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REVIEW

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Zooming in on mechanistic predator–prey ecology: Integrating camera traps with experimental methods to reveal the drivers of ecological interactions

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Abstract

1. Camera trap technology has galvanized the study of predator–prey ecology in wild animal communities by expanding the scale and diversity of predator–prey interactions that can be analysed. While observational data from systematic camera arrays have informed inferences on the spatiotemporal outcomes of predator–prey interactions, the capacity for observational studies to identify mechanistic drivers of species interactions is limited.

2. Experimental study designs that utilize camera traps uniquely allow for testing hypothesized mechanisms that drive predator and prey behaviour, incorporating environmental realism not possible in the laboratory while benefiting from the distinct capacity of camera traps to generate large datasets from multiple species with minimal observer interference. However, such pairings of camera traps with experimental methods remain underutilized.

3. We review recent advances in the experimental application of camera traps to investigate fundamental mechanisms underlying predator–prey ecology and present a conceptual guide for designing experimental camera trap studies.

4. Only 9% of camera trap studies on predator–prey ecology in our review use experimental methods, but the application of experimental approaches is increasing. To illustrate the utility of camera trap-based experiments using a case study, we

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propose a study design that integrates observational and experimental techniques to test a perennial question in predator–prey ecology: how prey balance foraging and safety, as formalized by the risk allocation hypothesis. We discuss applications of camera trap-based experiments to evaluate the diversity of anthropogenic influences on wildlife communities globally. Finally, we review challenges to conducting experimental camera trap studies.

5. Experimental camera trap studies have already begun to play an important role in understanding the predator–prey ecology of free-living animals, and such methods will become increasingly critical to quantifying drivers of community interactions in a rapidly changing world. We recommend increased application of experimental methods in the study of predator and prey responses to humans, synanthropic and invasive species, and other anthropogenic disturbances.

1 | INTRODUCTION

The consequences of predator–prey interactions permeate multiple scales of animal ecology, from decision-making and antipredator behaviour to trophic cascades and community turnover. While experimental evaluation of predator–prey theory is common in controlled laboratory studies with simplified systems, understanding of wild vertebrate predator–prey interactions has been largely gained from observational methods, including direct observations, animal captures and remote biologging technology (Smith, Drummer, Murphy, Guernsey, & Evans, 2004; Wilmers et al., 2015). Although much has been learned from observational approaches, they are limited in their capacity to uncover mechanistic drivers of predator–prey ecological dynamics. Field experiments that incorporate the complexity of natural conditions while isolating specific cues of risk or prey availability can uniquely provide mechanistic inference on predator and prey behaviour across a range of environmental contexts (Atkins et al., 2019; Suraci et al., 2017). Yet, such experiments remain rare due to the challenges of both manipulating and measuring responses to predators and prey in free-living wildlife.

In the last two decades, technical and analytical advances in camera trap (also trail camera or remote camera) methodologies have created emerging opportunities to study predator–prey interactions. Camera traps provide a non-invasive approach for detecting and monitoring wildlife that has been made more accessible through continued improvements in camera quality and cost-efficiency, and their use in addressing fundamental ecological questions is on the rise (Burton et al., 2015; Caravaggi et al., 2017; Frey, Fisher, Burton, & Volpe, 2017). Beyond monitoring, utilization of camera traps for observational research in predator–prey ecology has exploded in recent years (Figure 1), largely due to advances in statistical techniques, such as occupancy modelling and spatial capture–recapture analysis (Augustine

et al., 2018; Chandler & Royle, 2013; MacKenzie et al., 2017; Royle, Chandler, Sun, & Fuller, 2013; Sollmann et al., 2013).

Camera traps also have an unparalleled potential as an experimental tool to explore the causes and consequences of predator–prey interactions in complex and/or modified landscapes. Camera trap technology enables the integration of behavioural and spatio-temporal data to experimentally test predator–prey theory in field settings with complete predator and prey assemblages. Many of the features of camera traps that have spurred their rapid uptake in predator–prey ecology, including the capacity to collect large amounts of behavioural data from multiple species without an observer present, are also ideal for use in an experimental context. However, despite an exponential increase in the use of camera traps in wildlife research, integration with experimental methods remains relatively rare. Here, we review recent advances in the application of camera traps to observational and experimental research in predator–prey ecology and discuss new frontiers of experimental applications of camera traps, including opportunities to apply these methods in understanding and mitigating the effects of global change on wildlife. We illustrate the utility of integrating camera traps with experimental methods through a case study in which we propose an integrated study design to test the risk allocation hypothesis, a cornerstone of modern predator–prey theory.

2 | OBSERVATIONAL APPLICATIONS OF CAMERA TRAPS TO PREDATOR–PREY ECOLOGY: CONTRIBUTIONS AND SHORTCOMINGS

A systematic review of the literature (October 1994–December 2019; see Appendix S1 for details) revealed that, of 331 studies
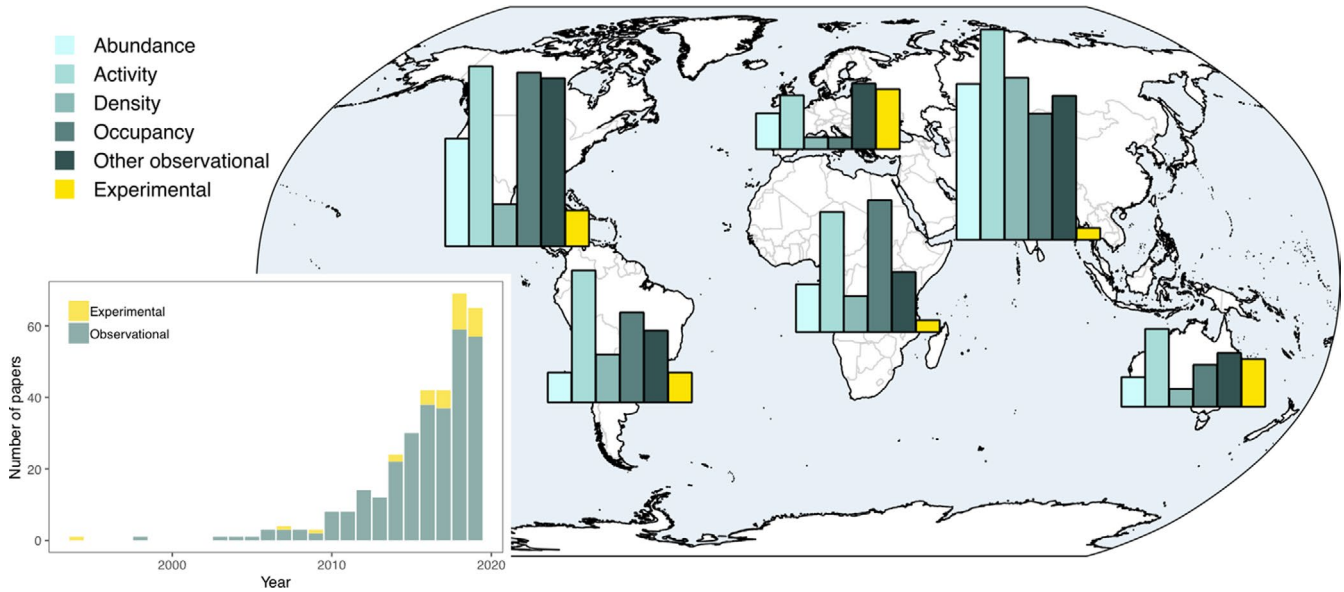
FIGURE 1 Distribution and number of experimental and observational camera trap (CT) studies on predators and/or prey by continent. Observational studies included in the inset figure include all predator–prey camera trap papers mentioning either *abundance*, *activity*, *density* or *occupancy*. Methods for literature search in Appendix S1. Bar height represents the number of studies (totals: Africa [45], Asia [80], Europe [34], North America [88], Oceania [39], South America [46]). Studies that measure more than one of the five examined keywords may contribute to multiple bars. Data include studies published through December 2019

