1 **Zooming in on mechanistic predator-prey ecology: integrating camera traps with**

2 **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 analyzed. 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 behavior, incorporating environmental realism not possible in the lab while benefiting from the distinct capacity of camera traps to generate large data sets 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 mention experimental methods, but the application of experimental approaches is increasing. To illustrate the utility of camera trap-based experiments using a case study, we 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

60   communities globally. Finally, we review challenges to conducting experimental camera

61   trap studies.

62   5. Experimental camera trap studies have already begun to play an important role in

63   understanding the predator-prey ecology of free-living animals, and such methods will

64   become increasingly critical to quantifying drivers of community interactions in a rapidly

65   changing world. We recommend increased application of experimental methods in the

66   study of predator and prey responses to humans, synanthropic and invasive species, and

67   other anthropogenic disturbances.

68

69   **Key-words**

70   antipredator behavior, camera trap, detection, experiments, landscape of fear, recognition, prey

71   selection

72

73   **Introduction**

74   The consequences of predator-prey interactions permeate multiple scales of animal ecology,

75   from decision-making and antipredator behavior to trophic cascades and community turnover.

76   While experimental evaluation of predator-prey theory is common in controlled laboratory

77   studies with simplified systems, understanding of wild vertebrate predator-prey interactions has

78   been largely gained from observational methods, including direct observations, animal captures,

79   and remote biologging technology (Smith *et al.* 2004; Wilmers *et al.* 2015). Although much has

80   been learned from observational approaches, they are limited in their capacity to uncover

81   mechanistic drivers of predator-prey ecological dynamics. Field experiments that incorporate the

82   complexity of natural conditions while isolating specific cues of risk or prey availability can

83   uniquely provide mechanistic inference on predator and prey behavior across a range of

84   environmental contexts (Suraci *et al.* 2017; Atkins *et al.* 2019). Yet such experiments remain

85   rare due to the challenges of both manipulating and measuring responses to predators and prey in

86   free-living wildlife.

87   In the last two decades, technical and analytical advances in camera trap (also trail

88   camera or remote camera) methodologies have created emerging opportunities to study predator-

89   prey interactions. Camera traps provide a non-invasive approach for detecting and monitoring

90   wildlife that has been made more accessible through continued improvements in camera quality

91   and cost-efficiency, and their use in addressing fundamental ecological questions is on the rise

92   (Burton *et al.* 2015; Caravaggi *et al.* 2017; Frey *et al.* 2017). Beyond monitoring, utilization of

93   camera traps for observational research in predator-prey ecology has exploded in recent years

94   (Fig. 1), largely due to advances in statistical techniques, such as occupancy modeling and

95   spatial capture-recapture analysis (Chandler & Royle 2013; Royle *et al.* 2013; Sollmann *et al.*

96   2013; MacKenzie *et al.* 2017; Augustine *et al.* 2018).

97   Camera traps also have an unparalleled potential as an experimental tool to explore the

98   causes and consequences of predator-prey interactions in complex and/or modified landscapes.

99   Camera trap technology enables the integration of behavioral and spatiotemporal data to

100   experimentally test predator-prey theory in field settings with complete predator and prey

101   assemblages. Many of the features of camera traps that have spurred their rapid uptake in

102   predator-prey ecology, including the capacity to collect large amounts of behavioral data from

103   multiple species without an observer present, are also ideal for use in an experimental context.

104   However, despite an exponential increase in the use of camera traps in wildlife research,

105   integration with experimental methods remains relatively rare. Here, we review recent advances

106   in the application of camera traps to observational and experimental research in predator-prey

107   ecology and discuss new frontiers of experimental applications of camera traps, including

108   opportunities to apply these methods in understanding and mitigating the effects of global

109   change on wildlife. We illustrate the utility of integrating camera traps with experimental

110   methods through a case study in which we propose an integrated study design to test the risk

111   allocation hypothesis, a cornerstone of modern predator-prey theory.

