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Reactive response to predation risk affects foraging time of hares, yet not their phosphorus intake

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Abstract

Antipredator responses could affect nutrient intake, which could lead to nutritional deficits. However, little is known about the antipredator response of small herbivores because most are nocturnal or crepuscular and therefore very difficult to study in the field. Therefore, we experimentally assessed the effect of a reactive response to predation risk on the nutrient (i.e., phosphorous) intake of the European hare (*Lepus europaeus*) using three different playback sounds. Additionally, we studied the time spent being costly vigilant, the time spent foraging, and the vegetation height in which the hares were present using accelerometers and GPS. Our results showed that elevated predation risk from our playback experiment did not affect the (1) phosphorus intake, (2) time spent being costly vigilant, and (3) time spent in tall vegetation. However, elevated predation risk did increase the time spent foraging. Possibly hares spent more time foraging with an increased predation risk because hares cannot seek refuge from predators. Additionally, the effect on phosphorus intake could be weak because phosphorous intake does not benefit a flight escape, while the reactive response acts late in the predation sequence limiting the effect on hare ecology. Prey anti-predator responses seem strongly related to the escape tactics of prey species that can differ between different habitats and the time of the day. More detailed field studies are necessary to get a better insight into species' anti-predator-food tactics.

Keywords Accelerometer · Nutrient intake · Risk effects · *Lepus europaeus* · Prey behavior · Playback experiments

Introduction

For predators to successfully feed on prey, they need to complete different sequential stages in the predation process, namely: search, detect (or encounter), chase, capture, handle and consume prey (Bateman et al. 2014). At each stage of the predation process, prey in their turn can use antipredator responses to reduce predation risk (Uetz and Hieber 1994; Creel and Creel 2002; Creel 2018). In particular, prey invests most antipredator effort in avoiding detection or becoming chased (Fuiman and Magurran 1994; but see Bateman et al. 2014), as the chance to avoid being killed presumably decreases further in the predation sequence (Endler 1991).

To reduce the probability of becoming detected by a predator, prey may avoid habitats with predators (Lima and Dill 1990), hide in dens (Olsson et al. 2008), spend more time in habitats that provide cover (e.g., tall vegetation) (Caro 2005; Hopewell et al. 2005), reduce movement (Eccard and Liesenjohann 2014; Weterings et al. 2016), or use camouflage (Stevens and Ruxton 2019). For example, elk moved to more dense vegetation to decrease their predation risk, after wolves arrived in Yellowstone National Park (Gude and Garrott 2003; Creel and Winnie 2005; Gude et al. 2006). Similarly, European hare spent more time in tall vegetation when red foxes were more active (Weterings et al. 2018).

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To reduce the probability of becoming chased, prey may spend more time vigilant to improve detection of approaching predators (Creel et al. 2017). Besides, prey can escape before the chase (Cooper and Frederick 2007) or select habitats that allow escaping at a later time (Heithaus et al. 2009), or show a predator that it has been seen (Holley 1993) to avoid becoming chased. For example, zebras increased their time spent vigilant when lions were present (Périquet et al. 2012). Furthermore, when predation risk increased, guinea pigs increased their time spent vigilant when the distance to cover increased (Cassini 1991). Similarly, during high predation risk, gerbils forage close to bush microhabitat, to allow escape into cover (Kotler et al. 1991).

Presumably, predation risk imposes constraints on prey by increasing the need to make alternative choices (Hawlena and Perez-Mellado 2009). The use of antipredator behavior depends on the context (Périquet et al. 2017) and comes with a cost, such as physiological costs (Zanette et al. 2014), movement costs (Weterings et al. 2016), foraging costs (Creel et al. 2017), nutritional costs (Christianson and Creel 2010) or energetic costs (MacLeod et al. 2014). Insight into the costs of antipredator behavior on nutrient intake is important, because prolonged nutritional deficits could eventually lead to a reduced birth- and survival rate (Creel and Christianson 2008; Cresswell 2010).

Increased vigilance can come at a cost to nutrient intake (i.e., costly vigilance) when an animal stops processing food (i.e., chewing, lubricating and swallowing), while scanning the environment (Hik 1994; Abramsky et al. 2002; Fortin et al. 2004; Creel 2018). For example, dark-eyed juncos foraged more on whole seeds when predation risk increased, to allow visual scanning of the surrounding, even though whole seeds were less profitable than seeds without a shell (Lima 1988). In contrast to prey in short vegetation, animals in tall vegetation stop processing food to improve auditory detection of approaching predators (Benhaiem et al. 2008), as visual detection of approaching predators in tall vegetation is difficult (Hopewell et al. 2005; Riginos and Grace 2008). As a consequence, spending time in tall vegetation can come at a cost to nutrient intake when the food in tall vegetation is nutrient-poor (i.e., in nitrogen and phosphorus) (Shipley 2007; but see Hodges and Sinclair 2003) or contains a high percentage of fibers that increases the handling time of food (Barboza et al. 2009). Nevertheless, prey can often compensate for the costs of antipredator behavior (Luttbeg et al. 2003). To compensate for the low-quality food or the increase in handling time, herbivores in tall vegetation could spend more time foraging (i.e., searching and cropping) to ingest sufficient nutrients (Heuermann et al. 2011). Additionally, as a result of stress, prey can adjust the composition of their diet, thereby changing the types of nutrients or energy ingested (Hawlena and Schmitz 2010b). However, animals may only show compensatory behavior in a specific context. For example, European hares in tall vegetation only spend more time foraging when the vegetation contains low edible biomass (Weterings et al. 2018).

Prey that better match their defense towards predators more often focus on escape tactics (i.e., reactive response), while species that poorly match their defense towards the predator more often focus on avoidance tactics (i.e., proactive response; Dellinger et al. 2019). Prey that is effective in avoiding predator detection is often less effective in escaping predators (Creel et al. 2014). Creel (2018) suggested that predation risk that is unpredictable and of short duration (i.e., an encounter) does not affect the nutrient intake of prey. However, this has not been tested yet for cryptic herbivores (Creel 2018), because nutrient intake for nocturnal or crepuscular herbivores is very difficult to observe or measure in the field, especially when in cover (Ashby 1972).

Therefore, we experimentally tested the short-term effect of a predator–prey encounter on the nutrient intake of a small herbivore. To understand this effect, we additionally studied the time spent costly vigilant, the vegetation height in which the animals were present, and the time spent foraging.

As a case study, we focused on the European hare (*Lepus europaeus*) as a cryptic herbivore, which is a widespread species in North-western Europe (NDFF 2020). The European hare is a solitary non-central place forager that is common in open grassland areas (Barnes and Tapper 1986) but can use tall vegetation as cover or resting places (Neumann et al. 2011). Predation risk strongly affects hare behavior and space use (Weterings et al. 2016, 2019). European hares spend approximately half of their active time being vigilant (Lush et al. 2015) and use crypsis or a flight response to escape predators (Focardi and Rizzotto 1999).

We hypothesize that after a predator–prey encounter in short vegetation, hares (1) spend more time in tall vegetation that provides more cover (Neumann et al. 2011; Weterings et al. 2018) (Table 1). As a consequence, in contrast to short vegetation, hares (2) spend more time costly vigilant in tall vegetation (Monclús and Rödel 2008; Trefry and Hik 2009) to improve auditory detection of approaching predators (Benhaiem et al. 2008). Following, in contrast to short vegetation, hares (3) will spend more time foraging in tall vegetation (Shipley 2007) to compensate for any losses in nutrient intake (Heuermann et al. 2011). Therefore, overall, we expect that a predator–prey encounter does not affect the nutrient intake of the European hare.

Materials and methods

Study site

All data used in this study were collected by Weterings et al. (2018) in 2014–2015 in a coastal dune landscape (52°33′N,

Table 1 Overview of hypotheses tested

No	Hypothesis	Justification	References
1	After a predator–prey encounter in short vegetation, hares spend more time in tall vegetation that provides more cover	To hide and escape from predators, hares will go to taller vegetation that provides more cover	Neumann et al. (2011), Weterings et al. (2018)
2	Hares spend more time costly vigilant in tall vegetation	Tall vegetation blocks visual detection of predators. To improve auditory detection of approaching predators prey species stop chewing and swallowing food	Benhaiem et al. (2008), Monclús and Rödel (2008), Trefry and Hik (2009)
3	In contrast to short vegetation, hares will spend more time foraging in tall vegetation to compensate for any losses in nutrient intake	Tall vegetation often contains a poor nutrient concentration that increases handling time during foraging, therefore to increase total nutrient intake hares will increase their time spend foraging	Shipley (2007), Weterings et al. (2018)

4°38′E) in the Netherlands. In this dune landscape, we focused on two study sites (275 and 50 ha) with a population of European hares (±15 hares/km^2). The areas consisted of patches of grass, thicket, brushwood, and forest.