using camera trap methods to investigate predator–prey interactions, 91% used solely observational approaches (Figure 1). Such observational approaches have indeed revolutionized predator–prey ecology, using innovative statistical techniques and large-scale camera trap datasets to reveal how predator and prey populations dynamically use space and time relative to one another, and providing insight into the nature and persistence of community assemblages (e.g. Astete et al., 2016; Rich et al., 2017; Rota et al., 2016). Spatial interactions between predator and prey have been examined using stratified random or systematic deployment of multiple cameras, which allows for detailed analyses of patterns of avoidance, association, co-occurrence and fine-scale space use (Rota et al., 2016; Weterings et al., 2019). Camera traps have also been implemented to examine how predators and prey partition time (Frey et al., 2017) and to quantify the degree of temporal overlap between two species (Ridout & Linkie, 2009) over daily (Monterroso, Alves, & Ferreras, 2013), monthly (e.g. lunar cycle; Pratas-Santiago, Gonçalves, da Maia Soares, & Spironello, 2016) or seasonal (Gelin et al., 2017) scales. Recent evidence from such studies suggests that prey responses to spatially distributed predation risk across a landscape vary with fluctuating temporal risk, that is, prey use riskier areas during safer times of the day (Bischof, Ali, Kabir, Habeed, & Nawaz, 2014) or the lunar cycle (Palmer, Fieberg, Swanson, Kosmala, & Packer, 2017). Camera trap surveys have also examined the influence of prey availability on predator spatiotemporal patterns by documenting variation in predator density or activity in response to seasonal prey migrations (Gelin et al., 2017) and prey activity patterns (Martín-Díaz et al., 2018). These observational camera trap studies have provided ecological information on cryptic species (Caravaggi

et al., 2017; Steinmetz et al., 2013), allowed for analysis of multiple interactions in complete predator and prey species assemblages (Palmer et al., 2017; Rich et al., 2017) and have been applied to understand global conservation challenges (Gaynor, Hojnowski, Carter, & Brashares, 2018).

A comprehensive analysis of the dynamics of predator–prey interactions requires mechanistic investigation of how prey perceive and respond to different risk cues, how predators detect and select for prey, and the state dependance and environmental dependence of decisions made by both players (Gaynor, Brown, Middleton, Power, & Brashares, 2019). Yet, it is challenging to identify the behavioural or environmental mechanisms that drive predator–prey interactions through observational camera trap studies alone. Additionally, full evaluations of predator–prey games, in which both predator and prey are dynamically responding to the behaviour of the other player (Lima, 2002), are often difficult to achieve with observational camera trap surveys. Such surveys typically focus on whether the distribution or activity of one player is predicted by the other, thus overlooking the two-way nature of predator–prey interactions. Rarely are attempts made to identify which player's response dominates, or furthermore, how predator and prey behaviour respond to one another (despite a long-acknowledged appreciation for these dynamics, e.g. Lima, 2002; Sih, 1984). There is a growing need for mechanistic studies that identify the behavioural drivers of predator–prey interactions for effective conservation and management of biological communities, particularly as global change alters predator and prey community assemblages, redesigns the playing field for predator–prey games through habitat modification and introduces novel sources of risk and reward.

3 | EXPERIMENTAL APPLICATIONS OF CAMERA TRAPS TO PREDATOR–PREY ECOLOGY: ONGOING DEVELOPMENTS AND NEW OPPORTUNITIES

Experimental studies using camera traps on free-ranging animal populations remain rare, comprising only 9% of studies in our systematic review on predator–prey interactions (Figure 1). However, current advancements in experimental methodologies and study designs offer novel approaches for investigating the fundamental mechanisms underlying predator–prey ecology in the field. Below, we describe current uses of camera traps in experimental research on predator–prey interactions and propose further development and application of new approaches (Table 1).

3.1 | Prey-focused experiments: Risk assessment and antipredator behaviour

Understanding how prey perceive and respond to predation risk has long been a major focus in ecology (Lima & Dill, 1990; McNamara & Houston, 1992), though isolating the salient sensory cues and cost–benefit trade-offs associated with the antipredator responses of wild prey remains a challenge. The relatively recent incorporation

TABLE 1 A conceptual guide for designing camera trap studies to address themes in predator–prey ecological research, with examples of specific experimental study designs and focal species

Treatment type	Research focus	Focal player	Experimental treatment	Cue	Example papers
Simulated risk cue	Predator detection Predator recognition Risk perception	Prey	Predator model	Visual	*,†Breviglieri and Romero (2016) (prey: frugivorous birds)
			Predator playback	Auditory	*Clinchy et al. (2016) (prey: European badger) *Smith et al. (2017) (prey: puma) *Suraci, Clinchy, Dill, Roberts, and Zanette (2016) (prey: raccoon)
			Predator scent	Olfactory	Carthey and Banks (2018) (prey: black rat) Kuijper et al. (2014) (prey: red deer) Sahlén et al. (2016) (prey: European ungulates)
			Habitat riskiness	Any	Farnworth, Innes, Kelly, Littler, and Waas (2018) (prey: weta spp.) Fležar et al. (2019) (prey: African ungulates)
Simulated prey cue	Attack rates Prey detection Prey recognition Prey selection	Predator	Prey model	Visual	*Hunter (2009) (predator: mammalian carnivores) Lawson et al. (2019) (predator: coyote)
			Prey playback	Auditory	No examples found
			Prey scent	Olfactory	Lawson et al. (2019) (predator: coyote)
	Predator diversity Survival	Prey	Prey model	Visual	Akcali et al. (2019) (prey: coral snake)
			Prey playback	Auditory	Natusch et al. (2017) (prey: metallic starling)
			Prey scent	Olfactory	Buzuleciu et al. (2016) (prey: diamond-backed terrapin) Natusch et al. (2017) (prey: metallic starling)
Prey subsidy/ addition	Attack rates Hunting behaviour Prey selection State-dependent predation	Predator	Bait, food supplements or prey proxy (e.g. artificial nests)	Presence	Dahl and Åhlén (2019) (predator: raccoon dog) Grüebler et al. (2018) (predator: little owl) Samplonius et al. (2016) (predator: pied flycatcher)
	Predator diversity Survival	Prey	Prey stocking Prey proxy (e.g. artificial nests)	Presence	Buehler, Bosco, Arlettaz, and Jacot (2017) (prey: woodlark) Luna et al. (2018) (prey: red-tailed tropicbird) Miyamoto, Squires, and Araki (2018) (prey: Masu salmon)
Risk elimination	Attack rates Risk perception Survival	Prey	Predator removal or exclosures	Presence	Hirsch et al. (2014) (prey: *Azteca* ant) van Veen and Wilson (2017) (prey: Jamaican rock iguana)
Prey food subsidy	Encounter risk Risk perception	Prey	Baiting Giving-up densities	Presence	Esparza-Carlos, Íñiguez-Dávalos, and Laundré (2018) (prey: collared peccary)

*Not identified by systematic review.

