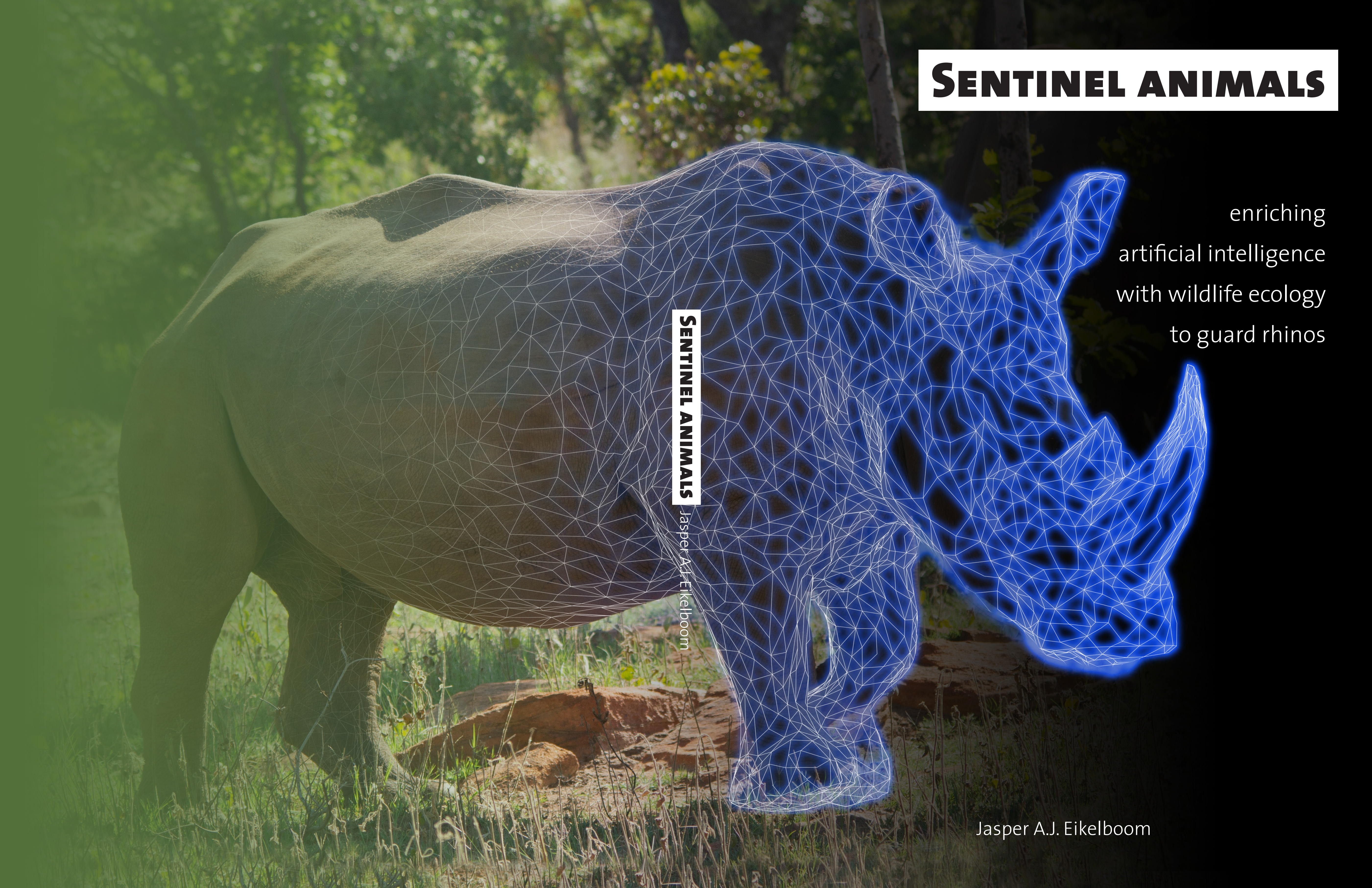


SENTINEL ANIMALS

Jasper A.J. Eikelboom

SENTINEL ANIMALS

enriching
artificial intelligence
with wildlife ecology
to guard rhinos

Jasper A.J. Eikelboom

Propositions

1. In our present epoch, creating and maintaining safe havens is the only key to nature conservation.
   (this thesis)

2. Although animal behaviour is fully predictable, humans do not have the capacity to understand it.
   (this thesis)

3. Hypothesis testing is weakened by model assumptions.

4. If ecosystems are characterized by alternative stable states, then recent global changes must encourage scientists to focus on the Earth's alternative future.

5. Constitutional freedom to profess religion drives inequity by legitimizing the behaviour of only an entitled group.

6. To achieve global sustainability, the average human birth rate needs to reduce to below replacement level.

Propositions belonging to the thesis, entitled

Sentinel animals: enriching artificial intelligence with wildlife ecology to guard rhinos

Jasper A.J. Eikelboom
Wageningen, 28 June 2021

Sentinel animals

enriching artificial intelligence with wildlife ecology to guard rhinos

Jasper A.J. Eikelboom

Thesis committee

Promotors:
Prof. Dr H.H.T. Prins
Professor emeritus of Resource Ecology
Wageningen University & Research

Prof. Dr F. van Langevelde
Professor of Wildlife Ecology and Conservation
Wageningen University & Research

Prof. Dr A. Doelman
Professor of Applied Analysis
Leiden University

Co-promotor:
Dr H.J. de Knegt
Lecturer, Wildlife Ecology and Conservation group
Wageningen University & Research

Other members:
Prof. Dr D. de Ridder, Wageningen University & Research
Prof. Dr B. Speckmann, Eindhoven University of Technology
Prof. Dr C.K. Hemelrijk, University of Groningen
Prof. Dr V. Rottschäfer, Leiden University & University of Amsterdam

This research was conducted under the auspices of the C.T. de Wit Graduate School of Production Ecology & Resource Conservation (PE&RC)

Sentinel animals
enriching artificial intelligence with wildlife ecology to guard rhinos

Jasper A.J. Eikelboom

Thesis
submitted in fulfilment of the requirements for the degree of doctor at
Wageningen University
by the authority of the Rector Magnificus
Prof. Dr A.P.J. Mol,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Monday 28 June 2021
at 1:30 p.m. in the Aula.

Jasper Arend Jan Eikelboom
Sentinel animals: enriching artificial intelligence with wildlife ecology to guard rhinos
288 pages

PhD thesis, Wageningen University, Wageningen, NL (2021)
With references, with summary in English, Dutch, Spanish and Chinese

ISBN 978-94-6395-770-0
DOI https://doi.org/10.18174/544693

Met dank aan mijn mede, mensen

Summary

English

Sentinel animals: enriching artificial intelligence with wildlife ecology to guard rhinos

The survival of both African rhinoceros species is under threat due to large-scale poaching. The pressure that poaching currently exerts on rhino populations is too large to solely wait for long-term conservation strategies, e.g., demand and corruption reduction campaigns, to take effect. Consequently, protection efforts aimed at the short-term survival of the rhino species seem to be urgently needed. Unfortunately, current rhino protection efforts fail to prevent large rhino population declines as conservation officers often fail to localize poachers before they can kill a rhino. Therefore I aimed to develop a poacher early warning system that provides conservation officers with more situational awareness, which can therefore decrease the risk of shootouts between poachers and conservation officers.

For this task I focused on developing a “sentinel-based poacher early warning system”, for which I envision nature reserves where abundant prey animals are tracked and where the movement responses of these animals are automatically used to detect the presence and infer the location of poachers. Hence the term: “sentinel”, as the animals themselves will take the role of game wardens. The benefit of such a system is that it could be working at all times and is not limited solely to rhino poachers. Apart from the obvious wildlife conservation challenge this thesis poses, it also tackles a major scientific challenge: to be able to detect abrupt changes in an environmental variable based on animal movement. In order to solve this challenge, a myriad of environmental and animal movement variables needed to be considered in interaction in a single model. This premise lead me to the use of a non-traditional statistical approach for wildlife ecologists: artificial intelligence.

This thesis brings together a number of coherent papers about wildlife conservation, movement ecology and artificial intelligence, aimed at investigating the necessity, analytics and applicability of a sentinel-based poacher early warning system. In **Chapter 2** I critically evaluated whether rhino protection efforts aimed at the short-term survival of the species are actually needed. I examined this by investigating if legal international rhino horn trade could be an ultimate solution for rhino poaching. Through an integrative review of scientific and grey literature about rhino horn trade legalization, I identified four main mechanisms through which a legal rhino horn market would influence the remaining wild rhino populations: 1) financial viability for private rhino owners, 2) rhino horn demand, 3) laundering of rhino horns, and 4) behaviour of rhino horn consumers. Subsequently, I determined through plausible reasoning that only the increased revenue for rhino farmers could potentially benefit rhino conservation. Conversely, the global demand for rhino horn is likely to increase to a level that cannot be met solely by legal supply. Moreover, corruption is omnipresent in countries along the trade routes, which has the potential to negatively affect rhino conservation. Finally, programmes aimed at reducing rhino horn demand will be counteracted through trade legalization by removing the stigma on consuming rhino horn. After combining these insights and comparing them with criteria for sustainable wildlife farming, I concluded that legalizing rhino horn trade will likely negatively impact the remaining wild rhino populations. To preserve rhino species I suggest to combine long- and short-term conservation approaches, by prioritizing the reduction of corruption within rhino horn trade, increasing the rhino population within well-protected 'safe havens' and implementing educational programmes and law enforcement targeted at rhino horn consumers.

In **Chapter 3** I investigated how much tropical animal populations in general are impacted by hunting, apart from solely considering African rhinos. I did this by analyzing how much human hunters alter the abundance and spatial distribution of animals in the tropics. Through a systematic review and a mixed effects meta-analysis I estimated that bird abundances declined on average by 58% (95% CI: 25-76%) and mammal abundances by 83% (95% CI: 72-90%) in hunted compared with unhunted areas. Mammal population densities were higher inside than outside protected areas, but hunting pressure reduced mammal abundances even within protected areas. Furthermore, I determined that bird populations were depleted within 7 kilometers and mammal populations within 40 kilometers from roads and settlements, which function as access points for hunters. These results signify that the impact of hunting on both the abundance and distribution of tropical animals is very large. Although these results suggest that the effect of hunting within protected areas is less detrimental than outside reserves, gazettement of protected areas seems insufficient to safeguard wildlife populations if not accompanied with improved reserve management, effective law enforcement and on-ground protection efforts.

In **Chapter 4** I studied the link between individual movement rules and emergent collective movement properties, which can both provide information about changes in the perceived environment of animals. For this I used an agent-based simulation model to investigate the indirect effects of fear and resources on animal group structures. In this model only the individual movement rules were directly affected by fear and resources, but through self-organization the effects of fear and resources also became apparent in the size of the formed groups. I specifically focused on the inherent variability in sizes of

groups that were generated from identical self-organizing processes. I found that the coefficient of variation of group size generally lied between 50 and 150% in these simulations, depending on both animal density and the resource scarcity/predation trade-off. Given that the variations of group size are already this large in homogeneous and deterministic scenarios, I consider group size an imprecise collective movement proxy for environmental conditions. Considering this imprecision of group size as a proxy and its time lag with changes in environmental conditions, group size can likely only be informative for slowly-evolving environmental conditions and will require information about the recent history of the animal group in order to be informative.

In **Chapter 5** I predicted the environment of animals based solely on their movement data. I specifically investigated how much of the variation in different environmental variables influenced animal movement in its multivariate entirety. I did this by linking high-resolution sensor data from cows in a controlled environment to various environmental variables through extensive feature engineering and machine learning to predict the environment from animal movement sensor data. Using this data-driven framework I demonstrated that it is possible to quantify environmental influence on animal movement with the performance metrics of machine learning regression algorithms. Depending on the chosen time window of feature engineering, the influence of environmental variables on different time scales can be studied. Furthermore, different types of animal movement features (e.g., individual- and collective-based, or GPS- and accelerometer-based) can be included separately or in combination in the framework. Even though the aim of this framework is to quantify the exact contribution of separate environmental variables on the total variation in animal movement, the core of this framework can be used to accurately predict environmental variation from animal movement as well.

In **Chapter 6** I developed a sentinel-based poacher early warning system in Welgevonden Game Reserve (South Africa). Using sensor data from 138 savanna ungulates combined with experimentally staged human intrusions, I algorithmically detected and localized poachers using animal movement data. I used a three-step analytical process to achieve this, namely: 1) animal behaviour classification, 2) poacher detection, and 3) poacher localization. In the first step I demonstrated the importance of interpreting animal movement as deviations from expectations given recent movement history and similar environmental conditions, given the complex relationship between the animals' heterogeneous environment and movement. I achieved an average precision of 46% to classify animal movement responses to humans versus all other movement. Even though this performance is quite an achievement (given the large class imbalance between normal and response behaviour, the inherent variability in animal movement, and environmental heterogeneity in the study area), it still leads to a substantial amount of misclassification. However, in the next two steps I considered the classified responses of all animals collectively in a spatiotemporal context, which allowed me to drastically improve upon this performance in the detection and localization of ‘poachers’. Periods with humans present in the area could be distinguished from periods without humans with 86% accuracy in a balanced validation design, and these humans were localized with less than 500m error in 54.2% of the experimentally staged poaching intrusions. This chapter thus demonstrates the feasibility of the main theme of this thesis, namely to use a sentinel-based poacher early warning system to detect and localize poachers.

In **Chapter 7** I investigated the performance of an automated animal detection algorithm for aerial imagery with the intention to gauge the potential of aerial imagery to supplement or replace animal-born sensors to track animals *en masse* in the near future. Using a deep learning approach I automatically identified large savanna herbivores inside images from an aerial wildlife survey in Kenya, after which I also classified the animal species using the same model. With this approach I managed to detect 90-95% of the number of individual animals that were found by four layers of human annotation, of which I correctly detected 2.8-4.0% extra animals that were missed by all humans. The model did result in 1.6-5.0 false positives per true positive, which emphasizes the importance of manual verification of automatic animal counts from aerial images. In this chapter I specifically demonstrated the potential of semi-automatic aerial animal counts to improve the precision and accuracy of animal population estimates. Furthermore, the results indicated that automated animal detections from aerial images have the potential to find more animals than humans can, especially when the algorithm is supplied with images taken at a fixed rate. Considering the aforementioned, I acknowledge the potential of aerial imagery to supplement *en masse* tracking with sensor tags. However, given that the detection chance of animals in images decreases substantially with horizontal distance to the camera, I expect animal tracking with cameras to be only suitable for relatively small areas.

Finally, in **Chapter 8** I synthesized my combined research in light of both wildlife conservation and wildlife ecology. I argued that the applicability of my developed sentinel-based poacher early warning system lies mainly in the aid it can provide to short-term wildlife protection efforts during the Anthropocene, which can concurrently reduce some of the negative effects associated with 'militarized conservation' (e.g., human rights violations). I plead for collaboration between conservationists working on short- and long-term conservation strategies, to maximize the efficacy of conservation by considering the occasional trade-off between conservation success in the Anthropocene and the development of a society that is in harmony with nature. Furthermore, I forecasted a large role for artificial intelligence in wildlife ecology research, which may drastically change the way scientific understanding is acquired in the near future. Exciting developments related to explainability and causality within artificial intelligence are currently being undertaken by computer scientists, but these scientists do require the input of ecologists to make these developments truly insightful and applicable to the real world.

Nederlands

Dieren als schildwacht: kunstmatige intelligentie met dierecologie verrijken om neushoorns te beschermen

Het voortbestaan van beide Afrikaanse neushoornsoorten wordt bedreigd door grootschalige stroperij. De druk die stroperij momenteel op neushoornpopulaties uitoefent is te groot om alleen maar het effect van beschermingsstrategieën voor de lange termijn af te wachten, zoals campagnes voor het verminderen van corruptie en de vraag naar neushoornhoorn. Daarom lijken beschermingsinspanningen dringend nodig die gericht zijn op het voortbestaan van de neushoornsoorten op de korte termijn. Helaas slagen de huidige inspanningen ter bescherming van neushoorns er niet in om een grote afname van de neushoornpopulatie te voorkomen, aangezien natuurbeschermers er vaak niet in slagen stropers te lokaliseren voordat dezen een neushoorn kunnen doden. Daarom wilde ik een vroegtijdig waarschuwingssysteem voor stropers ontwikkelen dat natuurbeschermers meer omgevingsbewustzijn biedt, waardoor het risico op schietpartijen tussen stropers en natuurbeschermers kan worden verminderd.

Voor deze taak heb ik me gefocust op het ontwikkelen van een "vroegtijdig waarschuwingssysteem voor stropers op basis van schildwachten", waarbij ik me natuurreservaten voor ogen heb waar prooidieren in grote aantallen worden gevolgd en waar de bewegingsreacties van deze dieren automatisch worden gebruikt om de aanwezigheid van stropers te detecteren en diens locatie af te leiden. Vandaar de term: "schildwacht", aangezien de dieren zelf de rol van natuurbeschermers op zich zullen nemen. Het voordeel van zo'n systeem is dat het constant actief kan zijn en niet alleen beperkt is tot neushoornstropers. Afgezien van de voor de hand liggende uitdaging omtrent dierbescherming die dit proefschrift stelt, pakt het ook een grote wetenschappelijke uitdaging aan: het kunnen detecteren van abrupte veranderingen in een omgevingsvariabele op basis van de bewegingen van dieren. Om deze uitdaging op te lossen moesten een groot aantal omgevings- en dierbewegingsvariabelen in interactie in één enkel model worden verwerkt. Dit uitgangspunt leidde me tot het gebruik van een niet-traditionele statistische benadering voor dierecologen: kunstmatige intelligentie.

Dit proefschrift brengt een aantal samenhangende artikelen over natuurbehoud, bewegingsecologie en kunstmatige intelligentie samen, gefocust op het onderzoeken van de noodzaak, analytiek en toepasbaarheid van een vroegtijdig waarschuwingssysteem voor stropers op basis van schildwachten. In **Hoofdstuk 2** heb ik kritisch geëvalueerd of beschermingsinspanningen die gericht zijn op het voortbestaan van de neushoornsoorten op de korte termijn daadwerkelijk nodig zijn. Dit deed ik door te onderzoeken of legale internationale handel in neushoornhoorns een definitieve oplossing zou kunnen zijn tegen het stropen van neushoorns. Door middel van een integrale literatuurstudie van wetenschappelijke en grijze literatuur over de legalisatie van neushoornhoornhandel, heb ik vier hoofdmechanismen geïdentificeerd waarmee een legale markt voor neushoornhoorns de resterende wilde neushoornpopulaties zou beïnvloeden: 1) de financiële levensvatbaarheid van particuliere neushoorn eigenaren, 2) de vraag naar neushoornhoorn, 3) het witwassen van neushoornhoorns, en 4) het gedrag van neushoornhoorn consumenten. Vervolgens stelde ik door middel van plausibel redeneren vast dat alleen de hogere inkomsten voor neushoornboeren mogelijk ten goede zouden komen aan het voortbestaan van neushoorns. Aan de andere kant zal de mondiale vraag naar neushoornhoorns waarschijnlijk toenemen tot een niveau wat te hoog is voor een legaal aanbod om volledig aan te voldoen. Bovendien is corruptie alomtegenwoordig in landen langs de neushoornhoorn handelsroutes, wat de bescherming van neushoorns negatief kan beïnvloeden. Ten slotte zullen programma's die gericht zijn op het verminderen van de vraag naar neushoornhoorn worden tegengewerkt door de handelslegalisatie aangezien dit het stigma op het consumeren van neushoornhoorn weg zal nemen. Na deze inzichten gecombineerd te hebben en te hebben vergeleken met criteria voor de duurzame veeteelt van wilde dieren, kwam ik tot de conclusie dat het legaliseren van de handel in neushoornhoorns waarschijnlijk een negatief effect zal hebben op de resterende wilde neushoornpopulaties. Om neushoornsoorten te behouden adviseer ik voor om lange en korte termijn beschermingsstrategieën te combineren, door prioriteit te geven aan het terugdringen van corruptie binnen de neushoornhoornhandel, de neushoornpopulaties te laten toenemen in goed beschermde 'veilige havens' en educatieve programma's en wetshandhaving gericht op neushoornhoorn consumenten te implementeren.

In **Hoofdstuk 3** heb ik onderzocht hoeveel de dierenpopulaties in de tropen over het algemeen worden beïnvloed door de jacht, in tegenstelling tot alleen Afrikaanse neushoorns in ogenschouw te nemen. Ik deed dit door te analyseren hoe groot het effect van jagers is op de hoeveelheid tropische dieren en diens ruimtelijke verspreiding. Door middel van een systematische review en een *mixed-effects* meta-analyse berekende ik dat de hoeveelheid vogels gemiddeld met 58% (95% BI: 25-76%) en zoogdieren met 83% (95% BI: 72-90%) zijn afgenomen in bejaagde ten opzichte van niet-bejaagde gebieden. De populatiedichtheid van zoogdieren was binnen beschermde gebieden hoger dan erbuiten, maar zelfs erbinnen verminderde de jachtdruk het aantal zoogdieren. Verder heb ik vastgesteld dat de vogelpopulaties binnen een radius van 7 kilometer van wegen en nederzettingen (die als toegangspunten voor jagers fungeren) waren afgenomen en de zoogdierpopulaties zelfs binnen 40 kilometer. Deze resultaten duiden erop dat het effect van de jacht op zowel de hoeveelheid als de verspreiding van tropische dieren erg groot is. Hoewel deze resultaten suggereren dat het effect van jagen in beschermde gebieden minder schadelijk is dan erbuiten, lijkt het aanwijzen van beschermde gebieden onvoldoende om dierenpopulaties te beschermen als het niet gepaard gaat met goed beheer, effectieve wetshandhaving en beschermingsinspanningen.

In **Hoofdstuk 4** heb ik het verband bestudeerd tussen de bewegingsregels van individuen en de daaruit volgende collectieve bewegingseigenschappen, welke beide informatie kunnen verschaffen over veranderingen in de waargenomen omgeving van dieren. Hiervoor heb ik een simulatiemodel gebaseerd op individuen gebruikt om de indirecte effecten van angst en voedsel op de groepsstructuren van dieren te onderzoeken. In dit model werden alleen de individuele bewegingsregels direct beïnvloed door angst en voedsel, maar door zelforganisatie werden de effecten van angst en voedsel ook zichtbaar in de grootte van de gevormde groepen. Ik heb me specifiek geconcentreerd op de inherente variabiliteit in de grootte van groepen die werden gegenereerd door identieke zelforganiserende processen. Ik ontdekte dat de variatiecoëfficiënt van de groepsgrootte in deze simulaties over het algemeen tussen de 50 en 150% lag, welke afhankelijk was van zowel de dierdichtheid als de balans tussen voedselschaarste en predatie. Aangezien de variaties in groepsgrootte al zo groot zijn in homogene en deterministische scenario's, beschouw ik groepsgrootte als een niet-precieze collectieve bewegingsproxy voor omgevingsvariabelen. Gezien deze lage precisie van groepsgrootte als een proxy en diens vertraging met veranderingen in omgevingsvariabelen, kan groepsgrootte waarschijnlijk alleen informatief zijn voor langzaam veranderende omgevingsvariabelen en zal informatie nodig zijn over de recente geschiedenis van de groep om informatief te kunnen zijn.

In **Hoofdstuk** 5 heb ik de omgeving van dieren voorspeld op basis van uitsluitend hun bewegingsdata. Ik heb specifiek onderzocht hoeveel van de variatie van verschillende omgevingsvariabelen de beweging van dieren in zijn multivariate geheel beïnvloedde. Ik deed dit door hoge resolutie sensordata van koeien in een gecontroleerde omgeving te koppelen aan verschillende omgevingsvariabelen door middel van uitgebreide kenmerkextractie en machinaal leren om de omgeving te voorspellen op basis van bewegingssensordata van dieren. Met behulp van dit data-gestuurde raamwerk heb ik aangetoond dat het mogelijk is om de invloed van de omgeving op de beweging van dieren te kwantificeren met de prestatiemetrieken van regressie-algoritmen voor machinaal leren. Afhankelijk van het gekozen tijdvenster van kenmerkextractie, kan de invloed van omgevingsvariabelen op verschillende tijdschalen worden bestudeerd. Bovendien kunnen verschillende soorten bewegingskenmerken van dieren (bijvoorbeeld individueel en collectief, of op GPS en versnellingsmeter gebaseerd) afzonderlijk of in combinatie in het raamwerk worden opgenomen. Hoewel het doel van dit raamwerk is om de exacte bijdrage van afzonderlijke omgevingsvariabelen aan de totale variatie in dierbewegingen te kwantificeren, kan de essentie van dit raamwerk ook worden gebruikt om de omgevingsvariatie nauwkeurig te voorspellen op basis van dierbeweging.

In **Hoofdstuk** 6 heb ik een vroegtijdig waarschuwingssysteem voor stropers ontwikkeld in Welgevonden Game Reserve (Zuid-Afrika). Met behulp van sensordata van 138 savannehoefdieren in combinatie met experimenteel geënsceneerde menselijke indringers, heb ik stropers algoritmisch gedetecteerd en gelokaliseerd met behulp van bewegingssensordata van dieren. Ik heb een analytisch proces van drie stappen gebruikt om dit te bereiken, namelijk: 1) classificatie van diergedrag, 2) detectie van stropers en 3) lokalisatie van stropers. In de eerste stap heb ik het belang aangetoond van het interpreteren van dierbewegingen als afwijkingen van verwachtingen op basis van de recente bewegingsgeschiedenis en vergelijkbare omgevingsomstandigheden, gezien de complexe relatie tussen de heterogene omgeving van dieren en hun beweging. Ik heb een gemiddelde precisie van 46% bereikt om de bewegingsreacties van dieren op mensen te classificeren ten opzichte van alle andere bewegingen. Hoewel deze precisie een behoorlijke prestatie is (gezien de grote klassendisbalans tussen normaal en responsgedrag, de inherente variabiliteit van dierbewegingen en de heterogeniteit in de omgeving in het studiegebied), leidt het toch tot een aanzienlijke mate van misclassificatie. In de volgende twee stappen heb ik echter de geclassificeerde reacties van alle dieren gezamenlijk in een tijdruimtelijke context bekeken, waardoor ik de prestatie bij het detecteren en lokaliseren van ‘stropers’ drastisch kon verbeteren. Perioden met mensen die in het gebied aanwezig waren, konden worden onderscheiden van perioden zonder mensen met een nauwkeurigheid van 86% in een gebalanceerd validatieontwerp. Verder werden deze mensen gelokaliseerd met een fout van minder dan 500 meter in 54,2% van de experimenteel geënsceneerde stroperij-inbraken. Dit hoofdstuk demonstreert dus de haalbaarheid van het hoofdthema van dit proefschrift, namelijk het gebruik van een vroegtijdig waarschuwingssysteem voor stropers op basis van schildwachten om stropers te detecteren en lokaliseren.

In **Hoofdstuk 7** heb ik de prestaties onderzocht van een geautomatiseerd dierdetectiealgoritme voor luchtfoto’s om het potentieel van luchtfoto’s te peilen als aanvulling op of vervanging van sensoren om dieren *en masse* te volgen in de nabije toekomst. Met behulp van een diep leren benadering identificeerde ik automatisch grote savanne-herbivoren in luchtfoto’s van een wildtelling in Kenia, waarna ik ook de diersoorten classificeerde met hetzelfde model. Met deze aanpak slaagde ik erin om 90-95% van het aantal individuele dieren te detecteren dat werd gevonden door vier lagen van menselijke annotatie, waarvan ik correct 2,8-4,0% extra dieren detecteerde die door alle mensen werden gemist. Het model resulteerde wel in 1,6-5,0 foutpositieven per echt positief, wat het belang benadrukt van handmatige verificatie van automatische wildtellingen op basis van luchtfoto’s. In dit hoofdstuk heb ik specifiek het potentieel aangetoond van semiautomatische wildtellingen vanuit de lucht om de precisie en nauwkeurigheid van dierpopulatie schattingen te verbeteren. Bovendien gaven de resultaten aan dat geautomatiseerde dier-detecties met luchtfoto’s het potentieel hebben om meer dieren te vinden dan mensen, vooral wanneer het algoritme foto’s krijgt aangeleverd die met een vaste frequentie zijn gemaakt. Gezien het bovenstaande bevestig ik het potentieel van luchtfoto’s als aanvulling voor het *en masse* volgen van dieren met sensors. Echter, gezien het feit dat de detectiekans van dieren in foto’s aanzienlijk afneemt met de horizontale afstand tot de camera, verwacht ik dat het volgen van dieren met camera’s alleen geschikt is voor relatief kleine gebieden.

Ten slotte heb ik in **Hoofdstuk 8** mijn totale onderzoek samengevat qua zowel natuurbehoud als dierecologie. Ik betoogde dat de toepasbaarheid van mijn ontwikkelde vroegtijdig waarschuwingssysteem voor stropers op basis van schildwachten voornamelijk ligt in de hulp die het op de korte termijn kan bieden aan beschermingsinspanningen van wilde dieren tijdens het Antropoceen, wat tegelijkertijd enkele van de negatieve effecten van 'gemilitariseerd natuurbehoud' kan verminderen (zoals mensenrechtenschendingen). Ik pleitte voor samenwerking tussen natuurbeschermers die werken aan zowel lange als korte termijn beschermingsstrategieën, om de effectiviteit van natuurbehoud te maximaliseren door rekening te houden met de af en toe voorkomende afweging tussen natuurbehoud in het Antropoceen en de ontwikkeling van een samenleving die in harmonie is met de natuur. Verder voorspelde ik een grote rol voor kunstmatige intelligentie in dierecologie onderzoek, wat de manier waarop wetenschappelijk inzicht wordt verworven in de nabije toekomst drastisch kan veranderen. Spannende ontwikkelingen met betrekking tot uitlegbaarheid en causaliteit binnen kunstmatige intelligentie worden momenteel ondernomen door informatici, maar deze wetenschappers hebben de input van ecologen nodig om deze ontwikkelingen daadwerkelijk inzichtelijk en toepasbaar te maken voor de echte wereld.

Español

Animales centinela: enriqueciendo la inteligencia artificial con ecología de vida silvestre para proteger a los rinocerontes

La supervivencia de las dos especies de rinocerontes Africanos está amenazada debido a la caza furtiva a gran escala. La presión de la caza furtiva en las poblaciones de rinocerontes es demasiado grande como para esperar solamente a que las estrategias de conservación a largo plazo tengan efecto, p. ej. las campañas de reducción de demanda y corrupción. Pareciera una necesidad urgente tener esfuerzos de protección enfocados a la supervivencia a corto plazo de ambas especies de rinoceronte. Desafortunadamente, los esfuerzos actuales de protección fallan en prevenir grandes reducciones de poblaciones de rinocerontes, mientras que los oficiales de conservación frecuentemente fallan en localizar a los cazadores antes de que maten a un rinoceronte. Por esto me enfoqué en desarrollar un sistema de alerta temprana de cazadores furtivos que proporcione a los oficiales de conservación más conciencia de la situación actual, y con el cual puedan reducir el riesgo de tiroteos entre cazadores furtivos y oficiales de conservación.

Para esta tarea me enfoqué en desarrollar un “sistema de alerta temprana de cazadores furtivos basado en centinela”, para lo cual visualizo reservas naturales donde abundantes animales de presa sean rastreados y donde las respuestas del movimiento de estos animales sean automáticamente usadas para detectar la presencia e inferir la ubicación de los cazadores furtivos. Por eso el término: “centinela”, ya que son los mismos animales los que tomarán el rol de guardabosques. El beneficio de tal sistema es que podría funcionar en todo momento y no es limitado solamente a los cazadores de rinocerontes. Además de los obvios desafíos de conservación de fauna silvestre que esta tesis plantea, también aborda un gran desafío científico: ser capaz de detectar cambios abruptos en una variable ambiental basada en el movimiento animal. Para resolver este desafío, una gran cantidad de variables ambientales y de movimiento animal necesitaron ser consideradas en interacción en un modelo único. Esta premisa me llevó a usar un enfoque estadístico no tradicional para los ecólogos de fauna silvestre: la inteligencia artificial.

Esta tesis reúne un numero de artículos relevantes acerca de la conservación de fauna silvestre, ecología del movimiento e inteligencia artificial, enfocados en investigar la necesidad, la analítica y la aplicabilidad de un sistema de alerta temprana de cazadores furtivos basado en centinela. En **el Capítulo 2** evalué críticamente si los esfuerzos de protección de rinocerontes enfocados en la supervivencia a corto plazo de las especies son realmente necesarios. Examiné esto investigando si el comercio legal internacional de los cuernos de rinoceronte podría ser una solución definitiva para la cacería furtiva de rinocerontes. Por medio de una revisión integradora de literatura científica y literatura gris de la legalización del comercio de cuernos de rinoceronte, identifiqué cuatro mecanismos principales a través de los cuales el mercado legal de cuernos de rinoceronte influiría las poblaciones silvestres

de rinocerontes: 1) viabilidad financiera de los propietarios privados de rinocerontes, 2) demanda de los cuernos de rinoceronte, 3) blanqueo de cuernos de rinoceronte, y 4) comportamiento de los consumidores de cuernos de rinoceronte. Subsecuentemente, determiné a través del razonamiento plausible que solamente un incremento en las ganancias de los criadores de rinocerontes podría beneficiar potencialmente la conservación de rinocerontes. En cambio, es probable que aumente la demanda global de cuernos de rinoceronte a un nivel que no puede ser cubierta solamente por el suministro legal. Además, la corrupción está omnipresente en países a lo largo de las rutas comerciales, las cuales tienen el potencial de afectar negativamente la conservación de rinocerontes. Finalmente, los programas enfocados en reducir la demanda de rinocerontes será contrarrestada por medio de la legalización comercial removiendo el estigma de consumir cuernos de rinoceronte. Después de combinar estas perspectivas y compararlas con criterios para la cría sustentable de fauna silvestre, concluí que legalizar el comercio de cuernos de rinoceronte posiblemente impactaría negativamente a las poblaciones silvestres de rinocerontes restantes. Para preservar las especies de rinoceronte, sugiero combinar enfoques de conservación a corto y largo plazo, priorizando la reducción de la corrupción en el comercio de cuernos, incrementando las poblaciones dentro de “refugios seguros” bien protegidos e implementar programas educativos así como el cumplimiento de la ley enfocado a los consumidores de cuernos de rinoceronte.

En **el Capítulo** 3 investigué qué tanto son impactadas, en general, las poblaciones tropicales de animales por la cacería, además de los rinocerontes Africanos. Hice esto analizando qué tanto alteran los cazadores la abundancia y distribución espacial de los animales en los trópicos. A través de una revisión sistemática y de un meta-análisis con efectos mixtos estimé que las abundancias de aves disminuyeron en promedio un 58% (95% IC: 25-76%) y las abundancias de mamíferos un 83% (95% IC: 72-90%) en áreas de cacería comparadas con áreas sin cacería. Las densidades poblacionales de mamíferos fueron más altas dentro de las áreas protegidas que fuera de las mismas, pero la presión de cacería redujo las abundancias de mamíferos incluso dentro de las áreas protegidas. Además, determiné que las poblaciones de aves y mamíferos desaparecieron, respectivamente, a los 7 y 40 kilómetros adyacentes a las carreteras y asentamientos humanos que funcionan como puntos de acceso para los cazadores. Estos resultados dan a conocer que el impacto de la cacería es muy grande tanto en la abundancia como en la distribución de animales tropicales. A pesar de que estos resultados sugieren que el efecto de la cacería dentro de las áreas protegidas es menos perjudicial que fuera de las reservas, delimitar áreas protegidas parece insuficiente para salvaguardas poblaciones de fauna silvestre si no se acompaña de un manejo mejorado de la reserva, cumplimiento efectivo de la ley y esfuerzos de protección sobre el terreno.

En **el Capítulo** 4 estudié el vínculo entre las reglas del movimiento individual y las propiedades de movimiento colectivo emergente, que pueden proveer información acerca de los cambios en el ambiente percibido de los animales. Para esto usé un modelo de simulación basado en agentes para investigar los efectos indirectos del miedo y de los recursos en las estructuras de los grupos de animales. En este modelo solamente las reglas de del movimiento individual fueron directamente afectadas por el miedo y por los recursos, pero por medio de la propia organización los efectos del miedo y de los recursos también fueron evidentes en el tamaño de los grupos formados. Específicamente me enfoqué en la variabilidad inherente de los tamaños de los grupos que fueron generados por procesos idénticos de organización propia. Encontré que los coeficientes de variación del tamaño de grupo generalmente fueron del 50% y 150% en estas simulaciones, dependiendo de la densidad animal y de la compensación entre la escasez de recursos y la depredación. Dado que las variaciones del tamaño del grupo son ya muy grandes en escenarios homogéneos y determinísticos, considero que el tamaño del grupo es un indicador impreciso del movimiento colectivo para las condiciones ambientales. Considerando esta imprecisión del tamaño de grupo como un indicador, así como su retraso de tiempo con los cambios en las condiciones ambientales, el tamaño de grupo podría solamente ser informativo para condiciones ambientales lentamente cambiantes y requerirá información acerca de la historia reciente del grupo animal para poder ser informativa.

En **el Capítulo 5** predije el ambiente de los animales basado solamente en los datos de su movimiento. Específicamente investigué qué tanto de la variación en diferentes variables ambientales influyó el movimiento animal en su totalidad multivariante. Hice esto vinculando datos de sensores de alta resolución de vacas en un entorno de condiciones ambientales controladas a través de una amplia ingeniería de funciones y aprendizaje automático para predecir el ambiente a partir de los datos de sensores del movimiento de animales. Usando este marco de referencia basado en datos demostré que es posible cuantificar la influencia ambiental en el movimiento animal con las métricas del rendimiento de los algoritmos de regresión del aprendizaje automático. Dependiendo de la ventana de tiempo elegida en la ingeniería de funciones, se puede estudiar la influencia de las variables ambientales a diferentes escalas de tiempo. Adicionalmente, se pueden incluir diferentes tipos de características del movimiento animal (p. ej. basadas en lo individual o en lo colectivo, o basadas en GPS y acelerómetro) por separado o en combinación con el marco de referencia. Aunque el propósito de este marco de referencia es cuantificar la contribución exacta de las variables ambientales por separado en la variación total del movimiento animal, el núcleo de este marco de referencia puede ser usado también para predecir de manera precisa la variación ambiental del movimiento animal.

En **el Capítulo 6** desarrollé un sistema de alerta temprana de cazadores furtivos basado en centinela en la reserva Welgevonden Game Reserve (Sudáfrica). Usando datos de sensores de 138 ungulados de la sabana combinados con intrusiones humanas experimentalmente escenificadas, detecté y localicé algorítmicamente cazadores furtivos usando datos del movimiento animal. Para lograr esto, utilicé un proceso analítico de tres pasos: 1) clasificación del comportamiento animal, 2) detección de cazadores furtivos, y 3) ubicación de los cazadores furtivos. En el primer paso demostré la importancia de interpretar el movimiento animal como desviaciones de las expectativas dada la historia del movimiento reciente y condiciones ambientales similares, dada la compleja relación entre el ambiente heterogéneo del ambiente animal y su movimiento. Logré una presión promedio de 46% para clasificar las respuestas del movimiento animal hacia el humano en comparación con los otros tipos de movimiento. Aunque este resultado es un gran logro (dado el gran desbalance de clase entre el comportamiento normal y el de respuesta, la inherente variabilidad en el movimiento animal, y la heterogeneidad ambiental en el área de estudio), esto aún conlleva una cantidad sustancial de clasificación errónea. Sin embargo, en los siguientes dos pasos consideré las respuestas clasificadas de todos los animales colectivamente en un contexto espaciotemporal, el cual me permitió mejorar drásticamente la detección y localización de "cazadores furtivos". Los periodos con humanos presentes en el área podrían ser distinguidos de los periodos sin humanos con una precisión de 86% en un diseño de validación balanceado, y estos humanos fueron localizados con un error de menos de 500m en el 54.2% de las intrusiones humanas experimentalmente escenificadas. Este capítulo entonces demuestra la factibilidad del tema principal de esta tesis, usar un sistema de alerta temprana de cazadores furtivos basado en centinela para detectar y localizar cazadores furtivos.

En **el Capítulo 7** investigué el desempeño de un algoritmo automatizado de detección animal para imágenes aéreas con la intención de calibrar el potencial de imágenes aéreas para suplementar o reemplazar sensores creados para rastrear animales *en masa* en un futuro cercano. Usando un enfoque de aprendizaje profundo identifiqué automáticamente grandes herbívoros de sabana en imágenes capturadas durante una campaña aérea de fauna silvestre en Kenia, después de la cual también clasifiqué las especies de animales usando el mismo modelo. Con este enfoque logré detectar el 90-95% del número de animales individuales que fueron encontrados por cuatro capas de anotación humana, de las cuales detecté correctamente 2.8-4.0% de animales adicionales que todos los humanos pasaron por alto. El modelo resultó en 1.6-5.0 falsos positivos por positivo verdadero, lo que enfatiza la importancia de la verificación manual de recuentos automáticos de animales a partir de imágenes aéreas. En este capítulo demostré específicamente el potencial de los recuentos aéreos semiautomatizados de animales para mejorar la precisión y exactitud de las estimaciones de poblaciones animales. Adicionalmente, los resultados indicaron que la detección automatizada en imágenes aéreas tiene el potencial de encontrar más animales que los humanos, especialmente cuando el algoritmo se suministra con imágenes tomadas a una velocidad constante. Considerando todo lo anterior, reconozco el potencial de las imágenes aéreas para suplementar rastreo *en masa* con sensores. Sin embargo, dado que la posibilidad de detección de animales en imágenes disminuye substancialmente con la distancia horizontal a la cámara, considero que el rastreo de animales con cámaras es apropiado solamente para áreas relativamente pequeñas.

Finalmente, en **el Capítulo 8** sinteticé mi investigación combinada a la luz de la conservación y ecología de la fauna silvestre. Argumenté que la aplicabilidad del sistema de

detección temprana de cazadores furtivos basado en centinela que desarrollé radica principalmente en la ayuda que este puede proveer a los esfuerzos de protección a corto plazo de la fauna silvestre durante el Antropoceno, lo cual puede concurrentemente reducir algunos de los efectos negativos asociados con la “conservación militarizada” (p. ej. las violaciones a los derechos humanos). Abogo por la colaboración entre conservacionistas trabajando en estrategias de conservación a corto y largo plazo para maximizar la eficacia de conservación considerando el equilibrio ocasional entre el éxito de la conservación en el Antropoceno y el desarrollo de una sociedad que esté en armonía con la naturaleza. Además, pronostiqué un papel importante de la inteligencia artificial en la investigación en ecología de la fauna y flora silvestre, el cual puede cambiar drásticamente la manera en que el conocimiento científico sea adquirido en el futuro cercano. Actualmente, científicos computacionales están llevando a cabo emocionantes desarrollos relacionados con la explicabilidad y la causalidad dentro de la inteligencia artificial, pero estos científicos requieren la participación de los ecólogos para hacer que los desarrollos sean verdaderamente perspicaces y aplicables en el mundo real.

中文

动物哨兵：结合野生动物生态学和人工智能来保护犀牛

由于大规模的偷猎行为，两种非洲犀牛的生存都受到严重的威胁。当前偷猎行为对犀牛种群造成的压力太大，以至于长期的保护策略（例如，减少需求和腐败的行动）难以落实干预。因此，我们迫切地需要针对犀牛物种生存的短期保护措施。然而，由于保护执法人员常常无法在犀牛被猎杀之前找到偷猎者的位置，当前的犀牛保护措施往往无法防止犀牛数量的大幅下降。因此，我的目标是开发一种可为保护人员提供更多态势感知的偷猎者预警系统，从而降低偷猎者与保护人员之间发生枪战的风险。

为此，我专注于开发一个“基于哨兵的偷猎者预警系统”。我构想在自然保护区内追踪足量的被捕食者，并自动通过这些动物的运动响应来识别偷猎者的存在并推断出他们的位置。这些被追踪的动物就是“哨兵”，而动物本身将扮演游戏管理员的角色。这种系统的好处是它可以持续工作，而不仅限于在犀牛偷猎者出现的时候。本论文除了解决前面提出的关于野生动物保护的挑战之外，还解决了一个重大科学挑战：基于动物运动轨迹来检测某个环境变量的突变。解决这一挑战需要在单个模型的交互中考虑大量的环境和动物运动变量，而这个前提使我想到了生态学家使用的一类非传统统计方法：人工智能。

本论文汇集了多篇有关野生动物保护、运动生态学和人工智能的子论文，旨在研究基于哨兵的偷猎者预警系统的必要性、可分析性和适用性。在**第2章**中，我评估了针对犀牛短期生存的保护措施的必要性。我从调查合法的国际犀牛角贸易是否可以作为控制犀牛偷猎的最终解决方案这个问题入手，通过总结和论述有关犀牛角贸易合法化的科学论文和灰色文献，确定了犀牛角贸易的合法化影响野生犀牛种群的四个主要机制：1）私人犀牛所有者的财务情况；2）犀牛角的需求；3）犀牛角的清洗；4）犀牛角消费者的行为。随后，我通过合理的推理确定，只有增加犀牛牧民的收入才能潜在地保护犀牛。然而，全球对犀牛角的需求可能会增加到仅靠合法供应无法满足的水平。此外，在贸易路线沿线的国家中，腐败无处不在，这可能对犀牛的保护产生消极影响。最后，减少犀牛角需求的计划或可能被通过消除食用犀牛角的污名来实现贸易合法化的行动所抵消。结合这些见解并将其与野生动物的可持续养殖标准进行比较后，我得出结论：犀牛角贸易的合法化可能会对剩余的野生犀牛种群产生负面影响。为了保护犀牛种群，我建议将长期和短期的保护策略结合起来，通过优先减少犀牛角贸易中的腐败，在受到良好保护的“安全港”内增加犀牛的数量，并对犀牛角消费者实施教育计划和法律干预。

除了单独考虑非洲犀牛之外，在**第3章**中我还研究了狩猎会多大程度地影响热带动物种群。为了回答这个问题，我定量分析了猎人改变热带地区动物丰度和空间分布的程度。通过系统综述和混合荟萃分析模型，我发现狩猎地区的鸟类平均丰度比非狩猎区少58%（95%CI：25-76%），而哺乳动物的平均丰度比非狩猎区少83%（95%CI：72-90%）。保护区内部的哺乳动物种群密度要高于保护区外，但即使在保护区内，狩猎压力也会降低哺乳动物的丰度。此外，鸟类种群在距离道路和居民区7公里以内耗尽，而哺乳动物在距离道路和居民区40公里以内耗尽，此标准可指示猎人的出入点。这些

结果表明，狩猎对热带动物的数量和分布的影响都非常大。尽管结果表明保护区内的狩猎危害要比保护区外小，但如果没有完善的保护区的管理、有效的执法和地面保护措施，单单通过保护区的设定似乎不足以保护野生动物种群。

在第4章中，我研究了动物个体运动规则与集体运动属性之间的联系，两者结合可提供有关动物感知环境变化的知识。为此，我使用了个体为本模型来研究恐惧和资源对动物群体结构的间接影响。在这个模型中，虽然只有个体的运动规则直接受到恐惧和资源的影响，但通过自组织过程，恐惧和资源也间接地影响着形成群组的规模。我特别关注由相同的自组织过程形成的群组规模的内在差异性。在我的模拟中，群组规模的差异系数通常在50%至150%之间，这取决于动物密度和资源稀缺程度/捕食的权衡。鉴于在同质和确定性场景中群组规模的差异已经如此之大，我认为群组规模不是一个能准确指示环境条件的运动指标。考虑到这种不精确性和其随环境变化而变化的滞后性，群体规模可能仅对缓慢变化的环境条件的指示具有参考价值，且这种参考价值需依赖于有关动物群体运动的近期历史信息。

在第5章中，我根据动物的运动数据预测了动物的环境。我特别关注不同环境变量作为多元整体对动物运动的影响的差异性。为此，我通过特征工程和机器学习的方法，将可控环境中奶牛的高分辨率传感器数据与各种环境变量相关联，从而利用动物运动的传感器数据来预测环境状况。通过这种数据驱动的方法框架，我证明了使用机器学习回归算法的性能指标可以量化环境对动物运动的影响。通过在特征工程中选择不同的时间窗口，我们可以分析环境变量在不同时间尺度上的影响。此外，不同类型的动物运动特征（例如，基于个体和基于集体的特征，或基于GPS定位和基于加速度的特征）可以被单独或共同包含在这个框架中。虽然此框架的初衷是量化单一环境变量对动物总体运动模式的确切贡献，但该框架的核心也可运用于动物运动对环境变化的预测。

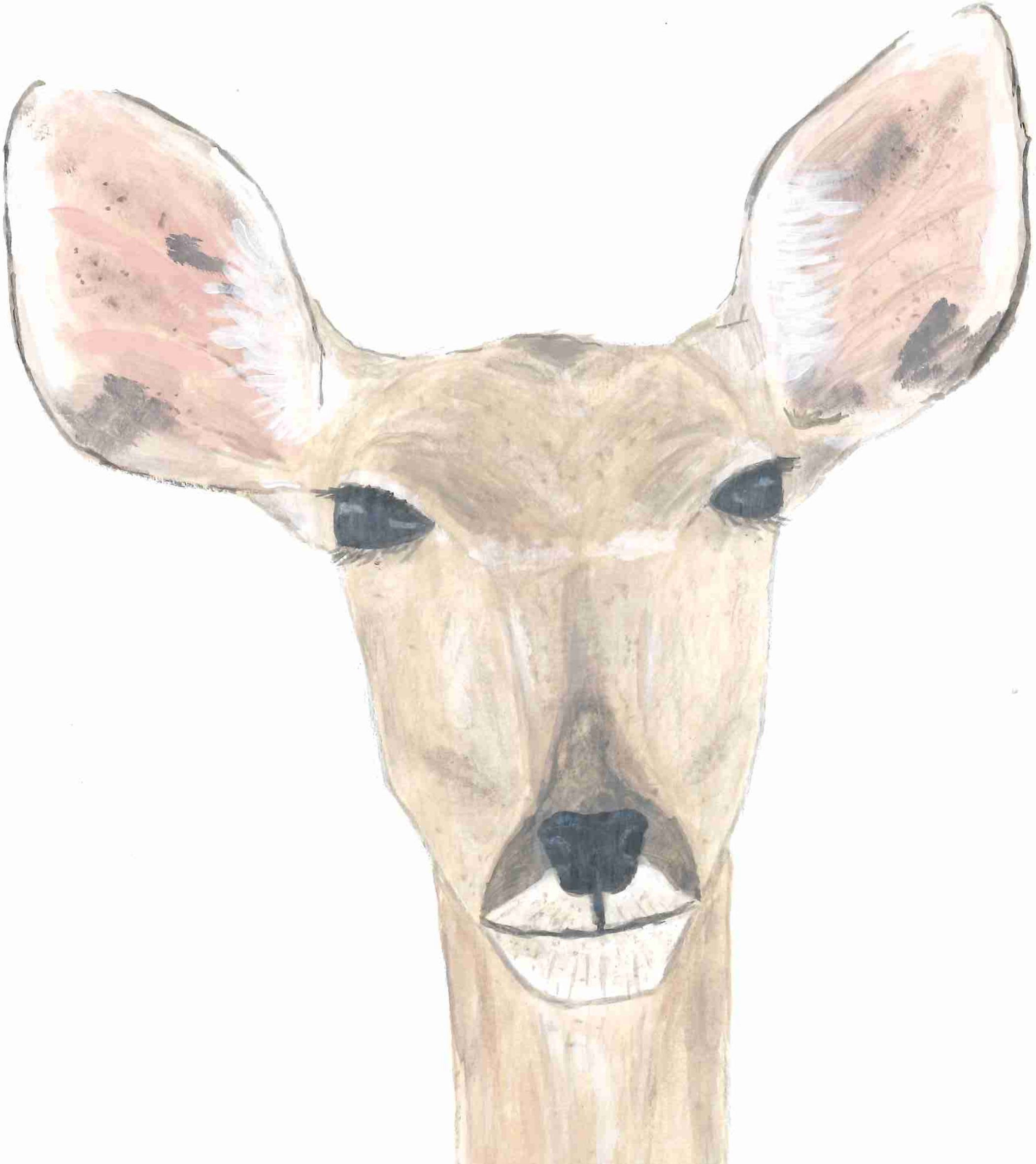
在第6章中，我在Welgevonden Game Reserve（南非）开发了一套基于哨兵的偷猎者预警系统。利用138只非洲稀树草原有蹄类动物的运动传感器数据以及分阶段进行的人类入侵实验，我通过算法检测并定位了偷猎者。这需要通过三步分析来实现，即：1）动物行为分类；2）偷猎者检测；3）偷猎者定位。在第一步中，鉴于异质环境与动物运动之间存在复杂的关系，我证明了基于近期运动历史与相似环境条件用偏离期望值的程度来解释动物运动模式的重要性。我对响应人为干扰下的动物运动与其他运动形式的区分度达到46%。虽然这已是很不错的推进了（鉴于正常行为和响应行为之间存在很大的类别失衡、动物运动的固有变异性以及研究区域中的环境异质性），但它仍然会产生大量的错误分类结果。因此，在接下来的两个步骤中，我考虑了所有动物在时空环境中的分类反应，这大大提高了对“偷猎者”的检测和定位精度。这种平衡验证模型对有人为干扰的与没有人类活动的时期的区分度高达86%，并且在实验性盗猎入侵中，我们对54.2%的偷猎者定位的误差都小于500米。因此，本章证明了本论文核心主题的可行性，即使用基于哨兵的偷猎者预警系统来检测和定位偷猎者。

在第7章中，我研究了应用航空影像对动物个体的自动检测算法，旨在评估航空图像在不久的将来协助或替代动物运动传感器来追踪动物群体的潜力。通过深度学习的方法，我从肯尼亚的一次航空野生生物调查影像中自动识别了非洲稀树草原上的草食性

动物，并使用相同的模型识别了动物的物种。我通过这种方法检测出了在四层实地调查中调查人员发现的90-95%的动物个体，此外，我还额外检测出了调查人员没有发现的2.8-4.0%的动物。当然，该模型的每个真阳性结果会伴随出现1.6-5.0个假阳性结果，这也强调了通过对航空影像的目视解译来验证动物自动计数结果的重要性。本章着重说明了半自动航空动物计数在提高动物种群数量估算的精确度和准确性方面的潜力。此外，研究结果表明，从航空影像中自动检测动物的方法或可比人类实地调查识别出更多的动物，尤其是当该算法应用于以固定速率拍摄的图像时。因此，航空影像有协助动物传感器进行大规模追踪的潜力。但是，鉴于对航空影像中动物的检测率会随着其距相机的水平距离的增加而大大降低，使用相机进行动物追踪仅适用于相对较小的区域。

最后，在**第8章**中，我结合了野生动物保护学和动物生态学对我的研究进行了总结。我认为，我开发的基于哨兵的偷猎者预警系统的应用价值主要在于它可以为人类世的短期野生动物保护提供帮助，同时可以减少“军事保护”可能带来的负面影响（例如侵犯人权）。我呼吁实施短期和长期保护战略的环境保护主义者相互合作，权衡野生动物保护与社会发展，贯彻人与自然和谐相处的理念，来最大程度地发挥保护效力。此外，我预期人工智能在野生动植物生态学研究中会发挥重要的作用，这可能在不久的将来会极大程度地改变科学理解的方式。目前，计算机科学家在人工智能的可解释性和因果关系领域，已实现了令人兴奋的发展，但是他们也需要生态学家的助力，来能使这些发展有更深刻的见解并适用于现实世界。

Contents



Chapter 1

Introduction

1.1 Rhino poaching

The Earth is well underway into the Anthropocene, meaning that humans globally dominate most contemporary environmental change (Lewis & Maslin, 2015). Due to these changes, biodiversity had been diminished over the past centuries and has been doing so at an accelerating rate over the past decades (IPBES, 2019). The most important direct drivers of biodiversity decline include land-use change, climate change, pollution, wildlife exploitation and invasive species, of which the relative importances differ per system and time scale (IPBES, 2019; Maxwell et al., 2016). Perhaps counterintuitively based on recent media reports, it is currently not climate change that is overall threatening the *IUCN Red List* species most, but wildlife exploitation (Maxwell et al., 2016).

One of the most worrying examples of wildlife exploitation over the past decade has been the African rhinoceros (white rhino *Ceratotherium simum* and black rhino *Diceros bicornis*) (WWF, 2021). Both African rhino species were once widespread and abundant in the African continent, but were gradually hunted to near-extinction after Western colonization ('t Sas-Rolfes, 2011). The globally most abundant rhino subspecies today (the southern white rhino, estimated at approximately 20,000 individuals in 2010 (Emslie et al., 2016; Rubino & Pienaar, 2017)) was once even considered extinct, until at the beginning of the 20th century a population of less than 20 individuals was rediscovered in the Hluhluwe-Umfolozi Park in South Africa. The other white rhino subspecies (the northern white rhino) has been hunted to extinction in the wild during the course of this study, since the last male died on 19 March 2018 (Njehia, 2018). The black rhino still had a population of around 100,000 individuals in the 1960s, which made it by far the globally most abundant rhino species at that time, but was poached to less than 2,500 individuals in the early 1990s ('t Sas-Rolfes, 2011). However, both African rhino species increased in number since the 1990s (primarily due to the effective conservation efforts in South Africa), which resulted in that approximately 95% (19,000 individuals) of all remaining white rhinos and 40% (1900 individuals) of all black rhinos lived in South Africa in 2010 (Emslie et al., 2016; Rubino & Pienaar, 2017). Unfortunately, roughly around 2010 as well, a resurgence of rhino poaching occurred due to a certain demand originating from Southeast Asia (Figure 1.1).

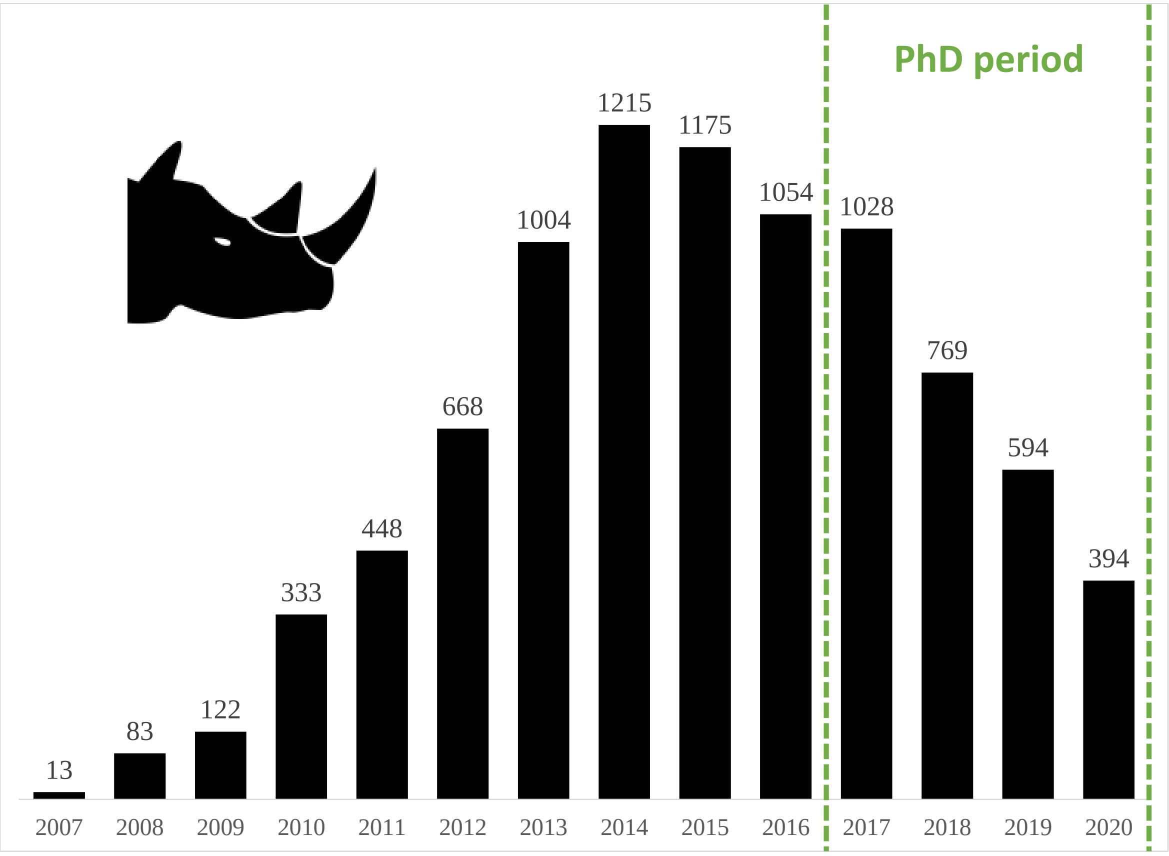


Figure 1.1: Number of recorded poached rhinos in South Africa from 2007 until 2020 (Save the Rhino, 2021). Note, and appreciate, that no Before-After-Control-Impact design (or any other statistics) has been employed to "test" the effect of my PhD on the recent reduction in rhino poaching. On the contrary, it is more likely that there are currently less rhinos to poach than less poachers (Ferreira & Pienaar, 2020).

Historically there has long been a demand for rhino horn from cultures in Southeast Asia, East Asia and the Middle-East, but in the past decade the demand from (and supply to) Southeast Asia increased dramatically (Milliken & Shaw, 2012). A large proportion of the Vietnamese people is now willing and able to buy rhino horn, mainly to use it as a status symbol (USAID Vietnam, 2018), and a large group of Chinese people currently demands rhino horn for traditional medicine (USAID Wildlife Asia, 2018). Facilitated by well-organized criminal networks (Ayling, 2013; Rademeyer, 2016; Van Uhm, 2012), this demand has led to unsustainable levels of rhino poaching in South Africa (Figure 1.2), which has lead some to forecast the imminent extinction of these species (Biggs et al., 2013; Haas & Ferreira, 2016). Given that there is no scientific evidence for the efficacy of rhino horn as a medicine (Cyranoski, 2018), the obvious, ultimate and preferable solution for rhino poaching is considered by many to be the reduction of demand for rhino horn

(Litchfield, 2013). Former rhino horn consumer countries, e.g., Japan and Yemen, have already been through this transition in the recent past (Prins & Okita-Ouma, 2013), so there could be a potential for a change in consumer behaviour in China and Vietnam as well. However, given the current dangerously high poaching levels and because such a transition in behaviour and culture will likely take time (especially since the market for medicinal rhino horn is increasing due to global promotions by the Chinese government, as supported by the World Health Organization (Cyranoski, 2018; WHO, 2013)), rhino protection efforts aimed at the short-term survival of the species seem to be urgently needed.

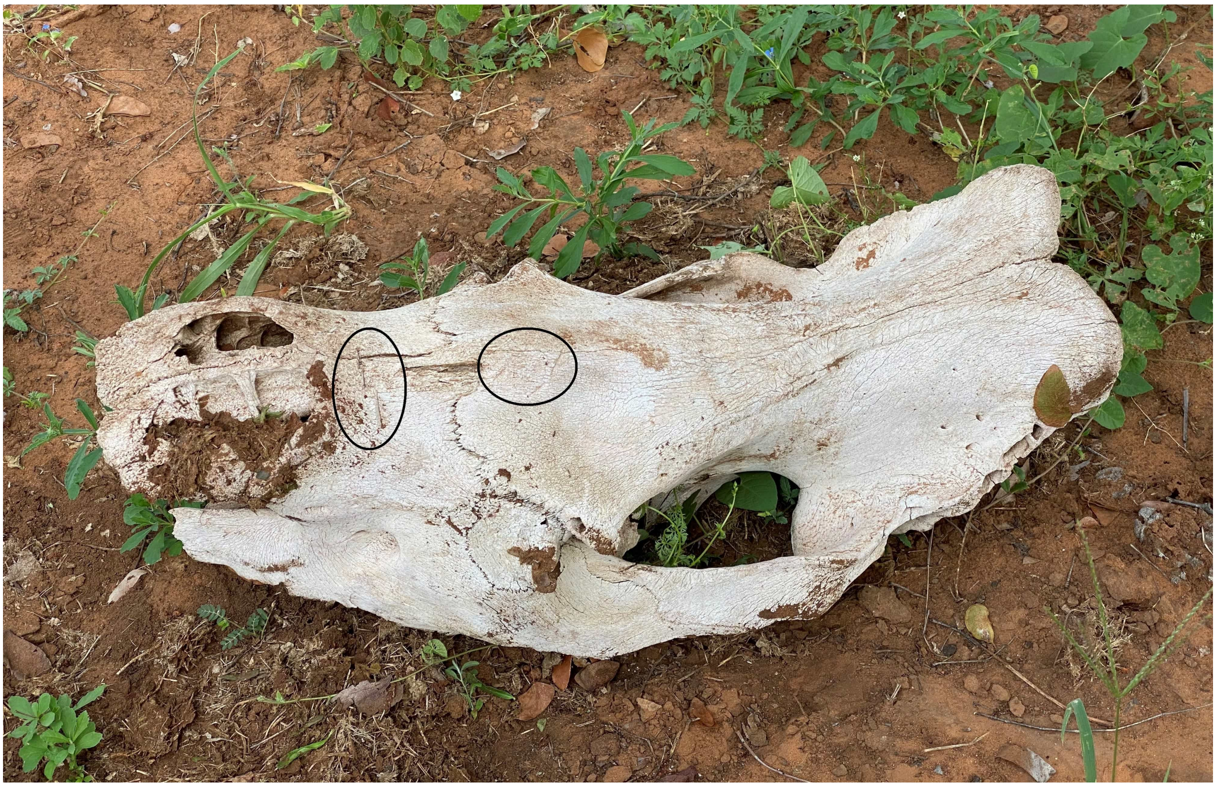


Figure 1.2: Poached white rhino skull that I found in Kruger National Park (South Africa) on 3 March 2020. Note the encircled axe marks at the bases of the former horns.

The rhino conservation sector, especially in South Africa, has responded to this alarming extinction risk in a number of ways. First, intensive patrols with anti-poaching rangers are being undertaken, fences have been built or improved around protected areas, scouting drones have been deployed, horns of living rhinos have been equipped with *RFID* chips and information technology has been included at various levels to stop poaching (Cambron et al., 2015; Conway-Smith, 2013; Penny et al., 2019; SANParks, 2015; Wildlife ACT, 2014). Second, education and awareness campaigns have been set up to decrease the illegal demand for rhino horn (African Wildlife Foundation, 2014; Greenfield & Veríssimo, 2019;

Save the Rhino, 2013; Veríssimo & Wan, 2019; WildAct Vietnam, 2019). Third, synthetic horns have been proposed to replace real ones and with that disturb the illegal market (Save the Rhino, 2016b). Fourth, cargo is being checked more intensively for animal body parts and negotiations with Asian governments are taking place to further enforce the ban on domestic sales of rhino horn in an effort to control the illegal trade (Save the Rhino, 2013, 2015). Fifth, horns of living rhinos have been dyed, poisoned or removed to devalue rhino horn (Ferreira et al., 2014; Rubino & Pienaar, 2017; Save the Rhino, 2016a). All these efforts have not been able to stop rhino poaching from taking place, but have possibly assisted in the decrease of rhino poaching events recorded in South Africa since 2014 (Figure 1.1). However, a grim reality is that Kruger National Park, the world's rhino poaching hotspot and (maybe former) rhino stronghold, experienced a 70% decline in their rhino population during the last decade (SANParks, 2020), of which the far majority disappeared between 2013 and 2018 (Ferreira & Pienaar, 2020). Currently there are only 3500 to 4000 rhinos left in Kruger National Park, which implies that there are nowadays simply less rhinos to poach.

1.2 Poacher early warning system

Sadly, poaching still continues to be a threat to the survival of African rhinos, as conservation officers often arrive too late at crime scenes (O'Donoghue & Rutz, 2016). Furthermore, deadly force used by poachers incites the authorities into intensified "militarized conservation", resulting in frequent shootouts between poachers and conservation officers (Duffy, 2014). An effective method for early poacher detection and localization is thus urgently needed, so that preventive action can be taken. With situational awareness, law enforcers can operate under safer conditions with reduced risk of fatalities and the potential to de-escalate conflicts. An effective poacher early warning system would thus contribute to the prevention of lethal violence, not only against wildlife, but also against conservation officers and poachers (Duffy, 2014).

Here I present such a poacher early warning system, based on the movement responses of sentinel animals. Humans often disturb animals when moving through a landscape, thereby changing the animals' movement (Frid & Dill, 2002; Tablado & Jenni, 2017). When the effect of humans on the movement of animals is adequately understood, the animals' perception about the presence and location of humans can be inferred from the animals' movement behaviour (Rosenzweig, 2007). Using this approach, animals can be used as sentinels to monitor the location of poachers through space and time, not much unlike canaries have been used as sentinels to monitor the presence of toxic gasses in mines.

1.3 Scientific background

The scientific background for the concept of a sentinel-based poacher early warning system is well in place. Prey species have evolved a suite of traits aimed at preventing them from being killed, e.g., via early predator detection and escape (Cooper & Blumstein, 2015). This often extrapolates to humans as well, since many prey species evolved together with human hunters, leading to anthropogenic disturbance stimuli triggering similar, or often even stronger, evasive responses (Frid & Dill, 2002; Zbyryt et al., 2018). Moreover, when one or several individuals in a group respond to a disturbance, the movement of all individuals and the entire group structure often changes (Helbing et al., 2000). This phenomenon can be described through a simple self-organizing process composed of inter-individual movement rules of attraction, repulsion and alignment (Couzin & Krause, 2003; Herbert-Read et al., 2015). Even small changes in individual movement rules can result in large and visually striking changes of collective movement patterns (Couzin et al., 2002; Krause & Ruxton, 2002), which can aid in the detection of anomalous movement patterns due to the presence of a poacher.

1.4 Scientific challenge

Despite the well-supported theoretical background for the concept of a sentinel-based poacher early warning system, some non-trivial scientific developments are still needed for the early warning system to work in practice. Generally speaking, being able to describe differences in animal movement given varying environmental conditions (e.g., the presence of a fear-inducing disturbance) is not the same as being able to detect a change in environmental conditions given information about animal movement. This contrast is two-fold: ecological (1) as well as statistical (2). First, animal behavior is known to be complex and context-dependent. Even simple movement variables such as mean displacement are often highly variable due to differences in time of day, season, weather conditions, vegetation patterns and landscape features (Nathan et al., 2008; Patterson et al., 2008). The effects of each of these environmental variables on animal movement can furthermore be multi-faceted, having both direct effects (e.g., dense tree cover slowing animals down by making a terrain difficult to traverse) as well as indirect effects (e.g., trees slowing animals down by inciting them to forage and at the same potentially inciting them to speed up due to the risk of ambush predators) (Fryxell et al., 2008; Nathan et al., 2008). Making it even more complex, environmental variables interact with each other in their effect on animal movement, e.g., animals can select areas with high tree cover during the day and more open areas during the night to decrease predation risk (Ager et al., 2003). Second, a statistical difference in a response variable (e.g., mean displacement of an animal) between two states of an environmental condition (e.g., dense versus open areas) does not necessarily mean that a sudden change in this condition can be detected by measuring and analyzing the response variable in real-time. A statistical difference in a response variable between two groups is acquired by comparing the distribution of an accumulation of many data records, often with a substantial variance within the same group. Such a statistical approach will not suffice when trying to detect a switch in the state of an environmental variable based on response variables, where I consider environmental state switches broadly (e.g., suitable to unsuitable forage habitat, day to night, center to edge of a social group, encountering a predator, etc.).

The detection of state switches in movement behaviour itself is a rapidly evolving field in movement ecology (Langrock et al., 2014; Patterson et al., 2008), but the detection of a state switch of an environmental variable based on animal movement less so. Environmental variables are known to influence animal movement via three mechanisms (Nathan et al., 2008): the animals' internal state ("*why move?*"), motion capacity ("*how to move?*") and navigation capacity ("*where to move?*"), which makes inference on the functional relationship between an environmental variable and animal movement complex. Moreover, given that the animals' environment is often heterogeneous, multiple environmental variables are often changing at the same time (Nathan et al., 2008). Past movement ecology research has therefore focused mainly on quantitatively describing animal movement and its state switches (e.g., via state-space modelling (Patterson et al., 2008)) and relating these patterns *post hoc* to environmental variables (Avgar et al., 2013; Signer & Ovaskainen, 2017; Wilmers et al., 2015). To be able to make direct predictions about an underlying environmental variable from animal movement, it is thus needed to substitute our lack of understanding about the functional relationship between the environment and animal movement.

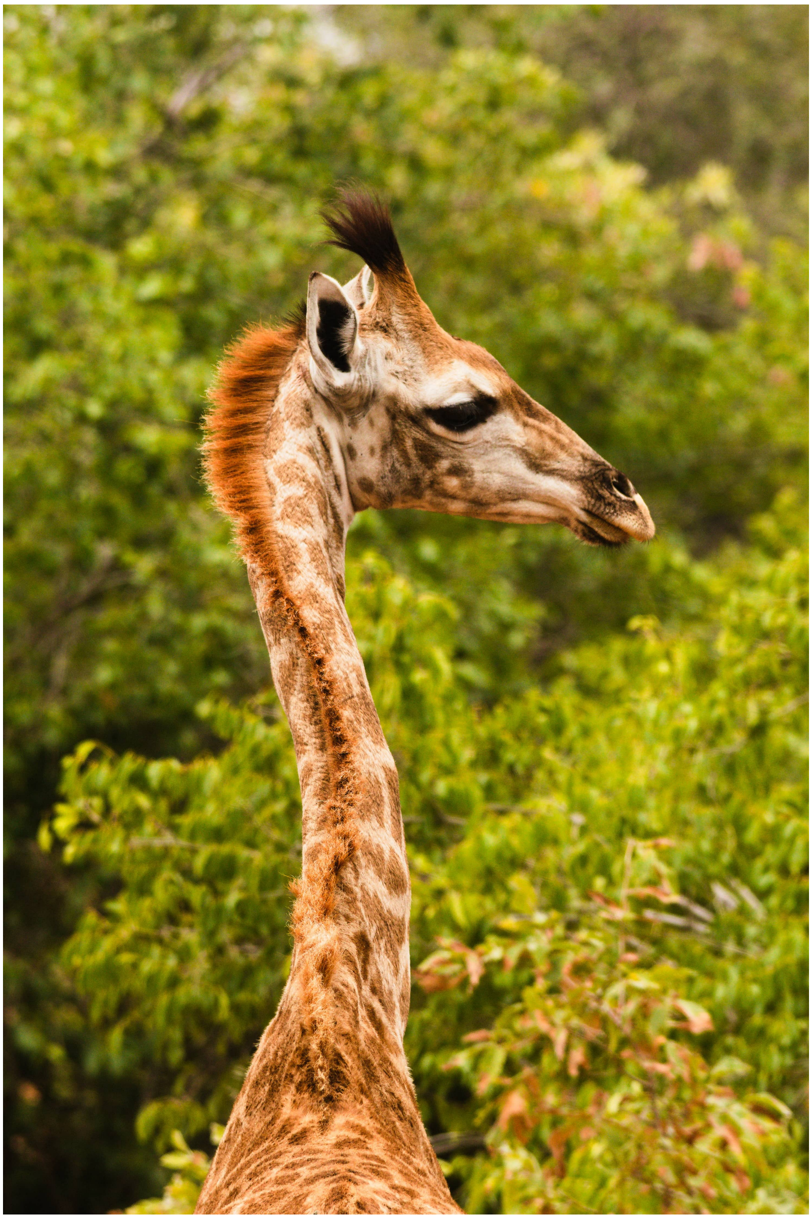
To develop this substitute for the goal to reliably infer an abrupt change of a single environmental variable from animal movement, a different statistical approach is required in which all other important environmental influences are accounted for. This approach requires that the interaction of many variables are combined in a single model that allows for complex data-driven relationships. Artificial intelligence offers such an approach. When combining many high-resolution animal trajectories with accurate environmental data about both the spatial (e.g., terrain and vegetation) and temporal aspects (e.g., time of day and weather), an estimate of "normal" animal behaviour given the prevailing conditions could be developed. Knowing the expected animal movement behaviour allows for the computation of the deviation of various movement features (both individual and collective), which can be used to train a data-driven machine learning classification model to detect the presence of a poacher.

The addition of this thesis to science lies mainly in the merging of two scientific fields: animal ecology and artificial intelligence. This thesis neither develops new fundamental ecological theories, nor does it develop new machine learning algorithms. However, what it does is combining previously acquired domain knowledge of animal ecology with the available toolbox provided by artificial intelligence into a framework that allows for the the detection of abrupt environmental changes from animal movement. Incorporating domain knowledge (viz., animal ecology) into a machine learning system is one of the most important aspects to make systems succeed in their tasks (DeepLearning.AI, 2021; Yu et al., 2010). Given the absence of an existing framework for the aforementioned task to which I could contribute, I did not set out to answer a specific overall research question in this thesis, but rather aimed at developing the full methodological framework and reflect on its mechanisms and uses.

1.5 Thesis outline

This thesis brings together a number of coherent research papers about wildlife conservation, movement ecology and artificial intelligence, aimed at investigating the necessity, analytics and applicability of a sentinel-based poacher early warning system. As such, some chapters focus on the societal challenge of poaching (Chapter 2; Chapter 3), while other chapters deal with the scientific challenge of predicting an environmental variable from animal movement (Chapter 4; Chapter 5), combine both challenges (Chapter 6), or focus on the eventual implementation of a sentinel-based poacher early warning system (Chapter 7). Each research chapter has on purpose been framed as broad as possible, to make its content also generally applicable outside the scope of this thesis.

In **Chapter 2** I critically evaluate whether rhino protection efforts aimed at the short-term survival of the species are actually needed. I examine this by investigating if legal international rhino horn trade would be an alternative ultimate solution for rhino poaching. Through an integrative review of scientific and grey literature about rhino horn trade legalization, I identify the main mechanisms by which a legal rhino horn market would influence the remaining wild rhino populations. Subsequently, I weigh through plausible reasoning the importance of these mechanisms on the predicted overall effect of a legal rhino horn trade on wild rhino populations. In **Chapter 3** I investigate how large the impact of hunting is on animal populations in general to gauge the potential of innovative protection efforts. I did this by analyzing how much human hunters alter the spatial distribution of animals in the tropics. Through a systematic review and a mixed effects meta-analysis I estimate the overall reduction in mammal and bird abundance in hunted versus unhunted sites. I focus here on the extent of population depletion by comparing population sizes with distances to human access points, both for protected and unprotected areas. In **Chapter 4** I study the link between individual movement rules and emergent collective movement properties, which can both provide information about changes in the perceived environment of animals. I use an agent-based simulation model to study the indirect effects of fear and resources on animal group structures. Only the individual movement rules are directly affected by fear and resources in this model, but through self-organization the effects of fear and resources also become apparent on a collective level. I specifically focus on the variation in group sizes that are generated from identical self-organizing processes. In **Chapter 5** I describe an analytical framework to predict the environment of animals based solely on their movement data. By doing this I investigate how much of the animal's environment influences their movement. Here I link high-resolution sensor data from cows in a controlled environment to various environmental variables by using extensive feature engineering and machine learning to predict the environment from animal movement sensor data. Using this data-driven approach I demonstrate that it is possible to quantify environmental influence on animal movement. In **Chapter 6** I combine the learned lessons from the previous two chapters into a sentinel-based poacher early warning system in Welgevonden Game Reserve (South Africa). Using sensor data from 138 savanna ungulates I first automatically classify flight responses caused by staged "poaching" intrusions undertaken by employees of the reserve. Secondly, I use the classified flight responses to automatically detect time periods with "poaching" intrusions. Thirdly, I use the sensor data of both fleeing and non-fleeing animals collectively to automatically localize the "poachers" through space and time. In **Chapter 7** I gauge the potential of aerial imagery to supplement or replace animal-born sensors to track animals *en masse* in the near future. For this I investigate the performance of an automated animal detection algorithm. Using a deep learning approach I automatically identify animals inside images from an aerial wildlife survey in Kenya, after which I also classify the animal species using the same model. Furthermore, I compare the precision and accuracy of population estimates that can be obtained with automatic animal detection versus those of manual aerial counts. Finally, in **Chapter 8** I synthesize my combined research in light of the scientific and societal challenges underlying the development of a sentinel-based poacher early warning system. Here I also look to the future and discuss the applicability of technology to aid nature conservation. Furthermore, next to wildlife conservation, I focus separately on the impact of my employed methods on ecological research. I discuss the potential of the interface between artificial intelligence and ecology, after which I suggest future research directions that could advance ecology as a science.



Chapter 2

Will legal international rhino horn trade save wild rhino populations?

This chapter is based on:

Eikelboom, J. A. J., Nuijten, R. J. M., Wang, Y. X. G., Schroder, B., Heitkönig, I. M. A., Mooij, W. M., van Langevelde, F., & Prins, H. H. T. (2020). Will legal international rhino horn trade save wild rhino populations? *Global Ecology and Conservation*, *23*, e01145. https://doi.org/10.1016/j.gecco.2020.e01145

Abstract

Wild vertebrate populations all over the globe are in decline, with poaching being the second-most-important cause. The high poaching rate of rhinoceros may drive these species into extinction within the coming decades. Some stakeholders argue to lift the ban on international rhino horn trade to potentially benefit rhino conservation, as current interventions appear to be insufficient. We reviewed scientific and grey literature to scrutinize the validity of reasoning behind the potential benefit of legal horn trade for wild rhino populations. We identified four mechanisms through which legal trade would impact wild rhino populations, of which only the increased revenue for rhino farmers could potentially benefit rhino conservation. Conversely, the global demand for rhino horn is likely to increase to a level that cannot be met solely by legal supply. Moreover, corruption is omnipresent in countries along the trade routes, which has the potential to negatively affect rhino conservation. Finally, programmes aimed at reducing rhino horn demand will be counteracted through trade legalization by removing the stigma on consuming rhino horn. Combining these insights and comparing them with criteria for sustainable wildlife farming, we conclude that legalizing rhino horn trade will likely negatively impact the remaining wild rhino populations. To preserve rhino species, we suggest to prioritize reducing corruption within rhino horn trade, increasing the rhino population within well-protected 'safe havens' and implementing educational programmes and law enforcement targeted at rhino horn consumers.