Research design and data collection

In October 2014 nine hares were caught with Speedset static hare nets (height 45 cm, with 13 cm full mesh; JB's Nets, Alexandria, UK), blindfolded (Paci et al. 2012), and kept in darkened boxes temporarily to reduce stress. Five hares were caught from the Koningsbos area and four hares from the Vennewater area. Hares were equipped with a lightweight GPS-ACC collar (69 g, 1.8% ± 0.2 SD of a hare's body weight) that included a radio link for wireless communication (Type A, E-obs GmBH, Gruenwald, Germany) to minimize disturbance of the hares. Sex and life stage were determined by Stroh's method (juvenile < 1 year/adult > 1 year). Healthy hares (weight 2981–4400 g) were tagged without sedation (Gerritsmann et al. 2012). All handling of the hares was approved by the Wageningen University Animal Experiment Committee (no. 2014034.b) and followed the EU Directive 2010/63 on the protection of animals used for scientific purposes.

To investigate the costs of a predator–prey encounter on European hare nutrient intake, we conducted a playback experiment between 16th of December 2014 and 21st of January 2015. Even though different cues can be used to trigger a response to increased predation risk (Prugh et al. 2019), playbacks are often used in field studies to investigate immediate responses to predator–prey encounters (Clinchy et al. 2012). Moreover, for species that rely more on sound than sight and smell, such as hares (Łopucki et al. 2017), playbacks are generally more meaningful in assessing prey response to encounters (Jarvis 2004). Furthermore, playbacks may often be more alarming than visual cues (Cohen et al. 2009). Hares that participated in the playback experiment were selected based on their spatial distribution to maximize the distance between individual hares treated. Based on the GPS locations of individual hares, hares within 300 m of each other were assigned the same treatment. We used playbacks of conspecific alarm calls of hares instead of playbacks of predators, because prey often responds more strongly to conspecific alarm calls than to playbacks of predators (Schmidt et al. 2008; Magrath et al. 2014). Conspecific alarm calls may warn conspecifics of predators (Smith 1965; Sherman 1977; Zuberbühler et al. 1999; Blumstein 2007), but may also communicate directly to predators that have been detected (Digweed and Rendall 2009a, b; Hasson 1991; Sherman 1985; Woodland et al. 1980).

The playback experiment consisted of three different treatments (1) playbacks of conspecific alarm calls of hares, (2) playbacks of sheep (control playback), and (3) no sound. The playback experiment consisted of three blocks of four days. In every treatment block, hares were either exposed to the treatments from audio boxes (Foxpro Fury2, FOXPRO inc. Lewistown) or to no sound at all (Supplementary materials 1, Table S1). Different treatments occurred within the same block; however, hare and sheep playbacks were never used both within the same block. The three treatment blocks were chosen to control for changes in daylight and weather conditions. Weather data were collected from the weather station in IJmuiden (approximately 10 km from Castricum) (Koninklijk Nederlands Meteorologisch Instituut 2020). After each treatment block there were at least five days without playbacks to avoid carry-over effects (e.g., Petrovan et al. 2012). Ten different combinations of three playback fragments of each 40 s were placed in random order. To avoid habituation, fragments were never used more than two times (McGregor et al. 1992). Playbacks were played for 40 s at 20:00 h (CET), because hare activity and foraging behavior peaked during that time (Hansen 1996), thereby increasing the chance of triggering anti-predator responses during foraging. Audio boxes were placed 50 m south from the core location of GPS activity of a given hare at 20:00 h on previous days (mean distance between boxes = 1117 ± 1882 m), with the largest speaker directed towards the north to standardize distribution of playbacks in different directions.

Costly vigilance and foraging time

To investigate time spent costly vigilant and time spent foraging, we recorded accelerometer (ACC) data of collared hares in three axes, every two minutes for 24 h a day with a frequency of 10.54 Hz per axis. To interpret the accelerometer data, a hand-held video camera was used to record behavior of collared hares in the field. We video-recorded the behavior of eight hares to account for individual variation between hares (see Brivio et al. 2021); six hares from this study site and two hares from another coastal dune habitat on Schiermonnikoog island. Behavioral observations of the latter two hares in a comparable habitat were only added to improve the classification of the accelerometer data of this study, not to explain our hypothesis, because the GPS collars used and the sampling design was exactly the same. The six hares in our two study sites were observed when hares were expected to be the most visible and active (7:00–10:00 and 13:00–16:00). We recorded a total of 9225 s of behavior (mean 1153 s ± 1509 SD per observation).

Vegetation height

To investigate the vegetation height, we measured the vegetation height at five orthogonal locations in six random 2 × 2 m quadrants in each of the 20 vegetation types ($n = 120$) (Agriculture; flower-rich grasslands; bulb fields; dune grasslands; Burnet rose, creeping willow-, blackberry thicket; bare sand; calcareous dune grassland; calcareous dune valleys; deciduous forest; coniferous forest; former agriculture; other; other forests; reed swamp; reed swamp communities; herbaceous, fault, and mantle communities; thickets; nutrient-rich grasslands; nutrient-rich pioneer communities, flood meadows, and pace vegetation; near-shore communities). Next, we recorded GPS locations of individual hares every 12 min for 24 h a day, and used ArcGIS (version 10.7) to link the GPS location of the hares with the average height of the vegetation type at that location.

Nutrient intake

To test the effect of predation risk on nutrient intake, the available food quantity (i.e., edible biomass) and the nutrient concentration of each vegetation type was measured. We collected samples of edible biomass for seven of the most important plant species in the diet of hares (i.e., *Festuca rubra*, *Agrostis capillaris*, *Poa pratensis*, *Holcus lanatus*, *Poa trivialis*, *Taraxacum officinale*, *Rubus caesisus*; Kuijper et al. 2008; Weterings et al. 2018) and a commercial flower bulb species using the hand-pluck method (de Vries and Schippers 1994). Edible biomass (i.e., the green plant parts that have a high nutritional value and are selected by hares; Homolka 1987) were collected by the hand-pluck method in six randomly placed circular plots (10 m radius) up to 50 cm in height in each vegetation type ($n = 120$). Plant parts were air-dried, stored, and chemically analyzed for the concentration of phosphorus (P). We chose phosphorus to investigate nutrient intake, because phosphorus plays an important role in the body of animals, involving the skeletal formation, energy storage, metabolism, nerve impulse transmission and muscle contraction (Barboza et al. 2009) that could facilitate flight from predators. Furthermore, phosphorus is considered one of the most important nutrients for hares (Miller 1968).

Data preparation

Costly vigilance and foraging time

The video recordings of hare behavior were used to label one-second segments of ACC data that only consisted of the same behavior. Hare behavior was classified into six postures (i.e., sitting, sitting alert, standing, standing on hind legs, movement, and jumping), and six activities (i.e., chewing, cropping, grooming, scratching, shaking, and stretching) using the software Avidemux (2.6.6). Labeled segments of ACC data (training data) were used to classify unlabeled segments ACC data into behaviors using Decision Tree (accuracy 80.96% ± 0.75 SD) in the AcceleRater software (Resheff et al. 2014). We used the time sitting alert as a proxy for the time spent costly vigilance, and cropping time as a proxy for foraging time. We chose cropping time instead of chewing time to determine the foraging time, because cropping time was classified with higher precision and recall than chewing time.

Even though there is a trade-off between foraging time and chewing time (Spalinger and Hobbs 1992), nutrient intake increases when chewing time as well as foraging time increases (Gross et al. 1993).

Vegetation height

To calculate the fraction of time hares spent in a certain vegetation height in an hour, the GPS location of the hares was linked to a high-resolution GIS map (1:5000) of the different vegetation types (Everts et al. 2008, 2009). However, whenever hares were present in multiple vegetation types within an hour, we calculated the weighted vegetation height.