†Authors used remote video cameras rather than motion-sensor camera trapsby.

FIGURE 2 Examples of measurements used to quantify predator–prey interactions in experimental camera trap studies. (a) Taxidermied animal mounts dyed to determine the effect of aposematic coloration and body shape on mammalian predator recognition of and response to potential prey (treatment type: simulated prey cue). (b) Motion-sensor playback experiments used to test puma fear of humans and synanthropic species, for example, domestic dogs (treatment type: simulated risk cue). Speaker and camera trap pictured. (c) Giving-up density (GUD) experiments used to measure red fox food-safety trade-offs in response to predator scent (treatment type: simulated risk cue). (d) Salmon stocked in artificial pools to measure size-specific predation rates (treatment type: prey subsidy/addition). Figures adapted from (a) Hunter (2009); (b) Suraci, Smith, et al. (2019); (c) Haswell, Jones, Kusak, and Hayward (2018) and (d) Miyamoto et al. (2018; photo reproduced from Miyamoto et al., 2018 with permission from CSIRO Publishing)
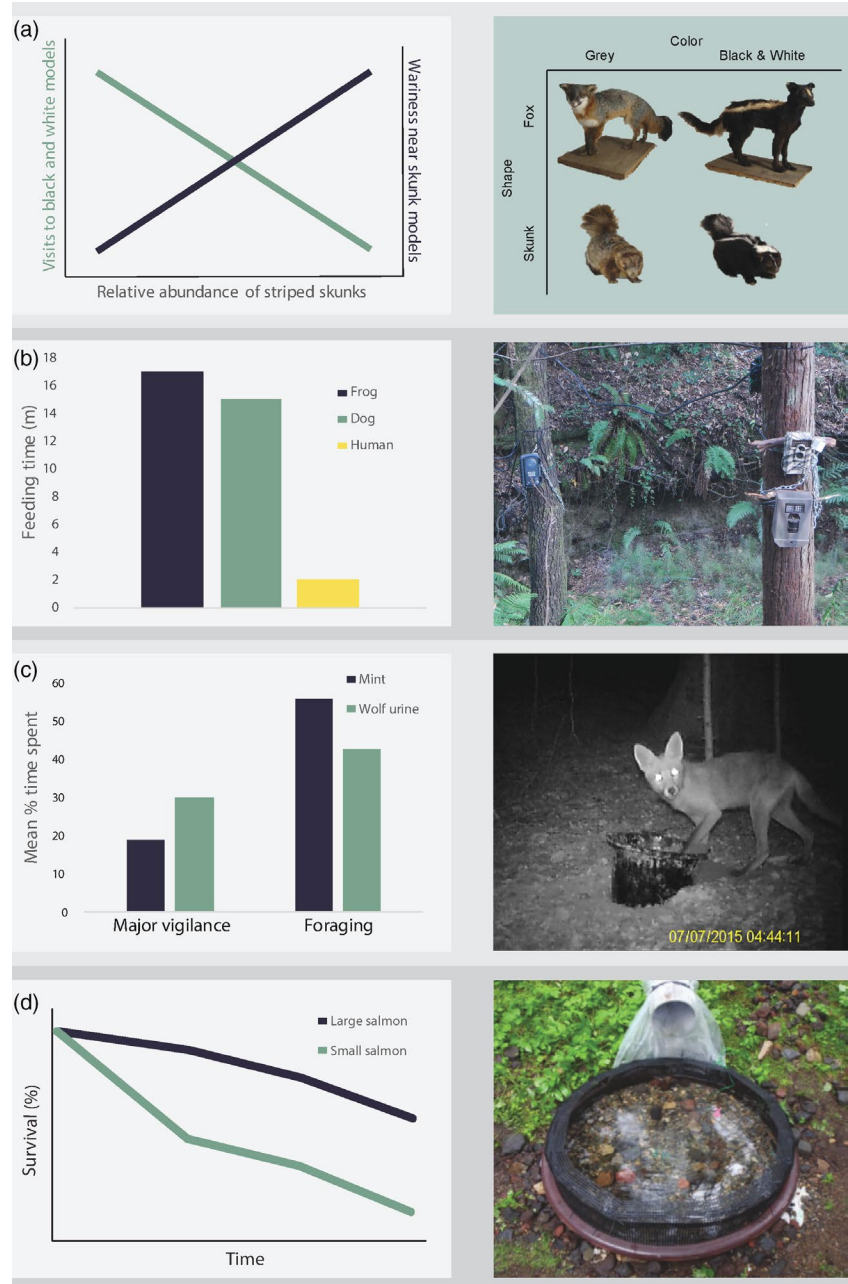
of camera traps into prey response studies, as detailed below, has allowed for increased investigation of antipredator behaviour in natural settings and with a wider range of prey, including cryptic species (Table 1; Figure 2). Through experimental study designs that simulate or eliminate risk, or subsidize predators or prey, camera traps can provide novel insight into how prey detect and respond to predators.

3.1.1 | Simulated risk cues

Spatial and temporal variation in risk is a fundamental determinant of behaviour and space use for many prey species (Brown, Laundré, & Gurung, 1999; Lima & Dill, 1990), and camera traps are an effective method for exploring prey spatiotemporal activity in response to predation risk. In observational studies, activity and detection rates of predators assessed from camera traps have been used as predictors of prey space use (Dorresteijn et al., 2015) and activity (Tambling et al., 2015). Camera traps have also been used to assess how prey distinguish between risky and safe habitat, for instance, by placing cameras across gradients of habitat cover (Abu Baker & Brown, 2014) or in areas with and without potentially dangerous habitat features (e.g. logs that impair escape; Kuijper, Bubnicki, Churski, Mols, & van Hooft, 2015) and quantifying variation in detection rates (i.e. the number of independent prey occurrences on camera) and vigilance behaviour (i.e. the proportion of prey detections in which the head was up and scanning; see Table 2). While these observational techniques are effective for examining risk avoidance behaviours associated with observable predator space

TABLE 2 A guide for identifying and measuring response variables in experimental camera trap studies of predator–prey ecology