2.1 Introduction

The majority of wild vertebrate populations are in severe decline and one-third of all mammal and bird species are currently under threat by unsustainable subsistence hunting, poaching and wildlife trade (IPBES, 2019; Rivalan et al., 2007; Scheffers et al., 2019). Large-scale poaching operations are taking place all over the world, heavily impacting the remaining number of rhinoceros, elephants, vultures, pangolins and numerous other animal species (Conrad, 2012; Fischer, 2004; Rademeyer, 2016). Their horns, tusks, claws, scales, bones and other body parts are smuggled in large quantities mainly to Southeast and East Asia, where they are processed into products that function as status symbols and traditional medicines (Milliken & Shaw, 2012). Illegal trafficking of animal products, e.g., rhino horn, is often undertaken by international crime groups, which can be both opportunistically formed collectives or structured and organised networks, that may have ties or are involved with conservation, tourism and/or trophy hunting industries (Ayling, 2013; Rademeyer, 2012, 2016; Van Uhm, 2012). Especially rhino horns are extremely valuable on the black market, being sold between US $ 30,000 and 65,000 per kg in Vietnam, thereby being worth more than gold, heroin or cocaine (Rademeyer, 2016; Van Uhm, 2012). The poachers may be locals that live near nature reserves who can earn between US $ 500 and 20,000 per poached rhino, depending on the role they fulfil (Rademeyer, 2016). However, there seems to be a trend towards more professionally outfitted and trained poachers (Van Uhm, 2016). Rhino horns are also harvested via ‘pseudo-hunting’, by using rhino trophy hunting as a cover-up for the illegal killing and trafficking of rhino horns to Southeast Asian markets (Ayling, 2013; Rademeyer, 2016; Van Uhm, 2018b).

The poaching rate of the two African rhinoceros species (the white rhino *Ceratotherium simum* and black rhino *Diceros bicornis*) increased significantly since 2007 (Figure 2.1), which has generated substantial global concern (African Wildlife Foundation, 2014; Biggs et al., 2013; Milliken & Shaw, 2012; Rubino & Pienaar, 2017). It has been estimated that African rhinos could already become extinct in the wild around the year 2036 (Haas & Ferreira, 2016). In 2010 it was estimated that South Africa was home to 95% (~19,000) of all remaining white rhinos and 40% (~1900) of all black rhinos (Emslie et al., 2016; Rubino & Pienaar, 2017). The survival of the South African rhino population could therefore likely determine the fate of both African rhinoceros species.

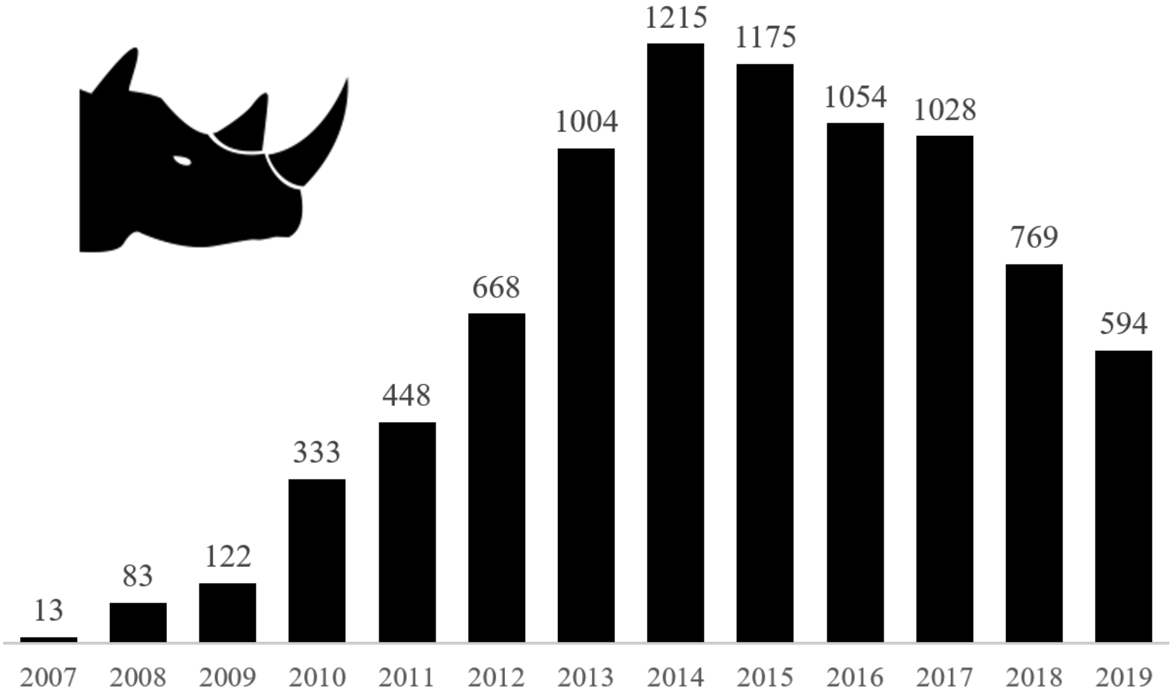


Figure 2.1: Number of recorded poached rhinos in South Africa from 2007 until 2019 (Save the Rhino, 2020).

The rhino conservation sector, especially in southern Africa, has responded to this alarming extinction risk in a number of ways. First, intensive patrols with anti-poaching rangers are being undertaken, fences have been built or improved around protected areas, scouting drones have been deployed, horns of living rhinos have been equipped with RFID chips and information technology has been included at various levels to stop poaching (Cambron et al., 2015; Conway-Smith, 2013; Penny et al., 2019; SANParks, 2015; Wildlife ACT, 2014). Second, education and awareness campaigns have been set up to decrease the illegal demand for rhino horn (African Wildlife Foundation, 2014; Greenfield & Veríssimo, 2019; Save the Rhino, 2013; Veríssimo & Wan, 2019; WildAct Vietnam, 2019). Third, synthetic horns have been proposed to replace real ones and with that disturb the illegal market (Save the Rhino, 2016b). Fourth, cargo is being checked more intensively for animal body parts and negotiations with Asian governments are taking place to further enforce the ban on domestic sales of rhino horn in an effort to control the illegal trade (Save the Rhino, 2013, 2015). Fifth, horns of living rhinos have been dyed, poisoned or removed to devalue rhino horn (Ferreira et al., 2014; Rubino & Pienaar, 2017; Save the Rhino, 2016a). All these efforts have not been able to stop rhino poaching from taking place, but have possibly assisted in the decrease of rhino poaching events recorded in South Africa from 2014 to 2019 (Figure 2.1). However, reduced rates of successfully tracking down rhino, because of their dwindling numbers, may also be invoked as an explanation for the decrease of poaching incidents. Furthermore, some state that the overall decrease of rhino poaching incidents is largely a result of the decrease in poaching in Kruger National Park, where protection was improved in response to the high poaching rate (Rademeyer, 2016). As a response, rhino poaching incidents have increased in other areas (Rademeyer, 2016), notably in Hluhluwe-Imfolozi Park and private game reserves. Unfortunately, the current poaching rate is still so high that it poses a serious threat to the survival of both African rhino species (Haas & Ferreira, 2016).

With the aim to reduce the rapid population decline of vulnerable species, international commercial trade bans of animal products have been implemented through CITES since 1975 (Ayling, 2013). International rhino horn trade has been banned since 1977, which was followed by a decrease in rhino poaching rate at first (Ayling, 2013). However, the increase in the population size of white rhino between 1977 and 2007 was likely not attributed to this trade ban, but to an increase in private ownership and trophy hunting (Leader-Williams et al., 2005) and the protection in the South African National Parks. Furthermore, the population size of black rhino has decreased substantially since the implementation of the trade ban from approximately 65,000 individuals in 1970 to 2400 individuals in 1995 (Leader-Williams et al., 2005). It is unlikely that the ban directly led to the increase of black rhino poaching, as this was likely caused by rapid economic and population growth in Southeast Asia (Milliken et al., 1993). Moreover, the poaching rate of both African rhino species increased dramatically since 2007 despite the trade ban (Figure 2.1).

Given the failure of an international trade ban to fully stop rhino poaching, a substantial number of scientists, policy makers, conservationists and rhino owners have argued to lift the current ban on international rhino horn trade as a potential solution for the ongoing rhino poaching crisis (Biggs et al., 2013; Rubino & Pienaar, 2020; Taylor et al., 2017). This was based on the reasoning of “use it, or lose it”, as substantiated by the Principles and Guidelines for the Sustainable Use of Biodiversity by the Convention on Biological Diversity (SCBD, 2004). Rhino horn, which is comprised only of keratin, can be harvested with no ill effect to the animal’s health (Biggs et al., 2013; Rubino & Pienaar, 2017). However, others are strongly opposed to lifting this ban for both ethical reasons and concerns about a further increase in rhino poaching (Cheung, Wang, et al., 2018; Prins & Okita-Ouma, 2013; Save the Rhino, 2018). This topic has been discussed during several CITES meetings, which led to votes in 2016 and 2019 that twice rejected proposals to lift the ban (CITES, 2019; Save the Rhino, 2018). Furthermore, scientists have been studying the potential effects of a rhino horn trade ban lift for approximately two decades now (Ayling, 2013; Biggs et al., 2013; Cheung, Wang, et al., 2018; Collins et al., 2016; Conrad, 2012; Fischer, 2004; Rivalan et al., 2007; Taylor et al., 2017). Overall, this debate has become polarized, which has led to an apparent deadlock in the discussion (Committee of Inquiry, 2016; Taylor et al., 2017).

The potential conservation benefit of legalizing an animal product market can be divided into two aspects: 1) a legal competing market could offset poaching, and 2) a legal market could provide financially viability to keep, protect and breed animal populations (see section 2.8). Past cases show that the legal commercialization of animal products can go both ways regarding the conservation of a species; with a (potentially) positive effect in the case of bison meat, crocodilian skins and trophy hunting, but with a (potentially) negative effect for elephant ivory and lion bones (see section 2.8). There are thus situational- and/or context-dependent mechanisms that determine how an animal population responds to a legal animal product trade (Tensen, 2016). It is important to gauge how the rhino populations could respond to a legalization of international rhino horn trade.

Here we present an integrative review on the pros and cons of legalizing international rhino horn trade for the sustained preservation of rhinos in the wild by drawing insight, plausible reasoning, modelling results and empirical data from scientific and grey literature of multiple disciplines (Snyder, 2019). In this review, we discuss four mechanisms (in no specific order) that change or come into play if international rhino horn trade would be legalized and how these mechanisms will potentially impact wild rhino populations (Figure 2.2). We identified the following mechanisms as the most frequently occurring ones in scientific literature, in grey literature, and in the arguments of conservationists, policy makers and private rhino owners: 1) financial viability for private rhino owners, 2) rhino horn demand, 3) laundering of rhino horns, and 4) behaviour of rhino horn consumers. These four mechanisms were selected by the authors after thoroughly familiarizing themselves with the topic through past work experience and reading top results from literature search engines about wildlife trade and farming, but without strong *a priori* hypotheses about how each of the mechanisms would influence the study's conclusion. The authors varied in their initial ideas about whether or not rhino horn trade could benefit rhino conservation, thereby limiting a potential researcher bias in the selection of the mechanisms. However, we do not suggest that the selected four mechanisms provide a complete description about what will happen if rhino horn trade is legalized, but we do posit these mechanisms to be of major importance. We collected and studied the literature *ad hoc* to get a thorough understanding about the mechanisms and how these would influence rhino populations in the case of a horn trade legalization. We did this by first reading the top results from literature search engines while searching for keywords related to these mechanisms and wildlife trade and farming. Upon noticing contradictions in views or knowledge gaps, we continued our search by using more specific keywords. These latter search results were often read with the purpose to retrieve an answer on specific questions, in order to get a complete overview of the effects of the mechanisms.

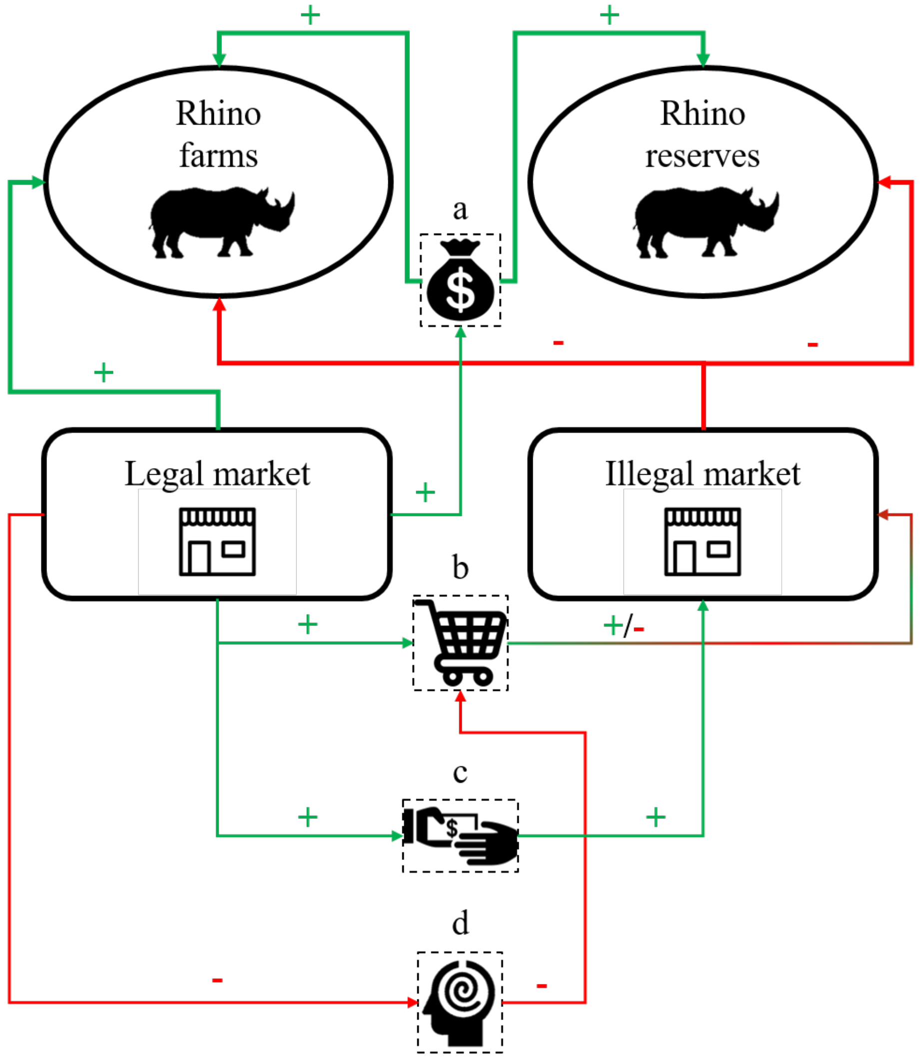


Figure 2.2: Conceptual diagram of the international legal rhino horn trade scenario with farmed and wild rhino populations, legal and illegal markets, and four identified mechanisms (as discussed in the four main sections of this study): a) financial viability for private rhino owners, b) rhino horn demand, c) laundering of rhino horns, and (d) behaviour of rhino horn consumers. Green arrows represent a potential positive effect (higher/larger source leads to a higher/larger destination), red arrows a potential negative effect (higher/larger source leads to a lower/smaller destination) and green/red arrows both a potential positive and negative effect. An improved financial viability for private rhino owners has been hypothesized to benefit both farmed and wild rhino populations, rhino horn demand has been hypothesized to increase with a legal market, laundering has been hypothesized to allow for an increase in illegal horn trade with a legalized market, and it has been hypothesized that programmes aimed at changing the behaviour of rhino horn consumers will be less effective with the existence of a stigma-removing legal rhino horn market.

After discussing the four aforementioned mechanisms, we combine our insights into a conclusion where we evaluate each mechanism and whether it will have a positive, negative, or still unknown effect on the future wild rhino population size. We weigh the relative importance of these mechanisms and their potential effect on the wild rhino population through plausible reasoning to come to an overall recommendation about legalizing international rhino horn trade. We conclude by giving suggestions for future research and for a policy agenda that would benefit rhino conservation the most according to our study. In our study we focus primarily on the two African rhino species and often in the setting of South Africa (as South Africa harbours the majority of all rhinos on Earth at present), even though we acknowledge the importance of other countries with rhino populations and the situation of the more rare Asian rhino species. Nevertheless, since illegal wildlife trade is an interlinked and global system, we posit that our review provides a valid overview for the situation of all rhino species by primarily considering the world's largest rhino population as a case study.

2.2 Financial viability of private rhino ownership

The majority of South African rhinos (both black and white) currently live in either government-owned national parks or privately owned game reserves and farms (Child et al., 2012; Knight et al., 2015). In national parks, large amounts of money are often spent on wildlife protection, paid for by revenues from tourism as well as by affluential external donors and the state (Annecke & Masubelele, 2016). Privately owned game reserves and farms on the other hand, need to be financially viable as a business model. For private rhino owners, the revenue from keeping rhinos on their lands traditionally comes from tourism, trophy hunting and live animal sales. When in the early 1990s the subsidy to agricultural commercial farmers stopped in South Africa, a large number of farmers reverted to game farming as South African law allowed for private ownership of wildlife (Child et al., 2012; Taylor et al., 2015). Private wildlife ownership is currently only allowed in South Africa, Namibia and Zimbabwe (Muir-Leresche & Nelson, 2000), where private wildlife owners have to abide to the national nature protection laws. Populations of large game animals have increased in southern Africa through this form of farming (Child et al., 2012). As 80% of the land in South Africa is privately owned (Cousins et al., 2008), it is thought that private ownership of rhino on these lands can play a critical role in the recovery and long-term conservation of the species (Collins et al., 2016; Rubino & Pienaar, 2017). It is estimated that 33% of the total rhino population in South Africa is now privately owned (Rademeyer, 2016; Rubino & Pienaar, 2017).

For private rhino owners, the increasing security costs of protecting their rhino from poaching pose a major problem (Rubino & Pienaar, 2020). Income from the traditional sources (tourism, trophy hunting and/or live sales) is in many cases not sufficient to cover the increased costs for protection and at the same time create a financially sustainable enterprise (Minnaar & Herbig, 2018; Rubino & Pienaar, 2017). It is estimated that in 2016, 70 of the approximate 400 private rhino owners in South Africa have removed rhinos from their land due to financial difficulties and the personal security risks posed by poachers, amounting to a loss of about 200,000 ha of land available for rhino conservation (CITES, 2016).

The problem sketched above has fuelled the plea for a lift on the trade ban and legalization of the market, with private rhino owners being prominent advocates (Private Rhino Owners Association, 2017; Rubino & Pienaar, 2020). Lifting the trade ban could enable private rhino owners to exploit an extra way of gaining revenue from keeping rhinos by selling sustainably harvested horns (Rubino et al., 2018). This increased revenue could in turn be used to pay for extra anti-poaching measures by private rhino owners. An additional advantage that is to be expected when legalizing the trade is that the viability of rhino farming will get an impulse, leading to more entrepreneurs and land-owners being interested in keeping rhinos. This will increase the population of captive rhinos, which benefits the global population of this threatened species. Although the conservation value of a captive population of rhinos is less than that of a healthy wild population (Redford et al., 2011), a captive population could be an important buffer in case rhinos become extinct in the wild.

Another frequently used argument is that tax raised from legally traded horns could flow back to the protection of wild rhino populations and can be invested in livelihood development for communities surrounding these parks, which currently form the cradle of poachers (Di Minin et al., 2015; Rademeyer, 2012). Di Minin et al., 2015 concluded in a modelling study that this reinvestment of profit from legal sales would actually be a prerequisite for a positive effect of legalizing the market on rhino conservation. Given that the black market price for rhino horn is currently between US $ 30,000 and 65,000 per kg and rhino horn farming is profitable from approximately US $ 11,500 per kg onwards (Rademeyer, 2016; Rubino et al., 2018), there is ample room for legal sales to yield substantial financial resources to potentially protect rhinos in such a way that poaching becomes less profitable (Collins et al., 2016; Di Minin et al., 2015). However, it is unlikely that most of the tax raised through rhino horn sales will be reinvested in wild rhino conservation, since health care, housing and education of previously disenfranchised people are politically more urgent for many African governments. Capitalist governments have independent processes of harvesting and distributing wealth, meaning that sectors that are taxed for a certain amount are not compensated with an equal amount of governmental funding. Furthermore, it is questionable whether private rhino owners are major stakeholders in wild rhino conservation or not, because they only have an indirect financial incentive to bargain with the government for a reinvestment of taxes to the protection of wild rhinos. Less poached rhino horns could of course lead to more consumers for farmed rhino horns, but the significance of this phenomenon will fade when there would be substantially more farmed rhinos than wild rhinos.

Legalizing the rhino horn trade would thus have two main advantages through the mechanism of increased revenue for rhino owners. First, the owners will have an incentive for sustaining a viable captive population of rhinos. Second, there will be money available for the protection of both private (through sustainably harvested horn sales) and wild rhinos (through taxes), which in turn can discourage poaching. However, it is unclear if a substantial amount of the raised taxes will be reinvested in the protection of wild rhinos.

2.3 Demand for rhino horn

The debate about whether or not to legalize international rhino horn trade often focuses on what will happen to the market demand (viz., in terms of quantity of rhino horn given current prices or potentially lower or higher prices), i.e., will the overall demand (legal, viz., supplied mainly by farms, and illegal, viz., supplied by poachers, combined) increase and how will the current illegal market respond to a legal market? To adequately answer these questions it should first be known how large the current demand for illegal rhino horn is. Some estimated the overall demand for rhino horn by looking solely at the current illegal supply, concluding that demand for rhino horn can be met with 5000 captive white rhinos through regular non-lethal harvesting of their horns in South Africa alone (Biggs et al., 2013; Milliken et al., 2009). However, there are many concerns about this estimation. First, the current illegal demand is already far greater than the current illegal supply (USAID Vietnam, 2018; USAID Wildlife Asia, 2018). The United States Agency for International Development concluded via interviewing 1400 Vietnamese people that are financially able to buy rhino horn (from five different cities that sustain a black market in rhino horn) that in Vietnam 10% of the people find it acceptable to buy or own rhino, of which 10% are currently wealthy enough to afford it (USAID Vietnam, 2018). This suggests that there is a demand for rhino horn from about a million people in Vietnam alone. In the 14 times more numerous Chinese population, the USAID surveyed 1800 people (from six different cities that have a rhino horn black market) and concluded that 16% have purchased rhino horn in the past, of which 8% in the past 12 months (USAID Wildlife Asia, 2018). China and Vietnam combined are thus home to millions of potential rhino horn consumers. Second, Kotze, 2014 argued that rhino horn farming will produce too few horns to meet the demand in the near future, considering the horn growth rate of only 6 cm per year on average (Pienaar et al., 1991) and the low reproduction rate of one calf per 3-5 years (Patton et al., 1999; Swaisgood et al., 2006). Third, Prins and Okita-Ouma, 2013 argued that Biggs et al., 2013 overlooked the demand for the other four rhino species; the suggested yield of legal supply is often based on rhino farming in southern Africa and overlooks Asian rhino species, which are not currently farmed and are desired for their horns nonetheless. To conclude, current illegal demand is likely far greater than current illegal supply, with the current estimation of potential buyers far exceeding the amount a legal supply could realistically meet in the (near) future (USAID Vietnam, 2018).

Current demand for rhino horn will likely not stay the same with a legalization of rhino horn trade and it should thus be estimated how the overall demand will change. First of all, future overall demand is likely to increase with economic and population growth in Asia, regardless of rhino horn trade legalization (Tensen, 2016; Vigne et al., 2007). Furthermore, if the trade ban is lifted new forces will start to influence the demand for rhino horn as well (Fischer, 2004). An important new force is the removal of the stigma that comes with buying illegal products. Although Biggs et al., 2013 assumed that with a legal rhino horn trade *"the demand does not escalate to dangerous levels as the stigma associated with the illegality of the product is removed"*, plenty of other studies argued that the demand will likely increase significantly because of the removal of the stigma (Collins et al., 2013; Fischer, 2004; Prins & Okita-Ouma, 2013), at least for law-abiding consumers (Fischer, 2004; USAID Vietnam, 2018; USAID Wildlife Asia, 2018). Another market force that could result in an increased demand after legalization is the reawakening of old markets, particularly markets that were active in the 1970s and 1980s in Taiwan, Japan, Singapore and Yemen (Prins & Okita-Ouma, 2013), which could thus reverse the decreased demand in these old markets (Graham-Rowe, 2011). In addition to traditional consumer countries, there are also new (e.g., African) countries that sell Traditional Chinese Medicines in their drug stores and where people start to believe that wildlife products (including rhino horn) can cure diseases (Cyranoski, 2018). These new local markets are often overlooked in the estimation of demand. Moreover, a substantial increase in demand (both legal or illegal) could further promote the tragic positive feedback loop between demand and the rhino extinction rate, which is coined the Anthropogenic Allee Effect (Challender & MacMillan, 2014; Hall et al., 2008). The Anthropogenic Allee Effect indicates that when the abundance of an animal species decreases, the demand for its products will increase due to its rarity (Hall et al., 2008). Accounting for all the aforementioned market forces, the overall demand for rhino horn is expected to grow significantly with a legalized market, although the recent COVID-19 pandemic may affect people's attitudes towards using products of wild animals in unforeseen ways (Lam et al., 2020).

Ideally, with a legal market that would be supplied mainly by rhino farmers, the illegal demand for poached horns would disappear or at least become substantially smaller. Unfortunately, how the illegal demand for rhino horn will respond exactly is uncertain (Fischer, 2004). From an economic perspective, illegal traders and farmers can compete with each other in multiple ways that could either benefit or devastate rhino conservation (Damania & Bulte, 2007). From a social perspective, people that fear heavy penalties for consuming illegal products will likely shift from the illegal to the legal market when effective law enforcement is in place. The same applies to people that care about animal welfare or conservation. These three deterrents have been mentioned by 71-76% of the

242 interviewed Vietnamese illegal rhino horn consumers (USAID Vietnam, 2018), so it can be assumed that a substantial portion of the current illegal consumers will consider switching to a legal market. On the other hand, some people have a preference for illegally harvested ('wild') horns, e.g., those that prefer to buy larger horns as a status symbol and those that believe that the suffering of the animal enhances the 'potency' of the medicine (Cheung, Mazerolle, et al., 2018; Hanley et al., 2018; Tensen, 2016). It is thus likely that an illegal market will always persist parallel to a legal market and this should not be neglected in the debate around the legalization.

Given the high likelihood of a substantially increasing demand with trade legalization, it is important to consider effective market forces to regulate this increase to avoid it leading to the detriment of wild rhino populations. Price is such a force that many studies proposed to influence the market demand (Milner-Gulland, 1993). However, the effect of price on the overall demand as well as on the illegal demand is ambiguous and may yield counterintuitive results. For the overall demand, lower prices make on the one hand rhino horn affordable to more buyers, which could lead to an increase in overall demand (USAID Vietnam, 2018). On the other hand, a lower price could also weaken the effect of the Anthropogenic Allee Effect, i.e., a lower price makes it less attractive for people that are after luxurious or rare products. For the illegal demand, Biggs et al., 2013 argued that lower prices in the legal market will likely diminish it. While it is true that a lower legal price can motivate people to move from the illegal to the legal market, it is not always the case. Like with marijuana, a legal market is more likely to reduce the illegal market when its price can compete with the illegal market (Morris, 2018). Wildlife product markets are very different from perfect competition markets, suggesting that lowering the price may not be a good strategy, as it is hard to make sure that the price in the legal market is always lower than the illegal price. For example, farmed tiger bones are 50-300% more expensive than from poached tigers (EIA, 2013). Also, illegal elephant tusks were sold for only a third of the price of legal tusks (Fischer, 2004). As for rhino farming, the minimum price for rhino horn to be profitable is approximately US $ 11,500 per kg (Rubino et al., 2018). If crime networks are able to supply horns at a lower price it is still likely that consumers will buy illegal products. However, 63% of the 242 Vietnamese illegal rhino horn consumers would be willing to pay more if the product is scientifically tested by a trusted supplier and 72% would still buy rhino horn with a 10% increase in price (USAID Vietnam, 2018). So a substantial portion of the current illegal consumers is likely to move to the legal market, even if legal prices cannot fully compete with illegal prices. On the other hand, consumers often overstate their willingness to pay a premium (Katt & Meixner, 2020). Furthermore, these results also show that price is only a minor concern to current rhino horn users (USAID Vietnam, 2018; USAID Wildlife Asia, 2018). This is backed up by the notion that demand for rhino horn is inelastic to price changes (Crookes & Blignaut, 2015; Milner-Gulland, 1993). For instance, the demand for rhino horn rose substantially in Yemen despite a 40% increase in price within four years (Vigne et al.,

2007) and modelling studies have suggested that reducing the price of rhino horn will not curb rhino poaching (Crookes, 2017). These results suggest that the overall demand for rhino horn is insensitive to an increase or decrease in price.

The improbability of price being able to control the demand urged researchers to look into social instead of economic forces. These social forces turned out to be more effective than price in a modelling study about the rhino horn case (Crookes & Blignaut, 2015). First, the consumption motives of rhino horn buyers in Southeast and East Asia should be known to be able to adequately respond to it. According to results of interviews with 242 Vietnamese illegal rhino horn buyers, the two main drivers of purchase are that rhino horns *"are worth their price no matter how expensive"* and *"indicate wealth, power and social status"* (USAID Vietnam, 2018). The status and cultural pride of the elite increases when the prices of 'must-have' status symbol products are high. The way to reduce the demand of these Vietnamese people are for example strategies related to heavy penalties and a focus on animal cruelty (USAID Vietnam, 2018). In a similar study, 140 Chinese illegal wildlife product buyers primarily mentioned that rhino horn *"brings good health"* and *"cures illness"* (USAID Wildlife Asia, 2018). In addition, an underestimated driver for buying rhino horn in China is the art and antiques market (Gao et al., 2016). Therefore, eliminating concerns about modern medical practices and increasing public awareness about animal conservation are key to reducing wildlife consumption in China. Understanding and anticipating the underlying consumption motives of rhino horn buyers thus seems more helpful in reducing demand than price changes.

In short, demand for rhino horn is currently much larger than supply and is expected to increase with economic and population growth in Asia (Tensen, 2016; USAID Vietnam, 2018; USAID Wildlife Asia, 2018; Vigne et al., 2007). With legalization of the market, demand is likely to increase further (in current, old and new markets) when the stigma around buying rhino horn is removed and potentially also due to the Anthropogenic Allee Effect (Challender & MacMillan, 2014; Hall et al., 2008). It will most likely be impossible to satisfy the demand with legal horns alone, due to a preference of some consumer groups for illegal ('wild') horns and the potentially lower price of illegal horns (Cheung, Mazerolle, et al., 2018; Hanley et al., 2018). The demand for illegal horn could however be reduced through a simultaneous increase in law enforcement combined with severe penalties for buying illegal horn (Tensen, 2016).

2.4 Laundering of rhino horns

The issues and debates about the demand for rhino horn suggest that legal and illegal markets are likely to co-exist after trade legalization, not only for consumers but also for suppliers (Fischer, 2004). Illegal rhino horn traders are likely to remain in business after trade legalization and could start laundering their products into the legal market (Collins et al., 2013; Fischer, 2004). This is the case with legal ivory trade as well, where 'ghost ivory' (post-1947 ivory being sold as pre-1947 ivory) and 'look-alikes' (e.g., elephant ivory fraudulently mislabelled as mammoth ivory) are being sold to the unsuspecting and uneducated buyers (CITES, 2019; Collins et al., 2017). Under such conditions, a legal market can actually give an incentive to illegal suppliers by lowering the chances of being caught in an illegal exchange, as corruption reduces the rhino horn confiscation rate (Fischer, 2004; Van Uhm, 2018b). For example, corruption amongst government officials, e.g., via threats and commission payments (Collins et al., 2016; Rademeyer, 2012), can allow for the entering of illegal products into legal markets (Bennett, 2015). A similar situation was found for the legal trade of ivory, in which eight of the twelve African countries that are home to the majority of elephant populations belong to the top 40% of the world's most corrupt countries (Transparency International, 2013; UNEP et al., 2013).

Widespread corruption exists and expands to all nodes in a trade chain (Bennett, 2015). Examples of wildlife trade related corruption exist in justice, economic and political systems (Wyatt et al., 2018), where acts of corruption on an individual level include bribes, patronage, diplomatic cover and permit abuse (Corruption Tracker, 2011; Nshuli, 2013; Walker, 2009; Wyatt et al., 2018). For example, a number of rhinos were actually poached by people who were employed to guard them in Africa during the 1970s and 1980s (Fischer, 2004). More recently in South Africa's Kruger National Park, police officers and rangers were directly involved in poaching (Anderson & Jooste, 2014). Similar situations were discovered in other rhino poaching hotspots in Africa as well (Smallhorne, 2013). For example in Kenya, the stronghold of the eastern black rhino (containing 87% of the subspecies' population), the internal government corruption worsened the problem of population decline (Anderson & Jooste, 2014).

Due to the aforementioned effects of corruption and laundering, legalizing rhino horn trade would at least need a highly regulated trading system if rhinos are to be preserved. A Central Selling Organization, the system with the largest control, was proposed by Biggs et al., 2013. To reduce the effects of corruption, they suggested to shorten the market chain between suppliers and buyers (Biggs et al., 2013). However, an illegal supply can in reality always be present as corruption within the Central Selling Organization could still support laundered poached horns to end up on the legal market (Bennett, 2015; Fischer, 2004). This was the case in the highly controlled diamond trade, where an estimated 5 to 10% of the world's legal diamond market consisted of 'blood diamonds' (Baker, 2015). Considering the huge demand for rhino horn and the small rhino population (USAID Vietnam, 2018), a potential 5% illegal horns would already be problematic for the survival of the species. Biggs et al., 2013 also proposed DNA profiling to track the legality of individual horns. However, this will not only inhibit the potential use of synthetic horns, but also that of buffalo horn and wood that circulate as 'rhino horn' and which currently comprise a substantial proportion of the market (Collins et al., 2013; Save the Rhino, 2016b). The demand for genuine rhino horn could therefore increase, together with the negative consequences (Collins et al., 2013). Furthermore, DNA profiling will likely increase the price of legal rhino horns.

In short, corruption is unfortunately a large problem worldwide, also along the rhino horn trade route in Africa and Asia (Emslie & Brooks, 1999; Wyatt et al., 2018). The illegal supply of rhino horn is therefore likely to increase when legalizing international rhino horn trade due to laundering and corruption (Van Uhm, 2018b), even with a highly regulated trading system (Bennett, 2015; Collins et al., 2013; Fischer, 2004).

2.5 Long-term behavioural change of rhino horn consumers

It is generally thought that the ultimate solution to stop rhino poaching lies in a change of the consumers' behaviour (Litchfield, 2013). The demand can be drastically reduced if not eliminated, by creating a uniform morality that it is wrong to purchase products that have such a clear negative effect on the survival of a threatened species and by providing alternatives to fulfil the need for the product (Litchfield, 2013). This can only be accomplished by a global change in consumer behaviour. Despite the efforts of non-governmental organisations and conservation incentives (Biggs et al., 2013; Holden et al., 2019; St John et al., 2010), this has not been achieved yet, as illustrated by the high poaching rates and large demand for rhino horn and other wildlife products (Save the Rhino, 2020; USAID Vietnam, 2018; USAID Wildlife Asia, 2018).

Environmental awareness programmes are believed to increase knowledge and concern (Sampei & Aoyagi-Usui, 2009), but there seems to be a value-action gap remaining in the general public (Kollmuss & Agyeman, 2002). Furthermore, the outcome of programmes to reduce consumer demand for wildlife products are only known for about 37% of the programmes, and the ecological impact has been reported for only 9% (Veríssimo & Wan, 2019). An extra complication in the rhino poaching crisis is the scale of the problem. While local awareness programmes can have strong positive effects on local environmental problems, e.g., overexploitation by subsistence hunting (Campos-Silva et al., 2017) or human wildlife conflicts (King et al., 2017), the illegal rhino horn trade represents an international conservation crisis that involves many stakeholders other than the local consumers (Milliken & Shaw, 2012; Sutherland et al., 2014). Especially with the current rise in popularity of Traditional Chinese Medicine, as promoted by the Chinese government (Cyranoski, 2018; Master, 2019) and supported by the World Health Organisation (Matthews-King, 2019; WHO, 2013), the market for perceived medicinal uses of rhino (and other wildlife) products is increasing (Master, 2019; Tang et al., 2018). Furthermore, half of all planned purchases of rhino horn products in Vietnam were motivated by the advice of a traditional medical doctor (USAID Vietnam, 2018). Current rhino horn buyers in Vietnam indicated that although they were aware of the extinction risk for rhinos, they do not feel responsible for the killing themselves as they *"are one of many consumers"*, *"do not kill the animals themselves"* or *"do not buy products regularly nor in high quantities"* (USAID Vietnam, 2018). These beliefs in combination with the commercial and governmental lobby for the use of Traditional Chinese Medicine make it difficult to campaign for the exact opposite However, the incrimination of pangolins as the origin of the COVID-19 pandemic may put traditional misuse of wild animals in a new unfavourable light (Lam et al., 2020).

In addition to environmental awareness programmes, law enforcement on the consumer side of the trade could also change the behaviour of potential buyers of rhino horn (Olmedo et al., 2018). Buyers of rhino horn in both Vietnam and China indicated that the top deterrents for future purchases are the link of rhino products to organised crime and the personal risk of violating the law (USAID Vietnam, 2018; USAID Wildlife Asia, 2018). When prioritized by the governments of consumer countries, more severe penalties for rhino horn owners could be implemented and effective law enforcement established. This has the potential to change the behaviour of consumers in both the short and long term (Olmedo et al., 2018).

Legalizing the market can be considered the complete opposite of campaigning to reduce consumer demand. By making it legal to sell and buy rhino horn products, the stigma around these products is removed and a signal that it is acceptable and useful to buy rhino horn is implicitly given (Biggs, Holden, et al., 2017). This may hamper critical thinking by consumers about their own behaviour and limit the impact of education programmes on the matter. As a comparison, legalization has increased the demand for other products in the past (see section 2.8). For marijuana the total consumption rose after legalization due to an increase in new users and extended consumption by regular users (Pacula, 2010). Furthermore, after legalizing crocodilian skin trade, the demand remained robust for the high-end products (alligator and crocodile skins) and increased dramatically for the lower-cost (caiman) products (MacGregor, 2002).

In the long term, involving consumers and informing them about the consequences of their choices is an essential aspect of saving the rhino as a species (Biggs, Cooney, et al., 2017). This can perhaps best be achieved by emphasizing the lack of efficacy of rhino-based Traditional Chinese Medicine by engaging professional medical doctors in China, who have essentially the same ethical standards as their counterparts in the U.S.A. (Nie et al., 2015). In the long run, such demand-reduction programmes may be more cost-effective and better able to tackle the complexity of the trade than increasing anti-poaching enforcement, independent of the initial price of wildlife products or ecological parameters (Challender & MacMillan, 2014; Holden et al., 2019). However, for demand-reduction programmes to become truly effective, conservationists need to adopt more rigorous impact evaluation strategies (Olmedo et al., 2018; 't Sas-Rolfes et al., 2019; Veríssimo & Wan, 2019). Nevertheless, given the current critical situation of rhino populations, more short-term measures, e.g., law enforcement (Olmedo et al., 2018), should be implemented as well to ensure the survival of the rhino species. In either scenario, legalizing the rhino horn market will likely hamper any demand-reduction strategy.

2.6 Discussion

Evaluating the effects of the four mechanisms separately on the rhino population in the situation of a legalized trade (Figure 2.3), we can summarize that 1) an improved financial viability of private rhino ownership will likely have a positive effect on the captive rhino population in countries that allow private wildlife ownership, i.e., South Africa, Namibia and Zimbabwe (Muir-Leresche & Nelson, 2000). However, it is questionable if this will lead to a substantial conservation benefit for wild rhino populations. 2) It will most likely be impossible to satisfy the demand with legal horns alone in the near future (Tensen, 2016; USAID Vietnam, 2018; USAID Wildlife Asia, 2018). Therefore, legal and illegal trade circuits would probably exist in parallel due to a preference of some consumer groups for illegal ('wild') horns and the potentially lower price of illegal horns (Cheung, Mazerolle, et al., 2018; Hanley et al., 2018; Rubino et al., 2018). 3) Corruption is widespread and likely to remain present in all nodes of the trade chain and can stimulate the illegal trafficking of poached rhino horns through laundering channels into the legal market (Van Uhm, 2018b), thereby keeping the poaching incentive alive. Furthermore, even in a tightly controlled market system corruption will most likely still allow for an influx of poached horns from African countries, as is the case with blood diamonds and ivory (Baker, 2015; Bennett, 2015; Fischer, 2004; Wasser et al., 2015). 4) Behavioural change of rhino horn consumers has often been suggested as the ultimate solution to stop rhino poaching, but legalizing the rhino horn market could likely negatively affect efforts taken in this direction (Biggs, Holden, et al., 2017). By legalizing the rhino horn market the stigma around buying illegal products of poached and threatened animals will be removed, which could cause an overall increasing interest in rhino horn (as happened for crocodilian skins and marijuana) in the future (MacGregor, 2002; Morris, 2018; Prins & Okita-Ouma, 2013).

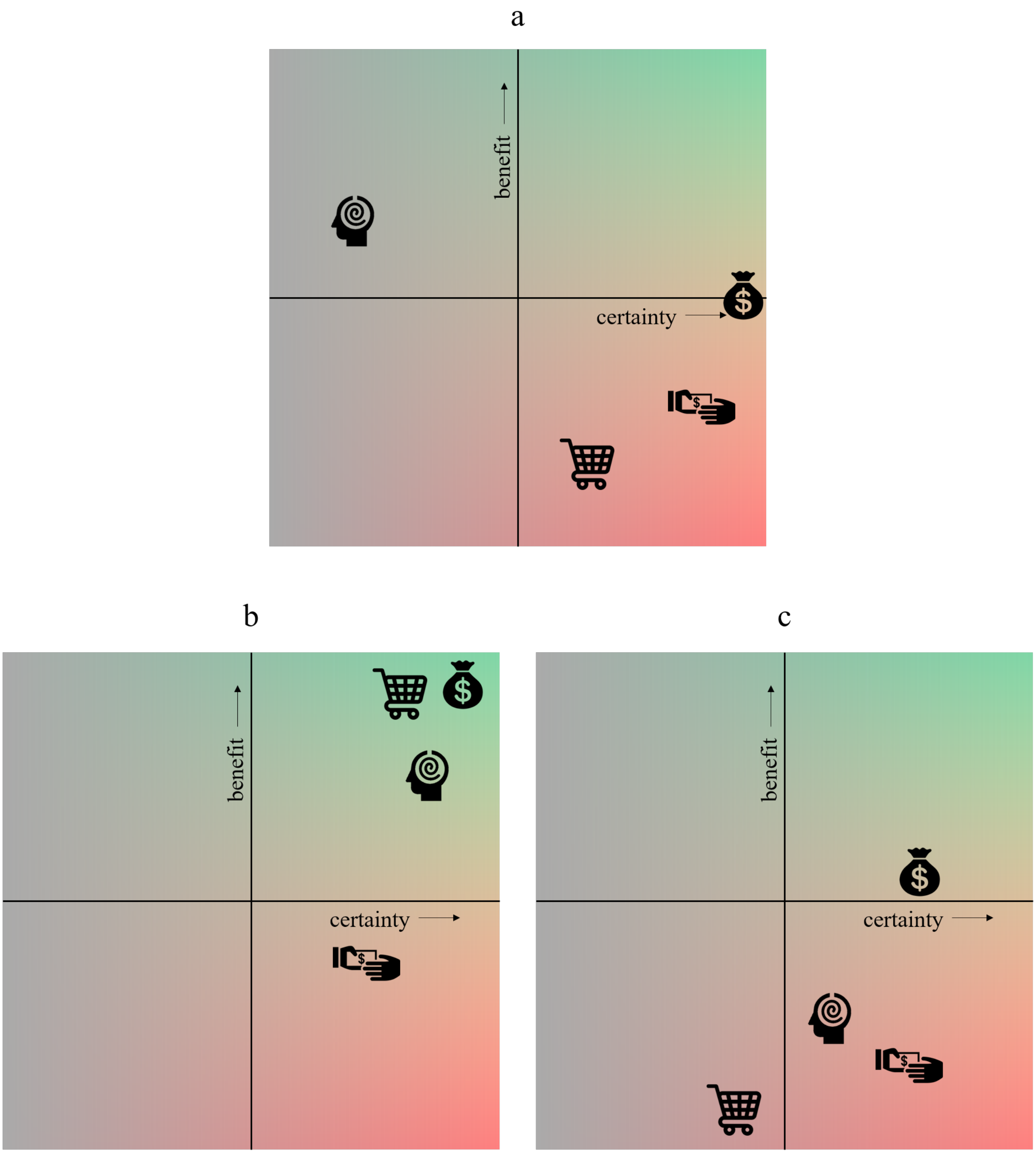


Figure 2.3: The mapped conservation benefit (y-axis, from red to green) and certainty (x-axis, from grey to transparent) of the four discussed mechanisms (financial viability for private rhino owners, rhino horn demand, laundering of rhino horns, and behaviour of rhino horn consumers) on rhino populations: a) business as usual scenario for wild rhinos, b) legal trade scenario for farmed rhinos, and c) legal trade scenario for wild rhinos. The symbols are identical to Figure 2.2.

Cases of trade legalization from the past show that the legal commercialization of animal products can go both ways regarding species' conservation; with a (potentially) positive effect in the case of bison meat, crocodilian skins and trophy hunting, but with a (potentially) negative effect for elephant ivory and lion bones (see section 2.8). To determine how the rhino populations will respond to the legalization of international rhino horn trade, it needs to be evaluated what makes a legal animal product market sustainable to benefit species conservation (SCBD, 2004; Tensen, 2016). Tensen, 2016 determined that wildlife farming (to supply legal products) can benefit species conservation only if five different criteria are met. First, consumers should show no preference for products originating from wild-caught animals. This likely does not apply to all buyers of rhino horn, as larger horns from poached rhinos function better as status symbols and horns from rhinos that suffered are believed by some to increase their medicinal potency (Cheung, Mazerolle, et al., 2018; Hanley et al., 2018). Second, a substantial part of the demand should be met and the demand should not increase due to a legalized market. This probably does not apply to rhino horns either, because demand is unlikely to be met by rhino farming in the near future (USAID Vietnam, 2018; USAID Wildlife Asia, 2018). Third, legal products should be more cost-efficient in order to combat the black market prices. This criterion likely does not apply to rhino horn as rhino horn farming was estimated to only be profitable without subsidies when horn is sold at a minimum price of US $ 11,500 per kg (Rubino et al., 2018). In contrast, poached rhino horn would probably still be profitable at a much lower price if the risks of rhino poaching do not increase substantially compared to the current situation (Conrad, 2012). Fourth, wildlife farming should not rely on wild populations for restocking. This would likely hold true for rhino farming if captive populations are well protected, because already more than 30% of all South African rhinos are privately owned and due to the aridification of farming grounds more area is expected to become available for rhino farming in the near future (Rademeyer, 2016; Rubino & Pienaar, 2017). Fifth, laundering of illegal products into the commercial trade should be absent. This will likely not be the case for rhino horn farming given the enormous value of the product, the trade network that is already involved and the corruption that is present in many African and Asian countries (Collins et al., 2013; Fischer, 2004; Wyatt et al., 2018). In short, the case of rhino horn farming complies with only one of the five criteria that are needed for wildlife farming to benefit species conservation. According to Tensen, 2016 even a minor violation of any of the criteria will result in a negative outcome of wildlife farming to species conservation, but even if a minor violation of these criteria could be compensated for by the other criteria then violating four out of five criteria will likely not result in a benefit for rhino conservation from farming rhino commercially. Similar to this prediction for the rhino horn trade, a modelling study deemed sustainable harvesting of elephant ivory to be impossible (Lusseau & Lee, 2016), and an assessment framework study deemed pangolin farming to be unable to yield a conservation benefit (Challender et al., 2019; Phelps et al., 2014).

Providing recommendations about scenarios that have never happened before (viz., legalizing international rhino horn trade) is challenging, as this is inherently coupled with a lack of empirical data. As a consequence, all our conclusions could only be determined with a certain level of certainty (Figure 2.3). In order to increase the certainty of inferences that can be made about potential effects of legal horn trade on wild rhino populations, we would suggest to focus future research on three topics. 1) Quantify and describe the current demand for rhino horn and the potential demand for legal rhino horn better. Although recent studies have taken important steps in this direction (USAID Vietnam, 2018; USAID Wildlife Asia, 2018), there is potential to better clarify the number of (potential) consumers, the amount of rhino horn they (want to) consume per time unit, the amount of money they are realistically willing to pay per unit of legal and illegal rhino horn, their reasons for purchasing rhino horn, and under which circumstances they are willing to switch to a legal market. This can be achieved through surveys and undercover intelligence in Southeast Asia. This information is critical to make more certain conclusions about whether or not there is potential for an illegal rhino horn market to exist in parallel to a legal market. 2) Rhino horn demand-reduction programmes should adopt more rigorous impact evaluation strategies. As demand-reduction is often a long-term process, studies should ideally be designed in such a way that it allows for demand-reducing strategies to be effective over multiple years and that the impact of the strategies are quantitatively evaluated for multiple times during this period. Because these programmes are arguably the only solution to stop the demand for rhino horn entirely and because these are likely to take a long time to take effect, efforts taken in this direction should be properly chosen, evaluated and ultimately optimized. 3) Economic and political avenues should be explored and substantiated about how a legal market of farmed rhino horns could benefit wild rhino populations in national parks and private game reserves. The financial benefit for rhino conservation related to farmed rhinos is clear, but it is not yet clear through which mechanisms this could benefit wild rhino populations. As both a healthy captive and wild population of rhinos could be important in preserving these species during the Anthropocene, the benefit of legal horn trade should be clear for the entire gradient of captive to wild rhino.

2.7 Conclusion

A legal rhino horn trade will most likely not be able to satisfy demand in the near future and will likely even lead to an increase in demand (Figure 2.3c). Omnipresent corruption in countries along the rhino horn trade routes will, together with demand for illegal (‘wild’) horns, facilitate the co-existence of legal and illegal markets. In addition, legalization will remove the stigma associated with the consumption of illegal products and will therefore counteract long-term behavioural change programmes targeted at consumers, which is arguably the ultimate solution to wildlife crime. Only one of our four considered mechanisms (an increased revenue for private rhino owners) will likely have a positive impact on rhino conservation, but primarily for the captive rhino populations in countries that allow private wildlife ownership. However, this one minor positive impact for rhino conservation will most likely not be able to offset the other negative impacts of trade legalization (Figure 2.3c). Based on this review, we therefore recommend not to legalize an international trade in rhino horn. Instead, we suggest to focus efforts on creating well-protected 'safe havens' for the remaining wild rhino populations to bridge the current period of high demand (short-term approach) and on programmes aimed at reducing rhino horn demand (long-term approach). We acknowledge that this strategy is not perfect, because rhinos are still poached in well-protected reserves and behavioural change programmes still need to improve and prove their effectiveness, which is why our proposed strategy requires substantial (international) effort.

One could argue that rhinos should be preserved as a species, instead of prioritizing rhinos in the wild. Focusing on preserving rhinos in the wild through a legal trade ban has the likely consequence that far less captive rhinos will be kept. Even though healthy wild animal populations are generally thought to have a higher conservation value than captive populations (Redford et al., 2011), if in spite of all efforts rhinos do become extinct in the wild, then it might complicate future reintroduction efforts to have fewer captive rhinos. This is a risk that should not be underestimated, which makes our suggested short-term approach of creating well-protected 'safe havens' for wild rhino populations all the more relevant (Welgevonden Game Reserve, 2020). Regardless of one's opinion to legalize an international rhino horn market or not, both anti- and pro-trade strategies to save the rhino from extinction are likely only possible after corruption has been reduced, more rhinos have been bred and illegal demand has been reduced (Committee of Inquiry, 2016). The debate about legalizing the rhino horn market should thus not prevent stakeholders from working together to achieve these goals (Sandbrook et al., 2019).

2.8 Supplementary materials

There has been a persistent drive for free markets and a trade-barrier free world during the last two centuries (Irwin, 1995; Wiseman & Ellig, 2007), also in developing countries (Rodriguez & Williams, 1994). It has even been argued that the environment can be best preserved through free trade (Schoenbaum, 1992; Yu, 1994), but there may be many hidden motives behind arguments in favour or against environment-related free trade (Soloway, 1999). The idea of legalizing trade of a product as a means to decrease related illegal activities and/or increase wildlife populations is not new. The first aspect of this legalization process is based on the argument that a legal competing market can offset criminal activities. For example, this aspect is one of the most important considerations for national governments to legalize drug use and sales. The potential for this to work has been demonstrated in several U.S. states, where the number of people involved in the illegal production and distribution of marijuana decreased drastically after the legalization of recreational marijuana use (Morris, 2018). The increase in marijuana demand due to its legalization has been more than offset by the reductions in crime associated with the legalization (Morris, 2018; Pacula, 2010). However, an important side note is that the decrease in criminal activities will be smaller in markets that are less competitive, viz., where the price of legal products cannot be reduced substantially compared to the original illegal price (Morris, 2018). Another related case are the so-called ‘blood diamonds’, viz., diamonds that are mined in war zones and sold to fuel the economy of invading or rebel armies. The Kimberley Process Certification Scheme was set up in 2003 as an international agreement to give ‘clean diamonds’ the legal certificates that are required for regulated trade. It has been estimated that blood diamonds now make up 5 to 10% of the world’s diamond market, compared to 25% before 2003 (Baker, 2015). However, the certification scheme failed to prevent the laundering of blood diamonds through bribery and international smuggling, thereby making it possible for blood diamonds to acquire certificates as well (Baker, 2015). By design, it also does not prevent human-rights abuses, natural resource exploitations or even crimes by government armies, which happened for example in Zimbabwe in 2008 (Baker, 2015).

The second aspect of the legalization process to increase wildlife populations, is about increasing the population size by making it financially viable to keep, protect and breed captive populations. This is not unlike trophy hunting in Africa, which has generated substantial financial support of conservation efforts for target species and natural areas when managed properly (Dickman et al., 2019; Leader-Williams et al., 2005; Lindsey et al., 2007). A specific example of this is the white rhino itself, of which the population has increased drastically due to private ownership and trophy hunting (Leader-Williams et al., 2005; Roe & Cremona, 2016). However, when poorly managed trophy hunting can have deleterious genetic effects, alter the age/sex structures or even result in population declines of target species (Crosmary et al., 2013; Loveridge et al., 2007; Milner et al., 2007; Packer et al., 2011). Furthermore, body parts of poached animals can be trafficked by being concealed as trophies, which has happened with rhino horns from South Africa (Ayling, 2013; Cota, 2013; Rademeyer, 2016). Another case where the animal population increased due to the animals' legal economic exploitation is the conservation of American bison, a species that went down in population from more than 60 million individuals around 1800 to 541 in 1889 and back up to approximately 15,000 wild and 500,000 farmed bison in 2010 (Aune et al., 2017; Environment News Service, 2010). Their conservation is to a large extent the result of private ownership and farming for meat and tourism (Lueck, 2002).

The combined process of reducing criminal activities, i.e., poaching and trafficking, and increasing the animal population size by legalizing trade also has cases from the past. International trade of African elephant ivory has been banned since 1989, which allowed some populations (especially the adequately protected) to recover (WWF, 2019). However, for elephant poaching in the Luanga valley (Zambia) the sole explanation for fluctuations in illegally killed elephants was resource allocation, viz., if more money was allocated to anti-poaching it resulted in fewer kills, regardless of the ban on ivory trade (Jachmann & Billiouw, 1997). Since 1997 two countries have been allowed to sell their stockpiles of ivory twice (Fischer, 2004). Some scientists and conservationists argued that these stockpile sales have led to an increase in elephant poaching rate (Hsiang & Sekar, 2019; Lemieux & Clarke, 2009; Sekar et al., 2018; Thornton et al., 2000), while others claimed these legal sales did not elicit a poaching response (Fischer, 2004). However, according to simple economic theory poaching should have decreased due to an increased ivory supply if the legal sales did not elicit a poaching response (Fischer, 2004). Furthermore, the lift of the ban would likely not have a positive effect on the elephant population size when unregulated domestic ivory markets exist nearby, because poached ivory can be smuggled abroad via these domestic markets (Lemieux & Clarke, 2009). Moreover, elephant poaching rates have increased substantially since 2003, with an estimated 50,000 poached elephants in 2013 out of an estimated 434,000 remaining individuals at the time (Wasser et al., 2015). A DNA study that was performed on seized ivory shipments showed that there are two poaching hotspots of African elephants since 1996: one in Tanzania / Mozambique and the other in Gabon / Republic of Congo / Central African Republic (Wasser et al., 2015). These countries are not allowed to sell their stockpiles of ivory themselves, but it demonstrates that massive poaching rates can still occur despite having trade bans or other regulations in place, likely facilitated by corruption and a lack of enforcement (Bennett, 2015; Wyatt et al., 2018).

A second case comparable to the partial elephant ivory trade ban lift, is the legal trade in crocodilian skins. Before the 1975 trade ban, wild crocodiles were in severe decline due to unsustainable harvesting of their skins (Hutton & Webb, 2002). This harvest rate decreased after the trade ban, but since legal harvesting of crocodilian skins in ranches was allowed since 1981 illegal harvesting came to a near-complete stop (Hutton & Webb, 2002), with a notable exception in Thailand where crocodiles were poached to near extinction due to skin laundering after the implementation of crocodile farming (Damania & Bulte, 2007). After the crocodilian skin trade legalization the demand remained robust for the high-end products (alligator and crocodile skins) and increased substantially for the lower-cost (caiman) products (MacGregor, 2002). Therefore the case of crocodilian skins could potentially provide a case of a sustainable legal wildlife market that has been able to displace unsustainable illegal harvesting (Hutton & Webb, 2002). Another explanation for the decrease in poaching could be that crocodile numbers are globally so low (except for saltwater crocodiles) that poaching is less profitable nowadays (Milman, 2015). Furthermore, recent trends in Egypt show that crocodile poaching is increasing again, with local Nile crocodile populations decreasing as a result (Schwartzstein, 2017). However, this increase in crocodile poaching in Egypt is most likely the cause of human-wildlife conflict where the skins are sold for a low price as a by-product (pers. comm. Mohamed Ezeldein Abdalatef, Crocodile Management Unit, Egyptian Environmental Affairs Agency, 23-11-2019). On the other hand, in the Classical antiquity, when the crocodile population was likely much higher than today, hunting and breeding of crocodiles was practiced simultaneously for the same purposes (Porcier et al., 2019; Van Uhm, 2018a). This could suggest that the decrease in crocodile poaching of the past decades was not necessarily a direct consequence of crocodile farming and that crocodile poaching could potentially increase in the near future (Porcier et al., 2019; Schwartzstein, 2017), but this cannot be concluded definitively at this stage.

The last case we highlight is the intertwined market of tiger and lion products. Stricter law enforcement led to a shift in demand from illegal tiger parts to easier attainable (and in part legal) lion products (Tensen, 2016). Consequently, the amount of lion bones exported from South Africa to Asia increased from 59 skeletons in 2008 to 1500 in 2018 (Kollapen, 2019; Williams et al., 2015). Most of these bones originate from breeding farms, where lions are kept under conditions that are considered by many as unacceptable (Ashcroft, 2019; Lindsey et al., 2012). When not butchered, these lions are often used for ‘canned hunting’ (Ashcroft, 2019; Lindsey et al., 2012), which many consider morally questionable. Due to the severe breaches of the South African animal welfare law, the South African high court declared the lion bones exportations quota (800 skeletons in 2017 and 1500 skeletons in 2018) to be unlawful and constitutionally invalid (Kollapen, 2019). However, if commercially bred lion bones could form a substitute for wild tiger bones, this market could theoretically have a positive conservation impact for both species if the supply would meet demand and part of the revenue would flow to lion and tiger conservation (Tensen, 2016). This new market must be controlled with extreme caution (apart from that it should shift to lion cruelty free ranching practices), because poaching of lions and other large cats is now increasing as well to replace illegal tiger parts in Asian markets (Bale, 2018; Fisher, 2018).

Chapter 3

The impact of hunting on tropical mammal and bird populations

This chapter is based on:

Benítez-López, A., Alkemade, R., Schipper, A. M., Ingram, D. J., Verweij, P. A., Eikelboom, J. A. J., & Huijbregts, M. A. J. (2017). The impact of hunting on tropical mammal and bird populations. *Science*, *356*(6334), 180–183. https://doi.org/10.1126/science.aaj1891

Abstract

Hunting is a major driver of biodiversity loss, but a systematic large-scale estimate of hunting-induced defaunation is lacking. We synthesized 176 studies to quantify hunting-induced declines of mammal and bird populations across the tropics. Bird and mammal abundances declined by 58% (25 to 76%) and by 83% (72 to 90%) in hunted compared with unhunted areas. Bird and mammal populations were depleted within 7 and 40 kilometers from hunters' access points (roads and settlements). Additionally, hunting pressure was higher in areas with better accessibility to major towns where wild meat could be traded. Mammal population densities were lower outside protected areas, particularly because of commercial hunting. Strategies to sustainably manage wild meat hunting in both protected and unprotected tropical ecosystems are urgently needed to avoid further defaunation.

3.1 Report

Global biodiversity loss is occurring at an unprecedented rate (Ceballos et al., 2015). Few undisturbed areas remain in the tropics (Gibson et al., 2011), but these are threatened by escalating road and infrastructure expansion, which promotes human accessibility to otherwise remote areas and facilitates illegal colonization and hunting (Laurance & Balmford, 2013; Laurance, Peletier-Jellema, et al., 2015; Peres & Lake, 2003). Hunting exerts a major pressure on wildlife, which can result in large population declines and local extirpations of wildlife populations in forests that appear structurally undisturbed (Redford, 1992). Overhunted "half-empty" or "empty ecosystems" are becoming common across the tropics (Milner-Gulland & Bennett, 2003). Indeed, the abundance of wildlife in natural ecosystems is more closely related to patterns of hunting than to factors such as forest type, habitat area, or habitat protection status (Harrison, 2011). A growing body of research is focusing on defaunation and its far-reaching cascading effects, including disruptions in seed dispersal mutualisms and a decline in total biomass (Abernethy et al., 2013; Dirzo et al., 2014). However, hunting-induced defaunation is a cryptic phenomenon that is difficult to monitor and, to date, no large-scale estimates of the impact of hunting on wildlife abundances are available.

Here, we analyze the impact of hunting on bird and mammal populations at a pantropical scale, in terms of both magnitude (decline in abundance) and spatial extent (depletion distances). We collated 176 studies, including 384 and 1938 effect sizes for 97 bird and 254 mammal species, respectively (see section 3.2; Figure 3.1), and estimated the overall reduction in mammal and bird abundance in hunted compared with unhunted sites with a mixed effects meta-analysis. As an effect size, we calculated response ratios (RR) between the abundance of each species in hunted (X_h) and unhunted sites (X_c) within each study ($RR = \log \frac{X_h}{X_c}$; (Hedges et al., 1999)). RR are therefore negative ($RR < 0$) or positive ($RR > 0$) if abundance estimates are lower or higher, respectively, because of hunting pressure. Based on the central-place foraging hypothesis, hunting intensity is generally higher in the proximity of hunters' access points (e.g., settlements and roads) (Abernethy et al., 2013; Peres & Lake, 2003), generating gradients of increasing species densities up to a distance where no effect is observed (i.e., species depletion distances). We used single meta-regression models to estimate species-depletion distances and to quantify how the impact of hunting varied depending on accessibility to urban markets for trade (travel time to major towns (Nelson, 2008)), region, type of hunting (commercial versus subsistence versus both), protection status (protected versus unprotected area), species body size, and feeding guild. Finally, we tested the relative importance of these moderators using an information-theoretic approach of several multiple meta-regression models including first- and second-order interactions.

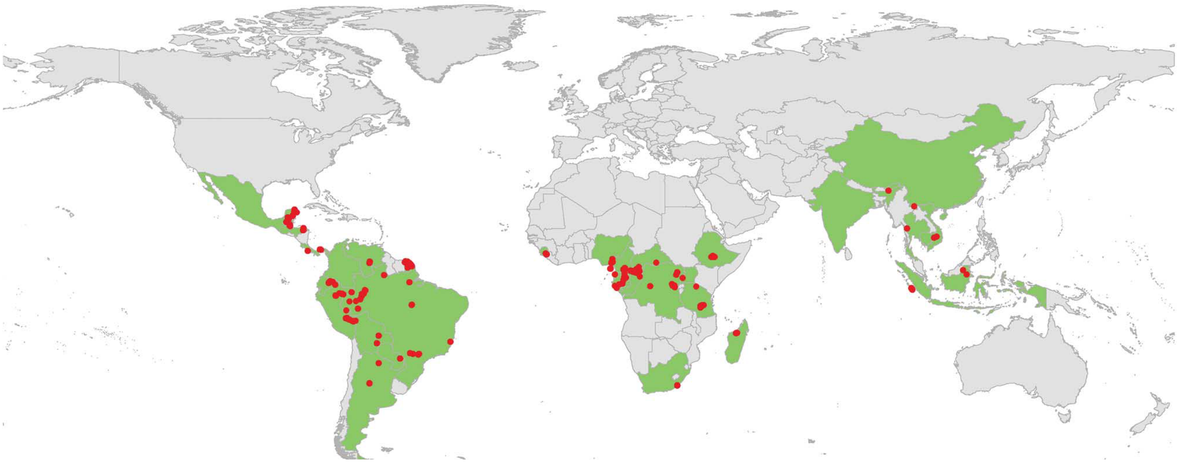


Figure 3.1: Geographical location of the 176 studies included in the meta-analysis. Locations as red dots. Countries that contain at least one study are in green color. Red dots may represent multiple effect sizes.

Overall, bird and mammal abundances were reduced by 58% (95% confidence interval (CI): 25, 76%) and 83% (95%CI: 72, 90%), respectively, in hunted areas (Figure 3.2). Hunting pressure had a larger effect on mammals than on birds, probably because hunters preferentially target larger species (Redford, 1992). Results were robust to potential publication bias for mammals and to Geary diagnostic tests and differences in study quality for both groups (Figure 3.6; Figure 3.7). Hunting-induced abundance reductions varied with distance to hunters' access points (distance, hereafter), accessibility to urban markets, protected area status and type of hunting, with distance being the most important moderator (Figure 3.3; Figure 3.4; Table 3.4). For birds, effect sizes were the lowest in proximity to hunters' access points ($RR_b = -3.17$, 95%CI: -2.62, -3.71, ∼95% loss at 500 m) and approximated 0 at a distance of 7 km (Figure 3.3A). For mammals, effect sizes first decreased from -0.76 (-1.30, -0.23) to -2.38 (-2.84, -1.78) within the first 700 m (∼90% loss), and then increased steadily up to 0 at ∼40 km from hunters' access points (Figure 3.3B). This initial higher RR may reflect the replacement of large-bodied mammals by smaller ones. Indeed, we found evidence of size-differential mammal defaunation for frugivores, carnivores, herbivores, and insectivores (Table 3.5; Table 3.6). Smaller mammals were consistently more abundant at higher hunting pressure than larger species (Figure 3.8), probably owing to release from predation pressure and competition as a result of (near) extirpation of medium- and large-sized mammals (Wright, 2003). Large-bodied frugivores, herbivores, and insectivores - including chimpanzees (*Pan troglodytes*), Western gorillas (*Gorilla gorilla*), and giant armadillos (*Priodontes maximus*) - are largely hunted for wild meat consumption and trade (Ripple et al., 2016). In turn, large carnivores, such as leopards (*Panthera pardus*) and jaguars (*Panthera onca*), are often persecuted because of livestock-wildlife conflicts, or their populations are reduced because of hunting-induced losses of prey species (Ripple et al., 2014).

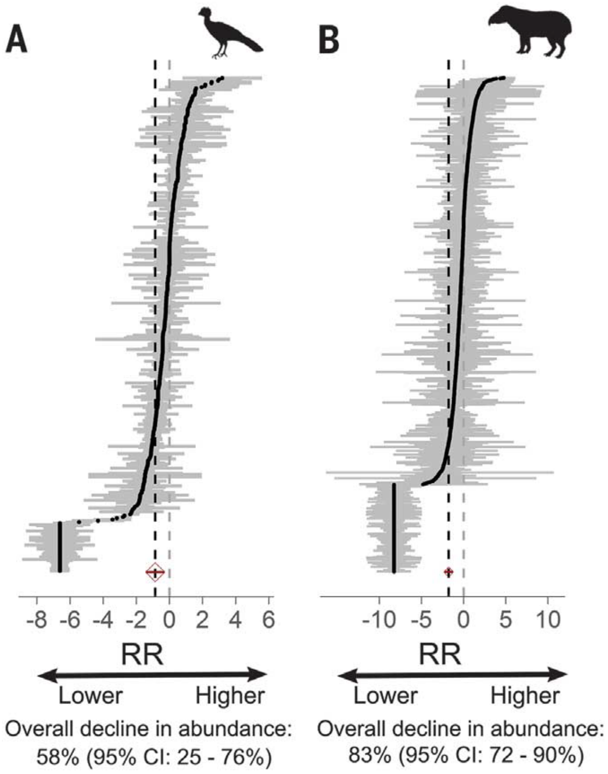


Figure 3.2: Forest plots of 384 and 1938 effect size estimates for birds and mammals, respectively. (A) Birds and (B) mammals. RR, response ratios (effect sizes), black dots with 95% confidence intervals (CI) as gray lines. Overall weighted mean effect size estimate, black dashed line and red diamond. 95%CI of weighted mean effect size, red line. $RR = 0$, dashed gray line. Extremely negative effect sizes indicate local extirpations.

Bird and mammal population abundances were lower in hunted areas with higher accessibility to urban markets (Figure 3.3C; Figure 3.3D). Effect sizes approached 0 within 1 to 2 days of travel time from the nearest major town. For mammals, this effect remained after controlling for other factors (Table 3.5). Across the tropics, the majority of consumed and traded wild meat and body parts comes from mammals, whereas birds are generally killed for a hunter's own consumption (Redford, 1992; Robinson & Bennett, 2000). However, for both species groups, the transition from subsistence to commercial hunting is having a massive impact on population densities (Figure 3.4). Current prospects of infrastructure expansion in the Amazon, Africa, and Asia will facilitate accessibility to remote areas (Clements et al., 2014; Laurance, Peletier-Jellema, et al., 2015; Laurance, Sloan, et al., 2015), boosting wild meat harvest and trade to meet urban demands (Milner-Gulland & Bennett, 2003) and, thus, increasing pressure on wildlife populations.

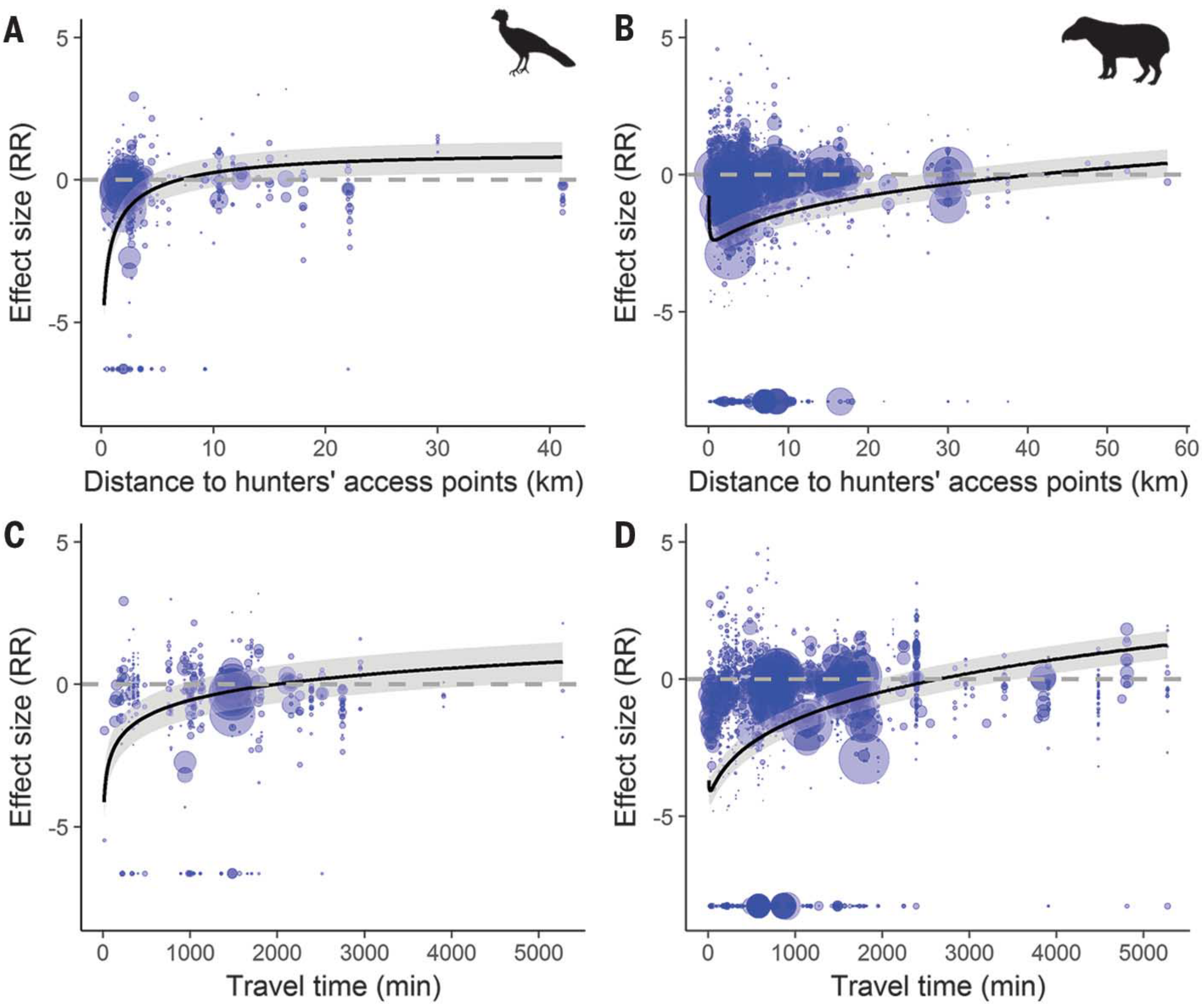


Figure 3.3: Change in species abundance with distance to hunters' access points and travel time to major towns. (A and B) Distance to hunter's access points and (C and D) travel time to major towns; for birds (A and C) and mammals (B and D). RR, response ratios. $RR = 0$, dashed gray line; predicted mean effect size (with 95%CI in gray), black lines. Size of data points (in blue) is proportional to the sampling variance. Results obtained with single meta-regressions.

Mammal population densities were higher inside than outside protected areas (Figure 3.4). However, hunting pressure reduced mammal abundances even within protected areas (Figure 3.4). Overhunting within protected areas is ubiquitous across the Amazon, Africa, and Asia (Harrison, 2011; Laurance et al., 2012). Although our results suggest that the effects within are less detrimental than outside reserves, gazettement of protected areas seems insufficient to safeguard wildlife populations if not accompanied with improved reserve management, effective law enforcement, and on-ground protection efforts (Laurance et al., 2012).

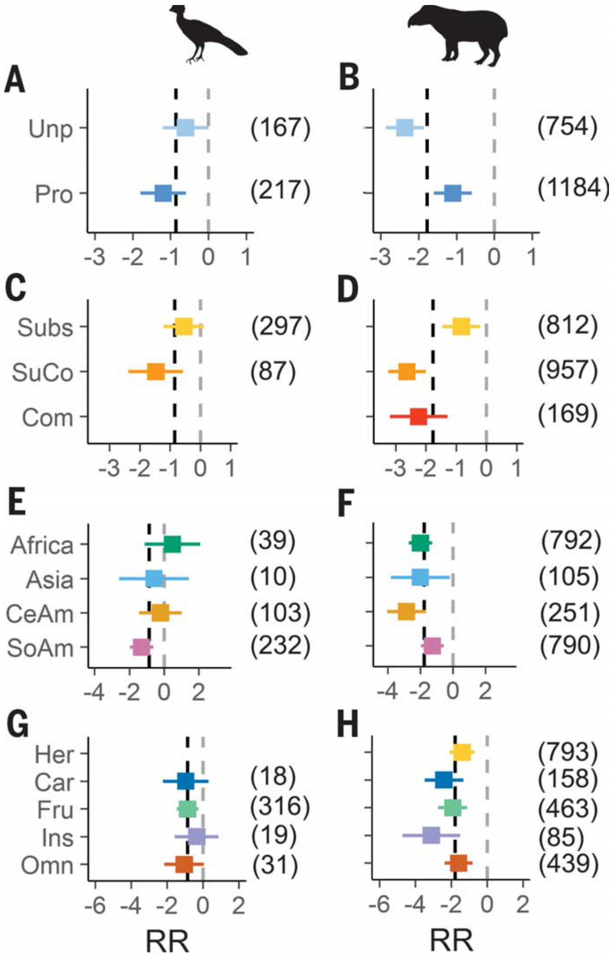


Figure 3.4: Change in species abundance for different levels of protection, type of hunting, regions, and feeding guilds. (A to H) Parameters as labeled for birds (left) and mammals (right). Number of effect sizes is shown between brackets. *RR*, response ratios. Mean weighted effect size, dashed black line; $RR = 0$, dashed gray line; Unp, unprotected areas; Prot, protected areas; Subs, subsistence hunting; SuCo, subsistence and commercial hunting; Com, commercial hunting; CeAm, Central America; SoAm, South America; Her, herbivores; Car, carnivores; Fru, frugivores; Ins, insectivores; and Omn, omnivores. Results obtained with single meta-regressions. None of the studies reported on bird hunting for commercial purposes solely.

Effect sizes were similar across regions for both taxa, although slightly lower in South America for birds (Figure 3.4). This indicates that overhunting affects mammal and bird populations similarly across the tropics. However, we found more studies in South America and Africa than Asia or Central America (Figure 3.1), which implies that our findings are more generalizable for the former two regions. It also points out an urgent need to focus research efforts in less-studied areas before wildlife populations are completely extirpated. Unfortunately, overhunting has already emptied most Asian forests (Milner-Gulland & Bennett, 2003), leaving few unhunted control areas left for comparisons.

The most important terms retained in our multiple meta-regression models were distance for both groups (Table 3.5; Table 3.6) and the interactions between guild, body size, and distance for mammals (see Figure 3.8 and explanations above). Our best models were significant according to omnibus tests (birds: $Q_M = 3157.5$, $p < 0.001$, McFadden pseudo-R^2: 0.29; mammals: $Q_M = 19207.3$, $p < 0.001$, McFadden pseudo-R^2: 0.18); however, residual heterogeneity was large (Table 3.6), indicating that hunting is a multi-faceted phenomenon influenced by additional factors, some of which were not included in our models (e.g., food security). Additionally, confounding variables such as small-scale habitat clearing and road disturbance are correlated with distance to settlements and roads (Benítez-López et al., 2010). However, we minimized their influence as much as possible by avoiding pairwise comparisons where disturbances other than hunting were apparent.

Overexploitation is a long-established major driver of wildlife population declines and extinctions in terrestrial ecosystems which, to date, has not been successfully mitigated and rather shows an increasing trajectory in recent decades (Maxwell et al., 2016). Pleistocene extinctions were triggered in part by human hunters (Sandom et al., 2014), and ongoing wildlife population declines and (near) extinctions of large-bodied species seem to share similar pathways. Consequently, defaunation is rendering tropical forests, savannas, and grasslands “empty” (Ripple et al., 2014), with populations so sparse that the strength of species interactions is declining dramatically. The subtle nature of this process makes it undetectable by remote-sensing techniques, which are key to monitor deforestation but prove futile to track on-ground changes in biodiversity and ecological functioning (Peres et al., 2006). Matching the findings of many regionally specific studies (Abernethy et al., 2013; Peres & Lake, 2003), our meta-analysis shows that large vertebrates of various functional groups are depleted in the vicinity of settlements and roads. Our estimated hunting-depletion distances can be used to assess ecosystem degradation as a result of current and future road developments and settlement establishment. Recently, Peres et al., 2016 estimated that 32.4% of the remaining forest across the Brazilian Amazon (~1 million km^2) is affected by hunting on the basis of hunting distances of 6 km from settlements. Our results, however, indicate that the Amazon forest area affected by hunting-induced defaunation might be much larger. By 2050, with millions of kilometers of roads planned in developing countries (Dulac, 2013), and human population and associated demand for wild meat increasing steadily, it is likely that the term “remoteness” will be a ghost of the past, with the last remnant half-depleted mammal and bird populations persisting in few protected areas. This can be ameliorated if we undertake coordinated strategies to expand the current network of protected areas, limit human encroachment around them, monitor hunting activities, and control overexploitation via law enforcement, if needed, while implementing alternative livelihood programs for wild meat–dependent communities.

3.2 Materials and methods

3.2.1 Search strategy

The relationship between hunting intensity and species abundance was quantified using data from peer-reviewed literature selected through a systematic literature search. Relevant studies published between 1970 and August 2015 were identified through literature searches in the ISI Web of Science and Google Scholar. The search was performed between July-October 2015 using the following search terms: (*road** OR *settlement** OR *village* OR *infrastructure**) AND (*access** OR *transect* OR *distance* OR **disturb** OR *proximity*) AND (*hunt** OR *bushmeat* OR *poach** OR *game*) AND (**diversity* OR *population* OR *abundan** OR **density* OR *encounter**). We also used ProQuest Dissertations and Theses repository (http://www.proquest.com/products-services/dissertations/) to access relevant PhD and MSc dissertations (i.e.: grey literature), and reviewed the references cited in relevant articles. Authors of relevant papers were also contacted for provision of any unpublished material or missing data. Relevant studies in other languages, mostly in Spanish and French, were also identified by cross-reference. Additionally, we obtained bibliographies from the OFFTAKE project (www.offtake.org) to complement our database of studies. No geographical or taxonomic restrictions were applied. A flowchart of the process and outcome of the literature search is provided in Figure 3.5.

3.2.2 Inclusion and exclusion criteria

We selected relevant studies according to title and abstract, and we finally selected studies that met the following criteria: 1) evaluates effect of hunting on wildlife populations, 2) contains abundance data on species or genus level, 3) reports abundance at increasing distance from access points, or at least at one proximate hunted area and one distant unhunted area (control), which in some cases included light hunting (Barrera Zambrano et al., 2007). Studies with potential confounding effects due to other disturbances (i.e.: hunted and logged area vs unhunted unlogged area) were discarded, unless all compared sites had the same level of disturbance (i.e.: sites with forests logged ca. 20 years ago, but with different hunting pressures and located at different distances from villages). Studies that reported on hunting on managed wild populations (i.e.: with release of farm-reared individuals) used for recreational hunting were not included.