Nutrient intake

We calculated the relative nutrient intake of hares by multiplying the time spent foraging by the phosphorus concentration in the edible biomass (Fig. 1).

The average edible biomass (g/m^2) was calculated for each vegetation type by summing the amount of edible biomass (g) of all plant species in one square meter of a vegetation type up to 50 cm in height. The average content of phosphorus in every vegetation type was calculated by averaging the percentage of phosphorus in the edible biomass present in the vegetation type, weighted by their volume per square meter up to 50 cm in height (see Weterings et al. 2018).

Data analysis

We explored the data using the protocol of Zuur et al. (2010) to identify potential statistical problems. Because all males were juveniles, we could not investigate the effect of life stage in our analysis. We used Generalized Additive Mixed Models (GAMMs) in R (R Core Team 2021; R package ‘mgcv’ version 1.9-0 (Wood 2017)) to test the effect of the treatment on the fraction of time spent costly vigilant by hares ($n = 1390$) (i.e., beta distribution), the average vegetation height ($n = 1227$) in which the hares were present (i.e., Gaussian distribution), the fraction of time spent foraging ($n = 1342$) (i.e., beta distribution) and on the phosphorous intake by hares ($n = 1342$) (i.e., Gaussian distribution). GAMMs describe highly nonlinear relationships between response and explanatory variables using smoothing functions (Guisan et al. 2002). In total we investigated 168 h (7 days times 24 h) of response by the hares. All four global models included the treatment, the control variables sex, body weight, temperature, wind speed, rainfall, prior treatment, time of day and the interaction treatment*time of day. Because hares shift between short and tall vegetation during a day at dusk and dawn (Schai-Braun et al. 2012), we included time of day and the interaction treatment*time of day in the analysis. The variable ‘prior treatment’ was added to control for any carryover effects by the treatment the day before. The prior treatment on the first day of a treatment block was categorized as no treatment. Additionally, we transformed (1) the amount of rainfall into presence-absence data, because the data mainly showed zeros, and (2) phosphorous intake ($\log(x + 1)$) because the data were right-skewed. We included vegetation height as an explanatory variable in the models that investigated time spent costly vigilant (Hopewell et al. 2005; Riginos and Grace 2008), foraging time (Heuermann et al. 2011) and phosphorous intake (Shipley 2007). However, vegetation height was excluded from the foraging time model and the phosphorous intake model due to multicollinearity. We found no multicollinearity between the other control variables. All continuous covariates were standardized to compare the effect size within and between models. Hare ID and treatment day block within hare ID were considered random factors. We excluded one hare from the analysis, because we did not identify its sex. A GAMM with cyclic smoother was used to model the effects during the time of day, to avoid discontinuity between subsequent days. Temporal autocorrelation among subsequent hours within a time block was addressed by including an autocorrelation structure, modeling a decreasing degree of autocorrelation with increasing temporal distance between data points. We chose an autoregressive (AR(1)) covariance type for individual time blocks at each site as this resulted in the best fit. The Akaike Information Criterion (AIC) was used to select the final model using the ‘base’ R-package (version 3.6.1). We validated the final model using the ‘MuMIn’ R-package (version 1.43.17) (Bartoń and Bartoń 2020) to plot the residuals against the predicted value and all the covariates.

Results

Compared to a playback of sheep and no playback, hares only spent more time foraging after an alarm call of a conspecific hare (Table 2).

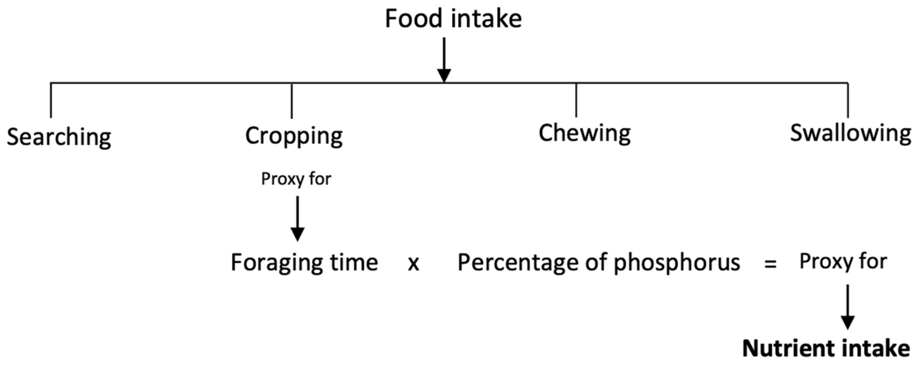

Fig. 1 The four-step process of food intake with the formula that shows the proxies used for foraging time and nutrient intake

Table 2 Results of the Generalized Additive Mixed Models (final models) on the effect of type of treatment on the costly vigilance, vegetation height in which the hares were present, foraging time, and phosphorous intake (log($x+1$)) of European hare (*Lepus europaeus*)

	Costly vigilance ($n=1390$)		Vegetation height ($n=1227$)		Foraging time ($n=1342$)		Phosphorous intake ($n=1342$)	
	ß^f ± SE	p	ß ± SE	p	ß ± SE	p	ß ± SE	p
Treatment Hare[a]	0.09 ± 0.12	0.45	−0.64 ± 1.02	0.53	0.45 ± 0.15	< 0.01	−0.01 ± 0.08	0.91
Treatment Sheep[a]	0.07 ± 0.13	0.59	−0.11 ± 1.16	0.92	−0.11 ± 0.20	0.60	−0.04 ± 0.09	0.67
Prior Treatment Control[a]							0.05 ± 0.08	0.55
Prior Treatment Hare[a]							−0.10 ± 0.13	0.45
Prior Treatment Sheep[a]							0.27 ± 0.09	< 0.01
Sex Male[b]			−0.91 ± 1.90	0.63				
Bodyweight[c]					−0.47 ± 0.17	0.007		
Rain[d]					−0.27 ± 0.10	0.01	−0.20 ± 0.05	< 0.01
Wind speed[c]					−0.09 ± 0.06	0.12		
Vegetation Height[c]	0.16 ± 0.03	< 0.01						
Time of day[c,e]	sm[g]	< 0.01	sm	< 0.01			sm	< 0.01
Random effects variances	$\sigma^2_{\text{Treatment day block}} = 0.049$ $\sigma^2_{\text{Hare}} = 0.452$		$\sigma^2_{\text{Treatment day block}} < 0.001$ $\sigma^2_{\text{Hare}} = 5.356$		$\sigma^2_{\text{Treatment day block}} = 0.990$ $\sigma^2_{\text{Hare}} = 0.270$		$\sigma^2_{\text{Treatment day block}} = 0.009$ $\sigma^2_{\text{Hare}} = 0.062$	

The results are based on 55 treatment day blocks, twelve days and nine hares in two study sites. The sample size is in hours.

[a] Reference category: treatment no sound

[b] Reference category: female

[c] Standardized covariates

[d] Reference category: absence of rain

[e] Smoothing function

[f] Regression coefficients

[g] sm = presented by a smoother

Costly vigilance

We found that the playback of conspecific alarm calls did not affect the amount of time the hares spent costly vigilant (Wald X^2 [2] = 0.343, $p = 0.710$). However, between 6 AM and 4 PM hares spent more time costly vigilant (Wald X^2 [8] = 8.303, $p < 0.001$; Fig. 2), more specifically when present in tall vegetation (Wald X^2 [1] = 22.605, $p < 0.001$).