Response category	Research focus	Camera-based response variable	Selected examples
Activity level; Attraction/ avoidance	Encounter risk Risk perception Predator detection Prey recognition Prey detection	Number of independent detections (of prey or predator species) on camera per unit time	Lawson et al. (2019) (predator: coyote) Sahlén et al. (2016) (prey: European ungulates)
		Total time (# photos, duration in video) spent at a camera site	Fležar et al. (2019) (prey: African ungulates) Garvey et al. (2017) (prey: small mammalian predators)
Feeding behaviour	Risk perception Predator detection	Visitation to or time spent at feeding stations (including GUDS)	Carthey and Banks (2018) (prey: black rat) *Suraci, Clinchy, et al. (2019) (prey: rodents)
		Time (# photos, duration in video) spent feeding on bait or natural prey.	*Cherry et al. (2015) (prey: white-tailed deer) *Smith et al. (2017) (prey: puma)
		Latency to discover provisioned food items/baits (duration of time between deployment and discovery)	*Suraci, Clinchy, et al. (2019) (prey: opossum)
Fleeing	Risk perception Predator recognition Predator detection	Binary response: whether or not prey immediately leaves the camera's field of view following predator (cue) exposure	*Smith et al. (2017) (prey: puma) *Suraci, Smith, et al. (2019) (prey: puma)
Investigation	Predator recognition	Time (# photos, duration in video) spent approaching and/or sniffing a predator odour cue	*Bytheway et al. (2013) (prey: black rats) Garvey et al. (2017) (prey: small mammalian predators)
Predator detection and attack rates	Prey recognition Prey selection Predator diversity Prey survival	Predator-specific investigation of and attacks on artificial prey, artificial nests or taxidermied mounts	Akcali et al. (2019) (predator: multiple snake predators) Buzuleciu et al. (2016) (predator: raccoon)
		Predator-specific visitation to areas of stocked prey	Miyamoto et al. (2018) (predator: multiple salmon predators)
Prey selection and consumption rate	Prey recognition Prey selection	Visual identification of food items brought to feeding locations	Grüebler et al. (2018) (predator: little owl) Samplonius et al. (2016) (predator: pied flycatcher)
Vigilance behaviour	Risk perception Predator recognition Predator detection	Time (# photos, duration in video) in which prey's head was up (above body midline), indicating attentiveness	Kuijper et al. (2014) (prey: red deer, boar) *Suraci et al. (2016) (prey: raccoon)
		Number of times a prey animal lifted its head in a photo sequence	Andersen et al. (2016) (prey: spotted-tailed quoll)

*Not identified by systematic review.

use and habitat characteristics, quantifying the relative importance of different indicators of risk on prey behaviour often requires experimental manipulations, given the many confounding factors such as environmental variation and food-safety trade-offs.

Little is known about which predator cues are most salient in driving antipredator behaviours, including altered habitat use and social behaviour and the trade-off between foraging and vigilance. To address this knowledge gap, experimental manipulation of visual, olfactory and/or auditory predator cues have recently been paired with camera traps to determine how the characteristics of these cues (e.g. age of scent cues, Bytheway, Carthey, & Banks, 2013; or predator identity, Carthey & Banks, 2018) affect prey behaviour. Olfactory predator cues are the most commonly utilized in camera trap studies (Smith et al., 2020), often by deploying predator scat or urine at camera traps to assess vigilance behaviour and space use (Andersen, Johnson, & Jones, 2016; Carthey & Banks, 2018; Kuijper et al., 2014; Sahlén

et al., 2016). Olfactory cues may indicate to prey that a predator uses the area but is not necessarily present and, as such, have been associated with a range of prey responses, from attraction (i.e. increased time spent at a camera trap site; Garvey et al., 2017) to avoidance (decreased time on camera; Fležar et al., 2019). In contrast, predator playbacks (auditory cues) are increasingly being combined with camera traps to simulate immediate risk of a present predator (Mugerwa, Preez, Tallents, Loveridge, & Macdonald, 2017; Smith et al., 2017; Suraci et al., 2016; Suraci, Clinchy, Zanette, & Wilmers, 2019; Suraci, Smith, Clinchy, Zanette, & Wilmers, 2019). Novel combinations of risk cues that execute a full factorial study design may be particularly effective at measuring species-specific perceptions of risk (e.g. pairing habitat manipulation with olfactory cues; Fležar et al., 2019), examining shifts in sentinel behaviour (e.g. comparing olfactory and visual predator cues; Zöttl, Lienert, Clutton-Brock, Millesi, & Manser, 2013) or testing the influence of group size on food-safety trade-offs

(e.g. pairing giving-up density [GUD] measures with olfactory cues; Carthey & Banks, 2015).

Predation risk can have important non-consumptive effects on prey populations and lower trophic levels, as mediated by costly behavioural responses, but it is often difficult to isolate these effects from those of actual consumption by predators in free-ranging populations. Camera trap experiments with simulated risk cues, which manipulate just the fear of predators and thus isolate these behavioural costs, have demonstrated that perceived risk from predators can cause prey to forego foraging (Clinchy et al., 2016; Smith et al., 2017) and avoid otherwise valuable habitat (Fležar et al., 2019; Sahlén et al., 2016). Beyond measuring immediate antipredator responses to risk, simulated risk cues can be used to quantify such costs of antipredator behaviour. Predator playbacks paired with camera traps have been used to document fear-induced trophic cascades by quantifying changes in species behaviour (e.g. detection rates, diel activity patterns and use of baited foraging stations; see Table 2) across trophic levels (Suraci et al., 2016; Suraci, Clinchy, et al., 2019) and camera traps paired with GUDs and scent cues have been used to estimate the potential for group foraging to mitigate such individual-level feeding costs through dilution or group vigilance (Carthey & Banks, 2015).

3.1.2 | Simulated prey cues and prey additions

Understanding predator impacts on prey demography and the relative importance of consumptive versus non-consumptive predator effects requires quantifying how frequently prey are subject to predator attacks and how likely they are to survive. Yet, opportunistic observations of predator attacks are relatively rare in natural settings and may not represent the full suite of predators from which a prey species experiences risk. Simulated prey cues or baiting with prey or prey proxies have therefore been used to estimate attack and survival rates of prey in diverse environmental contexts. Studies that pair simulated prey cues with camera traps can improve the quality and quantity of information on a prey species' predator diversity, predator-specific attack rates and how different prey cue types attract predators. A study using video camera traps to monitor model prey (coral snakes; *Micrurus* spp.) revealed the taxonomic composition of the snake predators and discrepancies between detection and attack rates (Akcali et al., 2019). To examine predator-specific attraction to prey auditory and olfactory cues, Natusch, Lyons, and Shine (2017) simulated metallic starling *Aplonis metallica* vocalizations and scent at camera trap stations, demonstrating that starling predators were primarily attracted to scent cues. Predator diversity and consequences of predation on prey demography can also be assessed by stocking and monitoring a population of focal prey; camera traps deployed on outdoor fish tanks and semi-natural streams identified the primary predator of Masu salmon, the influence of habitat and time of day on attack rates, the role of prey density on predator visitation, and the demographic class most impacted by predation (Miyamoto et al., 2018; Figure 2).