3.2.3 Data extraction

We extracted and stored the following data: the mean abundance of each species at each distance from hunters' access points, the sample size, and, depending on the study, the variance, standard deviation or standard error. These data were extracted from tables or graphs using GetData Graph Digitizer 2.26 (http://getdata-graph-digitizer.com/). Data extracted from graphs were plotted and visually inspected to verify that there were no errors during data extraction. Abundance estimates per species were expressed as a variety of metrics, including population density (individuals/km^2), group density (groups/km^2), encounter rates of groups, subgroups or individuals (e.g., number of encounters per 10 km of census effort) and number of photographs/camera trap-day in case of camera-trap surveys.

When species abundance was reported in distance intervals, we took the middle distance point of the interval as input distance. When only the hunting catchment area around the village was given, we calculated the hunting radius and took the middle of the radius as hunting distance. The effect of hunting on species populations was usually assessed in the core of the hunting catchment areas. In some cases hunting distances were not recorded and we calculated them in ArcGIS 10.2 after georeferencing the study sites (see below).

We also recorded data on the study characteristics: location (continent, country), biome (tropical, subtropical and montane forests, dry and montane grasslands, savanna and xerophilous deciduous forest), geographic coordinates, type of hunters' access points (roads, settlements, river networks, or roads and settlements), protected area status (protected, unprotected) and type of hunting (subsistence, commercial, both) (see Table S1 in Benítez-López et al., 2017). If coordinates were not available we retrieved them by georeferencing maps in the papers using ArcGIS 10.2 (Environmental Systems Research Institute, 2011). Additionally, we recorded data on the species' body mass (kg) and diet composition (%) from EltonTraits 1.0 (Wilman et al., 2014), and categorized species as frugivores ($>$ 50% of diet consists of fruits and seeds), carnivores ($>$ 50% of diet consists of vertebrates), insectivores ($>$ 50% of diet consists of invertebrates), herbivores ($>$ 50% of diet consists of plants and leaves) or omnivores (none of the previous categories apply). Species are defined here as single taxonomic species, or functional groups of ecologically analogous congeners that were not distinguished at species level (e.g., *Psophia spp.*, *Dasyprocta spp.*, *Saimiri spp.*, *Lagothrix spp.*, *Aras spp.*, *Amazonas spp.*). When abundances were reported for several species aggregated at genus level body mass and diet were averaged for all species included in the abundance estimation. When possible, we averaged trait data for species within the reported Genus known to occur in the area (according to IUCN range maps). Finally, we overlaid all study sites with available global data sets and extracted the following variables: human population density (1 km resolution, year 2000) (Center for International Earth Science Information Network et al., 2011), estimated travel time to the nearest town greater than 50000 inhabitants (as a proxy for accessibility to urban markets, 1 km resolution) (Nelson, 2008) and protected area status, from the World Database of Protected Areas accessed in August 2016 (IUCN & UNEP-WCMC, 2016). These operations were performed in ArcGIS 10.2 using a Mollweide equal area projection (Environmental Systems Research Institute, 2011). Prior to data analyses, we assessed for collinearity between our explanatory variables. Because human population density was correlated with travel time (Spearman $rho = -0.38$ and -0.55, for birds and mammals, respectively) we used only the latter in our models.

3.2.4 Data structure

The data was structured into Data Source, Study, and Species. A Data Source typically represents a single published paper, a technical report published by NGOs or a PhD or MSc thesis. In some cases a Data Source consists of both a published paper and a thesis used to complement the data on the paper (see Table S1 in Benítez-López et al., 2017). A single Data Source may contain one or more Studies, depending on whether data is reported for more than one village, or more than one site. A Study contains one or more Species for which abundance or density is reported at least at one hunted (although there could be more) and one control distance. A single Species may be reported in several Studies. All abundance measurements within a Study and for a Species must have been collected using the same sampling method so that observations within a Study can be reasonably compared and effect sizes calculated. For the same reason, observations among Studies, even for the same Species, should not be compared if there are methodological differences (line transect methods compared to camera traps).

3.2.5 Data availability and selected studies

The search string yielded 461 publications via ISI Web of Knowledge, which were complemented with the 100 first hits from Google Scholar. We also included 2 MSc Theses and 8 PhD theses found through ProQuest, and 55 cross-referenced articles. After removing duplicates, 603 publications were selected for abstract screening, out of which 285 fulfilled the criteria for full text screening. Four authors provided their full database on request. Additionally, we retrieved two databases from the A.P.E.S. database.

Finally we selected 101 data sources (among the peer-reviewed articles, theses and reports), with publication dates ranging between 1984 and 2016 (Figure 3.5). Our meta-analysis spanned 38 countries across the main tropical regions. Most data sources were from Africa (49) and South America (32), with the rest being from Asia (8) and Central America (12) (with Mexico included in the Central America category for analyses), with a clear geographical bias towards (sub) tropical regions (22.25 N to 32.27 S, Figure 3.1). In total we extracted 176 studies out of the 101 data sources, including 2322 effect sizes for a total of 347 species (Birds: 97 species and 384 effect sizes, Mammals: 250 species and 1938 effect sizes). Body mass of recorded species ranged from 0.06 kg to 3940.3 kg for mammals (median: 7.9 kg), and from 0.035 kg to 111 kg for birds (median: 1.2 kg).

3.2.6 Effect size metrics

We calculated log response ratios (RR, hereafter response ratios) as measure of effect size (Hedges et al., 1999; Lajeunesse, 2011):

$$RR = \ln \frac{\bar{X}_{ikh}}{\bar{X}_{ikc}} \tag{3.1}$$

For each study k, response ratios (RR) were calculated between the mean abundance $\bar{X}$ of any individual species i at hunting distance h from the access point and the mean abundance $\bar{X}$ of individual species i at a control distance c from the access point (unhunted distance) (see Benítez-López et al., 2010 and Alkemade et al., 2013 for similar approach). The control distance was either reported in the study as unhunted, in some cases after assessing hunting pressure at increasing distances from the access point; or was the most distant data point at which species abundance was estimated. Population densities in unhunted areas were assumed to be in equilibrium and approximate the carrying capacity (Milner-Gulland, 2001). Response ratios (RR) for any given species are therefore negative ($RR < 0$) if abundance estimates are lower due to hunting pressure (i.e.: closer to hunters' access points) and positive ($RR > 0$) if abundance estimates are higher regardless the distance to hunters' access points. Effect sizes close to zero ($RR \approx 0$) indicate little or no effect of hunting. Some ratios were zero for species completely extirpated in areas close to hunters' access points (mean abundance equals zero), precluding log-transformation. Therefore we transformed our effect sizes using a modification of the transformation $y' = \frac{y(N-1)+0.5}{N}$ proposed by Smithson and Verkuilen, 2006 to shrink [0,1] into (0,1) open intervals avoiding thus zeroes and ones. Since we only wanted to avoid zeroes, we used $y' = \frac{yN+0.5}{N}$, where y are unlogged ratios ($\frac{\bar{X}_{ikh}}{\bar{X}_{ikc}}$) and N is the number of effect sizes ($N_b = 384$ and $N_m = 1938$ for birds and mammals, respectively) resulting in a distribution of effect sizes slightly displaced towards larger values (mammals: before transformation: [0.000, 118.246], after transformation [0.00026, 118.24597]; birds: before transformation [0.00, 24.25], after transformation: [0.00133, 24.2513].

In all meta-analyses and meta-regressions, observed effect sizes (RRs) were weighed by the inverse of the sampling variances, which were calculated as:

$$\hat{\sigma}^2\left(RR\right) = \frac{SD^2_{ikh}}{N_{ikh}\bar{X}^2_{ikh}} + \frac{SD^2_{ikc}}{N_{ikc}\bar{X}^2_{ikc}} \tag{3.2}$$

Where RR represent the log response ratio, SD_{ikc} and SD_{ikh} represent the standard deviations of $\bar{X}_{ikc}$ and $\bar{X}_{ikh}$, respectively, with N_{ikc} and N_{ikh} as sample sizes (Hedges et al., 1999; Lajeunesse, 2011). Not all studies reported estimates of SD, variances or SE. In such cases, SD_{ikc} and SD_{ikh} could be estimated by assuming that the data follow a Poisson distribution, in which $\mu = \sigma^2$ and, therefore, $\bar{X}_{ikc} = \sigma^2_{ikc}$ (Sokal & Rohlf, 1981). Finally, for studies in which some species had zero densities ($\bar{X}_{ikh} = 0$, and thus $SD_{ikh} = 0$), a continuity correction factor ($k = 0.5$) was added to the numerator and denominator resulting in slightly higher variance estimates (Cox & Snell, 1970; J. Sweeting et al., 2004). Alternatively, we used two other methods for imputing missing SD and compared our results to our approach. We used "Bracken1992" approach to impute SD using the coefficient of variation from all complete cases (Bracken, 1992). Additionally we used the "HotDeckNN" approach, which applies Rubin and Schenker, 1991 resampling approach to fill gaps of missing SD from the SDs with complete information with means that are similar to missing SDs. For the "HotDeckNN" approach we imputed missing SD 100 times and recalculated 100 sampling variances and 100 meta-analytical estimates. These analyses were performed using *metagear* (Lajeunesse, 2016). The resulting estimates using these two approaches were similar to those obtained with the "Poisson" approach (Table 3.1), and therefore we used the latter in all our analyses.

Results are reported as RR and as percentage declines in abundance by back-transforming RR to unlogged ratios and multiplying by 100 (Percentage decline = $(1 - e^{RR})100$).

3.2.7 Data analyses

We ran multilevel mixed effects meta-analyses in *metafor* 1.9-8 (*rma.mv*, (Viechtbauer, 2010)) to control for non-independence in the data due to multiple effect sizes per study and species. All analyses were run separately for bird and mammal species. Several candidate random-effects structures were compared using the full candidate fixed-effects structure (see complex multiple meta-regression models below). We specified study identity and species identity as random effects in our models. Given that body mass is phylogenetically conserved at Order level in birds and mammals (Harvey & Pagel, 1991; McGill, 2008; Smith et al., 2004; Smith & Lyons, 2011), we assessed if model fit would improve by using the following nested random effects structure (Order/Species). Random effects were retained or discarded based on the models' BIC (Bayesian Information Criterion, which is more restrictive than AIC$_c$) (Burnham & Anderson, 2002). The final retained random effects structure was (1|Study) + (1|Species) for both birds and mammals (Table 3.3).

Our analyses were separated in three steps: random-effects meta-analysis, single mixed-effects meta-regression models and multiple mixed-effects meta-regression models. With the multilevel random-effects meta-analysis we assessed overall reductions in bird and mammal abundance in hunted vs unhunted sites. For these analyses we assessed heterogeneity by formal Cochran's Q-test tests (Q_E), which test whether the variability in the observed effect sizes or outcomes is larger than would be expected based on sampling variability alone. As expected for a biological meta-analysis (Nakagawa & Santos, 2012), there was significant residual heterogeneity in the random-effects meta-analysis for the birds dataset ($Q = 20256.1$, $p < 0.0001$), and for the mammal dataset ($Q = 441755.2$, $p < 0.0001$), which we tried to explain with different moderators (Table 3.2).

We ran single mixed-effects meta-regression models to assess the relationship between RR

and distance to hunters' access points (distance, hereafter), and variations in RR according to several categorical (factors) and continuous moderators (Table 3.2). Continuous variables were log-transformed and fitted as quadratic polynomials to account for non-linear relationships. Models with categorical factors were also run without the intercept to obtain the parameter estimates (mean effect sizes) of each level. The heterogeneity captured by the moderators of each independent meta-regression was assessed with omnibus tests (Q_M) (Table 3.4). p-values were adjusted for multiple hypothesis testing using Bonferroni corrections.

We also built multiple mixed-effects meta-regression models to examine variations in the relationship between species abundance (RR) and distance while controlling for the effect of guild, body mass, type of hunting, travel time and level of protection. Distance, body mass and travel time to major towns were standardized before the analyses. We included first-order and second-order interaction terms to account for variations in the slope of the relationship between effect sizes (RR) and distance, for different functional guilds and different body mass (Distance x Guild x BM), for different types of hunting (Distance x TypeHunting) and per level of protection (Distance x Protected). Model selection was done using the Bayesian information criterion (BIC) (Burnham & Anderson, 2002). If the most supported model included interaction terms, we tested them using Q_M and then we removed them to test main effects. We retained all main effects that were part of significant interaction terms regardless of their significance as main effects. Fixed factor estimates were considered statistically significant if the 95% confidence interval (CI) did not overlap zero. We checked profile likelihood plots to ensure the identifiability of the variance components in the model (σ_1^2: study-level variability, σ_2^2: species-level variability) and to test whether our more complex models were overparameterized (Figure 3.9) (Viechtbauer, 2010). Model fit was assessed with McFadden's adjusted pseudo-R^2. All parameter estimates are reported for best models run with REML (Restricted maximum likelihood). All analyses were performed in R 3.2.2 software (R Development Core Team, 2008).

3.2.8 Exploring potential publication bias and robustness of models

Publication bias was assessed using Funnel plots and Egger tests by including precision (1/SE) as covariate in *rma.mv* function, and using meta-analytic residuals (Egger et al., 1997). Rosenberg's fail safe-numbers were calculated to assess the robustness of our results to publication bias (Rosenberg, 2005). Egger tests suggest that the overall RR for mammals is robust, whereas there is a slight potential publication bias for birds (Figure 3.6). Rosenberg's fail safe-numbers were large enough for both mammals (54983163, $p < 0.0001$) and birds (331975, $p < 0.0001$) to be confident about the reliability of the estimates.

We used Geary diagnostic tests (Equation 3.3) to assess the accuracy of our RR (Lajeunesse, 2015). Effect sizes are deemed valid and accurate approximations when the standardized mean of either the control or treatment group is ≥ 3.

$$\frac{\bar{X}}{SD}\sqrt{N} \geq 3 \tag{3.3}$$

We performed a sensitivity analysis where the meta-analytic results from the complete dataset were compared to those where problematic cases detected by Geary tests were excluded. Effect sizes were still negative for both taxa even after excluding standardized means < 3 for hunted, control and hunted and control sites (Figure 3.7).

We used six main criteria to assess study quality:

1. Control area. When the authors reported abundance estimates on a clear unhunted area and/or unhunted distance (score 1). If the control area was unfrequently hunted or was hunted > 5 years ago (score 1). When the control area was under low hunting pressure or lightly hunted (score 0). Else the longest distance from hunters' access points is used as control (score 0).
2. When the authors assessed hunting pressure using metrics such as hunting signs in relation to distance to access points, or in a specific hunted area (score 1). If they specified a threshold distance up to which hunting occurs, or had evidence of hunting from other studies performed in the same area (score 1). If hunting evidence was not clearly assessed (score 0).
3. When the authors reported clear distance intervals or hunting distances (score 1). If hunting catchments were reported the hunting distance was estimated as the mid-distance of the hunting radius from the access point, or village (score 0). If distances to access points were extracted using GIS after georeferencing transects and villages or roads as access points (score 0).
4. When the authors reported the mean and the variance (or standard deviation, standard error, confidence interval) of the abundance estimates or these could be derived from raw data (score 1). If the variances (or other measure of error/variation around the abundance estimate) were not reported (score 0).
5. If species detectability was calculated and taken into account (e.g.: using DISTANCE software, adjusting the effective strip width via other methods, or using camera traps, for which detectability can be adjusted) (score 1). If detectability was not calculated (score 0).
6. If the effect size can be calculated at species level (score 1). If effect sizes were calculated for 2 or more species aggregated at genus level (due to difficulties of distinguishing between closely related species during surveys, i.e.: indirect signs of red duikers, or brocket deers) (score 0). This last criterion applies to individual effect sizes, not to the study as a whole.

We used the sum of the scores of the six criteria as an overall measure of quality, ranging from 1-2 ("low quality") to 3-4 ("medium quality") to 5-6 ("high quality"). Sensitivity analyses were done by rerunning the meta-analysis after subsequently excluding low quality studies, and then low and medium quality studies (i.e.: including only high quality studies). Results of the meta-analyses based on different data subsets were compared to evaluate the robustness of our results to differences in the quality of the studies included. Results were highly robust to differences in data quality, as reflected by similar effect sizes for different data subsets (Figure 3.7).

3.3 Supplementary materials

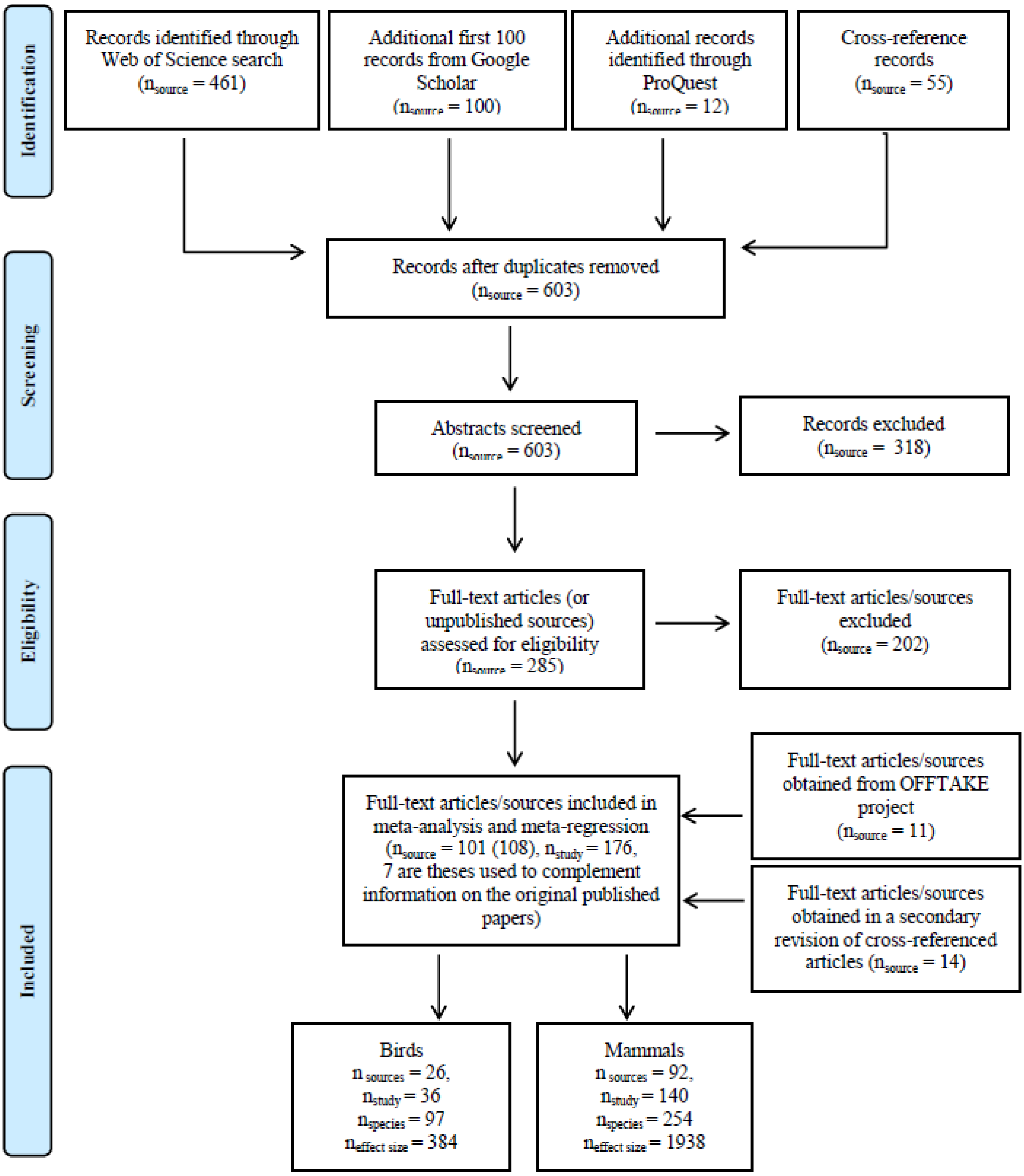


Figure 3.5: PRISMA flow chart showing the procedure of selecting publications.

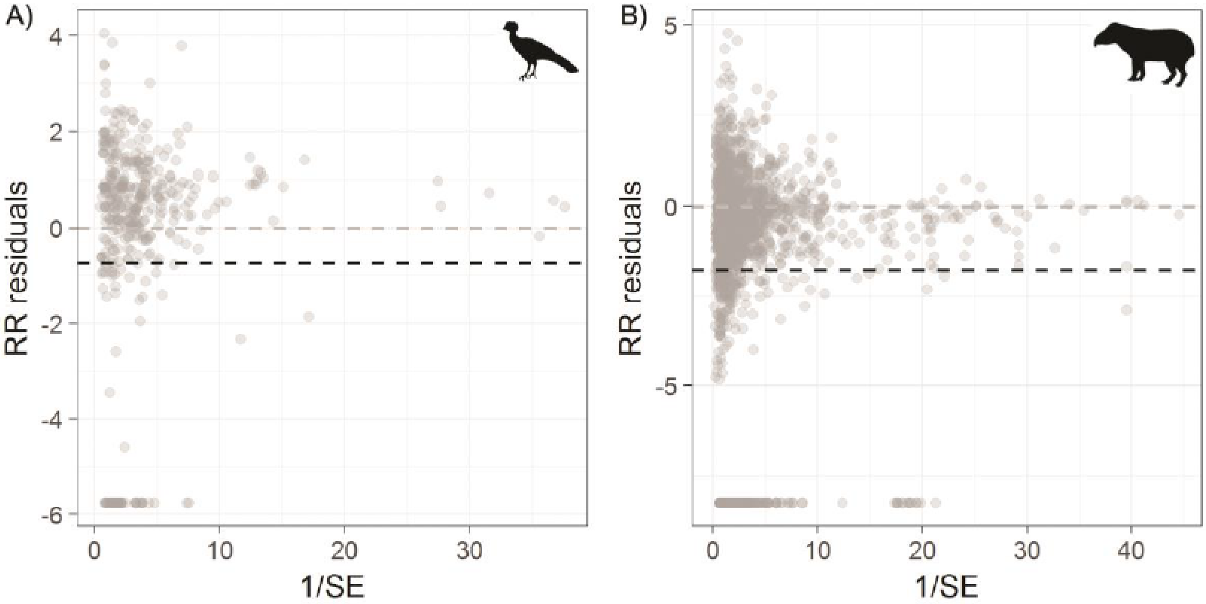


Figure 3.6: Funnel plots for (a) birds and (b) mammals. Funnel plots show the relationship between meta-analytic residuals and precision (SE^{-1}). Dashed lines indicates $RR = 0$ (zero line, black), and weighted mean effect size (gray). Egger test for birds: intercept = -0.74 (95% CI: -1.42,-0.05, $p = 0.0347$). Egger test for mammals: intercept = -0.05 (95% CI: -0.55, 0.44, $p = 0.8374$).

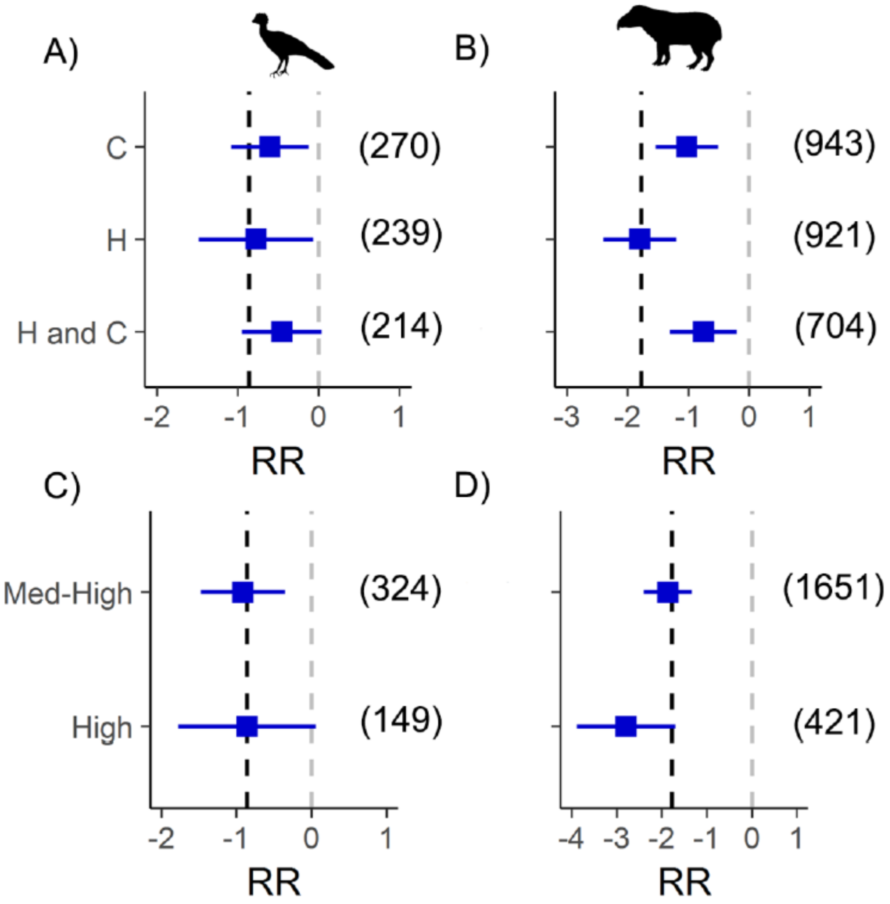


Figure 3.7: Forest plots for (a,c) birds and (b,d) mammals showing mean weighted effect sizes after exclusion of effect sizes with standardized means < 3, for hunted (H), control (C) and hunted and control means (HC). Forest plots in c) and d) show the robustness of our meta-analytical estimates to exclusion of studies with different quality levels. Med-High: excluding low quality studies; High: excluding low and medium quality studies. Number of effect sizes is shown between brackets. Dashed lines indicates $RR = 0$ (zero line, gray), and weighted mean effect size (black).

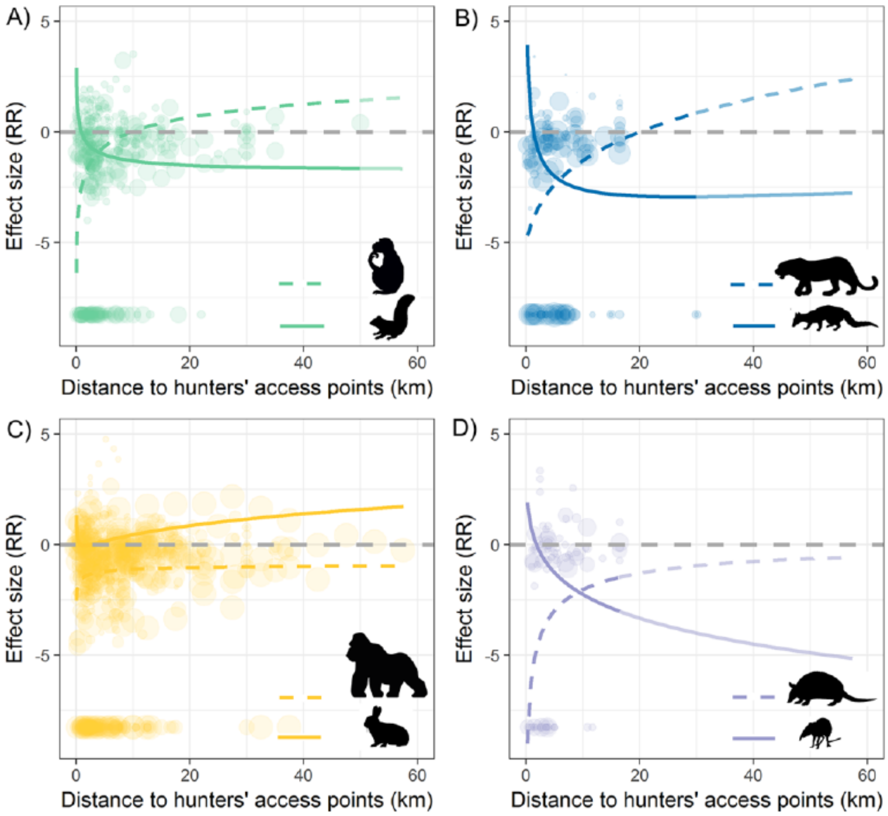


Figure 3.8: Relationship between *RR* and distance to hunters' access points for small and large mammal species representative of each feeding guild (a) frugivores (small: *Sciurus spp.*, ∼0.6kg, large: *Pan troglodytes*, 42.5 kg), (b) carnivores (small: *Genetta spp.*, ∼1.8 kg, large: *Panthera pardus*, 52 kg), (c) herbivores (small: *Sylvilagus brasiliensis*, 0.95 kg, large: *Gorilla gorilla*, 130 kg), (d) insectivores (small: *Rhynchocyon udzungwensis*, 0.71 kg, large: *Priodontes maximus*, 45 kg). Plots are shown for median travel times (∼600 min), and baseline levels of the other factors (subsistence hunting and no protected area, Table 3.5; Table 3.6). Colors as in Figure 3.3. Confidence intervals not shown. Point size is proportional to body mass. Predicted lines are extrapolated (faded color) for carnivores and insectivores to allow comparison with the other feeding guilds.

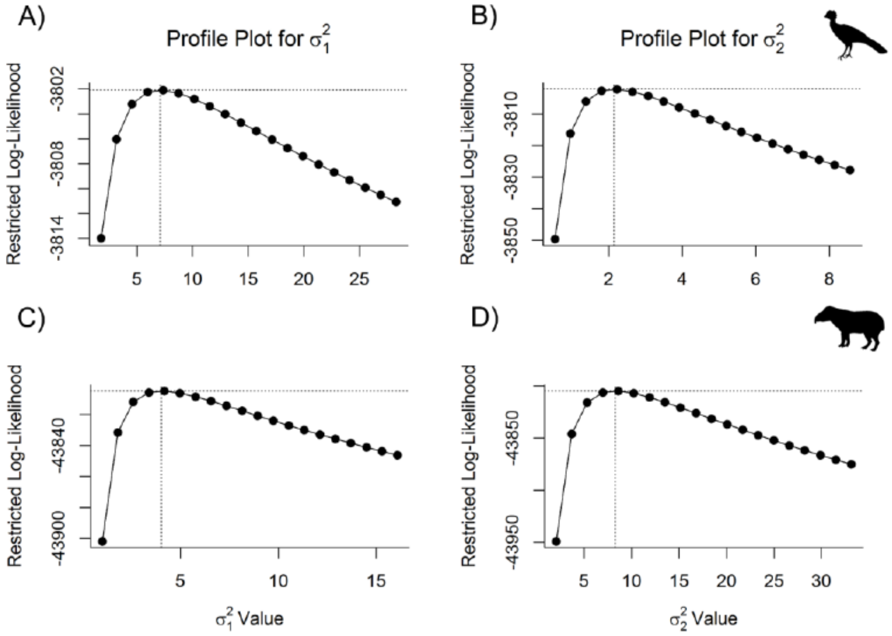


Figure 3.9: Profile likelihood plots of the variance components in the model (σ_1^2: study-level variability, σ_2^2: species-level variability) for birds (a,b) and mammals (c,d). Plots show a peak at the corresponding REML estimate (Birds: $\sigma_1^2 = 7.08$, $\sigma_2^2 = 2.14$; Mammals: $\sigma_1^2 = 4.02$; $\sigma_2^2 = 8.29$), indicating that our fitted models were not overparameterized. When the profiled likelihood is flat (over the entire parameter space or large portions of it), then this suggests that at least some of the parameters of the model are not identifiable and the parameter estimates obtained are to some extent arbitrary (Viechtbauer, 2010).

Table 3.1: Results of the meta-analysis under different SD imputation methods.

Class	Imputation	Weighted mean RR	Lower CI	Upper CI
Birds	Poisson	-0.859	-1.433	-0.285
	Bracken 1992	-0.773	-1.292	-0.255
	HotDeckNN	-0.837 (median) -0.835 (average)	-1.410 (median) -1.402 (average)	-0.264 (median) -0.268 (average)
Mammals	Poisson	-1.775	-2.273	-1.278
	Bracken 1992	-1.580	-2.062	-1.107
	HotDeckNN	-1.806 (median) -1.808 (average)	-2.312 (median) -2.316 (average)	-1.293 (median) -1.294 (average)

Table 3.2: Moderators included in the analyses. For continuous moderators, units and transformations are indicated; for categorical moderators (factors), levels of the factor are indicated.

Moderators		**Variable**	**Unit/levels**	**Transf.**	**Reason**
Species-level	*Guild* Carnivores Frugivores Herbivores Insectivores Omnivores	Factor	4 (birds); 5 (mammals)	n.a.	[1]
	Body mass	Continuous	kg	Log transf.	[2]
Study site-level	*Distance*	Continuous	km	Log transf.	[3]
	Travel time	Continuous	min.	Log transf.	[4]
	Region Africa Asia CAmerica SAmerica	Factor	4	n.a.	[5]
	Type of hunting Subsistence Commercial Both	Factor	2 (birds); 3 (mammals)	n.a.	[6]
	Protected areas Unprotected Protected	Factor	2	n.a.	[7]

---

[1] Large-scale hunting may affect functional guilds differently, with different consequences for ecosystem functioning (Peres et al., 2016).

[2] Large species are more heavily hunted.

[3] Species abundance increases with distance to hunters' access points and levels off beyond a certain threshold distance.

[4] Travel time to major towns is used as a proxy of accessibility to urban markets. Hunting pressure is expected to be higher in areas more accessible (with less travel time) to urban markets.

[5] Hunting-induced defaunation may vary regionally. For example, regions with more human population and historically more hunted (Africa) may be more defaunated (lower effect sizes) than regions with historically less human population (South America). Not included in model selection because it is confounded with "Type of hunting", plus it is not well balanced for birds.

[6] Commercial or subsistence and commercial hunting (both) may have a larger effect on wildlife populations than subsistence hunting.

[7] Hunting pressure is larger outside of protected areas.

Table 3.3: Results of model selection for fitting the random effects structure for birds and mammals. Models were run with a full fixed effects structure and compared using the Bayesian Information Criterion (BIC). The final random effects structure used in the meta-analysis is in bold: (1|Study + 1|Species). k: number of parameters.

Random effects	**Birds**		**Mammals**	
	BIC	***k***	**BIC**	***k***
(1|1)	16136.5	16	238433.6	37
(1|Study)	13161.0	17	142938.8	38
(1|Species)	9749.0	17	134129.6	38
(1|Order/Species)	9750.2	18	134137.2	39
(1|Study+1|Species)	**7696.4**	**18**	**87904.2**	**39**
(1|Study+1|Order/Species)	7699.3	19	87910.6	40
(1|Study+1|Order)	11722.9	18	134137.9	39

Table 3.4: Effect sizes (categorical moderators) and regression coefficients (continuous moderators) for birds and mammals. Average random-model effect sizes ("Mean Effect size") and 95% Confidence Intervals ("LCI" and "UCI") were calculated by Region, Functional Guild, Type of Hunting and Level of Protection, for birds and mammals separately. Average regression coefficients and 95% CI are shown for continuous moderators (Distance: distance to hunters' access points, Travel Time, Body mass). Models for continuous moderators included quadratic terms (Slope (q)). N: number of effect sizes, LRT: Likelihood ratio tests. Q_M: omnibus test (χ^2 distributed). Significant results are highlighted in bold. p-values and p-values corrected for multiple hypothesis testing using Bonferroni corrections are presented (p-adj).

Class	**Fixed effects/ Moderators**	**Mean eff. size/ Regr. coeff.**	**LCI**	**UCI**	**N**	**Model omnibus tests ($Q_{M,df}$)**
Birds	*Distance*				384	
	Intercept	-2.10	-2.63	-1.58		$Q_{M,2}$**=1605.5, p=0.0007**
	Slope	1.43	1.29	1.56		
	Slope (q)	-0.17	-0.21	-0.14		
	Body mass				384	
	Intercept	-0.90	-1.47	-0.32		$Q_{M,1}$=6.39, p=0.0805
	Slope	-0.37	-0.65	-0.08		
	Slope (q)					
	Travel time				384	
	Intercept	-6.14	-6.98	-5.30		$Q_{M,1}$**=395.45, p=0.0007**
	Slope	0.81	0.73	0.89		
	Slope (q)					
	Region					
	Africa	0.48	-1.13	2.09	39	$Q_{M,3}$**=14.89, p=0.0343**

Table 3.4 continued from previous page

Class	**Fixed effects/ Moderators**	**Mean eff. size/ Regr. coeff.**	**LCI**	**UCI**	**N**	**Model omnibus tests ($Q_{M,df}$)**
	Asia	-0.58	-2.60	1.43	10	
	CAmerica	-0.21	-1.45	1.03	103	
	SAmerica	-1.30	-1.98	-0.63	232	
	Guild					
	Carn	-0.98	-2.25	0.29	18	
	Frug	-0.87	-1.47	-0.26	316	$Q_{M,3}$=9.81, p=0.3066
	Herb					
	Insect	-0.36	-1.58	0.86	19	
	Omn	-1.06	-2.17	0.05	31	
	Hunting					
	Subsistence	-0.55	-1.21	0.11	297	**$Q_{M,1}$=11.85, p=0.0189**
	Commercial					
	Both	-1.48	-2.39	-0.57	87	
	Protection					
	Unprotected	-0.60	-1.21	-0.001	167	**$Q_{M,1}$=103.7, p=0.0007**
	Protected	-1.20	-1.80	-0.59	217	
Mammals	*Distance*				1938	
	Intercept	-2.36	-2.86	-1.87		**$Q_{M,2}$=12741.88, p=0.0007**
	Slope	0.10	0.08	0.13		
	Slope (q)	0.14	0.14	0.15		
	Body mass				1938	
	Intercept	-1.54	-2.12	-0.95		$Q_{M,1}$=2.18, p=0.9744
	Slope	-0.13	-0.32	0.05		
	Slope (q)					
	Travel time				1938	
	Intercept	-2.40	-3.02	-1.78		**$Q_{M,2}$=3497.42, p=0.0007**
	Slope	-1.08	-1.21	-0.95		
	Slope (q)	0.18	0.16	0.19		
	Region					
	Africa	-2.00	-2.72	-1.29	792	
	Asia	-2.02	-3.84	-0.20	105	**$Q_{M,3}$=57.18, p=0.0007**
	CAmerica	-2.87	-4.05	-1.68	251	
	SAmerica	-1.27	-1.97	-0.58	790	
	Guild					
	Carn	-2.41	-3.49	-1.33	158	
	Frug	-1.91	-2.73	-1.11	463	**$Q_{M,4}$=55.28, p=0.0007**
	Herb	-1.39	-2.08	-0.70	793	

Table 3.4 continued from previous page

Class	Fixed effects/ Moderators	Mean eff. size/ Regr. coeff.	LCI	UCI	N	Model omnibus tests ($Q_{M,df}$)
	Insect	-3.11	-4.71	-1.51	85	
	Omn	-1.59	-2.37	-0.81	439	
	Hunting					
	Subsistence	-0.83	-1.45	-0.22	823	$Q_{M,2}$=**76.47, p=0.0007**
	Commercial	-2.24	-3.20	-1.29	191	
	Both	-2.63	-3.25	-2.01	924	
	Protection					
	Unprotected	-2.37	-2.87	-1.87	754	$Q_{M,1}$=**2836.12, p=0.0007**
	Protected	-1.10	-1.60	0.60	1184	

Table 3.5: Model selection results for multiple meta-regression models relating RR to the following moderators: Distance: Distance to hunters' access point, BM: Body mass, TypeHunt: Type of Hunting, TravTime: Travel Time to the nearest major town, Guild, Prot: Protected area status. The most supported model is the one with the lowest BIC (Bayesian Information Criterion). Results are presented for birds and mammals. dBIC: Difference in BIC from the most supported model; weights: Akaike weights; k: number of fitted parameters. Model selection was applied to main effects first, and subsequently we assessed is model fit improved by adding first- and second-order interactions between distance and some of the moderators.

Class	Model	BIC	dBIC	weights	k
Birds	Distance + Distance^2 + BM x Distance + BM x Distance^2 + TypeHunt x Distance +TypeHunt x Distance^2 + Prot x Distance + Prot x Distance^2	7687.0	0.0	0.900	14
	Distance + Distance^2 + BM x Distance + BM x Distance^2+ TravTime + TypeHunt x Distance + TypeHunt x Distance^2 + Prot x Distance + Prot x Distance^2	7691.6	4.6	0.092	15
	Distance + Distance^2 + BM x Distance + BM x Distance^2 + Guild + TravTime + Distance x TypeHunt + Distance^2 x TypeHunt + Prot x Distance + Prot x Distance^2	7696.4	9.4	0.008	18

Table 3.5 continued from previous page

Class	Model	BIC	dBIC	weights	*k*
	Distance + Distance^2 + BM x Distance + BM x Distance^2 + TypeHunt x Distance + Prot x Distance + Prot x Distance^2	7779.1	92.1	0.000	13
	Distance + Distance^2 + BM x Distance + TypeHunt x Distance + Prot x Distance + Prot x Distance^2	7813.1	126.1	0.000	12
	Distance + Distance^2 + BM x Distance + BM x Distance^2 + TypeHunt x Distance + TypeHunt x Distance^2 + Prot x Distance	7823.0	135.9	0.000	13
	Distance + Distance^2 + BM + Distance x BM + BM x Distance^2 + TravTime + Guild + TypeHunt + Prot	8173.5	486.5	0.000	14
	Distance + Distance^2 + BM + Distance x BM + TravTime + Guild + TypeHunt + Prot	8180.8	493.8	0.000	13
	Distance + Distance^2 + BM + TravTime + Guild + TypeHunt + Prot x Distance + Prot x Distance^2	8465.9	778.9	0.000	14
	Distance + Distance^2 + BM + TravTime + Guild + TypeHunt + Prot x Distance	8606.6	919.6	0.000	13
	Distance + Distance^2 + BM + TravTime + Guild + TypeHunt x Distance + TypeHunt x Distance^2 + Prot	8972.2	1285.2	0.000	14
	Distance + Distance^2 + BM + TravTime + TypeHunt + Prot	8979.3	1292.3	0.000	9
	Distance + Distance^2 + BM + TravTime + TravTime^2 + Guild + TypeHunt + Prot	8985.6	1298.6	0.000	12
	Distance + Distance^2 + BM + TravTime + Guild + TypeHunt x Distance + Prot	8989.1	1302.1	0.000	13
	Null	10779.64	3092.6	0.000	3

Table 3.5 continued from previous page

Class	Model	BIC	dBIC	weights	*k*
Mammals	Distance + Distance^2 + BM + BM x Distance + BM x Distance^2 + TravTime + TravTime^2 + Guild + Guild x Distance + Guild x Distance^2 + Guild x BM + Guild x Distance x BM + TypeHunt + TypeHunt x Distance + TypeHunt x Distance^2 + Prot + Prot x Distance + Prot x Distance^2	87904.2	0.0	1.000	39
	Distance + Distance^2 + BM + BM x Distance + TravTime + TravTime^2 + Guild + Guild x Distance + Guild x Distance^2 + Guild x BM + Guild x Distance x BM + TypeHunt + Prot + Prot x Distance + Prot x Distance^2	88444.2	540.0	0.000	34
	Distance + Distance^2 + BM + BM x Distance + TravTime + TravTime^2 + Guild + Guild x Distance + Guild x Distance^2 + Guild x BM + Guild x Distance x BM + TypeHunt + Prot + Prot x Distance	88463.2	559.0	0.000	33
	Distance + Distance^2 + BM + BM x Distance + TravTime + TravTime^2 + Guild + Guild x Distance + Guild x Distance^2 + Guild x BM + Guild x Distance x BM + TypeHunt + TypeHunt x Distance +TypeHunt x Distance^2 + Prot	89612.5	1708.3	0.000	36
	Distance + Distance^2 + BM + BM x Distance + TravTime + TravTime^2 + Guild + Guild x Distance + Guild x Distance^2 + Guild x BM + Guild x Distance x BM + TypeHunt + TypeHunt x Distance + Prot	89691.9	1787.7	0.000	34
	Distance + Distance^2 + BM + BM x Distance + TravTime + TravTime^2 + Guild + Guild x Distance + Guild x Distance^2 + Guild x BM + Guild x Distance x BM + TypeHunt + Prot	90218.5	2314.3	0.000	32

Table 3.5 continued from previous page

Class	Model	BIC	dBIC	weights	*k*
	Distance + Distance^2 + BM + BM x Distance + TravTime + TravTime^2 + Guild + Guild x Distance + Guild x BM + Guild x Distance x BM + TypeHunt + Prot	90279.1	2374.9	0.000	28
	Distance + Distance^2 + BM + TravTime + TravTime^2 + Guild + TypeHunt + Prot + Prot x Distance	91689.3	3785.1	0.000	16
	Distance + Distance^2 + BM + TravTime + TravTime^2 + Guild + TypeHunt + Prot + Prot x Distance + Prot x Distance^2	91695.9	3791.7	0.000	17
	Distance + Distance^2 + BM + TravTime + TravTime^2 + Guild + TypeHunt + TypeHunt x Distance + TypeHunt x Distance^2 + Prot	92013.8	4109.6	0.000	19
	Distance + Distance^2 + BM + TravTime + TravTime^2 + Guild + TypeHunt +TypeHunt x Distance + Prot	92094.6	4190.4	0.000	17
	Distance + Distance^2 + BM + Distance x BM + Distance^2 x BM + TravTime + TravTime^2 + Guild + TypeHunt + Prot	92477.9	4573.7	0.000	17
	Distance + Distance^2 + BM + Distance x BM + TravTime + TravTime^2 + Guild + TypeHunt + Prot	92483.4	4579.2	0.000	16
	Distance + Distance^2 + BM + TravTime + TravTime^2 + Guild + TypeHunt + Prot	92590.2	4686.0	0.000	15
	Null	106903.6	18999.4	0.000	3

Table 3.6: Standardized coefficients of retained terms in best meta-regression models for birds and mammals. Distance: Distance to hunters' access point, BM: Body mass, SC: Subsistence and Commercial (both), C: Commercial. Main effects were tested after dropping interactions. Birds: McFadden's Pseudo $R^2 = 0.29$; $Q_{M,11} = 3157.5$ ($p<0.0001$), $Q_{E,372} = 16544.5$ ($p<0.0001$). Mammals: McFadden's Pseudo $R^2 = 0.18$, $Q_{M,36} = 19208.0$ ($p<0.0001$), $Q_{E,1391} = 237350.6$ ($p<0.0001$).

Class	Moderators	Estm.	SE	Z	$p_{\mathbf{estm}}$	$\mathbf{Q_m}$ (df)	$p_{\mathbf{Q}}$
Birds	Intercept	-0.61	0.58	-1.06	0.2913		
	Distance	3.91	0.20	19.49	<0.0001	1552.0 (2)	<0.0001
	Distance^2	-2.42	0.19	-12.98	<0.0001		
	BM	-0.14	0.16	-0.88	0.3799	0.8 (1)	0.3799
	TypeHunt (SC)	-1.63	0.97	-1.68	0.0920	2.8 (1)	0.0920
	Protected (Yes)	-0.07	0.08	-0.79	0.4271	0.6 (1)	0.4721
	Distance x BM	-0.12	0.09	-1.40	0.1608	690.8 (2)	<0.0001
	Distance^2 x BM	0.77	0.08	9.76	<0.0001		
	Distance x TypeHunt (SC)	-4.53	0.42	-10.72	<0.0001	115.4 (2)	<0.0001
	Distance^2 x TypeHunt (SC)	3.38	0.32	10.68	<0.0001		
	Distance x Prot (Yes)	-3.24	0.20	-16.09	<0.0001	465.5 (2)	<0.0001
	Distance^2 x Prot (Yes)	2.29	0.19	12.37	<0.0001		
Mammals	Intercept	-1.06	0.63	-1.69	0.0901		
	Distance	0.69	0.03	23.99	<0.0001	9123.7 (2)	<0.0001
	Distance^2	-0.03	0.02	-1.42	0.1550		
	BM	-0.13	0.56	-0.23	0.8218	3.8 (1)	0.0522
	TravTime	1.34	0.08	16.76	<0.0001	399.8 (2)	<0.0001
	TravTime^2	-1.25	0.09	-13.68	<0.0001		
	Guild (Carn)	-1.04	0.82	-1.28	0.2019	8.4 (4)	0.0767
	Guild (Herb)	0.38	0.67	0.57	0.5699		
	Guild (Invert)	-1.93	1.09	-1.77	0.0769		
	Guild (Omn)	-0.63	0.87	-0.73	0.4658		
	TypeHunt (C)	-1.98	0.57	-3.45	0.0006	27.1 (2)	<0.0001
	TypeHunt (SC)	-1.72	0.39	-4.38	<0.0001		
	Protected (Yes)	0.51	0.03	17.87	<0.0001	1004.3 (1)	<0.0001
	Distance x BM	1.12	0.03	32.26	<0.0001	1352.4 (2)	<0.0001
	Distance^2 x BM	-0.21	0.02	-12.55	<0.0001		
	Distance x Guild (Carn)	-1.23	0.15	-8.15	<0.0001	944.8 (8)	<0.0001

Table 3.6 continued from previous page

Class	Moderators	Estm.	SE	Z	p_{estm}	Q_m (df)	p_Q
	Distance x Guild (Herb)	-0.59	0.04	-15.14	<0.0001		
	Distance x Guild (Inver)	0.66	0.28	2.35	0.0189		
	Distance x Guild (Omn)	-1.17	0.05	-21.51	<0.0001		
	Distance^2 x Guild (Carn)	0.81	0.11	7.10	<0.0001		
	Distance^2 x Guild (Herb)	0.17	0.03	5.32	<0.0001		
	Distance^2 x Guild (Inver)	-0.51	0.21	-2.38	0.0174		
	Distance^2 x Guild (Omn)	0.26	0.03	7.55	<0.0001		
	BM x Guild (Carn)	-0.75	1.03	-0.72	0.4696	58.9 (4)	<0.0001
	BM x Guild (Herb)	-0.58	0.55	-1.05	0.2953		
	BM x Guild (Inver)	-1.39	1.18	-1.18	0.2392		
	BM x Guild (Omn)	-0.72	0.79	-0.91	0.3604		
	Distance x Type-Hunt (C)	-0.29	0.05	-5.22	<0.0001	566.1	<0.0001
	Distance x Type-Hunt (SC)	-0.28	0.04	-6.43	<0.0001		
	Distance^2 x Type-Hunt (C)	0.84	0.05	16.88	<0.0001		
	Distance^2 x Type-Hunt (SC)	0.38	0.04	9.58	<0.0001		
	Distance x Prot (Yes)	0.85	0.04	21.65	<0.0001	493.7	<0.0001
	Distance^2 x Prot (Yes)	-0.18	0.03	-5.70	<0.0001		
	Distance x BM x Guild (Carn)	1.02	0.11	9.51	<0.0001	1325.7	<0.0001
	Distance x BM x Guild (Herb)	-0.96	0.03	-30.36	<0.0001		

Table 3.6 continued from previous page

Class	Moderators	Estm.	SE	Z	$p_{\mathbf{estm}}$	$\mathbf{Q_m}$ (df)	$p_{\mathbf{Q}}$
	Distance x BM x Guild (Inver)	0.87	0.24	3.62	0.0003		
	Distance x BM x Guild (Omn)	-0.79	0.04	-19.49	<0.0001		

Chapter 4

Animal group size variation in a minimal attraction-repulsion agent-based model

This chapter is based on:

Eikelboom, J. A. J., Doelman, A., van Langevelde, F., & de Knegt, H. J. (*in draft*). Animal group size variation in a minimal attraction-repulsion agent-based model.

Abstract

Grouping behaviour of prey animals is thought to be mainly driven by fear of predation and resource scarcity. Fear of predation often leads to small inter-individual distances, while resource scarcity leads to the opposite. Consequently, it is believed that the number of individuals in a group (group size) is an emergent property of the trade-off between acquiring scarce resources and preventing predation. We analysed whether group size can be reliably used as a proxy for this trade-off, using a deterministic attraction-repulsion agent-based model in a homogeneous area. In our model, each individual experiences distance-dependent attraction and repulsion to all others in the area, where varying degrees of grouping behaviour emerge from the number and distance of intersections between the attraction and repulsion functions. We show that the coefficient of variation of group size generally lies between 50 and 150%, depending on both animal density and the trade-off between resource scarcity and predation. Given that the variations of group size are already this large in homogeneous and deterministic scenarios, we urge researchers to be cautious in using group size as a proxy for the resources/predation trade-off and consider inter-individual distance as a more direct and potentially more reliable alternative.

4.1 Background

In order to survive, the movement of animals is for a large part driven by two factors: resource availability (e.g., food) and fear of threats (e.g., predation) (Brown et al., 1999; Nathan et al., 2008). Resource scarcity induces animals to prioritize foraging behaviour and high predation risk induces animals to prioritize vigilance behaviour (Laundré et al., 2001). Given that these two behaviours often cannot be performed efficiently simultaneously, a trade-off exists between food acquisition and predator avoidance regarding optimal fitness (Lima, 1995). Emerging from individual movement, collective animal movement (e.g., group formation) is to a large extent also shaped by both resources and predation (Alexander, 1974; Couzin & Krause, 2003; Krause & Ruxton, 2002). In general, when the chance of predation is high it benefits an individual to live in a group with many individuals, through both the dilution (i.e., less chance to be chosen by a predator during an attack (Hamilton, 1971)) and the “many eyes” effect (i.e., benefiting from the vigilance of group members (Lima, 1995)). And although there are animal species that benefit from a sizeable group for resource acquisition (e.g., in order to defend territories with resources (Krause & Ruxton, 2002): contest competition), when resources are accessible to all competitors (i.e., scramble competition) it benefits an individual to live solitary in the absence of predators by having the monopoly on resources in its direct vicinity (Isbell, 1991). Considering prey species that are in scramble competition with their conspecifics, there is thus an apparent trade-off between resource availability and fear of predation regarding an ‘optimal’ group size (Couzin & Krause, 2003; Krause & Ruxton, 2002).

The proposed mechanisms by which individuals form groups of a certain size are derived from two main theories: 1) individuals selecting groups of a certain size (Krause & Godin, 2010), and 2) individuals forming groups through self-organizing processes of individual movement decisions (Couzin & Krause, 2003; Hoare et al., 2004). Both mechanisms are credible to occur in nature, possibly even occurring simultaneously for some species (Krause & Ruxton, 2002). However, the first of these two mechanisms is cognitively the most complex by assuming that animals are able to count conspecifics within a group, which is unlikely for large groups and/or species with lower cognitive abilities such as shoaling fish, swarming insects and flocking birds (Couzin & Krause, 2003). Furthermore, with the first mechanism, optimal group sizes are generally exceeded because solitary individuals continue to join already large groups (Hoare et al., 2004). Self-organization is thus the most parsimonious of these two mechanisms through which to explain the formation of group sizes that may appear optimal given the trade-off between searching for scarce resources and reducing predation risk (Couzin & Krause, 2003). These self-organizing models of collective behaviour have been build around individual movement decisions, in which often the radius of interaction with conspecifics and/or the magnitude of attraction and repulsion between individuals is a function of variables such as resource availability and fear of predation (Couzin et al., 2002; Couzin & Krause, 2003; Hoare et al., 2004).

In many studies the concept of optimal group size has been used to draw conclusions about resource availability (Isbell, 1991; Sinclair, 1977), predation risk (Fryxell et al., 2007; Sorato et al., 2012) or both (Brouwer et al., 2020; Hoare et al., 2004) by monitoring group sizes in the field. However, group sizes are often highly variable, resulting in broad frequency distributions when recording the sizes of groups (Hoare et al., 2004; Sinclair, 1977). This variability is not an issue in laboratory settings or during experiments where resource availability and fear perception can be controlled (Hoare et al., 2004), but it does become problematic under field conditions where resource availability and predation risk are largely unknown and which are often the actual variables of interest for which group size serves as a proxy (Fryxell et al., 2007; Sinclair, 1977). To substantiate this, a large variance in field-monitored group sizes can be caused by 1) heterogeneity in resource availability or predation risk across the study area, 2) complexity in animal behaviour (which is obviously driven by many more factors), as well as 3) a large inherent variability in the emergent properties of the group formation process even in the absence of environmental and behavioural heterogeneity. To draw reliable conclusions about resource availability and predation risk from monitored group sizes it is thus important to investigate the relative importance of each of these three aspects in their shaping of the variation in group sizes.

The inherent variability of group sizes caused by the group formation process itself can be studied with a minimal agent-based model with two types of forces: attraction (driven by predation risk) and repulsion (driven by resource scarcity). In a hypothetical situation with fear of predation and unlimited resources it is most beneficial for animals to all stack in the same location (attraction-only), and in the situation without fear of predation and with limited resources it is most beneficial for animals to distribute themselves perfectly overdispersed across the area (repulsion-only). Attraction-repulsion agent-based models have been used widely in biology, mathematics and physics research to study clustering, both to investigate equilibria (Bernoff & Topaz, 2011; Gazi & Passino, 2004; Leverentz et al., 2009; Liu & Xi, 2019; Sciortino et al., 2004) and collective movement patterns (Chen & Kolokolnikov, 2014; Eftimie et al., 2007; Romanczuk & Schimansky-Geier, 2012). From these modelling efforts it has become apparent that groups with alternate stable sizes can form in a single simulation from random initial locations, deterministic movement and homogeneous areas (Sciortino et al., 2004). How the variation in stable group sizes exactly relates to the underlying model parameters is of interest for this study.

Here we aim to investigate the inherent variability of group sizes that result from a deterministic and homogeneous self-organizing group formation process driven only by resources and fear. Using this approach we can measure the variance in group sizes that are caused solely by the group formation process, thereby avoiding the effects of environmental heterogeneity and other factors that influence animal behaviour. Our aim is thus not to provide a single realistic model for group size variation, but a simple model to gauge the effect of the inherent variability in the group formation process. To this end we have built an agent-based model in which each individual experiences distance-dependent forces to all other individuals: attraction (driven by predation risk) and repulsion (driven by resource scarcity), each force modelled with only one parameter. From the converged simulations of these models we computed the variances in group size and linked these to the different values of attraction, repulsion and animal density. To sample the entire probability distribution of stable group sizes, we ran multiple iterations of each unique model with random initial locations of the individuals.

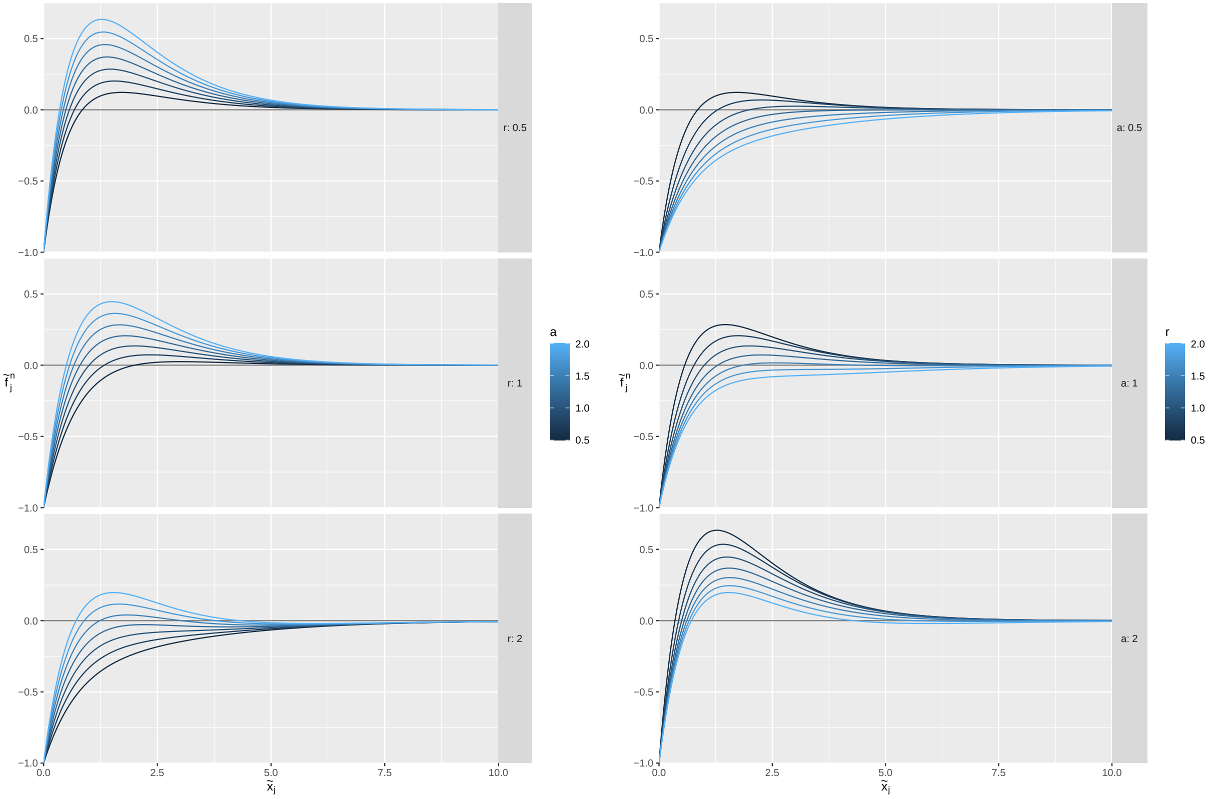
4.2 Modelling

Full details about the modelling are in the Methods section.

We modelled various numbers of individuals in one, two and three dimensions in areas of different sizes with an agent-based model. Each individual experienced both an attraction and a repulsion force to each other individual, for which the magnitude varied deterministically based on inter-individual distances. The net resultant vector of all these forces resulted in the movement of the individual. For every simulation the locations of the individuals were initiated with complete spatial randomness and the simulations ran until the locations converged to a stable position. The single-parameter function of the attraction force versus distance was chosen to be hump-shaped with a long tail: being low at close distances, high at intermediate distances and low at far distances. The single-parameter repulsion force function was chosen to decrease exponentially with distance: being high at close distances and low at far distances. These distance-dependent forces simulate the tendency of group-living prey animals to group together with conspecifics in the vicinity and to maintain a certain inter-individual distance (Gazi & Passino, 2004). We used the attraction parameter a as a proxy for predation risk and the repulsion parameter r as a proxy for resource scarcity and did not make assumptions about the functional relationship between predation risk versus a and resource scarcity versus r (other than being monotonically positive).

We chose our functions and underlying a and r parameters in such a way that the combination of the attraction and repulsion forces in a net attraction force (through subtracting the one from the other) led to three distinct scenarios of relationships (Figure 4.1): 1) when r had the upper hand over a, with the net attraction being negative for all possible distances; 2) when r and a were closer together in their influence on the system, with the net attraction being positive for a certain distance range and negative both before and after this range; and 3) when the balance between r and a is shifted even further, the net attraction being positive for all distances beyond a certain range. Based on the results of previous studies done on clustering with attraction-repulsion agent-based models (Gazi

& Passino, 2004; Liu & Xi, 2019; Sciortino et al., 2004), we expected the first scenario to result in overdispersed systems without group formation, the second scenario to result in systems where multiple groups can form, and the third scenario to result in systems that have the capacity to form one group with all individuals.



(a) a in legend and r in panels **(b)** r in legend and a in panels

Figure 4.1: Net attraction $\tilde{f}_j^n(\tilde{x}_j) = a\tilde{x}_j e^{-\tilde{x}_j} - e^{-\frac{\tilde{x}_j}{r}}$ versus distance $\tilde{x}_j$, for values of attraction a and repulsion r between 0.5 and 2.

We simulated all parameter combinations of the model 100 times with different random initial locations of the individuals. In order to retrieve the group sizes of the converged states of the simulations, we first tried various clustering algorithms (e.g., k-means, k-medoids, hierarchical clustering and brute-force packages that applied many different clustering algorithms at the same time) to differentiate the individuals into different groups. Unfortunately this proved to be too error-sensitive for our data, especially for situations where the distances between clusters were not much larger than the distances between individuals within the same cluster. Therefore we computed the distance matrices of the individuals and scaled the inter-individual distances based on the expected inter-individuals distances under complete spatial randomness (see Clustering subsection). From these transformed distance matrices we then identified the values that were substantially lower than expected and used these to derive an accurate estimation of the distributions of group sizes.

4.3 Results

By visualizing the end locations of the simulations (e.g., see Figure 4.2), we noticed that group formation was as expected largely influenced by both the balance in a and r as well as the density of individuals. Unexpectedly though, many simulations formed separate multi-individual groups instead of the expected single "supergroup" when the net attraction relationship did not became negative again after a certain distance range. Furthermore, there were simulations which were completely overdispersed into solely 1-individual groups, even when the net attraction was positive for a certain distance range. This is likely because the size of the simulated area extends on purpose far beyond the effective distance range of the net attraction function to resemble realistic natural scenarios and because the density of individuals is for certain simulations relatively low.

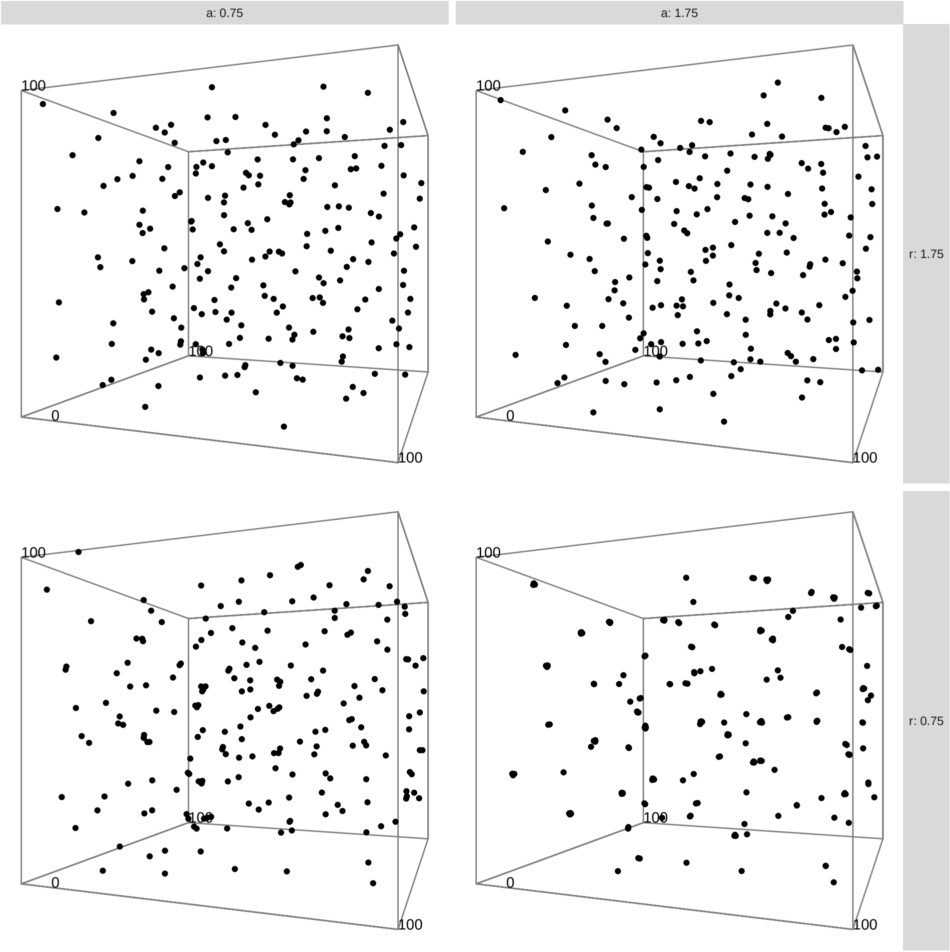


Figure 4.2: Converged states of 1 initialization of our model with 200 random initially distributed individuals inside a 3D toroidal landscape with a size s of 100, two different values of attraction a in the top panels and of repulsion r in the side panels. The two top visualizations display no clustering, the bottom left some clustering and the bottom right even more.

The transformed distance matrices allowed us to easily identify the individuals which were closer together than expected under complete spatial randomness (Figure 4.3), from which the distributions of kth neighbours within the same group and subsequently the probability distribution of an individual being in a group of a certain size could be derived.

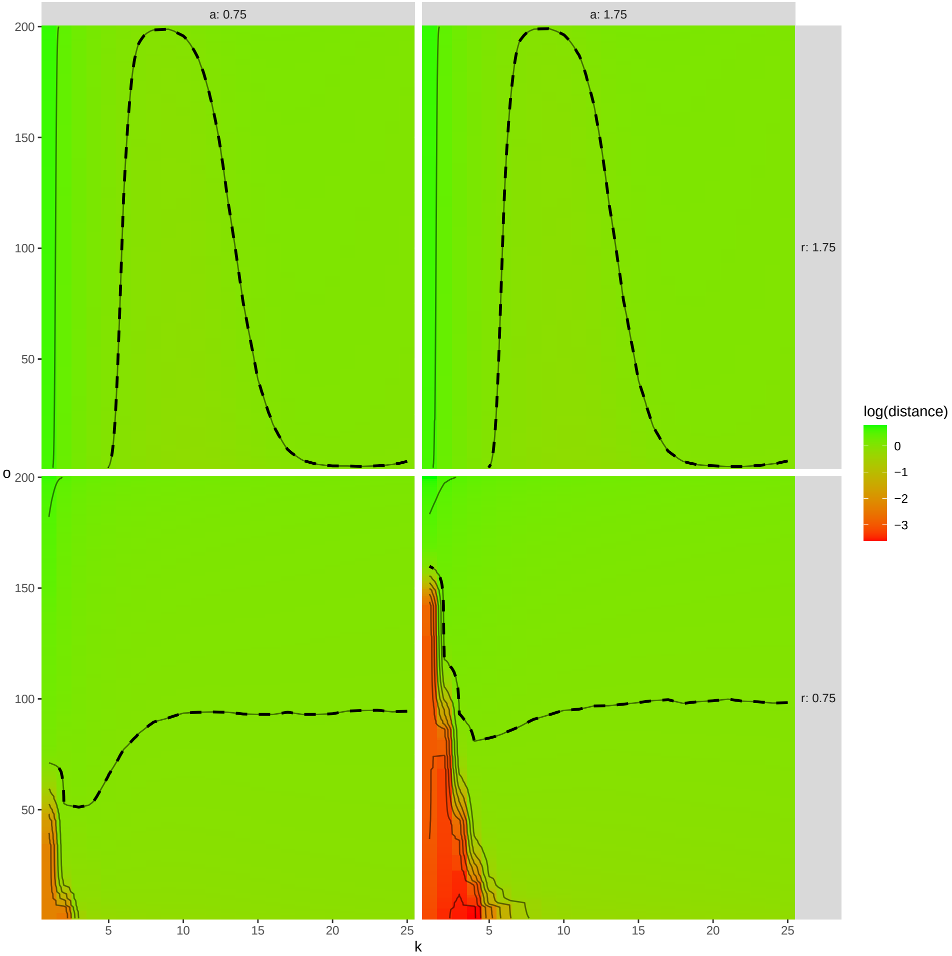
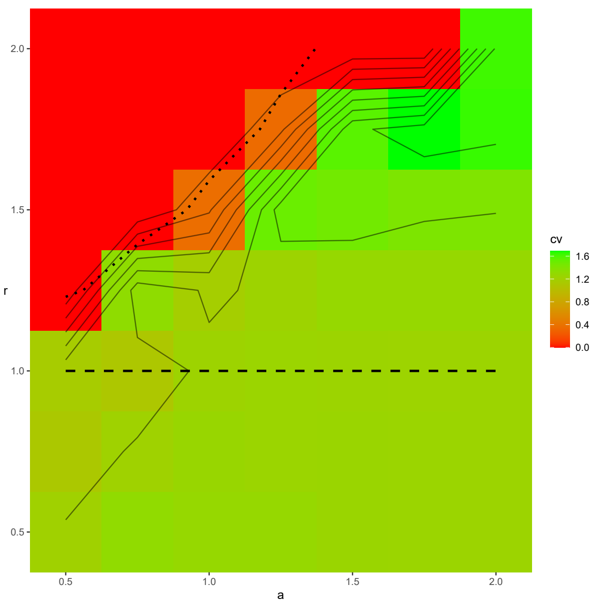
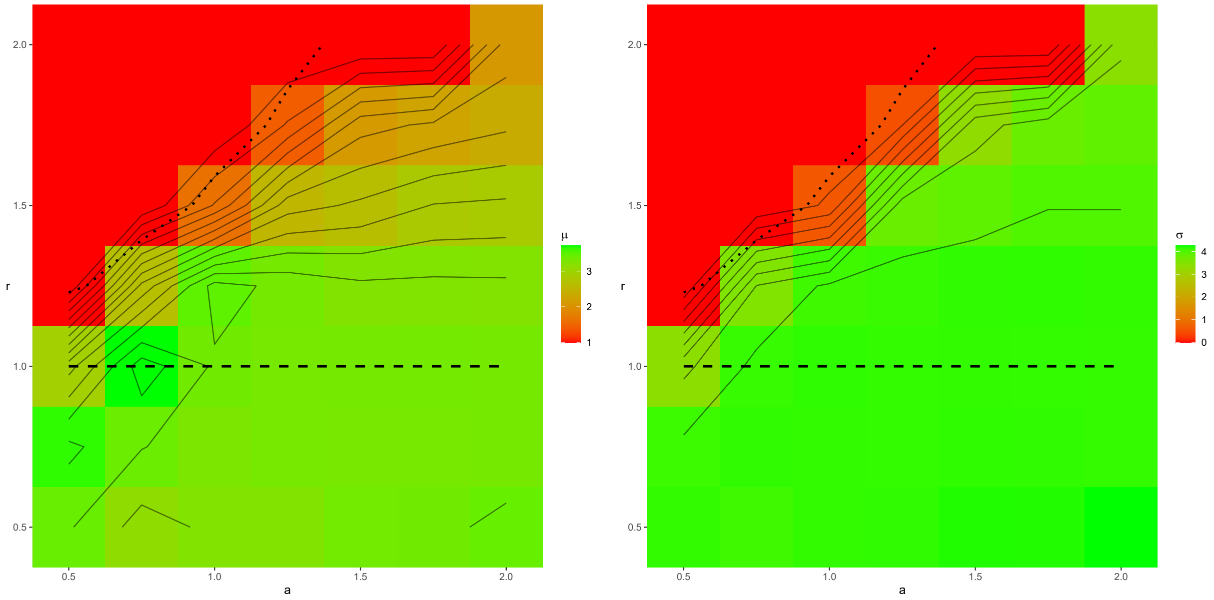


Figure 4.3: Average transformed distance matrices $\tilde{M}$ of the converged states of all 100 3D initializations as displayed in Figure 4.2, with the kth neighbour (until the 25th) on the x-axis, the ascending order o of distances on the y-axis, two different values of a in the top panels and of r in the side panels. The expected distance under complete spatial randomness is indicated with a dashed line. See Clustering subsection for details on the construction and use of these matrices.

After retrieving the distribution of group sizes for all parameter combinations of the model, we noticed that group size was as expected largely influenced by the difference between the distances for which the net attraction was zero (Figure 4.4, where the Lambert's W value is a mathematical proxy for the difference between these distances).



(a) Coefficient of variation

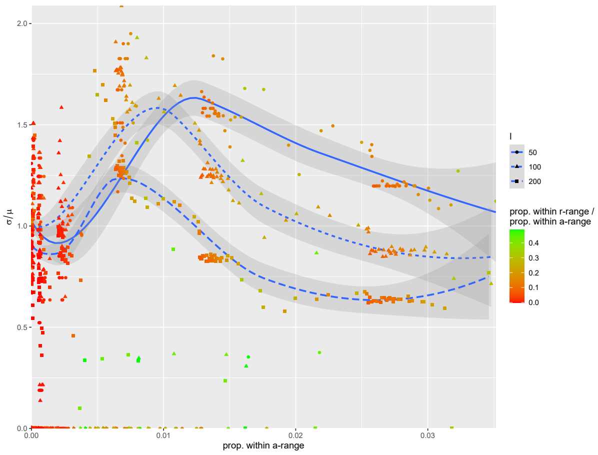


(b) Mean

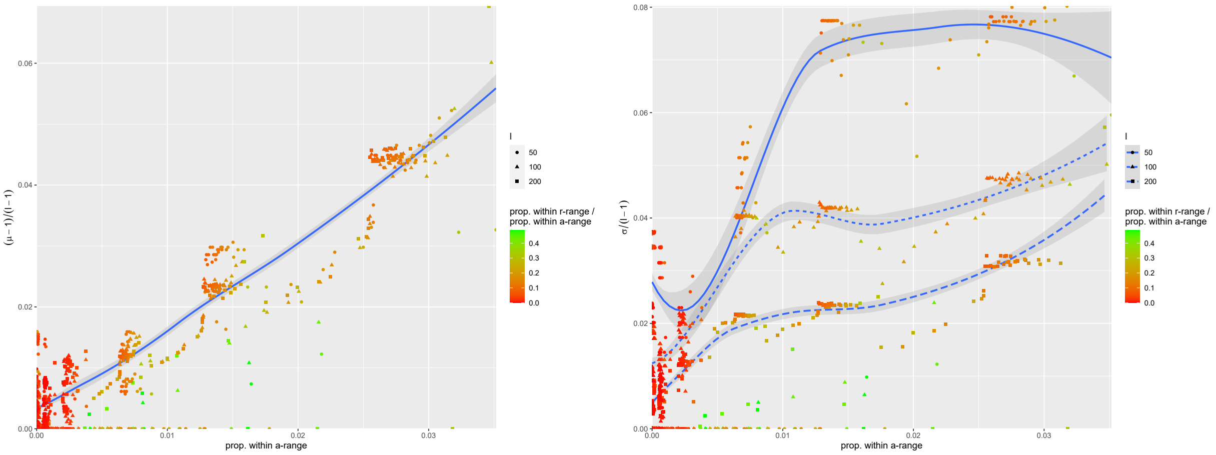
(c) Standard deviation

Figure 4.4: Group size versus attraction a (x-axis) and repulsion r (y-axis), for 1 dimension, 200 individuals and torus size 800. Coefficient of variation ($\frac{\sigma}{\mu}$) in Figure 4.4a, mean (μ) in Figure 4.4b and standard deviation (σ) in Figure 4.4c. The contour lines of 4.4b and 4.4c seem to follow the contour lines of the Lambert's W value for the intersections between the attraction and repulsion functions (Figure 4.6), of which the dashed (indicating the threshold between 1 and 2 intersections) and the dotted line (threshold between 2 and 0 intersections) are visualized here as well. This indicates a relationship between the mean and standard deviation of group size with the distance between the intersections of the attraction and repulsion functions.

Given all unique combinations of the parameters of our simulations, the same relative patterns as in Figure 4.4 were produced, but with differences in absolute values of group size. We then aimed to combine the balance between a and r (as expressed in Figure 4.4) with all other simulated variables into two interpretable variables: 1) the mean proportion of the total number of individuals within the attraction range (defined as zero for a repulsion-only model and otherwise defined as the largest distance with a value one-tenth of the value of the peak of net attraction) of each individual during initialization, and 2) the ratio between the mean proportion of the total number of individuals within the repulsion range (defined as the distance where the net attraction first becomes positive) of each individual during initialization and the former variable. These two variables seemed to describe the mean group size relative to the total number of individuals well (Figure 4.5b), but for the variation in group size the total number of simulated individuals also had a large influence (Figure 4.5a and 4.5c). Overall, the mean group size increases linearly with the proportion of individuals within the attraction range and increases even further when the proportion of individuals within the repulsion range is low relative to the proportion of individuals within the attraction range (Figure 4.5b). The same applies to the standard deviation of group size, although this relationship does not seem to be increasing linearly, but seemed to increase quicker for lower values of the proportion within the attraction range (Figure 4.5c). Furthermore, with smaller numbers of individuals the standard deviation of group size is noticeably larger. Dividing the standard deviation by the mean value of relative group size results in the coefficient of variation (Figure 4.5c), which appears to be hump-shaped and leveling off for larger larger values of the proportion within the attraction range. The coefficient of variation of relative group size lies approximately between 50 and 150% for the various parameter combinations.



(a) Coefficient of variation



(b) Mean

(c) Standard deviation

Figure 4.5: Group size proportional to number of individuals l (y-axis) versus average proportion of individuals under initial random distribution within every attraction range (x-axis), relative proportion within every repulsion range (color) and number of individuals l (shape). Coefficient of variation ($\frac{\sigma}{\mu}$) in Figure 4.5a, mean ($\frac{\mu-1}{l-1}$) in Figure 4.5b and standard deviation ($\frac{\sigma}{l-1}$) in Figure 4.5c. Trend lines computed independently of relative proportion within repulsion range and only when clustering occurred, using local polynomial regression fitting.

4.4 Discussion

In our study we have used an attraction-repulsion agent-based model to investigate the relationship between resource availability and predation risk versus animal group size. Using a single attraction parameter as a measure for predation risk and a single repulsion parameter as a measure for resource scarcity, we found that the mean relative group size increased with predation risk and resource availability, after having scaled the parameters for animal density. The standard deviation of relative group size behaved the same, but was noticeably larger for a smaller total number of animals and displayed a quicker increase for lower values of predation risk. As a result, the coefficient of variation of group size was highest for intermediate values of predation risk and depended on both the predation/resources trade-off and animal density. Overall, the coefficient of variation of group size generally lied between 50 and 150% in our simulations.

Our results show that mean animal group sizes increase with population density, predation risk and resource availability. Increased resource availability obviously allows for larger groups rather than causing it, as there is only a reason to cluster when there is a certain predation risk. Our results match well with empirical data, e.g., it has been shown that the mean group size increases with population density for fish (Niwa, 1998), with predation risk for birds (Sorato et al., 2012), resource availability for mammals (Sinclair, 1977), and all three factors for other taxa as well (Couzin & Krause, 2003; Krause & Ruxton, 2002). Furthermore, an increase in predation risk translated to an increased range of attraction in our model, while a decrease in resource availability translated to an increased range of repulsion. This approach of interaction ranges has been used directly in other modelling studies, which yielded comparable results to our study regarding the probability distributions of group size. For example, a decrease in the local interaction radius of modelled fish resulted in a smaller mean group size as well as a smaller spread of the group size distribution (Hoare et al., 2004).

The coefficient of variation of our modelled group sizes lies between 50 to 150% in homogeneous and deterministic scenarios, where the random initializations facilitated the observed variation. Given that there is such a large difference between the confidence limits of these group sizes, it is plausible that researchers who encounter such large differences in the field may actually interpret these as being caused by a difference in the predation/resources trade-off. There have for example been studies on ungulates (Thaker et al., 2010), rodents (Ebensperger & Wallem, 2002) and monkeys (Gillespie & Chapman, 2001) that have reported effects of a predation/resources trade-off on group sizes, while the variation in all group sizes was close to our reported variance here. This is potentially problematic, as the reported group sizes may thus have actually come from a single distribution (viz., with equal predation risk and resource availability).