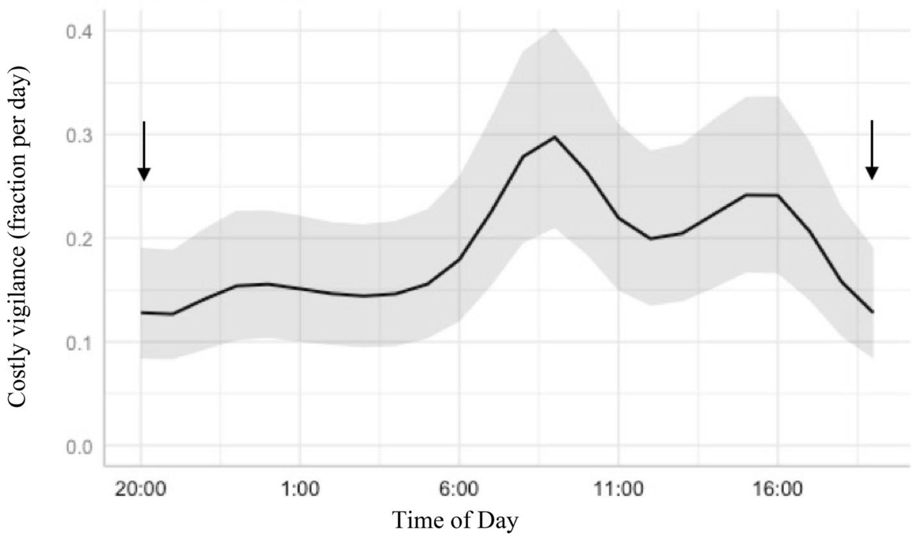

Fig. 2 Estimated marginal mean time spent costly vigilant (fraction per day) (grey band: 95% CI) plotted against time of day, based on 1390 h of observations of 9 hares in 2 sites. Start treatment was at 20:00 h (black arrows). Results based on Generalized Additive Mixed Model (GAMM)

Vegetation height

We found that the playback of conspecific alarm calls did not affect the average vegetation height in which hares were present (Wald X^2 [2] = 0.201, $p = 0.818$). However, between 6 AM and 4 PM (Wald X^2 [8] = 37.01, $p < 0.001$), hares spent significantly more time in taller vegetation (Fig. 3), which corresponds to the time when the hares spent more time costly vigilant.

Foraging time

Hares spent more time foraging after a playback of a conspecific alarm call compared to a playback of sheep, and no sound (Wald X^2 [2] = 10.42, $p = 0.005$); Fig. 4). Hares with a lower bodyweight spent more time foraging (Wald X^2 [1] = 7.16, $p = 0.007$). Furthermore, hares spent more time foraging in absence of rain compared to the presence of rain (Wald X^2 [1] = 6.49, $p = 0.011$). Finally, time of day was not significantly related to the time spent foraging (Wald X^2 [1] = 0.204, $p = 0.651$). Hares thus spent a similar amount of time per hour foraging throughout the day and the night.

Phosphorous intake

We found that the playback of conspecific alarm calls did not affect the phosphorus intake of hares (Wald X^2 [2] = 0.088, $p = 0.915$). However, the phosphorus intake of hares was

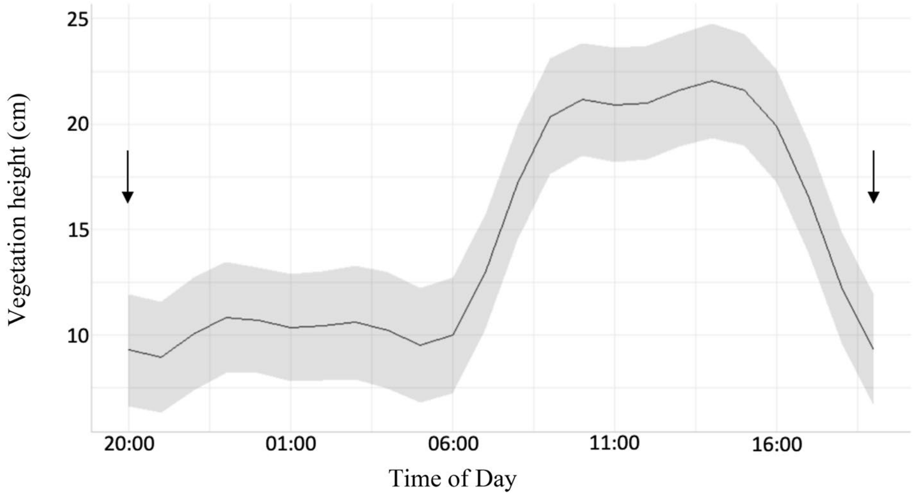

Fig. 3 Estimated marginal mean vegetation height per hour in which hares were found (grey band: 95% CI) plotted against time of the day, based on 1227 h of observations of 9 hares in 2 sites. Reference category: Treatment = control, Sex = females. Start treatment was at 20:00 h (black arrows). Results based on Generalized Additive Mixed Model (GAMM)

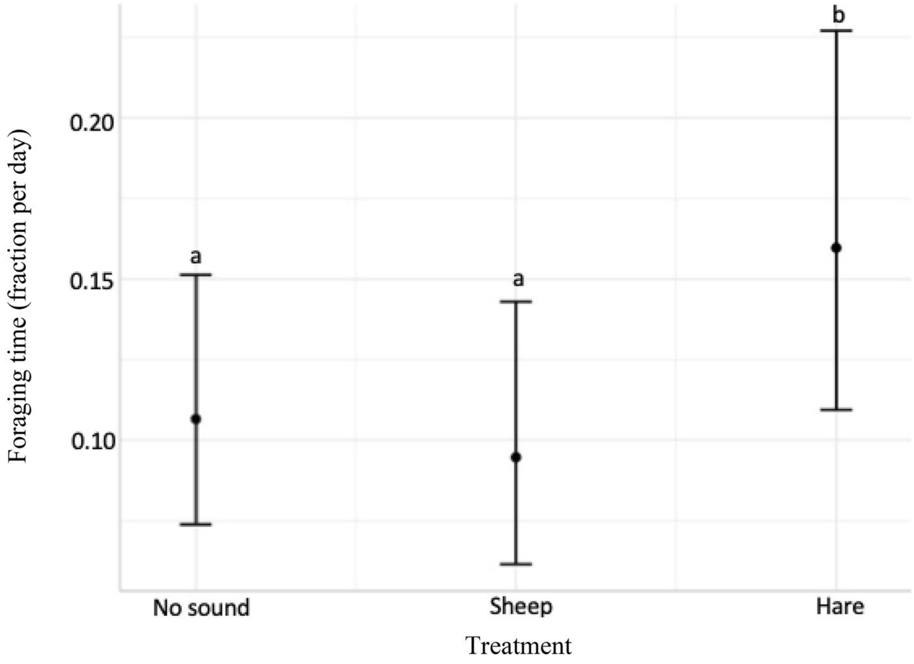

Fig. 4 Estimated marginal mean time spent foraging (fraction per day) (error bars: 95% CI) plotted against treatment, based on 1342 h of observations of 9 hares in 2 sites. Reference category: Bodyweight = 4253.15 g, Wind speed = 10.54 m/h, Rain = absence. Means with similar letters do not differ significantly. Results based on Generalized Additive Mixed Model (GAMM)

significantly affected by time of day (Wald X^2 [7] = 4.81, $p < 0.001$; Fig. 5), with a gradual increase in intake between 4AM and 4PM (i.e., during daytime in tall vegetation), after which the phosphorus intake decreased again (i.e., during night time in short vegetation). Moreover, hares had a significantly higher phosphorus intake in the absence of rain compared to the presence of rain (Wald X^2 [1] = 13.64, $p < 0.001$).

Discussion

We investigated the effect of a predator–prey encounter on the phosphorous intake of a small cryptic herbivore, the European hare. As a response to conspecific alarm calls, (1) hares did not increase their time spent costly vigilant in tall vegetation, (2) hares did not spend more time in tall vegetation, but (3) increased their time spent foraging in short and tall vegetation. Still, the phosphorus intake of hares was not affected. Therefore, the antipredator response of the European hare to our playback treatment did not come with a nutritional cost in phosphorus. Hares could possibly adjust their diet to compensate for losses in nutrient intake (Engelhart and Muller-Schwarze 1995; Epple et al. 1993; Pfister et al. 1990; Sullivan and Crump 1984). Alternatively, food intake could interact with safety to affect dietary responses to predation. For example, *L. catesbeianus* tadpoles adjust their body nutrient stoichiometry in response to predation risk (Guariento et al. 2015). Besides, Eurasian siskins that did not reduce their food intake rate with increased predation risk, showed more effective behavior to detect or escape from a predator, compared to individuals that did reduce their food intake (Pascual and Senar 2014). Additionally, hares that forage on an energy-rich diet that reduces gut-content weight could be more successful in escaping predators (Schai-Braun et al. 2015). Furthermore, in response to an encounter, prey possibly compensate for the loss in carbohydrates, which are spent during a flight response (Hawlena and Schmitz 2010a). In contrast, prey probably do not need to compensate for a loss in phosphorus or calcium, as these nutrients are not spent during an escape, but are required for stronger bones (Rinehart and Hawlena 2020). The latter could explain the lack of a nutritional cost in phosphorus as a result of the hare treatment observed in our study. Nevertheless, because the reactive response acts late in the predation sequence and occurs less frequent (see also Barnier et al. 2014; Christianson and Creel 2010), the effect on prey ecology at a population level would be limited (Creel 2018).