One of the most common experimental designs to study attack and survival rates of avian and reptilian prey involves artificial nests populated with quail, chicken or model eggs. Artificial nest studies comprised 29% of all experimental camera trap studies on predator–prey ecology in our literature search (Smith et al., 2020). The simplest design is to pair nests containing experimental eggs with a camera trap to monitor predator visitation and attack rates (Kämmerle, Niekrenz, & Storch, 2019; Luna, Varela, Brokordt, & Luna-Jorquera, 2018; Patterson, Kalle, & Downs, 2016; Ponce, Salgado, Bravo, Gutiérrez, & Alonso, 2018). Additional prey cues can also supplement traditional artificial nest experiments to identify predator attractants; a study on artificial terrapin nests found that the scent of disinterred soil was a stronger attractant for predators than terrapin scent or visual cues (Buzuleciu, Crane, & Parker, 2016).

3.1.3 | Risk elimination

As an alternative to simulating risk through the introduction of cues, another approach to quantifying the magnitude of risk effects on prey is to experimentally remove predators or install exclosures, thus eliminating risk. Experimental risk elimination allows for the study of prey behaviour and survival in the absence of the density- and trait-mediated effects of predation. In a long-term predator exclosure experiment, camera traps revealed that browsing herbivores increase feeding rates when risk was removed (as estimated from the number of photos in which herbivores were detected actively consuming provisioned baits), with cascading effects on oak (*Quercus* spp.) recruitment and understorey species composition (Cherry, Conner, & Warren, 2015; Cherry, Warren, & Conner, 2016). Removal or exclusion of predators has also been paired with camera traps to measure predation effects on nest size of colonial insects (Hirsch, Martinez, Kurten, Brown, & Carson, 2014) and nest survival of ground-nesting birds (Oppel et al., 2014) and reptiles (van Veen & Wilson, 2017).

3.2 | Predator-focused experiments: Predation patterns and hunting behaviour

Observations of predation in the wild are typically rare due to the spatiotemporal unpredictability of predation events and the influence of human observers on predator and prey behaviour. Prior to the development of camera trap technology, observations of hunting events in the field were largely limited to sightings of conspicuous diurnal predators in open habitats (e.g. Mills, Broomhall, & du Toit, 2004; Smith et al., 2004). A dearth of observations of predator behaviour has limited our understanding of the dynamics of predator–prey interactions, particularly predation itself (Lima, 2002). Although prey utilization can be determined through a number of methodologies (e.g. dietary scat analysis, stable isotope analysis or field tracking), predator hunting behaviour and selection of prey individuals based on their behaviour is much more challenging to observe through non-camera trap approaches. Camera traps provide

an opportunity to study lesser-known aspects of predator hunting behaviour, including prey detection, recognition and selection, as detailed below (see also Table 1).

3.2.1 | Simulated prey cues

Decisions made by predators about when, how and what to hunt can influence predator survival, fitness and competition dynamics. Camera traps are an innovative tool for experimentally studying the proximate cues (e.g. visual, auditory and olfactory) that predators use to detect their prey. Dying animal calls, feathers and chemical signals are regularly used as predator lures at camera trap stations with the purpose of refining delivery systems for predator control (Read, Bengsen, Meek, & Moseby, 2015), but these methods have yet to be broadly applied to studies of predator detection, recognition and preference for prey. Visual cues in the form of prey models are currently the most widely applied prey cue treatment in camera trap studies of predator behaviour. Realistic prey models and taxidermied animal mounts have been employed to examine attack rates on prey models in vigilant and non-vigilant postures (Cresswell, Lind, Kaby, Quinn, & Jakobsson, 2003), prey detection (Lawson, Fogarty, & Loss, 2019), the influence of camouflage on attack rates (Atmeh, Andruszkiewicz, & Zub, 2018) and the role of aposematic coloration in prey selection and hunting behaviour (Hunter, 2009).

Few studies have addressed the responses of predators to prey chemical (but see: Schiefelbein, 2016), auditory or scent cues (but see: Lawson et al., 2019), though pairing such cues with camera traps provides a straightforward means of testing how predators detect and locate their prey. Additionally, presentations of wild prey to a captive predator (Janson, Monzón, & Baldovino, 2014) or captive prey to wild predators (Garrote et al., 2012) could be paired with small arrays of camera traps to evaluate detection distance and post-detection behaviour. Extension of these camera trap techniques is easily applicable to other studies of prey recognition and discrimination, and could provide investigators with additional information about prey partitioning in multi-predator systems or native prey recognition by invasive predators.

3.2.2 | Prey or proxy subsidies and baits

Experimental prey subsidies, while rarely used in predator-focused studies, can be used to quantify detection and utilization of prey, state-dependent hunting behaviours and the impact of prey availability on predator fitness. As in prey-focused studies, artificial nests that are baited with real eggs can be employed as a tool in predator-focused research to observe hunting behaviour by a focal predator species (Dahl & Åhlén, 2019). By altering the internal condition of individual predators, supplemental feeding treatments paired with camera traps at predator nests have been used

to test the relationship between food availability and diet, parental care strategies and nestling survival in avian predators (Grüebler et al., 2018). Prey subsidies that alter the timing of food availability have revealed how phenological mismatch between predator and prey can cause a diet shift in insectivorous birds (Samplonius, Kappers, Brands, & Both, 2016). Because foraging decisions are often state-dependent and internal state is often challenging to assess in the field, experiments that alter food availability to predators provide important nuance to understandings of predator diet preferences and prey utilization.

4 | CASE STUDY: INTEGRATING CAMERA TRAPS AND EXPERIMENTAL METHODS TO TEST THE RISK ALLOCATION HYPOTHESIS

Many of the advances in camera trap-based experiments described above focus on the immediate response of a single predator or prey individual to a cue or subsidy. However, integration of such targeted experiments with larger-scale manipulations could be used to address questions concerning the context dependency of animal responses to predators or prey across scales. To illustrate this approach, and to concretize the value of integrating camera traps with experimental methods more generally, we propose a multi-scale experimental design to test a cornerstone of predator–prey theory, the Risk Allocation Hypothesis.

For most prey animals, basic activities such as foraging are thought to increase the risk of predation, setting up a fundamental trade-off between time devoted to minimizing risk and time devoted to foraging or other crucial behaviours (Lima & Dill, 1990; Sih, 1980). The behavioural adjustments that prey make to balance safety and foraging are also a primary mechanism by which the non-consumptive effects of predators can cascade across food webs, as predator-induced suppression of foraging may, in turn, affect the prey's impact on its resource (Schmitz, Krivan, & Ovadia, 2004; Suraci et al., 2016). Understanding the implications of this 'food-safety trade-off' for prey populations remains a major area of research interest in ecology and a fertile area for experimental investigations of predator–prey dynamics in natural systems.