112

113   **Observational Applications of Camera Traps to Predator-Prey Ecology: Contributions and**

114   **Shortcomings**

115   A systematic review of the literature (October 1994 - December 2019; see Appendix 1 for

116   details) revealed that, of 331 studies using camera trap methods to investigate predator-prey

117   interactions, 91% used solely observational approaches (Fig. 1). Such observational approaches

118   have indeed revolutionized predator-prey ecology, using innovative statistical techniques and

119   large-scale camera trap datasets to reveal how predator and prey populations dynamically use

120   space and time relative to one another, and providing insight into the nature and persistence of

121   community assemblages (e.g. Astete *et al.* 2016, Rota *et al.* 2016, Rich *et al.* 2017). Spatial

122   interactions between predator and prey have been examined using stratified random or

123   systematic deployment of multiple cameras, which allows for detailed analyses of patterns of

124   avoidance, association, co-occurrence, and fine-scale space use (Rota *et al.* 2016; Weterings *et*

125   *al.* 2019). Camera traps have also been implemented to examine how predators and prey partition

126   time (Frey *et al.* 2017) and to quantify the degree of temporal overlap between two species

127   (Ridout & Linkie 2009) over daily (Monterroso, Alves, & Ferreras 2013), monthly (e.g., lunar

128   cycle; Pratas-Santiago *et al.* 2016), or seasonal (Gelin *et al.* 2017) scales. Recent evidence from

129   such studies suggests that prey responses to spatially-distributed predation risk across a

130   landscape vary with fluctuating temporal risk, i.e., prey use riskier areas during safer times of the

131   day (Bischof *et al.* 2014) or the lunar cycle (Palmer *et al.* 2017). Camera trap surveys have also

132   examined the influence of prey availability on predator spatiotemporal patterns by documenting

133   variation in predator density or activity in response to seasonal prey migrations (Gelin *et al.*

134   2017) and prey activity patterns (Martín-Díaz *et al.* 2018). These observational camera trap

135   studies have provided ecological information on cryptic species (Steinmetz et al. 2013,

136   Caravaggi et al. 2017), allowed for analysis of multiple interactions in complete predator and

137   prey species assemblages (Palmer *et al.* 2017; Rich *et al.* 2017), and have been applied to

138   understand global conservation challenges (Gaynor *et al.* 2018).

139   A comprehensive analysis of the dynamics of predator-prey interactions requires

140   mechanistic investigation of how prey perceive and respond to different risk cues, how predators

141   detect and select for prey, and the state- and environmental-dependence of decisions made by

142   both players (Gaynor *et al.* 2019). Yet, it is challenging to identify the behavioral or

143   environmental mechanisms that drive predator-prey interactions through observational camera

144   trap studies alone. Additionally, full evaluations of predator-prey games, in which both predator

145   and prey are dynamically responding to the behavior of the other player (Lima 2002), are often

146   difficult to achieve with observational camera trap surveys. Such surveys typically focus on

147   whether the distribution or activity of one player is predicted by the other, thus overlooking the

148   two-way nature of predator-prey interactions. Rarely are attempts made to identify which

149   player's response dominates, or furthermore, how predator and prey behavior respond to one

150   another (despite a long-acknowledged appreciation for these dynamics, e.g., Sih 1984; Lima

151   2002). There is a growing need for mechanistic studies that identify the behavioral drivers of

152   predator-prey interactions for effective conservation and management of biological communities,

153   particularly as global change alters predator and prey community assemblages, redesigns the

154   playing field for predator-prey games through habitat modification, and introduces novel sources

155   of risk and reward.

156

157   **Experimental Applications of Camera Traps to Predator-Prey Ecology: Ongoing**

158   **Developments and New Opportunities**

159   Experimental studies using camera traps on free-ranging animal populations remain rare,

160   comprising only 9% of studies in our systematic review on predator-prey interactions (Fig. 1).

161   However, current advancements in experimental methodologies and study designs offer novel

162   approaches for investigating the fundamental mechanisms underlying predator-prey ecology in

163   the field. Below, we describe current uses of camera traps in experimental research on predator-

164   prey interactions and propose further development and application of new approaches (Table 1).