Group compactness is a more direct proxy for grouping tendency than group size in situations where group formation is driven by local interaction rules, given that the distance between individuals follows directly from the interaction rules and group size is an emergent property of this self-organizing process (Couzin & Krause, 2003). For example, it has been shown that fish groups become more compact with increased predation risk (Herbert-Read et al., 2017). Furthermore, group compactness seemed to be more important than group size in the preference of certain fish species (Frommen et al., 2009), and group compactness also seemed more important than group size in the reduction of predation risk through a “confusion effect” (Scott-Samuel et al., 2015). However, group compactness has generally been used far less in the literature than group size to gauge the predation/resources trade-off, especially for terrestrial animals (Fryxell et al., 2007; Isbell, 1991; Sinclair, 1977; Sorato et al., 2012; Thaker et al., 2010). This is of course not surprising, given that it is easier to measure group size than group compactness, as compactness must preferably be monitored over a longer period of time and often requires equipment like cameras and tracking software while a single count suffices for group size. However, given the large inherent variability in group size given the same predation/resources trade-off, the usefulness and reliability of group compactness as a field proxy for this trade-off should be investigated for multiple species and study areas.

In this study we focused on purpose solely on the inherent variability of group sizes that result from a deterministic and homogeneous self-organizing group formation process, thereby leaving out other processes. Extra complexity in more realistic models can further amplify the variation in group sizes that we found (e.g., through local environmental heterogeneity or animal movement being dependent on more factors) or dampen it (e.g., forward persistence in movement that could lead to fission and fusion dynamics, which potentially leads to group sizes that become more ‘averaged out’ over time). It would therefore be recommendable for future research to also investigate the relative importance regarding the variability in group sizes of environmental heterogeneity and animal behaviour complexity in interaction with this simple group formation process.

4.5 Conclusion

We demonstrate self-organizing animal group formation with an attraction-repulsion agent-based model, for which the group sizes increase with predation risk, resource availability and population density. Even though this process is deterministic and homogeneous, the group sizes have a coefficient of variation between 50 and 150% depending on the aforementioned parameters. Such large variations in a single process are problematic when group sizes in the field are gauged on having resulted from differences in the predation/resources trade-off. We therefore urge researcher to investigate the usefulness and reliability of group compactness as a more direct proxy for the predation/resources trade-off.

4.6 Methods

4.6.1 Agent-based Model

Our agent-based model is composed of l individuals of which each individual experiences attraction $\overrightarrow{f_j^a}$ and repulsion $\overrightarrow{f_j^r}$ forces to all other conspecifics j based on their distance x_j. For each point in time these forces sum up to one vector per individual $\overrightarrow{f^n}$, which determines the movement of that individual at that point in time.

$$\overrightarrow{f^n}(x_j) = \sum_{j=1}^{l-1} \overrightarrow{f_j^n}(x_j)$$

$$\overrightarrow{f_j^n}(x_j) = \overrightarrow{f_j^a}(x_j) - \overrightarrow{f_j^r}(x_j)$$

$$\overrightarrow{f_j^a}(x_j) = \alpha\beta x_j e^{-\beta x_j}$$

$$\overrightarrow{f_j^r}(x_j) = \gamma e^{-\delta x_j}$$

$\overrightarrow{f^n} \in (-\infty, \infty)$, movement vector

$\overrightarrow{f_j^n} \in (-\infty, \infty)$, net attraction to conspecific j of l individuals

$\overrightarrow{f_j^a} \in (-\infty, \infty)$, gross attraction to conspecific j of l individuals

$\overrightarrow{f_j^r} \in (-\infty, \infty)$, repulsion from conspecific j of l individuals

$x_j \in [0, \infty)$, distance from conspecific j of l individuals

$\alpha \in (0, \infty)$, attraction height parameter

$\beta \in (0, \infty)$, attraction rate parameter

$\gamma \in (0, \infty)$, repulsion height parameter

$\delta \in (0, \infty)$, repulsion rate parameter

4.6.2 Nondimensionalization

Given that our model is not specifically designed for a certain animal species, the absolute values of x_j and $\overrightarrow{f^n}$ have no inherent meaning. Therefore, both dimensions of the net attraction function $\overrightarrow{f_j^n}$ can be scaled to relative dimensions. This results in a simpler scaled net attraction function $\tilde{f}_j^n$ with two instead of four parameters.

$$\overrightarrow{f_j^n}(x_j) = \alpha\beta x_j e^{-\beta x_j} - \gamma e^{-\delta x_j}$$

$$\tilde{f}_j^n(\tilde{x}_j) = \frac{\alpha\beta x_c \tilde{x}_j e^{-\beta x_c \tilde{x}_j} - \gamma e^{-\delta x_c \tilde{x}_j}}{w_c^n} \Leftarrow \tilde{f}_j^n = \frac{\overrightarrow{f_j^n}}{w_c^n}, \tilde{x}_j = \frac{x_j}{x_c}$$

$$w_c^n = \gamma, x_c = \beta^{-1} \Rightarrow \tilde{f}_j^n\left(\tilde{x}_j\right) = \frac{\alpha}{\gamma}\tilde{x}_j e^{-\tilde{x}_j} - e^{-\frac{\delta}{\beta}\tilde{x}_j}$$

$$\tilde{f}_j^n\left(\tilde{x}_j\right) = a\tilde{x}_j e^{-\tilde{x}_j} - e^{-\frac{\tilde{x}_j}{r}} \Leftarrow a = \frac{\alpha}{\gamma}, r = \frac{\beta}{\delta}$$

$\tilde{f}_j^n \in [-1, \infty)$, scaled net attraction to conspecific j

$\tilde{x}_j \in [0, \infty)$, scaled distance from conspecific j

$a \in (0, \infty)$, scaled attraction parameter

$r \in (0, \infty)$, scaled repulsion parameter

4.6.3 Intersections

The intersections between the attraction and repulsion functions, i.e., when $\tilde{f}_j^n = 0$, determine at which distances to a conspecific an individual remains stationary in the absence of other conspecifics. With multiple conspecifics, these intersections will determine the distances between conspecifics within the same group and the distances between groups. Note that the solution is a Lambert's W function, which can have zero, one or two solutions (Figure 4.6).

$$\tilde{f}_j^n\left(\tilde{x}_j\right) = 0$$

$$a\tilde{x}_j e^{-\tilde{x}_j} - e^{-\frac{\tilde{x}_j}{r}} = 0$$

$$a\tilde{x}_j e^{-\tilde{x}_j} - e^{\left(1-\frac{1}{r}\right)\tilde{x}_j} e^{-\tilde{x}_j} = 0$$

$$e^{-\tilde{x}_j}\left(a\tilde{x}_j - e^{\left(1-\frac{1}{r}\right)\tilde{x}_j}\right) = 0$$

$$e^{-\tilde{x}_j} = 0, a\tilde{x}_j - e^{\left(1-\frac{1}{r}\right)\tilde{x}_j} = 0$$

$$\tilde{x}_j \notin \mathbb{R}, e^{\left(1-\frac{1}{r}\right)\tilde{x}_j} = a\tilde{x}_j$$

$$\frac{e^{\left(1-\frac{1}{r}\right)\tilde{x}_j}}{\tilde{x}_j} = a$$

$$\tilde{x}_j e^{\left(\frac{1}{r}-1\right)\tilde{x}_j} = a^{-1}$$

$$r = 1 \Rightarrow \tilde{x}_j = a^{-1}$$

$$e^u \frac{u}{\frac{1}{r}-1} = a^{-1} \Leftarrow u = \left(\frac{1}{r}-1\right)\tilde{x}_j$$

$$e^u u = \frac{\frac{1}{r}-1}{a}$$

$$u = W\left(\frac{1-r}{ar}\right)$$

$$r \neq 1 \Rightarrow \tilde{x}_j = -\frac{rW\left(\frac{1-r}{ar}\right)}{r-1}$$

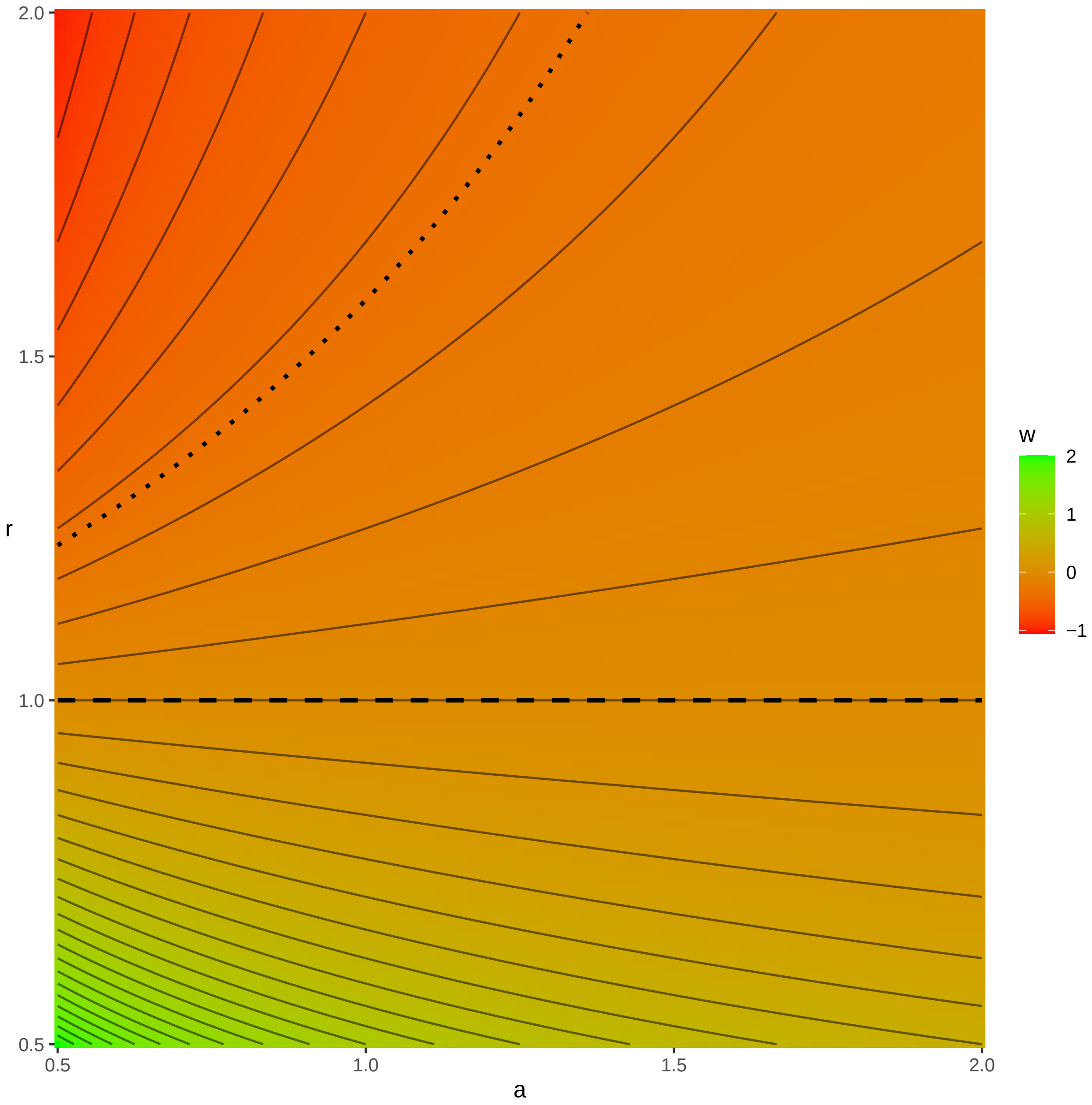


Figure 4.6: $w\left(a, r\right) = \frac{1-r}{ar}$, the input value of Lambert's W function for intersections. w higher than 0 (dashed line) gives 1 intersection, w between 0 and $-e^{-1}$ (dotted line) gives 2 intersections, and w lower than $-e^{-1}$ gives 0 intersections.

4.6.4 Peaks

Following the same equation solving techniques as for the intersections, the peaks of $\tilde{f}_j^n$ can also be derived.

$$\frac{d\tilde{f}_j^n}{d\tilde{x}_j} = 0$$

$$\frac{e^{-\frac{\tilde{x}_j}{r}}}{r} - ae^{-\tilde{x}_j}\left(\tilde{x}_j - 1\right) = 0$$

$$r = 1 \Rightarrow \tilde{x}_j = a^{-1} + 1$$

$$r \neq 1 \Rightarrow \tilde{x}_j = 1 - \frac{rW\left(-\frac{e^{1-\frac{1}{r}}(r-1)}{ar^2}\right)}{r-1}$$

4.6.5 Simulations

We simulated l individuals 100 times with random initial locations inside a d dimensional torus of size s with scaled attraction a and scaled repulsion r. We used a torus to prevent edge effects of the simulation area and chose the size of the torus to be an order of magnitude larger than the effective interaction range of the individuals to limit the effects of the torus on the movement process. We simulated our model using Euler integration with a custom-build adaptive step size routine until all movements converged. We performed these simulations for all combinations of:

$$l \in \{50, 100, 200\}$$

$$d \in \{1, 2, 3\}$$

$$s \in 2^{3-d}\{100, 200, 400\}$$

$$a \in \left\{\tfrac{l}{4}\right\}_{l=1}^{8}$$

$$r \in \left\{\tfrac{l}{4}\right\}_{l=1}^{8}$$

Given that in a d-dimensional torus there are 2^d straight paths between two points, we computed at each time step in the simulations the sum of all $2^d\left(l-1\right)$ scaled net attraction vectors $\tilde{f}_j^n\left(\tilde{x}_j\right)$ over toroidal distances $\tilde{x}_j$ per individual j.

4.6.6 Clustering

Unfortunately it proved to be too error-sensitive to directly determine the number of clusters and their sizes for each converged simulation. Therefore we computed for each simulation the minimum toroidal Euclidian distance matrix M and averaged it out element-wise for the 100 iterations of each parameter combination of the simulation. Finally, we transformed M to $\tilde{M}$ so that it quantifies the deviation from the expected distance to the kth neighbour under complete spatial randomness, by:

1. Sorting the rows per column in ascending order.

2. Sorting the columns per row in ascending order, to retrieve a matrix of columns with ascending distances to the kth neighbour.
3. Removing all columns larger than

$$(l-1)\,\frac{\psi\left(\frac{s}{2}\right)^d}{s^d} = (l-1)\,\frac{\psi}{2^d},$$

where ψ is the volume of a d dimensional ball with unit size

$$\psi = \frac{\pi^{\frac{d}{2}}}{\Gamma\left(\frac{d}{2}+1\right)},$$

to include only the k neighbours that with complete spatial randomness are inside a d dimensional ball of diameter s within a d dimensional cube of size s.

4. Scaling every column by the expected average distance to the kth neighbour under complete spatial randomness (Bhattacharyya & Chakrabarti, 2008)

$$\frac{\left(\Gamma\left(\frac{d}{2}+1\right)\right)^{\frac{1}{d}}}{\sqrt{\pi}}\,\frac{\Gamma\left(k+\frac{1}{d}\right)}{\Gamma(k)}\,\frac{\Gamma(l)}{\Gamma\left(l+\frac{1}{d}\right)}s = \left(\frac{1}{\psi}\right)^{\frac{1}{d}}\frac{\Gamma\left(k+\frac{1}{d}\right)}{\Gamma(k)}\,\frac{\Gamma(l)}{\Gamma\left(l+\frac{1}{d}\right)}s,$$

which (given that l is rather large) can be reduced with Stirling's approximation to

$$\left(\frac{1}{\psi}\right)^{\frac{1}{d}}\frac{\Gamma\left(k+\frac{1}{d}\right)}{\Gamma(k)}\left(\frac{1}{l}\right)^{\frac{1}{d}}s,$$

which can be approximated for large values of k with

$$\left(\frac{1}{\psi}\right)^{\frac{1}{d}}k^{\frac{1}{d}}\left(\frac{1}{l}\right)^{\frac{1}{d}}s = s\left(\frac{k}{\psi l}\right)^{\frac{1}{d}}.$$

4.6.7 Point Process Model

From $\tilde{M}$ the number of clusters with a certain size were derived by identifying the matrix cells with a substantially lower value than 1 (see Figure 4.3, bottom row). After having identified these cells with a lower value, the probability distribution of each individual being in a cluster of a certain size could easily be determined. To verify that this procedure matched the actual group size distribution, we computed $\tilde{M}$ for a custom-build Point Process Model with known group sizes and (based on the known group sizes) marked the matrix cells that signified distances within a cluster (Figure 4.7). We performed this procedure with Point Process Models using all combinations of the following parameters:

1. Mean $\mu\left(\tilde{N}\right)$ of the Beta distribution of the number of clusters N, where $N = \left[1+\tilde{N}(l-1)\right], \in \{0.5, 0.7, 0.9\}$

2. Standard deviation $\sigma\left(\tilde{N}\right)$ of the Beta distribution of N relative to the maximum possible standard deviation $(\mu(1-\mu))$, $\in \{0.5, 0.7, 0.9\}$
3. Concentration $\lambda(\tilde{\kappa})$ of the symmetric Dirichlet distribution of the number of individuals κ per cluster (with the number of categories of the distribution being fixed at N), where $\kappa = [\tilde{\kappa} l]$, $\in \{1, 10, 100\}$
4. Repulsion coefficient ω of the clusters as a function of cluster size κ, where the location of all cluster centres g are simulated in a single ABM using $\tilde{f}_g^n(\tilde{x}_g) = -\tilde{x}_g - (\omega(\kappa_g - 1) - \epsilon)\sqrt{d\left(\frac{s}{2}\right)^2}$, with $\epsilon = \min_{\kappa_g=1}^{l}(\omega(\kappa_g - 1)) - 1$, $\in \{-2, 0, 2\}$
5. Inter-individual distance θ within each cluster, simulated with a separate ABM for each cluster using $\tilde{f}_m^n(\tilde{x}_m) = \frac{1}{1+e^{-\frac{5}{\theta}(\tilde{x}_m - \theta)}} - \frac{1}{2}$, $\in \{0.5, 1, 2\}$
6. Number of individuals l, $\in \{50, 100, 200\}$
7. Number of dimensions d, $\in \{1, 2, 3\}$
8. Torus size s, $\in 2^{3-d}\{100, 200, 400\}$

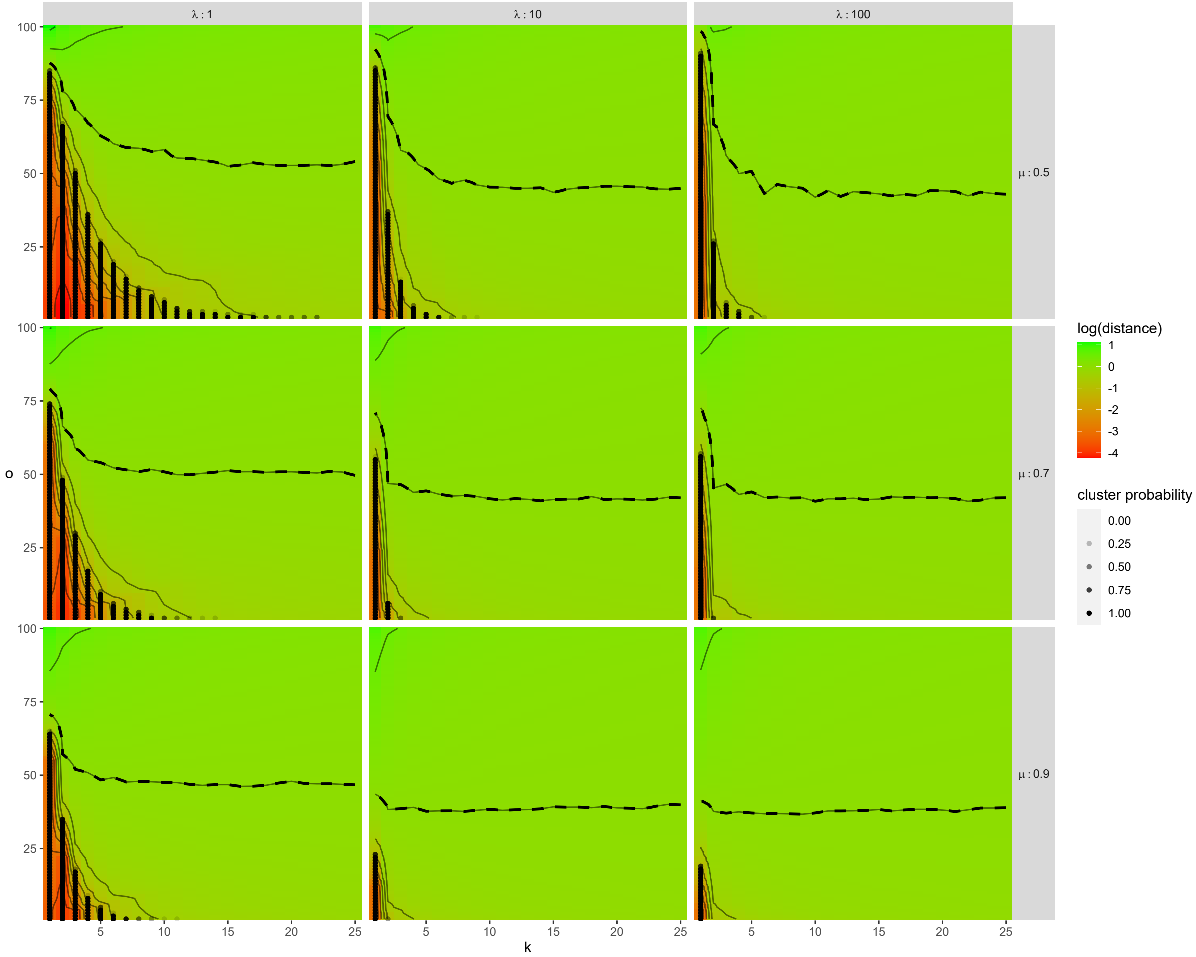


Figure 4.7: Average transformed distance matrices $\tilde{M}$ of the converged states of all 100 Point Process Model initializations, with the kth neighbour (until the 25th) on the x-axis, the ascending order o of distances on the y-axis, all values of group size concentration λ in the top panels and all values of mean number of clusters μ in the side panels. All other parameters of the model are set at the median value for this figure. The black dots signify the distances that are known to be from within a cluster, which matches accurately with the low values of $\tilde{M}$.

Chapter 5

Inferring an animal's environment through biologging: quantifying the environmental influence on animal movement

This chapter is based on:

Eikelboom, J. A. J., de Knegt, H. J., Klaver, M., van Langevelde, F., van der Wal, T., & Prins, H. H. T. (2020). Inferring an animal's environment through biologging: quantifying the environmental influence on animal movement. *Movement Ecology*, *8*(1), 40. https://doi.org/10.1186/s40462-020-00228-4

Abstract

Animals respond to environmental variation by changing their movement in a multifaceted way. Recent advancements in biologging increasingly allow for detailed measurements of the multifaceted nature of movement, from descriptors of animal movement trajectories (e.g., using GPS) to descriptors of body part movements (e.g., using tri-axial accelerometers). Because this multivariate richness of movement data complicates inference on the environmental influence on animal movement, studies generally use simplified movement descriptors in statistical analyses. However, doing so limits the inference on the environmental influence on movement, as this requires that the multivariate richness of movement data can be fully considered in an analysis. We propose a data-driven analytic framework, based on existing methods, to quantify the environmental influence on animal movement that can accommodate the multifaceted nature of animal movement. Instead of fitting a simplified movement descriptor to a suite of environmental variables, our proposed framework centres on predicting an environmental variable from the full set of multivariate movement data. The measure of fit of this prediction is taken to be the metric that quantifies how much of the environmental variation relates to the multivariate variation in animal movement. We demonstrate the usefulness of this framework through a case study about the influence of grass availability and time since milking on cow movements using machine learning algorithms. We show that on a one-hour timescale 37% of the variation in grass availability and 33% of time since milking influenced cow movements. Grass availability mostly influenced the cows' neck movement during grazing, while time since milking mostly influenced the movement through the landscape and the shared variation of accelerometer and GPS data (e.g., activity patterns). Furthermore, this framework proved to be insensitive to spurious correlations between environmental variables in quantifying the influence on animal movement. Not only is our proposed framework well-suited to study the environmental influence on animal movement; we argue that it can also be applied in any field that uses multivariate biologging data, e.g., animal physiology, to study the relationships between animals and their environment.

5.1 Background

Analysing animal movement is fundamental to ecology, because movement is arguably the most important way for animals to respond to their environment (Nathan et al., 2008). Quantifying the environmental influence on animal movement is therefore an important practice in ecology (Avgar et al., 2013; Signer & Ovaskainen, 2017). As animal movement is inherently multifaceted, with aspects related to the movement of the animal through the landscape and aspects related to the movement of body parts, the movement process cannot be described with simplified descriptors without loss of information. On the contrary, a plethora of emergent patterns can be identified through these multifaceted movement descriptors, e.g., activity types (such as walking, foraging or resting) and collective movement properties (Benaissa et al., 2017; Sumpter et al., 2018). Technological advancements in the field of biologging currently allow for data on animal movement to be acquired at finer temporal and spatial scales and in increasing volumes, e.g., data on animal movement speed, movement path tortuosity, tri-axial acceleration of body parts, and heart rate patterns can now relatively easily be acquired (Cooke et al., 2004; McClintock et al., 2017; Wilmers et al., 2015). These technological advancements provide opportunities to increase ecological understanding by analysing the full multivariate complexity of animal movement (McClintock et al., 2017; Wilmers et al., 2015). This multivariate complexity of movement is not fully used in recent studies to infer the environmental influence on animal movement. Instead, quantifying the environmental influence on animal movement is currently often done through relating simplified movement descriptors, e.g., animal distributions, net displacements, diffusion rates, or distributions of step lengths and turning angles, to a suite of environmental variables, e.g., through canonical analyses, linear mixed models, semivariance approaches, diffusion approximations, step-selection functions, hidden Markov models, or state-space models (Avgar et al., 2013; Patterson et al., 2009; Patterson et al., 2008; Peres-Neto et al., 2006; Signer & Ovaskainen, 2017; Thurfjell et al., 2014; Turchin, 1998). Many of these approaches were not designed specifically for animal movement data, but are approaches that function generally well in quantifying the relationship of independent variables with one or several dependent variables. Although the simplification of movement descriptors prior to analyses is a useful practice to acquire ecological understanding, it almost necessarily leads to a reduction in the quantified environmental influence on multivariate animal movement as this influence may not become fully apparent in the simplified movement descriptors. Even more so considering that there are often multiple behavioural phenotypes that individuals of the same species can produce in a given set of environments (Dingemanse et al., 2010), which can also be influenced by different internal states between individuals (Nathan et al., 2008). This consequently challenges the way that the analysis should be approached, as a multivariate analytic framework is required to quantify the overall influence of environmental variables on fine-scale multivariate animal movement data.

Data-driven machine learning methods provide a toolset to be able to model multivariate animal movement data and have been adopted by many animal ecologists over the past years (Hughey et al., 2018; Wang, 2019). These machine learning methods have been used to automatically detect and classify animal species in images (Eikelboom et al., 2019), to track moving animals in videos (Risse et al., 2017), to follow animal body postures and track body parts in videos (Hughey et al., 2018), to flag when animals become sick using animal-mounted biologging sensors and videos (Van Hertem et al., 2014), and to classify animal activities from biologging sensors (Wang, 2019). Although machine learning has proven to be useful for movement ecology, it is often only used as a tool to transform raw data (e.g., images, videos, accelerometer readings) into informative data (e.g., species labels, animal locations, animal activity labels) (Hughey et al., 2018; Wang, 2019). After these informative data have been generated, ecologists often use more traditional statistical methods to relate these data to environmental variables (Avgar et al., 2013; Signer & Ovaskainen, 2017; Wilmers et al., 2015). Machine learning has certainly generated ecological understanding via this way, but we posit that machine learning can also be used to acquire ecological understanding by directly relating animal movement data to environmental variables.

Here we propose a machine learning-based analytic framework, based on existing methods, to quantify the overall influence of an environmental variable on multivariate animal movement. After introducing the general framework, we demonstrate the usefulness of this framework with a case study about the influence of grass availability, time since milking, and wind speed on cow movements. Apart from quantifying the degree of coupling between the environment and cow movements, this case study shows that applying this framework can yield ecological insights. Finally, we discuss possible usages and constraints of this analytic framework. We contend that this framework contributes to the toolbox of ecologists studying the relationship between the environment and animal movement, behaviour, and physiology.

5.2 Methods

Our analytic framework quantifies the influence of an environmental variable on animal movement by utilizing the multivariate richness of movement data. Instead of building a model to predict a simplified animal movement descriptor from a set of environmental predictors, i.e., the route of causal inference, we turn this around and build a model to predict an environmental variable from a large number of animal movement variables. By using animal movement variables, the model of this framework predicts a perceived environmental variable by the animal (Cooke et al., 2004; Manning et al., 2004). Although predicting an environmental variable from movement data is the goal of the model, it is an intermediate step of the framework in order to quantify environmental influence on animal movement. In this framework it is key to use as many informative movement variables as possible, which could be meaningful human-constructed ecological (e.g., variables related to multiple classified animal activities), mathematical and/or physical variables, or abstract variables from an automated (deep learning) feature extraction algorithm. When effort is made to extract as many informative variables as possible from the animal movement data, chances are maximized that most of the variation of the environmental variable under scrutiny that is present in the data is captured. Furthermore, instead of creating the model as the end product during the analysis, the environmental variable should be predicted on a separate test dataset as the final step of the analysis. This follows from a data-driven and machine learning philosophy, in which complex multivariate models can be built that are not overfitted and therefore generalize better to new datasets. When distinguishing the train and test dataset, the test set used in the prediction of the environmental variable needs to be from a different temporal range than the train set that is used in the model building phase, due to autocorrelation in animal movement data that can otherwise cause the model to overfit (Arlot & Celisse, 2010). The range of values in the test set of environmental variables (whether or not these are under scrutiny) should be comparable to the range of values in the train set, to prevent incorrect extrapolation. After generating model predictions on the test set, the coefficient of determination (R^2) quantifies the fit of this predicted environmental variable from animal movement data to the measured environmental variable on a known scale and can thus be considered a metric on how much of the variation in the environmental variable influenced animal movement in a multivariate fashion (Figure 5.8) (Nakagawa & Schielzeth, 2013). The measure of fit of the null model (i.e., no environmental influence) should be chosen depending on the algorithm that is used, which is $R^2 = 0$ for algorithms that are able to always predict the mean of the response variable (e.g., Support Vector Regression and Random Forest Regression), even when the input variables are white noise. The measure of fit of this null model will then form the baseline value for which there is a 0% environmental influence and an R^2 of 1 can always be interpreted as 100% environmental influence. Of course R^2 should only be used as the measure of fit when modelling a continuous environmental response variable. With a discrete environmental variable, a classification approach should be undertaken, which is outside the scope of this study. However, to compare the influence of different environmental variables with each other fairly, the same measure of fit should be used.

In order to demonstrate the usefulness of the proposed analytic framework, we applied this framework to a case study about the influence of resource availability (here grass biomass), time since milking, and wind speed on the movement of eight dairy cows in a pasture (Figure 5.1). When animals are facing resource depletion, movement characteristics (through the landscape and of body parts), and emergent patterns like group (herd) characteristics, and time allocated to specific activities (e.g., foraging) often change, because animals need to invest more time and/or energy in searching for and acquiring resources (De Knegt et al., 2007; Emlen, 1966). Cows in a pasture are a good model for such a case study, because this provides a relatively homogenous foraging arena. Time since milking is another variable that could substantially influence the movement of dairy cows, because it has been shown that the lactation stage of cows (a variable that is intuitively linked to time since milking regarding its effect on cow behaviour) influences the relative distribution of their activity patterns (Bewley et al., 2010; Nielsen et al., 2000). Wind speed provided a good test case for our framework, because it was moderately correlated ($r = 0.37$) with grass biomass. We expected this correlation to be spurious and the effect of wind speed on cow movement to be negligible, because conditions were mild during the experiment (0-9 m/s).

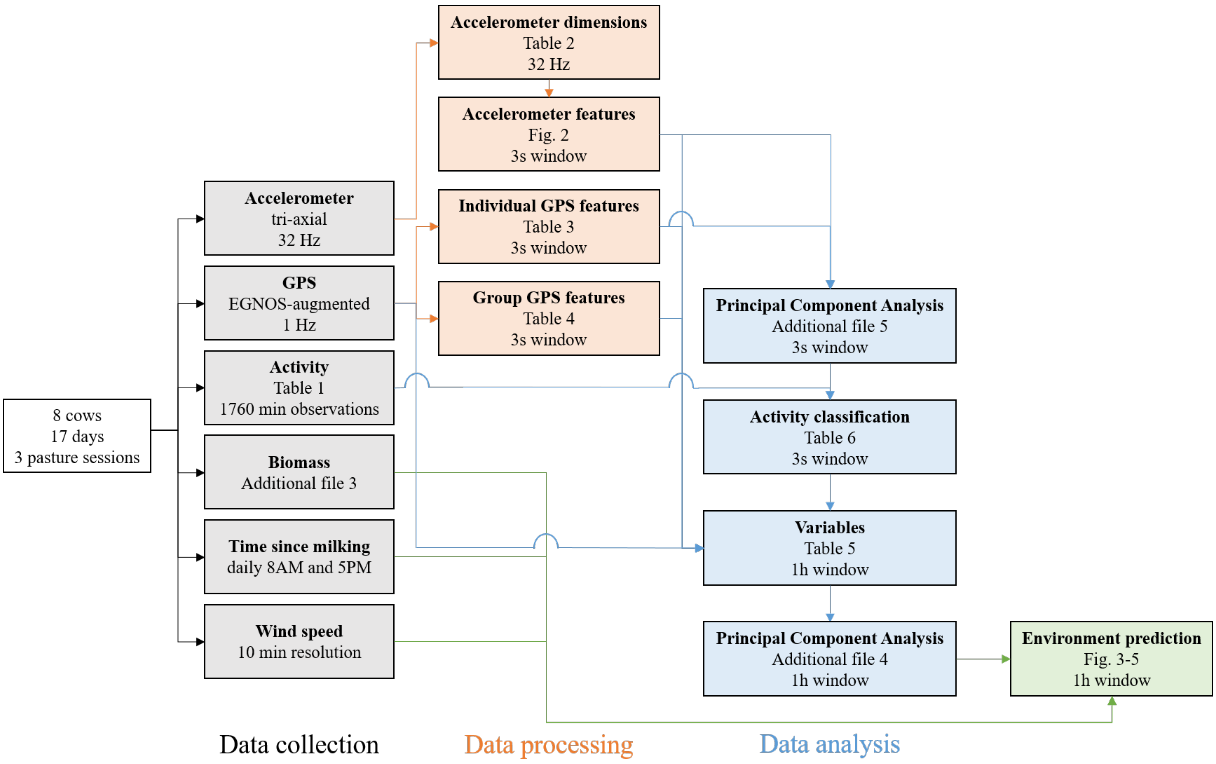


Figure 5.1: Flow chart of the summarized methodological approach for the case study.

The exact methodological approach that we describe for this case study is one possible implementation of our proposed analytical framework (Figure 5.1). However, there are numerous possible implementations of this framework for other studies, which may be influenced by the problem statement, experimental setup, animal movement sensors, environmental data types, data quantity, etc. However, the property that all implementations should have in common is that the environmental influence on animal movement is quantified by predicting environmental variables from movement descriptors in a data-driven (viz., machine learning) approach, which uses the coefficient of determination as a measure to quantify this influence. This framework is fully based on existing machine learning methods that are already widely used in movement ecology (Hughey et al., 2018; Wang, 2019). For example, the classification of animal activities from biologging data are often performed in a similar way, where movement features are extracted from the data and linked to known (supervised) or unknown (unsupervised) output values via a data-driven algorithm (Benaissa et al., 2017; Martiskainen et al., 2009; Vázquez Diosdado et al., 2015; Wang, 2019). In this framework we apply the same principle, but in a different setting, to predict the environment from multivariate animal movement. Furthermore, the interpretation of the coefficient of determination is atypical as well, where this measure is often used in movement ecology as solely a measure of model fit without an ecological meaning.

5.2.1 Data collection

For this case study eight adult female Holstein-Friesian dairy cows were kept in controlled pastures that were small enough so that foraging lead to resource depletion over the course of several days. The experiment ran from 25 April until 11 May 2017. During the experiment, the cows' movements were recorded continuously with e-Track neck collars (Noldus InnovationWorks, Wageningen, Netherlands), containing an EGNOS-augmented GPS receiver and a tri-axial accelerometer sensor. The cows were continuously kept on pasture at Carus animal facility in Wageningen, Netherlands (51°59'8" N, 5°39'11" E), and could move freely around as a single group during the experiment. Over the course of this period, we relocated the cows between three 0.32 ha pasture plots (sequentially five, six and six consecutive days in each plot). At every pasture switch the cows were housed inside the Carus facility for one night where they were offered fodder, so that they were not hungry at the start of a new pasture plot session. Furthermore, the cows were taken inside for milking and feeding every morning between 7:30 and 8:30 CEST and solely for milking every afternoon between 16:30 and 17:00 CEST. The time the cows spent on pasture was short enough to assume that the pasture did not increase in grass quality because of re-growth after grazing and only decreased in grass availability (Ferraro & Oesterheld, 2002). The short duration of the pasture sessions (approximately one day longer than when a commercial farmer would have moved the cows, as judged by the farm manager) ensured that the cows were not hungry, but only had to put more effort into foraging when time progressed. Furthermore, the collaring process did not put the cows under noticeable stress, more so because they were accustomed to continuously wearing a neck collar.

The sensors in the cows' neck collars recorded GPS and accelerometer data during the experiment. The data were stored with a millisecond-accurate timestamp on a local SD memory card, which was replaced every one to five days together with the battery. GPS data were stored on the SD card with a one second interval. The accelerometer data were sampled with a variable frequency of 25-500 Hz, which were later down-sampled and linearly interpolated to a constant 32 Hz signal. Both the GPS and the accelerometer did not record data during some hardcoded multi-hour periods of inactivity, which were variable in duration and time of day, to save battery power. However, the time between GPS fixes was exactly 1 second in more than 99% of the cases. The precision of the GPS fixes was high, with 98% of the fixes having a Horizontal Dilution of Precision (HDOP) of less than two (a dimensionless unit; two is considered "excellent" precision). All GPS fixes with an HDOP of more than five, which were 0.5% of all fixes, were considered to be untrustworthy and filtered out of the final dataset. We also tested the accelerometer data for precision by placing the sensor on a stable, non-moving surface while it recorded for several minutes. The fluctuations in the recorded signal of all three accelerometer axes were small, 0.06 m/s^2 between the lowest and highest value, and were considered negligible and thus ignored.

Activity (or behaviour) observations were conducted on work days from 25 April to 9 May 2017. A single person visually classified the activities using focal-animal sampling with a pre-defined ethogram (Table 5.1). All activity types in the ethogram (grazing, walking, standing, standing while ruminating, lying, lying while ruminating) were mutually exclusive. Each individual cow was observed continuously for ten minutes in the morning (10:00-13:00 CEST) and ten minutes in the afternoon (13:00-17:00 CEST), in random order, resulting in a total observation time of 1760 minutes. During the observations, the start and end times of each displayed activity type from the ethogram were recorded. We conducted these observations to acquire annotations for an activity classification model. Representative acceleration plots of the three axes for the different activity types are provided (Figure 5.9).

Table 5.1: Ethogram. Descriptions of the recorded, mutually exclusive activity types.

Activity	**Description**
Grazing	Foraging behaviour by chewing grass from the pasture whilst standing still or slowly moving with the head down
Walking	Taking at least two steps without grazing, either with the head up or down
Standing without ruminating	Standing on all four legs with head erect, without swinging its head from side to side and without ruminating
Lying down without ruminating	All four legs tucked underneath the torso or lying down on one side of its body without ruminating
Ruminating while standing	Masticating regurgitated feed, swallowing masticated feed or regurgitating feed while standing with head erect
Ruminating while lying down	Masticating regurgitated feed, swallowing masticated feed or regurgitating feed while lying down

We measured resource availability as dry matter grass biomass in kilograms per hectare, excluding stubble biomass. We determined time-varying biomass levels using a combination of field-measured biomass levels at specific time points, satellite-based biomass estimates derived from the Normalized Difference Vegetation Index (NDVI), and modelling of grass dynamics (see section 5.6). Wind speed (m/s, mean speed 10 m above ground) were recorded at 10 minute resolution during the experiments with a weather station on a grass pasture at the Veenkampen, Wageningen, Netherlands. This weather station is located one kilometre west of the pasture plots used for the experiments.

5.2.2 Data processing

We used the pre-processed 32 Hz, tri-axial accelerometer signal as input for the accelerometer feature extraction. First, we converted all the records in the three-dimensional accelerometer dataset to 21 dimensions using multiple geometric transformations, i.e., resultant vectors, angles, solid angles, volumes and areas (Table 5.2). These dimensions constitute all geometric transformations of angles and distances in one, two and three dimensions. Considering that tri-axial accelerometer readings describe the movement forces in three dimensions, geometric transformations make sense from a physics perspective. More transformations could be considered, but these may lack to provide additional information to the feature set. Second, we divided the resulting dataset into non-overlapping time windows. We tried all window sizes in the range of 1 until 30 seconds and optimized this window size as a hyperparameter regarding the activity classification performance, where 3 s turned out to be the optimal window size (Table 5.8). For every time window we computed multiple statistics per accelerometer dimension per cow, e.g., mean, standard deviation, quantiles and Fast Discrete Fourier Transform (FFT) parameters (Figure 5.2). These statistics were chosen to provide summary statistics about both the time-invariant and sequential aspects of the data, given that accelerometer data also includes patterns in the frequency domain regarding animal activity (e.g., head movement of cows during grazing has a strong cyclic behaviour). We computed the FFT with the base R 3.6.2 stats package (R Development Core Team, 2008), of which we used the maximum FFT value as the dominant amplitude, the corresponding period of the dominant amplitude as the dominant period, and finally the sum of all squared FFT values as the spectral energy. Our list of computed statistics is not all-encompassing and more statistics can be thought of to describe patterns in the data, but these statistics are similar to the ones that are often used in activity classification with accelerometers (Bao & Intille, 2004; Shoaib et al., 2015). Furthermore, as these statistics were mainly used in the activity classification part of the analysis, we deemed the computed statistics sufficient when it resulted in a high performance during activity classification. Overall, computing all statistics for each dimension resulted in 210 accelerometer features per time window per cow.

Table 5.2: Dimensions extracted from the accelerometer data.

Name	**Formula**	**Description**
x	x	raw accelerometer reading in the x axis
y	y	raw accelerometer reading in the y axis
z	z	raw accelerometer reading in the z axis
r_{xyz}	$\left\lVert\begin{matrix}x\\y\\z\end{matrix}\right\rVert$	magnitude of resultant vector
r_{xy}	$\left\lVert\begin{matrix}x\\y\end{matrix}\right\rVert$	magnitude of resultant vector in x,y plane
r_{xz}	$\left\lVert\begin{matrix}x\\z\end{matrix}\right\rVert$	magnitude of resultant vector in x,z plane
r_{yz}	$\left\lVert\begin{matrix}y\\z\end{matrix}\right\rVert$	magnitude of resultant vector in y,z plane
θ_{xy}	$\arctan\frac{y}{x}$	angle of resultant vector in x,y plane
θ_{xz}	$\arctan\frac{z}{x}$	angle of resultant vector in x,z plane
θ_{yz}	$\arctan\frac{z}{y}$	angle of resultant vector in y,z plane
θ_{z}	$\arctan\frac{z}{\left\lVert\begin{matrix}x\\y\end{matrix}\right\rVert}$	angle of resultant vector with x,y plane collapsed to 1 line

Table 5.2 continued from previous page

Name	Formula	Description
θ_y	$\arctan \frac{y}{\left\Vert \begin{matrix} x \\ z \end{matrix} \right\Vert}$	angle of resultant vector with x,z plane collapsed to 1 line
θ_x	$\arctan \frac{x}{\left\Vert \begin{matrix} y \\ z \end{matrix} \right\Vert}$	angle of resultant vector with y,z plane collapsed to 1 line
Ω_x	$\arcsin \frac{yz}{\left\Vert \begin{matrix} x \\ y \\ 0 \end{matrix} \right\Vert \left\Vert \begin{matrix} x \\ 0 \\ z \end{matrix} \right\Vert}$	solid angle of resultant pyramid base projected along x axis
Ω_y	$\arcsin \frac{xz}{\left\Vert \begin{matrix} x \\ y \\ 0 \end{matrix} \right\Vert \left\Vert \begin{matrix} 0 \\ y \\ z \end{matrix} \right\Vert}$	solid angle of resultant pyramid base projected along y axis
Ω_z	$\arcsin \frac{xy}{\left\Vert \begin{matrix} x \\ 0 \\ z \end{matrix} \right\Vert \left\Vert \begin{matrix} 0 \\ y \\ z \end{matrix} \right\Vert}$	solid angle of resultant pyramid base projected along z axis
V_{xyz}	xyz	volume of resultant cuboid
A_x	yz	area of resultant pyramid base projected along x axis
A_y	xz	area of resultant pyramid base projected along y axis
A_z	xy	area of resultant pyramid base projected along z axis
A_{xyz}	$\frac{1}{2} \left\Vert \begin{bmatrix} x \\ y \\ 0 \end{bmatrix} \times \begin{bmatrix} x \\ 0 \\ z \end{bmatrix} \right\Vert$	area of resultant triangle

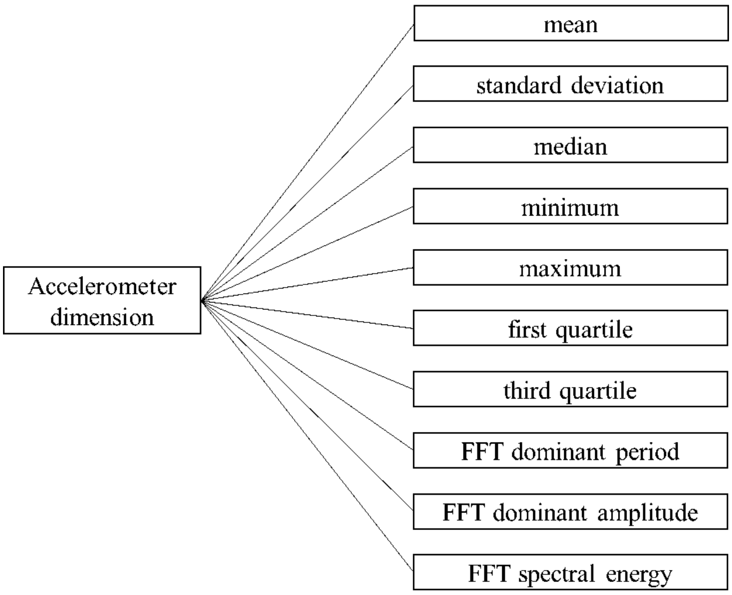


Figure 5.2: Statistics calculated per time window, cow and accelerometer dimension. FFT stands for Fast Fourier Transform.

We used the filtered 1 Hz GPS data as input for the GPS feature extraction. First, we transformed all the latitude, longitude coordinates to Cartesian coordinates by projecting them to zone 31N of the UTM system (EPSG 32631). Second, we extracted a number of individual GPS features from the projected GPS coordinates per time window per cow, related to speed, turning angle, tangential velocity, mean squared displacement, and first passage time (Table 5.3), which are widely used metrics for path-level analyses in movement ecology (Seidel et al., 2018). The time windows were exactly the same as the time windows used in the extraction of the accelerometer features. Third, we extracted a number of group GPS features from the projected GPS data per time window per cow, related to group shape, group area, and distances and directions to other cows (Table 5.4), which are low-level geometric metrics similar to those used for 2D point clouds in computational geometry (Weinmann et al., 2017). We determined which individual and group GPS features to compute by drawing fake GPS trajectories and animal clusters, after which we discussed which geometrical properties (e.g., tangential velocity: the linear speed of an animal moving along a circular path) could be extracted from these patterns. Furthermore, we computed ecological properties of animal trajectories that were known to us (e.g., Mean Squared Displacement: a measure of the deviation of the position of an animal with respect to a reference position over time) and searched the literature and animal movement related R packages for other ecological properties (e.g., First Passage Time: the time required for an animal to cross a circle with a given radius). We do not suggest that the provided list of computed features is all-encompassing, but we do suggest that spending time and effort in the engineering of features (or optimizing the architecture of a neural network in a deep learning approach) is an important part of our suggested framework. The more informative variation that is extracted from the raw data, the better the model could potentially perform and thus the better the quantified environmental influence on animal movement matches reality. Overall, computing both the individual and group GPS features resulted in 38 GPS features per time window per cow.

Table 5.3: Individual GPS features extracted per time window and cow.

Dimension	**Statistic**	**Description**
Distance	Net gross ratio	Distance between first and last position divided by sum of distances of all segments
Speed	Mean	-
	Standard deviation	-
	Median	-
	Minimum	-
	Maximum	-
	First quartile	-
	Third quartile	-
	Autocorrelation function index	Autocorrelation value at a lag of 1 second
	Brownian motion scaling parameter	See Equation 5.1
Turning angle	ρ	Length of the mean resultant vector
	Autocorrelation function index of the absolute turning angles	Autocorrelation value at a lag of 1 second
Absolute tangential velocity	Mean	-
	Standard deviation	-
	Median	-
	Minimum	-
	Maximum	-
	First quartile	-
	Third quartile	-
	Autocorrelation function index	Autocorrelation value at a lag of 1 second
Mean Squared Displacement	Diffusion coefficient	The value of a in the fitted model $\text{MSD} = a\tau^b$ on MSD values for τ from 1 to 6

Table 5.3 continued from previous page

Dimension	**Statistic**	**Description**
	Diffusion power coefficient	The value of b in the fitted model $\mathrm{MSD} = a\tau^b$ on MSD values for τ from 1 to 6
First Passage Time	Mean, 5m radius	-
	Variance of log, 5m radius	-
	Autocorrelation function index, 5m radius	Autocorrelation value at a lag of 1 second
	Radius with maximum variance of log (integers from 1 to 10m)	-
	Linear regression coefficient log radius vs. log mean FPT	-

$$B = \sqrt{\frac{\sum \frac{\begin{bmatrix} \left(\frac{\Delta x(t=1)}{\sqrt{\Delta t}} - \frac{\sum \frac{\Delta x}{\Delta t}}{n}\right) & \cdots & \left(\frac{\Delta x(t=n)}{\sqrt{\Delta t}} - \frac{\sum \frac{\Delta x}{\Delta t}}{n}\right) \\ \left(\frac{\Delta y(t=1)}{\sqrt{\Delta t}} - \frac{\sum \frac{\Delta y}{\Delta t}}{n}\right) & \cdots & \left(\frac{\Delta y(t=n)}{\sqrt{\Delta t}} - \frac{\sum \frac{\Delta y}{\Delta t}}{n}\right) \end{bmatrix} \begin{bmatrix} \left(\frac{\Delta x(t=1)}{\sqrt{\Delta t}} - \frac{\sum \frac{\Delta x}{\Delta t}}{n}\right) & \left(\frac{\Delta y(t=1)}{\sqrt{\Delta t}} - \frac{\sum \frac{\Delta y}{\Delta t}}{n}\right) \\ \vdots & \vdots \\ \left(\frac{\Delta x(t=n)}{\sqrt{\Delta t}} - \frac{\sum \frac{\Delta x}{\Delta t}}{n}\right) & \left(\frac{\Delta y(t=n)}{\sqrt{\Delta t}} - \frac{\sum \frac{\Delta y}{\Delta t}}{n}\right) \end{bmatrix}}{n} \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}}{2}} \tag{5.1}$$

In which B is the Brownian motion scaling parameter and n the number of records.

Table 5.4: Group GPS features extracted per time window and cow.

Dimension	**Statistic**	**Description**
Net distances to other cows	Mean	-
	Median	-
	Minimum	-
	# cows within 2m radius	-
	# cows within 4m radius	-
	# cows within 8m radius	-
	# cows within 16m radius	-

Table 5.4 continued from previous page

Dimension	Statistic	Description
All mean cow coordinates	Group elongation index, ϕ	Variance explained by the first principal component through the mean x and y coordinates of all cows. Value lies by definition between 0.5 (when completely non-elongated, e.g., an exact circle) and 1 (when all coordinates lie on a straight line). Afterwards scaled between 0 and 1, by subtracting 0.5 and multiplying by 2.
	Group area proxy	$\pi\sigma^2(1-\phi)$; where σ is the standard deviation of the first principal component values. This measure assumes that the area can be estimated by considering the group as an ellipse. When completely non-elongated the area is $\pi\sigma^2$ (where the variance σ^2 is a proxy for the extent of the direction of elongation) and when fully elongated the area is 0.
Directions to other cows	ρ	Length of the mean resultant vector
	Periphery index	Maximum difference between consecutive directions, minus $\frac{2\pi}{\#\text{cows}-1}$ and divided by 2π

5.2.3 Data analysis

We used the accelerometer features and individual GPS features per time window per cow for which activity observations were undertaken as input data for the activity classification models (Figure 5.2; Table 5.3), which we first converted to principal components. We linked the time-matched activity observations to these input data and used the activity type as output variable for the classification models. We trained a multi-class classification model for the activity types: grazing, walking, standing and lying down. As a second step after the main activity classification we also trained a binary classification model for ruminating, with an extra input variable that indicated standing versus lying down. We tried for both classification models a Support Vector Machine (SVM) with a Radial Basis Function (RBF) kernel and a one-against-one approach, implemented in the e1071 package for R 3.6.2 (Meyer et al., 2017; R Development Core Team, 2008), and a Random Forest (RF) with 500 trees, implemented in the randomForest package (Liaw & Wiener, 2002). To prevent overfitting due to autocorrelation in the data we randomly assigned each hour of the dataset into a train (80%) or test set (20%) and performed 5-fold cross-validation on the train set, which was also split per hour at each of the 5 cross-validation iterations (Arlot & Celisse, 2010). To find the optimal hyperparameters for the models (number of principal components and time window size for both SVM and RF; *cost*, *gamma* and class weights for SVM; and *mtry*, *sample size* and *node size* for RF), we used an extensive grid search on a High Performance Cluster of Wageningen University, Netherlands (Table 5.8). We started the grid search with a coarse resolution search that covered a large range of all hyperparameters, to make sure that the global optimum was covered and to get a feel for the performance landscape. We zoomed in with a finer resolution during a second grid search and finished with an even more zoomed in and finer resolution during a final grid search. We determined the optimal classification model and hyperparameters by selecting for the highest mean balanced accuracy during cross-validation (Equation 5.2). The classification models with the highest performance during cross-validation were then evaluated for performance on the test dataset. Finally, we used the models to predict the displayed activity type (grazing, walking, standing or lying down) and whether or not the cows were ruminating, for all the time windows and cows with available sensor data.

$$\text{mean balanced accuracy} = \frac{\sum_{x=1}^{n} \frac{1}{2}\left(\frac{TP_x}{P_x} + \frac{TN_x}{N_x}\right)}{n} \tag{5.2}$$

Where x is a class; n is the number of classes; TP is the number of true positives; P is the number of positives; TN is the number of true negatives; and N is the number of negatives.

We computed the dataset for the environmental variable predictions per cow over one-hour time windows. The window size that is chosen has of course an influence on the results, as the effect of an environmental variable on animal movement data varies with temporal scales (McClintock et al., 2014). In short, the window size that is chosen represents the scale at which the animals' behavioural decisions are made (McClintock et al., 2014). The choice of this temporal scale should therefore be chosen in line with the study's aim and based upon ecological considerations, which are different for every study. We chose a window size of one hour for a combination of two reasons: 1) it makes sense from an ecological point of view, as the considered environmental variables likely influence cow behaviour on this temporal scale, and 2) because it traded off the number of resulting data records (number of rows in the dataset after applying the one hour window) and the convergence of variables well; meaning that the resulting dataset consists of hundreds of records (thereby being enough for a data-driven machine learning approach) and each record was based on 1200 (one hour divided by 3 seconds) underlying records or more (thereby making sure that the inherent heterogeneity of animal movement is taken into account by averaging it out over a large enough period). The calculated variables consisted of multiple variable sets, based on the source of the data (GPS or accelerometer), organizational level (group or individual), transformation type, and variables conditional on foraging (Table 5.5). We did not consider variables conditional on other activity types than foraging, because the cows sometimes did not display one of the other activity types during a one hour time window. This resulted in a total of 548 variables per cow per one-hour time window. We standardized these variables (to zero mean and unit variance) per combination of day/night and cow ID to account for differences in nocturnal and diurnal activities of cows and individual differences in movement characteristics, group characteristics, and activities. These standardized variables were used as input for a principal component analysis, but were first one by one visually checked for symmetric unimodality by inspecting the histograms and normal Q-Q plots. Two of the 548 variables displayed signs of bimodality and eight variables appeared to be somewhat heavy-tailed. Due to the low number of variables that showed these deviations and due to the small severity of these deviations, we decided not to correct these ten variables and thus left all standardized variables untransformed. Moreover, symmetric unimodality is not an actual requirement of a principal component analysis, but it does result in a better centring and scaling of the principal components. After that we converted the standardized variables to principal components separately for the GPS and accelerometer variables and linked these principal components to the mean grass biomass, time since milking, and wind speed values per hour (Table 5.7; Figure 5.10; Figure 5.11). To prevent overfitting of the model due to autocorrelation of the time series, we trained the model on the data of all cows from two of the three pasture plot sessions (n = 600, viz., number of rows in the train set) and tested the model on the data of all cows from the other pasture plot session (n = 259, viz., number of rows in the test set). We used the second pasture plot session as our test set, because its range of biomass values fell within the range of biomass values of the first and third pasture plot session.

Table 5.5: Calculated variable sets per cow over one-hour time windows.

Variable set	Statistic	Transformed data
Individual GPS	All statistics from Table 5.3	1 Hz GPS data
Proportion activity	Proportion	Predicted activity per three-seconds window (Table 5.1)
Individual GPS distribution parameters while grazing	Mean and standard deviation of log-transformed data	Median speed and median absolute tangential velocity per three-seconds window while grazing (Table 5.3)
Median group GPS	Median	Group GPS features per three-seconds window (Table 5.4)
SD group GPS	Standard deviation	Group GPS features per three-seconds window (Table 5.4)

Table 5.5 continued from previous page

Variable set	Statistic	Transformed data
Median individual GPS while grazing	Median	Individual GPS features per three-seconds window while grazing (Table 5.3)
SD individual GPS while grazing	Standard deviation	Individual GPS features per three-seconds window while grazing (Table 5.3)
Median group GPS while grazing	Median	Group GPS features per three-seconds window while grazing (Table 5.4)
SD group GPS while grazing	Standard deviation	Group GPS features per three-seconds window while grazing (Table 5.4)
Median accelerometer while grazing	Median	Accelerometer features per three-seconds window while grazing (Figure 5.2)
SD accelerometer while grazing	Standard deviation	Accelerometer features per three-seconds window while grazing (Figure 5.2)

To predict the environmental variables we built a Support Vector Regression (SVR) model with a RBF kernel and a Random Forest Regression (RFR) with 1000 trees on the train set with both GPS and accelerometer principal components, with only GPS components, and with only accelerometer components. These models are time-invariant, as they assume independence between the data records, and are particularly well-suited to model complex interactions between a large number of variables. To find the optimal hyperparameters for the models (number of principal components for both SVR and RFR; and *cost*, *gamma* and *epsilon* for SVR), we used a grid search (following the same procedure as during the grid search of the activity classification) on a High Performance Cluster of Wageningen University, Netherlands (Table 5.7). We did not optimize any other RFR hyperparameter, because the performance improved barely compared to the default values during a trial analysis. We determined the optimal hyperparameters by selecting for the highest R^2 on the test set (Equation 5.3). Ideally, (cross-)validation is performed before a test set evaluation to prevent overfitting in hyperparameter space, but the limited quantity of data records in our case study prevented us from setting aside more data from the train set. However, we prevented overfitting in hyperparameter space by not optimizing the hyperparameters of the RFR and by limiting the amount of hyperparameter values that were tested for the SVR.

$$R^2 = 1 - \frac{\sum_i (y_i - f_i)^2}{\sum_i (y_i - \bar{y})^2} \tag{5.3}$$

Where y is the vector of actual values and f is the vector of predicted values.

5.3 Results

The general cline of grass biomass is predicted by both models, but the steepness is not entirely captured (Figure 5.3). The time since milking cline is quite accurately matched from 0.5 to 6.5 hours, but after 6.5 hours it levels off for both models (Figure 5.3). For wind speed both models were not able to make accurate predictions (Figure 5.3). Overall the SVR models outperformed RFR in predicting the environmental variables from cow movement data (Table 5.7). When analysing the explained variation of the models with only accelerometer or GPS datasets, the qualitative differences between the explained variation of the different response variables for both algorithms are comparable (Figure 5.4). However, SVRs are apparently better capable of using the interaction between variables in the mixed-sensor dataset to increase the explained variation, while RFRs are hardly able to do so with our data (Figure 5.4; Figure 5.5). Both models indicate that grass biomass influences accelerometer data substantially more than GPS data, while the reverse is true for time since milking (Figure 5.4; Figure 5.5). Furthermore, for time since milking the explained variation by accelerometer data is largely shared with GPS data (Figure 5.5). Finally, the optimization of the hyperparameters was also done on datasets of each cow separately, which resulted into approximately the same hyperparameters and performance when compared to the model for all cows combined. Therefore, we concluded that cows responded to changes in resource availability and time since milking in approximately the same manner and we thus decided to use the models for all cows combined.

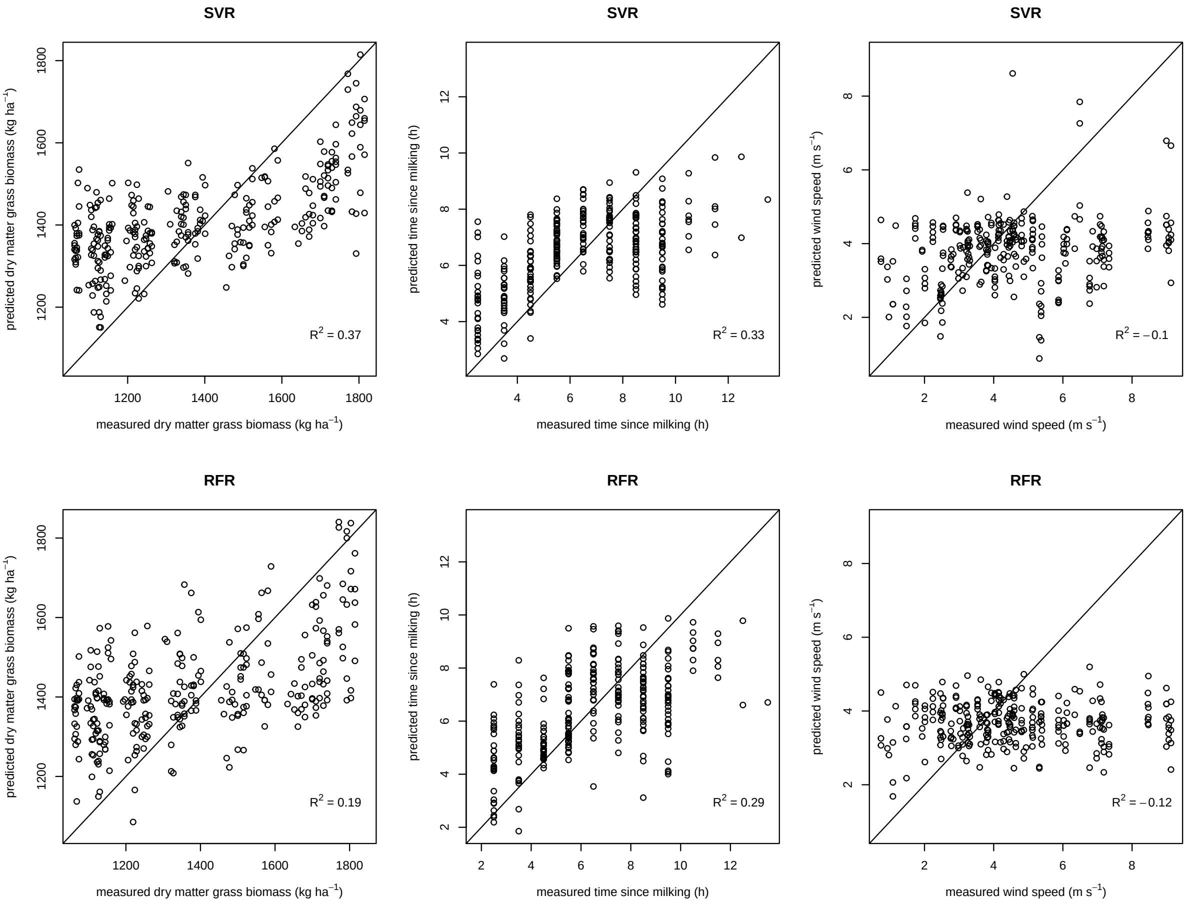


Figure 5.3: Left to right: measured versus predicted grass biomass, time since milking and wind speed using GPS and accelerometer data. Top: Support Vector Regression predictions. Bottom: Random Forest Regression predictions.

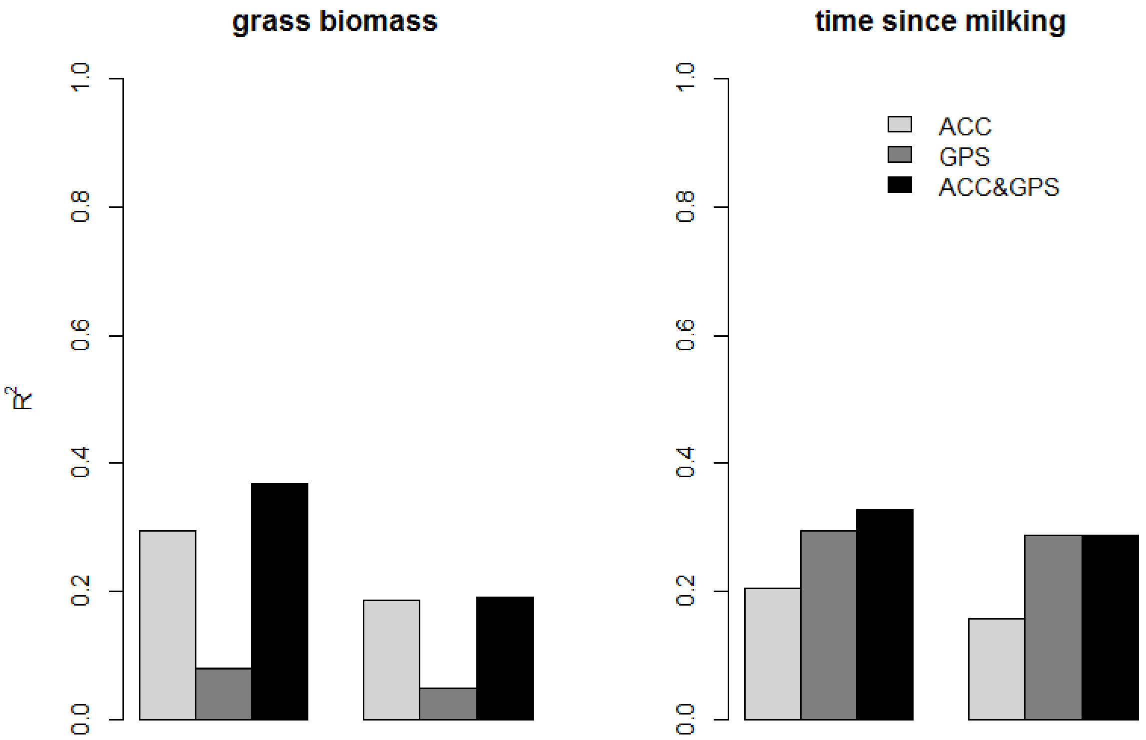


Figure 5.4: Explained grass biomass and time since milking variation using Support Vector Regression models (SVR) and Random Forest Regression Models (RFR) with a GPS, accelerometer (ACC) and combined dataset.

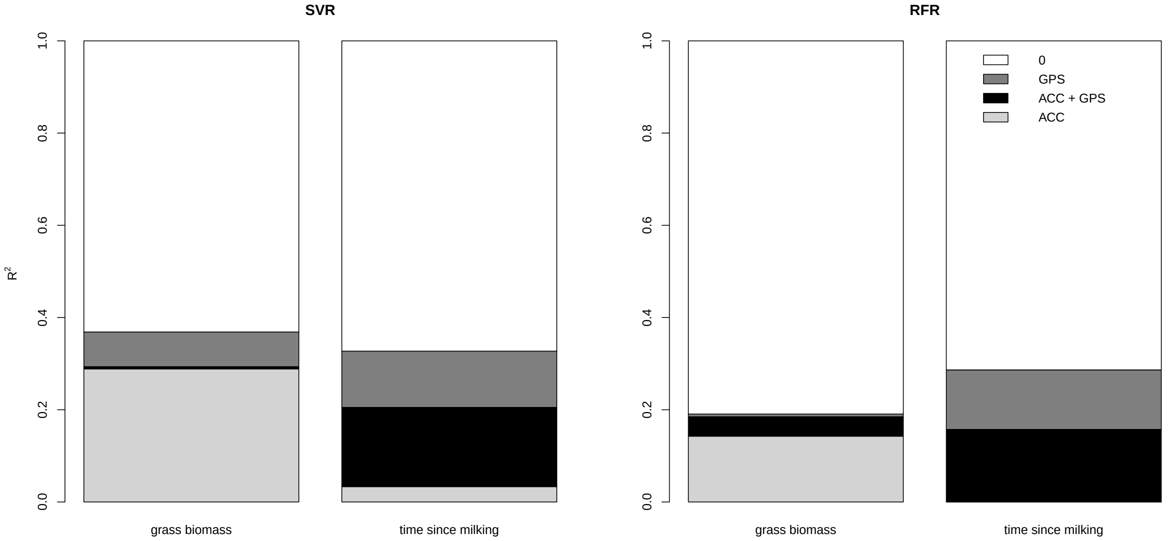


Figure 5.5: Variation partitioning of accelerometer (ACC) and GPS data with Support Vector Regression models (SVR) and Random Forest Regression models (RFR) for grass biomass and time since milking.

Some of the variables used in our model were based on the automated activity classifications of the cows' sensor data and visual observations. SVMs outperformed RFs for all these activity classification tasks with our data, so we only used the predictions of the SVMs. The best performing SVM classification model of the main activity types achieved 91.7% mean balanced accuracy on the test set and the best performing SVM model of rumination 90.9% (Table 5.8). While we maximized the mean balanced accuracy during cross-validation, also kappa, Matthews Correlation Coefficient, mean F_1 and mean True Skill Statistic were maximized at the same time (Table 5.6). Moreover, the confusion matrices of both models show that, in addition to a high accuracy, the relative frequency of misclassification of each activity type was approximately equal (Table 5.9). This means that the models were not overclassifying a specific activity type over another. Furthermore, we have found no substantial inter- or intra-cow activity classification performance differences. We thus considered the SVM activity classification models good enough to reliable predict the activity types based on the movement sensor data, even more so because the classification performance was higher or comparable to other cow activity classification studies (Benaissa et al., 2017; Martiskainen et al., 2009; Vázquez Diosdado et al., 2015).

Table 5.6: Performance measures on the test set of the best performing SVM activity classification models (*g = grazing; w = walking; s = standing; l = lying*) (Kuhn, 2020).

	Main activity types	**Rumination**
Balanced accuracy	μ = 91.7% (*g=94.2%; w=84.5%; s=90.2%; l=97.9%*)	90.9%
Accuracy	94.2%	90.9%
Kappa	88.0%	79.8%
Matthews Correlation Coefficient	88.0%	80.0%
True Skill Statistic	μ = 83.4% (*g=88.3%; w=69.0%; s=80.4%; l=95.8%*)	81.8%
F_1	μ = 88.0% (*g=96.6%; w=76.6%; s=83.4%; l=95.6%*)	86.6%
Precision	μ = 90.0% (*g=95.9%; w=84.9%; s=85.1%; l=94.2%*)	82.8%
Recall	μ = 86.5% (*g=97.3%; w=69.8%; s=81.7%; l=97.0%*)	90.9%
Negative predictive value	μ = 97.4% (*g=93.9%; w=98.0%; s=98.3%; l=99.4%*)	95.4%
True negative rate	μ = 96.9% (*g=91.0%; w=99.2%; s=98.6%; l=98.8%*)	90.9%

5.4 Discussion

In the case study we quantified (on a one-hour resolution) that 37% of the variation in resource availability influenced cow movements (consisting of movement through the landscape, body part movement, and emergent patterns like group characteristics, and displayed activities) and time since milking influenced it for 33%, while wind speed did not influence it noticeably (Figure 5.3; Figure 5.4; Figure 5.5). These results support our expectations that both resource availability and time since milking are important in shaping the movement of cows, but that wind speed (during relatively mild conditions) is not. Furthermore, it seems that the moderate correlation between resource availability and wind speed was indeed spurious. This framework proved to be insensitive to this spurious correlation, as it did quantify the influence of wind speed on cow movement to be 0%. Furthermore, the Support Vector Regression (SVR) models performed overall better than the Random Forest Regression (RFR), especially when confronted with a dataset with both GPS and accelerometer variables, but the qualitative patterns when comparing the three different environmental influences to single-sensor movement datasets were the same for both algorithms. Due to the SVRs higher performance, we do consider it to be the better alternative over RFR for this analytical framework when dealing with hyperdimensional datasets, especially when variables from multiple sensors are mixed. Moreover, we found that resource availability influenced accelerometer variables (29%) more than GPS variables (8%), but this influence on GPS variables still was largely independent from accelerometer variables (less than 1% of the total variation was shared). This indicates that, at this temporal scale and with these computed movement variables, the individual movement of cows through the landscape and the spatial group characteristics hardly contained any signature of resource availability and that almost all of the influence of resource availability on cow movements became apparent from the accelerometer variables of the cows' neck during grazing. The accelerometer variables of the cows' neck during grazing, being descriptive for bite frequency and bite force (Table 5.2; Figure 5.2; Table 5.5), probably link more explicitly to grazing behaviour than GPS variables do. These accelerometer variables are probably influenced more by resource availability than GPS variables, because grazing behaviour in cows is closely linked to resource availability (Drescher et al., 2003). The opposite was found for time since milking, which influenced GPS variables (29%) more than accelerometer variables (21%), with a lot of their explained variation being shared (17% of the total variation). This links well to our previous argument about that the accelerometer variables are shaped for a large part by the cows' neck movement during grazing, which is intuitively more heavily influenced by grass biomass than by time since milking. Previous studies also found that the lactation stage, a variable that we expected to be linked to time since milking regarding its effect on cow behaviour, influences the relative distribution of cow activity patterns and cow movement through the landscape (Bewley et al., 2010; Nielsen et al., 2000). This supports our finding about a higher influence on GPS variables with a large shared influence with accelerometer variables, because the movement through the landscape is measured by GPS variables and the activity patterns are measured by both GPS and accelerometer variables. Finally, the estimated model parameters were similar for all cows, indicating that the cows responded to changes in resource availability and time since milking in the same way. However, it should be noted that all the results that are presented above are of course context dependent. With a different experimental setup, e.g., indoor instead of pasture housing or different ranges of environmental variable values, the quantified influences can change. As is the case with nearly all modelling efforts, this framework is also only able to provide sensible results about the system for which data is available.

Our case study illustrates how the proposed analytic framework can quantify the influence of an ecological variable on animal movement. Having this quantification as the goal of the analytic framework, human interpretation and understanding of the correlative relationships within the model is initially of lesser importance. The goal is to build a model that can predict as much of the variation in the measured environmental variable as possible, by not limiting the model's complexity to facilitate human interpretation. Only then the aim is to quantify the overall influence of the environmental variable on animal movement. This analysis could be followed by a stage where the researcher is selective in the choice of movement variables, to study which movement variables are mainly influenced by the environmental variable. Due to the way the framework is set up, the environmental influence on multivariate animal movement will by definition always be higher or equal to the environmental influence on a subset of the animal movement variables. Thus, using this framework to first determine the environmental influence on multivariate animal movement and afterwards determine the influence on specific subsets of movement variables, allows for an analysis that shows in which movement variables the environmental influence is most or least visible. This is demonstrated in our case study, where resource availability mainly influenced accelerometer variables and much less GPS variables, indicating that resource availability was more tightly linked to the cows' movement of body parts than to their movement through the landscape. The opposite was true for time since milking, where also the explained variation by the accelerometer data was largely shared with GPS data. Furthermore, this framework allows for a comparison between the influences of multiple environmental variables to animal movement whilst being insensitive to moderate spurious correlations between environmental variables, which is also shown in our case study with regards to the influence of wind speed. Therefore, this framework could be well suited for exploratory analyses of the link between environment and animal movement.

In our framework the influence of the environment on animal movement is quantified, but the difference with previous studies (using low-dimensional movement descriptors (Avgar et al., 2013; Signer & Ovaskainen, 2017)) is that our result is quantified by how much of the variation in the environment can be predicted by observing the movement (instead of the other way around). Terming this quantified measure "environmental contribution", it should be noted that the environmental contribution to animal movement (i.e., the variation in an environmental variable that is traceable in animal movement data) is not the same as the environmental dependency of animal movement (i.e., the variation in animal movement that is dependent on an environmental variable), where potentially the environmental contribution can be large but the dependency small or vice versa. To accommodate for a multivariate analysis of animal movement we determine environmental contribution instead of the easier interpretable environmental dependency. In movement ecology usually the environmental dependency of animal movement is the focus of analyses, as this allows for the determination of the direction and strength of the environmental influence on an animal movement variable. Therefore, post hoc analyses that link environmental variables to a simplified animal movement descriptor can supplement our proposed multivariate analytic framework in order to study the route of causal inference (Avgar et al., 2013; Signer & Ovaskainen, 2017).

Various factors in the relationship between the environment and animal movement influence the quantification of the environmental influence on animal movement (Figure 5.6). First, many environmental variables are correlated and interact with each other in their influence on the animal's decision making and, thus, movement (Nathan et al., 2008). When the influence of a single environmental variable on animal movement is under scrutiny, these correlations and interactions with other environmental variables need to be taken into consideration. In the proposed analytic framework we do not distinguish between the independent, shared, and interaction influences of environmental variables on animal movement (Peres-Neto et al., 2006), which is different from the independent and shared influence on multiple subsets of the movement variables as described in our case study. As a consequence, both the direct and indirect influences of an environmental variable on animal movement are combined into a single metric. Future research could potentially be aimed at the distinction between these influence types of multiple environmental variables on multivariate animal movement, e.g., by using multi-target (Support Vector) regression and variation partitioning procedures (Borchani et al., 2015; Melki et al., 2017). Furthermore, when the influence of an environmental variable on animal movement is quantified, it is important that the movement itself does not influence the environmental variable directly at that point in space and time as well. Social proximity is for example an important variable in the shaping of individual animal movement, but individual movement parameters also directly shape collective movement patterns (Couzin et al., 2002). The fit of a model with social proximity as response variable and individual movement variables as input data would then not be solely the influence of an environmental variable anymore. This could consequently yield unrealistically large values of the explained variance, which should be prevented.

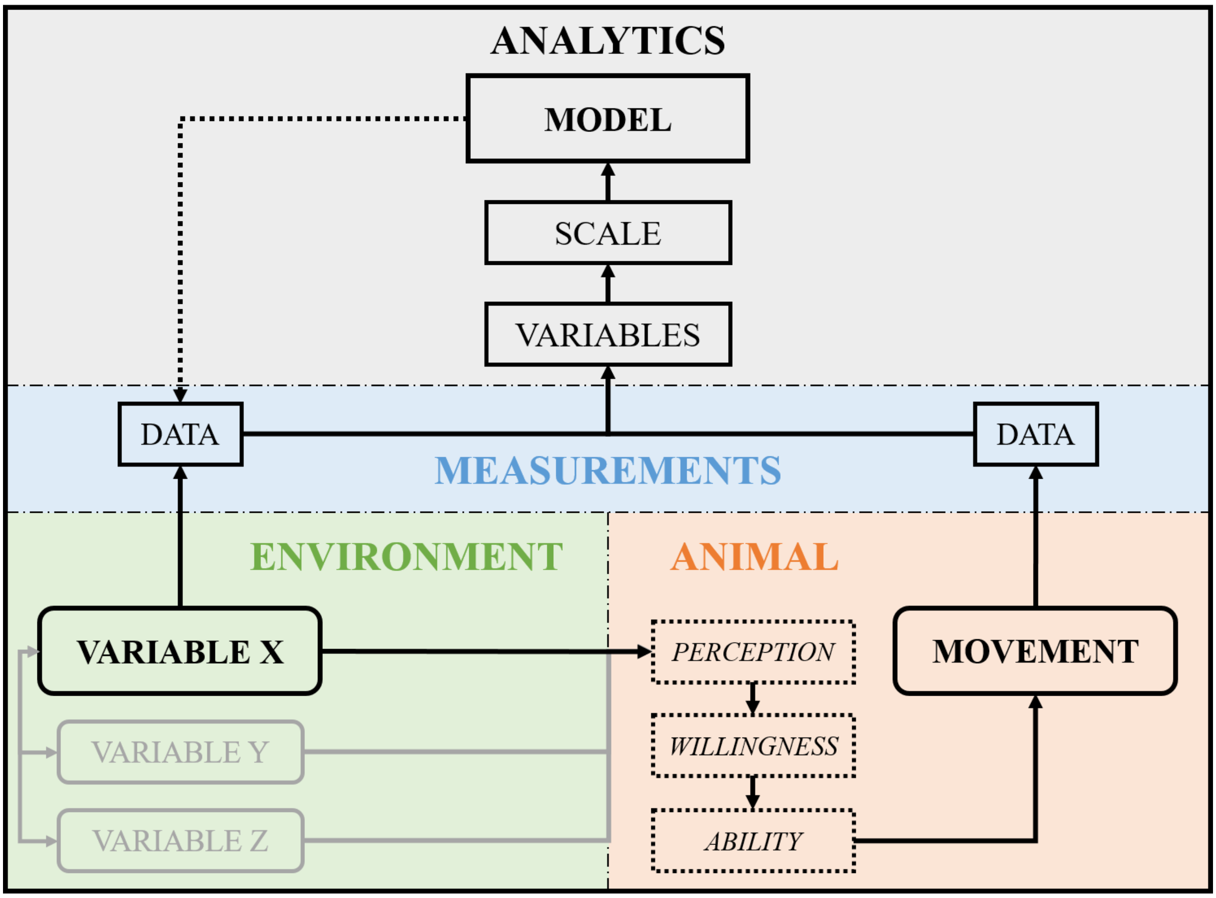


Figure 5.6: Conceptual model of the relationship between an environmental variable, animal movement and a predictive model to determine the influence of an environmental variable on multivariate animal movement. Dotted blocks are latent variables, rounded blocks are measurable variables, greyed out blocks are unmeasured variables, and straight blocks are known variables, values, or objects. The dotted arrow displays the predictive analysis following up on the model building phase.