The time spent costly vigilant did not increase as a result of the 'risky' playback of conspecific alarm calls of hares. It is unlikely that this behavioral response was shown because of the type of playback used, as hares did respond to our cue by increasing their time spent foraging. Besides, playbacks of conspecific alarm calls are used successfully to trigger antipredator behavior in many other studies (e.g., Blumstein et al. 2001; Cameron and du Toit 2005; Lung and Childress 2007; McDonough and Loughry 1995). Our results did show that in contrast to short vegetation, hares in tall vegetation spent more time being costly vigilant, probably to improve auditory detection of approaching predators due to low visibility (Marboutin and Aebischer 1996; Benhaiem et al. 2008; Riginos and Grace 2008). Differences in (costly) vigilance seemed, therefore, more related to differences in visibility due to vegetation cover than a change in predation risk initiated by our playback.

As a response to the treatment simulating a predator–prey encounter, we hypothesized that prey would shift habitat and move to taller vegetation containing more cover (Neumann et al. 2011). In contrast, hares did not move to tall vegetation, but moved to tall vegetation during the transition from night to day. Hares shift from tall to short vegetation during dusk and vice versa during dawn (Schai-Braun

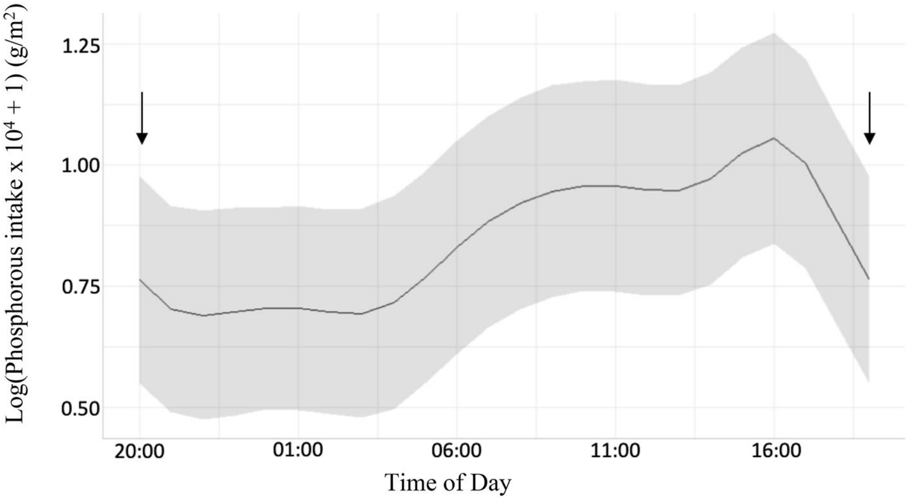

Fig. 5 Estimated marginal means of phosphorous intake (95% CI) plotted against time of the day, based on 1342 h of observations of 9 hares in 2 sites. Reference category: Treatment = control, Rain = no rain, Prior treatment = no treatment, Bodyweight (z-score) = 0. Start treatment was at 20:00 h (black arrows). Results based on Generalized Additive Mixed Model (GAMM)

et al. 2012). Possibly, hares did not shift habitat to avoid predators in open vegetation, because their defense matched predator attack ecology in open and short vegetation during the night (Dellinger et al. 2019). Short vegetation allows hares to detect approaching predators (Hewson 1977) and to escape predators by flight (Weterings et al. 2016). However, hares only use flight as an escape tactic in open habitat during the night, and make use of crypsis in closed habitat during the day. We, therefore, suggest that hares have an advantage escaping predation in short vegetation during the night, while they have an advantage avoiding predation in tall vegetation during the day (Dellinger et al. 2019).

In contrast to the control treatment, playback of conspecific alarm calls increased the time spent foraging by hares throughout the day, no matter the length of the vegetation. Prey species increase their time spent foraging during high levels of predation risk, when this risk is uniformly spread over the landscape (i.e., they have no place to hide) and missed opportunity costs for foraging are therefore low (Eccard et al. 2008; Eccard and Liesenjohann 2014). This could apply to the European hare, which as a non-central place forager, does not have a refuge or burrow. However, snowshoe hares (*Lepus americanus*) (also a non-central place forager) did show a decrease in time spent foraging at high predation risk (Liu et al. 2014). Small mammals that can hide, decrease their time spend foraging during high predation risk (Verdolin 2006). Nevertheless, Mazza et al. (2019) showed that prey that could outrun their predator seem to accept predation risk rather than avoid predation risk and adjust their foraging behavior, compared to prey that cannot outrun their predator (see also Dellinger et al. 2019). Besides, our prey could behaved more boldly during winter time, because the available food choices are limited during this season (Kervola 2019). Moreover, if the risk of starvation is high, prey will forage in unsafe habitats (Sih 1980, 1982).

In contrast to studies that report hares resting in cover during day time (see e.g., Tapper and Barnes 1986), our results show that hares foraged in cover during the day. Possibly hares require a specific nutritional diet that can only be satisfied by foraging in two different types of habitats (i.e., short and tall vegetation) (see e.g., sparrows; Tinbergen 1980), as mobile species often use multiple habitats to fulfill their biological needs (Firle et al. 1998; Doniol-Valcroze et al. 2012). Interestingly, during day time (between 8:00 a.m. and 18:00 p.m.) when hares were found in tall vegetation, hares had a higher phosphorus intake in contrast to night time when hares were found in short vegetation. Furthermore, our results do show that hares with a lower bodyweight spent more time foraging. This could be an effect of the life stage of hares, or could corroborate with the hypothesis of mass-dependent predation risk (MDPR) (see Gosler et al. 1995; Kullberg et al. 1996; MacLeod et al. 2005). Nevertheless, we think that earlier scientists did not observe hares foraging during the day time, because hares spent most of their time in cover during day time and are thus very difficult to observe (e.g., Marboutin and Aebischer 1996). Most recent studies did not use accelerometers that can continuously record behavior of small mammals during their circadian rhythm, even in concealed habitats (see e.g., Botts et al. 2020). However, variation between individuals (e.g., in sex, age, body size, collar tightness) may affect the recorded values of accelerometers and need to be considered during data analysis (Brivio et al. 2021).

Overall, we found that playback of conspecific alarm calls of hares did not affect the antipredator responses of hares including their phosphorus intake. Animals consume food resources as a complex mixture of nutrients in varying levels of availability to maximize their response to predation (Zaguri et al. 2022), while minimizing the effects of toxics (Kirmani et al. 2010). In contrast to the consumption of phosphorus, hares could select an energy-rich diet, enabling them to run faster and escape from predators (Schai-Braun et al. 2015) (see hypothesis of mass-dependent predation risk: MacLeod et al. 2005), while meeting their daily energy demands. Additionally, the nutritional costs of an encounter can also affect the consumption of carbohydrates by prey, as carbohydrates are spent during the flight response. Furthermore, prey anti-predator responses (i.e., vigilance or a habitat shift) seem strongly related to the escape tactics of prey species that can differ between different habitats, while it can also differ during the time of the day. After all, more detailed field studies on the effects of predation risk on the nutrient intake of prey species are necessary to get a better insight into species' anti-predator-food tactics.

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Data availability Data is available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.05qfttf95).

Declarations

Conflict of interest The authors declare they have no conflict of interest.