165

166   *Prey-Focused Experiments: Risk Assessment and Antipredator Behavior*

167   Understanding how prey perceive and respond to predation risk has long been a major focus in

168   ecology (Lima & Dill 1990; McNamara & Houston 1992), though isolating the salient sensory

169   cues and cost-benefit tradeoffs associated with the antipredator responses of wild prey remains a

170   challenge. The relatively recent incorporation of camera traps into prey response studies, as

171   detailed below, has allowed for increased investigation of antipredator behavior in natural

172   settings and with a wider range of prey, including cryptic species (Table 1, Fig. 2). Through

173   experimental study designs that simulate or eliminate risk, or subsidize predators or prey, camera

174   traps can provide novel insight into how prey detect and respond to predators.

175

176 <u>Simulated Risk Cues</u>

177 Spatial and temporal variation in risk is a fundamental determinant of behavior and space use for

178 many prey species (Lima & Dill 1990; Brown, Laundré, & Gurung 1999), and camera traps are

179 an effective method for exploring prey spatiotemporal activity in response to predation risk. In

180 observational studies, activity and detection rates of predators assessed from camera traps have

181 been used as predictors of prey space use (Dorresteijn *et al.* 2015) and activity (Tambling *et al.*

182 2015). Camera traps have also been used to assess how prey distinguish between risky and safe

183 habitat, for instance, by placing cameras across gradients of habitat cover (Abu Baker & Brown

184 2014) or in areas with and without potentially dangerous habitat features (e.g., logs that impair

185 escape; Kuijper *et al.* 2015) and quantifying variation in detection rates (i.e., the number of

186 independent prey occurrences on camera) and vigilance behavior (i.e., the proportion of prey

187 detections in which the head was up and scanning; see Table 2). While these observational

188 techniques are effective for examining risk avoidance behaviors associated with observable

189 predator space use and habitat characteristics, quantifying the relative importance of different

190 indicators of risk on prey behavior often requires experimental manipulations, given the many

191 confounding factors such as environmental variation and food-safety trade-offs.

192   Little is known about which predator cues are most salient in driving antipredator

193 behaviors, including altered habitat use and social behavior and the trade-off between foraging

194 and vigilance. To address this knowledge gap, experimental manipulation of visual, olfactory,

195 and/or auditory predator cues have recently been paired with camera traps to determine how the

196 characteristics of these cues (e.g., age of scent cues, Bytheway, Carthey, & Banks 2013; or

197 predator identity, Carthey & Banks 2018) affect prey behavior. Olfactory predator cues are the

198   most commonly utilized in camera trap studies (Appendix 1), often by deploying predator scat or

199   urine at camera traps to assess vigilance behavior and space use (Kuijper *et al.* 2014; Andersen,

200   Johnson, & Jones 2016; Sahlén *et al.* 2016; Carthey & Banks 2018). Olfactory cues may indicate

201   to prey that a predator uses the area but is not necessarily present and, as such, have been

202   associated with a range of prey responses, from attraction (i.e., increased time spent at a camera

203   trap site; Garvey *et al.* 2017) to avoidance (decreased time on camera; Fležar *et al.* 2019). In

204   contrast, predator playbacks (auditory cues) are increasingly being combined with camera traps

205   to simulate immediate risk of a present predator (Mugerwa *et al.* 2017; Suraci *et al.* 2016, 2019;

206   Smith *et al.* 2017). Novel combinations of risk cues that execute a full factorial study design may

207   be particularly effective at measuring species-specific perceptions of risk (e.g., pairing habitat

208   manipulation with olfactory cues; Fležar *et al.* 2019), examining shifts in sentinel behavior (e.g.

209   comparing olfactory and visual predator cues; Zöttl *et al.* 2013), or testing the influence of group

210   size on food-safety tradeoffs (e.g., pairing giving-up density (GUD) measures with olfactory

211   cues; Carthey & Banks 2015).