This trade-off was formalized by Lima and Bednekoff's (1999) highly influential Risk Allocation Hypothesis (RAH), which recognized that the time prey devote to vigilance versus foraging is not just a function of the immediate presence or absence of predators, but is affected by the long-term temporal pattern of exposure to predation risk. Therefore, prey should forage most intensely during brief pulses of safety in an otherwise risky environment and be most vigilant during brief pulses of risk in an otherwise safe environment (Lima & Bednekoff, 1999). Experimental tests in laboratory settings have generally supported the predictions of the RAH (reviewed in Ferrari, Sih, & Chivers, 2009), as have observational studies on large mammal predators and prey (Costelloe & Rubenstein, 2018; Creel, Winnie, Christianson, & Liley, 2008; Gude, Garrott, Borkowski, &
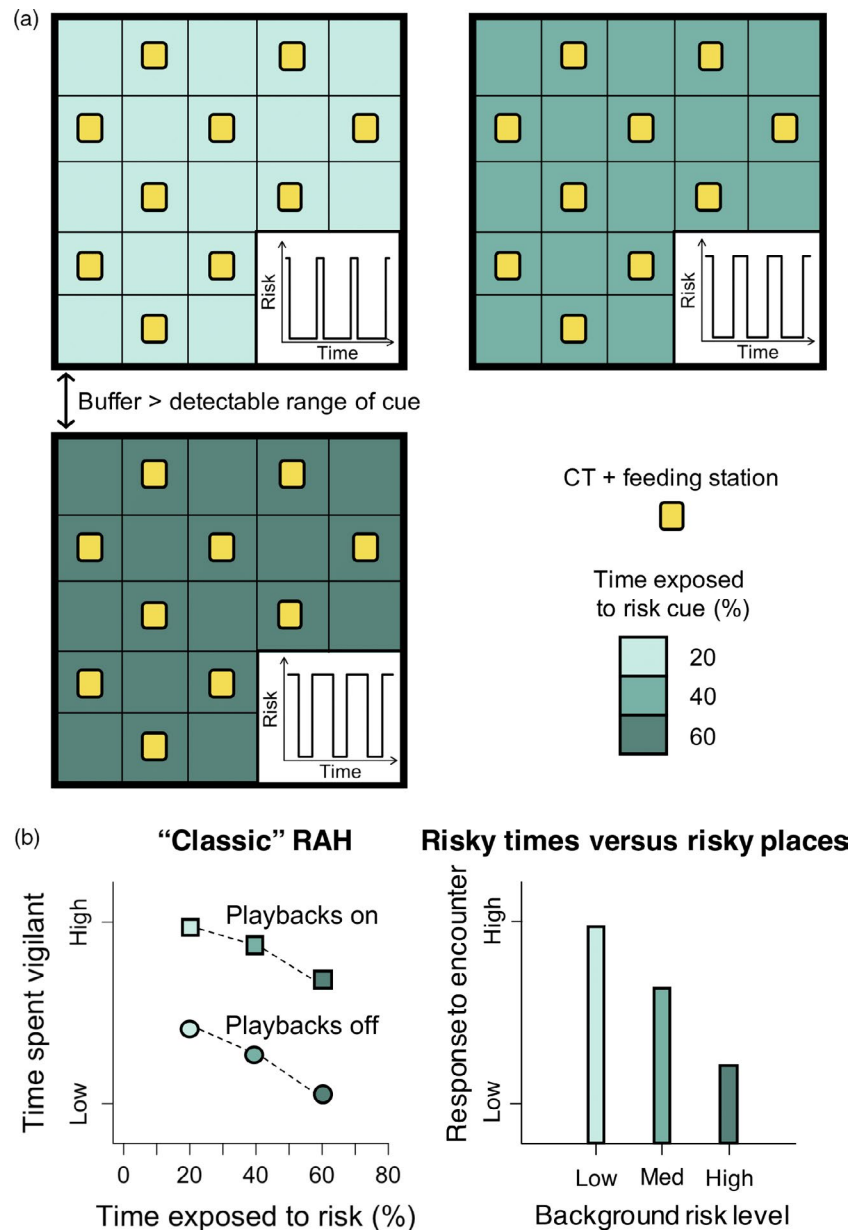
FIGURE 3 Illustration of the proposed study design for integrating camera traps (CT) and experimental methods to test the Risk Allocation Hypothesis (RAH). The RAH addresses a perennial question in predator–prey ecology, that is, how prey balance foraging and safety to optimize antipredator behaviour. (a) Spatial layout of the proposed experiment. Each experimental replicate consists of three grids of playback speakers broadcasting predator vocalizations at varying intensity (here 20%, 40% and 60% of the time). Camera traps and GUDs or feeding stations (yellow boxes) are deployed systematically across each grid to monitor prey vigilance/foraging. The inset in each grid illustrates the set schedule of predator cue presentation, allowing prey to predict risky versus safe periods (playbacks on = high risk, playbacks off = low risk; Ferrari et al., 2009). Under the 'classic' formulation of the RAH (based on proportion of time a prey animal spends at risk), prey foraging intensity is measured during both risky and safe periods at each level of overall predation risk. The same design can be used to test the risky times versus risky places hypothesis (see text for details) by deploying motion-sensitive playback systems (Suraci et al., 2017) at camera traps/feeding stations to simulate immediate predator encounters (risky times) against varying background levels of risk (risky places). (b) Expected results of both the 'classic' RAH formulation (left panel, adapted from Lima & Bednekoff, 1999) and the risky times versus risky places formulation (right panel). In the left panel, average time spent vigilant is compared both between risky (playbacks on) and safe (playbacks off) periods and across overall risk levels. In the right panel, responsiveness to an immediate predator encounter is compared between background levels of predation risk

King, 2006). Experimental tests of the RAH with free-living wildlife remain rare, however, leaving open important questions regarding the role of temporal variability of risk in shaping prey responses and potential cascading effects.

As previously noted by Moll et al. (2017), testing the RAH in natural systems may be achieved through the integration of camera traps with the experimental presentation of predator cues (e.g. scent and/or vocalization playbacks). We envisage a study design

(Figure 3a) based on the proportion of time that a prey animal spends in relatively risky versus safe situations, as described in Lima and Bednekoff's (1999) original model. In this design, replicate experimental plots matched for baseline levels of predator activity are exposed to predator cues (e.g. via grids of playback speakers; Suraci, Clinchy, et al., 2019; Suraci, Smith, et al., 2019) on a regular schedule such that prey animals have the opportunity to learn the temporal sequence of risky and safe periods (Ferrari et al., 2009). Camera traps are deployed across the experimental plots and paired with GUDs or feeding stations, allowing researchers to monitor foraging/vigilance during both risky and safe periods. The proportion of time at risk is varied between plots, for example, by presenting playbacks 20%, 40% and 60% of the time. The RAH predicts that vigilance will be lowest (and foraging most intense) during safe periods (when playbacks are off) in the high-risk treatment, and that vigilance will be highest during risky periods (playbacks on) in the low-risk treatment (Figure 3b, left panel). The RAH also makes the somewhat counterintuitive prediction that vigilance during risky periods will be lower in the high-risk than in low-risk treatment because of an animal's requirement to meet energetic demands through some minimum amount of time spent foraging.