References

Abramsky Z, Rosenzweig M, Subach A (2002) The costs of apprehensive foraging. Ecology 83(5):1330–1340. https://doi.org/10.1890/0012-9658(2002)083[1330:TCOAF]2.0.CO;2

Ashby KR (1972) Patterns of daily activity in mammals. Mammal Rev 1:171–185. https://doi.org/10.1111/j.1365-2907.1972.tb00088.x

Barboza P, Parker K, Hume I (2009) Integrative wildlife nutrition. Springer, Berlin. https://doi.org/10.1007/978-3-540-87885-8

Barnes R, Tapper S (1986) Consequences of the myxomatosis epidemic in Britain's rabbit (*Oryctolagus cuniculus* L.) population on the numbers of brown hares (*Lepus europaeus* Pallas). Mammal Rev 16(3–4):111–116. https://doi.org/10.1111/j.1365-2907.1986.tb00030.x

Barnier F, Valeix M, Duncan P, Chamaillé-Jammes S, Barre P, Loveridge A, Macdonald D, Fritz H (2014) Diet quality in a wild grazer declines under the threat of an ambush predator. P Roy Soc B-Biol Sci 281(1785):20140446. https://doi.org/10.1098/rspb.2014.0446

Bartoń K, Bartoń M (2020) MuMIn: multi-model inference.–R package ver. 1.43.17

Bateman AW, Vos M, Anholt BR (2014) When to defend: antipredator defenses and the predation sequence. Am Nat 183(4):847. https://doi.org/10.1086/675903

Benhaiem S, Delon M, Lourtet B, Cargnelutti B, Aulagnier S, Hewison A, Morellet N, Verheyden H (2008) Hunting increases vigilance levels in roe deer and modifies feeding site selection. Anim Behav 76(3):611–618. https://doi.org/10.1016/j.anbehav.2008.03.012

Blumstein D (2007) The evolution of alarm communication in rodents: structure, function, and the puzzle of apparently altruistic calling in rodents. In: Wolff JO, Sherman PW (eds) Rodent societies. University of Chicago Press, Chicago, pp 317–327

Blumstein DT, Daniel JC, Evans CS (2001) Yellow-footed rock-wallaby group size effects reflect a trade-off. Ethology 107:655–664. https://doi.org/10.1046/j.1439-0310.2001.00699.x

Botts RT, Eppert AA, Wiegman TJ, Blankenship SR, Rodriguez A, Wagner AP, Ullrich SE, Allen GR, Garley WM, Asselin EM, Mooring MS (2020) Does moonlight increase predation risk for elusive mammals in Costa Rica? Trop Conserv Sci 13:1–21. https://doi.org/10.1177/1940082920952405

Brivio F, Bertolucci C, Marcon A, Cotza A, Apollonio M, Grignolio S (2021) Dealing with intra-individual variability in the analysis of activity patterns from accelerometer data. Hystrix 32(1):41–47

Cameron EZ, du Toit JT (2005) Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*. Anim Behav 69:1337–1344. https://doi.org/10.1016/j.anbehav.2004.08.015

Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, IL

Cassini MH (1991) Foraging under predation risk in the wild guinea pig *Cavia aperea*. Oikos 62(1):20–24. https://doi.org/10.2307/3545441

Christianson D, Creel S (2010) A nutritionally mediated risk effect of wolves on elk. Ecology 91(4):1184–1191. https://doi.org/10.1890/09-0221.1

Clinchy M, Sheriff M, Zanette L (2012) Predator induced stress and the ecology of fear. Funct Ecol 27(1):56–65. https://doi.org/10.1111/1365-2435.12007

Cohen H, Kozlovsky N, Richter-Levin G, Zohar J (2009) Post-traumatic stress disorder in animal models. In: Soreq H, Friedman A, Kaufer D (eds) Stress - from molecules to behaviour. Wiley, Weinheim, pp 263–282

Cooper WE, Frederick WG (2007) Optimal flight initiation distance. J Theor Biol 244:59–67. https://doi.org/10.1016/j.jtbi.2006.07.011

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

Creel S, Christianson D (2008) Relationships between direct predation and risk effects. Trends Ecol Evol 23(4):194–201. https://doi.org/10.1016/j.tree.2007.12.004

Creel S, Creel NM (2002) The African wild dog: behavior, ecology and conservation. Princeton University Press, Princeton. https://doi.org/10.1515/9780691207001

Creel S, Winnie J (2005) Response of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Anim Behav 69(5):1181–1189. https://doi.org/10.1016/j.anbehav.2004.07.022

Creel S, Schuette P, Christianson D (2014) Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behav Ecol 25(4):773–784. https://doi.org/10.1093/beheco/aru050

Creel S, Droge E, M'soka J, Smit D, Becker MS, Christianson D, Schuette P (2017) The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey. Ecology 98(8):2081–2092. https://doi.org/10.1002/ecy.1885

Cresswell W (2010) Predation in bird populations. J Ornithol 152(S1):251–263. https://doi.org/10.1007/s10336-010-0638-1

De Vries MF, Schippers P (1994) Foraging in a landscape mosaic: general introduction. Oecologia 100(1–2):107–117. https://doi.org/10.1007/BF00317137

Dellinger JA, Shores CR, Craig A, Heithaus MR, Ripple WJ, Wirsing AJ (2019) Habitat use of sympatric prey suggests divergent antipredator responses to recolonizing wolves. Oecologia 189:487–500. https://doi.org/10.1007/s00442-018-4323-z

Digweed S, Rendall D (2009a) Predator-associated vocalizations in North American red squirrels, *Tamiasciurus hudsonicus*: are alarm calls predator specific? Anim Behav 78(5):1135–1144. https://doi.org/10.1016/j.anbehav.2009.07.030

Digweed S, Rendall D (2009b) Predator-associated vocalizations in North American red squirrels (*Tamiasciurus hudsonicus*): to whom are alarm calls addressed and how do they function? Ethology 115(12):1190–1199. https://doi.org/10.1111/j.1439-0310.2009.01709.x

Doniol-Valcroze T, Lesage V, Giard J, Michaud R (2012) Challenges in marine mammal habitat modelling: evidence of multiple foraging habitats from the identification of feeding events in blue whales. Endanger Species Res 17:255–268. https://doi.org/10.3354/esr00427

Eccard JA, Liesenjohann T (2014) The importance of predation risk and missed opportunity costs for context-dependent foraging patterns. PLoS ONE 9(5):e94107. https://doi.org/10.1371/journal.pone.0094107

Eccard JA, Pusenius J, Sundell J, Halle S, Ylönen H (2008) Foraging patterns of voles at heterogeneous avian and uniform mustelid predation risk. Oecologia 157:725–734. https://doi.org/10.1007/s00442-008-1100-4

Endler JA (1991) Interactions between predators and prey. In: Krebs JR, Davies NB (eds) Behavioural ecology, 3rd edn. Blackwell, Oxford, pp 169–196

Engelhart A, Muller-Schwarze D (1995) Responses of beaver (*Castor canadensis* KUHL) to predator chemicals. J Chem Ecol 21:1349–1364. https://doi.org/10.1007/BF02027567

Epple G, Mason JR, Nolte DL, Campell DL (1993) Effects of predator odors on feeding in the mountain beaver (*Aplodontia rufa*). J Mammal 74:715–722. https://doi.org/10.2307/1382293

Everts H, Pranger P, Tolman E, De Vries J (2008) Vegetation mapping subareas Egmond-Bakkum 2007. Report number: 653 EGG. EGG Consult, Groningen, The Netherlands. https://doi.org/10.1007/978-90-313-7318-5_54

Everts H, Pranger P, Tolman E, De Vries J (2009) Vegetation mapping subareas Castricum 2008. Report number: 739 EGG. EGG Consult, Groningen, The Netherlands

Firle S, Bommarco R, Ekbom B, Natiello M (1998) The influence of movement and resting behavior on the range of three carabid beetles. Ecology 79(6):2113–2122. https://doi.org/10.1890/0012-9658(1998)079[2113:TIOMAR]2.0.CO;2

Focardi S, Rizzotto M (1999) Optimal strategies and complexity: a theoretical analysis of the anti-predatory behavior of the hare. Bull Math Biol 61(5):829–848. https://doi.org/10.1006/bulm.1999.0114

Fortin D, Boyce MS, Merrill EH, Fryxell JM (2004) Foraging costs of vigilance in large mammalian herbivores. Oikos 107(1):172–180. https://doi.org/10.1111/j.0030-1299.2004.12976.x

Fuiman LA, Magurran AE (1994) Development of predator defences in fishes. Rev Fish Biol Fish 4:145–183. https://doi.org/10.1007/BF00044127

Gerritsmann H, Stalder G, Seilern-Moy K, Knauer F, Walzer C (2012) Comparison of S(+)-ketamine and ketamine, with medetomidine, for field anaesthesia in the European brown hare (*Lepus europaeus*). Vet Anaesth Analg 39(5):511–519. https://doi.org/10.1111/j.1467-2995.2012.00754.x