212   Predation risk can have important non-consumptive effects on prey populations and

213   lower trophic levels, as mediated by costly behavioral responses, but it is often difficult to isolate

214   these effects from those of actual consumption by predators in free-ranging populations. Camera

215   trap experiments with simulated risk cues, which manipulate just the fear of predators and thus

216   isolate these behavioral costs, have demonstrated that perceived risk from predators can cause

217   prey to forego foraging (Clinchy *et al.* 2016, Smith *et al.* 2017) and avoid otherwise valuable

218   habitat (Sahlén *et al.* 2015, Fležar *et al.* 2019). Beyond measuring immediate antipredator

219   responses to risk, simulated risk cues can be used to quantify such costs of antipredator behavior.

220   Predator playbacks paired with camera traps have been used to document fear-induced trophic

221   cascades by quantifying changes in species behavior (e.g., detection rates, diel activity patterns,

222   use of baited foraging stations; see Table 2) across trophic levels (Suraci *et al.* 2016, 2019a) and

223   camera traps paired with GUDs and scent cues have been used to estimate the potential for group

224   foraging to mitigate such individual-level feeding costs through dilution or group vigilance

225   (Carthey & Banks 2015).

226

227   <u>Simulated Prey Cues and Prey Additions</u>

228   Understanding predator impacts on prey demography and the relative importance of consumptive

229   vs. non-consumptive predator effects requires quantifying how frequently prey are subject to

230   predator attacks and how likely they are to survive. Yet opportunistic observations of predator

231   attacks are relatively rare in natural settings and may not represent the full suite of predators

232   from which a prey species experiences risk. Simulated prey cues or baiting with prey or prey

233   proxies have therefore been used to estimate attack and survival rates of prey in diverse

234   environmental contexts. Studies that pair simulated prey cues with camera traps can improve the

235   quality and quantity of information on a prey species' predator diversity, predator-specific attack

236   rates, and how different prey cue types attract predators. A study using video camera traps to

237   monitor model prey (coral snakes; *Micrurus* spp.) revealed the taxonomic composition of the

238   snake predators and discrepancies between detection and attack rates (Akcali *et al.* 2019). To

239   examine predator-specific attraction to prey auditory and olfactory cues, Natusch, Lyons, &

240   Shine (2017) simulated metallic starling (*Aplonis metallica*) vocalizations and scent at camera

241   trap stations, demonstrating that starling predators were primarily attracted to scent cues.

242   Predator diversity and consequences of predation on prey demography can also be assessed by

243   stocking and monitoring a population of focal prey; camera traps deployed on outdoor fish tanks

244   and semi-natural streams identified the primary predator of Masu salmon, the influence of habitat

245   and time of day on attack rates, the role of prey density on predator visitation, and the

246   demographic class most impacted by predation (Miyamoto, Squires, & Araki 2017; Fig. 2).

247   One of the most common experimental designs to study attack and survival rates of avian

248   and reptilian prey involves artificial nests populated with quail, chicken, or model eggs. Artificial

249   nest studies comprised 36% of all experimental camera trap studies on predator-prey ecology in

250   our literature search (Appendix 1). The simplest design is to pair nests containing experimental

251   eggs with a camera trap to monitor predator visitation and attack rates (Patterson, Kalle, &

252   Downs 2016; Luna *et al.* 2018; Ponce *et al.* 2018; Kämmerle, Niekrenz, & Storch 2019).

253   Additional prey cues can also supplement traditional artificial nest experiments to identify

254   predator attractants; a study on artificial terrapin nests found that the scent of disinterred soil was

255   a stronger attractant for predators than terrapin scent or visual cues (Buzuleciu, Crane, & Parker

256   2016).