The RAH has been adapted to compare the relative effects of 'risky times' (i.e. immediate encounters with a predator) and 'risky places' (i.e. spatial locations of high background predation risk) on prey antipredator behaviour (Creel et al., 2008; Gude et al., 2006). Such a comparison could be readily incorporated into the above study design using motion-sensitive playback systems (Suraci et al., 2017) deployed at camera trap-monitored GUD or feeding stations to simulate an immediate predator encounter against different background levels of predator activity, the latter simulated by varying cue presentation intensity as illustrated in Figure 3a. Under this formulation, the RAH predicts that prey will be more responsive to a predator encounter (e.g. exhibit a greater increase in vigilance) where background levels of risk (e.g. predator cue intensity) are lower (Figure 3b, right panel). It is important to note that, as with all cue-based experiments, the potential for prey to habituate to predator cues is a critical consideration for the proposed RAH study design. Researchers considering this or similar designs will need to ensure that prey are no more likely to habituate to cues in the high-risk than in the low-risk treatments. We consider the issue of habituation in detail below (see 'Challenges to implementing experimental camera trap research' section) and offer some considerations for mitigating its effects.

5 | PREDATOR–PREY INTERACTIONS IN A CHANGING WORLD

Ecological communities globally are in flux as invasive species, land use change and human activity permeate even the most remote landscapes. Understanding predator–prey interactions can inform conservation initiatives, such as efforts to mitigate detrimental impacts of invasive species, promote restoration of

extirpated species and manage outcomes of changing community composition (Ritchie et al., 2012). Observational applications of camera trap technology have been instrumental in documenting anthropogenic effects on predator–prey interactions through anthropogenic disturbance (Kays et al., 2017) or habitat modification (Muhly, Semeniuk, Massolo, Hickman, & Musiani, 2011), facilitating global studies describing the impacts of humans on wildlife (Gaynor et al., 2018). Experimental approaches that address human impacts on predator–prey interactions remain rare, but may prove critical to management decisions in the near future. Given the myriad forms that human 'disturbance' can take, the capacity for camera trap-based experiments to provide a mechanistic understanding of the most important drivers of anthropogenic impacts on wildlife interactions may help refine conservation strategies.

Several studies have combined camera traps with experimental or quasi-experimental designs to provide valuable insights into how human activity affects predators and prey. The anthropogenic addition (e.g. introduction, restoration) or removal (e.g. extirpation) of predators to or from a community can have major effects on prey behaviour and population dynamics. Experimental work pairing camera traps with predator cues has allowed researchers to quantify the time required for prey to develop appropriate antipredator responses to invasive predators (Carthey & Banks, 2016; Steindler, Blumstein, West, Moseby, & Letnic, 2018), or to lose costly responses to extirpated predators (Le Saout et al., 2015). In addition to directly altering the predator–prey community, anthropogenic activity can impact predator–prey interactions by altering the landscape within which they occur. For instance, Sahlén et al. (2016) paired camera traps with predator scent to show that land clearing by humans (e.g. for agriculture) mediates perceived predation risk in several European ungulate species, with ungulates increasing use of open areas in the presence of predator cues.

Camera trap-based experiments have played a major role in an emerging field of research examining how the fear of humans as predators affects wildlife. This work is based on the premise that, because humans are a primary source of mortality for many wildlife species (Darimont, Fox, Bryan, & Reimchen, 2015), these species may respond to humans as any prey responds to its predators (i.e. with avoidance and/or reductions in foraging behaviour). Indeed, these novel experiments have demonstrated that both large carnivores and mesocarnivores respond fearfully to perceived human presence, resulting in reduced feeding time at baits or kill sites (Clinchy et al., 2016; Smith et al., 2017; Suraci, Smith, et al., 2019), and that these responses can scale up to affect wildlife behaviour and predator–prey interactions at the landscape level (Suraci, Clinchy, et al., 2019). The role of humans as sources of perceived risk for wildlife has important conservation implications given the steady expansion of human presence into wildlife habitat (Venter et al., 2016), and is thus likely to remain a key focus of camera trap experiments.

The ability of camera trap-based experiments to isolate specific disturbance types in their impacts on free-living predators and prey lends itself to several important future directions in understanding

the effects of global change on wildlife behaviour. For instance, recent evidence suggests that noise pollution (e.g. from vehicle traffic or industrial activity) can interfere with the hunting abilities of auditory predators such as bats and owls (Senzaki, Yamaura, Francis, & Nakamura, 2016; Siemers & Schaub, 2011). Current studies that control the intensity (amplitude, duration) of noise pollution in an experimental or quasi-experimental context (Kleist, Guralnick, Cruz, Lowry, & Francis, 2018; Mulholland et al., 2018) could be expanded to identify mechanisms for observed physiological and demographic responses to noise by deploying camera traps to quantify the severity of noise-induced foraging reductions in free-living predators. Similarly, artificial light at night may substantially alter the behaviour of visual predators or crypsis-dependent prey (Longcore & Rich, 2004), and could readily be manipulated in the presence of camera traps to quantify effects on, for example, prey foraging behaviour or predator hunting success. Data from observational camera trap studies have demonstrated that anthropogenic disturbance affects the diel activity patterns of wildlife on a global scale (Gaynor et al., 2018), including in response to reintroduced (Tambling et al., 2015) or invasive predators (Bogdan, Jůnek, & Vymyslická, 2016). Experimentally pairing camera traps with specific disturbance types (e.g. light, noise pollution, human or other predator cues) may help identify and mitigate the primary drivers of such impacts on wildlife activity.

Human-induced changes in animal behaviour and interactions are a global phenomenon, and global camera trap datasets are currently leading to new insights about biodiversity loss and conservation (Beaudrot et al., 2016). Calls for the standardization of camera trap protocols and data sharing have been made to increase opportunities for understanding anthropogenic influences on key predator–prey interactions (Steenweg et al., 2017). We support similar standardization of data collected from camera trap experiments around the world. For example, playback experiments that use the same decibel range, collect standard measures of fleeing and vigilance behaviour, and maintain a similar distance between speaker and focal animal could be compiled to compare the effects of different kinds of anthropogenic disturbances across a species' range or to assess differential responses by various taxa to anthropogenic sound cues. Here, at the leading edge of experimental camera trap studies, standardization of protocols will promote longitudinal, comparative studies that capture the diversity of anthropogenic environmental changes impacting wildlife populations.