In the relationship between the environment and animal movement, the animal's internal state ("*why move?*"), motion capacity ("*how to move?*"), and navigation capacity ("*where to move?*") are also involved (Nathan et al., 2008). The animal's internal state is composed of many different factors, e.g., physiological "need" (hunger, fear, etc.), physical characteristics (age, sex, body condition, etc.), and personality differences (laziness, level of sociality, etc.), that combined result in a certain response by the animal when confronted with a set of environmental variables at certain moment in time (Nathan et al., 2008). We translate this combined net effect of the internal state factors into the willingness of the animal to respond to the environment (Figure 5.6). The motion and navigation capacity can be translated into the ability of the animal to respond. Another factor that is involved, even before the animal can decide whether it is willing and able to respond, is the animal's perception of the environment (Manning et al., 2004). Only when an animal can observe changes or differences in an environmental variable can it decide to respond in a certain way. Because of the aforementioned latent variables - perception, willingness, and ability - the movement of the animal is not purely a deterministic function of a fixed set of environmental variables (Nathan et al., 2008). These latent variables can thus cause a partial environmental influence on animal movement. Furthermore, these latent variables are in part individual-specific (Nathan et al., 2008), which is why differences between individuals should be taken into consideration by standardizing the movement variables per individual and/or adding individual identifiers as variables to the model.

Other factors, which are more data-related, also influence the quantification of the environmental influence on animal movement (Figure 5.6). First, environment and animal movement are linked through sensor measurements, which influence the outcome of the analysis through varying sensor types, resolution, extent, and precision. Second, the movement variables that are computed from the animal movement data to describe the movement process determine how much of the environmental influence on animal movement is traceable in the data. Therefore it is key to extract as many informative movement variables from the animal movement data as possible in this proposed framework (or optimize the architecture of a neural network in a deep learning approach), because ideally all inherent variation needs to be extracted from the movement data to quantify the total environmental influence and to compare the influence of different environmental variables fairly. In our case study, the best performing models had a selected number of principal components with a relatively low cumulative proportion of variance, especially for the GPS variables (Table 5.7; Figure 5.10; Figure 5.11), which suggests that enough variation had been extracted from the raw data to make a good prediction about the environmental influence on animal movement. Although the best performing model does not necessarily equate a good model, so it could theoretically also be that we missed to extract some extra informative variables from the raw data, which could otherwise have resulted in an even better performing model. Third, the temporal scale at which these variables are computed determine the temporal scale for which the influence of the environmental variable on animal movement is quantified. As the effect of an environmental variable on animal movement data varies with temporal scales, the choice of the temporal scale of the variables is relevant (McClintock et al., 2014). Finally, the algorithm that is used to predict an environmental variable from animal movement data influences the level of fit that can be attained, which is demonstrated in our case study with SVR outperforming RFR on all occasions. Algorithms that can model complex interactions between variables are often able to make better predictions of the response variable, e.g., RFR, SVR, and Neural Network Regression, likewise are algorithms that take into account the sequence of time series data, e.g., Recurrent Neural Network. Quantitative comparisons between the influences of different environmental variables on animal movement can thus only be done reliably when the same algorithm is used on the same underlying animal movement dataset.

Apart from only using the R^2 of the model predictions to acquire ecological insights, the patterns of the observed vs. predicted plots can also potentially generate insight. For an environmental variable to influence animal movement, the animal's perception, willingness, and ability are conditionalities (Figure 5.6). Therefore, certain parts of the environmental variable's range might be better predicted by the model than other parts. It could be argued that this could be an explanation for the better SVR predictions during intermediate grass biomass compared to low and high biomass levels, thereby creating a lower overall slope of the predictions compared to the observations (Figure 5.3). However, apart from animal perception, willingness, and ability, other factors might also influence patterns of the observed vs. predicted plot Figure 5.6). In this case the algorithm might be the underlying cause for the lower overall slope of the SVR biomass predictions, due to a "regression toward the mean" characteristic (Figure 5.12). Furthermore, the overall gradient of the time since milking predictions follows the measurements quite accurately for both models from 0.5 to 6.5 hours, but after 6.5 hours it levels off (Figure 5.3). This suggests that until 6.5 hours cows continue to change their movement in response to the time since they were last milked, but after 6.5 hours there is no noticeable change in movement anymore. Besides a potential behavioural ecological cause for this pattern, it could also be (partially) caused by correlations with other time variables due to our experimental setup where the cows were milked two times a day around the same time of day. Follow-up studies could focus on these predicted time since milking patterns, where the experimental setup should contain multiple groups of cows that are milked at different times of the day. Finally, apart from concluding that wind speed probably has no noticeable effect on cow movement in this study (Figure 5.3), it becomes clear that the model performance suffered from some higher wind speed values in the test set compared to the train set (thereby generating an R^2 lower than 0).

5.5 Conclusions

We developed an analytical framework from existing methods that can quantify the environmental influence on animal movement while preserving the multifaceted nature of the movement process. Apart from providing a measure of the tightness of coupling between an environmental variable and animal movement, the prediction of an environmental variable from animal movement data can be a useful application in itself as the unique property of this predicted variable is that it represents the perceived environmental variable by the animals. This framework demonstrates that the possible applications of machine learning methods extend beyond the ability to transform raw into informative data to acquire ecological understanding, and that machine learning can also be used to directly relate movement data to environmental variables.

The applicability of our multivariate analytic framework extends beyond animal movement. With the recent increase in biologging practices, more and more variables of animal data are acquired (Cooke et al., 2004; McClintock et al., 2017; Wilmers et al., 2015). These data do not only encompass animal movement, but for example also animal physiology, which can be related to environmental variables as well using the same framework as presented in this study (Cooke et al., 2004; McClintock et al., 2017; Wilmers et al., 2015), e.g., by relating heart rate patterns to terrain characteristics or physical fitness metrics to climate conditions. Apart from using this analytic framework to quantify environmental influence on animal biologging data, the computation of perceived environmental variables can allow researchers and managers to monitor the perceived habitat of animal species (Cooke et al., 2004; Manning et al., 2004). This way, the habitat quality in natural areas, e.g., in terms of resources, can be assessed more precisely regarding the needs of specific, sensor-equipped, focal animals (Cooke et al., 2004; Rosenzweig, 2007). Furthermore, with the results presented here, the management of pasture-fed cattle can be optimized by detecting the appropriate time to move cattle to a more resource-rich area or towards a milking machine, without measuring resource availability or milk content in the udder directly. Finally, we argue that our proposed data-driven analytic framework to quantify environmental influence on animal biologging data is a valuable tool for explorative and comparative analyses on the relationship between the environment and animal movement, behaviour, and physiology.

5.6 Supplementary materials

We measured resource availability as dry matter grass biomass in kilograms per hectare, excluding stubble biomass. We determined time-varying biomass levels using a combination of field-measured biomass levels at specific time points, satellite-based biomass estimates derived from the Normalized Difference Vegetation Index (NDVI), and modelling of grass dynamics. The biomass field-measure was determined directly with an EC-09 electronic rising plate pasture meter (JenQuip, Feilding, New Zealand) by using the mean of 16 measurements spread equally across a pasture plot. These measurements were done roughly halfway each pasture session. For the satellite-measures, we used the Sentinel-2A (10m resolution), PlanetScope (3.125m resolution) and RapidEye (5m resolution) satellite image data to determine the NDVI inside the three pasture plots. The days for which satellite images were acquired aligned roughly with the beginning and the end of each pasture session. NDVI was calibrated against biomass using ground-truth pasture plots in and around Wageningen, Netherlands, 2016 (Wageningen University & Research & Noldus, 2017).

To estimate the biomass value at any point in time during the experiment and to account for uncertainties in the measurements, we fitted an exponential decay function through the biomass measurements using numerical optimization for the decay rate coefficient (Equation 5.4). For this we combined the biomass measurements of the plate pasture meter and the satellite images.

$$r = \frac{2000}{a_n} e^{-bx} + 800 \tag{5.4}$$

Where r is biomass in kilogram dry matter per hectare, excluding stubble; a_n is a coefficient that determines the intercept of the function, which has a unique value for each pasture plot session; b is a coefficient that determines the rate of the exponential decay, which has the same value for all pasture plot sessions; and x is the time in days starting at zero on 12:00 PM CEST of the first day of each pasture plot session. We first determined a_n for each of the three plots separately by dividing 2000 by the biomass measurement for $x = 0$. Then we multiplied all measurements from plot n by a_n and afterwards pooled all converted measurements into one dataset. Optimizing the decay rate coefficient in the aforementioned function for this combined dataset resulted in an acceptable fit of the estimated data to the measured data ($R^2 = 0.69$; Figure 5.7). These estimated data do not perfectly fit true absolute biomass levels, but nonetheless capture the trend in biomass over time.

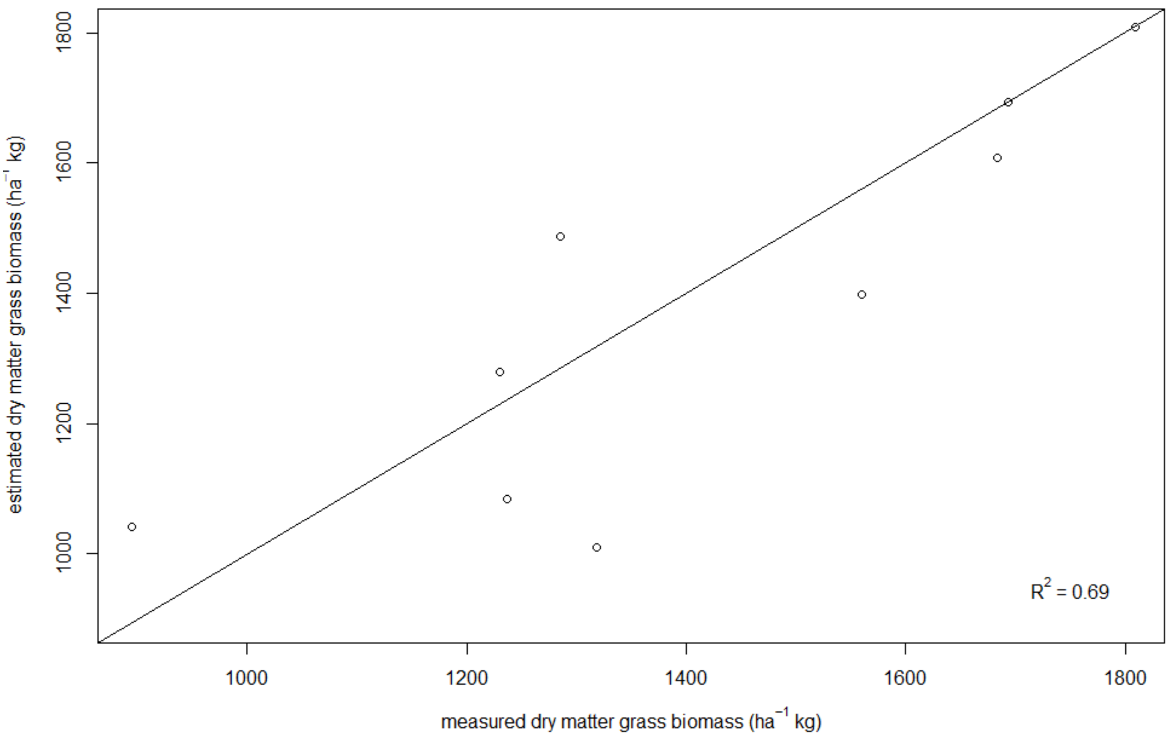


Figure 5.7: Measured versus estimated grass biomass (kilogram dry matter per hectare, excluding stubble) during the experiment.

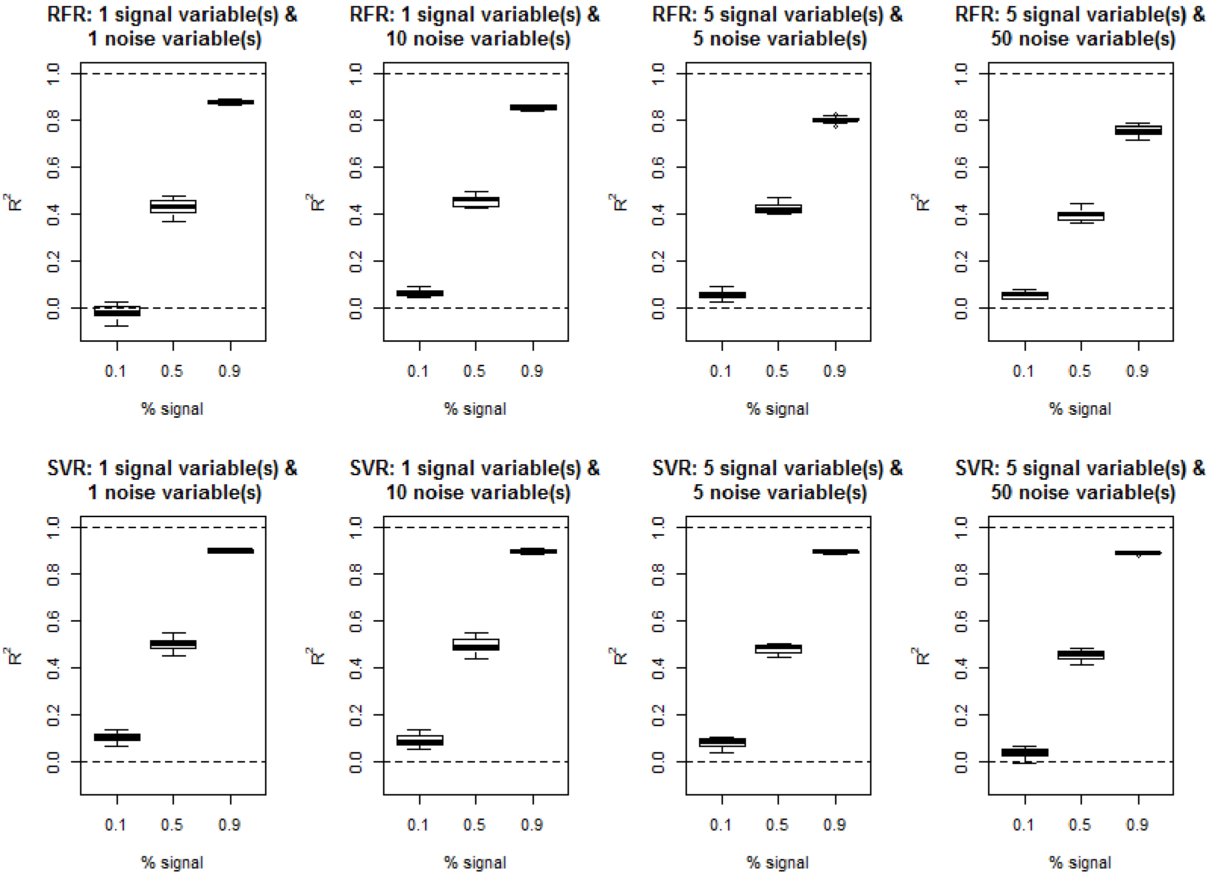


Figure 5.8: Boxplots of the explained variation (using separate train, validation and test sets) of 10 repeated simulations per combination of: algorithm (Random Forest Regression and Support Vector Regression); number of variables with a linear relationship to the response variable and number of noise variables (1/1, 1/10, 5/5, 5/50); and percentage of noise versus signal added around response variable (10%, 50%, 90%). It becomes clear that (especially SVRs) are accurately capable to predict the percentage of the response variable that contributed to the input variables until very high noise levels.

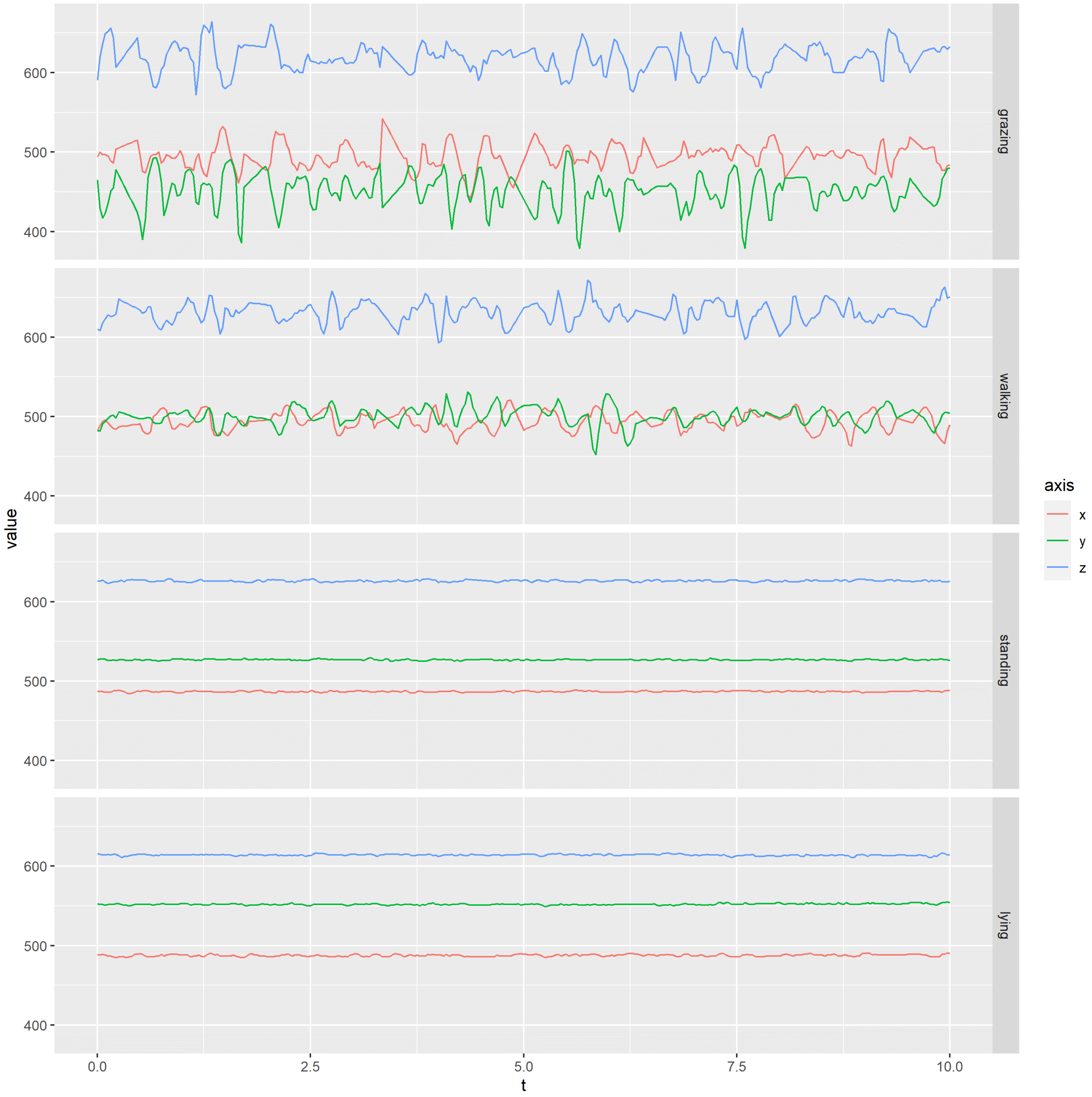


Figure 5.9: Representative acceleration plots of the three axes vs time in seconds for the different activity types.

Table 5.7: Hyperparameters and performance of the best performing SVR and RFR models.

Model	**Response**	**Data**	#PC$_{\text{ACC}}$	#PC$_{\text{GPS}}$	c	γ	ϵ	R^2
SVR	Biomass	ACC	29	n.a.	$10^{2.25}$	$10^{-2.25}$	0	.29
SVR	Biomass	GPS	n.a.	6	$10^{2.25}$	$10^{-1.5}$	10^{-9}	.08
SVR	Biomass	ACC+GPS	29	9	$10^{2.25}$	$10^{-2.25}$	1	.37
SVR	Milk time	ACC	21	n.a.	$10^{0.5}$	$10^{-1.5}$	1	.21
SVR	Milk time	GPS	n.a.	7	10^{0}	10^{-1}	1	.29
SVR	Milk time	ACC+GPS	10	29	$10^{0.5}$	$10^{-1.75}$	1	.33
SVR	Wind speed	ACC	3	n.a.	$10^{1.75}$	$10^{-1.25}$	1	-.10
SVR	Wind speed	GPS	n.a.	31	$10^{3.5}$	10^{0}	1	-.12
SVR	Wind speed	ACC+GPS	3	0	$10^{1.75}$	$10^{-1.25}$	1	-.10
RFR	Biomass	ACC	33	n.a.	n.a.	n.a.	n.a.	.18
RFR	Biomass	GPS	n.a.	11	n.a.	n.a.	n.a.	.05
RFR	Biomass	ACC+GPS	33	9	n.a.	n.a.	n.a.	.19
RFR	Milk time	ACC	49	n.a.	n.a.	n.a.	n.a.	.16
RFR	Milk time	GPS	n.a.	11	n.a.	n.a.	n.a.	.29
RFR	Milk time	ACC+GPS	0	11	n.a.	n.a.	n.a.	.29
RFR	Wind speed	ACC	122	n.a.	n.a.	n.a.	n.a.	-.13
RFR	Wind speed	GPS	n.a.	92	n.a.	n.a.	n.a.	-.26
RFR	Wind speed	ACC+GPS	3	1	n.a.	n.a.	n.a.	-.12

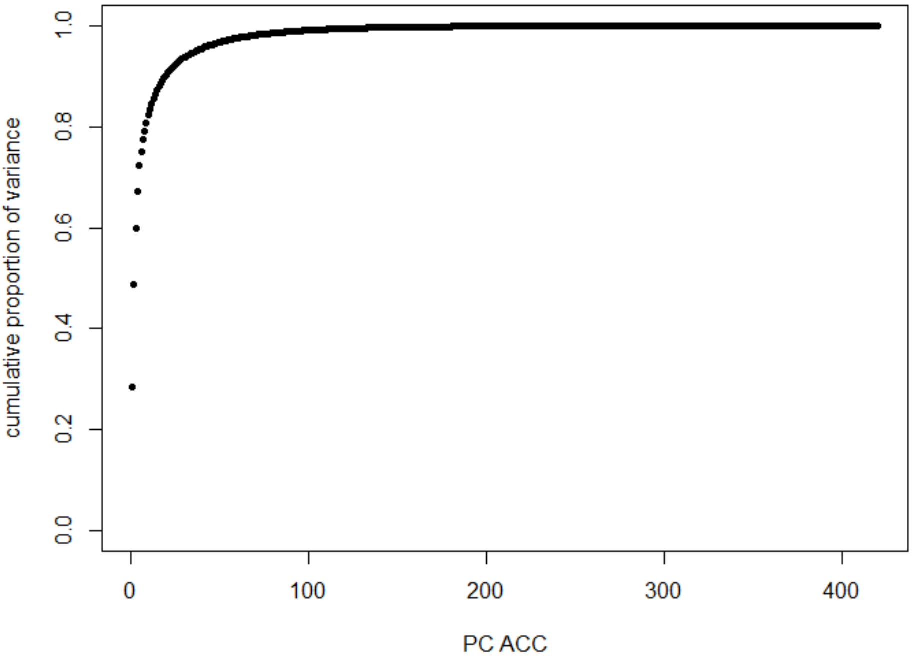


Figure 5.10: Accelerometer principal components versus cumulative proportion of variance.

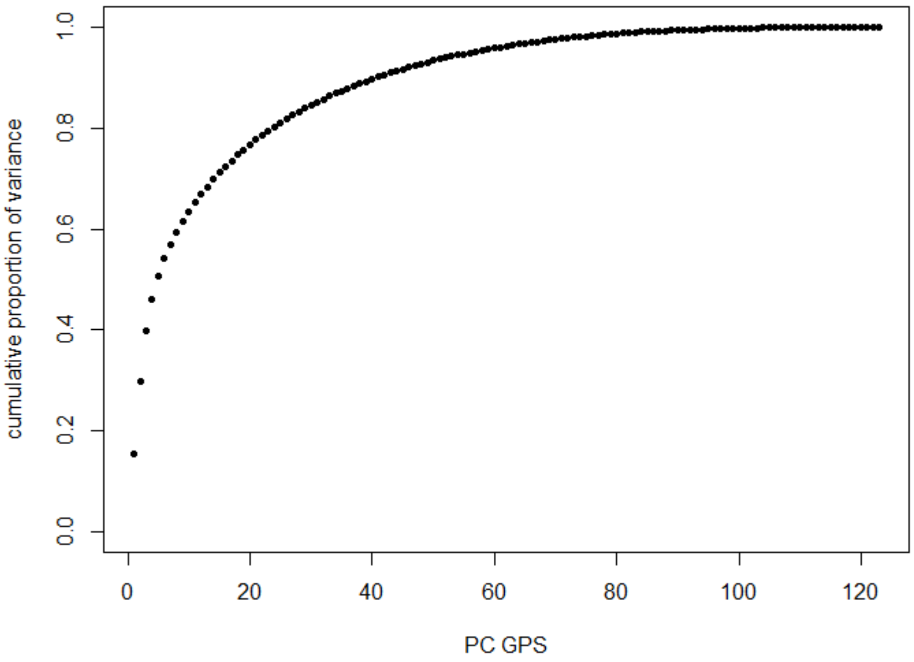


Figure 5.11: GPS principal components versus cumulative proportion of variance.

Table 5.8: Hyperparameters of the best performing SVM activity classification models.

	Main activity types	**Rumination**
window size	3 s	
principal components	210 (0.999990 cum. expl. var.)	5 (0.765970 cum. expl. var.)
gamma	$10^{-4.7}$	$10^{-2.2}$
cost	$10^{3.3}$	10^{6}
class weights	1:1:1:1	1:1

Table 5.9: Confusion matrices of the best performing SVM activity classification models on the test set, for a) main activity types (g = grazing; w = walking; s = standing; l = lying); and b) rumination (0 = not ruminating; 1 = ruminating).

		actual			
	a)	*g*	*w*	*s*	*l*
predicted	*g*	**1769**	46	25	4
	w	12	**118**	5	4
	s	23	5	**188**	5
	l	14	0	12	**422**

b)	*0*	*1*
0	**560**	27
1	56	**269**

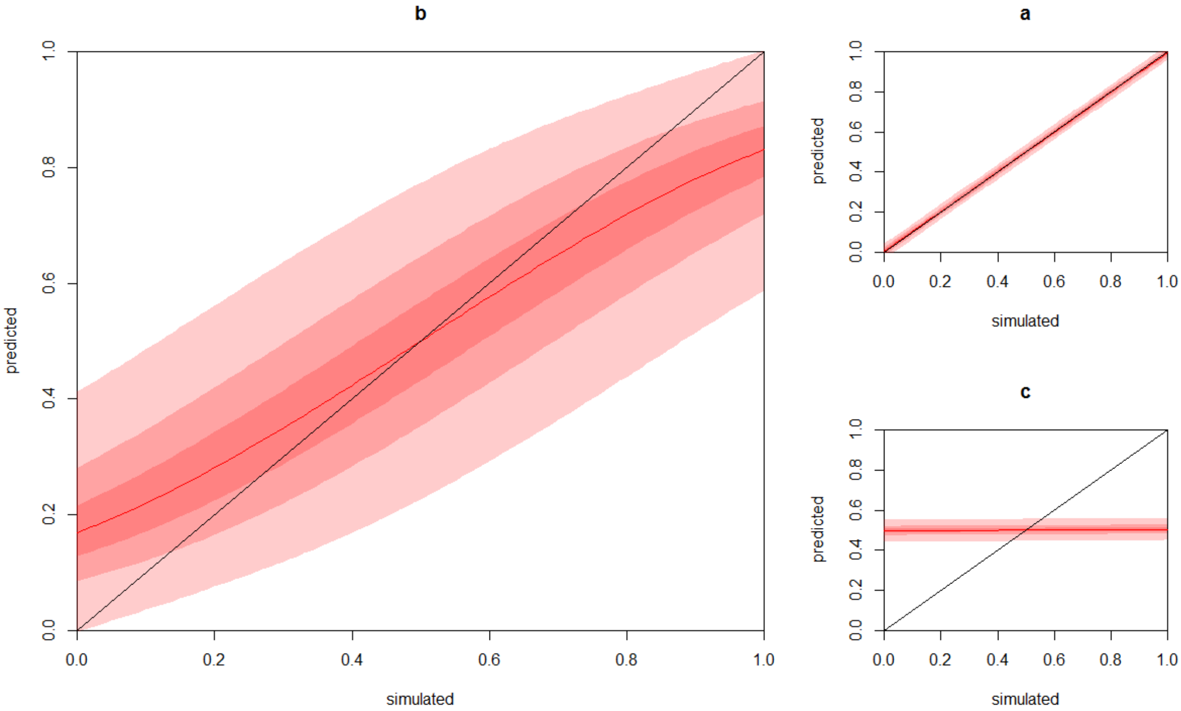


Figure 5.12: Simulated data vector $\left(y = \frac{[0..200]}{200}\right)$ versus the quantiles ($p = \{0.05, 0.2, 0.35, 0.5, 0.65, 0.8, 0.95\}$) of 10^6 predicted data vectors by the best performing Support Vector Regression models (a: $cost = 10^4$, $gamma = 10^{-3}$, $epsilon = 10^{-5}$; b: $cost = 10^2$, $gamma = 10^{-1}$, $epsilon = 10^{-1}$; c: $cost = 10^1$, $gamma = 10^{-5}$, $epsilon = 10^{-5}$). The models were trained on the odd elements of 106 different sets of two simulated input data vectors (a: $x_1 \sim N(\mu = y, \sigma = 0.025)$, $x_2 \sim N(\mu = y, \sigma = 0.05)$; b: $x_1 \sim N(\mu = y, \sigma = 0.25)$, $x_2 \sim N(\mu = y, \sigma = 0.5)$; c: $x_1 \sim N(\mu = y, \sigma = 2.5)$, $x_2 \sim N(\mu = y, \sigma = 5)$), and afterwards the predictions were made using the even elements of the input vectors. From these simulations it becomes clear that with a decreasing signature of the response variable in the input variables (a to c), the predictions increasingly get regressed toward the mean. In other words, the smaller the signature of the response variable in the input variables is, the more the model predictions will be located around the mean of the response variable instead of around the gradient of the response variable.

Chapter 6

Timely poacher detection and localization using sentinel animal movement

This chapter is based on:

*de Knegt, H. J., *Eikelboom, J. A. J., van Langevelde, F., Spruyt, W. F., & Prins, H. H. T. (2021). Timely poacher detection and localization using sentinel animal movement. *Scientific Reports, 11*, 4596. https://doi.org/10.1038/s41598-021-83800-1

* *these authors contributed equally*

Abstract

Wildlife crime is one of the most profitable illegal industries worldwide. Current actions to reduce it are far from effective and fail to prevent population declines of many endangered species, pressing the need for innovative anti-poaching solutions. Here, we propose and test a poacher early warning system that is based on the movement responses of non-targeted sentinel animals, which naturally respond to threats by fleeing and changing herd topology. We analyzed human-evasive movement patterns of 135 mammalian savanna herbivores of four different species, using an internet-of-things architecture with wearable sensors, wireless data transmission and machine learning algorithms. We show that the presence of human intruders can be accurately detected (86.1% accuracy) and localized (less than 500m error in 54.2% of the experimentally staged intrusions) by algorithmically identifying characteristic changes in sentinel movement. These behavioral signatures include, among others, an increase in movement speed, energy expenditure, body acceleration, directional persistence and herd coherence, and a decrease in suitability of selected habitat. The key to successful identification of these signatures lies in identifying systematic deviations from normal behavior under similar conditions, such as season, time of day and habitat. We also show that the indirect costs of predation are not limited to vigilance, but also include 1) long, high-speed flights; 2) energetically costly flight paths; and 3) suboptimal habitat selection during flights. The combination of wireless biologging, predictive analytics and sentinel animal behavior can benefit wildlife conservation via early poacher detection, but also solve challenges related to surveillance, safety and health.

6.1 Introduction

Wildlife trade is a low-risk, yet high-profit crime, ranking fourth in terms of revenue after trade in drugs, humans and arms (Scheffers et al., 2019). Wildlife crime is driven by a rapidly expanding wealthy class in some cultures that views animal parts as medicine or status-enhancing luxury goods (Felbab-Brown, 2017). The demand for animal parts has led to escalating prices (Chen, 2016), which consequently fuels poaching. As one of the main causes for biodiversity decline (Ceballos et al., 2017), poaching increasingly threatens the existence of wildlife, notably pangolins, rhinos, elephants and tigers. Ultimately, losses of these and other species can reshape entire ecosystems via cascading effects.

Although the ultimate solution is to reduce the global demand for wildlife products, efforts to do so have not been successful enough (Veríssimo & Wan, 2019). Local efforts thus often aim at deterring poachers, mainly through ranger patrols. Deadly force used by poachers incites conservation authorities into intensified 'militarized conservation', resulting in frequent shootouts between poachers and conservation officers (Duffy, 2014). Sadly, poaching of wildlife still continues to be a threat to the preservation of many wildlife species (Scheffers et al., 2019), as anti-poaching rangers often arrive too late at crime scenes (O'Donoghue & Rutz, 2016). An effective method for early poacher detection and localization is thus urgently needed, so that preventive action can be taken. With situational awareness, law enforcers can operate under safer conditions with reduced risk of fatalities and potential to de-escalate conflicts. An effective poacher early warning system (EWS) thus contributes to preventing lethal violence, not only against wildlife, but also against conservation officers and poachers (Duffy, 2014).

Animal sentinels, especially those that are abundant and no targets themselves, may provide an early warning that poachers are *en route*. Prey species may be good sentinels as these species have evolved a suite of traits aimed at preventing them from being killed, e.g., via early predator detection and escape (Cooper & Blumstein, 2015). This often extrapolates to humans as well, since many prey species evolved together with human hunters, leading to anthropogenic disturbance stimuli triggering similar, or often even stronger, evasive responses (Frid & Dill, 2002; Zbyryt et al., 2018). Until now, practical constraints have hampered the development of a sentinel-based EWS (Katzner & Arlettaz, 2020). Although wireless sensors can generate large volumes of data, the areas in which poaching occurs often lack infrastructure that allows real-time wireless communication of sufficient bandwidth (O'Donoghue & Rutz, 2016). Moreover, animal behavior is known to be complex and context-dependent, thus an EWS needs to be able to handle rich contextual data when identifying behavioral abnormalities linked to anthropogenic disturbances. Fortunately, advances in technology, computing and analytics have now alleviated these constraints (Williams et al., 2020). We therefore tested the concept of whether the behavior of sentinel animals can be used to detect and localize human intrusions using wearable biologging sensors and predictive algorithms (Figure 6.4).

We tested the sentinel-based EWS in an African savanna, home to several targeted species (e.g., pangolin, elephant, rhino and lion) that coexist with an assemblage of mammalian prey species that could be potential sentinels. We deployed wearable GPS and tri-axial accelerometer sensors on 138 animals equally over four species (plains zebra, blue wildebeest, common eland and impala) in a 1200ha fenced, predator-free area inside Welgevonden Game Reserve (WGR), South Africa (Figure 6.1). These sensors transmitted data wirelessly via a LoRa network connected to a backhaul. During a period of seven months, WGR park officials executed 57 intrusions mimicking poachers (referred to as 'experimental intrusions'). Data collected in the absence of experimental intrusions were used to characterize undisturbed behavior, allowing quantification of the degree of abnormality of movement behavior at any point in time. During all these experimental intrusions and matched controls, a median of 47 sensors yielded data for further analyses.

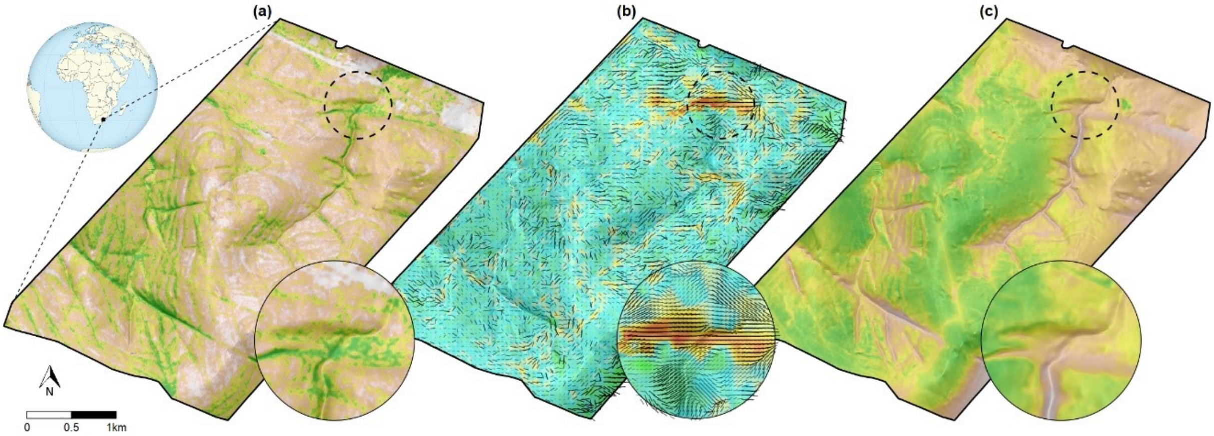


Figure 6.1: Overview of the study area with three examples of how normal behavior varies spatially: (a) topography and tree cover in the study area (white to green with increasing tree cover); (b) movement speed (third quartile) and directionality of wildebeest during the afternoon (blue to red with increasing speed; length and darkness of line segments indicates the degree of directional preference and orientation indicates the preferred movement direction); and (c) modelled habitat suitability of wildebeest during the afternoon as function of habitat characteristics (white to green with increasing suitability). The inset figures exemplify the importance of considering environmental context in the early warning system, since fast, straight and directional movements through low suitability areas are part of the sentinels' normal behavior. Thus, solely detecting fast and straight movements may not suffice as early warning indicators. All maps were generated in R3.5.0 using GIS, location and modelled data (R Core Team, 2020).

We engineered a large set of potentially meaningful and ecologically relevant features, describing the geometry of individual trajectories as well as emergent herd topologies and various characteristics of the animal-environment interplay (split into 4 main classes: individual geometry, accelerometer-based, collective movement features, and indices of space usage; and 12 sub-classes; and various standardizations of features to capture deviations from normal behavior, see Table 6.2). Then, we applied a multi-step dimensionality reduction approach (first across a subset of features within sub-classes to collapse the ecologically related features into a low-dimensional characterization, then across the set of selected principal components from all classes to reduce multicollinearity; see section 6.4) and segmented the dataset into experimental intrusions and controls. Data during experimental intrusions were randomly matched with control data of the same period, one or two days earlier or later, when no intrusion took place. To generate predictive signatures for the EWS, we followed a three-step process: (1) behavioral response classification focusing on detecting evasive anti-predator behavior by each individual separately, followed by (2) intrusion detection focusing on a system classification through integrating signals over all individuals, and (3) intrusion localization. We allocated each experimental intrusion or control segment to either the training phase or the evaluation phase, applying a leave-one-group-out cross-validation approach on these segments to make the best use of all data (see section 6.4 for details).

6.2 Results

Exploration of the animals' reaction to the experimental intrusions highlighted several broad characterizations of their response. First, the experimental intrusions triggered nearby sentinels to divert their movement away from the perceived treat while increasing their speed, body acceleration and directional persistence (Figure 6.2). This, together with elevated variation in such features, resulted in more directional, brisk, straight and erratic movements. These evasive flights lasted on average 47 minutes per fleeing group of zebra (SD=28, n=29), 39 minutes for wildebeest (SD=33, n=15), 46 minutes for eland (SD=18, n=15), and 43 minutes for impala (SD=14, n=14). Second, the difference between the sentinels' response behavior and their normal behavior was larger when comparing the individuals' movement in the same spatial (location and habitat) and temporal (seasonal and diurnal) context. Third, the sentinels selected sub-optimal habitat and chose flight paths that incurred higher energetic costs via faster and uncommon uphill movement in response to the experimental intrusions, possibly in an effort to find refuge (Figure 6.2; Figure 6.3). Fourth, apart from alterations in the geometry of individual movement trajectories, patterns of collective geometry changed in the vicinity of the experimental intrusions. Generally, nearby individuals tended to form groups with more synchronized and aligned movements (Figure 6.2f).

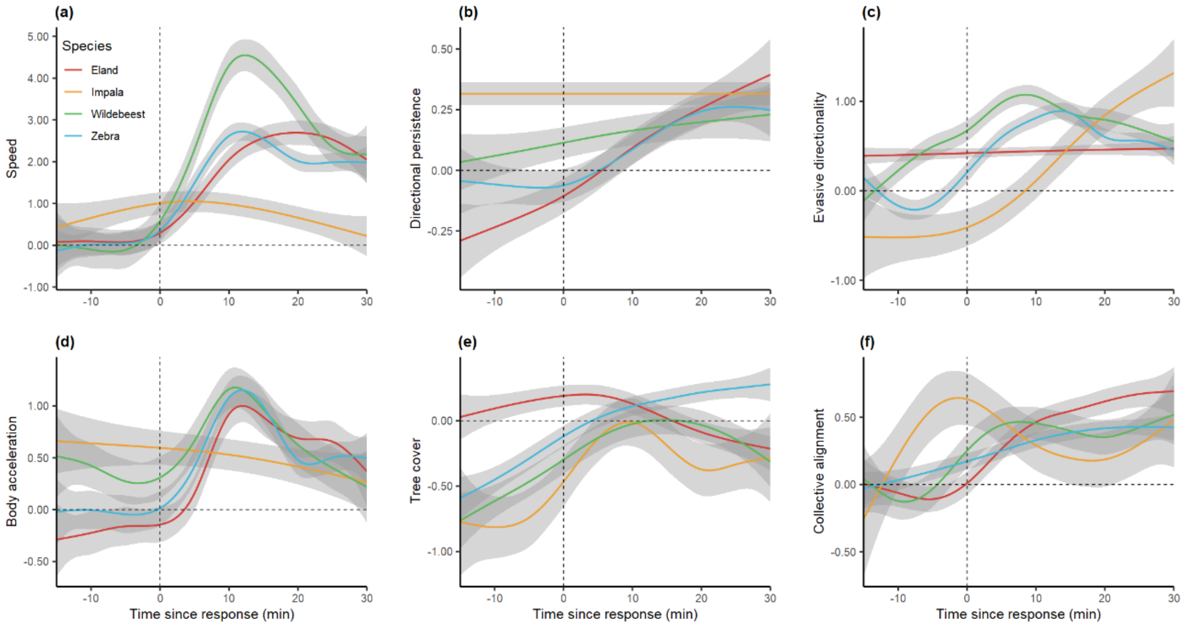


Figure 6.2: A sample of the 2117 computed animal movement features characterizing the sentinels' behavior near experimental intrusions, shown here as function of the time since the annotated start of their response behavior (i.e., 'flight' and 'regroup' as described in the main text). All y-axes show standardized values (zero-mean and unit-variance when undisturbed), and the shaded area around each line (i.e., sentinel species) depicts pointwise 95% CI of a General Additive Model. When encountering the experimental intrusions, the sentinels moved faster (a), straighter (b), away from the intrusion (c), and with higher body acceleration (d). The sentinel species that prefer more grass-dominated habitats (i.e., lower tree cover) tended to move towards areas with higher tree cover (e) and thus lower habitat suitability. Moreover, encountering the intrusions induced more aligned collective movement (f).

We trained a Support Vector Machine (SVM) to algorithmically classify the animal's response behavior as either undisturbed (i.e., calm or normal) or disturbed (a summary label for the above-described responses). We were able to achieve an average precision of classification (i.e., the area under the precision-recall curve) of 46%. Depending on the chosen value of the response probability decision boundary, the classification performance achieved up to 100% precision, or 100% recall, with a maximum F_1-score of 47% (Figure 6.5). Comparing the SVM's average precision on various subsets of the data resulted in three noteworthy variations in predictability of response behavior: (1) intrusion type (on foot 52%, by vehicle 14%), (2) species (eland 47%, impala 17%, wildebeest 29%, zebra 57%), and (3) time of day (morning 48%, noon 26%, afternoon 53%). A higher predictability near humans on foot compared to motorized vehicles suggests a stronger behavioral response to the former and is in line with other findings (Cooper & Blumstein, 2015; Stankowich, 2008). A lower predictability for impala and wildebeest may imply that these animals exhibit a broader suite of response behaviors, possibly including antipredator responses not included here (e.g., 'freezing' or 'threat inspection' behavior). For impala, being the smallest of our sentinel species, it may furthermore be caused by a high-quality food requirement inducing them to delay escape and hence reduce the associated opportunity costs (Cooper & Blumstein, 2015). The lower predictability around noon could be due to the midday heat inducing animals to accept a higher risk and lower their energy expenditure of costly risk-avoidance behavior, thereby creating less pronounced signatures in the data.

Following animal behavior classification, we were able to distinguish intrusions from controls with 86.1% accuracy (82.6% precision, 89.2% recall) using logistic regression, exclusively using the movement data of the sentinels (Table 6.1). The odds of an intrusion increased considerably with higher SVM-predicted probabilities of response behavior, the degree of local spatial autocorrelation therein, and a decrease in spatial clustering of sentinels that were predicted to be undisturbed. Including more features in the detection classifier boosted its predictive accuracy to 91% (Figure 6.7), but also increased the risk of lowering its generalizability to other areas due to potential overfitting. The true positive rate was 84.2%, and there was no apparent positive relationship between the probability that an intrusion was correctly detected and the number of working sensors (logistic regression, p=0.260).

Table 6.1: Confusion matrix of the poacher detection algorithm. Bold numbers indicate correct predictions.

		Truth	
		Control	Intrusion
Prediction	Control	**52**	10
	Intrusion	5	**47**

Following detection, we predicted the location of the intrusion relative to the position, movement direction and SVM-predicted response probabilities of the sentinels. We summarized the performance of the localization prediction through the Euclidian distance between the peak prediction and the true location of the intrusion, followed by computing the spatial error of the 10 most dense probability surfaces per experimental intrusion. In 20.8% of them the predictions were highly accurate, namely within 100m from the true location, increasing to 41.7% and 54.2% respectively, for distances up 300m and 500m (Figure 6.3b).

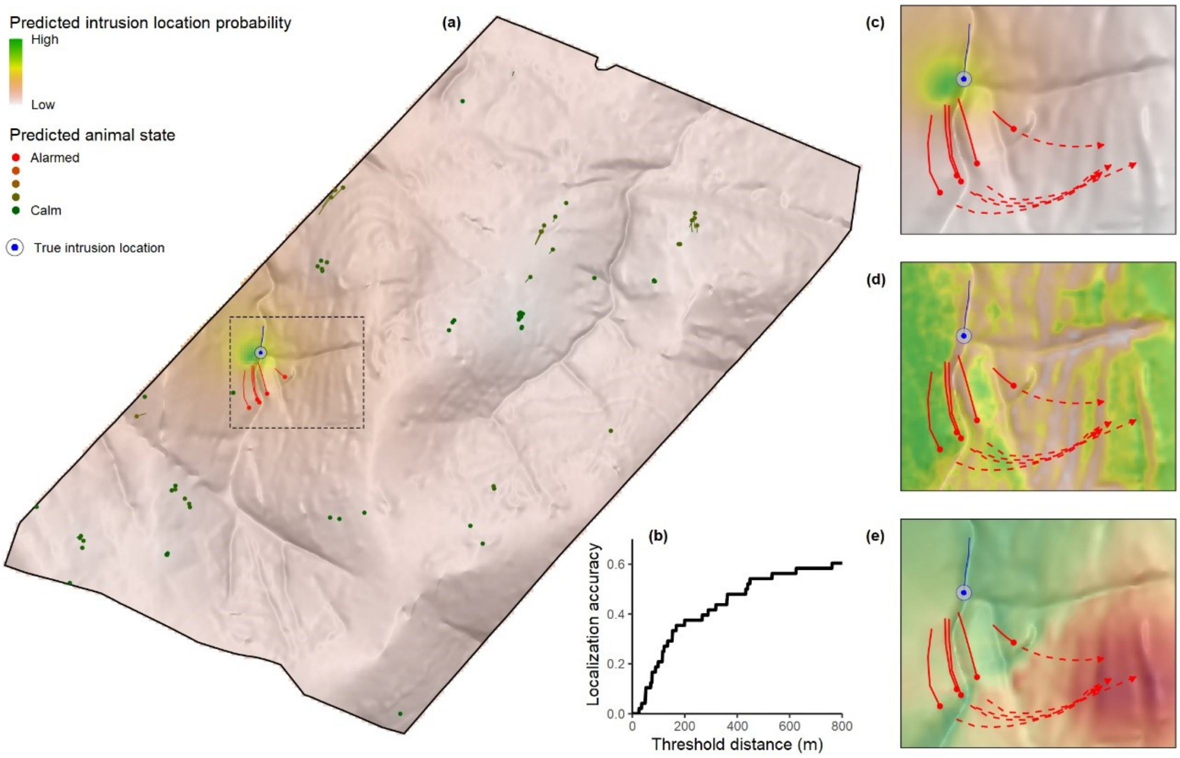


Figure 6.3: Spatial performance of our early warning system. Panel (a) shows the predicted spatial probability surface for the intrusion's location (based on data from the sentinel animals only) for one of the experimental intrusions. For all experiments where the intrusion was algorithmically detected (82.5%), the spatial localization accuracy as function of threshold distance (b) shows that 54.2% of these correctly detected intrusions could be localized with a spatial error of less than 500m and 20.8% within 100m. The dashed focal area shown in panel (a) is highlighted in panels (c-e), where the sentinels' (here: wildebeest) movements in the next 10 minutes is indicated with dashed lines. Panel (c) shows the spatial localization prediction of the intrusion. The evasive movements of the fleeing wildebeest are fast compared to their normal movement at that location (Figure 6.1b), and highly aligned. While fleeing, the wildebeest move through habitat with a low suitability (d, see Figure 6.1c), and towards areas that are energetically costly to reach (e, movement costs are computed based on topography and relative to their current position, where the cost of movement is assumed to be inversely proportional to movement speed on an incline as computed using Tobler's hiking function). All maps were generated in R3.5.0 using GIS, location and modelled data (R Core Team, 2020).

6.3 Discussion

Our study thus clearly demonstrates that sentinel animal behavior can be used to detect poachers, since predictable signatures in behavioral responses to disturbance stimuli can be used to detect and locate human intrusions. Indeed, the sentinels took systematic and detectable evasive action when experimental intruders came near.

The sentinels increased their movement speed and body acceleration as they generally do during anti-predator responses (Cooper & Blumstein, 2015), whilst moving away from the perceived threat with higher directional persistence (Figure 6.2). They did so for a considerable amount of time per flight response (45 minutes on average), longer than only instantaneously running away, thereby substantially trading off energy for safety (Gallagher et al., 2017). This signal became even more pronounced in the context of the individuals' normal behavior given the prevailing conditions (season, time of day and habitat), since a systematic deviation from normality is key to successful identification of disturbed behavior. It thus proved to be important to explicitly consider the spatial-temporal context of the movement-environment interplay when using sentinel movement metrics as early warning indicators. Solely using movement speed as indicator (Ihwagi et al., 2018) without incorporating environmental conditions is therefore not very informative (Figure 6.1).

These findings suggest that the sentinels elevated their energy expenditure while fleeing, in line with theory on energy landscapes and the landscape of fear (Cooper & Blumstein, 2015; Gallagher et al., 2017; Halsey, 2016; Wilson et al., 2012). However, not only did experimental intrusions trigger faster-than-normal movement, but the sentinels also tended to utilize the terrain by moving uphill, thereby increasing their energy expenditure (Figure 6.3). Moreover, the sentinels seemed to alter their decision-making during evasive actions, selecting less optimal habitat than they would do when undisturbed (Figure 6.2e; Figure 6.3d). This suggests that anti-predator trade-offs relates to energy trade-offs and that perceived threats can induce resource avoidance (Gaynor et al., 2019). Together, these consequences of anti-predator behavior can incur significant energetic and opportunity costs (Gaynor et al., 2019). These energetic costs are generally not considered in the indirect costs of predation within the landscape of fear framework, but are now increasingly being recognized (Gallagher et al., 2017; Gaynor et al., 2019). Our findings suggest that anti-predator behavior not only incur costs in terms of trading off foraging and resting for vigilance, but also in terms of increased costs due to 1) performing long, high-speed flights; 2) choosing energetically costly flight paths; and 3) selecting suboptimal habitats during flights.

Although the study of collective behavior of animals within groups has predominantly relied on controlled laboratory-based studies and theoretical models (Calabrese et al., 2018; Westley et al., 2018), our high-resolution data on manifold large terrestrial mammals allowed the detailed computation of collective movement properties in their natural habitat in relation to perceived threats. The sentinels increased group coherence when intruders were near (Figure 6.2f), presumably in an effort to find safety in numbers (Hamilton, 1971), whilst at the same time avoiding the likelihood of collisions by increasing alignment during escape (Evans et al., 2019). These findings support predictions from theoretical studies (Bode et al., 2010) and controlled laboratory experiments (Ioannou et al., 2017).

Central to these findings is that the responsive and evasive behavior of animal sentinels can be used to algorithmically detect and localize poachers. A sentinel-based EWS is robust against adaptive behavior of poachers, as an abundance of sentinels cannot easily be manipulated and fooled (Berdahl et al., 2013; Lima, 1995). Additionally, shooting sentinel animals would give away the poacher's position, both via its acoustic signal (O'Donoghue & Rutz, 2016) as well as through the sensor data of the shot animal. Moreover, if hackers were to tap into the dataflow, only the locations of the sentinels may be revealed, but not those of targeted species. Applying biologging technology directly to targeted species is risky, and will rule out preventive intervention as it only enables the *post hoc* identification of mortalities (O'Donoghue & Rutz, 2016). Instead, the responsive behavior of untargeted sentinels crossing path with poachers *en route* provides an early warning and situational awareness to anti-poaching personnel.

Our proposed sentinel-based EWS critically hinges on the premise that sentinel animals respond reactively to human intrusions. This requires that these sentinels have evolved with natural and human predators, and that they have maintained their anti-predator behavior (Charuvi et al., 2020). In African savannas, apex predators like lion and leopard are generally present and fear of the human "super-predator" (Darimont et al., 2015; Suraci et al., 2019) is pervasive throughout mammal communities in Africa (Zanette & Clinchy, 2020). However, empirical evidence shows that response to natural predators and humans varies across contexts and with predator mode: sit-and-wait ambush predators induce different responses than cursorial predators (Miller et al., 2014; Thaker et al., 2011), and humans on foot are generally more evocative than other anthropogenic stimuli (e.g., motorized vehicles) (Cooper & Blumstein, 2015; Stankowich, 2008). To prey, illicit human activity in conservation areas may be rarer and less predictable than encounters with natural predators. Human encounters could therefore be more stressful, since lack of predictability is a well-established trigger of reactive responses like flight (Creel, 2018). Several studies suggest that free-roaming animals not only respond differently to human presence than to natural predators, but also that human presence evokes stronger responses (Ciuti et al., 2012; Proffitt et al., 2009; Zbyryt et al., 2018). Since our study was intentionally conducted in a predator-free environment, the next logical step is to include the sentinels' responses to their natural predators in the EWS. Although we currently lack the knowledge and data to separate human-induced from predator-induced behavioral shifts in wild-living animals (Goumas et al., 2020; Montgomery et al., 2020), the behavior and approach movements of natural predators is expected to be sufficiently different from that of humans to successfully do so.

The main advantage of our proposed sentinel-based EWS is its ability to filter out periods without poaching activity, thereby prioritizing model sensitivity over specificity. However, in African savannas it is generally a rare event for a sentinel to encounter a human. Therefore, given our current false positive rate of 8.8%, many false positives will be generated over time when an EWS is actually deployed. The poacher detections by the EWS will thus require an extra layer of verification by, e.g., visually inspecting the patterns in localizations generated by the EWS or dispatching an Unmanned Aerial Vehicle to the detected poacher location. Known locations of legal human activity should then be taken into account as well, e.g., roads or camps with tourists who could trigger responses by animals. The role of this EWS is not that of a fully automatic system to directly dispatch an anti-poaching unit, but to help wildlife reserves make informed decisions about managing their anti-poaching resources.

Using animal sentinels as a lens to the environment is in itself not new, as they have long been employed to detect human exposure to biological and chemical hazards (e.g., canaries in coal mines) (Rabinowitz et al., 2008; Reif, 2011), and more recently to detect the onset of natural disasters (Wikelski et al., 2020; Woith et al., 2018), epileptic seizures (Catala et al., 2019) or outbursts of violence (Bakeman et al., 2019). Elucidating the hitherto hidden information in the behavior of animals with cutting-edge technology can help us gauge the conditions of life on Earth (Wikelski & Tertitski, 2016). More specifically, this approach can expose illicit human activities, such as illegal fishing (Weimerskirch et al., 2020) and, as shown here, poaching. Our study is the first to document the use of untargeted sentinel behavior as an early warning against wildlife crime, yet our approach is generalizable beyond animals as sentinels. Similar methods could be utilized to detect anomalous behavior of people in crowds in response to a perceived threat (Mehran et al., 2009). Harnessing the collective sensing capacities of sentinels will thus not only innovate wildlife conservation and help turn protected areas into safe havens, it has the potential to advance many other applications as well.

6.4 Methods

6.4.1 Study system and species

This study was performed in Welgevonden Game Reserve (WGR), a privately owned game reserve in the Limpopo province, South Africa (24°10'S; 27°45'E to 24°25'S; 27°56'E). The reserve is located in the mountainous Waterberg region. WGR was established on former agricultural lands in the early 1980s and the main occurring vegetation types are Waterberg Mountain Bushveld and Sour Bushveld. The Waterberg region has a temperate climate, with two distinct seasons, characterized by the rainfall regime: a dry season ranging from April to September and a wet season ranging from October to March, with an average annual precipitation in WGR of 634 mm. Our study area is an enclosed breeding camp within WGR, with a size of approximately 1200 ha. Main predator species such as lion, cheetah and spotted hyena were excluded from this study area, as well as elephant and rhino.

WGR equipped 35 impala (*Aepyceros melampus*), 34 blue wildebeest (*Connochaetes taurinus*), 35 plains zebra (*Equus burchellii*) and 34 common eland (*Taurotragus oryx*) with a GPS and accelerometer sensor equipped custom made collar; an estimated 23% of the individual impalas present in the area, 48% of the eland, 40% of the wildebeest and 40% of the zebra. However, due to malfunctioning and errors made in the sensor development process, only 83 of the sensors yielded data at any point in time, thus lowering the effective density of sentinel animals. During the experimental intrusions (see below), the median number of data-yielding sensors was 47, and minimally 30. The animal movement data were recorded day and night and transmitted wirelessly in near real-time to five long-range low-power LoRa radiocommunication gateways in the study area, from where data packages were routed to an on-line data warehouse via a 3G/4G backhaul. The deployment of these sentinel animals were approved by the board and CEO of WGR as a management action and was performed in accordance with relevant guidelines and regulations.

6.4.2 Experimental intrusions

Between September 2017 and March 2018, WGR employees performed experimental intrusions (lasting ca. 2 hours) on foot and by car through the study area, at varying locations and movement routes through the study area, independent from the locations of the sentinel animals. The movement of the intrusions were tracked by GPS, and the relevant metadata for each intrusion recorded (mode of transport, group size, start time, end time). The intrusions were distributed in a stratified way over the mornings, middays and afternoons (with time slots relative to specific solar positions: sunrise, solar noon and sunset). Furthermore, the intrusions were temporally spread in such a way to avoid a disturbance overflow for the sentinel animals, by performing a maximum of five experiments per week and a maximum of two experiments per day (and then only with one intrusion in the morning and one in the afternoon).

6.4.3 Data gathering

The animal sensors gathered location data via GPS and overall dynamic body accelerations (Gleiss et al., 2011) (ODBA) via a tri-axial accelerometer (range ±2g; sampling frequency 100Hz, down-sampled to 10Hz prior to analysis). The GPS was scheduled to record spatial position at irregular intervals depending on the level of activity as gauged by ODBA. All sensors were scheduled to record locations every 15 minutes in the absence of sufficient activity (given that successive fixes were further than 5m apart, else a geofence was applied and the new coordinate was omitted to save bandwidth and battery power, thereby assuming that the animal still was at its previous location). The GPS fix rate was increased up to 2- or 10-minute intervals (depending on two different sensor settings) when ODBA indicated sufficient activity (after checking for the geofence). ODBA data were sampled continuously and summarized per 15 second window in a mean, maximum and variance value.

The experimentally intruding groups were outfitted with handheld GPS devices that recorded their location every 5 seconds and these groups logged and timestamped all their pre-defined activities and metadata on a tablet using CyberTracker during their intrusion (CyberTracker, 2017). Most cars traveling through the study area were tracked by GPS as well to filter the animal data for disturbances by cars unrelated to the experimental intrusions.

Weather data (temperature, radiation, precipitation and wind) in the study area were recorded on a 3-minute resolution with a weather station in the north of the study area. We assumed the 1200 ha study area to be sufficiently small to assume the weather station data to be representable for the prevailing weather conditions throughout the study area. GIS data of the study area (summarized in Table 6.2) consisted of information on topography, infrastructure (e.g., fences, roads, powerlines, etc.) and vegetation cover (supervised classification of 25cm resolution aerial imagery into four classes: trees, herbaceous/grass, sand/soil and other/built-up area).

All further data processing and algorithm development was done in the software R3.5.0 (R Core Team, 2020).

6.4.4 Data pre-processing

To link the animal location data with the intrusion location data, as well as to correct for the substantial level of positional noise present in the animal location data, we modelled the animal location data to regular 1-minute resolution trajectories using the following five steps. First, we filtered out large obvious errors (e.g., obvious outliers and irregularities such as locations far outside the study area) from the data. Second, we corrected systematic medium-scale outliers: ‘spikes’ that occurred due to positional outliers. Such spike-like outliers were visible during sensor testing while following known straight-line trajectories along an airstrip, thereby confirming that these spike-like geometries most likely resulted from positional error rather than true animal movement. Points were classified as anomalous spike points when (a) the displacement to and away from this point was high (>500m), (b) when the distance between the locations before and after this point was small, and (c) when the turning angle at this point approached 180 degrees. Therefore, we corrected the locations that were classified as spike-like anomalies by shifting them closer to the straight line between the neighboring points. The extent of this shift was set relative to the degree of spikiness of the points (the spikier the pattern, the larger the shift towards the midpoint of the adjacent coordinates). Third, after filtering and correcting the original locations we smoothed the timeseries of x/y coordinates at each original timepoint with a Kalman smoother using a dynamic linear model. Fourth, we linearly interpolated the locations to a 10 second resolution based on ODBA, where we considered the animal to be stationary between multiple timepoints if the accelerometer signal suggested the animal was not moving. Fifth, we fitted an X-spline through the data, where we gave the linearly ODBA-interpolated locations a smaller weight, and sampled the fitted spline on a regular 1-minute resolution. These pre-processing steps resulted in the modelled animal trajectory data, composed of spatial locations every minute, and averaged ODBA statistics per step (i.e., the segments between consecutive coordinates). These data were used as input for the next steps in the analyses. In contrast to the animal data, the raw intrusion data were of a high temporal resolution and spatial accuracy so that we only needed to subset the data in order to acquire 1-minute resolution time-synchronized intrusion trajectories.

The first three parts of the data pre-processing were only needed because of firmware issues in our custom-made sensors. Without these issues, a simple denoising technique like a Kalman filter will suffice.

6.4.5 Feature engineering and processing

We computed a plethora of human-engineered features from the animal trajectories, ODBA data, weather data and several GIS layers with environmental data from the study area (summarized in Table 6.2). All features were computed such that they could not directly be linked to specific points in space or time (by computing movement features relative to the environmental variables), so that only behavioral patterns and abnormalities therein could be linked to intrusion presence. After engineering these base features, we transformed certain features (after visual inspection of the histograms) to approximately symmetric distributions using logarithms. Then we truncated the distributions to the lower and upper 0.001 percentile to correct possible outliers. After that, we standardized all computed features to zero mean and unit variance per species. We also computed scaled versions of selected features by subtracting the mean and dividing by the variance of the selected features per reference set to capture deviations from normal behavior: (1) per area (characterized by a 30 by 30 m neighborhood around each grid cell), (2) per time of day (morning, midday, afternoon) in a period of five weeks around each intrusion or control, (3) per area per time of day per five weeks, and (4) per individual sentinel per time of day per five weeks (Table 6.2). Furthermore, after computing and standardizing the features, we computed more features by applying moving window computations (5 minutes centered, 10 and 20 minutes lagging, and the difference between these: 5 minutes centered minus 10 and 20 minutes lagging) on the standardized features to capture (the change in) the recent history of animal movement descriptors (mean and standard deviation of all features, fitted Mean Squared Displacement exponential function parameters, net-gross distance ratio and variance of log First Passage Times). Finally, we discretized all features to ordinal values to avoid odd-, fat- and heavy-tailed distributions. In total we computed 2117 features describing different aspects of movement geometry of individual trajectories, herd topology and the interactions with landscape variation.

6.4.6 Subsetting and dimensionality reduction

Before analyzing the computed animal movement features, we applied some filtering on the data. We removed all periods with an experimental intrusion during which there were less than 30 active animal sensors in total. We also removed data of both animals and intrusion when they were close to the reserve's main gate in order to avoid dilution of the data with other known disturbances. This resulted in 57 intrusions that were selected for further analyses. For every intrusion we selected control data of the same period one or two days earlier or later during which no intrusion took place, resulting in an approximately balanced intrusion-control dataset. Furthermore, we removed data from animals that were located within 250 m and within 20 minutes of a vehicle moving through the area that was not part of our experiment.

For each feature, we computed 4 importance metrics based on binary labelled data: records associated to locations within 1 km from the intrusion (subscript 1) versus an equally-sized random selection of data points during control periods (subscript 0): Mahalanobis distance, marginality (computed as $\frac{\mu_1 - \mu_0}{\sigma_0}$, for sample mean μ and sample standard deviation σ), specialization (computed as $\frac{\sigma_1}{\sigma_0}$) and the Mean Decrease Accuracy of a Random Forest classifier (with default hyperparameters). We then ranked the features according to their importance and selected a feature for further analyses if it occurred in the top 125 features for any of the 4 importance measures described above (resulting in a total of 361 selected features). Subsequently, we converted the selected features per main feature class (Table 6.2) to principal components, keeping those principal components that capture the most variation (in total 95%), which resulted in 99 selected components in total. Finally, we transformed these components again via a second principal component analysis, now across all the selected 99 components. In subsequent training of the animal behavior classifier, we optimized the total number of included components as a hyperparameter, which resulted in the first 8 principal components in the best performing classifier.

6.4.7 Labelling

We labelled the sentinel movement data through visual inspection of the animal and intruder trajectories, where we considered the animals' behavior to be undisturbed when the animal was not near an intrusion, or when the animal was close to an intrusion yet did not visually display a change in behavior. However, when the animal was near the intrusion and displayed a sudden or gradual behavioral change in response to intrusion proximity, we labelled the data as 'flight' (changing the movement direction away from the intrusion, possibly with increased speed) or 'regroup' (when individuals clustered together). In total, only ca. 1% of the animal data were associated to either flight or regroup behavior (which we will refer to as 'response' behavior). A few animals also appeared to exhibit behavior we could label as 'freeze', i.e., halting movement in the proximity of the intrusion, yet this class was too underrepresented to be accurately predicted and hence dropped from the final dataset. Furthermore, we assigned a qualitative measure of intensity to each labelled behavioral response ('low', 'medium', 'high') to describe how visually pronounced this response was. Besides the supervised labelling based on visual inspection of behavioral responses via video animations of the trajectories, we also labelled data using an unsupervised k-means nearest neighbor classifier, where we clustered the feature space consisting of the 99 features selected as described above into 25 clusters per species.

6.4.8 Animal behavior classification

We trained an RBF kernel C-classification Support Vector Machine (SVM) with a subsequent moving window over the outputted probabilities to distinguish undisturbed vs. response behavior. In the training datasets we only included the data separated by more than 1 km from the intrusion and labelled as 'undisturbed', and removed 90% thereof to train algorithms with a more balanced dataset. Furthermore, we only trained and validated on data with intrusions present in the area. We trained another SVM to distinguish the flight response from the regroup response. All computations were done in R 3.5.0 with the e1071 package on the Linux High Performance Cluster of Wageningen University and Research. We optimized the following hyperparameters and model settings during the training phase for the Average Precision via a grid search (with the selected values between brackets):

- gamma (undisturbed-response: $10^{-3.2}$; flight-regroup: $10^{-2.0}$);
- cost (undisturbed-response: $10^{-2.2}$; flight-regroup: $10^{-1.5}$);
- number of principal components to include as features (undisturbed-response: 8; flight-regroup: 12);

- species-specific models vs. one model with species dummy variables included in the features (species-specific models);
- specific models for the different times of day vs. one model with time of day dummy variables (one model);
- response intensities to include in the training data (only medium and high intensities);
- weights to assign to the classes (equal weights);
- the quantile to be computed of the SVM probabilities by the moving window (100%, i.e., maximum value);
- the alignment of the moving window (centered);
- the size of the moving window (15 minutes on both sides).

The best model was selected via a leave-one-intrusion-out cross-validation approach. We summarized the predictive performance by computing the Average Precision of the least occurring class (i.e., 'response' for the undisturbed-response model: 46%, Figure 6.5; and 'regroup' for the flight-regroup model: 80%, Figure 6.6). After having computed these probabilities with an SVM and a temporal window smoother, we tried to improve the predicted performance by including the predicted animal response probabilities of nearby animals. However, this spatial explicit approach hardly improved the predictive performance, indicating that the spatial contextualization of behavioral response was sufficiently captured by the computed features. We therefore did not include this spatial contagion effect of predicted animal response probabilities in the final analysis.

6.4.9 System classification - detection

Based on the predicted SVM response probabilities and feature cluster analysis, we computed summary features per 15 minutes of each intrusion and control period. These summary features related to the odds ratios of the probability of association of unsupervised clusters with intrusions vs. controls, the SVM predicted probabilities of behavioral response, and several features describing the values (and its spatial structure, e.g., clustering or autocorrelation) of these SVM predicted response probabilities. After computing summary features per 15 minutes, we summarized them even further for the intrusions vs. controls using the following eight statistics: mean, standard deviation, minimum, maximum, mean of the lagged differences, standard deviation of the lagged differences, minimum of the lagged differences and maximum of the lagged differences.

After computing the summary features, we build a logistic regression classifier to distinguish intrusions from controls. To create a parsimonious model, we iteratively added features to the model and evaluated its performance after each iteration. We evaluated the performance based on the model accuracy and performed validation through 25 times 2-fold cross-validation in a stratified way (by 25 times choosing a balanced random sample of intrusions and controls). We determined the sequence of adding features to the model by performing an independent two-sample t-test for each feature between the intrusions and controls. The feature with the largest t-value was then added to the model. After each feature addition, we removed its correlation with the remaining features using linear regressions with the added feature as independent variable and the remaining features as dependent variables, from which we extracted the residuals, standardized them to zero mean and unit variance, and applied the t-tests again. The (original) feature with the largest t-value was then added to the model again. This procedure was repeated until all features were ordered corresponding to their "importance". We then performed logistic regressions without interactions between the features for an increasing number of features (Figure 6.7). The model already performed quite accurately with only 7 features (86.1% accuracy ± SD 3.3%, precision 82.6% ± SD 6.9%, recall 89.2% ± SD 5.1%). However, with 20 features and 2-way interactions the model achieved the maximum accuracy (90.9%).

6.4.10 System classification - localization

The data gathered during intrusions that were correctly predicted as such by the detection classifier were used to train the intrusion localization algorithm. The probability surface of the location of the intrusion was fitted relative to that of the sentinel animals using:

$$O_{i,j} \sim \frac{p_j \left(f_{wn}\left(\theta_{i,j}, \mu_j, \rho_1\right) f_{ln}\left(\gamma_{i,j}, \mu_1, \sigma_1\right)\right) \left(1 - p_j\right) \left(f_{wn}\left(\theta_{i,j}, \mu_j, \sigma_0\right) f_{ln}\left(\gamma_{i,j}, \mu_0, \sigma_0\right)\right)}{f_{wn}\left(\theta_{i,j}, \mu_j, \rho_0\right) f_{ln}\left(\gamma_{i,j}, \mu_0, \sigma_0\right)}$$

where $O_{i,j}$ is the odds ratio of intrusion presence at location i evaluated for individual j, p_j is the SVM-predicted probability that individual j is exhibiting response behavior. The function f_{wn} is the wrapped normal probability density function, $\theta_{i,j}$ is the direction from location i to the location of the focal animal j, μ_j is the movement direction of individual j, ρ_1 and ρ_0 are the standard deviations of the unwrapped distributions. The function f_{ln} is the lognormal probability density function, where $\gamma_{i,j}$ is the distance of location i to j, μ_1 and μ_0 as well as σ_1 and σ_0 are the log-normal distribution parameters (respectively log-mean and log-sd).

The parameters μ_1, σ_1 and ρ_1 capture the geometry of intrusion-animal topology for animals that exhibited a predicted behavioral response to the intrusion. Similarly, μ_0, σ_0 and ρ_0 are the corresponding parameters for animals that were predicted to be undisturbed. The parameters μ_1, $log\left(\sigma_1\right)$ and $log\left(\rho 1\right)$ were fitted to the data assuming a 3rd order polynomial relationship to t_s: the time (in minutes) since the start of the predicted behavioral response (using the maximum F_1 classification score). Since the behavioral response signature is lost over time, we truncated t_s to 45 minutes (thus $t_s > 45$ minutes was set to $t_s = 45$). The parameters μ_0, σ_0 and ρ_0 were estimated using the data of the controls and with randomly generated intrusion locations in the study area, in order to correct for the effects of geometry of the study area on the predicted response surfaces.

The probability surface P_i was then calculated as:

$$P_i = \alpha \sum_j O_{i,j}$$

where α is a normalization constant so that P_i integrates to 1 over the area covered by the rectangular axis-aligned bounding box around the study area.

To measure the prediction accuracy of each localization surface, we simplified each surface to a point coordinate located at the location of maximum probability, and computed the Euclidian distance to the known true position of the intrusion. We then summarized each experimental intrusion by selecting the 10 prediction surfaces with the most condense highest probability density, i.e., those in which the top 5% probability density is contained in the smallest, most condense, area. The spatial error of the localization prediction associated with these selected predictions was further summarized by taking the average Euclidian distance over the 10 selected predictions.

6.5 Supplementary materials

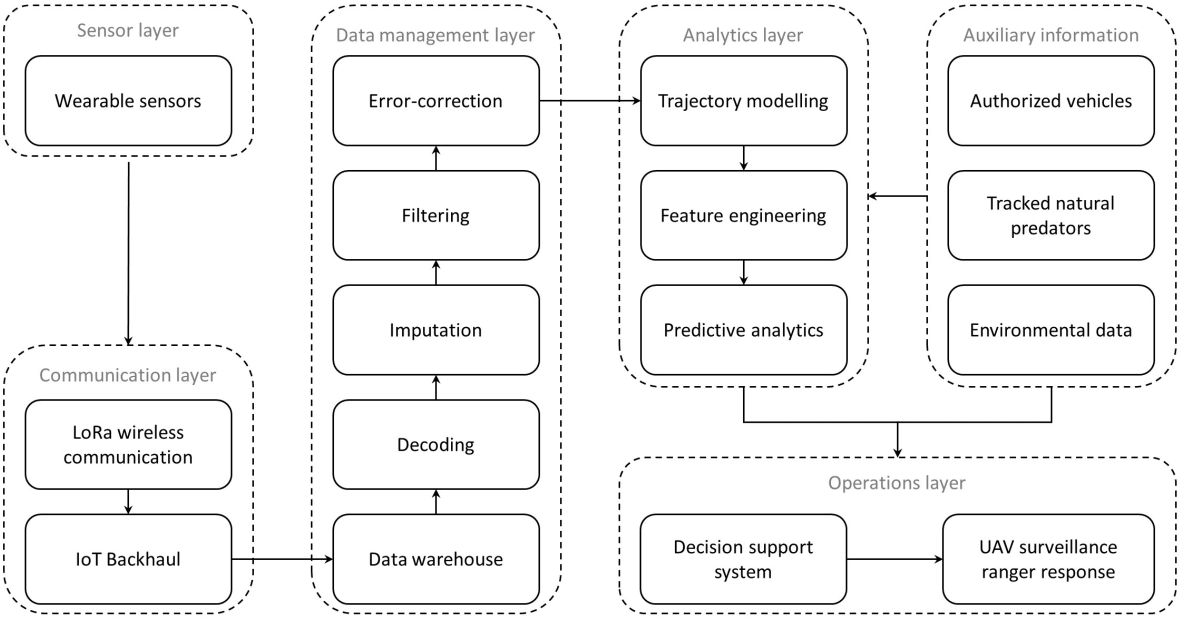


Figure 6.4: Schematic diagram of our proposed sentinel-based poacher early warning system.

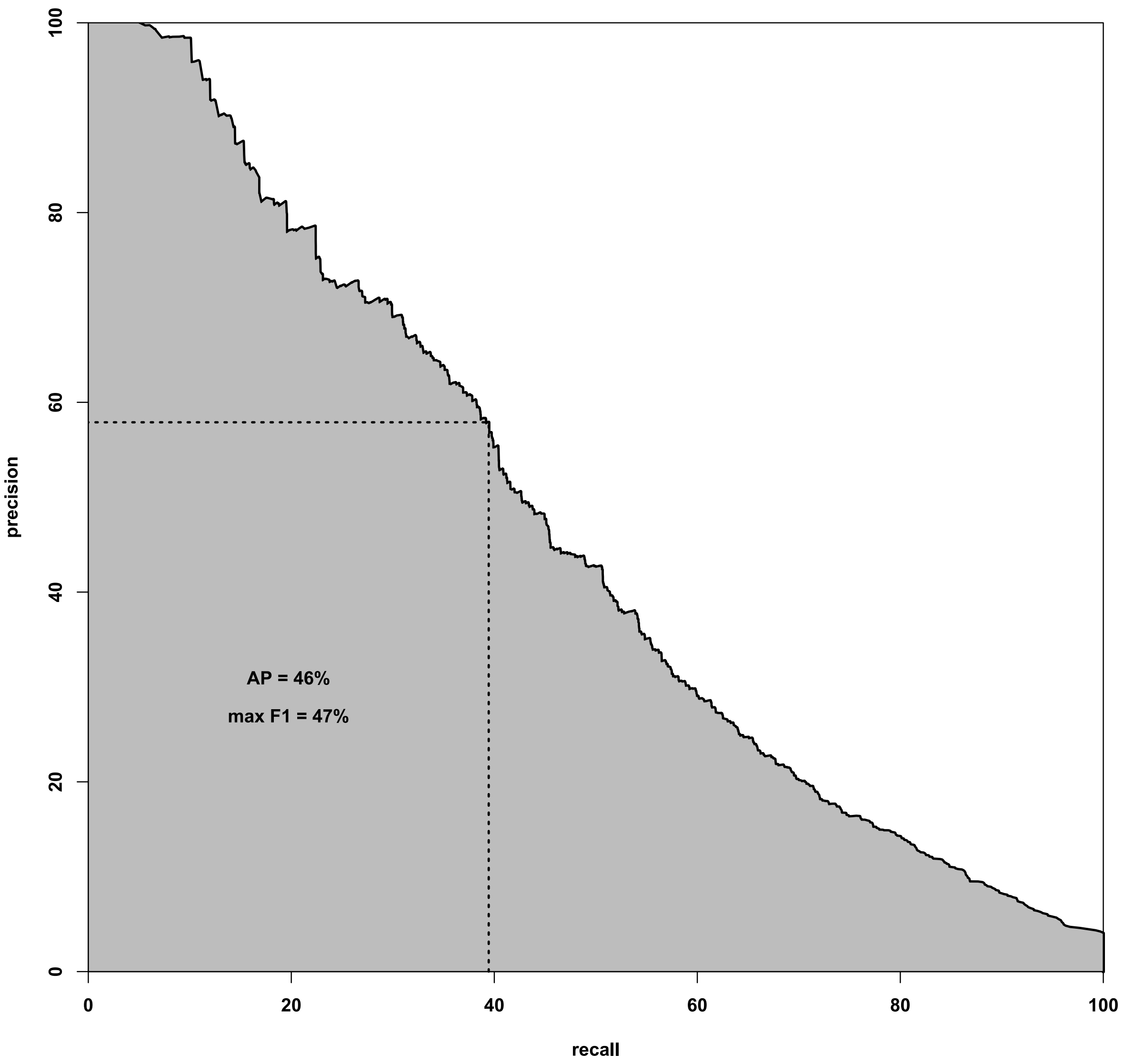


Figure 6.5: Precision-recall curve for ‘response’ of the undisturbed-response model. The dotted line indicates the maximum harmonic mean of precision and recall (F_1-score).