257

258   Risk Elimination

259   As an alternative to simulating risk through the introduction of cues, another approach to

260   quantifying the magnitude of risk effects on prey is to experimentally remove predators or install

261   exclosures, thus eliminating risk. Experimental risk elimination allows for the study of prey

262   behavior and survival in the absence of the density- and trait-mediated effects of predation. In a

263   long-term predator exclosure experiment, camera traps revealed that browsing herbivores

264   increase feeding rates when risk was removed (as estimated from the number of photos in which

265   herbivores were detected actively consuming provisioned baits), with cascading effects on oak

266   (*Quercus* spp.) recruitment and understory species composition (Cherry, Conner, & Warren

267   2015; Cherry, Warren, & Conner 2016). Removal or exclusion of predators has also been paired

268   with camera traps to measure predation effects on nest size of colonial insects (Hirsch *et al.*

269   2014) and nest survival of ground-nesting birds (Oppel *et al.* 2014) and reptiles (van Veen &

270   Wilson 2017).

271

272   *Predator-Focused Experiments: Predation Patterns and Hunting Behavior*

273   Observations of predation in the wild are typically rare due to the spatiotemporal unpredictability

274   of predation events and the influence of human observers on predator and prey behavior. Prior to

275   the development of camera trap technology, observations of hunting events in the field were

276   largely limited to sightings of conspicuous diurnal predators in open habitats (e.g., Mills,

277   Broomhall, & Toit 2004, Smith et al. 2004). A dearth of observations of predator behavior has

278   limited our understanding of the dynamics of predator-prey interactions, particularly predation

279   itself (Lima 2002). Although prey utilization can be determined through a number of

280   methodologies (e.g., dietary scat analysis, stable isotope analysis, or field tracking), predator

281   hunting behavior and selection of prey individuals based on their behavior is much more

282   challenging to observe through non-camera trap approaches. Camera traps provide an

283   opportunity to study lesser-known aspects of predator hunting behavior, including prey

284   detection, recognition, and selection, as detailed below (see also Table 1).

285

286   <u>Simulated Prey Cues</u>

287   Decisions made by predators about when, how, and what to hunt can influence predator survival,

288   fitness, and competition dynamics. Camera traps are an innovative tool for experimentally

289   studying the proximate cues (e.g., visual, auditory, and olfactory) that predators use to detect

290   their prey. Dying animal calls, feathers, and chemical signals are regularly used as predator lures

291   at camera trap stations with the purpose of refining delivery systems for predator control (Read

292   *et al.* 2015), but these methods have yet to be broadly applied to studies of predator detection,

293   recognition, and preference for prey. Visual cues in the form of prey models are currently the

294   most widely applied prey cue treatment in camera trap studies of predator behavior. Realistic

295   prey models and taxidermied animal mounts have been employed to examine attack rates on prey

296   models in vigilant and non-vigilant postures (Cresswell *et al.* 2003), prey detection (Lawson,

297   Fogarty, & Loss 2019), the influence of camouflage on attack rates (Atmeh *et al.* 2018), and the

298   role of aposematic coloration in prey selection and hunting behavior (Hunter 2009).

299   Few studies have addressed the responses of predators to prey chemical (but see:

300   Schiefelbein 2016), auditory, or scent cues (but see: Lawson, Fogarty, & Loss 2019), though

301   pairing such cues with camera traps provides a straightforward means of testing how predators

302   detect and locate their prey. Additionally, presentations of wild prey to a captive predator

303   (Janson, Monzón, & Baldovino 2014) or captive prey to wild predators (Garrote *et al.* 2012)

304   could be paired with small arrays of camera traps to evaluate detection distance and post-

305   detection behavior. Extension of these camera trap techniques are easily applicable to other

306   studies of prey recognition and discrimination, and could provide investigators with additional

307   information about prey partitioning in multi-predator systems or native prey recognition by

308   invasive predators.