6 | CHALLENGES TO IMPLEMENTING EXPERIMENTAL CAMERA TRAP RESEARCH

While the integration of camera traps with experimental methods can help to overcome key issues associated with observational studies (e.g. by providing a mechanistic understanding of predator or prey responses), there are nonetheless several important considerations that may impact the feasibility of camera trap experiments and/or the interpretation of their results. Cameras are

imperfect detectors (i.e. not all animals present in the vicinity of a camera trap will be detected), and thus all camera trap-based studies, including experiments, will be subject to issues of detectability (Burton et al., 2015). This may present challenges in some experimental studies if detectability differs between experimental treatments in ways that are not accounted for in the analysis. It is worth noting, however, that the probability of detecting an animal on camera is, at least in part, a function of that animal's behaviour near the camera site (Neilson, Avgar, Burton, Broadley, & Boutin, 2018). Thus, when other environmental variables are adequately controlled for, changes in detection rates between experimental treatments (e.g. lower detection rates of prey during predator treatments) can actually serve as a response variable in camera trap studies (e.g. Suraci, Clinchy, et al., 2019; see also Table 2). Responses to light and noise emitted by camera traps vary among individual animals, as some may preferentially avoid camera trap sites while others are more likely to investigate, but this has not been shown to produce significant differences in outcomes (Meek, Ballard, Fleming, & Falzon, 2016). Low detectability may also lead to issues with data acquisition rates for studies in which target species are particularly rare or cryptic, or when detectability differs substantially among target species. In such cases, the use of attractants or placement of cameras along known travel routes may help to increase detection rates but, of course, must be balanced against the potential effects on animal behaviour.

As illustrated by many of the research examples described above, combining camera traps with the experimental presentation of risk cues is an increasingly common approach to assessing the mechanisms and costs of prey responses to predation risk. However, despite their broad utility, interpretation of camera trap experiments with predator cues requires careful attention to the magnitude of the cue and whether cue type and intensity match the objectives of the study (Prugh et al., 2019). Without such consideration, predator cue experiments risk exposing animals to cue levels that do not correspond to those experienced by wild populations, complicating inference to natural systems. Researchers pairing camera traps with predator cues should make clear whether their objective is to mimic the magnitude of naturally occurring predator cues, demonstrate the potential for animals to respond to specific cues types or quantify responses to an immediate and isolated predator encounter. Quantifying and replicating the amount and combination of predator cues that prey actually experience in nature remains a key challenge for predator–prey ecology in general, and thus care is required when integrating predator cues into camera trap studies.

A related issue is the possibility that animals will habituate to experimental manipulations given that, for instance, experimentally presented predator cues are dissociated from actual predation risk. In general, predator cue field experiments will likely be most successful when conducted in environments in which the prey actually co-occur with the predator of interest. In such situations, interactions between predator and prey outside of the context of the experiment may help to reinforce the perceived

risk from the experimentally presented cue. Additionally, there are several measures researchers can take to minimize the effects of habituation in camera trap-based field experiments. When animals can be targeted individually, researchers can take steps to only expose individuals to a treatment once during a study (e.g. Smith et al., 2017), or to limit the total number of exposures and separate them by long time periods to minimize opportunities for learning. Previous field experiments deploying predator cues over protracted periods (e.g. several weeks) have used multiple cue types, random presentation of cues and regular movement of cues sources across the landscape to minimize the effects of habituation (e.g. Suraci, Clinchy, et al., 2019; Zanette, White, Allen, & Clinchy, 2011). The onset or intensity of habituation can, in some cases, be estimated directly from camera trap data by measuring changes in behavioural response variables (e.g. proportion of images in which prey exhibit vigilance) over time (Suraci et al., 2016). Habituation to experimental cues can also be a conservation or management concern, as it may reduce antipredator behaviours when prey encounter real cues. Habituation is a critical consideration for all studies presenting predator or prey cues to animals, and researchers should consider conducting pilot studies to determine the appropriate amount of treatment exposure to minimize habituation.

For many species, direct observations of predator–prey interactions in nature are exceedingly rare and thus difficult and costly to study. A key advantage of integrating camera traps with experimental methods is that the occurrence of such predator–prey interactions can be substantially increased by manipulating or simulating the presence of either predator or prey, thus avoiding the logistical challenges of detecting actual interactions in the wild. Such experimental approaches nonetheless come with their own suite of logistical challenges, which must be considered when planning camera trap experiments. Experimental manipulations may need to be checked regularly (e.g. daily, weekly) to ensure that experimental equipment is working and to refresh baits or olfactory cues. Experiments that are conducted over large spatial scales can therefore demand extensive labour to maintain. Studies that directly manipulate the presence of predators or prey (e.g. through removals, additions or exclosures) will also require substantial financial and labour commitments to conduct trapping or maintain fencing, and for monitoring to ensure that density manipulations were successful. Furthermore, camera vandalism and theft can add considerable cost, incentivizing sub-optimal camera placement (Meek, Ballard, & Falzon, 2016). As with any study, these potential logistical challenges associated with camera trap experiments must be weighed against the potential benefits when planning fieldwork.

7 | CONCLUSIONS

The study of predator–prey interactions has undergone a renaissance in recent decades largely due to the ability of camera traps

to monitor free-living predators and prey in their natural habitat over large spatial scales. Combining camera traps with experimental methods may provide the next major advance in predator–prey ecology by isolating the drivers of animal behaviour and thus clarifying the mechanisms behind observed spatiotemporal patterns of predator and prey activity. Such approaches have already begun to make substantial contributions to our understanding of how prey detect, recognize and respond to their predators (including humans; see Table 1). Experimental investigations of the factors influencing the predator side of the predator–prey game—that is, predator detection and selection of prey or the rate and success of predator attacks—have progressed more slowly, highlighting an important area for future research. In addition to the opportunity that camera trap-based experiments provide to bring rigorous tests of fundamental predator–prey theory out of the laboratory and into the field, these methods are also poised to play a crucial role in applied ecology and conservation by allowing researchers to quantify the relative impact of multiple anthropogenic disturbance types on wildlife. While experimental camera trap studies remain rare, the relatively rapid uptake of this approach over the last 5 years (Figure 1, inset) suggests this will become an increasingly common component of the ecologist's toolkit, with the potential to substantially increase our understanding of predator–prey dynamics in natural systems.

Extensions of the work reviewed here include examining the interactions between predator–prey pairs and other trophic levels (e.g. scavengers, resources or intraguild predators) and integrating experimental studies with longitudinal camera trap surveys. For example, a growing literature on applications of experimental techniques to link predation risk, prey behaviour and resource biomass has begun to investigate the mechanisms of trait-mediated trophic cascades (e.g. Atkins et al., 2019; Suraci et al., 2016). At the global scale, extensive use of food provisioning at camera traps has allowed for analyses of relationships within scavenger communities (e.g. Sebastián-González et al., 2019). Similar experimental techniques that evaluate the mechanisms underlying predator–prey interactions should be expanded to understand broader patterns in population and community dynamics.

AUTHORS' CONTRIBUTIONS
All authors conceived of the study, contributed to the systematic review and edited the manuscript; J.A.S., J.P.S., J.S.H., K.M.G., C.B.K., M.S.P. and L.B. developed the conceptual framing and wrote the manuscript; J.A.S., J.P.S. and J.S.H. made the figures; J.P.S. and J.A.S. developed the proposed experimental design; J.A.S. led the systematic review.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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