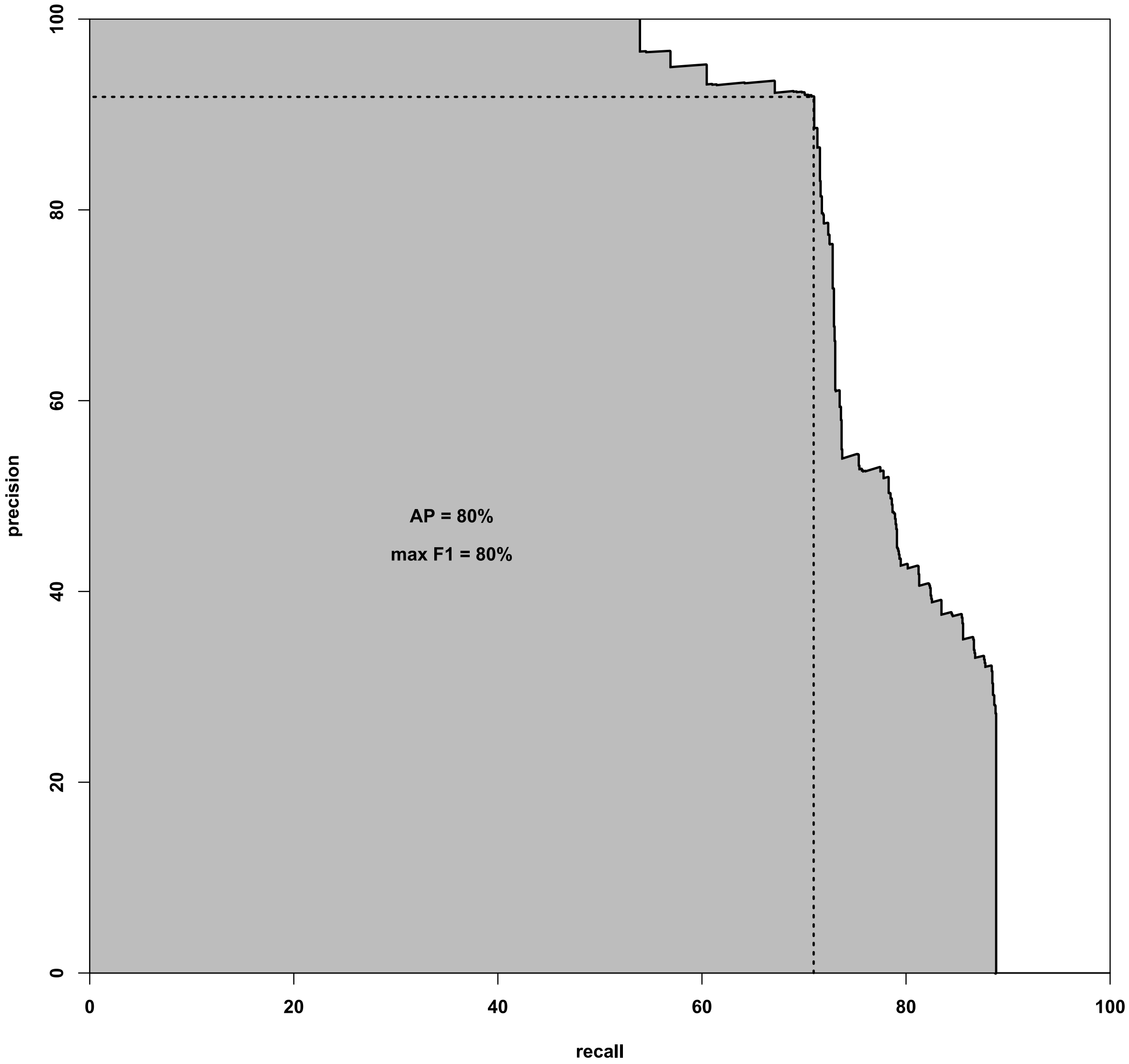


Figure 6.6: Precision-recall curve for 'regroup' of the flight-regroup model. The dotted line indicates the maximum harmonic mean of precision and recall (F_1-score).

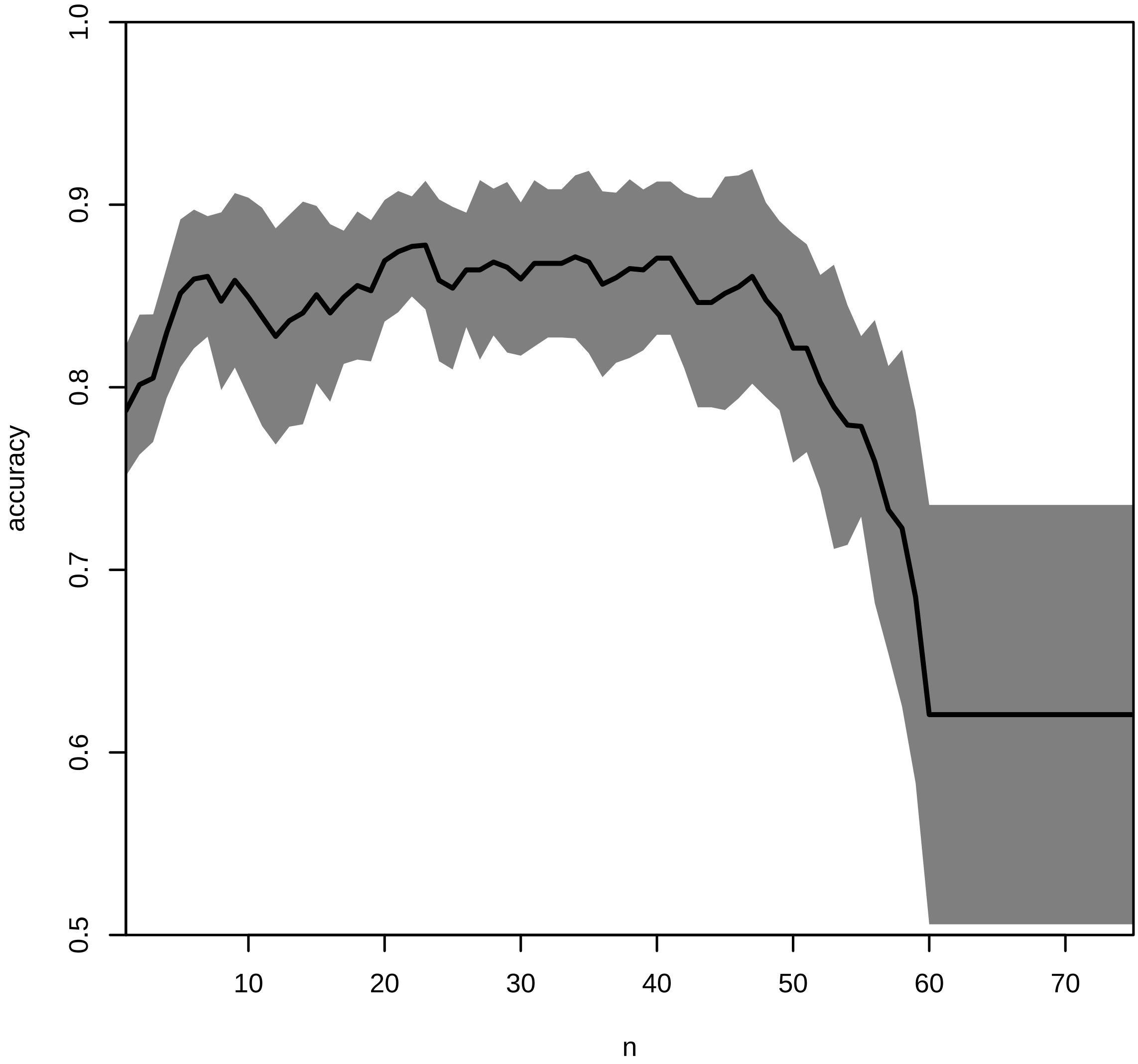


Figure 6.7: Accuracy vs. the number of features of the intrusion classification logistic regressions.

Table 6.2: Computed features per record. To capture deviations from normal behavior, features were scaled 0) per species and selected features were also scaled 1) per area (a 30 x 30 m neighborhood centered on each grid cell), 2) per time of day (morning, midday, afternoon) in the five weeks around each experimental intrusion or control, 3) per area per time of day per five weeks, and 4) per individual per time of day per five weeks. The means and variances used for scaling were computed from data in the absence of experimental intrusions. In total, this resulted in 2117 computed features (the set below, plus species identification and time of day; morning, midday or afternoon).

Main class	Sub class	Feature	Scaling
Individual movement geometry	Speed	Speed	0,2,3,4
		Scale parameter of a fitted SSM for speed[1]	0,1,3
		Shape parameter of a fitted SSM for speed[1]	0,1,3
		Value of the cumulative distribution function given a fitted SSM for speed[1]	0,1,3
		Log-likelihood of a fitted SSM for speed[1]	0
		Scaled deviation from maximum value of the pdf of a fitted SSM for speed[1] (with negative values when speed < mode)	0
	Relative headings	Absolute turning angle (TA)	0,2,3,4
		Cosine TA	0,2,3,4
		Concentration parameter of a fitted SSM for TA[2]	0,1,3
		Log-likelihood of a fitted SSM for TA[2]	0
		Scaled deviation from maximum value of the pdf of a fitted SSM for TA[2]	0
		Absolute centripetal turning angle	0,2,3,4
		Cosine centripetal turning angle	0,2,3,4
		Cosine relative angle to terrain aspect	0
		Cosine relative angle to feeding site	0
		Cosine relative angle to average movement direction	0,1,3

Table 6.2 continued from previous page

Main class	Sub class	Feature	Scaling
		Cosine relative angle to nearest track	0
		Cosine relative angle to nearest road	0
		Cosine relative angle to wind direction	0
		Cosine relative angle to terrain aspect, weighted for slope	0
		Cosine relative angle to feeding site, weighted for distance to feeding site	0
		Cosine relative angle to average movement direction, weighted for rho of movement directions	0,1,3
		Cosine relative angle to nearest track, weighted for distance to track	0
		Cosine relative angle to nearest road, weighted for distance to road	0
		Cosine relative angle to wind direction, weighted for wind speed	0
	Acceleration	Acceleration	0,2,3,4
		Angular acceleration	0,2,3,4
		Centripetal acceleration	0,2,3,4
		Centripetal angular acceleration	0,2,3,4
		Tangential acceleration	0,2,3,4
	Velocity	Absolute tangential velocity	0,2,3,4
		Centripetal velocity	0,2,3,4
	Compound features	First Passage Time (FPT) at 3m radius	0,2,3,4
		FPT at 9m radius	0,2,3,4
		FPT at 27m radius	0,2,3,4
		Slope of the radius vs FPT relationship	0,2,3,4
		Rate of exponential decay of the Velocity Autocorrelation Function (VAF) up to 15-minute time lag	0,2,3,4
		Rate of exponential decay of the VAF up to 30-minute time lag	0,2,3,4

Table 6.2 continued from previous page

Main class	Sub class	Feature	Scaling
Accelerometer-based features	Fraction moved	Estimated fraction of time moving	0,1,2,3,4
	Mean	Mean mean acceleration	0,2,3,4
		Mean standard deviation acceleration	0,2,3,4
		Mean peak acceleration	0,2,3,4
	Standard deviation	Standard deviation average acceleration	0,2,3,4
		Standard deviation standard deviation acceleration	0,2,3,4
		Standard deviation peak acceleration	0,2,3,4
Collective movement features (both computed across species, as well as for conspecifics only)	Relative angles	Cosine of relative heading compared to the weighted mean of headings of surrounding animals[3]	0,2,3,4
		Length of the weighted resultant vector of headings of surrounding animals[3]	0,2,3,4
		Cosine of relative heading compared to the weighted mean of headings of surrounding animals[3], multiplied by the weighted resultant vector length	0
		Cosine of relative heading compared to the weighted mean of headings of surrounding animals, multiplied by the weighted resultant vector length and sum of weights[3]	0
		Cosine of the relative heading towards the herd-center (the distance weighted mean coordinate of nearby animals[3])	0,2,3,4
	Distance	Distance towards the herd-center	0,2,3,4
		Distance towards the nearest animal	0,2,3,4
		Sum of distance-based weights[3]	0,2,3,4
Indices of space usage (at both the individual and species level)	Index of Habitat Suitability[4] (HSI)	HSI value at location of next record ('used')	0

Table 6.2 continued from previous page

Main class	Sub class	Feature	Scaling
		Mean and sd of HSI value in neighboring grid cells	0
		Measure of step selection: (used - mean) / sd	0
	Utilization distribution via Kernel Density Estimation[5] (KDE)	KDE value at location of next record ('used')	0
		Mean and sd of KDE value in neighboring grid cells	0
		Measure of step selection: (used - mean) / sd	0

---

[1] Fitted state-space model (SSM) for speed using a lognormal distribution, where the scale parameter and the logarithm of the shape parameter are related to environmental predictors via a linear predictor.

[2] Fitted SSM for turning angle using a wrapped Cauchy distribution where the expectation is 0 (i.e. no change of direction) and the concentration parameter (via logit link) related to environmental predictors via a linear predictor.

[3] The weight of surrounding animals decays with distance from the focal individual proportional to a normal distribution with mean 0 and standard deviation of 100m (scaled to have weight 1 at distance 0).

[4] MaxEnt habitat suitability prediction based on environmental predictors fitted per species per time of day in a window of 5 weeks around an experiment/control.

[5] Using an isotropic bivariate gaussian kernel with a bandwidth of 10m.

Chapter 7

Improving the precision and accuracy of animal population estimates with aerial image object detection

This chapter is based on:

Eikelboom, J. A. J., Wind, J., van de Ven, E., Kenana, L. M., Schroder, B., de Knegt, H. J., van Langevelde, F., & Prins, H. H. T. (2019). Improving the precision and accuracy of animal population estimates with aerial image object detection. *Methods in Ecology and Evolution*, *10*(11), 1875–1887. https://doi.org/10.1111/2041-210X.13277

Abstract

Animal population sizes are often estimated using aerial sample counts by human observers, both for wildlife and livestock. The associated methods of counting remained more or less the same since the 1970s, but suffer from low precision and low accuracy of population estimates. Aerial counts using cost-efficient Unmanned Aerial Vehicles or microlight aircrafts with cameras and an automated animal detection algorithm can potentially improve this precision and accuracy. Therefore, we evaluated the performance of the multi-class convolutional neural network *RetinaNet* in detecting elephants, giraffes and zebras in aerial images from two Kenyan animal counts. The algorithm detected 95% of the number of elephants, 91% of giraffes, and 90% of zebras that were found by four layers of human annotation, of which it correctly detected an extra 2.8% of elephants, 3.8% giraffes, and 4.0% zebras that were missed by all humans, whilst detecting only 1.6 to 5.0 false positives per true positive. Furthermore, the animal detections by the algorithm were less sensitive to the sighting distance than humans were. With such a high recall and precision we posit it is feasible to replace manual aerial animal count methods (from images and/or directly) by only the manual identification of image bounding boxes selected by the algorithm and then use a correction factor equal to the inverse of the undercounting bias in the calculation of the population estimates. This correction factor causes the standard error of the population estimate to increase slightly compared to a manual method, but this increase can be compensated for when the sampling effort would increase by 23%. However, an increase in sampling effort of 160 to 1050% can be attained with the same expenses for equipment and personnel using our proposed semi-automatic method compared to a manual method. Therefore, we conclude that our proposed aerial count method will improve the accuracy of population estimates and will decrease the standard error of population estimates by 31 to 67%. Most importantly, this animal detection algorithm has the potential to outperform humans in detecting animals from the air when supplied with images taken at a fixed rate.

7.1 Introduction

Estimating population sizes of animals is key in nature conservation (Davis & Winstead, 1980; Norton-Griffiths, 1978; Van Lavieren, 1982) and large-scale animal husbandry (Andrew et al., 2017; Chamoso et al., 2014). Accurate animal population estimates are important for farmers to determine the value of their companies and for game managers to optimize hunting strategies (Hearne et al., 2000; Mwakiwa et al., 2016; Van Lavieren, 1982), while precise estimates are important to follow population trends of rare and/or valuable wildlife species (Van Lavieren, 1982). Most of the animal population estimates are based on sample counts, where animals are only counted in a part of the area and the counts are afterwards extrapolated, which is cheaper and less time-consuming than total counts (Jachmann, 2001; Norton-Griffiths, 1978; Van Lavieren, 1982). Very often aerial counts are performed, which are the only practical way to estimate the population sizes of some animal species (Davis & Winstead, 1980; Jachmann, 2001; Norton-Griffiths, 1978; Van Lavieren, 1982). Although aerial counts are recommended for open landscapes without too much vegetation or terrain features blocking the view of the observers, many animal counts in forested areas are also performed from the air (LeResche & Rausch, 1974; Van Lavieren, 1982). The present-day method of estimating animal populations from aerial counts has not changed substantially since the 1970s (Jachmann, 2001; Nichols et al., 1996; Redfern et al., 2002), and suffers from imprecise and inaccurate population estimates (Davis & Winstead, 1980; Fleming & Tracey, 2008; Jachmann, 2001; LeResche & Rausch, 1974; Rabe et al., 2002; Stott & Olson, 1972; Van Lavieren, 1982). Low sampling efforts, e.g., sampled kilometres, are more rule than exception in aerial counts due to the high associated costs (De Bie & Kessler, 1983; DHV Consulting Engineers, 1980; Norton-Griffiths, 1978; Redfern et al., 2002). Decreasing the costs of aerial counts could lead to an increase in sampling effort and an increase in the precision and accuracy of population estimates (Davis & Winstead, 1980; Jolly, 1969a; Van Lavieren, 1982).

Achieving accurate and precise population estimates from aerial sample counts is notoriously difficult. When comparing aerial counts to the actual population size (often estimated using multiple and/or thorough ground counts) in environments that are not completely open, aerial counts generally underestimate the number of animals by 8 to 80% (Davis & Winstead, 1980; De Bie & Kessler, 1983; Dunn et al., 2002; Fleming & Tracey, 2008; LeResche & Rausch, 1974; Stott & Olson, 1972). This underestimation bias in aerial sample counts can be corrected by multiplying population estimates with a correction factor per species per stratum, viz., vegetation or terrain type, often based on a comparison of a subsample with thorough ground counts or a double-observer approach (Cook & Jacobson, 1979; Jachmann, 2002; Jolly, 1969b; Nichols et al., 2000; Norton-Griffiths, 1978; Van Lavieren, 1982). More elaborate methodological designs, i.e., distance sampling methods, make these correction factors also dependent on the animal sighting distance (Buckland et al., 2004). The correction factors that are used can be extremely large, even for very open savanna ecosystems factors as large as 13 have been reported (De Bie & Kessler, 1983), which have a large impact on the precision of population estimates (Jolly, 1969b). Sampling effort should ideally be based on preliminary surveys, but is in practice often dictated by logistics and financial considerations (Van Lavieren, 1982). Consequently, most population estimates from aerial sample counts have such low precision that only large changes of the population can be detected (Davis & Winstead, 1980). The underestimation bias depends not only on the animal species and environmental characteristics of a certain stratum, but also on sampling effort and human skill related factors (Caughley et al., 1976; Van Lavieren, 1982). Increasing the sampling effort by flying slower, lower, with narrower transects, and/or more transects, should result in an increase in accuracy and precision (Jolly, 1969a, 1969b; Norton-Griffiths, 1978; Van Lavieren, 1982). On the other hand, having a method that would not depend so much on the skill, fitness, and visual responses of different observers and pilots, could also increase the accuracy and precision of population estimates (Christie et al., 2016; Norton-Griffiths, 1978; Sirmacek et al., 2012; Van Lavieren, 1982).

An increase in sampling effort can most easily be obtained by an increase in sampling efficiency, which can be realized by a decrease in financial costs per sampling unit (Norton-Griffiths, 1978). To simultaneously increase the sampling efficiency and standardize the animal detection system, Unmanned Aerial Vehicles (UAVs) or microlight aircrafts with cameras and an automated image object detection algorithm are considered an alternative to manned aircrafts with human observers (Colefax et al., 2018; Linchant et al., 2015; Rey et al., 2017; Sirmacek et al., 2012). In the past decade this proposed method has been explored and tested in various studies (Hodgson et al., 2018; Kellenberger et al., 2018; Rey et al., 2017; Van Gemert et al., 2014). At first this method seemed too far-fetched to apply in practice (Van Gemert et al., 2014), but lately, due to developments in deep learning image recognition, the performance of this method increased enough to accurately and fully automatically count animals in homogeneous and open landscapes (Andrew et al., 2017; Chamoso et al., 2014; Hodgson et al., 2018), or semi-automatically in more challenging landscapes (Kellenberger et al., 2018; Rey et al., 2017). At present, semi-automatic aerial counts with UAVs or microlights and an image object detection algorithm supplemented by human verification of the algorithm's output, could be a feasible alternative to manual aerial counts (from images and/or directly) in any area where these manual aerial counts are appropriate (Kellenberger et al., 2018; Rey et al., 2017). The current challenges for this semi-automatic method are the small animals (in terms of pixel dimensions) in large images and the algorithms' ability to distinguish between species. However, the recent rapid development of Convolutional Neural Networks (CNNs) in image object detection has the potential to solve these issues (He et al., 2016; Lin et al., 2017; Lin et al., 2018).

Replacing manual aerial sample counts by the proposed semi-automatic method thus has the potential to improve the accuracy and precision of animal population estimates due to an increased sampling efficiency and a standardized animal detection system. In this study we evaluate the performance of a fully convolutional multi-class one-stage detector, called *RetinaNet* (Lin et al., 2018), to detect elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), and plains zebras (*Equus quagga*) in aerial images from two savanna animal counts in Kenya, 2014 and 2015. The performance of this algorithm is then used to compute the difference in sampling effort that is required to compensate for the gain or loss of precision due to the over- or undercounting bias of the algorithm compared to human counts. Moreover, we compare the accuracy of population estimates using manual versus semi-automatic aerial counts by comparing the human and algorithm detections of animals versus the distance to the aircraft, because most factors that cause animal counts to be biased are dependent on the sighting distance (Van Lavieren, 1982). Furthermore, we evaluate the costs of manual versus semi-automatic aerial counts and determine how much the sampling efficiency will improve when manual aerial counts are replaced with semi-automatic counts for the same total expenditure. Finally, we combine both the cost analysis and the animal detection algorithm to compute how much the precision of population estimates can improve when manual aerial counts are replaced with semi-automatic aerial counts.

7.2 Materials and methods

7.2.1 Data collection

All 561 images used in this study were collected by Kenya Wildlife Service during aerial sample animal counts with plane-mounted cameras in the Tsavo National Parks (Kenya, March 2014) and in the Laikipia-Samburu Ecosystem (Kenya, May 2015). These nature reserves are savanna ecosystems with varying tree-grass ratios. During the animal counts the images were manually taken by human observers upon spotting animal groups that were too large to count accurately while in the air, typically groups larger than five animals. The images were taken at speeds of 170 to 200 km/h between 90 and 120 m above the ground, facing both the left and right sides of the plane, and tilted slightly towards the ground creating strip widths of on average 200 m per camera. This resulted in the animals being small in the images, on average 50 by 50 pixels in images of 5000 by 3000 pixels, often poorly visible for the human eye. The images were pre-selected by Kenya Wildlife Service for the presence of elephant, giraffe and/or zebra, not excluding the presence of other animal species (e.g., impala (*Aepyceros melampus*), eland antelope (*Taurotragus oryx*), cattle (*Bos taurus*), and Cape buffalo (*Syncerus caffer*)), and annotated on an image-level detailing the number of individuals per species in the image. These numbers were estimated based upon human inspection of the images after the actual aerial animal count. We annotated the images on an animal-level by defining rectangular bounding boxes around the animals. These bounding boxes were finally checked and corrected by another author. Due to varying aircraft altitude and tilt, and various landscape, vegetation and animal characteristics, the animals in the images have different sizes, orientations, and body postures, and are possibly close to or behind each other, or partly visible because of vegetation and terrain (Figure 7.1).

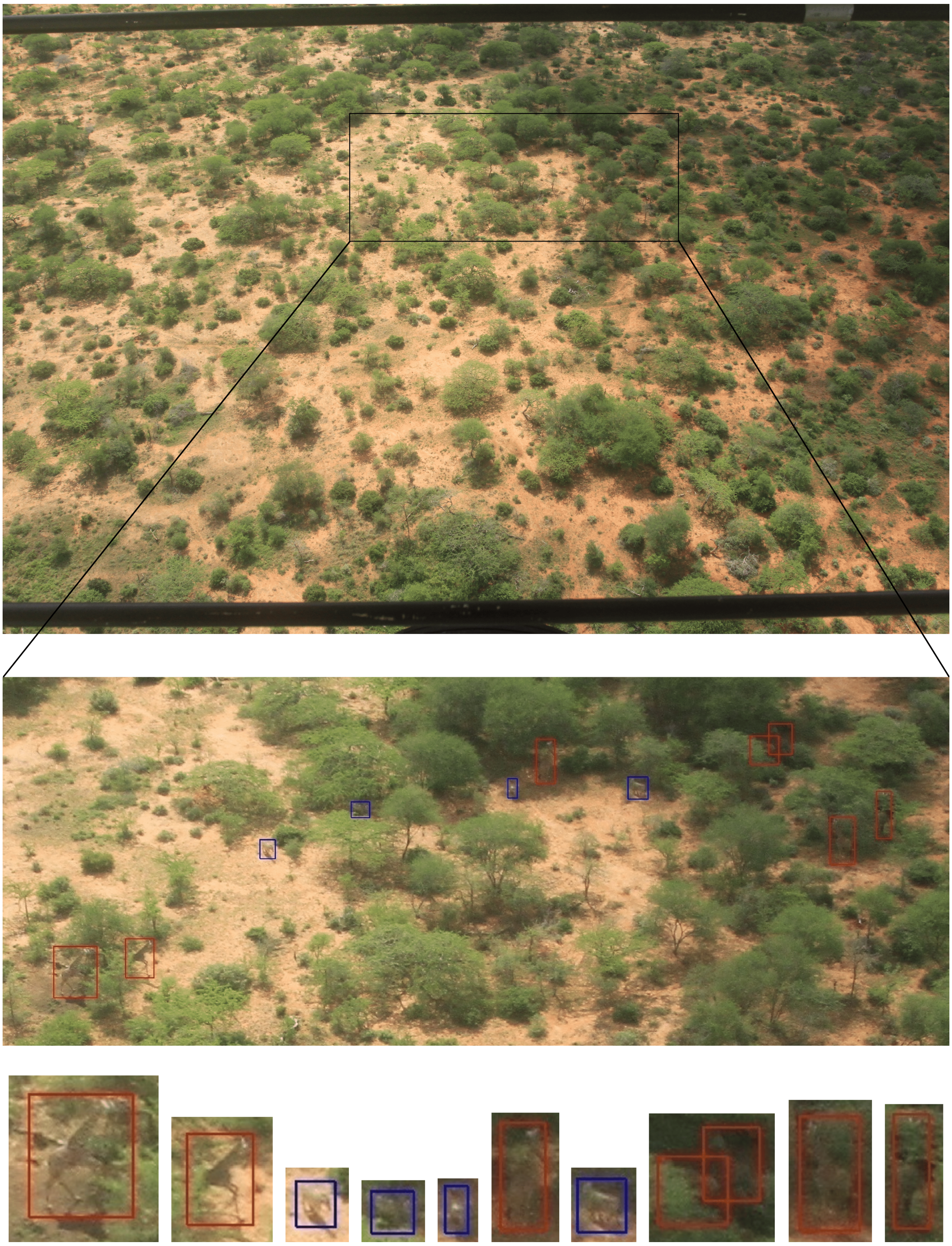


Figure 7.1: Example of an image containing giraffe and zebra. Top: entire image; Middle: part of image zoomed in, with annotated bounding boxes (red for giraffe and blue for zebra). Bottom: annotated animals from left to right.

7.2.2 Detection algorithm

We used the fully convolutional multi-class one-stage detector *RetinaNet* to detect animals in the aerial images (Lin et al., 2018). The architecture of *RetinaNet* is composed of a backbone network and two task-specific subnetworks (Figure 7.2). This algorithm takes entire images as input, constructs feature maps at different scale levels, generates region proposals at each scale level by means of “anchors”, and performs classification and bounding box regression for each anchor to predict the presence and location of objects in the input images. By using the *Focal Loss* function, training focusses on cases that are hard to classify, leading to high detection accuracy. For details about *RetinaNet* we refer to the study that proposed this algorithm (Lin et al., 2018).

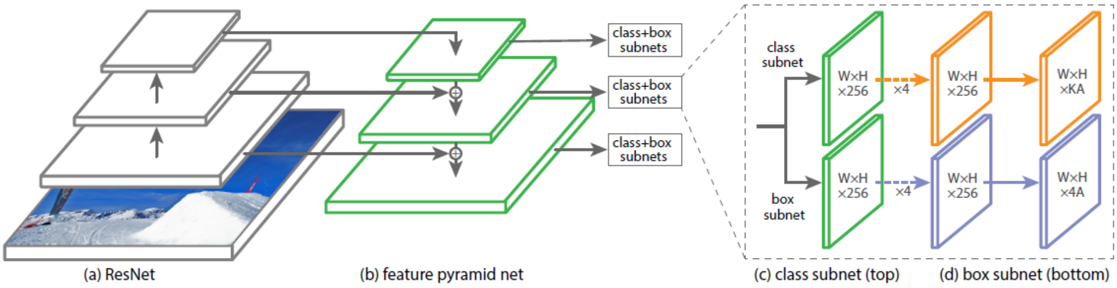


Figure 7.2: The architecture of *RetinaNet*, figure from Lin et al., 2018: a backbone network that consists of a feedforward *ResNet* (He et al., 2016) (a), connected to a Feature Pyramid Network (Lin et al., 2017) (b), computes a convolutional feature map over the entire input image at different scales. These feature maps are then input for two subnetworks: the first subnetwork computes the object classification (c) and the second subnetwork performs the bounding box regression (d).

We specifically used keras-retinanet 0.5.0 (Fizyr, 2018), an implementation of *RetinaNet* in Python 3.6.5 (Anaconda custom 64-bit) using Keras 2.2.4 with OpenCV 3.4.1, TensorFlow 1.11.0, GCC 7.2.0, pip 18.1, and numpy 1.14.5. Training and detection was done with a NVIDIA Tesla V100 16GB Graphics Processing Unit of an Amazon instance type p3.2xlarge (Amazon Web Services, 2018), running on Ubuntu 16.04.5 LTS (Linux 4.4.0-1069-aws) with CUDA 9.0.176. *ResNet-50* was used as the backbone and the algorithm was initialized with pre-trained weights on *ImageNet* (Deng et al., 2009). The algorithm was trained for 50 epochs with a batch size of 1 image and again for 50 epochs with a batch size of 2 images, which took on average 7 minutes per epoch for a batch size of 1 and 5 minutes for a batch size of 2. Batch sizes up to 7 were possible within the memory constraints of the system, but to limit the total computation time we stopped training at the batch size that performed less than the smaller batch size.

The 561 images were randomly divided into a training (70%), validation (10%), and test (20%) set (Table 7.1). The division of sets is thus based solely on the number of images, while some images contained many examples of a species, others contained only one example. However, the number of examples for each separate species closely approaches the 70/10/20 ratio that was used for the division of images. The original annotations in the images consisted of 1319 elephant, 1109 giraffe, and 1877 zebra in total. The images could not be used in their entirety as training input for the algorithm due to memory limitations. Therefore, the training images were first divided into 42 (7 by 6) equal-sized "tiles" each with 200 pixels overlap on all sides, resulting in tiles of on average 900 by 700 pixels. The overlap between tiles sometimes resulted in the same animal being present in several tiles, but made sure that every annotated animal was at least once fully present in a tile. Sometimes animals were only partly covered in a tile, but then we cut off a part of the tile to remove as much of this partly covered animal without removing the fully covered animals in the tile. We only trained the algorithm with the annotations from animals of which the bounding box were entirely covered in the tile, all partly covered animals were considered background. Also all the animals of species other than our three focal species were considered background. Furthermore, all training tiles were horizontally mirrored to be used as extra training data. We only used the tiles that contained at least one fully covered animal as training input for the algorithm, which resulted in approximately 10% of all the generated tiles. As the same example of an individual animal was sometimes present in several overlapping training tiles and because the total amount of training tiles was doubled due to the mirroring, the total number of training examples was 300% larger than the number of unique animal examples in the training images. For every 18 animals in the training set there was on average one partly covered animal.

Table 7.1: Number of images, tiles, and animal examples of each species per training, validation, and test set.

Set	**Images**	**Tiles**	**Species**	**Animals**
Training	393	3200	Elephant	2640
			Giraffe	2160
			Zebra	4182
Validation	56	n.a.	Elephant	140
			Giraffe	93
			Zebra	219
Test	112	n.a.	Elephant	288
			Giraffe	261
			Zebra	301

7.2.3 Algorithm evaluation

After each epoch during training, the resulting algorithm was saved and evaluated on a validation set. Detection was done on whole images and took on average 1.5 seconds per image, during which the images simply had to be forwarded through the trained algorithm. The algorithm that performed the best on the validation set was eventually evaluated on a test set, which also consisted of whole images.

The annotated bounding boxes were compared with the predicted bounding boxes per species using the Intersection over Union (IoU) measure, defined as the area of overlap divided by the area of union. A combination of an annotated box and a predicted box was potentially considered a True Positive (TP) when the IoU was equal to or larger than a certain threshold. However, every annotation and every prediction could only be used once to generate a TP, where priority was given to the combination with the largest IoU. Every prediction that was not coupled with an annotation after this process was considered a potential False Positive (FP) and every annotation that was not coupled with a prediction a False Negative (FN). Finally, we checked if the FPs were not actually TPs that were missed by the four layers of human annotation: 1, taking a photograph from the air upon spotting a group of animals; 2, counting the individual animals per species per image; 3, defining rectangular bounding boxes around the animals; and 4, checking and correcting the annotations. We chose a relatively low IoU threshold of 0.3, because the accurate positions of animals in the image is often of no importance for animal counts and the annotation of the bounding boxes around the animals was often ambiguous due to occlusions.

To evaluate the algorithm performance over all bounding boxes in all images, precision/recall curves per species were used (Equation 7.1; Equation 7.2). These curves were computed by varying the threshold for the class prediction probability (score confidence threshold) that was given by the algorithm to each bounding box. The Average Precision (AP), defined as the area below the precision/recall curve, was used to quantify the algorithm's performance in detecting a specific animal species. The mean Average Precision (mAP) of all three animal species was used to quantify the overall algorithm's performance. The algorithm with the highest mAP on the validation set was then evaluated on the test set.

$$\text{Precision} = \frac{\#TP}{\#TP + \#FP} \tag{7.1}$$

$$\text{Recall} = \frac{\#TP}{\#TP + \#FN} \tag{7.2}$$

Where $\#TP$ is the number of True Positives, $\#FP$ the number of False Positives, and $\#FN$ the number of False Negatives.

Furthermore, to provide a comparison of the difference in accuracy between human observers and the algorithm, the proportion of detections were visualized versus the horizontal distance to the aircraft for both the humans (annotations) and the algorithm (predictions). As the visual field on the ground of both humans and cameras from the air is a trapezoid, the ground area per pixel at the top of the image is larger than at the bottom of the image. This area is proportional to the distance from the aircraft to the ground, so a geometric expectation of the animal detections versus the distance to the aircraft can be formulated as more animals are expected to be present in a larger area. Therefore, the animal detection method that is more accurate and thus less influenced by the distance to the aircraft, should have a detection curve that is more similar to the geometric expectation.

7.2.4 Population estimate precision

The over- or undercounting bias by the algorithm compared to the manually annotated animals requires an extra correction factor for the population estimate on top of the regularly used correction factor for manual counts. The extrapolation of population sizes based on insight gathered in previously undertaken surveys, for example using aerial/ground count comparisons, distance sampling methods, and/or double-observer approaches, can thus still be used but should now be supplemented with this extra correction factor. This counting bias can be computed by dividing the algorithm's recall with the humans' recall, with the inverse of this counting bias to be used as the correction factor. This should be done per species and ideally per stratum, viz., vegetation or terrain type, as well. This correction factor can be larger or smaller than one, depending on whether the algorithm counts less or more animals than humans did. When the population estimate is multiplied with a constant correction factor, the standard error of the population estimate changes with the same factor. To compensate for the change in standard error of the estimate, a change in sampling effort of the area is needed. Equation 7.3 summarizes the solution about how much the sampling effort needs to change to achieve a standard error of the (semi-)automatic method that is equal to the manual method (see section 7.5):

$$N = r^{-2} \tag{7.3}$$

Where N is the index detailing how much the number of sampling units needs to change, and r is the counting bias.

To compute to what extent the standard error of the population estimate can decrease by spending the same amount of finances on our proposed semi-automatic aerial count method as on a manual aerial count method, first the costs per sampled kilometre were compared (see section 7.5). Using the sampled kilometres as a unit to calculate the costs of an aerial count is a common practice in wildlife management (Norton-Griffiths, 1978). A difference in costs of a factor k in favour of the semi-automatic method can be translated to an increase in sampled kilometres by k when the same total amount of finances are spent. An increase in sampled kilometres by k would result on average, either with equal- or unequal sized sampling units, in an increase in sampling units by k when the same strip width is sampled. The decrease in a population estimate's standard error with an increase in sampling units by k can be computed, thereby taking into account the initial change in standard error by r^{-1} (see section 7.5):

$$S = \left(r\sqrt{k}\right)^{-1} \tag{7.4}$$

Where S is the index detailing what the standard error of the population estimate from semi-automatic counts will be compared to manual counts by spending the same amount of finances on the semi-automatic method as on the manual method, and k is the increase in sampling units.

7.3 Results

7.3.1 Algorithm evaluation

The algorithms trained with a batch size of 1 performed overall better than the algorithms with a batch size of 2 (Figure 7.3), with the algorithm from epoch 36 of a batch size of 1 having achieved the largest mAP (0.81) on the validation set (Figure 7.8).

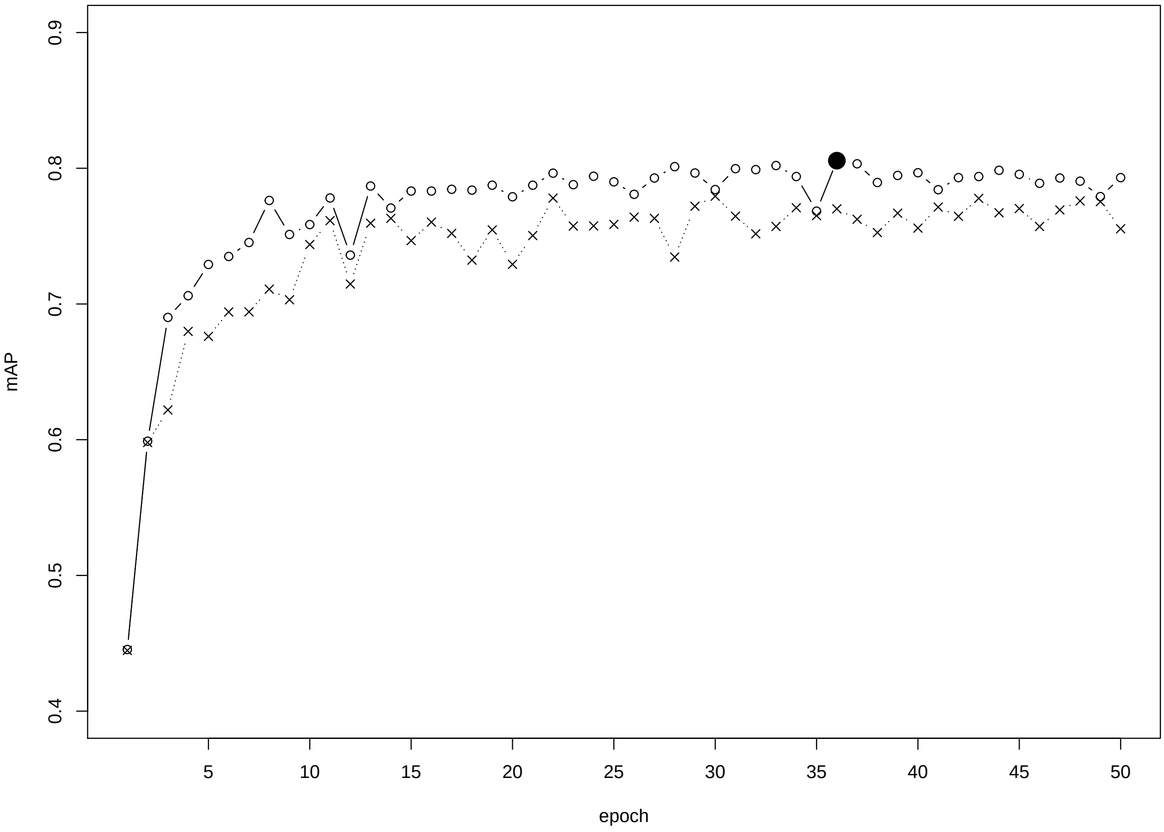


Figure 7.3: Mean Average Precision (mAP) obtained on the validation set for the algorithms of the 50 epochs from both a batch size of 1 (solid line with dots) and 2 (dashed lined with crosses). The solid dot marks the algorithm that performed the best on the validation set ($mAP \approx 0.81$).

The best performing algorithm on the validation set was applied to the test set and achieved a mAP of 0.77, with an AP of 0.81 on elephant, 0.79 on giraffe, and 0.72 on zebra (Figure 7.4). When applied to the training images, this algorithm achieved a mAP of 0.86, with an AP of 0.87 on elephant, 0.92 on giraffe, and 0.80 on zebra (Figure 7.9). This suggests that the training set size is acceptable, but possibly the detection of giraffe (the least occurring species in our dataset) would improve with more training data (Table 7.1). The maximum recall reached was 0.92 for elephant, 0.87 for giraffe, and 0.86 for zebra, with elephant having an accompanying precision of 0.26, giraffe of 0.38, and zebra of 0.17 (Figure 7.4). The maximum F_1-score, i.e., the harmonic mean of the recall and precision, was 0.76 for elephant, 0.78 for giraffe, and 0.71 for zebra (Figure 7.4). F_1-scores are good performance indicators when the algorithm is considered to be used in a fully automatic animal detection system. The predicted bounding boxes with a score above the mean of the score thresholds corresponding to the maximum F_1-scores detect many of the annotated animals, but miss the inconspicuous ones to prevent predicting many FPs (Figure 7.5). There was little confusion between species at this score threshold, for elephant 4% of the predictions were on other species, for giraffe 5%, and for zebra 1%.

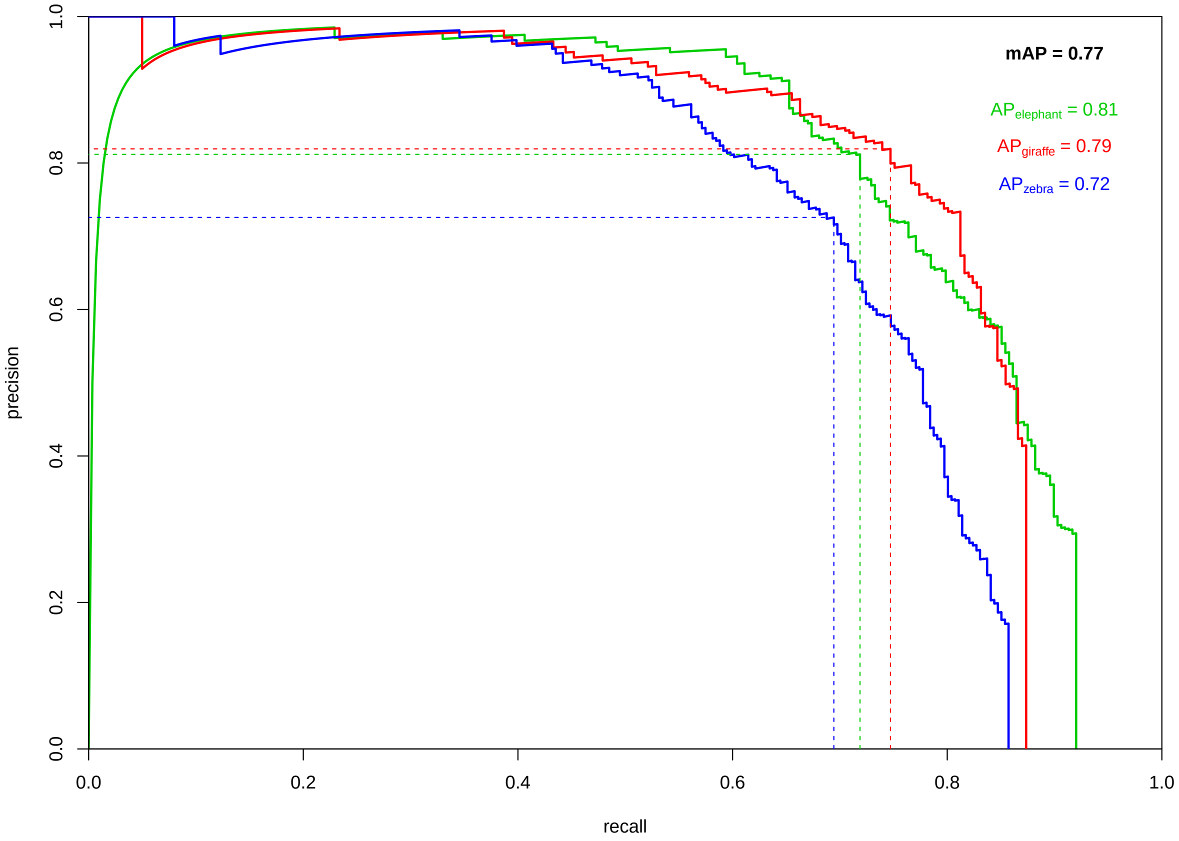


Figure 7.4: Precision/recall curves of the animal detection algorithm for elephant ($AP \approx 0.81$), giraffe ($AP \approx 0.79$), and zebra ($AP \approx 0.72$) on the test set ($mAP \approx 0.77$). The precision/recall combinations with the highest F_1-scores (0.76 for elephant, 0.78 for giraffe, and 0.71 for zebra) are marked with dashed lines.

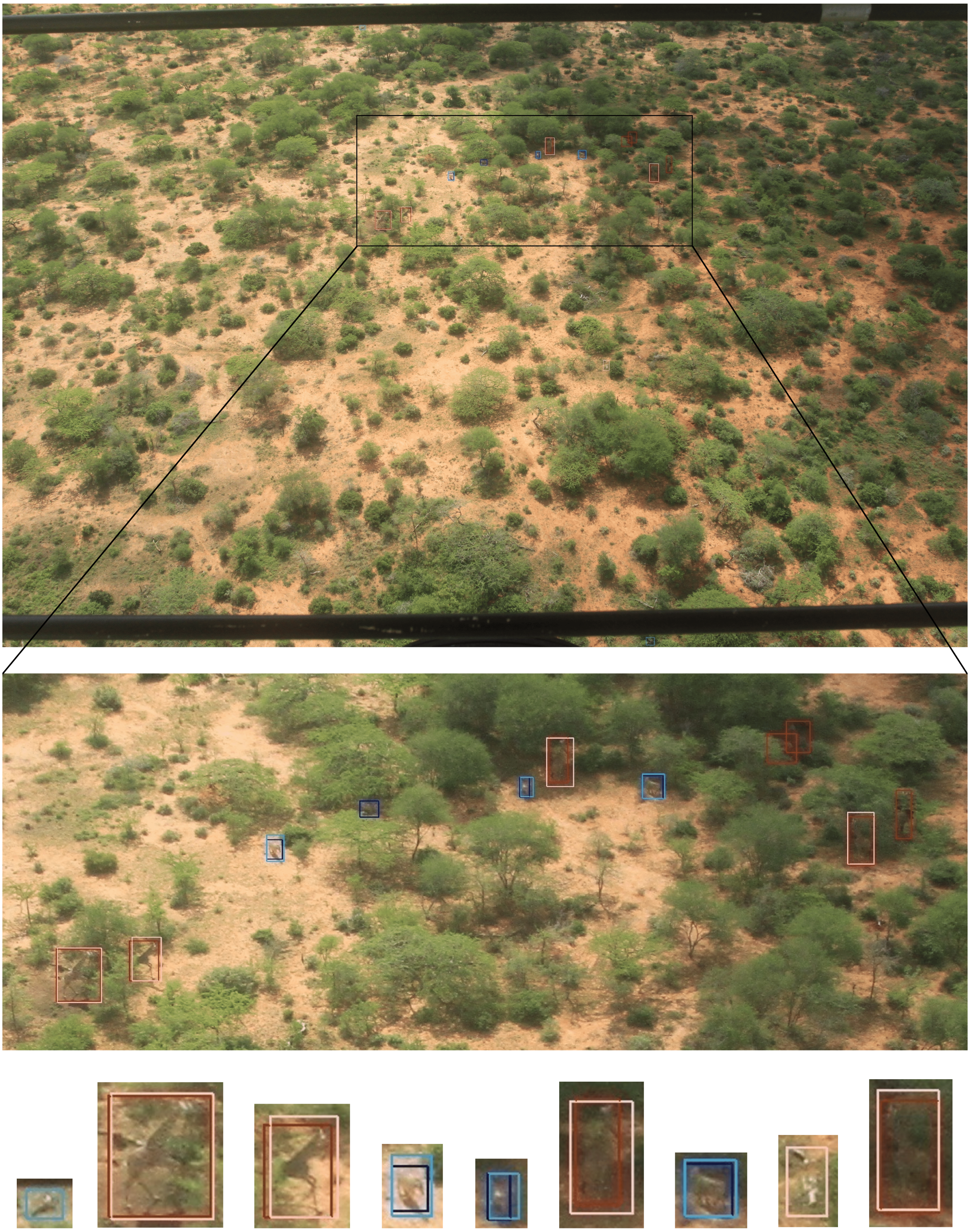
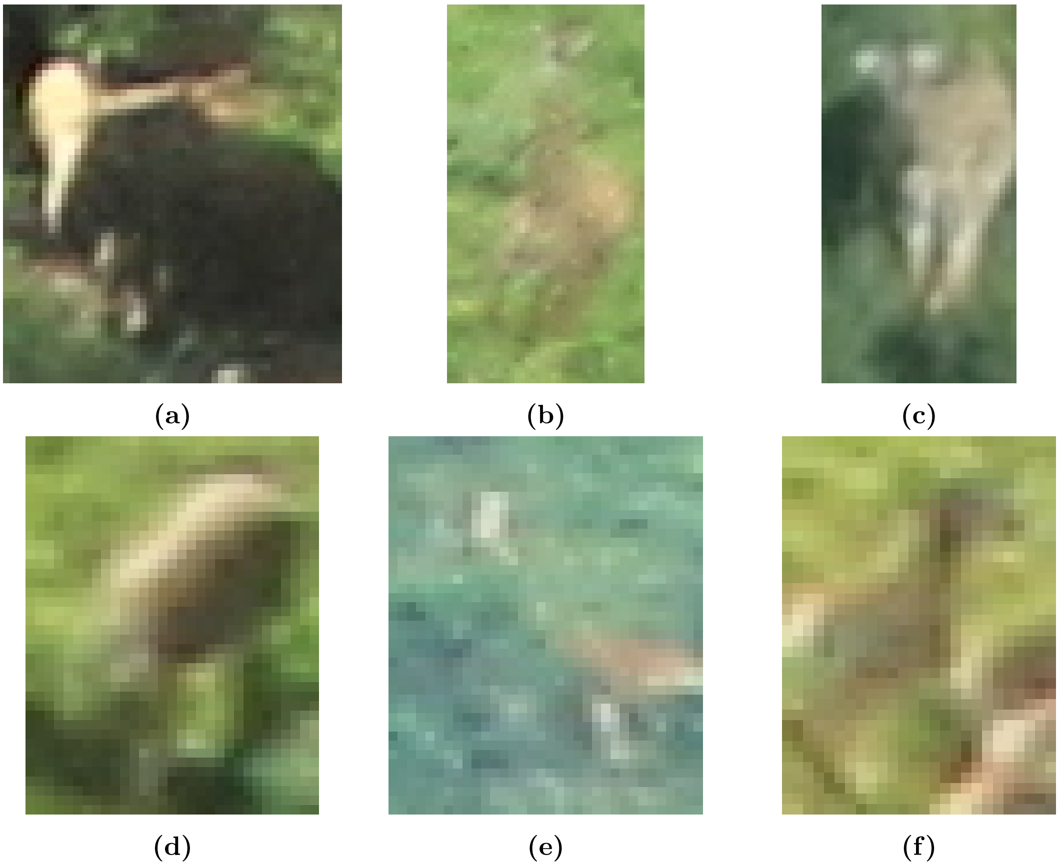


Figure 7.5: Predicted bounding boxes using a score confidence threshold corresponding to the mean of the scores with the maximum F_1-score. The presented image is the same as Figure 7.1, including the annotated bounding boxes. The predicted bounding boxes have lighter colour than the annotated bounding boxes (red for giraffe and blue for zebra). Top: entire image; Middle: part of image zoomed in. Bottom: predicted bounding boxes from left to right.

The top 17% of the FPs with the highest score confidences (361 bounding boxes, with a score confidence between 1 and 0.4) were visually checked to determine if they were not actually TPs that were missed by the four layers of human annotation. It turned out that 20 of these detected bounding boxes (4 elephants, 8 giraffes, and 8 zebras) were actually correctly predicted, but missed during annotations (Figure 7.6a; Figure 7.6b; Figure 7.6c). Furthermore, 25 other detected bounding boxes (10 elephants, 6 giraffes, and 9 zebras) could potentially also be TPs but were too vague to be determined with certainty (Figure 7.6d; Figure 7.6e; Figure 7.6f). We considered this task of verifying detected bounding boxes comparable to verifying human-annotated bounding boxes and also considerably easier and quicker than when scanning entire images for the presence of animals, with the effect of fatigue and visual context being far less important as it was near impossible for a human to overlook an animal within a small bounding box.



(a) (b) (c)

(d) (e) (f)

Figure 7.6: Examples of (a,d) an elephant, (b,e) giraffe, and (c,f) zebra that were missed by four layers of human annotation, but detected by the algorithm. Top examples (a-c) are clear TPs, bottom examples (d-f) are potential TPs.

We estimated that the algorithm found 30 animals in total (8 elephants, 10 giraffes, and 12 zebras) that were not found by the four layers of human annotation. When plotting the cumulative number of FPs, clear TPs and potential TPs versus the score threshold, 30 animals is clearly a conservative estimate when assuming that all the FPs until the minimum score would have been evaluated (Figure 7.11). To compute the counting bias of the algorithm compared to humans, we divided the algorithm's maximum recall with the recall of the humans (using all the TPs found by both the humans and the algorithm as the total). This resulted in an undercounting bias of $\frac{\frac{TP_{\text{model}}}{TP_{\text{total}}}}{\frac{TP_{\text{human}}}{TP_{\text{total}}}} = \frac{\frac{265+8}{288+8}}{\frac{288}{288+8}} \approx 0.95$ for elephant, $\frac{\frac{228+10}{261+10}}{\frac{261}{261+10}} \approx 0.91$ for giraffe, and $\frac{\frac{258+12}{301+12}}{\frac{301}{301+12}} \approx 0.90$ for zebra.

The cumulative proportions of detections by both the human annotators and the algorithm were compared versus the horizontal distance to the aircraft (Figure 7.7). The cumulative algorithm detections were more in line with the geometric expectation of animal detections ($R^2 = 0.97$) than the human detections were ($R^2 = 0.85$), with the algorithm detections following the pattern of the expectation well. The human detections display a clear optimum between 125 and 200 m from the aircraft (where the slope of the cumulative human detections is substantially larger than the slope of the geometric expectation and the cumulative model detections), but perform less well below and above this distance range.

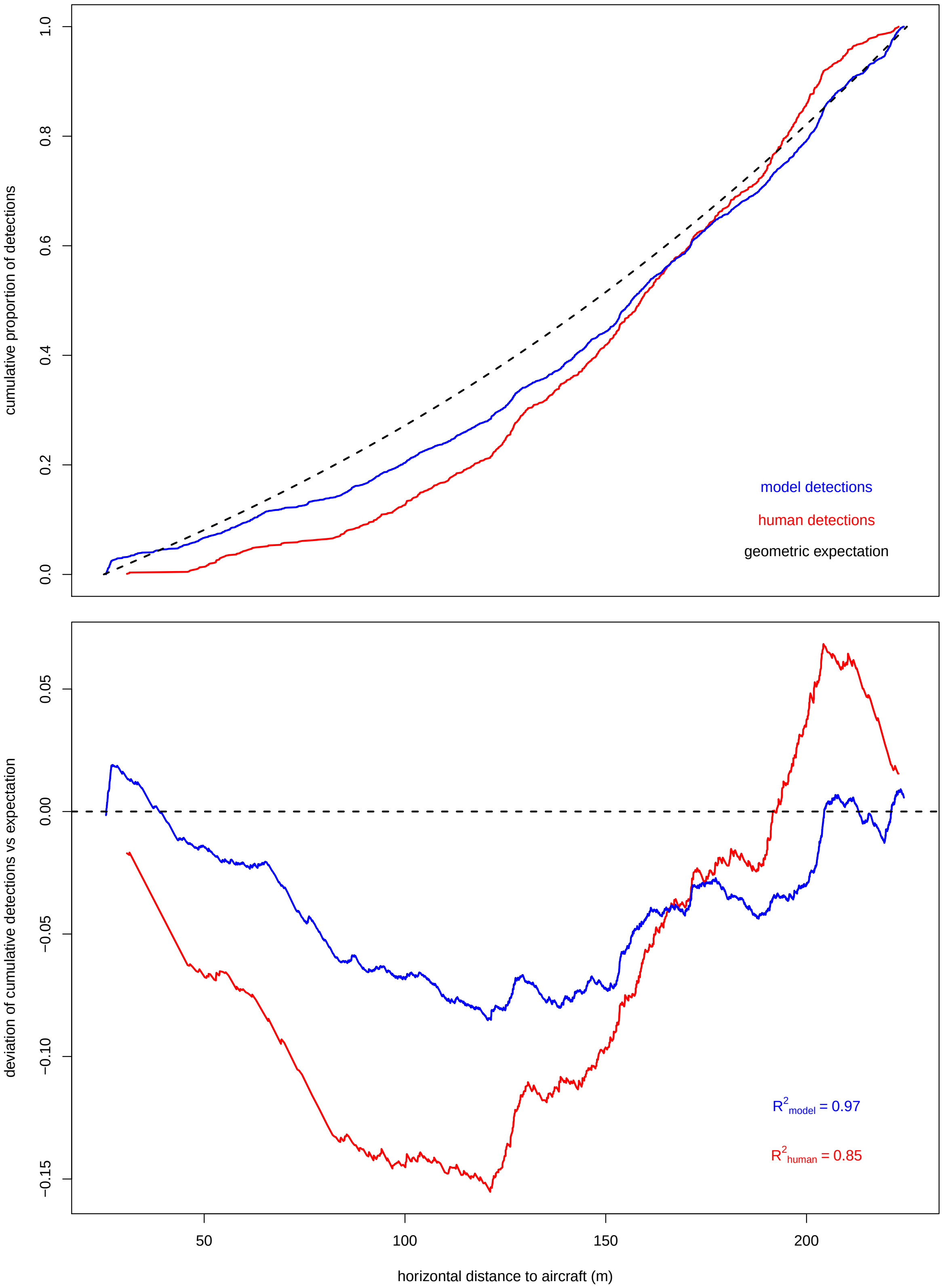


Figure 7.7: Top: the cumulative proportion of animal detections by both the algorithm and human observers versus horizontal distance to the aircraft (m). The geometric expectation is computed based on the trapezoid shape of the visual field on the ground from the air of a human eye and a camera. Bottom: the deviation from the geometric expectation of both the cumulative proportion of animal detections by the algorithm and human observers.

7.3.2 Population estimate precision

Using the minimum of the three aforementioned values of the algorithm's undercounting bias compared to human annotations ($r = 0.9$), it follows from Equation 7.3 that the increase (N) in sampling units that is needed to achieve a decrease in standard error of the population estimate (S_Y) equal to r is:

$$N = \frac{n_{\text{automatic}}}{n_{\text{manual}}} = r^{-2} = 0.9^{-2} \approx 1.23$$

The costs per sampled kilometre of various helicopter and fixed-wing manual count methods, using direct observations, manual image verification, and a combination, were compared with the expected costs of our proposed semi-automatic method using UAVs and microlights with an animal detection algorithm (see section 7.5), from which follows that the costs can be reduced by a factor 2.6 to 11.5. Using these factors ($k = 2.6$ to $k = 11.5$) and the undercounting bias ($r = 0.9$), it follows from Equation 7.4 that the factor by which the standard error of the population estimate will change (S) is:

$$S = \frac{S_{Y,\text{automatic}}}{S_{Y,\text{manual}}} = \left(r\sqrt{k}\right)^{-1} = \left(0.9\sqrt{2.6}\right)^{-1} \approx 0.69$$

to

$$S = \left(0.9\sqrt{11.5}\right)^{-1} \approx 0.33$$

7.4 Discussion

Our animal detection algorithm detected 92% of all the human-identified elephants, 87% of the human-identified giraffes, and 86% of the human-identified zebras in the aerial imagery from two Kenyan savanna animal counts. Furthermore, the algorithm correctly detected an extra 2.8% of elephants, 3.8% giraffes, and 4.0% zebras that were missed by four layers of human annotation. Having an algorithm that has a minimum undercounting bias of 90% compared to humans, will result in a correction factor of 0.9-1 for the animal population estimates and thus an increase of 11% in the standard error of the population estimates. This increase in standard error can be compensated for with an increase in sampling effort, e.g., sampled kilometres, of 23%. However, we conclude that the costs per sampled kilometre can be reduced with 160 to 1050% when manual aerial counts are replaced by counts with UAVs or microlights and image object detection software, where detected bounding boxes have to be verified by humans. Moreover, with our algorithm there will be only 2.9 false positive bounding boxes per true positive for elephant, 1.6 for giraffe, and 5.0 for zebra, when the maximum number of animals are correctly detected by the algorithm. With this semi-automatic aerial animal count method it is thus possible to sample 160 to 1050% more units, e.g., kilometres, for the same costs, which will result in an increase of the accuracy of animal population estimates and an overall decrease of the standard error of 31 to 67%. Furthermore, this standard error will likely decrease even more in practice, because UAVs or microlights carrying cameras with zoom lenses can probably fly higher than manned aircrafts whilst still being able to count the animals. This will increase the sampling efficiency further. Finally, the animal detections by the algorithm were less sensitive to the sighting distance than the human detections were. This highlights the fact that an animal detection algorithm is less sensitive to factors like the speed the landscape is passing by, the angle of vision to the ground, the “size” of the animals, and visual cues triggering a focus. This indicates that a semi-automatic method will result in more accurate population estimates than a manual method, as human observers had a clear optimum in animal detections between 125 and 200 m from the aircraft.

Our animal detection algorithm performed better than previously published algorithms for aerial imagery of mammals in similar habitats (Kellenberger et al., 2018; Rey et al., 2017; Sirmacek et al., 2012), whilst also being able to differentiate between animal species. Furthermore, this is likely the first evidence of an algorithm detecting animals that multiple layers of humans were not able to detect. Therefore, we posit that this algorithm is likely to outperform humans in the detection of animals from an aircraft when images are taken at a fixed interval, instead of only when animals are spotted by human observers.

As with many new technological developments, implementing this semi-automatic method requires some initial work and potentially schooling of personnel. An animal detection algorithm should first be trained for a new area and animal species and verified with manual count data to compute performance measures. However, previously collected aerial image footage can potentially be used as input data for this task. Annotating the images by drawing bounding boxes around the animals is the most time-consuming part of this process, which took us on average two minutes per image per person. Training and validating the algorithm is a matter of hours when running the analysis on a dedicated server with pre-installed software. As with all deep learning applications, performance improves with more training data, which implicates that rare species will be more difficult to distinguish from other species. In a semi-automatic approach this can be dealt with by merging for example all medium-sized antelopes into one class for the algorithm, with humans doing afterwards the species determination. Moreover, as cameras can be equipped with zoom lenses and can generate high-resolution images, the potential can be explored to count smaller animal species as well than done in manual aerial counts. Furthermore, some argued that UAVs are less suited for animal counts compared to manned aircrafts because of their smaller action radius (Christie et al., 2016). We concur that UAV flying can be restricted to the pilot’s line of sight due to national legislations, which causes microlights to be more ideal for semi-automatic game counts in large, hilly and/or densely vegetated areas. However, because of the low costs of UAV equipment versus manned aircrafts, it is possible for a single UAV pilot to transport multiple batteries, mobile battery chargers, and/or UAVs for a single animal count and therefore still cover a large area per day. Moreover, factors that influence animal visibility still impact the semi-automatic counts, just like they impact manual aerial animal counts. However, practices that can be employed to correct manual aerial counts for varying animal visibility, e.g., detection curves in distance sampling methods (probability of spotting an animal vs. distance to aircraft), sighting-probability models (probability of spotting an animal vs. various external factors), area division in strata, and ground count comparisons (Buckland et al., 2004; Norton-Griffiths, 1978), can still be applied to semi-automatic counts. In this study we computed a single correction factor in order to derive the potential increase in population estimates' precision, but this should in practice be done per species per stratum and can be a function of sighting distance and external factors as well. With semi-automatic counts there is also the potential to estimate the fraction of animals that are missed by both humans and the algorithm together by using the double-observer approach during the model building phase (where one observer is now the algorithm), which could give extra information about the actual population sizes (Cook & Jacobson, 1979; Nichols et al., 2000). Furthermore, as UAVs and microlights can carry on-board sensors that accurately monitor and record speed, altitude and tilt, and the aerial imagery allows all kind of landscape, terrain and vegetation characteristics to be recorded for every part of the count, it is now possible to further modernize aerial animal count practices. All these external data can be used to create detection curves that are not fixed for a certain area or stratum, but dynamic over the whole count. Therefore, the computation of population estimates can potentially be done in a more continuous fashion without the need to choose a discrete set of strata.

Using our proposed semi-automatic aerial animal count method, instead of manual aerial counts, with the same total expenditure will result in a better accuracy and precision of animal population estimates. This semi-automatic method is influenced far less by factors such as animal group size, aircraft speed, and observer fatigue, experience, and skill, because it is far less dependent on human observations. This causes the counts of the semi-automatic method to be more consistent over a variety of conditions than manual counts. As the performance of image object detection algorithms and the action radius and autonomy of UAVs improve rapidly (Christie et al., 2016; Lin et al., 2018), we contend that the population estimates of this semi-automatic aerial animal count method will improve even further over time and that aerial animal counts can become fully automatic in the near future.

7.5 Supplementary materials

7.5.1 Population estimate calculations

The change in sampling effort that is needed depends on the chosen sampling method (Jolly, 1969a): 1, equal-sized units; 2, unequal-sized units using the ratio method; or 3, equal- or unequal-sized units selecting with probability proportional to size. Here the third method is considered, as this is the most generally applicable of the three methods and the other two methods can be translated into this method. Moreover, the standard error of this method can be calculated in a straightforward way without having to include variables for the standard error of the sample unit areas:

$$S_Y = \sqrt{\frac{Z^2}{n} s_d{}^2}, \text{ with } s_d{}^2 = \frac{1}{n-1}\left(\left(\sum_i d_i{}^2\right) - \frac{\left(\sum_i d_i\right)^2}{n}\right) \tag{7.5}$$

Where S_Y is the standard error of the population estimate in the stratum, Z the total area of the stratum, n the number of sampled units (e.g., transects) in the stratum, s_d the standard error of the densities of counted animals over the sampled units, and d_i the density of counted animals in unit i (Jolly, 1969a). Only sample counts with a census area consisting of a single stratum are considered here, to be able to give one value for the change in sampling effort that is required. The procedure to compute the standard error of the population estimate with stratification of the census area is the same as for a non-stratified sample count, but then the procedure needs to be applied on each stratum separately and the square root of the sum of variances taken to get the standard error for the total area (Norton-Griffiths, 1978).

Using Equation 7.5 combined with the algorithm's counting bias results in the population estimate's standard error of the (semi-)automatic method:

$$S_{Y,\text{automatic}} = r^{-1} S_{Y,\text{manual}} \tag{7.6}$$

Where r is the counting bias.

When s_d is assumed to be known or converged to an approximately constant value before all the planned units have been sampled, then s_d can be considered independent of n. Equation 7.5 could therefore be rewritten to get a function for n:

$$S_Y = \sqrt{\frac{z^2}{n} s_d{}^2} = \frac{Z}{\sqrt{n}} s_d,$$

$$\sqrt{n} = \frac{Z}{S_Y} s_d,$$

$$n = \left(\frac{Z}{S_Y} s_d\right)^2 = \frac{Z^2}{S_Y{}^2} s_d{}^2 \tag{7.7}$$

Because of Equation 7.6 $S_{Y,\text{automatic}}$ needs to be multiplied by r to compensate for its change by r^{-1} compared to $S_{Y,\text{manual}}$. The change in n that is needed to compensate for this can then be computed:

$$N = \frac{n_{\text{automatic}}}{n_{\text{manual}}} = \frac{\frac{Z^2}{(rS_Y)^2} {s_d}^2}{\frac{Z^2}{{S_Y}^2} {s_d}^2} = \frac{\frac{Z^2}{r^2 {S_Y}^2}}{\frac{Z^2}{{S_Y}^2}} = r^{-2} \frac{\frac{Z^2}{{S_Y}^2}}{\frac{Z^2}{{S_Y}^2}} = r^{-2} \tag{7.8}$$

Where N is the index detailing how much the number of sampling units needs to change to achieve a $S_{Y,\text{automatic}}$ that equals $S_{Y,\text{manual}}$.

The decrease in a population estimate's standard error with an increase in sampling units by k can be computed, thereby taking into account the initial change in standard error by r^{-1}:

$$S = \frac{S_{Y,\text{automatic}}}{S_{Y,\text{manual}}} = \frac{r^{-1} \frac{Z}{\sqrt{kn}} s_d}{\frac{Z}{\sqrt{n}} s_d} = r^{-1} \sqrt{k}^{-1} \frac{\frac{Z}{\sqrt{n}}}{\frac{Z}{\sqrt{n}}} = \left(r\sqrt{k}\right)^{-1} \tag{7.9}$$

Where S is the index detailing what the standard error of the population estimate from semi-automatic counts will be compared to manual counts by spending the same amount of finances on the semi-automatic method as on the manual method, and k is the increase in sampling units.

7.5.2 Operating costs

The costs per sampled kilometre were compared for five different count methods (Table 7.2): 1, manned aerial counts without images; 2, manned aerial counts with manual image verification for large groups; 3, manned aerial counts with fully manual image verification; 4, microlight aerial counts with semi-automatic image verification; 5, and Unmanned Aerial Vehicle (UAV) counts with semi-automatic image verification. These manual count methods are often advised and employed (Jachmann, 2001; Norton-Griffiths, 1978; Rabe et al., 2002; Redfern et al., 2002), with the first two being most prevalent. The first manual method has been compared for both helicopter and fixed-wing counts, while the other manual methods are only compared for fixed-wing counts. The costs for manual image verification assume that small animals (50 by 50 pixels) have to be searched by humans in large images (5000 by 3000 pixels). For the second method the images are taken by two human observers from the plane, and for the third method the images are taken automatically at a fixed interval. The costs for semi-automatic counts are based on a pre-trained animal detection algorithm for which four bounding boxes have to be manually verified per TP (the mean performance of the algorithm with the three species considered in this study).

Table 7.2: The costs breakdown per sampled kilometre of five different count methods. Manual 1: Manned, no images / manual air counts (both for helicopter and fixed-wing). Manual 2: Manned, manual air counts with image verification only for large groups. Manual 3: Manned, manual image verification. Semi-automatic 1: Microlight, semi-automatic image verification. Semi-automatic 2: UAV, semi-automatic image verification.

	Manual 1: helicopter	**Manual 1: fixed-wing**	**Manual 2: fixed-wing**	**Manual 3: fixed-wing**	**Semi-automatic 1: microlight**	**Semi-automatic 2: UAV**
Aircraft, equipment	$ 9.44	$ 1.09	$ 1.09	$ 1.09	$ 0.21	$ 0.48
Pilot	$ 3.39	$ 0.47	$ 0.47	$ 0.47	$ 0.47	$ 1.15
Recorder	$ 0.91	$ 0.38	$ 0.38	n.a.	n.a.	n.a.
Observer 1	$ 0.17	$ 0.38	$ 0.38	n.a.	n.a.	n.a.
Observer 2	$ 0.17	$ 0.38	$ 0.38	n.a.	n.a.	n.a.
Images verifier	n.a.	n.a.	$ 0.77	$ 14.91	$ 0.01	$ 0.01
Ground team, fuel, catering	$ 0.57	$ 1.69	$ 1.69	$ 0.56	$ 0.56	$ 0.28
Aircraft fuel	$ 0.67	$ 0.69	$ 0.69	$ 0.69	$ 0.29	n.a.
Total	**$ 15.32**	**$ 5.08**	**$ 5.85**	**$ 17.72**	**$ 1.54**	**$ 1.92**

The costs of the fixed-wing manual method were obtained from the Kenya Wildlife Service as the average costs per kilometre of the May 2015 aerial game count in the Laikipia-Samburu Ecosystem, Kenya (Table 7.4). The costs of the helicopter manual method were obtained from the August 2017 aerial game count in Welgevonden Game Reserve, South Africa (Table 7.3). We converted the local currencies to US dollars to compare the costs equally between countries. No correction was applied to account for international differences between average costs for services and goods, because the cost of living for both countries was comparable at that time (NUMBEO, 2016). The costs of the semi-automatic method were obtained by using the costs breakdown of the manual game counts, thereby leaving out or reducing the costs that were not needed for this method (Table 7.4). Furthermore, microlight fuel and operating costs were based on South African hourly rates of an Aquilla 582 and an average flying speed of 50 km/h (Microlighters, 2012). UAV operating costs were based on standard South African daily rates of 6000 to 8500 ZAR (J. Swart 2018-12-06, pers. comm.) and an average flying speed of 50 km/h.

Table 7.3: The cost breakdown of method manual 1, with helicopter (using a Bell Jet Ranger). The costs were determined using the 2017 Welgevonden Game Reserve aerial census. Costs are excl. VAT. Calculation is based on a total sampled area of 380 km^2 with a 300 m inter-transect distance. The USD-ZAR exchange rate of 28-08-2017 was used (XE, 2017).

Manual 1: helicopter	**Total area**	**km^{-2}**	**km^{-1}**	**km^{-1}**
Aircraft, equipment	R 156,000.00	R 410.53	R 123.16	$ 9.44
Pilot	R 56,022.00	R 147.43	R 44.23	$ 3.39
Recorder	R 15,120.00	R 39.79	R 11.94	$ 0.91
Observer 1	R 2,760.00	R 7.26	R 2.18	$ 0.17
Observer 2	R 2,760.00	R 7.26	R 2.18	$ 0.17
Ground team, fuel, catering	R 9,420.00	R 24.79	R 7.43	$ 0.57
Aircraft fuel	R 11,037.60	R 29.05	R 8.71	$ 0.67
Total	**R 253,119.60**	**R 666.10**	**R 199.83**	**$ 15.32**

Table 7.4: The cost breakdown of method manual 2, with fixed-wing (using a Cessna 182 and Cessna 206). The costs were determined using the 2015 Laikipia-Samburu Ecosystem aerial census. Costs are excl. VAT. Calculation is based on a total transect length of 6871 km. The USD-KES exchange rate of 10-05-2015 was used (XE, 2015). The costs for the fixed-wing manual 1 method were determined by leaving out the costs for the images verifier, for the fixed-wing manual 3 method they were determined by leaving out the costs for the recorder and the two observers (also regarding the ground team costs) and by increasing the costs for the images verifier with a factor 19.37 (equal to the increase in the number of images when the same game count was done with images at a 2 second fixed interval, resulting in 10 images per km when flying at 180 km/h), and for the automatic methods they were determined by leaving out the costs for the recorder and the two observers (also regarding the ground team costs) and by decreasing the costs for the images verifier of method 3 with a factor 1500 (equal to the decrease in pixels when on average 4 bounding boxes of 50 by 50 pixels per image of 5000 by 3000 pixels are detected by the algorithm, the number of detected bounding boxes will in practice be probably much lower and thereby decreasing the costs even more).

Manual 2: fixed-wing	**Total area**	**km^{-1}**	**km^{-1}**
Aircraft, equipment	K 716,458.59	K 104.27	$ 1.09
Pilot	K 309,575.76	K 45.06	$ 0.47
Recorder	K 252,000.00	K 36.68	$ 0.38
Observer 1	K 252,000.00	K 36.68	$ 0.38
Observer 2	K 252,000.00	K 36.68	$ 0.38
Images verifier	K 504,000.00	K 73.35	$ 0.77
Ground team, fuel, catering	K 1,108,229.60	K 161.29	$ 1.69
Aircraft fuel	K 449,912.20	K 65.48	$ 0.69
Total	**K 3,844,176.14**	**K 559.48**	**$ 5.85**

7.5.3 Model performance figures

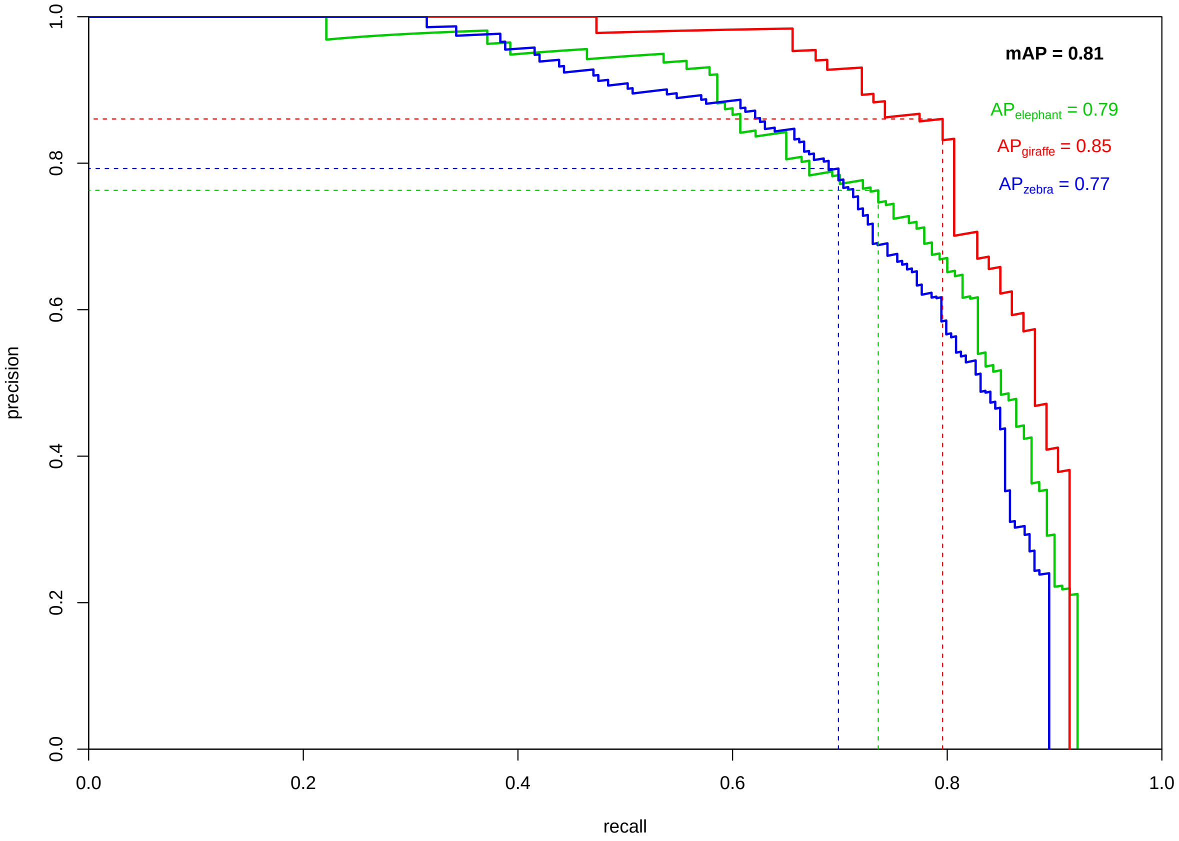


Figure 7.8: Precision/recall curves of the animal detection algorithm for elephant ($AP \approx 0.79$), giraffe ($AP \approx 0.85$), and zebra ($AP \approx 0.77$) on the validation set ($mAP \approx 0.81$). The precision/recall combinations with the highest F_1-scores (0.75 for elephant, 0.83 for giraffe, and 0.74 for zebra) are marked with dashed lines.

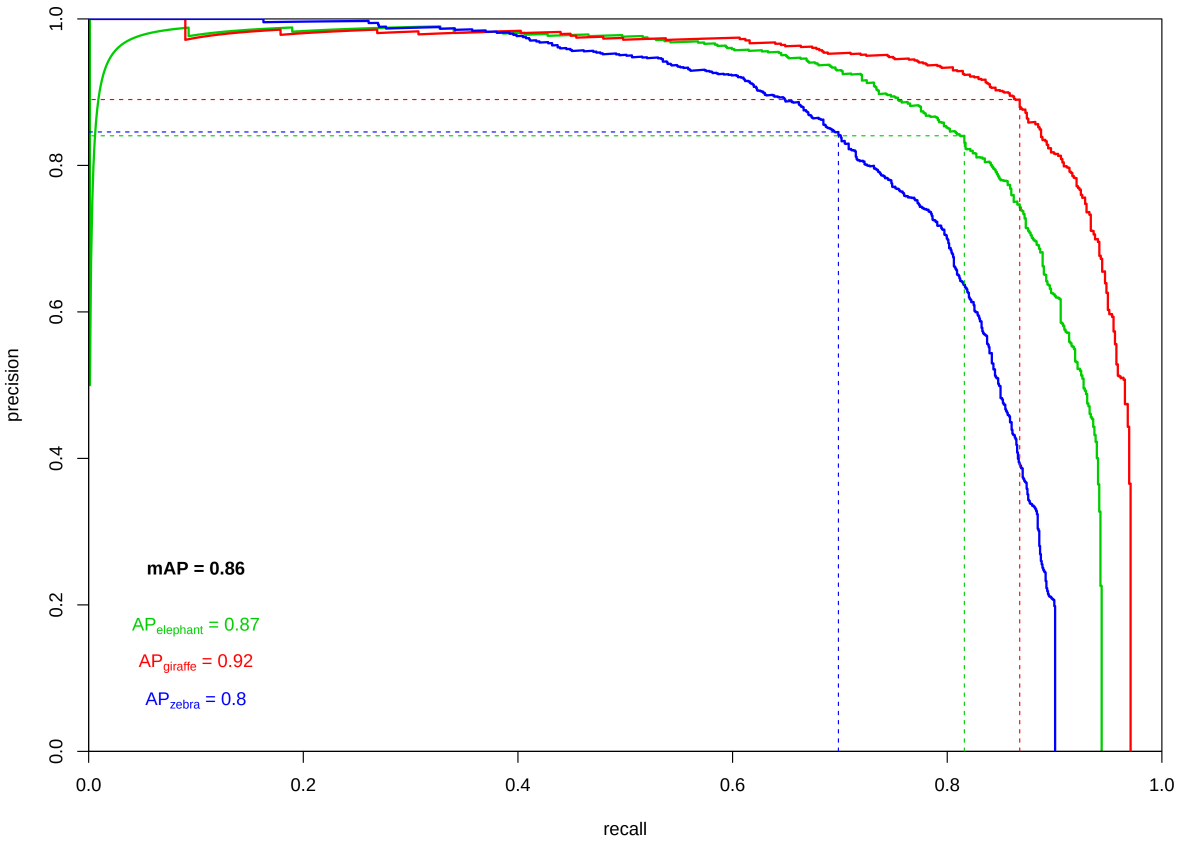


Figure 7.9: Precision/recall curves of the animal detection algorithm for elephant ($AP \approx 0.87$), giraffe ($AP \approx 0.92$), and zebra ($AP \approx 0.80$) on the training images ($mAP \approx 0.86$). These images were not directly used in the training process, but from these images the training tiles were extracted. The precision/recall combinations with the highest F_1-scores (0.83 for elephant, 0.88 for giraffe, and 0.77 for zebra) are marked with dashed lines.