309

310   <u>Prey or Proxy Subsidies and Baits</u>

311   Experimental prey subsidies, while rarely used in predator-focused studies, can be used to

312   quantify detection and utilization of prey, state-dependent hunting behaviors, and the impact of

313   prey availability on predator fitness. As in prey-focused studies, artificial nests that are baited

314   with real eggs can be employed as a tool in predator-focused research to observe hunting

315   behavior by a focal predator species (Dahl & Åhlén 2019). By altering the internal condition of

316   individual predators, supplemental feeding treatments paired with camera traps at predator nests

317   have been used to test the relationship between food availability and diet, parental care strategies,

318   and nestling survival in avian predators (Grüebler *et al.* 2018). Prey subsidies that alter the

319   timing of food availability have revealed how phenological mismatch between predator and prey

320   can cause a diet shift in insectivorous birds (Samplonius *et al.* 2016). Because foraging decisions

321   are often state-dependent and internal state is often challenging to assess in the field, experiments

322   that alter food availability to predators provide important nuance to understandings of predator

323   diet preferences and prey utilization.

324

325   **Case Study: Integrating Camera Traps and Experimental Methods to Test the Risk**

326   **Allocation Hypothesis**

327   Many of the advances in camera trap-based experiments described above focus on the immediate

328   response of a single predator or prey individual to a cue or subsidy. However, integration of such

329   targeted experiments with larger-scale manipulations could be used to address questions

330   concerning the context-dependency of animal responses to predators or prey across scales. To

331   illustrate this approach, and to concretize the value of integrating camera traps with experimental

332   methods more generally, we propose a multi-scale experimental design to test a cornerstone of

333   predator-prey theory, the Risk Allocation Hypothesis.

334   For most prey animals, basic activities such as foraging are thought to increase the risk of

335   predation, setting up a fundamental tradeoff between time devoted to minimizing risk and time

336   devoted to foraging or other crucial behaviors (Sih 1980; Lima & Dill 1990). The behavioral

337   adjustments that prey make to balance safety and foraging are also a primary mechanism by

338   which the non-consumptive effects of predators can cascade across food webs, as predator-

339   induced suppression of foraging may in turn affect the prey's impact on its resource (Schmitz,

340   Krivan, & Ovadia 2004; Suraci *et al.* 2016). Understanding the implications of this "food-safety

341   tradeoff" for prey populations remains a major area of research interest in ecology and a fertile

342   area for experimental investigations of predator-prey dynamics in natural systems.

343   This trade-off was formalized by Lima and Bednekoff's (1999) highly influential Risk

344   Allocation Hypothesis (RAH), which recognized that the time prey devote to vigilance vs.

345   foraging is not just a function of the immediate presence or absence of predators, but is affected

346   by the long-term temporal pattern of exposure to predation risk. Therefore, prey should forage

347   most intensely during brief pulses of safety in an otherwise risky environment and be most

348   vigilant during brief pulses of risk in an otherwise safe environment (Lima & Bednekoff 1999).

349   Experimental tests in laboratory settings have generally supported the predictions of the RAH

350   (reviewed in Ferrari, Sih, & Chivers 2009), as have observational studies on large mammal

351   predators and prey (Gude *et al.* 2006; Creel *et al.* 2008; Costelloe & Rubenstein 2018).

352   Experimental tests of the RAH with free-living wildlife remain rare, however, leaving open

353   important questions regarding the role of temporal variability of risk in shaping prey responses

354   and potential cascading effects.

355   As previously noted by Moll *et al.* (2017), testing the RAH in natural systems may be

356   achieved through the integration of camera traps with the experimental presentation of predator

357   cues (e.g., scent and/or vocalization playbacks). We envisage a study design (Fig. 3a) based on

358   the proportion of time that a prey animal spends in relatively risky vs. safe situations, as

359   described in Lima and Bednekoff's (1999) original model. In this design, replicate experimental

360   plots matched for baseline levels of predator activity are exposed to predator cues (e.g., via grids

361   of playback speakers; Suraci *et al.* 2019) on a regular schedule such that prey animals have the

362   opportunity to learn the temporal sequence of risky and safe periods (Ferrari, Sih, & Chivers

363   2009). Camera traps are deployed across the experimental plots and paired with GUDs or

364   feeding stations, allowing researchers to monitor foraging/vigilance during both risky and safe

365   periods. The proportion of time at risk is varied between plots, e.g., by presenting playbacks 20,

366   40, and 60% of the time. The RAH predicts that vigilance will be lowest (and foraging most

367   intense) during safe periods (when playbacks are off) in the high-risk treatment, and that

368   vigilance will be highest during risky periods (playbacks on) in the low-risk treatment (Fig. 3b,

369   left panel). The RAH also makes the somewhat counterintuitive prediction that vigilance during

370   risky periods will be lower in the high-risk than in low-risk treatment because of an animal's

371   requirement to meet energetic demands through some minimum amount of time spent foraging.