Gosler AG, Greenwood JJD, Perrins CM (1995) Predation risk and the cost of being fat. Nature 377:621–623. https://doi.org/10.1038/377621a0

Gross J, Shipley L, Hobbs N, Spalinger D, Wunder B (1993) Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. Ecology 74(3):778–791. https://doi.org/10.2307/1940805

Gariento RD, Carneiro LS, Jorge JS, Borges AN, Esteves FA, Caliman A (2015) Interactive effects of predation risk and conspecific density on the nutrient stoichiometry of prey. Ecol Evol 5(21):4747–4756. https://doi.org/10.1002/ece3.1740

Gude J, Garrott B (2003) Lower Madison Valley wolf-ungulate research project 2002–2003 annual report. Montana State University, Bozeman

Gude JA, Garrott RA, Borkowski JJ, King F (2006) Prey risk allocation in a grazing ecosystem. Ecol Appl 16(1):285–298. https://doi.org/10.1890/04-0623

Guisan A, Edwards J, Thomas C, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol Model 157:89–100. https://doi.org/10.1016/S0304-3800(02)00204-1

Hansen K (1996) European hare (*Lepus europaeus*) time budget of nine different nocturnal activities in a Danish farmland. In Proc XXII IUGB Congress, Sofia, Bulgaria, p. 167–173

Hasson O (1991) Pursuit-deterrent signals: communication between prey and predator. Trends Ecol Evol 6(10):325–329. https://doi.org/10.1016/0169-5347(91)90040-5

Hawlena D, Perez-Mellado V (2009) Change your diet or die: predator-induced shifts in insectivorous lizard feeding ecology. Oecologia 161:411–419. https://doi.org/10.1007/s00442-009-1375-0

Hawlena D, Schmitz OJ (2010a) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. Am Nat 176(5):537–556. https://doi.org/10.1086/656495

Hawlena D, Schmitz OJ (2010b) Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. PNAS 107(35):15503–15507. https://doi.org/10.1073/pnas.1009300107

Heithaus MR, Wirsing AJ, Burkholder D, Thomson J, Dill LM (2009) Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. J Anim Ecol 78(3):556–562. https://doi.org/10.1111/j.1365-2656.2008.01512.x

Heuermann N, van Langevelde F, van Wieren S, Prins H (2011) Increased searching and handling effort in tall swards lead to a Type IV functional response in small grazing herbivores. Oecologia 166(3):659–669. https://doi.org/10.1007/s00442-010-1894-8

Hewson R (1977) Food selection by brown hares (*Lepus capensis*) on cereal and turnip crops in north-east Scotland. J Appl Ecol 14(3):779–785. https://doi.org/10.2307/2402809

Hik DS (1994) Predation risk and the snowshoe hare cycle. Ph.D. Thesis, University of British Columbia, Vancouver

Hodges KE, Sinclair ARE (2003) Does predation risk cause snowshoe hares to modify their diets? Can J Zool 81(12):1973–1985. https://doi.org/10.1139/z03-192

Holley AJF (1993) Do brown hares signal to foxes? Ethology 94:21–30. https://doi.org/10.1111/j.1439-0310.1993.tb00544.x

Homolka M (1987) The diet of brown hare (*Lepus europaeus*) in central Bohemia. Folia Zool 36(2):103–110

Hopewell L, Rossiter R, Blower E, Leaver L, Goto K (2005) Grazing and vigilance by Soay sheep on Lundy island: influence of group size, terrain and the distribution of vegetation. Behav Process 70(2):186–193. https://doi.org/10.1016/j.beproc.2005.04.009

Jarvis E (2004) Learned birdsong and the neurobiology of human language. Ann N Y Acad Sci 1016(1):749–777. https://doi.org/10.1196/annals.1298.038

Kervola A (2019) Automatic camera traps in monitoring small mammals: the effect of predation risk on activity and foraging in winter and spring. Ph.D. Thesis, Environmental Science

Kirmani SN, Banks PB, McArthur C (2010) Integrating the costs of plant toxins and predation risk in foraging decisions of a mammalian herbivore. Oecologia 164(2):349–356. https://doi.org/10.1007/s00442-010-1717-y

Koninklijk Nederlands Metereologisch Instituut. (2020). Klimatologie: daggegevens van het weer in Nederland. Retrieved on June 15 2020, from http://projects.knmi.nl/klimatologie/daggegevens/selectie.cgi

Kotler BP, Brown JS, Hasson O (1991) Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249–2260. https://doi.org/10.2307/1941575

Kuijper D, Beek P, Van Wieren S, Bakker J (2008) Time-scale effects in the interaction between a large and a small herbivore. Basic Appl Ecol 9:126–134. https://doi.org/10.1016/j.baae.2006.08.008

Kullberg C, Fransson T, Jakobsson S (1996) Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). P Roy Soc B-Biol Sci 263(1377):1671–1675. https://doi.org/10.1098/rspb.1996.0244

Lima SL (1988) Vigilance and diet selection: a simple example in the dark-eyed junco. Can J Zool 66:593–596. https://doi.org/10.1139/z88-087

Lima S, Dill L (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68(4):619–640. https://doi.org/10.1139/z90-092

Liu R, DeAngelis DL, Bryant JP (2014) Dynamics of herbivores and resources on a landscape with interspersed resources and refuges. Theor Ecol 7(2):195–208. https://doi.org/10.1007/s12080-013-0210-8

Łopucki R, Klich D, Gielarek S (2017) Do terrestrial animals avoid areas close to turbines in functioning wind farms in agricultural landscapes? Environ Monit Assess 189(7):343. https://doi.org/10.1007/s10661-017-6018-z

Lung MA, Childress MJ (2007) The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. Behav Ecol 18:12–20. https://doi.org/10.1093/beheco/arl066

Lush L, Ellwood S, Markham A, Ward A, Wheeler P (2015) Use of tri-axial accelerometers to assess terrestrial mammal behaviour in the wild. J Zool 298(4):257–265. https://doi.org/10.1111/jzo.12308

Luttbeg B, Rowe L, Mangel M (2003) Prey state and experimental design affect relative size of trait- and density-mediated indirect effects. Ecology 84(5):1140–1150. https://doi.org/10.1890/0012-9658(2003)084[1140:PSAEDA]2.0.CO;2

MacLeod R, Barnett P, Clark JA, Cresswell W (2005) Body mass change strategies in blackbirds *Turdus merula*: the starvation-predation risk trade-off. J Anim Ecol 74:292–302. https://doi.org/10.1111/j.1365-2656.2005.00923.x

MacLeod CD, MacLeod R, Learmonth JA, Cresswell W, Pierce GJ (2014) Predicting population-level risk effects of predation from the responses of individuals. Ecology 95(7):2006–2015

Magrath R, Haff T, Fallow P, Radford A (2014) Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biol Rev 90(2):560–586. https://doi.org/10.1111/brv.12122

Marboutin E, Aebischer NJ (1996) Does harvesting arable crops influence the behaviour of the European hare *Lepus europaeus*? Wildlife Biol 2(2):83–91. https://doi.org/10.2981/wlb.1996.036

Mazza V, Jacob J, Dammhahn M, Zaccaroni M, Eccard JA (2019) Individual variation in cognitive style reflects foraging and anti-predator strategies in a small mammal. Sci Rep 9(1):10157–10159. https://doi.org/10.1038/s41598-019-46582-1

McDonough CM, Loughry WJ (1995) Influences on vigilance in nine-banded armadillos. Ethology 100:50–60. https://doi.org/10.1111/j.1439-0310.1995.tb00314.x

McGregor P, Catchpole C, Dabelsteen T, Falls J, Fusani L, Gerhardt H, Gilbert F, Horn A, Klump G, Kroodsma D, Lambrechts M, McComb K, Nelson D, Pepperberg I, Ratcliffe L, Searcy W, Weary D (1992) Design of playback experiments: the Thornbridge Hall NATO ARW consensus. In: McGregor PK (ed) Playback and studies of animal communication. NATO ASI Series, vol 228. Springer, Boston

Miller GR (1968) Evidence for selective feeding on fertilized plots by red grouse, hares, and rabbits. J Wildl Manage 32(4):849–853. https://doi.org/10.2307/3799560