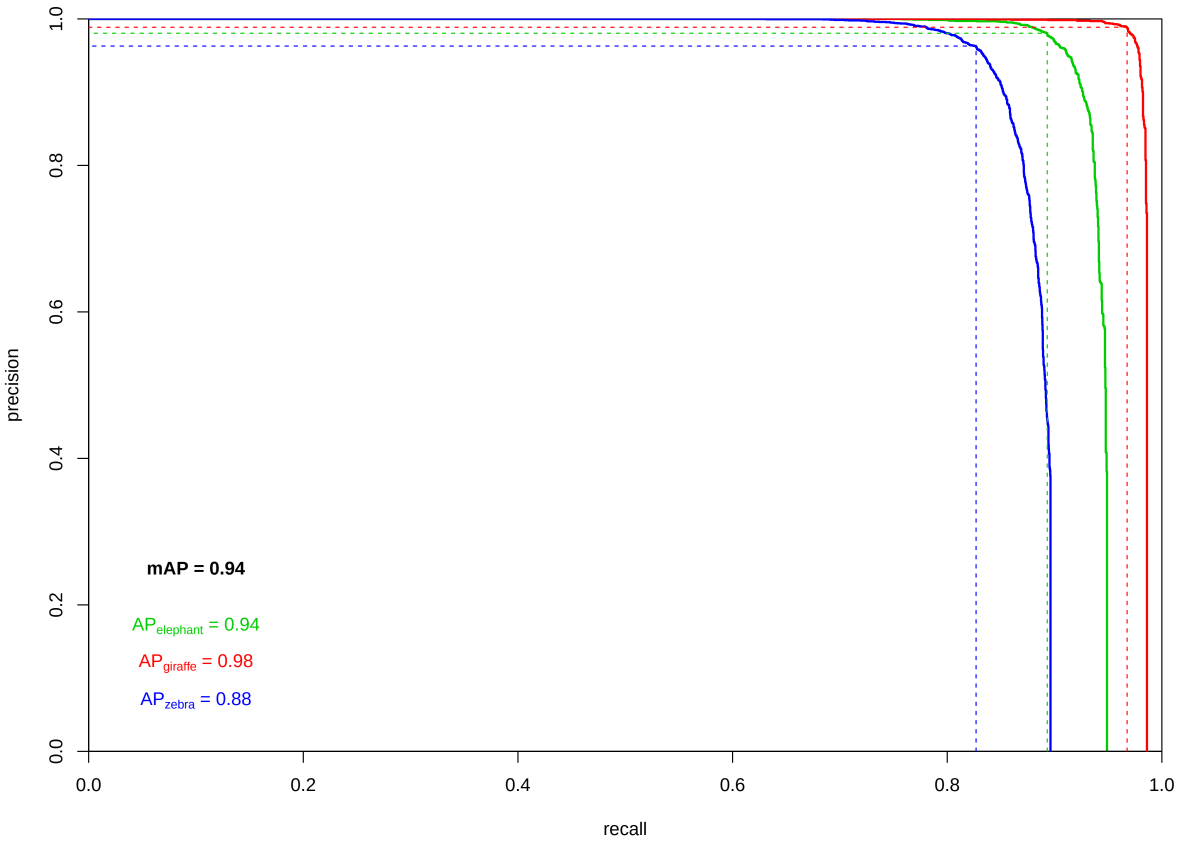


Figure 7.10: Precision/recall curves of the animal detection algorithm for elephant ($AP \approx 0.94$), giraffe ($AP \approx 0.98$), and zebra ($AP \approx 0.88$) on the training tiles ($mAP \approx 0.94$). The precision/recall combinations with the highest F_1-scores (0.93 for elephant, 0.98 for giraffe, and 0.89 for zebra) are marked with dashed lines.

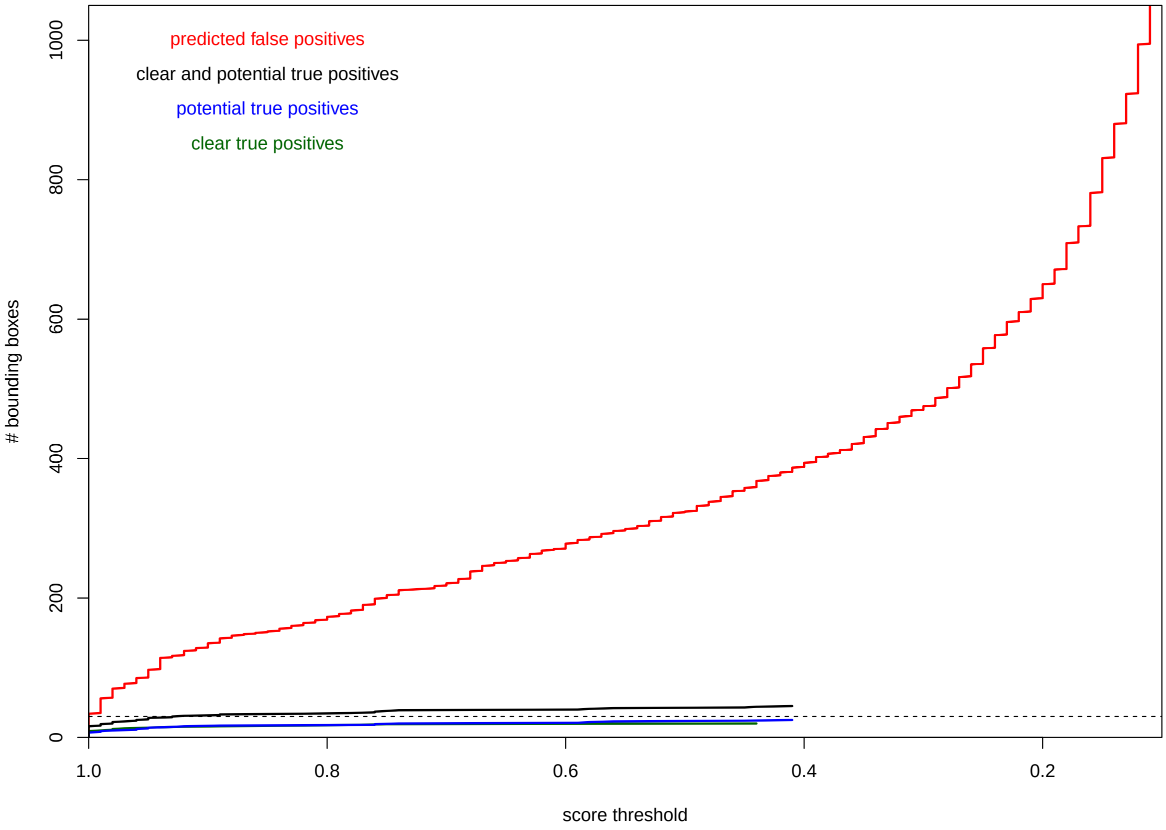


Figure 7.11: Cumulative number of false positives and the cumulative number of true positives that were not annotated by humans, versus the score threshold. We stopped evaluating the false positives below a score threshold of 0.4, due to time constraints. The dotted horizontal line indicates 30 animals, which is the number that we chose as an estimate for the total number of animals that the algorithm detected and the humans did not.

Chapter 8

Synthesis

8.1 Introduction

The survival of both African rhino species is currently under threat due to large-scale poaching (Biggs et al., 2013; Ferreira & Pienaar, 2020; Haas & Ferreira, 2016). These poaching efforts are driven by a demand for rhino horn in Southeast Asia, which is at an all-time high due to recent population and economic growth (Milliken & Shaw, 2012). This demand for rhino horn comes mainly from a desire to use horns as a status symbol and in traditional medicine (USAID Vietnam, 2018; USAID Wildlife Asia, 2018), for which the efficacy of the latter has not been scientifically demonstrated (Cyranoski, 2018). Unfortunately the market for traditional (Chinese) medicine continues to increase, especially due to global promotions by the Chinese government and with the support of the World Health Organization (Cyranoski, 2018; WHO, 2013). Protection efforts aimed at the short-term survival of the African rhino species seem thus to be urgently needed (Ferreira & Pienaar, 2020).

The South African authorities and conservation managers have responded extensively to the increase in rhino poaching. Probably the most important and costly of the numerous rhino protection efforts that have been undertaken is the large-scale deployment of anti-poaching patrols (Duffy, 2014). Given that most conservation officers have to patrol very large areas, they often arrive too late to save a rhino from being poached (O'Donoghue & Rutz, 2016). Furthermore, deadly force used by poachers incites the authorities into intensified "militarized conservation", resulting in frequent shootouts between poachers and conservation officers (Duffy, 2014). It would therefore be beneficial for rhinos, conservation officers and poachers if the authorities have more situational awareness, as the risk of fatalities in all three groups would decrease.

In this thesis I aimed to develop a system that can give conservation authorities more situational awareness to detect poachers, so that the loss of both animal and human life can be reduced. I proposed a "sentinel-based poacher early warning system" for this goal, for which I envision nature reserves where abundant savanna prey animals are tracked and where the movement responses of these animals are automatically used to detect the presence and infer the location of poachers. Hence the term: "sentinel", as the animals themselves will take the role of game wardens.

Apart from the obvious wildlife conservation challenge this thesis poses, it also tackles a major scientific challenge: to be able to detect abrupt changes in an environmental variable based on animal movement. In order to solve this challenge, a myriad of environmental and animal movement variables needed to be considered in interaction in a single model. This premise lead me to the use of a non-traditional statistical approach for animal ecologists: artificial intelligence.

This thesis brings together a number of coherent papers about wildlife conservation, movement ecology and artificial intelligence, aimed at investigating the necessity, analytics and applicability of a sentinel-based poacher early warning system. Consequently, this thesis has both a major conservation as well as a major scientific component to it. Furthermore, having undertaken this research at the Wildlife Ecology and Conservation group of Wageningen University, I also consider both components to be important to discuss in further detail. Therefore, I aim to give substantial attention to both the wildlife conservation as well as the wildlife ecology component in the rest of this synthesis. First, I will discuss each of my research chapters in relation to both or either of these components (section 8.2). The findings of the first two chapters (section 8.2.1; section 8.2.2) relate mostly to the societal challenge of poaching, the findings of the next three chapters mostly to the scientific challenge of predicting an environmental variable from animal movement (section 8.2.3; section 8.2.4; section 8.2.5) and the findings of the final chapter mostly to the applied scientific challenge of implementing *en masse* animal tracking needed for the sentinel-based poacher early warning system (section 8.2.6). While discussing the findings of these chapters, I will base my discussions on my own research as well as on studies done by others. The discussion of the findings of each separate chapter is followed by a general conclusion of this thesis about the necessity, analytics and applicability of a sentinel-based poacher early warning system (section 8.3). After that I will look ahead to the future of both wildlife conservation (section 8.4.1) and wildlife ecology (section 8.4.2). Here I will present my view on how this thesis relates to the broader fields of wildlife conservation and ecology. I will discuss the potential and role of a sentinel-based poacher early warning system within wildlife conservation and will set forth my vision on the future of wildlife conservation. Furthermore, I will discuss both the benefits that artificial intelligence has provided wildlife ecology, as well as its shortcomings. I will then continue with suggestions on how artificial intelligence can advance the field of wildlife ecology further, after which I will conclude with my ideas on how this advancement will impact the general process of scientific inquiry.

8.2 Findings

8.2.1 Legal international rhino horn trade

In Chapter 2 I investigated the potential of a legal international rhino horn trade to help save wild rhino populations from extinction. In Western countries the most often heard ultimate solution for rhino poaching is the reduction of demand for rhino horn (Litchfield, 2013). Given that this solution likely takes a substantial amount of time (if to be successful at all of course), it makes sense to focus on rhino protection efforts to bridge the period of high demand and poaching pressure. However, especially in South Africa, there is an other often-heard ultimate solution for rhino poaching: international rhino horn trade legalization (Rubino & Pienaar, 2020). This solution does not necessarily require a substantial amount of time to implement, so this would reduce the need for protection efforts to save rhinos from extinction. The argument for trade legalization is that the production through non-lethal horn harvesting from farmed rhinos could offset the market for poached horns (Biggs et al., 2013).

I demonstrated with an integrative literature review that the success of a legal international rhino horn trade regarding the preservation of wild rhino populations will mostly depend on four mechanisms: 1) financial viability for private rhino owners, 2) rhino horn demand, 3) laundering of rhino horns, and 4) behaviour of rhino horn consumers. Of these four mechanisms only the first will likely have a positive impact on rhino conservation, but primarily for the captive rhino populations in countries that allow private wildlife ownership. However, a legal rhino horn trade will most likely not be able to satisfy demand in the near future and will likely even lead to an increase in demand. Omnipresent corruption in countries along the rhino horn trade routes will, together with demand for illegal ('wild') horns, facilitate the co-existence of legal and illegal markets. In addition, legalization will remove the stigma associated with the consumption of illegal products and will therefore counteract long-term behavioural change programmes targeted at consumers. Therefore, I argue that international rhino horn trade legalization will likely not benefit wild rhino populations.

After having concluded this, it thus makes sense to continue to focus on the long-term strategy of reducing consumer demand for rhino horn and the short-term strategy to improve the protection of rhinos, of which this thesis focuses on the latter. This conclusion is not only applicable to African rhinos, but applies to other important target species as well: e.g., African elephants (Lusseau & Lee, 2016) and pangolins (Challender et al., 2019).

8.2.2 The impact of hunting

In Chapter 3 I analysed both the magnitude and spatial extent of the impact of hunting on tropical mammal and bird populations. The use of this study for the overall goal of this thesis is two-fold: 1) to determine how much animals in general (apart from solely considering African rhinos) are impacted by hunting, and 2) to determine how animals change their distribution in response to human hunters. Through an extensive meta-analysis I demonstrated that bird and mammal abundances declined on average respectively by 58% and 83% in hunted compared with unhunted areas and their populations were significantly depleted respectively within 7 and 40 kilometers from hunters' access points. Mammal population densities were higher inside than outside protected areas, but hunting pressure reduced mammal abundances even within protected areas. This makes clear that the impact of hunting on tropical animal populations in general is very large, which is echoed by other studies (Harrison, 2011; Maxwell et al., 2016). The extent over which populations have been depleted also clarifies that the animals' distributions have been severely impacted. Although these results suggest that the effect of hunting within protected areas is less detrimental than outside reserves, gazettement of protected areas seems insufficient to safeguard wildlife populations if not accompanied with improved reserve management, effective law enforcement and on-ground protection efforts.

From these results it does not become apparent yet whether animals actively avoid dangerous areas or that these areas are continuously being depleted of animals. However, mammal abundances decreased on average until 700 meters from hunters' access points until they started to increase again. This is counter-intuitive when based solely on hunting pressure, as you would expect prey abundances to be lowest at the centre of a central-place predator (which a human hunter is (Abernethy et al., 2013)). This initial higher mammal abundance may reflect the replacement of large bodied mammals by smaller ones, as I also found evidence that larger mammals were more heavily impacted by hunting than smaller ones. Given that it does not make sense that hunting pressure on smaller mammals increases until a certain distance from hunters' access points, the initial population increase of smaller mammals is probably due to their release from predation pressure and competition as a result of the (near) extirpation of large mammals (Wright, 2003).

This hypothesised phenomenon still does not differentiate between the two possible explanations of either the mammals' active avoidance of dangerous areas or the continuous depletion of mammals due to the combination of both hunting and natural predation. Although many studies demonstrated that the indirect effects of predation are often more important than its direct (lethal) effect regarding animal behaviour, fitness and distribution (Brown et al., 1999; Laundré et al., 2001), I do hypothesize here that the direct effect of hunting by humans (viz., animal population depletion) is more important than the indirect effect (viz., the active avoidance of the hunted region by animals). I base my hypothesis on the observation that the animal abundances do not seem to increase substantially above the baseline abundance in unhunted regions after being away more than 7 (for birds) and 40 (for mammals) kilometers from the hunters' access points. The animal abundances tend to level off at their baseline level, indicating an actual depletion of animals near roads instead of a migration of animals to areas further away. Especially for mammals this also ecologically makes sense, as an area with a radius of 40 kilometers is much larger than most tropical mammals' home ranges are, making it unlikely that mammals have this hunting area inside their home range that they actively have to avoid.

8.2.3 Animal group size variation

In Chapter 4 I simulated the effect of fear and resource availability on animal group size. I did this using a minimal agent based model in which groups formed through a self-organizing process driven solely by two inter-individual movement rules: attraction and repulsion. From this study it became apparent that both fear and resource availability, as well as the total density of animals in an area, have a very clear positive effect on group size. So even in the case when individual animals do not consciously and actively select for groups with a certain size, fear and resources still have a prominent effect on group size through self-organization (Couzin & Krause, 2003; Krause & Ruxton, 2002).

This observation is very useful when trying to infer environmental conditions from observing animal movement, as the collective patterns are more pronounced than the subtle individual movement changes that underlie them (Couzin et al., 2002). However, from the modelling results it also became apparent that there is an important drawback of relying on animal group size to infer environmental conditions. Even in this simple, deterministic and homogeneous movement model, there was a large variance in animal group size (resulting in a coefficient of variation of 50 to 150%) solely because of the random initial locations of the animals. This large inherent variability in the self-organizing group formation process could even be amplified in field conditions due to environmental heterogeneity and more complex animal behaviour (Nathan et al., 2008). Furthermore, when aiming to detect abrupt changes in environmental conditions (e.g., an encounter with a predator) group size will likely not be a reliable proxy to detect this, as group formation is dependent on the presence of other animals in the neighborhood. So even if a group will get certain properties after an abrupt environmental change that could cause it to merge with other groups, it can only do so after it encounters other animals (Couzin & Krause, 2003). This time lag in animal group size from environmental changes even applies to the situation of when a group 'wants' to become smaller (Couzin & Krause, 2003; Krause & Ruxton, 2002).

Group size will thus only be an accurate proxy for long-term prevailing environmental conditions (e.g., landscape of fear), but not for abrupt environmental changes (e.g., predator encounter). However, although group size is an accurate proxy for prevailing environmental conditions, it certainly is not a precise estimate given its large coefficient of variation. Concluding from this, I consider group compactness (viz., the distance between individuals within the same group) a more reliable proxy for both prevailing environmental conditions as well as abrupt environmental changes, because this follows directly from changes in net attraction between individuals. When developing a system based on animal movement that aims to provide insight in perceived prevailing environmental conditions, group size could still be an insightful proxy, but the recent history of the size of the groups should then be taken into account as well. In other words, a change in group size likely tells more about environmental conditions than the absolute number of animals in a group at a specific point in time. Also for other collective metrics such as group compactness (and possibly for individual movement metrics as well) the relative changes are likely more important than their absolute values. However, when aiming for a system that detects abrupt environmental changes (e.g., detecting poachers from animal movement), group size will likely not be a reliable proxy even when relative changes in recent history are taken into account, given the time-lag in the group formation process.

8.2.4 Quantifying environmental influence on animal movement

In Chapter 5 I developed a data-driven analytical framework to study environmental influence on animal movement. This framework makes use of the performance metrics of machine learning regression algorithms to quantify the influence of environmental variables on animal movement. Depending on the chosen time window of feature engineering, the influence of environmental variables on different time scales can be studied. Furthermore, different types of animal movement features (e.g., individual- and collective-based, or GPS- and accelerometer-based) can be included separately or in combination in the framework.

Even though the aim of this framework is to quantify the overall contribution of environmental variables on the total variation in animal movement, the core of this framework can be used to accurately predict environmental variation from animal movement as well. This does require a slight adaptation of the framework in which the time-component is explicitly used to make predictions about the environment, which is in line with my earlier observation about the importance of relative changes in movement metrics over time (Chapter 4). To be more specific, a moving-window approach (e.g., using a filter or smoother) or a prediction model that uses previous predictions for the next prediction (e.g., a Recurrent Neural Network or a 1-dimensional Convolutional Neural Network) could boost the prediction of the environmental variable from animal movement data to a level that is higher than the actual contribution of this environmental variable to animal movement.

This adaptation could make this framework also a good tool to infer environmental conditions from animal movement data. However, even though the time scale of the analysis can be chosen to be small, I do not think this regression-based approach will work well to detect abrupt changes in environmental conditions from animal movement, especially not when these abrupt changes are rare occurrences. This is in part because the model fitting will likely be flooded with data from baseline conditions, because the framework is aimed at deriving accurate predictions along the entire gradient of the environmental variable. This capability of the framework is of less interest when trying to detect abrupt changes in environmental conditions, which makes a classification approach more appropriate than a regression approach. Furthermore, when trying to make accurate predictions about both prevailing environmental conditions and abrupt changes in environmental conditions, it could benefit model performance to incorporate data on other environmental variables to be able to better interpret the variation in animal movement data. This last requirement has (on purpose) not been incorporated in the analytical framework of this chapter, as it won't allow for quantitative comparisons between the influences of different environmental variables on animal movement. However, in the next chapter I actually aimed to accurately detect abrupt changes in the animals' environment, which led me to implement the aforementioned changes in the analytical framework.

8.2.5 Poacher detection using sentinel animal movement

In Chapter 6 I algorithmically detected and localized poachers using animal movement data, which demonstrates the feasibility of the main theme of this thesis. I used a three-step analytical process to achieve this, namely: 1) animal behaviour classification, 2) poacher detection, and 3) poacher localization. In the first step I achieved an average precision of 46% to classify animal movement responses to humans versus all other movement. Even though this performance is quite an achievement (given the class imbalance of 1 versus 100, the inherent variability in animal movement, and heterogeneity in the environment of the study area), it still leads to a substantial amount of misclassification. However, given that in the next two steps of the analytical process I considered the classified responses of all animals collectively in a spatiotemporal context, I managed to drastically improve upon this performance in the detection and localization of ‘poachers’. Periods with humans present in the area could be distinguished from periods without humans with 86% accuracy in a balanced validation design, and these humans were localized with less than 500m error in 54.2% of the experimentally staged poaching intrusions.

Here I would like to discuss three learned lessons that are relevant when trying to infer context from animal movement algorithmically, which are unfortunately not always correctly executed in peer-reviewed ecological research. First, the engineering of features relative to ‘normal’ behaviour. Although I acknowledge that areas with certain environmental characteristics have a higher probability to harbor poachers, e.g., areas with low visibility, I intentionally wanted to create an algorithm that could reliably detect animal responses to poachers in all types of environment. Therefore I wanted to make sure that the prediction of disturbed animal behaviour is not a direct consequence of the environment. Consequently, I avoided the use of explicit environmental features in my model. For example, although the experimental intrusions took place every time at different locations in the study area, it could be that certain areas were used more often by the ‘poachers’ than others. If I had included environmental features in my model directly, the model could have learned mostly from these environmental features (independent of an interaction with animal movement features) to increase the probability of disturbed movement. This is why I only included animal movement features in my model, but made sure that these features were computed so that these were relative to ‘normal’ animal behaviour. In the definition of ‘normal’ animal behaviour is where the environmental variables were used. Using this approach, it can for example be computed that an impala moved twice as fast as expected given the surrounding tree cover and slope, without using the values for tree cover and slope directly as features in the poacher detection algorithm. An added benefit of this approach compared to directly including environmental features with movement features in the model, is that in the same way the recent history of (individual) animal movement can be taken into account in the definition of ‘normal’ animal behaviour. This observation of how to correctly include environmental features in my model is part of a growing awareness in the artificial intelligence community about the generalization of machine learning models (DeepLearning.AI, 2021). Not including features that could describe patterns that are specific to a study area or experimental design is important in order to avoid model biases, especially because these biases cannot be tested for with the acquired data.

Second, unbiased model validation approaches of animal movement. Given that movement data are time series, the data have inherent autocorrelation. The actual amount of autocorrelation is dependent on for example the GPS frequency and the consistency of the animals' behaviour, but nonetheless a certain amount of autocorrelation is always present. Due to this autocorrelation, a random split of movement data for model validation will cause the validation set to not be independent of the train set (Arlot & Celisse, 2010). This leads to misleading model performance values and potentially model overfitting (Arlot & Celisse, 2010). A stratified dataset splitting design is therefore recommended for movement data (Arlot & Celisse, 2010), e.g., per individual animal or per large blocks of time.

Third, the use of meaningful performance metrics. Accuracy is very often used as a classification model performance metric, likely because of its simple interpretation. Also in studies about animal activity classification from sensor data, accuracy is often used as the main performance metric when presenting the study's results (Chakravarty et al., 2019; de Weerd et al., 2015; Gerencsér et al., 2013; Homburger et al., 2014; Ladds et al., 2016; Shamoun-Baranes et al., 2012; Tatler et al., 2018). However, when there is a class imbalance (which is often the case when classifying animal activity, such as in the studies cited in the previous sentence), accuracy gives a distorted impression of model performance (Thabtah et al., 2020). For example, the accuracy of my animal behaviour classification model that I presented in this chapter is higher than 99%, which implies a near-perfect model. Obviously the reason for this high accuracy is that 99% of the data is of a single class, so having a model predict only that class will already result in an accuracy of 99%. Using accuracy as a performance metric for classification models is thus only appropriate for a balanced class design, or possibly when specifically mentioning a 'baseline' value for the accuracy given the class imbalance. Other classification performance metrics give a better impression about model performance in the case of class imbalance, e.g., F_1-score (the harmonic mean between precision and recall) or area-under-the-curve metrics such as average precision (which are also independent of the decision boundary). Therefore I urge ecologists to use class-balance-independent metrics in the evaluation of their models and presentation of their results, given that the classes and states of natural phenomena are rarely balanced.

8.2.6 Animal population estimates with image detection

In Chapter 7 I used deep learning computer vision techniques to automatically detect large savanna herbivores in aerial images. With this approach I managed to detect 90-95% of the number of individual animals that were found by four layers of human annotation, of which I correctly detected 2.8-4.0% extra animals that were missed by all humans. The model did result in 1.6-5.0 false positives per true positive, which emphasizes the importance of manual verification of automatic animal counts from aerial images. In this chapter I demonstrated the potential of semi-automatic aerial animal counts to improve the precision and accuracy of animal population estimates. Furthermore, the results from this study indicated that automated animal detections from aerial images have the potential to find more animals than humans can from both the air and images, especially when the algorithm is supplied with images taken at a fixed rate. The implication of this is rather important, because it will result in larger and more precise population estimates of animal species. Moreover, this effect will be even more pronounced for cryptic and rare animal species (Norton-Griffiths, 1978), which could lead to more favourable population estimates for endangered animal species.

Being that as it is, this result was actually not the reason why I performed this study. Monitoring animal movement *en masse* (for example to monitor their perceived environment, e.g., the presence of poachers, such as in this thesis) is an expensive and often intrusive undertaking. Technological advancements that were made during the last decades did already decrease the severity of these two issues by developing smaller and cheaper sensor tags that are solar-powered, but I expect it will nonetheless still be a costly and intrusive undertaking to tag a large enough number of sentinels in for example Kruger National Park (South Africa) to safeguard all their rhinos. However, technology continues to develop, which will likely make animal tracking even less expensive and less intrusive in the near future. A possible technological development (one that you hear often when talking to people who are laymen regarding sensor technology) are implantable trackers, but to the best of my knowledge there currently is not yet a technological solution in sight that will overcome the problem of *in vivo* power supply for long-term tracking. Therefore I explored the potential of an alternative way to track animals in this chapter, using imagery from aerial platforms to supplement or possibly replace tracking with sensor tags.

Recent studies have also demonstrated, just like I did, promising results to detect animals from the air (Kellenberger et al., 2018) and even from space (Duporge et al., 2020). Granted, animal detection in images is not the same as animal tracking, but the step that is needed to achieve this is not that substantial, given that object tracking can ‘simply’ be performed by using subsequent object detections over the video frames (Bochinski et al., 2017). Moreover, the required methods that are needed to achieve image-based animal tracking in natural environments have recently been almost fully developed (Haalck et al., 2020). Considering the aforementioned, I thus acknowledge the potential of aerial imagery to track wildlife continuously in the near future and to potentially supplement *en masse* tracking with sensor tags. However, I also found in this chapter that the detection chance of animals in images decreases substantially when the horizontal distance to the camera increases, likely because of occlusions, animals' smaller pixel dimensions and unfavorable angles (Buckland et al., 2004). This is why I expect animal tracking with cameras from for examples Unmanned Aerial Vehicles, blimps or elevated terrain to be only suitable for relatively small areas. Obviously, horizontal distances from the camera become less problematic with higher altitudes of the camera, but then other problems start to take effect. For example, being further away from the Earth's surface makes the pixel dimensions of the animals smaller and cloud cover will block line of sight (for cameras in both the visual and thermal infrared spectrum) for extended periods of time. Furthermore, when cameras from satellites would be used for this goal, then obviously geosynchronous satellites are needed as image snapshots from non-synchronous satellites will likely be temporally too far apart to infer accurate and reliable movement trajectories. However, current cameras from geosynchronous satellites (which are primarily used for weather monitoring) have a pixel resolution of approximately 1 km for visual and 4 km for infrared cameras (Bureau of Meteorology, 2011), which is way too coarse to detect and track animals. All in all, I expect that *en masse* animal tracking will still be heavily reliant on sensor tags in the near future.

8.3 Conclusion

All in all, I can conclude that improved protection efforts are very much needed in order to safeguard the survival of African rhinos (Chapter 2) and tropical animal populations in general (Chapter 3). A sentinel-based poacher early warning system can help fulfil this task (Chapter 6). I demonstrate that both individual and collective animal movement features (Chapter 4; Chapter 5; Chapter 6), as well as animal body movement and movement through the landscape (Chapter 5; Chapter 6), provide information about the animals' environment that is needed for a sentinel-based poacher early warning system to function. I also show that it is possible to automatically predict the animals' environment and abrupt changes therein with an artificial intelligence framework using feature engineering techniques that are rooted in domain knowledge of animal ecology (Chapter 5; Chapter 6). Given the complex relationship between the animals' heterogeneous environment and movement, I demonstrate the importance of interpreting animal movement as deviations from expectations given recent movement history and similar environmental conditions (Chapter 4; Chapter 5; Chapter 6) and provide the analytical framework to do so (Chapter 5; Chapter 6). Finally, I show the potential of deep learning image detection to automatically track sentinel animals *en masse* with aerial imagery of small poaching-critical areas (Chapter 7).

8.4 Outlook

8.4.1 Wildlife conservation

With this thesis I have provided *proof of concept* of a sentinel-based poacher early warning system, which could lead to more situational awareness for conservation officers and subsequently less poaching incidents. However, a few more developments are needed to provide *proof of production* and successfully use this early warning system in practice. First, as discussed in section 8.2.6 about Chapter 7, tracking animals *en masse* is a costly and intrusive undertaking. Given that wildlife conservation is often needed most in developing countries (Cincotta et al., 2000), the financial aspect could be a limiting factor. Luckily there has been a trend towards cheaper, less intrusive and longer-lasting animal sensors over the past decades, but it will nonetheless be beneficial to limit the amount of tagged sentinels as much as possible. Therefore, future research should be aimed at investigating the trade-off between sentinel density and poacher detectibility, in order to determine a minimum sentinel density for which poachers can still be localized timely and accurately. Next to solely investigating sentinel density, the division of sentinel species should also be investigated. Some animal species simply perform better as sentinels compared to others (Chapter 6), but animal species also occupy different habitats. A good division between sentinel species could thus assure adequate spatial coverage with a good performance. Second, Chapter 6 has on purpose been performed in a predator-free area, in order to prevent unknown disturbances to the monitored animals. Because of this, I have not yet been able to demonstrate that sentinel movement can be used to differentiate between the presence of poachers and predators. Research aimed at making this distinction should therefore be a priority in order to make this early warning system applicable in areas with predators. Several studies have already suggested that free-roaming animals respond differently and more strongly to humans compared to natural predators (Ciuti et al., 2012; Proffitt et al., 2009; Zbyryt et al., 2018), which suggests that it should be possible to algorithmically classify sentinel movement as a response to either humans or predators. If not, sequential disturbance localizations by the model could potentially also be used to make inferences about the type of disturbance. Third, the poacher early warning system should in practice be able to operate in real-time, but I have not yet demonstrated this. The steps that are currently taken by the system (feature engineering, dimension reduction and prediction) will result in delay piling up. I chose the setup of feature engineering and subsequent dimension reduction, because *a priori* I did not know the most useful features to compute for the task. For future research this approach should be optimized, ideally by directly computing a limited number of features without dimension reduction, so that the classification can be performed in real-time. Given that only 8 principal components were used down the line to classify disturbed animal movement, I expect that it should be computationally possible to build a real-time sentinel-based poacher early warning system. Fourth, although not a necessity, there are possibilities to further improve the performance of the system. Deep learning could for example be employed to improve the classification of disturbed sentinel behaviour, given that deep learning has in recent years demonstrated to yield superior performance over standard machine learning techniques for many different classification tasks (Chapter 5; Chapter 7). I especially expect sequential deep learning models (e.g., 1-dimensional Convolutional Neural Networks and Recurrent Neural Networks) to be promising for these time series data. Furthermore, due to faulty sensor firmware, Chapter 6 has been build around very noisy data, which required substantial amounts of preprocessing before I could reliably use the data for the classification and localization task. When using location data with more common spatial errors, I expect the performance of the sentinel-based poacher early warning system to be better. Finally, (on-board) animal activity classification with accelerometers could potentially improve the classification of disturbed sentinel behaviour as well.

Although improving the performance of the sentinel-based poacher early warning system is obviously beneficial for its efficacy, care should be taken here. The way this poacher early warning system has been envisioned from the start was that it could be used as an extra layer of information to provide conservation officers with more situational awareness in the field. This way it will hopefully lead to less fatalities of animals, conservation officers and poachers. However, it has never been the ultimate aim to develop an autonomous poacher arresting system, nor should it in my opinion be. Human decision-making is essential to make sure that law enforcement is conducted ethically (Peny, 2012), which is thus important to consider when it could for example be possible to make arrests (or even kills) with Unmanned Aerial Vehicles. As such, I argue that a certain amount of false positives in the poacher early warning system is useful in the sense that it requires humans to evaluate the system's predictions, e.g., by visually inspecting the predictions behind a computer or by scouting areas on foot or from the air. This way, human involvement in poacher law enforcement is a prerequisite in order for the early warning system to function. Admittedly, there are downsides to false positives as well, e.g., that it could lead to a certain amount of distrust in the system by conservation officers. Nonetheless, the chance of achieving a false positive rate of zero for this system is probably not that large for the near future, given that the focus lies first and foremost on developing a false negative rate (which is by definition in trade-off with false positive rate) of zero in order to detect all poachers (Chapter 6). However, even if at some point a perfectly performing poacher early warning system would be developed, it remains imperative that humans keep involved in evaluating the system's predictions: a 'human-in-the-loop' deployment (DeepLearning.AI, 2021). Not only for ethical reasons, but also to keep the system failure-free in case mistakes creep in over time, which would otherwise propagate indefinitely (Kellenberger, 2020).

Although this thesis is centered around the preservation of African rhino species, the developed sentinel-based poacher early warning system is obviously not restricted solely to rhino poachers. As such, this system is a new example of multiple technological developments that have been deployed to safeguard wildlife reserves. Other examples include ‘smart’ fences with acoustic fibre surveillance (Hernandez, 2019), scouting Unmanned Aerial Vehicles (SANParks, 2015), information intelligence with cameras and license plate recognition (Welgevonden Game Reserve, 2021), and direct poacher localization with radar (Martin, 2017). Wildlife reserves, especially the ones harboring target animals, are thus slowly being converted to intensively monitored fortresses with the help of technology (Duffy, 2014). This development, which thus also includes my sentinel-based poacher early warning system, is viewed by some as part of the growing ‘militarized conservation’ approach to protect wildlife and is often concurrently viewed as a worrying development (Duffy et al., 2019). In short, the three main points of critique against militarized conservation are human rights violations, questionable efficacy and the potential to hamper long-term conservation (Duffy, 2014; Duffy et al., 2019; Shrestha & Lapeyre, 2018).

I posit that it is incorrect to attribute the same negative consequences that are assigned to militarized conservation in general, to all anti-poaching technology. It is certainly true that the use of technology coincides with (and often results from) the increasingly military approach to wildlife conservation, especially in sub-Saharan Africa (Duffy et al., 2019). However, this does not mean that it can be logically concluded that these technological developments will have the same negative consequences. It is stated that anti-poaching technologies can be a large financial sink and can broaden the gap between local communities and conservation agencies (Duffy, 2014; Duffy et al., 2019; Shrestha & Lapeyre, 2018), but at the same time it can also provide positive effects that could counteract major negative effects of militarized conservation. For example, the (arguably) most prominent point of critique against militarized conservation are human rights violations (Duffy, 2014; Duffy et al., 2019), which most notably comes from the large number of poachers who have been killed by conservation officers (Duffy, 2014). On the other hand, technological tools that help track down poachers more accurately (e.g., this sentinel-based poacher early warning system) will reduce the number of surprise encounters between poachers and conservation officers. Moreover, from a more suspicious viewpoint, it also means that there will be less opportunities to stage fake defensive poacher casualties. If poachers can be arrested safely, there will be arguably no other argument to defend a shoot-on-sight policy than the acknowledgment of a poor judicial system. So when there are technological systems in place that can provide early indicators about the poachers’ whereabouts, it will consequently become more difficult to justify shoot-on-sight policies.

To address the other two main points of critique against militarized conservation strategies: first, protecting target animals from poachers directly is indeed a short-term strategy focused on symptom relief, which I also stated myself at the start of this thesis (Chapter 1). Conversely, the conservation strategies that are advocated for by opponents of militarized conservation (i.e., solving the issue of corruption, reducing demand for wildlife products, increasing regional stability, and reevaluating human-nature relationships (Büscher & Fletcher, 2019; Duffy, 2014; Duffy et al., 2019)) are all long-term conservation strategies. Many target animals (e.g., rhino, elephant, gorilla) are so endangered and their products so in demand that there simply is too little time to solely wait for these long-term strategies to take effect. Therefore, I see anti-poacher protections efforts (which is not necessarily the same as militarized conservation) as a strategy that is needed to bridge the current precarious period until long-term strategies can take their full effect. Perhaps these long-term effects will never be sufficient to make anti-poacher protection efforts superfluous, but hopefully it will significantly reduce the need for it. Second, broadening the gap between local communities and conservation agencies should indeed be avoided in order not to jeopardize conservation in the long run. As stated in the previous paragraph, I posit that poacher tracking technologies can help to reduce the fatalities of poachers (who are often from neighbouring communities) and incentivize a better-functioning judicial process, which would actually counteract the main negative consequence of militarized conservation as well (Duffy, 2014). However, I do acknowledge that the way a new anti-poaching technology is implemented will have an important effect on the efficacy of long-term conservation, especially related to the inclusion of local communities (Duffy, 2014). There are certainly examples of how technology has been implemented in the wrong way regarding community-conservation relationships (Duffy et al., 2019; Shrestha & Lapeyre, 2018), but this does not mean that technology cannot be implemented to the benefit of both parties (Jordan et al., 2013), nor does it necessarily mean that anti-poacher protection efforts (with or without technology) are motivated by neo-colonial or even racial politics (Duffy et al., 2019).

The discussion about anti-poaching technology and militarized conservation ties in with a larger debate about the future of wildlife conservation through ‘new conservationism’ (i.e., accepting the Anthropocene to let nature ‘evolve’ and use it to support human development (Marris, 2011)) versus ‘neoprotectionism’ (i.e., putting nature back in charge by separating humans and nature on an unprecedented global scale (Wilson, 2016)), which is also referred to as ‘social conservationism versus nature protectionism’ or ‘sharing versus sparing’ (Büscher & Fletcher, 2019; Miller et al., 2011). The risk of polarization due to a debate about such conflicting views is high, especially within a small community of conservationists who are up against a daunting task of ‘saving nature’ in our current human-dominated world. Therefore I applaud initiatives that aim to bring these two opposing views closer together (Marris, 2014; Marvier, 2014; Miller et al., 2011), or even aim to transcend this division of views (Büscher & Fletcher, 2019).

Approaching conservation in the Anthropocene from a ‘neoprotectionism’ versus a ‘new conservationism’ viewpoint is fundamentally different regarding an ethical values perspective (Büscher & Fletcher, 2019; Miller et al., 2011), although some new conservationists do argue that it’s not (Marris, 2014; Marvier, 2014). This difference primarily boils down to whether or not the ultimate aim is to preserve ‘pristine’, ‘untouched’ or ‘wild’ nature. However, I fear that if conservationists are hellbent on either of these two aims that there can be no satisfactory outcome. First, regarding neoprotectionism, I argue that it is impossible to preserve true natural wilderness and that wild places are possibly already a ghost of the past. For example, in this thesis I've shown that human infrastructure negatively impacts mammal populations up to 40 kilometers away, due to the infrastructure's function as an access point for hunters into natural areas (Chapter 3). Given this large spatial extent, there are hardly any unimpacted places left and it won't be long until all are gone given the ongoing human population expansions in the tropics (Chapter 3). Moreover, it may seem that solutions such as the 'Half-Earth Project' or the 'One Planet Summit' could remedy this impact by protecting massive amounts of land and water (Wilson, 2016), but even if these areas are to be implemented then this implementation will inherently impact the nature within it as well. If our society continues to function mostly in a capitalistic way, then these proposed natural areas will also need protection against humans who aim to exploit its resources. This will likely mean fencing, monitoring, intensive management and technological solutions aimed at reducing these exploitations (Chapter 2; Chapter 6), which will almost by definition make these areas managed instead of wild. Second, regarding new conservationism, it will mean that animals that do not 'fit' into our Anthropocene world will not be allowed by us to survive as a species. These 'incompatible' species include for example species of megaherbivores and predators, species with valuable body parts, species that get outcompeted or annihilated by invasive species, and shy species that do not tolerate human presence well. Taking this a step further, according to some it is actually even only meaningful to save animal species within broader social, cultural and environmental contexts (Büscher & Fletcher, 2019; Dawson, 2016; Heatherington, 2012; Sodikoff, 2012). However, our current contexts will likely not remain the same in the future (just like they haven't been in the past), but animal species can (often) go extinct only once. This premise will thus mean that we should at this point in time brand certain animal species as remnants of the Holo- or Pleistocene and deny these species a future in which it could potentially be possible to coexist sustainably with humans again (Figure 8.1). This way we could end up with only a small selection of surviving animal (and plant) species, as our changing social, cultural and environmental contexts will possibly continue to become incompatible for other species over the course of time.

THE RHINOCEROS FULFILS THE MISSION OF THE OX.

Figure 8.1: Farmer ploughing his fields with a harnessed rhinoceros, said to illustrate a scene in lower Egypt, but the rhino looks distinctly Indian (Rookmaaker, 2020). First published by Jacolliot, 1884.

So it is admirable and arguably visionary to aim to transcend this polarizing debate by proposing a new system of ethical values that will make nature conservation future-proof regarding our current and emerging political, economical and social climate (Büscher & Fletcher, 2019). However, the proposed approach of 'convivial conservation' does unfortunately not provide solutions or methods on how to practice nature conservation in the Anthropocene (Büscher & Fletcher, 2019). Simply put, if convivial conservation were to be fully implemented then there would not be an Anthropocene anymore. If the human nature would have moved away from the stereotypical '*homo economicus*' towards a state in which it lives in harmony with nature (Büscher & Fletcher, 2019), then humans would only have the capacity to be the dominant force on Earth instead of actually being it. This means that convivial conservation, how commendable it may be as a long-term conservation strategy, is not a solution to the predicament of how to conserve nature during the time that the Earth is still in the Anthropocene. Within this time period I envision my sentinel-based poacher early warning system as a necessary tool to safeguard the survival of endangered target animals, just as I acknowledge the importance of heavily and technologically monitored protected areas that are well-managed. Moreover, 'sharing' conservation strategies will also be useful for certain species, for example to ensure the survival of pollinators with nature-inclusive agricultural practices. However, bridging the Anthropocene with as many animal species as possible should not be an excuse for hampering the implementation of long-term conservation strategies such as convivial conservation (Büscher & Fletcher, 2019). Ultimately it would benefit nature the most if we were indeed to transcend from the Anthropocene, which signifies that we should divide our focus over both short- and long-term conservation goals. Perhaps counterintuitively, this does not mean we should divide conservation approaches as well, but rather cooperate more so that both short- and long-term conservation approaches work most efficiently as a whole (Büscher & Fletcher, 2019; Marris, 2014; Marvier, 2014; Miller et al., 2011). Hopefully this will result in my sentinel-based poacher early warning system to be superfluous in the next century.

8.4.2 Wildlife ecology and artificial intelligence

Artificial intelligence (AI) has been a central theme and tool in this thesis (Chapter 1; Chapter 5; Chapter 6; Chapter 7), mainly because of its ability to provide accurate predictions in the analyses of big data within wildlife ecology research. I have used AI to predict environmental variables from animal trajectories (Chapter 5; Chapter 6), classify activity from animal body acceleration patterns (Chapter 5) and detect various animal species in images (Chapter 7). Other examples include the tracking of moving animals in videos (Risse et al., 2017), the following of animal body postures and body parts in videos (Hughey et al., 2018), the detection of when animals become sick using animal sensors and videos (Van Hertem et al., 2014), and the classification of animal calls from sound data (Xie et al., 2019). These developments have provided ecologists with unprecedented amounts of useful and interpretable information to help answer their research questions, which would otherwise not have been possible to acquire or would have taken years of tedious and invasive field observations (Hughey et al., 2018; Wang, 2019)

The algorithms that are used in the aforementioned studies are often referred to by ecologists and other domain scientists as being “black boxes”, mainly in a slightly disapproving way (Lucas, 2020). A black box signifies in this context an algorithm with high predictive power, but with little ability to provide understanding of how the prediction came to be. Actually there exists a trade-off between predictive power and interpretability for AI algorithms (Kuhn & Johnson, 2013; Lundberg & Lee, 2017), but it is true that mainly the algorithms with high predictive power (and thus often low interpretability) have spurred recent developments in “big data ecology” and consequently gained most attention by wildlife ecologists (Hughey et al., 2018; Lucas, 2020). So although these algorithms have provided ecologists with useful interpretable information, by themselves these algorithms have not often directly provided understanding about the studied ecological processes (Chapter 5). This is in contrast to traditional (often frequentist) statistics, which are mostly employed for the task of directly gaining understanding of an ecological phenomenon by testing hypotheses. The lack of fully grasping or appreciating this contrast could very well be a contributing factor to the widespread critique amongst ecologists on the predictive focus of AI (Lucas, 2020).

So AI has generally been used in wildlife ecology to acquire informative data from raw data, while traditional statistics are often used to acquire understanding from these informative data (Chapter 5; Lucas, 2020). However, there is also a large potential to harness the predictive power of AI to directly provide ecological understanding (Lucas, 2020). This potential includes techniques that are relatively unknown to ecologists as well as techniques that are still in development. First, model performance metrics can be used as a proxy to draw inferences about how well the input variables relate to the response variable (Chapter 5; Lucas, 2020). Second, variable importance metrics can be used to draw inferences about the importance of each included variable on the performance of the model, in which the effect of interactions with other variables can be included as well (Lucas, 2020; Molnar, 2019). Third, sensitivity analyses can be performed on subsets of the data to get a feeling of how the various input variables influence the response variable (Lucas, 2020; Molnar, 2019). Fourth, an actively ongoing area of research is Explainable Artificial Intelligence (XAI) that aims to make fitted black box AI algorithms understandable by humans (Bastani et al., 2017; Doshi-Velez & Kim, 2017; Jain & Wallace, 2019; Lipton, 2016; Lundberg & Lee, 2017; Lyddon et al., 2018; Miller, 2019; Mittelstadt et al., 2019; Ribeiro et al., 2016; Samek et al., 2017). Fifth, another ongoing area of research is Causal Representation Learning (CRL) that aims to develop AI algorithms that can capture causal relationships instead of focusing fully on correlation (Bengio et al., 2019; Mitrovic et al., 2020; Pearl, 2000, 2009; Pearl & Mackenzie, 2019; Schölkopf, 2019; Schölkopf et al., 2021; Sgaier et al., 2020; Zhao & Hastie, 2021).

Both XAI and CRL techniques are currently being developed mostly solely by computer scientists, which is potentially problematic for domain scientists, e.g., wildlife ecologists. The nature of automated explanations and causality is far from clear, with their definitions being actively debated subjects in both the cognitive and computer sciences (Confalonieri et al., 2019; Miller, 2019; Mittelstadt et al., 2019; Pearl & Mackenzie, 2019; Zhao & Hastie, 2021). The criteria of what constitutes good model explainability, understanding and insight can even differ per scientific discipline, application and data type (Confalonieri et al., 2019). Moreover, the different ultimate aims that domain scientists have for considering the use of XAI and CRL techniques will also impact the implementation of explainability and causality in these techniques (Mittelstadt et al., 2019; Sgaier et al., 2020). As such, it will benefit wildlife ecologists to actively work together with computer scientists by developing XAI and CRL techniques that are most useful to them, regarding their data types and their research questions (Sutherland et al., 2013). For example, a large part of XAI research focuses on explaining which image parts contributed to a certain classification (Jain & Wallace, 2019; Samek et al., 2017), which may be of interest to (for example) medicine and engineering research but not so much to wildlife ecology. In wildlife ecology the interest lies mainly in the relationship of animals with their environment (Nathan et al., 2008; Sutherland et al., 2013), which thus makes the focus of XAI more on sensor data by relating a variety of monitored environmental variables to animal behaviour and emergent properties (e.g., Chapter 5; Chapter 6). However, most ecological findings from explorative data-driven studies are still obtained by manual feature engineering (e.g., Chapter 6), while there is a large potential for automated pattern recognition. Also regarding CRL techniques there are clear aims for wildlife ecologists. These aims boil down primarily to filtering out spurious correlations in the complex web of interactions between animals and their environment (Sutherland et al., 2013), which is especially important when a constant environmental process influences animal behaviour with a large variance (e.g., Chapter 4). This aim is certainly also one of the pillars of current CRL research, but it is not the only aim and its implementation is likely not universal for all scientific disciplines and data types (Bengio et al., 2019; Schölkopf et al., 2021).

So what will be the consequence for the process of scientific inquiry in wildlife ecology if AI can be used to directly provide understanding from big multivariate datasets in the near future? Will the golden standard of the scientific method (i.e., making observations, forming hypotheses and testing these hypotheses) be replaced by automated pattern recognition, like some have claimed or considered (Appenzeller, 2017; Falk, 2019)? The main argument of people who claim that AI will change scientific inquiry is that understanding will become obsolete if correlations can provide perfect predictions (Anderson, 2008). However, this is actually only an opinion about the value or relevance of scientific inquiry, which is a separate debate and does not consider the potential of AI to change the process of scientific inquiry to provide understanding. Although my thoughts have gone back and forth on this topic for a while, I posit that the method of scientific inquiry will not and should not change if AI can directly provide understanding. Clearly the potential of automated pattern recognition is huge for wildlife ecologists, given the complex and multifaceted interactions of animals with their heterogeneous environment, but it can simply be considered a more advanced technique of making observations (Forde

& Paganini, 2019; Lucas, 2020; The Royal Society & The Alan Turing Institute, 2018). The aforementioned XAI and CRL developments will not automate the formulation and testing of hypotheses, nor does it formulate a complete alternative process for scientific inquiry. Developing and testing hypotheses will thus remain an integral part of research in wildlife ecology, which is up to researchers to perform (Forde & Paganini, 2019; Lucas, 2020). On the other hand, I also posit that not all studies should adhere to the full process of scientific inquiry. For example, an explorative study of a new and large dataset (e.g., using automated data-driven pattern recognition) without formal hypothesis testing could potentially be more informative to readers who aim to draft their own hypotheses than a study that aims to draft and test an hypothesis on the same dataset. Moreover, I think it is important to emphasize that hypothesis testing is not necessarily the same as significance testing. Sometimes it seems that ecologists consider significance testing (rather than hypothesis testing) the golden standard of scientific inquiry, but this view greatly limits the potential analyses that can be performed to test hypotheses (e.g., Bayesian inference and model selection techniques (Burnham & Anderson, 2002; Nickerson, 2000)) and increases the risk of viewing hypotheses as statements that can be accepted or rejected instead of having a probability of not being true (Kruschke, 2013).

8.5 Summarizing remarks

With this thesis I hope to have demonstrated the potential of artificial intelligence for both wildlife conservation and wildlife ecology. I hope that sometime in the near future the Earth will have transcended from the Anthropocene due to a sustainable transformation of the global human society, but until then wildlife continues to deserve our protection from ourselves. I also foresee a large role for artificial intelligence in wildlife ecology research, which may drastically change the way scientific understanding is acquired in the near future. Exciting developments related to explainability and causality within artificial intelligence are currently being undertaken by computer scientists, but they do require the input of ecologists to make these developments truly insightful and applicable to the real world. Let's embrace these new ways of data analysis and spur ecological discovery.

References

Abernethy, K. A., Coad, L., Taylor, G., Lee, M. E., & Maisels, F. (2013). Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1625), 20120303. https://doi.org/10.1098/rstb.2012.0303

African Wildlife Foundation. (2014). Tools of the Trade Starring Jackie Chan (Mandarin). https://youtu.be/sLbLlk3Nsp0

Ager, A. A., Johnson, B. K., Kern, J. W., & Kie, J. G. (2003). Daily and seasonal movements and habitat use by female Rocky Mountain Elk and Mule Deer. *Journal of Mammalogy*, *84*(3), 1076–1088. https://doi.org/10.1644/BBa-020

Alexander, R. D. (1974). The Evolution of Social Behavior. *Annual Review of Ecology and Systematics*, *5*(1), 325–383. https://doi.org/10.1146/annurev.es.05.110174.001545

Alkemade, R., Reid, R. S., van den Berg, M., de Leeuw, J., & Jeuken, M. (2013). Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. *Proceedings of the National Academy of Sciences*, *110*(52), 20900–20905. https://doi.org/10.1073/pnas.1011013108

Amazon Web Services. (2018). Amazon EC2 P3 Instances. https://aws.amazon.com/ec2/instance-types/p3/

Anderson, B., & Jooste, J. (2014). Wildlife Poaching: Africa's Surging Trafficking Threat. *Africa Security Brief*, (28), 1–8.

Anderson, C. (2008). The end of theory: The data deluge makes the scientific method obsolete. *Wired magazine*, *06*(23), 10–12. http://www.uvm.edu/pdodds/files/papers/others/2008/anderson2008a.pdf

Andrew, W., Greatwood, C., & Burghardt, T. (2017). Visual Localisation and Individual Identification of Holstein Friesian Cattle via Deep Learning. *Proceedings of the IEEE International Conference on Computer Vision*, 22–29. https://doi.org/10.1109/ICCVW.2017.336

Annecke, W., & Masubelele, M. (2016). A Review of the impact of militarisation: The case of rhino poaching in kruger national park, South Africa. *Conservation and Society*, *14*(3), 195–204. https://doi.org/10.4103/0972-4923.191158

Appenzeller, T. (2017). The AI revolution in science. *Science*. https://www.sciencemag.org/news/2017/07/ai-revolution-science

Arlot, S., & Celisse, A. (2010). A survey of cross-validation procedures for model selection. *Statistics Surveys*, *4*, 40–79. https://doi.org/10.1214/09-SS054

Ashcroft, M. (2019). Lord Ashcroft's exclusive revelations about "horrific" captive-bred lion farming. https://lordashcroftpolls.com/2019/04/lord-ashcrofts-exclusive-revelations-about-horrific-captive-bred-lion-farming/

Aune, K., Jørgensen, D., & Gates, C. (2017). Bison bison (errata version published in 2018). https://doi.org/10.2305/IUCN.UK.2017-3.RLTS.T2815A45156541.en

Avgar, T., Mosser, A., Brown, G., & Fryxell, J. (2013). Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *Journal of Animal Ecology*, *82*(1), 96–106. https://doi.org/10.1111/j.1365-2656.2012.02035.x

Ayling, J. (2013). What Sustains Wildlife Crime? Rhino Horn Trading and the Resilience of Criminal Networks. *Journal of International Wildlife Law and Policy*, *16*(1), 57–80. https://doi.org/10.1080/13880292.2013.764776

Bakeman, U., Eilam, H., Schild, C. M., Grinstein, D., Eshed, Y., Laster, M., Fride, E., & Anavi-Goffer, S. (2019). Detection of Impending Aggressive Outbursts in Patients with Psychiatric Disorders: Violence Clues from Dogs. *Scientific Reports*, *9*(1), 1–11. https://doi.org/10.1038/s41598-019-52940-w

Baker, A. (2015). Blood diamonds. https://time.com/blood-diamonds/

Bale, R. (2018). Where Jaguars Are 'Killed to Order' for the Illegal Trade. https://www.nationalgeographic.com/animals/2018/09/wildlife-watch-news-jaguar-poaching-trafficking-suriname/

Bao, L., & Intille, S. S. (2004). Activity Recognition from User-Annotated Acceleration Data. In A. Ferscha & F. Mattern (Eds.), *Pervasive computing* (pp. 1–17). Springer.

Barrera Zambrano, V. A., Zambrano Moncada, J., & Stevenson, P. R. (2007). Diversity of regenerating plants and seed dispersal in two canopy trees from Colombian Amazon forests with different hunting pressure. *Revista de Biología Tropical*, *56*(3). https://doi.org/10.15517/rbt.v56i3.5727

Bastani, O., Kim, C., & Bastani, H. (2017). Interpreting Blackbox Models via Model Extraction. *arXiv*.

Benaissa, S., Tuyttens, F., Plets, D., de Pessemier, T., Trogh, J., Tanghe, E., Martens, L., Vandaele, L., Van Nuffel, A., Joseph, W., & Sonck, B. (2017). On the use of on-cow accelerometers for the classification of behaviours in dairy barns. *Research in Veterinary Science*, (August). https://doi.org/10.1016/j.rvsc.2017.10.005

Bengio, Y., Deleu, T., Rahaman, N., Ke, R., Lachapelle, S., Bilaniuk, O., Goyal, A., & Pal, C. (2019). A Meta-Transfer Objective for Learning to Disentangle Causal Mechanisms. *arXiv*.

Benítez-López, A., Alkemade, R., Schipper, A. M., Ingram, D. J., Verweij, P. A., Eikelboom, J. A. J., & Huijbregts, M. A. J. (2017). The impact of hunting on tropical mammal and bird populations. *Science*, *356*(6334), 180–183. https://doi.org/10.1126/science.aaj1891

Benítez-López, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation*, *143*(6), 1307–1316. https://doi.org/10.1016/j.biocon.2010.02.009

Bennett, E. L. (2015). Legal ivory trade in a corrupt world and its impact on African elephant populations. *Conservation Biology*, *29*(1), 54–60. https://doi.org/10.1111/cobi.12377

Berdahl, A., Torney, C. J., Ioannou, C. C., Faria, J. J., & Couzin, I. D. (2013). Emergent Sensing of Complex Environments by Mobile Animal Groups. *Science*, *339*(6119), 574–576. https://doi.org/10.1126/science.1225883

Bernoff, A. J., & Topaz, C. M. (2011). A Primer of Swarm Equilibria. *SIAM Journal on Applied Dynamical Systems*, *10*(1), 212–250. https://doi.org/10.1137/100804504

Bewley, J., Boyce, R., Hockin, J., Munksgaard, L., Eicher, S., Einstein, M., & Schutz, M. (2010). Influence of milk yield, stage of lactation, and body condition on dairy cattle lying behaviour measured using an automated activity monitoring sensor. *Journal of Dairy Research*, *77*(1), 1–6. https://doi.org/10.1017/S0022029909990227

Bhattacharyya, P., & Chakrabarti, B. K. (2008). The mean distance to the n th neighbour in a uniform distribution of random points: an application of probability theory. *European Journal of Physics*, *29*(3), 639–645. https://doi.org/10.1088/0143-0807/29/3/023

Biggs, D., Cooney, R., Roe, D., Dublin, H. T., Allan, J. R., Challender, D. W., & Skinner, D. (2017). Developing a theory of change for a community-based response to illegal wildlife trade. *Conservation Biology*, *31*(1), 5–12. https://doi.org/10.1111/cobi.12796

Biggs, D., Courchamp, F., Martin, R., & Possingham, H. P. (2013). Legal trade of Africa's Rhino horns. *Science*, *339*(6123), 1038–1039. https://doi.org/10.1126/science.1229998

Biggs, D., Holden, M. H., Braczkowski, A., Cook, C. N., Milner-Gulland, E. J., Phelps, J., Scholes, R. J., Smith, R. J., Underwood, F. M., Adams, V. M., Allan, J., Brink, H., Cooney, R., Gao, Y., Hutton, J., Macdonald-Madden, E., Maron, M., Redford, K. H., Sutherland, W. J., & Possingham, H. P. (2017). Breaking the deadlock on ivory. *Science*, *358*(6369), 1378–1381. https://doi.org/10.1126/science.aan5215

Bochinski, E., Eiselein, V., & Sikora, T. (2017). High-Speed tracking-by-detection without using image information. *2017 14th IEEE International Conference on Advanced Video and Signal Based Surveillance (AVSS)*, (August), 1–6. https://doi.org/10.1109/AVSS.2017.8078516

Bode, N. W., Faria, J. J., Franks, D. W., Krause, J., & Wood, A. J. (2010). How perceived threat increases synchronization in collectively moving animal groups. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1697), 3065–3070. https://doi.org/10.1098/rspb.2010.0855

Borchani, H., Varando, G., Bielza, C., & Larrañaga, P. (2015). A survey on multi-output regression. *Wiley Interdisciplinary Reviews: Data Mining and Knowledge Discovery*, *5*(5), 216–233. https://doi.org/10.1002/widm.1157

Bracken, M. B. (1992). Effective Care of the Newborn Infant. In J. C. Sinclair & M. B. Bracken (Eds.), *Effective care of the newborn infant* (pp. 13–20). Oxford University Press.

Brouwer, L., Cockburn, A., & van de Pol, M. (2020). Integrating Fitness Components Reveals That Survival Costs Outweigh Other Benefits and Costs of Group Living in Two Closely Related Species. *The American Naturalist*, *195*(2), 201–215. https://doi.org/10.1086/706475

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Buckland, S., Anderson, D., Burnham, K., Laake, J., Borchers, D., & Thomas, L. (2004). *Advanced Distance Sampling*. Oxford University Press.

Bureau of Meteorology. (2011). About environmental satellites. http://www.bom.gov.au/australia/satellite/about_satellites.shtml

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer.

Büscher, B., & Fletcher, R. (2019). Towards Convivial Conservation. *Conservation and Society*, *17*(3), 283–296.

Calabrese, J. M., Fleming, C. H., Fagan, W. F., Rimmler, M., Kaczensky, P., Bewick, S., Leimgruber, P., & Mueller, T. (2018). Disentangling social interactions and environmental drivers in multi-individual wildlife tracking data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170007. https://doi.org/10.1098/rstb.2017.0007

Cambron, M. E., Brode, C., Butler, P., & Olszewkski, G. (2015). Poacher detection at fence crossing. *SoutheastCon 2015*, 1–2. https://doi.org/10.1109/SECON.2015.7132898

Campos-Silva, J. V., Peres, C. A., Antunes, A. P., Valsecchi, J., & Pezzuti, J. (2017). Community-based population recovery of overexploited Amazonian wildlife. *Perspectives in Ecology and Conservation*, *15*(4), 266–270. https://doi.org/10.1016/j.pecon.2017.08.004

Catala, A., Grandgeorge, M., Schaff, J. L., Cousillas, H., Hausberger, M., & Cattet, J. (2019). Dogs demonstrate the existence of an epileptic seizure odour in humans. *Scientific Reports*, *9*(1), 1–7. https://doi.org/10.1038/s41598-019-40721-4

Caughley, G., Sinclair, R., & Scott-Kemmis, D. (1976). Experiments in Aerial Survey. *The Journal of Wildlife Management*, *40*(2), 290–300. https://doi.org/10.2307/3800428

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, 201704949. https://doi.org/10.1073/pnas.1704949114

Center for International Earth Science Information Network, Columbia University, International Food Policy Research Institute, The World Bank, & Centro Internacional de Agricultura Tropical. (2011). Global Rural-Urban Mapping Project (GRUMP), version 1: Population Density Grid. https://doi.org/10.7927/H4R20Z93

Chakravarty, P., Cozzi, G., Ozgul, A., & Aminian, K. (2019). A novel biomechanical approach for animal behaviour recognition using accelerometers. *Methods in Ecology and Evolution*, *10*(6), 802–814. https://doi.org/10.1111/2041-210X.13172

Challender, D. W. S., & MacMillan, D. C. (2014). Poaching is more than an Enforcement Problem. *Conservation Letters*, *7*(5), 484–494. https://doi.org/10.1111/conl.12082

Challender, D. W., Sas-Rolfes, M., Ades, G. W., Chin, J. S., Ching-Min Sun, N., Chong, J. l., Connelly, E., Hywood, L., Luz, S., Mohapatra, R. K., de Ornellas, P., Parker, K., Pietersen, D. W., Roberton, S. I., Semiadi, G., Shaw, D., Shepherd, C. R., Thomson, P., Wang, Y., ... Nash, H. C. (2019). Evaluating the feasibility of pangolin farming and its potential conservation impact. *Global Ecology and Conservation*, *20*, e00714. https://doi.org/10.1016/j.gecco.2019.e00714

Chamoso, P., Raveane, W., Parra, V., & González, A. (2014). UAVs Applied to the Counting and Monitoring of Animals. In Springer (Ed.), *Ambient intelligence - software and applications* (pp. 71–80). https://doi.org/10.1007/978-3-319-07596-9

Charuvi, A., Lees, D., Glover, H. K., Rendall, A. R., Dann, P., & Weston, M. A. (2020). A physiological cost to behavioural tolerance. *Behavioural Processes*, *181*(November 2019), 104250. https://doi.org/10.1016/j.beproc.2020.104250

Chen, F. (2016). Poachers and Snobs: Demand for Rarity and the Effects of Antipoaching Policies. *Conservation Letters*, *9*(1), 65–69. https://doi.org/10.1111/conl.12181

Chen, Y., & Kolokolnikov, T. (2014). A minimal model of predator-swarm interactions. *Journal of The Royal Society Interface*, *11*, 20131208. https://doi.org/10.1098/rsif.2013.1208

Cheung, H., Mazerolle, L., Possingham, H. P., & Biggs, D. (2018). Medicinal Use and Legalized Trade of Rhinoceros Horn From the Perspective of Traditional Chinese Medicine Practitioners in Hong Kong. *Tropical Conservation Science*, *11*, 1–8. https://doi.org/10.1177/1940082918787428

Cheung, H., Wang, Y., & Biggs, D. (2018). China's reopened rhino horn trade. *Science*, *362*(6421), 1369. https://doi.org/10.1126/science.aav9392

Child, B. A., Musengezi, J., Parent, G. D., & Child, G. F. (2012). The economics and institutional economics of wildlife on private land in Africa. *Pastoralism: Research, Policy and Practice*, *2*, 18. https://doi.org/10.1186/2041-7136-2-18

Christie, K., Gilbert, S., Brown, C., Hatfield, M., & Hanson, L. (2016). Unmanned aircraft systems in wildlife research: Current and future applications of a transformative technology. *Frontiers in Ecology and the Environment*, *14*(5), 241–251. https://doi.org/10.1002/fee.1281

Cincotta, R. P., Wisnewski, J., & Engelman, R. (2000). Human population in the biodiversity hotspots. *Nature*, *404*(6781), 990–992. https://doi.org/10.1038/35010105

CITES. (2016). *Information document for amendment proposal CoP17 Prop. 7 (CoP17 Inf. 17)* (tech. rep.). CITES Management Authority. Johannesburg, South Africa.

CITES. (2019). Updates on decisions made on proposals to amend Appendices I and II at CoP18. https://cites.org/eng/updates_decisions_cop18_species_proposals

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012). Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *PLoS ONE*, *7*(11), e50611. https://doi.org/10.1371/journal.pone.0050611

Clements, G. R., Lynam, A. J., Gaveau, D., Yap, W. L., Lhota, S., Goosem, M., Laurance, S., & Laurance, W. F. (2014). Where and How Are Roads Endangering Mammals in Southeast Asia's Forests? *PLoS ONE*, *9*(12), e115376. https://doi.org/10.1371/journal.pone.0115376

Colefax, A., Butcher, P., & Kelaher, B. (2018). The potential for unmanned aerial vehicles (UAVs) to conduct marine fauna surveys in place of manned aircraft. *ICES Journal of Marine Science*, *75*(1), 1–8. https://doi.org/10.1093/icesjms/fsx100

Collins, A., Cox, C., & Pamment, N. (2017). Culture, Conservation and Crime: Regulating Ivory Markets for Antiques and Crafts. *Ecological Economics*, *135*, 186–194. https://doi.org/10.1016/j.ecolecon.2017.01.018

Collins, A., Fraser, G., & Snowball, J. (2013). Rhino Poaching: Supply and Demand Uncertain. *Science*, *340*(6137), 1167–1167. https://doi.org/10.1126/science.340.6137.1167-a

Collins, A., Fraser, G., & Snowball, J. (2016). Issues and concerns in developing regulated markets for endangered species products: The case of rhinoceros horns. *Cambridge Journal of Economics*, *40*(6), 1669–1686. https://doi.org/10.1093/cje/bev076

Committee of Inquiry. (2016). *Summary Report* (tech. rep.). Ministry of Environmental Affairs. Johannesburg, South Africa.

Confalonieri, R., Besold, T. R., Weyde, T., Creel, K., Lombrozo, T., Mueller, S., & Shafto, P. (2019). What makes a good explanation? Cognitive dimensions of explaining intelligent machines. *CogSci 2019*, (July 24-27), 25–26.

Conrad, K. (2012). Trade bans: A perfect storm for poaching? *Tropical Conservation Science*, *5*(3), 245–254. https://doi.org/10.1177/194008291200500302

Conway-Smith, E. (2013). South Africa sics drones on rhino poachers. https://www.pri.org/stories/2013-01-11/south-africa-sics-drones-rhino-poachers

Cook, R., & Jacobson, J. (1979). A Design for Estimating Visibility Bias in Aerial Surveys. *Biometrics*, *35*(4), 735–742. https://doi.org/10.2307/2530104

Cooke, S., Hinch, S., Wikelski, M., Andrews, R., Kuchel, L., Wolcott, T., & Butler, P. (2004). Biotelemetry: A mechanistic approach to ecology. *Trends in Ecology and Evolution*, *19*(6), 334–343. https://doi.org/10.1016/j.tree.2004.04.003

Cooper, W. E., & Blumstein, D. T. (2015). *Escaping From Predators: An Integrative View of Escape Decisions* (W. E. Cooper & D. T. Blumstein, Eds.). Cambridge University Press.

Corruption Tracker. (2011). Ivory smuggling exposes massive graft at ports: Tanzania Corruption Tracking System. http://www.corruptiontracker.or.tz/dev/index.php?option=com_content&view=article&id=199%3Aivory-smugglingexposes-massive-graft-at-ports&catid=26%3Awhat-mediasays&Itemid=50&lang=br

Cota, R. (2013). South Africa's Trophy Hunt Industry Linked to Rhino Horn Trafficking ... Again. http://annamiticus.com/2013/08/06/south-africas-trophy-hunt-industry-linked-to-rhino-horn-trafficking-again/

Cousins, J. A., Sadler, J. P., & Evans, J. (2008). Exploring the role of private wildlife ranching as a conservation tool in South Africa: Stakeholder perspectives. *Ecology and Society*, *13*(2), 43. https://doi.org/10.5751/ES-02655-130243

Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002). Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology*, *218*(1), 1–11. https://doi.org/10.1006/yjtbi.3065

Couzin, I. D., & Krause, J. (2003). Self-Organization and Collective Behavior in Vertebrates. *Advances in the study of behavior* (pp. 1–75). Academic Press. https://doi.org/10.1016/S0065-3454(03)01001-5

Cox, D. R., & Snell, E. J. (1970). *Analysis of Binary Data*. Methuen.

Creel, S. (2018). The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. *Ecology Letters*, *21*(7), 947–956. https://doi.org/10.1111/ele.12975

Crookes, D. J. (2017). Does a reduction in the price of rhino horn prevent poaching? *Journal for Nature Conservation*, *39*, 73–82. https://doi.org/10.1016/j.jnc.2017.07.008

Crookes, D. J., & Blignaut, J. N. (2015). Debunking the myth that a legal trade will solve the rhino horn crisis: A system dynamics model for market demand. *Journal for Nature Conservation*, *28*, 11–18. https://doi.org/10.1016/j.jnc.2015.08.001

Crosmary, W. G., Loveridge, A. J., Ndaimani, H., Lebel, S., Booth, V., Côté, S. D., & Fritz, H. (2013). Trophy hunting in Africa: Long-term trends in antelope horn size. *Animal Conservation*, *16*(6), 648–660. https://doi.org/10.1111/acv.12043

CyberTracker. (2017). CyberTracker. https://www.cybertracker.org/

Cyranoski, D. (2018). Why Chinese medicine is heading for clinics around the world. *Nature*, *561*(7724), 448–450. https://doi.org/10.1038/d41586-018-06782-7

Damania, R., & Bulte, E. H. (2007). The economics of wildlife farming and endangered species conservation. *Ecological Economics*, *62*(3-4), 461–472. https://doi.org/10.1016/j.ecolecon.2006.07.007

Darimont, C. T., Fox, C. H., Bryan, H. M., & Reimchen, T. E. (2015). The unique ecology of human predators. *Science*, *349*(6250), 858–860. https://doi.org/10.1126/science.aac4249

Davis, D., & Winstead, R. (1980). Estimating the Numbers of Wildlife Populations. In S. Schemnitz (Ed.), *Wildlife management techniques manual* (Fourth Ed., pp. 221–245). The Wildlife Society.

Dawson, A. (2016). *Extinction: a radical history*. OR Books.

De Bie, S., & Kessler, J. (1983). *An aerial resource inventory of the national park "Boucle du Baoule"(Mali, West Africa) 1980 - 1981* (tech. rep.). Projet de Recherche sur l' Utilisation Rationelle du Gibier au Sahel (RURGS) & Nature Conservation Department, Agricultural University Wageningen. Wageningen, Netherlands.

De Knegt, H., Hengeveld, G., Van Langevelde, F., De Boer, W., & Kirkman, K. (2007). Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology*, *18*(6), 1065–1072. https://doi.org/10.1093/beheco/arm080

DeepLearning.AI. (2021). The Batch. https://www.deeplearning.ai/the-batch/

de Knegt, H. J., Eikelboom, J. A. J., van Langevelde, F., Spruyt, W. F., & Prins, H. H. T. (2021). Timely poacher detection and localization using sentinel animal movement. *Scientific Reports*, *11*, 4596. https://doi.org/10.1038/s41598-021-83800-1

Deng, J., Dong, W., Socher, R., Li, L., Li, K., & Fei-Fei, L. (2009). ImageNet: A large-scale hierarchical image database. *Proceedings of the IEEE Conference on Computer Vision and Pattern Recognition*, 248–255. https://doi.org/10.1109/CVPRW.2009.5206848

de Weerd, N., van Langevelde, F., van Oeveren, H., Nolet, B. A., Kölzsch, A., Prins, H. H. T., & de Boer, W. F. (2015). Deriving Animal Behaviour from High-Frequency GPS: Tracking Cows in Open and Forested Habitat. *PLOS ONE*, *10*(6), e0129030. https://doi.org/10.1371/journal.pone.0129030

DHV Consulting Engineers. (1980). *Countrywide Animal and Range Assessment Project. Volume IV - Special Subject Report: Animal Populations.* (tech. rep.). Republic of Botswana, Ministry of Commerce, Industry, Department of Wildlife National Parks, and Tourism & Commission of the European Communities, European Development Fund. Republic of Botswana.

Di Minin, E., Laitila, J., Montesino-Pouzols, F., Leader-Williams, N., Slotow, R., Goodman, P. S., Conway, A. J., & Moilanen, A. (2015). Identification of policies for a sustainable legal trade in rhinoceros horn based on population projection and socioeconomic models. *Conservation Biology*, *29*(2), 545–555. https://doi.org/10.1111/cobi.12412

Dickman, A., Cooney, R., Johnson, P. J., Louis, M. P., & Roe, D. (2019). Trophy hunting bans imperil biodiversity. *Science*, *365*(6456), 874–874. https://doi.org/10.1126/science.aaz0735

Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, *25*(2), 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*(6195), 401–406. https://doi.org/10.1126/science.1251817

Doshi-Velez, F., & Kim, B. (2017). Towards A Rigorous Science of Interpretable Machine Learning. *arXiv*.

Drescher, M., Heitkönig, I., & Prins, H. (2003). Forage availability and accessibility determine the functional response of herbivores in complex resources. In M. Drescher (Ed.), *Grasping complex matter: Large herbivore foraging in patches of heterogeneous resources* (pp. 17–35).

Duffy, R. (2014). Waging a war to save biodiversity: the rise of militarized conservation. *International Affairs*, *90*(4), 819–834. https://doi.org/10.1111/1468-2346.12142

Duffy, R., Massé, F., Smidt, E., Marijnen, E., Büscher, B., Verweijen, J., Ramutsindela, M., Simlai, T., Joanny, L., & Lunstrum, E. (2019). Why we must question the militarisation of conservation. *Biological Conservation*, *232*, 66–73. https://doi.org/10.1016/j.biocon.2019.01.013

Dulac, J. (2013). *Global land transport infrastructure requirements: Estimating road and railway infrastructure capacity and costs to 2050* (tech. rep.). International Energy Agency. Paris, France.

Dunn, W., Donnelly, J., & Krausmann, W. (2002). Using thermal infrared sensing to count elk in the southwestern United States. *Wildlife Society Bulletin*, *30*(3), 963–967.

Duporge, I., Isupova, O., Reece, S., Macdonald, D. W., & Wang, T. (2020). Using very-high-resolution satellite imagery and deep learning to detect and count African elephants in heterogeneous landscapes. *Remote Sensing in Ecology and Conservation*, rse2.195. https://doi.org/10.1002/rse2.195

Ebensperger, L. A., & Wallem, P. K. (2002). Grouping increases the ability of the social rodent, Octodon degus , to detect predators when using exposed microhabitats. *Oikos*, *98*(3), 491–497. https://doi.org/10.1034/j.1600-0706.2002.980313.x

Eftimie, R., de Vries, G., Lewis, M. A., & Lutscher, F. (2007). Modeling Group Formation and Activity Patterns in Self-Organizing Collectives of Individuals. *Bulletin of Mathematical Biology*, *69*, 1537–1565. https://doi.org/10.1007/s11538-006-9175-8

Egger, M., Smith, G. D., Schneider, M., & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *BMJ*, *315*(7109), 629–634. https://doi.org/10.1136/bmj.315.7109.629

EIA. (2013). *Hidden in Plain Sight: China's Clandestine Tiger Trade* (tech. rep.). Environmental Investigation Agency. London, UK.

Eikelboom, J. A. J., de Knegt, H. J., Klaver, M., van Langevelde, F., van der Wal, T., & Prins, H. H. T. (2020). Inferring an animal's environment through biologging:

quantifying the environmental influence on animal movement. *Movement Ecology*, *8*(1), 40. https://doi.org/10.1186/s40462-020-00228-4

Eikelboom, J. A. J., Nuijten, R. J. M., Wang, Y. X. G., Schroder, B., Heitkönig, I. M. A., Mooij, W. M., van Langevelde, F., & Prins, H. H. T. (2020). Will legal international rhino horn trade save wild rhino populations? *Global Ecology and Conservation*, *23*, e01145. https://doi.org/10.1016/j.gecco.2020.e01145

Eikelboom, J. A. J., Wind, J., van de Ven, E., Kenana, L. M., Schroder, B., de Knegt, H. J., van Langevelde, F., & Prins, H. H. T. (2019). Improving the precision and accuracy of animal population estimates with aerial image object detection. *Methods in Ecology and Evolution*, *10*(11), 1875–1887. https://doi.org/10.1111/2041-210X.13277

Emlen, J. (1966). The Role of Time and Energy in Food Preference. *The American Naturalist*, *100*(916), 611–617. https://doi.org/10.1086/282455

Emslie, R., & Brooks, M. (1999). *African Rhino: Status Survey and Conservation Action Plan* (tech. rep.). IUCN. Gland, Switzerland.

Emslie, R. H., Milliken, T., Talukdar, B., Ellis, S., Adcock, K., & Knight, M. H. (2016). *African and Asian Rhinoceroses - Status, Conservation and Trade. A report from the IUCN Species Survival Commission (IUCN SSC) African and Asian Rhino Specialist Groups and TRAFFIC to the CITES Secretariat pursuant to Resolution Conf. 9.14 (Rev. CoP15)* (tech. rep.).

Environment News Service. (2010). Restoring North America's Wild Bison to Their Home on the Range. http://www.ens-newswire.com/ens/mar2010/2010-03-03-01.html

Environmental Systems Research Institute. (2011). ArcGIS Desktop.

Evans, D. A., Stempel, A. V., Vale, R., & Branco, T. (2019). Cognitive Control of Escape Behaviour. *Trends in Cognitive Sciences*, *23*(4), 334–348. https://doi.org/10.1016/j.tics.2019.01.012

Falk, D. (2019). How artificial intelligence is changing science. *Quanta magazine*, *3*(11). https://www.quantamagazine.org/how-artificial-intelligence-is-changing-science-20190311/

Felbab-Brown, V. (2017). *The Extinction Market*. Oxford University Press.

Ferraro, D., & Oesterheld, M. (2002). The effect of defoliation on grass growth: A quantitative review. *Oikos*, *98*(1), 125–133. https://doi.org/10.1034/j.1600-0706.2002.980113.x

Ferreira, S., Hofmeyr, M., Pienaar, D., & Cooper, D. (2014). Chemical horn infusions: A poaching deterrent or an unnecessary deception? *Pachyderm*, *55*, 54–61.

Ferreira, S. M., & Pienaar, D. (2020). Evaluating uncertainty in estimates of large rhinoceros populations. *Pachyderm*, *61*, 97–108.

Fischer, C. (2004). The complex interactions of markets for endangered species products. *Journal of Environmental Economics and Management*, *48*(2), 926–953. https://doi.org/10.1016/j.jeem.2003.12.003

Fisher, A. (2018). As Tigers Become Rarer, Poachers Are Targeting Lions. https://www.nationalgeographic.com/news/2018/06/wildlife-watch-illegal-trade-lions-teeth-claws-poaching/

Fizyr. (2018). Keras RetinaNet 0.5.0. https://github.com/fizyr/keras-retinanet/tree/0.5.0

Fleming, P., & Tracey, J. (2008). Some human, aircraft and animal factors affecting aerial surveys: how to enumerate animals from the air. *Wildlife Research*, *35*, 258–267. https://doi.org/10.1071/WR07081

Forde, J. Z., & Paganini, M. (2019). The Scientific Method in the Science of Machine Learning. *arXiv*.

Frid, A., & Dill, L. M. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, *6*(1), 11. https://doi.org/10.5751/ES-00404-060111

Frommen, J. G., Hiermes, M., & Bakker, T. C. M. (2009). Disentangling the effects of group size and density on shoaling decisions of three-spined sticklebacks (Gasterosteus aculeatus). *Behavioral Ecology and Sociobiology*, *63*(8), 1141–1148. https://doi.org/10.1007/s00265-009-0767-9

Fryxell, J. M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T., & Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19114–9. https://doi.org/10.1073/pnas.0801737105

Fryxell, J. M., Mosser, A., Sinclair, A. R. E., & Packer, C. (2007). Group formation stabilizes predator–prey dynamics. *Nature*, *449*(7165), 1041–1043. https://doi.org/10.1038/nature06177

Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. (2017). Energy Landscapes and the Landscape of Fear. *Trends in Ecology and Evolution*, *32*(2), 88–96. https://doi.org/10.1016/j.tree.2016.10.010

Gao, Y., Stoner, K. J., Lee, A. T., & Clark, S. G. (2016). Rhino horn trade in China: An analysis of the art and antiques market. *Biological Conservation*, *201*, 343–347. https://doi.org/10.1016/j.biocon.2016.08.001

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology & Evolution*, *34*(4), 355–368. https://doi.org/10.1016/j.tree.2019.01.004

Gazi, V., & Passino, K. M. (2004). A class of attractions/repulsion functions for stable swarm aggregations. *International Journal of Control*, *77*(18), 1567–1579. https://doi.org/10.1080/00207170412331330021

Gerencsér, L., Vásárhelyi, G., Nagy, M., Vicsek, T., & Miklósi, A. (2013). Identification of Behaviour in Freely Moving Dogs (Canis familiaris) Using Inertial Sensors. *PLoS ONE*, *8*(10), e77814. https://doi.org/10.1371/journal.pone.0077814

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, *478*(7369), 378–381. https://doi.org/10.1038/nature10425

Gillespie, T., & Chapman, C. (2001). Determinants of group size in the red colobus monkey (Procolobus badius): an evaluation of the generality of the ecological-constraints model. *Behavioral Ecology and Sociobiology*, *50*(4), 329–338. https://doi.org/10.1007/s002650100371

Gleiss, A. C., Wilson, R. P., & Shepard, E. L. (2011). Making overall dynamic body acceleration work: On the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution*, *2*(1), 23–33. https://doi.org/10.1111/j.2041-210X.2010.00057.x

Goumas, M., Lee, V. E., Boogert, N. J., Kelley, L. A., & Thornton, A. (2020). The Role of Animal Cognition in Human-Wildlife Interactions. *Frontiers in Psychology*, *11*(November). https://doi.org/10.3389/fpsyg.2020.589978

Graham-Rowe, D. (2011). Biodiversity: Endangered and in demand. *Nature*, *480*(7378), S101–S103. https://doi.org/10.1038/480S101a

Greenfield, S., & Veríssimo, D. (2019). To What Extent Is Social Marketing Used in Demand Reduction Campaigns for Illegal Wildlife Products? Insights From Elephant Ivory and Rhino Horn. *Social Marketing Quarterly*, *25*(1), 40–54. https://doi.org/10.1177/1524500418813543

Haalck, L., Mangan, M., Webb, B., & Risse, B. (2020). Towards image-based animal tracking in natural environments using a freely moving camera. *Journal of Neuroscience Methods*, *330*, 108455. https://doi.org/10.1016/j.jneumeth.2019.108455

Haas, T. C., & Ferreira, S. M. (2016). Conservation Risks: When Will Rhinos be Extinct? *IEEE Transactions on Cybernetics*, *46*(8), 1721–1734. https://doi.org/10.1109/TCYB.2015.2470520

Hall, R. J., Milner-Gulland, E. J., & Courchamp, F. (2008). Endangering the endangered: The effects of perceived rarity on species exploitation. *Conservation Letters*, *1*(2), 75–81. https://doi.org/10.1111/j.1755-263X.2008.00013.x

Halsey, L. G. (2016). Terrestrial movement energetics: current knowledge and its application to the optimising animal. *The Journal of Experimental Biology*, *219*(10), 1424–1431. https://doi.org/10.1242/jeb.133256

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*(2), 295–311. https://doi.org/10.1016/0022-5193(71)90189-5

Hanley, N., Sheremet, O., Bozzola, M., & MacMillan, D. C. (2018). The Allure of the Illegal: Choice Modeling of Rhino Horn Demand in Vietnam. *Conservation Letters*, *11*(3), e12417. https://doi.org/10.1111/conl.12417

Harrison, R. D. (2011). Emptying the Forest: Hunting and the Extirpation of Wildlife from Tropical Nature Reserves. *BioScience*, *61*(11), 919–924. https://doi.org/10.1525/bio.2011.61.11.11

Harvey, P. H., & Pagel, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press.

He, K., Zhang, X., Ren, S., & Sun, J. (2016). Deep Residual Learning for Image Recognition. *Proceedings of the IEEE Conference on Computer Vision and Pattern Recognition*, 770–778. https://doi.org/10.1109/CVPR.2016.90

Hearne, J., Korrûbel, J., & Koch, K. (2000). Modelling to optimise consumptive use of game. *Annals of Operations Research*, *95*, 269–284. https://doi.org/10.1023/A:1018950007473

Heatherington, T. (2012). From ecocide to genetic rescue: can technoscience save the wild? In G. Sodikoff (Ed.), *The anthropology of extinction: Essays on culture and species death* (pp. 39–66). Bloomington, Indiana University Press.

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, *80*, 1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2

Helbing, D., Farkas, I., & Vicsek, T. (2000). Simulating dynamical features of escape panic. *Nature*, *407*(6803), 487–490. https://doi.org/10.1038/35035023

Herbert-Read, J. E., Buhl, J., Hu, F., Ward, A. J. W., & Sumpter, D. J. T. (2015). Initiation and spread of escape waves within animal groups. *Royal Society open science*, *2*(4), 140355. https://doi.org/10.1098/rsos.140355

Herbert-Read, J. E., Rosén, E., Szorkovszky, A., Ioannou, C. C., Rogell, B., Perna, A., Ramnarine, I. W., Kotrschal, A., Kolm, N., Krause, J., & Sumpter, D. J. T. (2017). How predation shapes the social interaction rules of shoaling fish. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1861), 20171126. https://doi.org/10.1098/rspb.2017.1126

Hernandez, M. (2019). We're helping to save the rhino - here's how. https://gblogs.cisco.com/uki/help-save-this-rhino-heres-how/

Hoare, D., Couzin, I., Godin, J.-G., & Krause, J. (2004). Context-dependent group size choice in fish. *Animal Behaviour*, *67*(1), 155–164. https://doi.org/10.1016/j.anbehav.2003.04.004

Hodgson, J., Mott, R., Baylis, S., Pham, T., Wotherspoon, S., Kilpatrick, A., Segaran, R., Reid, I., Terauds, A., & Koh, L. (2018). Drones count wildlife more accurately and precisely than humans. *Methods in Ecology and Evolution*, *9*, 1160–1167. https://doi.org/10.1111/2041-210X.12974

Holden, M. H., Biggs, D., Brink, H., Bal, P., Rhodes, J., & McDonald-Madden, E. (2019). Increase anti-poaching law-enforcement or reduce demand for wildlife products? A framework to guide strategic conservation investments. *Conservation Letters*, *12*(3), e12618. https://doi.org/10.1111/conl.12618

Homburger, H., Schneider, M. K., Hilfiker, S., & Lüscher, A. (2014). Inferring Behavioral States of Grazing Livestock from High-Frequency Position Data Alone. *PLoS ONE*, *9*(12), e114522. https://doi.org/10.1371/journal.pone.0114522

Hsiang, S., & Sekar, N. (2019). Does legalization reduce black market activity? Evidence from a global ivory experiment and elephant poaching data. *NBER Working Paper Series*, (22314), 49. https://doi.org/10.3386/w22314

Hughey, L. F., Hein, A. M., Strandburg-Peshkin, A., & Jensen, F. H. (2018). Challenges and solutions for studying collective animal behaviour in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170005. https://doi.org/10.1098/rstb.2017.0005

Hutton, J., & Webb, G. (2002). Legal Trade Snaps Back: Using the Experience of Crocodilians to Draw Lessons on Regulation of the Wildlife Trade. *Proceedings of the 16th Working Meeting of the Crocodile specialist Group of the Species Survival Commission of IUCN - The World Conservation Union*, 1–10.

Ihwagi, F. W., Thouless, C., Wang, T., Skidmore, A. K., Omondi, P., & Douglas-Hamilton, I. (2018). Night-day speed ratio of elephants as indicator of poaching levels. *Ecological Indicators*, *84*, 38–44. https://doi.org/10.1016/j.ecolind.2017.08.039

Ioannou, C. C., Ramnarine, I. W., & Torney, C. J. (2017). High-predation habitats affect the social dynamics of collective exploration in a shoaling fish. *Science Advances*, *3*(5). https://doi.org/10.1126/sciadv.1602682

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (tech. rep.). Bonn, Germany. https://www.ipbes.net/global-assessment-report-biodiversity-ecosystem-services

Irwin, D. A. (1995). Multilateral and bilateral trade policies in the world trading system: an historical perspective. In J. De Melo & A. Panagariya (Eds.), *New dimensions in regional integration* (pp. 90–119). Cambridge University Press. https://doi.org/10.1017/cbo9780511628511.008

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*(2), 143–155. https://doi.org/10.1093/beheco/2.2.143

IUCN, & UNEP-WCMC. (2016). The World Database on Protected Areas (WDPA). https://www.iucn.org/theme/protected-areas/our-work/worlddatabase-%0Aprotected-areas

J. Sweeting, M., J. Sutton, A., & C. Lambert, P. (2004). What to add to nothing? Use and avoidance of continuity corrections in meta-analysis of sparse data. *Statistics in Medicine*, *23*(9), 1351–1375. https://doi.org/10.1002/sim.1761

Jachmann, H. (2001). *Estimating abundance of African wildlife: an aid to adaptive management*. Kluwer Academic Publishers.

Jachmann, H. (2002). Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology*, *39*, 841–852. https://doi.org/10.1046/j.1365-2664.2002.00752.x

Jachmann, H., & Billiouw, M. (1997). Elephant Poaching and Law Enforcement in the Central Luangwa Valley, Zambia. *Journal of Applied Ecology*, *34*(1), 233–244. https://doi.org/10.2307/2404861

Jacolliot, L. (1884). *Les animaux sauvages*. Librairie illustrée.

Jain, S., & Wallace, B. C. (2019). Attention is not Explanation. *Proceedings of the 2019 Conference on Empirical Methods in Natural Language Processing and the 9th International Joint Conference on Natural Language Processing (EMNLP-IJCNLP)*, 11–20.

Jolly, G. (1969a). Sampling methods for aerial censuses of wildlife populations. *East African Agricultural and Forestry Journal*, *34*, 46–49. https://doi.org/10.1080/00128325.1969.11662347

Jolly, G. (1969b). The treatment of errors in aerial counts of wildlife populations. *East African Agricultural and Forestry Journal*, *34*, 50–55. https://doi.org/10.1080/00128325.1969.11662348

Jordan, C., Urquhart, G., & Kramer, D. (2013). On Using Mental Model Interviews to Improve Camera Trapping: Adapting Research to Costeño Environmental Knowledge. *Conservation and Society*, *11*(2), 159–175. https://doi.org/10.4103/0972-4923.115725

Katt, F., & Meixner, O. (2020). A systematic review of drivers influencing consumer willingness to pay for organic food. *Trends in Food Science & Technology*. https://doi.org/10.1016/j.tifs.2020.04.029

Katzner, T. E., & Arlettaz, R. (2020). Evaluating Contributions of Recent Tracking-Based Animal Movement Ecology to Conservation Management. *Frontiers in Ecology and Evolution*, *7*, 519. https://doi.org/10.3389/fevo.2019.00519

Kellenberger, B., Marcos, D., & Tuia, D. (2018). Detecting Mammals in UAV Images: Best Practices to address a substantially Imbalanced Dataset with Deep Learning. *Remote Sensing of Environment*, *216*, 139–153. https://doi.org/10.1016/j.rse.2018.06.028

Kellenberger, B. (2020). *Interactive Machine Vision for Wildlife Conservation* (Doctoral dissertation). Wageningen University. https://doi.org/10.18174/511122

King, L. E., Lala, F., Nzumu, H., Mwambingu, E., & Douglas-Hamilton, I. (2017). Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. *Conservation Biology*, *31*(4), 743–752. https://doi.org/10.1111/cobi.12898

Knight, M., Emslie, R., Smart, R., & Balfour, D. (2015). *Biodiversity Management Plan for The White Rhinoceros (Ceratotherium simum) in South Africa 2015-2020* (tech. rep.). Department of Environmental Affairs. Pretoria, South Africa.

Kollapen, J. (2019). *Lion Bones Judgement* (tech. rep.). High Court of South Africa. Pretoria, South Africa. https://www.scribd.com/document/420943204/Lion-Bones-Judgment

Kollmuss, A., & Agyeman, J. (2002). Mind the Gap: Why do people act environmentally and what are the barriers to pro-environmental behavior? *Environmental Education Research*, *8*(3), 239–260. https://doi.org/10.1080/13504620220145401

Kotze, D. (2014). Why legalising trade in horn will hasten the demise of rhinos. *Africa Geographic Magazine*, *22*. https://magazine.africageographic.com/weekly/issue-22/rhino-horn-trade-south-africa-china-selling-out/

Krause, J., & Godin, J.-G. J. (2010). Shoal Choice in the Banded Killifish (Fundulus diaphanus, Teleostei, Cyprinodontidae): Effects of Predation Risk, Fish Size, Species Composition and Size of Shoals. *Ethology*, *98*(2), 128–136. https://doi.org/10.1111/j.1439-0310.1994.tb01063.x

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

Kruschke, J. K. (2013). Bayesian estimation supersedes the t test. *Journal of Experimental Psychology: General*, *142*(2), 573–603. https://doi.org/10.1037/a0029146

Kuhn, M. (2020). caret: Classification and Regression Training. https://cran.r-project.org/package=caret

Kuhn, M., & Johnson, K. (2013). *Applied Predictive Modeling*. Springer.

Ladds, M. A., Thompson, A. P., Slip, D. J., Hocking, D. P., & Harcourt, R. G. (2016). Seeing It All: Evaluating Supervised Machine Learning Methods for the Classification of Diverse Otariid Behaviours. *PLOS ONE*, *11*(12), e0166898. https://doi.org/10.1371/journal.pone.0166898

Lajeunesse, M. J. (2011). On the meta-analysis of response ratios for studies with correlated and multi-group designs. *Ecology*, *92*(11), 2049–2055. https://doi.org/10.1890/11-0423.1

Lajeunesse, M. J. (2015). Bias and correction for the log response ratio in ecological meta-analysis. *Ecology*, *96*(8), 2056–2063. https://doi.org/10.1890/14-2402.1

Lajeunesse, M. J. (2016). Facilitating systematic reviews, data extraction and meta-analysis with the METAGEAR package for R. *Methods in Ecology and Evolution*, *7*(3), 323–330. https://doi.org/10.1111/2041-210X.12472

Lam, T. T.-Y., Shum, M. H.-H., Zhu, H.-C., Tong, Y.-G., Ni, X.-B., Liao, Y.-s., Wei, W., Cheung, W. Y.-m., Li, W.-J., Li, L.-f., Leung, G. M., Holmes, E. C., Hu, Y.-l., & Guan, Y. (2020). Identifying SARS-CoV-2 related coronaviruses in Malayan pangolins. *Nature*. https://doi.org/10.1038/s41586-020-2169-0

Langrock, R., Hopcraft, J. G. C., Blackwell, P. G., Goodall, V., King, R., Niu, M., Patterson, T. A., Pedersen, M. W., Skarin, A., & Schick, R. S. (2014). Modelling group dynamic animal movement. *Methods in Ecology and Evolution*, *5*(2), 190–199. https://doi.org/10.1111/2041-210X.12155

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear"in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, *79*(8), 1401–1409. https://doi.org/10.1139/z01-094

Laurance, W. F., & Balmford, A. (2013). A global map for road building. *Nature*, *495*(7441), 308–309. https://doi.org/10.1038/495308a

Laurance, W. F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C. J. A., Sloan, S. P., Laurance, S. G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K. S., Cannon,

C. H., Cao, M., Carroll, R., Chapman, C., … Zamzani, F. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, *489*(7415), 290–294. https://doi.org/10.1038/nature11318

Laurance, W. F., Peletier-Jellema, A., Geenen, B., Koster, H., Verweij, P., Van Dijck, P., Lovejoy, T. E., Schleicher, J., & Van Kuijk, M. (2015). Reducing the global environmental impacts of rapid infrastructure expansion. *Current Biology*, *25*(7), R259–R262. https://doi.org/10.1016/j.cub.2015.02.050

Laurance, W. F., Sloan, S., Weng, L., & Sayer, J. A. (2015). Estimating the Environmental Costs of Africa's Massive Development Corridors. *Current Biology*, *25*(24), 3202–3208. https://doi.org/10.1016/j.cub.2015.10.046

Leader-Williams, N., Milledge, S., Adcock, K., Brooks, M., Conway, A., Knight, M., Mainka, S., Martin, E. B., & Teferi, T. (2005). Trophy hunting of black rhino Diceros bicornis: Proposals to ensure its future sustainability. *Journal of International Wildlife Law and Policy*, *8*(1), 1–11. https://doi.org/10.1080/13880290590913705

Lemieux, A. M., & Clarke, R. V. (2009). The International Ban on Ivory Sales and its Effects on Elephant Poaching in Africa. *British Journal of Criminology*, *49*(4), 451–471. https://doi.org/10.1093/bjc/azp030

LeResche, R., & Rausch, R. (1974). Accuracy and Precision of Aerial Moose Censusing. *The Journal of Wildlife Management*, *38*(2), 175–182. https://doi.org/10.2307/3800722

Leverentz, A. J., Topaz, C. M., & Bernoff, A. J. (2009). Asymptotic Dynamics of Attractive-Repulsive Swarms. *SIAM Journal on Applied Dynamical Systems*, *8*(3), 880–908. https://doi.org/10.1137/090749037

Lewis, S. L., & Maslin, M. A. (2015). Defining the Anthropocene. *Nature*, *519*(7542), 171–180. https://doi.org/10.1038/nature14258

Liaw, A., & Wiener, M. (2002). Classification and Regression by randomForest. *R News*, *2*(3), 18–22. https://cran.r-project.org/doc/Rnews/

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Lin, T., Dollár, P., Girshick, R., He, K., Hariharan, B., & Belongie, S. (2017). Feature Pyramid Networks for Object Detection. *Proceedings of the IEEE Conference on Computer Vision and Pattern Recognition*, *1*(2), 4. https://doi.org/10.1109/CVPR.2017.106

Lin, T., Goyal, P., Girshick, R., He, K., & Dollár, P. (2018). Focal Loss for Dense Object Detection. *Proceedings of the IEEE Transactions on Pattern Analysis and Machine Intelligence*, 2999–3007. https://doi.org/10.1109/ICCV.2017.324

Linchant, J., Lisein, J., Semeki, J., Lejeune, P., & Vermeulen, C. (2015). Are unmanned aircraft systems (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. *Mammal Review*, *45*, 239–252. https://doi.org/10.1111/mam.12046

Lindsey, P. A., Roulet, P. A., & Romañach, S. S. (2007). Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*, *134*(4), 455–469. https://doi.org/10.1016/j.biocon.2006.09.005

Lindsey, P. A., Balme, G. A., Booth, V. R., & Midlane, N. (2012). The significance of African lions for the financial viability of trophy hunting and the maintenance of wild land. *PLoS ONE*, *7*(1), e29332. https://doi.org/10.1371/journal.pone.0029332

Lipton, Z. C. (2016). The Mythos of Model Interpretability. *Communications of the ACM*, *61*(10), 35–43. https://doi.org/10.1145/3233231

Litchfield, C. A. (2013). Rhino Poaching: Apply Conservation Psychology. *Science*, *340*(6137), 1168–1168. https://doi.org/10.1126/science.340.6137.1168-a

Liu, Y., & Xi, Y. (2019). Colloidal systems with a short-range attraction and long-range repulsion: Phase diagrams, structures, and dynamics. *Current Opinion in Colloid & Interface Science*, *39*, 123–136. https://doi.org/10.1016/j.cocis.2019.01.016

Loveridge, A. J., Searle, A. W., Murindagomo, F., & Macdonald, D. W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, *134*(4), 548–558. https://doi.org/10.1016/j.biocon.2006.09.010

Lucas, T. C. D. (2020). A translucent box: interpretable machine learning in ecology. *Ecological Monographs*, *90*(4), e01422. https://doi.org/10.1002/ecm.1422

Lueck, D. (2002). The extermination and conservation of the American bison. *Journal of Legal Studies*, *31*(S2), S609–S652. https://doi.org/10.1086/340410

Lundberg, S., & Lee, S.-I. (2017). A Unified Approach to Interpreting Model Predictions. *Advances in Neural Information Processing Systems*, *2*, 4766–4775.

Lusseau, D., & Lee, P. C. (2016). Can We Sustainably Harvest Ivory? *Current Biology*, *26*(21), 2951–2956. https://doi.org/10.1016/j.cub.2016.08.060

Lyddon, S. P., Walker, S. G., & Holmes, C. C. (2018). Nonparametric learning from Bayesian models with randomized objective functions. *Advances in Neural Information Processing Systems*, 2071–2081.

MacGregor, J. (2002). International trade in crocodilian skins: review and analysis of the trade and industry dynamics for market-based conservation. *Proceedings of the 16th Working Meeting of the Crocodile specialist Group of the Species Survival Commission of IUCN - The World Conservation Union*, 12–18.

Manning, A., Lindenmayer, D., & Nix, H. (2004). Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos*, *104*(3), 621–628. https://doi.org/10.1111/j.0030-1299.2004.12813.x

Marris, E. (2011). *Rambunctious garden: saving nature in a post-wild world*. Bloomsbury.

Marris, E. (2014). 'New conservation' is an expansion of approaches, not an ethical orientation. *Animal Conservation*, *17*(6), 516–517. https://doi.org/10.1111/acv.12129

Martin, G. (2017). Meerkat surveillance system helping reduce Kruger poaching. https://www.defenceweb.co.za/security/border-security/meerkat-surveillance-system-helping-reduce-kruger-poaching/

Martiskainen, P., Järvinen, M., Skön, J., Tiirikainen, J., Kolehmainen, M., & Mononen, J. (2009). Cow behaviour pattern recognition using a three-dimensional accelerometer and support vector machines. *Applied Animal Behaviour Science*, *119*(1-2), 32–38. https://doi.org/10.1016/j.applanim.2009.03.005

Marvier, M. (2014). New Conservation Is True Conservation. *Conservation Biology*, *28*(1), 1–3. https://doi.org/10.1111/cobi.12206

Master, F. (2019). As China pushes traditional medicine globally, illegal wildlife trade flourishes. https://www.reuters.com/article/us-china-tcm/as-china-pushes-traditional-medicine-globally-illegal-wildlife-trade-flourishes-idUSKCN1R90D5

Matthews-King, A. (2019). World Health Organisation's recognition of traditional Chinese medicine 'could push species into extinction'. https://www.independent.co.uk/news/health/china-medicine-wildlife-poaching-conservation-world-health-organisation-a8933061.html

Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, *536*(7615), 143–145. https://doi.org/10.1038/536143a

McClintock, B., Johnson, D., Hooten, M., Ver Hoef, J., & Morales, J. (2014). When to be discrete: the importance of time formulation in understanding animal movement. *Movement Ecology*, *2*, 21. https://doi.org/10.1186/s40462-014-0021-6

McClintock, B., London, J., Cameron, M., & Boveng, P. (2017). Bridging the gaps in animal movement: Hidden behaviors and ecological relationships revealed by integrated data streams. *Ecosphere*, *8*(3), e01751. https://doi.org/10.1002/ecs2.1751

McGill, B. J. (2008). Exploring Predictions of Abundance from Body Mass Using Hierarchical Comparative Approaches. *The American Naturalist*, *172*(1), 88–101. https://doi.org/10.1086/588044

Mehran, R., Oyama, A., & Shah, M. (2009). Abnormal crowd behavior detection using social force model. *2009 IEEE Conference on Computer Vision and Pattern Recognition*, (2), 935–942. https://doi.org/10.1109/CVPR.2009.5206641

Melki, G., Cano, A., Kecman, V., & Ventura, S. (2017). Multi-target support vector regression via correlation regressor chains. *Information Sciences*, *415-416*, 53–69. https://doi.org/10.1016/j.ins.2017.06.017

Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A., & Leisch, F. (2017). e1071: Misc Functions of the Department of Statistics. https://cran.r-project.org/package=e1071

Microlighters. (2012). Operating cost on standard Aquilla 582. http://www.microlighters.co.za/viewtopic.php?f=1&t=19639#p190570

Miller, J. R., Ament, J. M., & Schmitz, O. J. (2014). Fear on the move: Predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology*, *83*(1), 214–222. https://doi.org/10.1111/1365-2656.12111

Miller, T. R., Minteer, B. A., & Malan, L.-C. (2011). The new conservation debate: The view from practical ethics. *Biological Conservation*, *144*(3), 948–957. https://doi.org/10.1016/j.biocon.2010.04.001

Miller, T. (2019). Explanation in artificial intelligence: Insights from the social sciences. *Artificial Intelligence*, *267*, 1–38. https://doi.org/10.1016/j.artint.2018.07.007

Milliken, T., Emslie, R. H., & Talukdar, B. (2009). *African and Asian Rhinoceroses – Status, Conservation and Trade (CoP15 Doc. 45.1 Annex)* (tech. rep.). CITES. Gland, Switzerland.

Milliken, T., Nowell, K., & Thomsen, J. B. (1993). *The Decline of the Black Rhino in Zimbabwe: Implications for Future Rhino Conservation*, TRAFFIC East/Southern Africa.

Milliken, T., & Shaw, J. (2012). *The South Africa – Viet Nam Rhino Horn Trade Nexus: A deadly combination of institutional lapses, corrupt wildlife industry professionals and Asian crime syndicates* (tech. rep.). TRAFFIC. Johannesburg, South Africa.

Milman, O. (2015). Human activity 'driving half of world's crocodile species to extinction'. https://www.theguardian.com/environment/2015/sep/08/human-activity-driving-half-of-worlds-crocodile-species-to-extinction

Milner, J. M., Nilsen, E. B., & Andreassen, H. P. (2007). Demographic side effects of selective hunting in ungulates and carnivores: Review. *Conservation Biology*, *21*(1), 36–47. https://doi.org/10.1111/j.1523-1739.2006.00591.x

Milner-Gulland, E. J. (1993). An econometric analysis of consumer demand for ivory and rhino horn. *Environmental & Resource Economics*, *3*(1), 73–95. https://doi.org/10.1007/BF00338321

Milner-Gulland, E. J. (2001). Hunting and Bushmeat Utilization in the African Rain Forest: Perspectives Toward a Blueprint for Conservation Action. In M. I. Bakarr, G. A. B. Fonseca, R. Mittermeier, A. B. Rylands, & K. W. Painemilla (Eds.), *Hunting and bushmeat utilization in the african rain forest: Perspectives toward a blueprint for conservation action*. Center for Applied Biodiversity Science.

Milner-Gulland, E., & Bennett, E. L. (2003). Wild meat: the bigger picture. *Trends in Ecology & Evolution*, *18*(7), 351–357. https://doi.org/10.1016/S0169-5347(03)00123-X

Minnaar, A., & Herbig, F. (2018). The impact of conservation crime on the South African rural economy: A case study of rhino poaching. *Acta Criminologica: Southern African Journal of Criminology*, *31*(4), 147–168. https://journals.co.za/content/journal/10520/EJC-159791abf8

Mitrovic, J., McWilliams, B., Walker, J., Buesing, L., & Blundell, C. (2020). Representation Learning via Invariant Causal Mechanisms. *arXiv*.

Mittelstadt, B., Russell, C., & Wachter, S. (2019). Explaining Explanations in AI. *Proceedings of the Conference on Fairness, Accountability, and Transparency - FAT* '19*, 279–288. https://doi.org/10.1145/3287560.3287574

Molnar, C. (2019). *Interpretable machine learning: A Guide for Making Black Box Models Explainable*. https://christophm.github.io/interpretable-ml-book/

Montgomery, R. A., Macdonald, D. W., & Hayward, M. W. (2020). The inducible defences of large mammals to human lethality. *Functional Ecology*, *34*(12), 2426–2441. https://doi.org/10.1111/1365-2435.13685

Morris, J. (2018). Does Legalizing Marijuana Reduce Crime? https://reason.org/wp-content/uploads/does-legalizing-marijuana-reduce-crime.pdf

Muir-Leresche, K., & Nelson, R. (2000). *Private Property Rights to Wildlife: The Southern African Experiment* (No. 2), International Centre for Economic Research.

Mwakiwa, E., Hearne, J., Stigter, J., De Boer, W., Henley, M., Slotow, R., Van Langevelde, F., Peel, M., Grant, C., & Prins, H. (2016). Optimization of net returns from wildlife consumptive and non-consumptive uses by game reserve management. *Environmental Conservation*, *43*(2), 128–139. https://doi.org/10.1017/S0376892915000296

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Nakagawa, S., & Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, *26*(5), 1253–1274. https://doi.org/10.1007/s10682-012-9555-5

Nathan, R., Getz, W., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052–19059. https://doi.org/10.1073/pnas.0800375105

Nelson, A. (2008). *Travel time to major cities: A global map of accessibility* (tech. rep.). Global Environment Monitoring Unit: Joint Research Centre of the European Commission. Ispra, Italy.

Nichols, J., Conroy, M., Jarman, P., Smith, A., Southwell, C., Lancia, R., Bishir, J., & Dickman, C. (1996). Techniques for Estimating Abundance and Species Richness. In D. Wilson, F. Cole, J. Nichols, R. Rudran, & M. Foster (Eds.), *Measuring and monitoring biological diversity: Standard methods for mammals* (pp. 177–234). Smithsonian Institution Press.

Nichols, J., Hines, J., Sauer, J., Fallon, F., Fallon, J., & Heglund, P. (2000). A Double-Observer Approach for Estimating Detection Probability and Abundance from Point Counts. *The Auk*, *117*(2), 393–408. https://doi.org/10.2307/4089721

Nickerson, R. S. (2000). Null hypothesis significance testing: A review of an old and continuing controversy. *Psychological Methods*, *5*(2), 241–301. https://doi.org/10.1037/1082-989X.5.2.241

Nie, J.-B., Smith, K. L., Cong, Y., Hu, L., & Tucker, J. D. (2015). Medical professionalism in China and the United States: a transcultural interpretation. *The Journal of Clinical Ethics*, *26*(1), 48–60. http://www.ncbi.nlm.nih.gov/pubmed/25794294

Nielsen, B., Veerkamp, R., & Lawrence, A. (2000). Effects of genotype, Feed type and lactational stage on the time budget of dairy cows. *Acta Agriculturae Scandinavica A: Animal Sciences*, *50*(4), 272–278. https://doi.org/10.1080/090647000750069467

Niwa, H.-S. (1998). School Size Statistics of Fish. *Journal of Theoretical Biology*, *195*(3), 351–361. https://doi.org/10.1006/jtbi.1998.0801

Njehia, J. (2018). World's last male northern white rhino dies. https://www.reuters.com/article/us-kenya-rhino/worlds-last-male-northern-white-rhino-dead-kenyan-conservancy-idUSKBN1GW0IT

Norton-Griffiths, M. (1978). *Counting Animals: Revised second edition* (tech. rep.). African Wildlife Leadership Foundation. Nairobi, Kenya.

Nshuli, R. (2013). Les conditions de travail des ecogardes sur le terrain: Le metier d'ecogardes: statut, missions, risques, valorisation. *Journees des aires protegees d'afrique centrale* (p. 22). RAPAC.

NUMBEO. (2016). Cost of Living Index for Country 2016 Mid-Year. https://www.numbeo.com/cost-of-living/rankings_by_country.jsp?title=2016-mid

O'Donoghue, P., & Rutz, C. (2016). Real-time anti-poaching tags could help prevent imminent species extinctions. *Journal of Applied Ecology*, *53*(1), 5–10. https://doi.org/10.1111/1365-2664.12452

Olmedo, A., Sharif, V., & Milner-Gulland, E. (2018). Evaluating the Design of Behavior Change Interventions: A Case Study of Rhino Horn in Vietnam. *Conservation Letters*, *11*(1), e12365. https://doi.org/10.1111/conl.12365

Packer, C., Brink, H., Kissui, B. M., Maliti, H., Kushnir, H., & Caro, T. (2011). Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania. *Conservation Biology*, *25*(1), 142–153. https://doi.org/10.1111/j.1523-1739.2010.01576.x

Pacula, R. L. (2010). *Examining the Impact of Marijuana Legalization on Marijuana Consumption: Insights from the Economics Literature*, RAND Corporation. https://www.rand.org/content/dam/rand/pubs/working_papers/2010/RAND_WR770.pdf

Patterson, T., Basson, M., Bravington, M., & Gunn, J. (2009). Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology*, *78*(6), 1113–1123. https://doi.org/10.1111/j.1365-2656.2009.01583.x

Patterson, T., Thomas, L., Wilcox, C., Ovaskainen, O., & Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology and Evolution*, *23*(2), 87–94. https://doi.org/10.1016/j.tree.2007.10.009

Patton, M., Swaisgood, R., Czekala, N., White, A., Fetter, G., Montagne, J., Rieches, R., & Lance, V. (1999). Reproductive cycle length and pregnancy in the southern white rhinoceros (Ceratotherium simum simum) as determined by fecal pregnane analysis and observations of mating behavior. *Zoo Biology*, *18*(2), 111–127. https://doi.org/10.1002/(SICI)1098-2361(1999)18:2⟨111::AID-ZOO3⟩3.0.CO;2-0

Pearl, J. (2000). *Causality: Models, Reasoning and Inference*. Cambridge University Press.

Pearl, J. (2009). Causal inference in statistics: An overview. *Statistics Surveys*, *3*, 96–146. https://doi.org/10.1214/09-SS057

Pearl, J., & Mackenzie, D. (2019). *The Book of Why: The New Science of Cause and Effect.* Penguin Books Ltd.

Penny, S. G., White, R. L., Scott, D. M., MacTavish, L., & Pernetta, A. P. (2019). Using drones and sirens to elicit avoidance behaviour in white rhinoceros as an anti-poaching tactic. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1907), 20191135. https://doi.org/10.1098/rspb.2019.1135

Peny, J. (2012). Technology Ethics for Law Enforcement. *American International Journal of Contemporary Research*, *2*(2), 124–133.

Peres, C. A., Barlow, J., & Laurance, W. F. (2006). Detecting anthropogenic disturbance in tropical forests. *Trends in Ecology & Evolution*, *21*(5), 227–229. https://doi.org/10.1016/j.tree.2006.03.007

Peres, C. A., Emilio, T., Schietti, J., Desmoulière, S. J. M., & Levi, T. (2016). Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences*, *113*(4), 892–897. https://doi.org/10.1073/pnas.1516525113

Peres, C. A., & Lake, I. R. (2003). Extent of Nontimber Resource Extraction in Tropical Forests: Accessibility to Game Vertebrates by Hunters in the Amazon Basin. *Conservation Biology*, *17*(2), 521–535. https://doi.org/10.1046/j.1523-1739.2003.01413.x

Peres-Neto, P., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrix: estimation and comparison of fractions. *Ecology*, *87*(10), 2614–2625. https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

Phelps, J., Carrasco, L. R., & Webb, E. L. (2014). A Framework for Assessing Supply-Side Wildlife Conservation. *Conservation Biology*, *28*(1), 244–257. https://doi.org/10.1111/cobi.12160

Pienaar, D., Hall-Martin, A., & Hitchins, P. (1991). Horn growth rates of free-ranging white and black rhinoceros. *Koedoe*, *34*(2). https://doi.org/10.4102/koedoe.v34i2.426

Porcier, S. M., Berruyer, C., Pasquali, S., Ikram, S., Berthet, D., & Tafforeau, P. (2019). Wild crocodiles hunted to make mummies in Roman Egypt: Evidence from synchrotron imaging. *Journal of Archaeological Science*, *110*(May), 105009. https://doi.org/10.1016/j.jas.2019.105009

Prins, H. H. T., & Okita-Ouma, B. (2013). Rhino Poaching: Unique Challenges. *Science*, *340*(6137), 1167–1168. https://doi.org/10.1126/science.340.6137.1167-b

Private Rhino Owners Association. (2017). DEA Gazette Notice 74 of 2017 'Great News' to rhino owners. www.rhinoalive.com/dea-gazette-notice-74-2017-greatnews-rhino-owners/

Proffitt, K. M., Grigg, J. L., Hamlin, K. L., & Garrott, R. A. (2009). Contrasting Effects of Wolves and Human Hunters on Elk Behavioral Responses to Predation Risk.

Journal of Wildlife Management, *73*(3), 345–356. https://doi.org/10.2193/2008-210

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Development Core Team. (2008). R: A language and environment for statistical computing. http://www.r-project.org

Rabe, M., Rosenstock, S., & DeVos Jr., J. (2002). Review of big-game survey methods used by wildlife agencies of the western United States. *Wildlife Society Bulletin*, *30*(1), 46–52. https://doi.org/10.2307/3784634

Rabinowitz, P., Wiley, J., Odofin, L., Wilcox, M., & Dein, F. J. (2008). Animals as sentinels of chemical terrorism agents: An evidence-based review. *Clinical Toxicology*, *46*(2), 93–100. https://doi.org/10.1080/15563650701664905

Rademeyer, J. (2012). *Killing for profit: Exposing the illegal rhino horn trade*. Penguin Random House.

Rademeyer, J. (2016). *Tipping Point: Transnational organised crime and the 'war' on poaching* (tech. rep.). The Global Initiative against Transnational Organized Crime. Geneva, Switzerland.

Redfern, J., Viljoen, P., Kruger, J., & Getz, W. (2002). Biases in estimating population size from an aerial census: a case study in the Kruger National Park, South Africa. *South African Journal of Science*, *98*, 455–461.

Redford, K. H. (1992). The Empty Forest. *BioScience*, *42*(6), 412–422. https://doi.org/10.2307/1311860

Redford, K. H., Amato, G., Baillie, J., Beldomenico, P., Bennett, E. L., Clum, N., Cook, R., Fonseca, G., Hedges, S., Launay, F., Lieberman, S., Mace, G. M., Murayama, A., Putnam, A., Robinson, J. G., Rosenbaum, H., Sanderson, E. W., Stuart, S. N., Thomas, P., & Thorbjarnarson, J. (2011). What Does It Mean to Successfully Conserve a (Vertebrate) Species? *BioScience*, *61*(1), 39–48. https://doi.org/10.1525/bio.2011.61.1.9

Reif, J. S. (2011). Animal sentinels for environmental and public health. *Public Health Reports*, *126*(SUPPL. 1), 50–57. https://doi.org/10.1177/00333549111260s108

Rey, N., Volpi, M., Joost, S., & Tuia, D. (2017). Detecting animals in African Savanna with UAVs and the crowds. *Remote Sensing of Environment*, *200*, 341–351. https://doi.org/10.1016/j.rse.2017.08.026

Ribeiro, M. T., Singh, S., & Guestrin, C. (2016). Why Should I Trust You?: Explaining the Predictions of Any Classifier. *Proceedings of the ACM SIGKDD International Conference on Knowledge Discovery and Data Mining*, 1135–1144. https://doi.org/10.1145/2939672.2939778

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, *343*(6167), 1241484–1241484. https://doi.org/10.1126/science.1241484

Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P. A., Macdonald, D. W., Machovina, B., Newsome, T. M., Peres, C. A., Wallach, A. D., Wolf, C., & Young, H. (2016). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*, *3*(10), 160498. https://doi.org/10.1098/rsos.160498

Risse, B., Mangan, M., Pero, L. D., & Webb, B. (2017). Visual Tracking of Small Animals in Cluttered Natural Environments Using a Freely Moving Camera. *IEEE International Conference on Computer Vision (ICCV)*, 2840–2849.

Rivalan, P., Delmas, V., Angulo, E., Bull, L. S., Hall, R. J., Courchamp, F., Rosser, A. M., & Leader-Williams, N. (2007). Can bans stimulate wildlife trade? *Nature*, *447*(7144), 529–530. https://doi.org/10.1038/447529a

Robinson, J. G., & Bennett, E. L. (2000). *Hunting for Sustainability in Tropical Forests*. Columbia University Press.

Rodriguez, A., & Williams, M. D. (1994). The Effectiveness of Proposed Antitrust Programs for Developing Countries. *N. C. J. Int'l L. & Com. Reg.*, *19*(2), 209–232.

Roe, D., & Cremona, P. (2016). Informing decisions on trophy hunting. https://www.iucn.org/sites/dev/files/iucn_sept_briefing_paper_-_informingdecisionstrophyhunting.pdf

Romanczuk, P., & Schimansky-Geier, L. (2012). Swarming and pattern formation due to selective attraction and repulsion. *Interface Focus*, *2*(6), 746–756. https://doi.org/10.1098/rsfs.2012.0030

Rookmaaker, K. (2020). Rhinoceros pulling a plough - fact or fiction? *Pachyderm*, *61*, 176–178.

Rosenberg, M. S. (2005). The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, *59*(2), 464–468. https://doi.org/10.1111/j.0014-3820.2005.tb01004.x

Rosenzweig, M. (2007). On foraging theory, humans and the conservation of diversity: a prospectus. In D. Stephens, J. Brown, & R. Ydenberg (Eds.), *Foraging: Behavior and ecology* (pp. 400–411). University of Chicago Press.

Rubin, D. B., & Schenker, N. (1991). Multiple imputation in health-care databases: An overview and some applications. *Statistics in Medicine*, *10*(4), 585–598. https://doi.org/10.1002/sim.4780100410

Rubino, E. C., & Pienaar, E. F. (2017). Applying a conceptual framework to rhinoceros conservation on private lands in South Africa. *Endangered Species Research*, *34*, 89–102. https://doi.org/10.3354/esr00844

Rubino, E. C., & Pienaar, E. F. (2020). Rhinoceros ownership and attitudes towards legalization of global horn trade within South Africa's private wildlife sector. *Oryx*, *54*(2), 244–251. https://doi.org/10.1017/S0030605318000030

Rubino, E. C., Pienaar, E. F., & Soto, J. R. (2018). Structuring Legal Trade in Rhino Horn to Incentivize the Participation of South African Private Landowners. *Ecological Economics*, *154*, 306–316. https://doi.org/10.1016/j.ecolecon.2018.08.012

Samek, W., Binder, A., Montavon, G., Lapuschkin, S., & Muller, K.-R. (2017). Evaluating the Visualization of What a Deep Neural Network Has Learned. *IEEE Transactions on Neural Networks and Learning Systems*, *28*(11), 2660–2673. https://doi.org/10.1109/TNNLS.2016.2599820

Sampei, Y., & Aoyagi-Usui, M. (2009). Mass-media coverage, its influence on public awareness of climate-change issues, and implications for Japan's national campaign to reduce greenhouse gas emissions. *Global Environmental Change*, *19*(2), 203–212. https://doi.org/10.1016/j.gloenvcha.2008.10.005

Sandbrook, C., Fisher, J. A., Holmes, G., Luque-Lora, R., & Keane, A. (2019). The global conservation movement is diverse but not divided. *Nature Sustainability*, *2*(4), 316–323. https://doi.org/10.1038/s41893-019-0267-5

Sandom, C., Faurby, S., Sandel, B., & Svenning, J.-C. (2014). Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1787), 20133254. https://doi.org/10.1098/rspb.2013.3254

SANParks. (2015). Media Release: SANParks receives air support for anti-poaching operations. https://www.sanparks.org/about/news/?id=56336

SANParks. (2020). *South African National Parks Annual Report 2019-2020* (tech. rep.). SANParks. Pretoria, South Africa.

Save the Rhino. (2013). Tackling the demand for rhino horn. https://www.savetherhino.org/rhino_info/thorny_issues/tackling_the_demand_for_rhino_horn

Save the Rhino. (2015). The transportation industry and the illegal wildlife trade. https://www.savetherhino.org/rhino_info/thorny_issues/the_transportation_industry_and_the_illegal_wildlife_trade

Save the Rhino. (2016a). Dyeing rhino horn and elephant ivory. https://www.savetherhino.org/rhino_info/thorny_issues/dyeing_rhino_horn_and_elephant_ivory

Save the Rhino. (2016b). Synthetic / bio-fabricated rhino horn: Will it save the rhino? https://www.savetherhino.org/rhino_info/thorny_issues/synthetic_rhino_horn_will_it_save_the_rhino

Save the Rhino. (2018). A legal trade in rhino horn. https://www.savetherhino.org/thorny-issues/legal-trade-in-rhino-horn/

Save the Rhino. (2020). Poaching stats. https://www.savetherhino.org/rhino-info/poaching-stats/

Save the Rhino. (2021). Poaching stats. https://www.savetherhino.org/rhino-info/poaching-stats/

SCBD. (2004). *Addis Ababa Principles and Guidelines for the Sustainable Use of Biodiversity Published* (tech. rep.). Secretariat of the Convention on Biological Diversity. Montreal, Canada.

Scheffers, B. R., Oliveira, B. F., Lamb, I., & Edwards, D. P. (2019). Global wildlife trade across the tree of life. *Science*, *366*(6461), 71–76. https://doi.org/10.1126/science.aav5327

Schoenbaum, T. J. (1992). Free International Trade and Protection of the Environment: Irreconcilable Conflict? *The American Journal of International Law*, *86*(4), 700–727. https://doi.org/10.2307/2203788

Schölkopf, B. (2019). Causality for Machine Learning. *arXiv*.

Schölkopf, B., Locatello, F., Bauer, S., Ke, N. R., Kalchbrenner, N., Goyal, A., & Bengio, Y. (2021). Towards Causal Representation Learning. *arXiv*.

Schwartzstein, P. (2017). Crocodile Poaching Booms as Egypt Tourism Crumbles. https://www.nationalgeographic.com/news/2017/06/crocodiles-illegal-hunting-egypt-nile/

Sciortino, F., Mossa, S., Zaccarelli, E., & Tartaglia, P. (2004). Equilibrium Cluster Phases and Low-Density Arrested Disordered States: The Role of Short-Range Attraction and Long-Range Repulsion. *Physical Review Letters*, *93*(5), 055701. https://doi.org/10.1103/PhysRevLett.93.055701

Scott-Samuel, N. E., Holmes, G., Baddeley, R., & Cuthill, I. C. (2015). Moving in groups: how density and unpredictable motion affect predation risk. *Behavioral Ecology and Sociobiology*, *69*(6), 867–872. https://doi.org/10.1007/s00265-015-1885-1

Seidel, D. P., Dougherty, E., Carlson, C., & Getz, W. M. (2018). Ecological metrics and methods for GPS movement data. *International Journal of Geographical Information Science*, *32*(11), 2272–2293. https://doi.org/10.1080/13658816.2018.1498097

Sekar, N., Clark, W., Dobson, A., Coelho, P. C. F., Hannam, P. M., Hepworth, R., Hsiang, S., Kahumbu, P., Lee, P. C., Lindsay, K., Pereira, C. L., Wasser, S. K., & Nowak, K. (2018). Ivory crisis: Growing no-trade consensus. *Science*, *360*(6386), 276–277. https://doi.org/10.1126/science.aat1105

Sgaier, B. S. K., Huang, V., & Charles, G. (2020). The Case for Causal AI. *Stanford Social Innovation Review*, (Summer), 50–56.

Shamoun-Baranes, J., Bom, R., van Loon, E. E., Ens, B. J., Oosterbeek, K., & Bouten, W. (2012). From Sensor Data to Animal Behaviour: An Oystercatcher Example. *PLoS ONE*, *7*(5), e37997. https://doi.org/10.1371/journal.pone.0037997

Shoaib, M., Bosch, S., Incel, O., Scholten, H., & Havinga, P. (2015). A Survey of Online Activity Recognition Using Mobile Phones. *Sensors*, *15*(1), 2059–2085. https://doi.org/10.3390/s150102059

Shrestha, Y., & Lapeyre, R. (2018). Modern Wildlife Monitoring Technologies: Conservationists versus Communities? A Case Study: The Terai-Arc Landscape, Nepal. *Conservation and Society*, *16*(1), 91–101.

Signer, J., & Ovaskainen, O. (2017). Detecting the influence of environmental covariates on animal movement: a semivariance approach. *Methods in Ecology and Evolution*, *8*(5), 561–570. https://doi.org/10.1111/2041-210X.12692

Sinclair, A. R. E. (1977). *The African Buffalo: A Study of Resource Limitation of Populations*. University of Chicago Press.

Sirmacek, B., Wegmann, M., Cross, A., Hopcraft, J., Reinartz, P., & Dech, S. (2012). Automatic population counts for improved wildlife management using aerial photography. *Proceedings of the International Congress on Environmental Modelling and Software*, (July), 1–8.

Smallhorne, M. (2013). Think local to save rhino. https://mg.co.za/article/2013-11-01-00-think-local-to-save-rhino

Smith, F. A., Brown, J. H., Haskell, J. P., Lyons, S. K., Alroy, J., Charnov, E. L., Dayan, T., Enquist, B. J., Morgan Ernest, S. K., Hadly, E. A., Jones, K. E., Kaufman, D. M., Marquet, P. A., Maurer, B. A., Niklas, K. J., Porter, W. P., Tiffney, B., & Willig, M. R. (2004). Similarity of Mammalian Body Size across the Taxonomic Hierarchy and across Space and Time. *The American Naturalist*, *163*(5), 672–691. https://doi.org/10.1086/382898

Smith, F. A., & Lyons, S. K. (2011). How big should a mammal be? A macroecological look at mammalian body size over space and time. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2364–2378. https://doi.org/10.1098/rstb.2011.0067

Smithson, M., & Verkuilen, J. (2006). A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods*, *11*(1), 54–71. https://doi.org/10.1037/1082-989X.11.1.54

Snyder, H. (2019). Literature review as a research methodology: An overview and guidelines. *Journal of Business Research*, *104*, 333–339. https://doi.org/10.1016/j.jbusres.2019.07.039

Sodikoff, G. (2012). *The anthropology of extinction: essays on culture and species death.* Bloomington, Indiana University Press.

Sokal, R. R., & Rohlf, F. J. (1981). *Biometry: The Principles and Practice of Statistics in Biological Research* (2nd ed.). Freeman.

Soloway, J. A. (1999). Environmental Trade Barriers under NAFTA: the MMT Fuel Additives Controversy. *Minnesota Journal of Global Trade*, *8*(1), 55–96.

Sorato, E., Gullett, P. R., Griffith, S. C., & Russell, A. F. (2012). Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Animal Behaviour*, *84*(4), 823–834. https://doi.org/10.1016/j.anbehav.2012.07.003

St John, F. A. V., Edwards-Jones, G., & Jones, J. P. G. (2010). Conservation and human behaviour: lessons from social psychology. *Wildlife Research*, *37*(8), 658–667. https://doi.org/10.1071/WR10032

Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*, *141*(9), 2159–2173. https://doi.org/10.1016/j.biocon.2008.06.026

Stott, R., & Olson, D. (1972). An Evaluation of Waterfowl Surveys on the New Hampshire Coastline. *The Journal of Wildlife Management*, *36*(2), 468–477. https://doi.org/10.2307/3799077

Sumpter, D., Szorkovszky, A., Kotrschal, A., Kolm, N., & Herbert-Read, J. (2018). Using activity and sociability to characterize collective motion. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170015. https://doi.org/10.1098/rstb.2017.0015

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, *22*(10), 1578–1586. https://doi.org/10.1111/ele.13344

Sutherland, W. J., Aveling, R., Brooks, T. M., Clout, M., Dicks, L. V., Fellman, L., Fleishman, E., Gibbons, D. W., Keim, B., Lickorish, F., Monk, K. A., Mortimer, D., Peck, L. S., Pretty, J., Rockström, J., Rodríguez, J. P., Smith, R. K., Spalding, M. D., Tonneijck, F. H., & Watkinson, A. R. (2014). A horizon scan of global conservation issues for 2014. *Trends in Ecology & Evolution*, *29*(1), 15–22. https://doi.org/10.1016/j.tree.2013.11.004

Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C., Hails, R. S., Hays, G. C., Hodgson, D. J., Hutchings, M. J., Johnson, D., Jones, J. P. G., Keeling, M. J., Kokko, H., Kunin, W. E., . . . Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, *101*(1), 58–67. https://doi.org/10.1111/1365-2745.12025

Swaisgood, R. R., Dickman, D. M., & White, A. M. (2006). A captive population in crisis: Testing hypotheses for reproductive failure in captive-born southern white rhinoceros females. *Biological Conservation*, *129*(4), 468–476. https://doi.org/10.1016/j.biocon.2005.11.015

't Sas-Rolfes, M. (2011). *Saving African Rhinos: A Market Success Story* (tech. rep.). PERC. Bozeman, U.S.A.

‘t Sas-Rolfes, M., Challender, D. W., Hinsley, A., Veríssimo, D., & Milner-Gulland, E. (2019). Illegal Wildlife Trade: Scale, Processes, and Governance. *Annual Review of Environment and Resources*, *44*(1), 201–228. https://doi.org/10.1146/annurev-environ-101718-033253

Tablado, Z., & Jenni, L. (2017). Determinants of uncertainty in wildlife responses to human disturbance. *Biological Reviews*, *92*, 216–233. https://doi.org/10.1111/brv.12224

Tang, H., Huang, W., Ma, J., & Liu, L. (2018). SWOT analysis and revelation in traditional Chinese medicine internationalization. *Chinese Medicine*, *13*(1), 5. https://doi.org/10.1186/s13020-018-0165-1

Tatler, J., Cassey, P., & Prowse, T. A. A. (2018). High accuracy at low frequency: detailed behavioural classification from accelerometer data. *The Journal of Experimental Biology*, *221*(23), jeb184085. https://doi.org/10.1242/jeb.184085

Taylor, A., Balfour, D., Brebner, D. K., Coetzee, R., Davies-Mostert, H., Lindsey, P. A., Shaw, J., & 't Sas-Rolfes, M. (2017). Sustainable rhino horn production at the pointy end of the rhino horn trade debate. *Biological Conservation*, *216*, 60–68. https://doi.org/10.1016/j.biocon.2017.10.004

Taylor, A., Lindsey, P. A., & Davies-Mostert, H. (2015). *An assessment of the economic, social and conservation value of the wildlife ranching industry and its potential to support the green economy in South Africa* (tech. rep.). Endangered Wildlife Trust. Johannesburg, South Africa. https://doi.org/10.13140/RG.2.1.1211.1128

Tensen, L. (2016). Under what circumstances can wildlife farming benefit species conservation? *Global Ecology and Conservation*, *6*, 286–298. https://doi.org/10.1016/j.gecco.2016.03.007

Thabtah, F., Hammoud, S., Kamalov, F., & Gonsalves, A. (2020). Data imbalance in classification: Experimental evaluation. *Information Sciences*, *513*, 429–441. https://doi.org/10.1016/j.ins.2019.11.004

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M., & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: Effects on the spatial distribution of African ungulates. *Ecology*, *92*(2), 398–407. https://doi.org/10.1890/10-0126.1

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., & Slotow, R. (2010). Group Dynamics of Zebra and Wildebeest in a Woodland Savanna: Effects of Predation Risk and Habitat Density. *PLoS ONE*, *5*(9), e12758. https://doi.org/10.1371/journal.pone.0012758

The Royal Society, & The Alan Turing Institute. (2018). *The AI revolution in scientific research* (tech. rep.). https://royalsociety.org/-/media/policy/projects/ai-and-society/AI-revolution-in-science.pdf?la=en-GB&hash=5240F21B56364A00053538A0BC29FF5F

Thornton, A., Perry, C., Rufus, J., Powell, M., & Bell, D. (2000). *Lethal experiment: how the CITES-approved ivory sale led to increased elephant poaching* (tech. rep.). Environmental Investigation Agency. London, UK.

Thurfjell, H., Ciuti, S., & Boyce, M. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, *2*(1), 1–12. https://doi.org/10.1186/2051-3933-2-4

Transparency International. (2013). Corruption Perceptions Index 2013. https://www.transparency.org/cpi2013/results

Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates Inc.

UNEP, CITES, IUCN, & TRAFFIC. (2013). *Elephants in the dust - the African elephant crisis. A rapid response assessment* (tech. rep.). United Nations Environment Programme. Birkeland, Norway. https://portals.iucn.org/library/node/10345

USAID Vietnam. (2018). *Research Study on Consumer Demand for Elephant, Rhino and Pangolin Parts and Products in Vietnam* (tech. rep.). GlobeScan.

USAID Wildlife Asia. (2018). *Research Study on Consumer Demand for Elephant, Pangolin, Rhino and Tiger Parts and Products in China* (tech. rep.). GlobeScan.

Van Gemert, J., Verschoor, C., Mettes, P., Epema, K., Koh, L., & Wich, S. (2014). Nature Conservation Drones for Automatic Localization and Counting of Animals. *Workshop at the European Conference on Computer Vision*, *September*, 255–270. https://doi.org/10.1007/978-3-319-16178-5{_}17

Van Hertem, T., Viazzi, S., Steensels, M., Maltz, E., Antler, A., Alchanatis, V., Schlageter-Tello, A. A., Lokhorst, K., Romanini, E. C., Bahr, C., Berckmans, D., & Halachmi, I. (2014). Automatic lameness detection based on consecutive 3D-video recordings. *Biosystems Engineering*, *119*, 108–116. https://doi.org/10.1016/j.biosystemseng.2014.01.009

Van Lavieren, L. (1982). *Wildlife Management in the Tropics - with special emphasis on South East Asia: A guidebook to the warden. Part 1 - Introduction, Taking fielnotes & Wildlife census methods.* School of Environmental Conservation Management.

Van Uhm, D. (2012). Organised crime in the wildlife trade. *Centre for Information and Research on Organised Crime Newsletter*, *10*(2), 2–4.

Van Uhm, D. (2016). Illegal trade in wildlife and harms to the world. In A. Spapens, R. White, & W. Huisman (Eds.), *Environmental crime in transnational context.* Ashgate Publishing Ltd.

Van Uhm, D. (2018a). The social construction of the value of wildlife: A green cultural criminological perspective. *Theoretical Criminology*, *22*(3), 384–401. https://doi.org/10.1177/1362480618787170

Van Uhm, D. (2018b). Wildlife and laundering: Interaction between the under and upper world. In A. Spapens, R. White, D. Van Uhm, & W. Huisman (Eds.), *Green crimes and dirty money* (pp. 197–211). Routledge. https://doi.org/10.4324/9781351245746

Vázquez Diosdado, J., Barker, Z., Hodges, H., Amory, J., Croft, D., Bell, N., & Codling, E. (2015). Classification of behaviour in housed dairy cows using an accelerometer-based activity monitoring system. *Animal Biotelemetry*, *3*(1), 15. https://doi.org/10.1186/s40317-015-0045-8

Veríssimo, D., & Wan, A. K. Y. (2019). Characterizing efforts to reduce consumer demand for wildlife products. *Conservation Biology*, *33*(3), 623–633. https://doi.org/10.1111/cobi.13227

Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software*, *36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Vigne, L., Martin, E., & Okita-Ouma, B. (2007). Increased demand for rhino horn in Yemen threatens eastern Africa's rhinos. *Pachyderm*, *43*, 73–86.

Wageningen University & Research, & Noldus. (2017). *GrazingSpace: Final Report* (tech. rep.). European Space Agency. Noordwijk, Netherlands.

Walker, J. (2009). *Ivory's ghosts: the white gold of history and the fate of elephants.* Atlantic Monthly Press.

Wang, G. (2019). Machine learning for inferring animal behavior from location and movement data. *Ecological Informatics*, *49*, 69–76. https://doi.org/10.1016/j.ecoinf.2018.12.002

Wasser, S. K., Brown, L., Mailand, C., Mondol, S., Clark, W., Laurie, C., & Weir, B. S. (2015). Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. *Science*, *349*(6243), 84–87. https://doi.org/10.1126/science.aaa2457

Weimerskirch, H., Collet, J., Corbeau, A., Pajot, A., Hoarau, F., Marteau, C., Filippi, D., & Patrick, S. C. (2020). Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of nondeclared fishing. *Proceedings of the National Academy of Sciences*, *117*(6), 3006–3014. https://doi.org/10.1073/pnas.1915499117

Weinmann, M., Jutzi, B., Mallet, C., & Weinmann, M. (2017). Geometric Features and Their Relevance for 3D Point Cloud Classification. *ISPRS Annals of Photogrammetry, Remote Sensing and Spatial Information Sciences*, *IV-1/W1*, 157–164. https://doi.org/10.5194/isprs-annals-IV-1-W1-157-2017

Welgevonden Game Reserve. (2020). Conservation Management Vision. https://www.welgevonden.org/conservation-management-vision/

Welgevonden Game Reserve. (2021). Opening of the Greater Marakele Security Cluster Sattellite Joint Operations Centre. https://www.welgevonden.org/news/opening-of-the-greater-marakele-security-cluster-satellite-joint-operations-centre/

Westley, P. A. H., Berdahl, A. M., Torney, C. J., & Biro, D. (2018). Collective movement in ecology: from emerging technologies to conservation and management. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170004. https://doi.org/10.1098/rstb.2017.0004

WHO. (2013). *WHO Traditional Medicine Strategy 2014-2023* (tech. rep.). World Health Organization. Hong Kong SAR, China.

Wikelski, M., Mueller, U., Scocco, P., Catorci, A., Desinov, L., Belyaev, M., Keim, D., Pohlmeier, W., Fechteler, G., & Mai, P. M. (2020). Potential short-term earthquake forecasting by farm-animal monitoring. *bioRxiv*. https://doi.org/10.1101/2020.01.19.911313

Wikelski, M., & Tertitski, G. (2016). Living sentinels for climate change effects. *Science*, *352*(6287), 775–776. https://doi.org/10.1126/science.aaf6544

WildAct Vietnam. (2019). WildAct. http://www.wildact-vn.org/

Wildlife ACT. (2014). GPS and VHF tracking collars used for wildlife monitoring. http://wildlifeact.com/blog/gps-and-vhf-tracking-collars-used-for-wildlife-monitoring/

Williams, H. J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., de Grissac, S., Demšar, U., English, H. M., Franconi, N., Gómez-Laich, A., Griffiths, R. C., Kay, W. P., Morales, J. M., Potts, J. R., Rogerson, K. F., Rutz, C., Spelt, A., Trevail, A. M., Wilson, R. P., & Börger, L. (2020). Optimizing the use of biologgers for movement ecology research. *Journal of Animal Ecology*, *89*(1), 186–206. https://doi.org/10.1111/1365-2656.13094

Williams, V. L., Newton, D., Loveridge, A. J., & Macdonald, D. W. (2015). *Bones of Contention : An Assessment of the South African Trade in African Lion Panthera leo Bones and Other Body Parts* (tech. rep.). TRAFFIC and WildCRU. Cambridge, UK, Oxford, UK.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, *95*(7), 2027–2027. https://doi.org/10.1890/13-1917.1

Wilmers, C., Nickel, B., Bryce, C., Smith, J., Wheat, R., & Yovovich, V. (2015). The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology*, *96*(7), 1741–1753. https://doi.org/10.1890/14-1401.1

Wilson, E. O. (2016). *Half-Earth: Our Planet's Fight for Life*. Liferight Publishing.

Wilson, R. P., Quintana, F., & Hobson, V. J. (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1730), 975–980. https://doi.org/10.1098/rspb.2011.1544

Wiseman, A. E., & Ellig, J. (2007). The Politics of Wine: Trade Barriers, Interest Groups, and the Commerce Clause. *The Journal of Politics*, *69*(3), 859–875. https://doi.org/10.1111/j.1468-2508.2007.00580.x

Woith, H., Petersen, G. M., Hainzl, S., & Dahm, T. (2018). Review: Can Animals Predict Earthquakes? *Bulletin of the Seismological Society of America*, *108*(3A), 1031–1045. https://doi.org/10.1785/0120170313

Wright, S. J. (2003). The myriad consequences of hunting for vertebrates and plants in tropical forests. *Perspectives in Plant Ecology, Evolution and Systematics*, *6*(1-2), 73–86. https://doi.org/10.1078/1433-8319-00043

WWF. (2019). Still poached for ivory. http://wwf.panda.org/knowledge_hub/endangered_species/elephants/african_elephants/afelephants_threats/index.cfm

WWF. (2021). Rhino. https://www.worldwildlife.org/species/rhino

Wyatt, T., Johnson, K., Hunter, L., George, R., & Gunter, R. (2018). Corruption and Wildlife Trafficking: Three Case Studies Involving Asia. *Asian Journal of Criminology*, *13*(1), 35–55. https://doi.org/10.1007/s11417-017-9255-8

XE. (2015). Current and Historical Rate Tables. https://www.xe.com/currencytables/

XE. (2017). Current and Historical Rate Tables. https://www.xe.com/currencytables/

Xie, J., Hu, K., Zhu, M., Yu, J., & Zhu, Q. (2019). Investigation of Different CNN-Based Models for Improved Bird Sound Classification. *IEEE Access*, *7*, 175353–175361. https://doi.org/10.1109/ACCESS.2019.2957572

Yu, D. (1994). Free Trade Is Green, Protectionism Is Not. *Conservation Biology*, *8*(4), 989–996. https://doi.org/10.1046/j.1523-1739.1994.08040989.x

Yu, T., Simoff, S., & Jan, T. (2010). VQSVM: A case study for incorporating prior domain knowledge into inductive machine learning. *Neurocomputing*, *73*, 2614–2623. https://doi.org/10.1016/j.neucom.2010.05.007

Zanette, L. Y., & Clinchy, M. (2020). Ecology and Neurobiology of Fear in Free-Living Wildlife. *Annual Review of Ecology, Evolution, and Systematics*, *51*, 297–318. https://doi.org/10.1146/annurev-ecolsys-011720-124613

Zbyryt, A., Bubnicki, J. W., Kuijper, D. P., Dehnhard, M., Churski, M., & Schmidt, K. (2018). Do wild ungulates experience higher stress with humans than with large carnivores? *Behavioral Ecology*, *29*(1), 19–30. https://doi.org/10.1093/beheco/arx142

Zhao, Q., & Hastie, T. (2021). Causal Interpretations of Black-Box Models. *Journal of Business & Economic Statistics*, *39*(1), 272–281. https://doi.org/10.1080/07350015.2019.1624293

Acknowledgements

Many people were involved in the development of this thesis. Actually too many to try to list here all without a substantial risk of missing some names in the process. That's why I want to thank here all people who directly or indirectly assisted me during my PhD project over the past four years. Although there is still a lot of solitary grinding involved in a PhD project, it is almost impossible to complete it without collaboration.

In particular I would like to thank my family for their patience with me. Too often did our conversation stall while we walked with our dogs, sat at our (Christmas) dining table or travelled to our horses, because my mind was still in the 'equation-solving-mode'. I would be lying if I were now to promise that it won't happen again, but I sincerely believe that it will occur less often now that I've finished this important chapter (and I've become a bit better in equation solving).

I would also like to sincerely thank my supervisors for their support, disagreements, lessons, quirks and friendship. Most importantly I've learned from you what it is really like to be a scientist. Therefore I came to appreciate the value of being one, even (or often especially) when my role as a scientist contradicts with my personal views.

I owe my (former) colleagues and students from the Wildlife Ecology and Conservation group also my gratitude, all in particular. Whether they are now living in Wageningen, Oxford, Helsinki, Pretoria, Nairobi or somewhere else, they made my stay at the group very enjoyable. Having now been more than a year in the COVID-lockdown, I can say that I really miss the coffee breaks during which we talked about work, hobbies, frustrations and our views about basically everything in the world.

Finally, I want to state how grateful I am for the opportunities that were given to me by the management of Welgevonden Game Reserve. You're doing an amazing job for the conservation of African wildlife, where many reserves do well to learn from. Not only were you invaluable in the development and execution of the 'anti-poaching project', you really went the extra mile for me personally. Always inviting my wife to come along with me, organising dinners with us, arranging seats for us in the helicopter game counts (from which I am still nauseous by the way), taking us along on game captures and facilitating transport for us to and from wherever we wanted in South Africa: you were amazing!

About the author

Jasper Eikelboom was born in Zwolle, the Netherlands on April 9, 1991. He grew up in the Sallandian towns Wijhe and Hardenberg, where his pets and movies such as "Jungle Book" and "Walking with Dinosaurs" made him enthusiastic about wildlife. Whilst getting his tonsils removed in the hospital at the age of 11, it was the book "The Wilderness Family" by Kobie Krüger that made him determined to become a veterinarian in the Kruger National Park, South Africa. Eventually the beauty of Mathematics drew him more towards science rather than veterinary medicine, but his passion for the African savanna never left him. During his studies of Earth Sciences, Environmental Biology and Geography Education at Utrecht University, he was mainly angry at the current state of the world and considered science too fundamental and nature conservation too focused on symptom relief to make a difference. This made him decide to become a Mathematics high school teacher after his studies and spend as much free time on a fight against human overpopulation (without any culling of course). Becoming older, calmer and perhaps even a bit wiser, he decided that this was not the path for him and re-evaluated his feelings towards the impact of science and nature conservation. At the age of 25 he went on his first trip to his beloved Kruger National Park and at the same time got married there (with his 100% non-African, but Dutch former girlfriend). Being in the area where he always wanted to be, he asked around about getting a job in and making a change to nature conservation. There they pointed him back towards the Netherlands to go and find professor Prins at Wageningen University. Half a year later he started with his PhD on rhino conservation in South Africa at Prins' group, being very lucky that the preceding PhD candidate decided to quit. Always having wildlife conservation as his passion to guide him in his career, it is the wrangling with data and interaction with colleagues and students that makes him get out of bed on a day-to-day basis. It makes him therefore all the happier that he can continue his work at the Wildlife Ecology and Conservation group as a postdoctoral researcher.

Peer-reviewed journal publications

*de Knegt, H. J., *Eikelboom, J. A. J., van Langevelde, F., Spruyt, W. F., & Prins, H. H. T. (2021). Timely poacher detection and localization using sentinel animal movement. *Scientific Reports, 11*, 4596. https://doi.org/10.1038/s41598-021-83800-1

Eikelboom, J. A. J., de Knegt, H. J., Klaver, M., van Langevelde, F., van der Wal, T., & Prins, H. H. T. (2020). Inferring an animal's environment through biologging: quantifying the environmental influence on animal movement. *Movement Ecology*, *8*(1), 40. https://doi.org/10.1186/s40462-020-00228-4

Eikelboom, J. A. J., Nuijten, R. J. M., Wang, Y. X. G., Schroder, B., Heitkönig, I. M. A., Mooij, W. M., van Langevelde, F., & Prins, H. H. T. (2020). Will legal international rhino horn trade save wild rhino populations? *Global Ecology and Conservation*, *23*, e01145. https://doi.org/10.1016/j.gecco.2020.e01145

Eikelboom, J. A. J., Wind, J., van de Ven, E., Kenana, L. M., Schroder, B., de Knegt, H. J., van Langevelde, F., & Prins, H. H. T. (2019). Improving the precision and accuracy of animal population estimates with aerial image object detection. *Methods in Ecology and Evolution*, *10*(11), 1875–1887. https://doi.org/10.1111/2041-210X.13277

Benítez-López, A., Alkemade, R., Schipper, A. M., Ingram, D. J., Verweij, P. A., Eikelboom, J. A. J., & Huijbregts, M. A. J. (2017). The impact of hunting on tropical mammal and bird populations. *Science*, *356*(6334), 180–183. https://doi.org/10.1126/science.aaj1891

In preparation

Eikelboom, J. A. J. (*in draft*). Classifying animal behaviour with movement sensor data: a deep learning meta-analysis.

Eikelboom, J. A. J., Doelman, A., van Langevelde, F., & de Knegt, H. J. (*in draft*). Animal group size variation in a minimal attraction-repulsion agent-based model.

Xu, Y., van der Jeugd, H., Si, Y., Prins, H. H. T., Fouchier, R. A. M., Guillemain, M., Caizergues, A., Li, Z., Eikelboom, J. A. J., Xu, C., Thorup, K., von Rönn, J., Gong, P., & de Boer, W. F. (*in draft*). Range shifts of migratory hosts facilitate avian influenza panzootics via crossroads of flyways.

Li, W., Funk, M., Eikelboom, J. A. J., & Brombacher, A. (*in revision*). Visual Exploration of Movement Relatedness for Multi-species Ecology Analysis. https://arxiv.org/abs/2001.11163

Other publications

Eikelboom, J. A. J., & Wind, J. (2014). Overpopulation. *Apple App Store*, Smartphone and tablet app. https://appsto.re/nl/L_S_3.i

Eikelboom, J. A. J. (2013). An essay on the ecological and socio-economic effects of the current and future global human population size. *Utrecht University Repository*, MSc thesis. https://doi.org/1874/290490

Other achievements

CELTMAN! Extreme Scottish Triathlon (15 June 2019). 17h 4min 41s.

Affiliation of co-authors

Wildlife Ecology and Conservation Group, Wageningen University, NL

- Jasper A.J. Eikelboom
- Rascha J.M. Nuijten
- Yingying X.G. Wang
- Bradley Schroder
- Ignas M.A. Heitkönig
- Frank van Langevelde
- Henrik J. de Knegt
- Maayke Klaver
- Johan Wind
- Eline van de Ven
- Lekishon M. Kenana

Dep. of Animal Sciences, Wageningen University, NL

- Herbert H.T. Prins

Spatial Knowledge Systems, Wageningen Environmental Research, NL

- Tamme van der Wal

Dep. of Aquatic Ecology, Netherlands Inst. of Ecology, NL

- Wolf M. Mooij

Mathematical Inst., Leiden University, NL

- Arjen Doelman

Inst. for Wetland and Water Research, Radboud University, NL

- Ana Benítez-López
- Mark A.J. Huijbregts

Copernicus Inst. of Sustainable Development, Utrecht University, NL

- Pita A. Verweij

PBL, Netherlands Environmental Assessment Agency, NL

- Rob Alkemade
- Aafke M. Schipper

School of Life Sciences, University of Sussex, UK

- Daniel J. Ingram

Board of Directors, Welgevonden Game Reserve, SA

- W. François Spruyt

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Detecting poachers by monitoring animal herd dynamics

Post-graduate courses (6 ECTS)

- Machine learning; Stanford University (coursera) (2017)
- R and big data; PE&RC (2017)
- A career in movement ecology; British Ecological Society (2018)
- Consumer-resource interactions; PE&RC (2018)
- Bayesian statistics; PE&RC (2018)

Deficiency, refresh, brush-up courses (4.6 ECTS)

- R programming; Johns Hopkins University (coursera) (2017)
- Dynamic models in R: programming, parameter estimation and model selection; PE&RC (2017)
- Programming in Matlab; BioSB (2017)
- Git workshop; WUR (2017)
- Linux for HPC basic course; WUR (2018)
- HPC basic course; WUR (2018)
- HPC advanced course; WUR (2018)
- Meet artificial intelligence in the cloud; WUR (2019)

Laboratory training and working visits (0.9 ECTS)

- Aerial game counts; Welgevonden Game Reserve, Sunrise Aviation & Agricultural Research Council, South Africa (2017)

Invited review of journal manuscripts (4 ECTS)

- Pachyderm: rhino population estimates (2020)
- Wildlife Research: thermal IR in aerial wildlife surveys (2020)
- IEEE Access: image animal gender differentiation (2020)
- Journal of Zoology: drones for wildlife monitoring (2020)

Competence strengthening / skills courses (3.7 ECTS)

- PhD Workshop carousel; WGS (2017)
- Competence assessment; WGS (2017)
- Scientific writing; WGS (2018)
- Brain training; WGS (2018)
- Presentation workshop session for Dies Natalis; Wageningen in'to Languages (2019)
- An Introduction to LaTeX; PE&RC (2019)

Scientific integrity / ethics in science activity (0.6 ECTS)

- Scientific integrity; WGS (2018)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.8 ECTS)

- PE&RC First years weekend (2017)
- PE&RC Day: preventing the end of the world - how science can save the planet (2017)
- PE&RC Day: exploring sustainability - now and for the future, winning pitch for call for institutional collaboration (2019)
- PE&RC Last year afternoon (2020)
- PE&RC Afternoon event (2020)

National scientific meetings / local seminars / discussion groups (4.7 ECTS)

- Animal movement analysis; REG, EZO, BPH & BEG (2018–2020)
- Breed4Food seminar: scientific developments in tracking and monitoring animals in groups (2019)

International symposia, workshops and conferences (5.8 ECTS)

- NAEM: Ecology and conservation - using sensor technology and machine learning to understand animal behaviour; Lunteren, the Netherlands (2018)

- Dies Natalis WUR ceremony: innovation for conservation - pushing technological frontiers: advanced instrumentation and analytics for wildlife protection; Wageningen, the Netherlands (2019)
- Workshop: monitoring and analysis of movement of crowds and herds - automated aerial animal counts; Wageningen, the Netherlands (2019)
- Wildlife research and conservation: smart tags for smart animals - advanced instrumentation and analytics for wildlife protection; Berlin, Germany (2019)

Societally relevant exposure (0.45 ECTS)

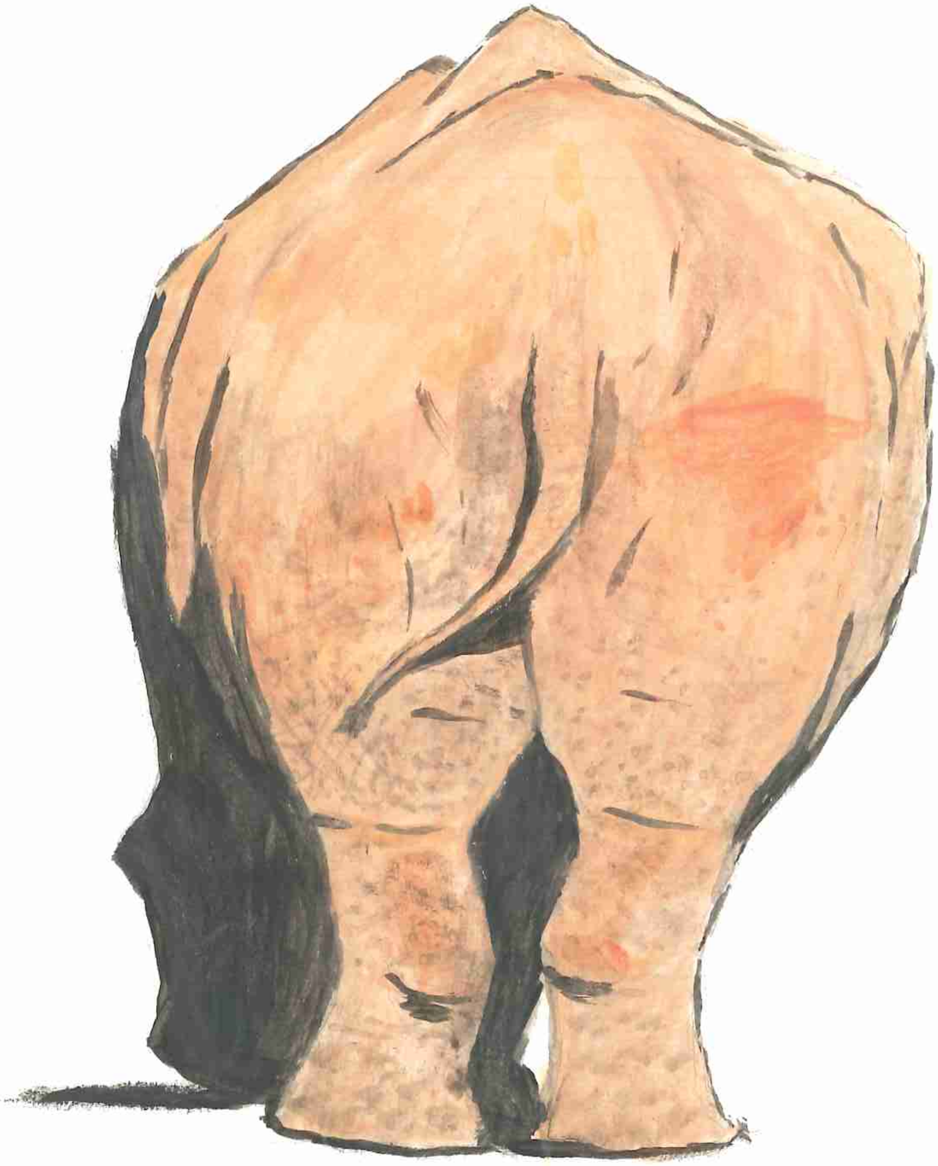
- Resource article: jacht rooft tropisch bos leeg (2017)
- Resource article: big brother in de jungle (2019)
- WUR YouTube movie: saving rhinos with data (2019)
- Radio 1 Nieuwsweekend, de Volkskrant & de Ingenieur: zender een zebra, vind een stroper (2021)

Lecturing / supervision of practicals / tutorials (3.6 ECTS)

- Animal ecology (2017, 2018)
- Ecological methods I (2017, 2018)
- Ecological modelling and data analysis in R (2018)
- Introduction in animal ecology (2019)
- Wildlife ecology and conservation (2019)
- Models for ecological systems (2019, 2020)
- Trends in forest and nature conservation (2019, 2020)
- Data science for ecology (2020)

MSc thesis supervision (6 ECTS)

- African ungulate automated behaviour
- Cow automated behaviour classification
- African ungulate vigilance and flight behaviour
- African ungulate landscape of fear
- Oystercatcher automated behaviour classification
- African mammal aerial image detection
- Rhino poaching prevention through deep learning
- African mammal aerial video tracking
- Barnacle geese decision-making
- African ungulate movement modelling versus environmental heterogeneity
- Animal sensor data systematic review
- African elephant movement behaviour in interaction with cars
- Honeybee sound classification



This research received funding from the Netherlands Organization for Scientific Research (NWO program “Advanced Instrumentation for Wildlife Protection”), the European Space Agency (ESA Contract No. “4000117990/16/NL/CLP”) and the Graduate School for Production Ecology and Resource Conservation (PE&RC call “Institutional Collaboration”).

Cover by Creart Graphics
Artwork by Daniëlle Eikelboom
Photographs by Jasper Eikelboom

Printed by ProefschriftMaken with financial support from Wageningen University