Monclús R, Rödel HG (2008) Different forms of vigilance in response to the presence of predators and conspecifics in a group-living mammal, the European rabbit. Ethology 114(3):287–297. https://doi.org/10.1111/j.1439-0310.2007.01463.x

NDFF Verspreidingsatlas Zoogdieren (2020) *Lepus europaeus* Pallas - Haas. Retrieved on April 14 2020, from https://www.verspreidingsatlas.nl/8496115

Neumann F, Schai-Braun S, Weber D, Amrhein V (2011) European hares select resting places for providing cover. Hystrix 22(2):291–299

Olsson O, Brown JS, Helf KL (2008) A guide to central place effects in foraging. Theor Popul Biol 74(1):22–33. https://doi.org/10.1016/j.tpb.2008.04.005

Paci G, Ferretti M, Bagliacca M (2012) Reducing visual stimulations in European hares (*Lepus europaeus* Pallas) captured for translocation. Ital J Anim Sci 11(3):e51–e51. https://doi.org/10.4081/ijas.2012.e51

Pascual J, Senar JC (2014) Antipredator behavioural compensation of proactive personality trait in male Eurasian siskins. Anim Behav 90:297–303. https://doi.org/10.1016/j.anbehav.2014.02.002

Périquet S, Todd-Jones L, Valeix M, Stapelkamp B, Elliot N, Wijers M, Pays O, Fortin D, Madzikanda H, Fritz H, Macdonald DW, Loveridge AJ (2012) Influence of immediate predation risk by lions on the vigilance of prey of different body size. Behav Ecol 23(5):970–976. https://doi.org/10.1093/beheco/ars060

Périquet S, Richardson P, Cameron EZ, Ganswindt A, Belton L, Loubser E, Dalerum F, Wright J (2017) Effects of lions on behaviour and endocrine stress in plains zebras. Ethology 123(9):667–674. https://doi.org/10.1111/eth.12638

Petrovan S, Ward A, Wheeler P (2012) Habitat selection guiding agri-environment schemes for a farmland specialist, the brown hare. Anim Conserv 16(3):344–352. https://doi.org/10.1111/acv.12002

Pfister JA, Muller-Schwarze D, Balph DF (1990) Effects of predator fecal odors on feed selection by sheep and cattle. J Chem Ecol 16:573–583. https://doi.org/10.1007/BF01021787

Prugh L, Sivy K, Mahoney P, Ganz T, Ditmer M, van de Kerk M, Gilbert S, Montgomery R (2019) Designing studies of predation risk for improved inference in carnivore-ungulate systems. Biol Conserv 232:194–207. https://doi.org/10.1016/j.biocon.2019.02.011

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Resheff Y, Rotics S, Harel R, Spiegel O, Nathan R (2014) AcceleRater: a web application for supervised learning of behavioral modes from acceleration measurements. Mov Ecol 2(1):27. https://doi.org/10.1186/s40462-014-0027-0

Riginos C, Grace J (2008) Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. Ecology 89(8):2228–2238. https://doi.org/10.1890/07-1250.1

Rinehart S, Hawlena D (2020) The effects of predation risk on prey stoichiometry: a meta-analysis. Ecology 101(7):e03037. https://doi.org/10.1002/ecy.3037

Schai-Braun S, Rödel HG, Hackländer K (2012) The influence of daylight regime on diurnal locomotor activity patterns of the European hare (*Lepus europaeus*) during summer. Mamm Biol 77(6):434–440. https://doi.org/10.1016/j.mambio.2012.07.004

Schai-Braun S, Reichlin TS, Ruf T, Klansek E, Tataruch F, Arnold W, Hackländer K (2015) The European hare (*Lepus europaeus*): a picky herbivore searching for plant parts rich in fat. PLoS ONE 10(7):e0134278. https://doi.org/10.1371/journal.pone.0134278

Schmidt K, Lee E, Ostfeld R, Sieving K (2008) Eastern chipmunks increase their perception of predation risk in response to titmouse alarm calls. Behav Ecol 19(4):759–763. https://doi.org/10.1093/beheco/arn034

Sherman P (1977) Nepotism and the evolution of alarm calls. Science 197(4310):1246–1253. https://doi.org/10.1126/science.197.4310.1246

Sherman P (1985) Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? Behav Ecol Sociobiol 17(4):313–323. https://doi.org/10.1007/BF00293209

Shipley L (2007) The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. Oikos

116(12):1964–1974. https://doi.org/10.1111/j.2007.0030-1299.15974.x

Sih A (1980) Optimal behavior: can foragers balance two conflicting demands. Science 210:1041–1043. https://doi.org/10.1126/science.210.4473.1041

Sih A (1982) Foraging strategies and the avoidance of predation by an aquatic insect. Ecology 63:786–796. https://doi.org/10.2307/1936799

Smith J (1965) The evolution of alarm calls. Am Nat 99(904):59–63. https://doi.org/10.1086/282349

Spalinger D, Hobbs N (1992) Mechanisms of foraging in mammalian herbivores: new models of functional response. Am Nat 140(2):325–348. https://doi.org/10.1086/285415

Stevens M, Ruxton GD (2019) The key role of behaviour in animal camouflage. Biol Rev Biol Proc Camb Philos Soc 94(1):116–134. https://doi.org/10.1111/brv.12438

Sullivan TP, Crump DR (1984) Influence of mustelid scent-gland compounds on suppression of feeding by snowshoe hares (*Lepus americanus*). J Chem Ecol 10:1809–1821. https://doi.org/10.1007/BF00987363

Tapper SC, Barnes RFW (1986) Influence of farming practice on the ecology of the brown hare (*Lepus europaeus*). J Appl Ecol 23(1):39–52. https://doi.org/10.2307/2403079

Tinbergen JM (1980) Foraging decisions in starlings (*Sturnus vulgaris* l.). Ardea 69:1–67. https://doi.org/10.5253/arde.v69.p1

Trefry S, Hik D (2009) Eavesdropping on the neighbourhood: collared pika (*Ochotona collaris*) responses to playback calls of conspecifics and heterospecifics. Ethology 115(10):928–938. https://doi.org/10.1111/j.1439-0310.2009.01675.x

Uetz GW, Hieber CS (1994) Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms. Behav Ecol 5:326–333. https://doi.org/10.1093/beheco/5.3.326

Verdolin JL (2006) Meta-analysis of foraging and predation risk tradeoffs in terrestrial systems. Behav Ecol Sociobiol 60:457–464. https://doi.org/10.1007/s00265-006-0172-6

Weterings MJA, Zaccaroni M, van der Koore N, Zijlstra LM, Kuipers HJ, van Langevelde F, van Wieren SE (2016) Strong reactive movement response of the medium-sized European hare to elevated predation risk in short vegetation. Anim Behav 115:107–114. https://doi.org/10.1016/j.anbehav.2016.03.011

Weterings MJA, Moonen S, Prins HHT, Wieren SE, Langevelde F (2018) Food quality and quantity are more important in explaining foraging of an intermediate-sized mammalian herbivore than predation risk or competition. Ecol Evol 8(16):8419–8432. https://doi.org/10.1002/ece3.4372

Weterings MJA, Ewert SP, Peereboom JN, Kuipers HJ, Kuijper DPJ, Prins HHT, Jansen PA, van Langewelde F, van Wieren SE (2019) Implications of shared predation for space use in two sympatric leporids. Ecol Evol 9(6):3457–3469. https://doi.org/10.1002/ece3.4980

Wood S (2017) Generalized additive models: an introduction with R, 2nd edn. Chapman and Hall/CRC, Boca Raton

Woodland D, Jaafar Z, Knight M (1980) The "pursuit deterrent" function of alarm signals. Am Nat 115(5):748–753. https://doi.org/10.1086/283596

Zaguri M, Kandel S, Lavie N, Hawlena D (2022) Methodological limitations and conceptual implications of nutritional estimations. Oikos. https://doi.org/10.1111/oik.08467

Zanette LY, Clinchy M, Suraci JP (2014) Diagnosing predation risk effects on demography: can measuring physiology provide the means? Oecologia 176(3):637–651. https://doi.org/10.1007/s00442-014-3057-9

Zuberbühler K, Jenny D, Bshary R (1999) The predator deterrence function of primate alarm calls. Ethology 105(6):477–490. https://doi.org/10.1046/j.1439-0310.1999.00396.x

Zuur F, Ieno N, Elphick S (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1(1):3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x