372   The RAH has been adapted to compare the relative effects of "risky times" (i.e.,

373   immediate encounters with a predator) and "risky places" (i.e., spatial locations of high

374   background predation risk) on prey antipredator behavior (Gude *et al.* 2006; Creel *et al.* 2008).

375   Such a comparison could be readily incorporated into the above study design by using motion-

376   sensitive playback systems (Suraci *et al.* 2017) deployed at camera trap-monitored GUD or

377   feeding stations to simulate an immediate predator encounter against different background levels

378   of predator activity, the latter simulated by varying cue presentation intensity as illustrated in

379   Figure 3a. Under this formulation, the RAH predicts that prey will be more responsive to a

380   predator encounter (e.g., exhibit a greater increase in vigilance) where background levels of risk

381   (e.g., predator cue intensity) is lower (Fig. 3b, right panel). It is important to note that, as with all

382   cue-based experiments, the potential for prey to habituate to predator cues is a critical

383   consideration for the proposed RAH study design. Researchers considering this or similar

384   designs will need to ensure that prey are no more likely to habituate to cues in the high-risk than

385   in the low-risk treatments. We consider the issue of habituation in detail below (see "Challenges

386   to implementing experimental camera trap research" section) and offer some considerations for

387   mitigating its effects.

388

389   **Predator-Prey Interactions in a Changing World**

390   Ecological communities globally are in flux as invasive species, land use change, and human

391   activity permeate even the most remote landscapes. Understanding predator-prey interactions can

392   inform conservation initiatives, such as efforts to mitigate detrimental impacts of invasive

393   species, promote restoration of extirpated species, and manage outcomes of changing community

394   composition (Ritchie *et al.* 2012). Observational applications of camera trap technology have

395   been instrumental in documenting anthropogenic effects on predator-prey interactions through

396   anthropogenic disturbance (Kays *et al.* 2017) or habitat modification (Muhly *et al.* 2011),

397   facilitating global studies describing the impacts of humans on wildlife (Gaynor *et al.* 2018).

398   Experimental approaches that address human impacts on predator-prey interactions remain rare,

399   but may prove critical to management decisions in the near future. Given the myriad forms that

400   human "disturbance" can take, the capacity for camera trap-based experiments to provide a

401   mechanistic understanding of the most important drivers of anthropogenic impacts on wildlife

402   interactions may help refine conservation strategies.

403   Several studies have combined camera traps with experimental or quasi-experimental

404   designs to provide valuable insights into how human activity affects predators and prey. The

405   anthropogenic addition (e.g., introduction, restoration) or removal (e.g., extirpation) of predators

406   to or from a community can have major effects on prey behavior and population dynamics.

407   Experimental work pairing camera traps with predator cues has allowed researchers to quantify

408   the time required for prey to develop appropriate antipredator responses to invasive predators

409   (Carthey & Banks 2016; Steindler *et al.* 2018), or to lose costly responses to extirpated predators

410   (Le Saout *et al.* 2015). In addition to directly altering the predator-prey community,

411   anthropogenic activity can impact predator-prey interactions by altering the landscape within

412   which they occur. For instance, Sahlén *et al.* (2016) paired camera traps with predator scent to

413   show that land clearing by humans (e.g., for agriculture) mediates perceived predation risk in

414   several European ungulate species, with ungulates increasing use of open areas in the presence of

415   predator cues.

416   Camera trap-based experiments have played a major role in an emerging field of research

417   examining how the fear of humans as predators affects wildlife. This work is based on the

418   premise that, because humans are a primary source of mortality for many wildlife species

419   (Darimont *et al.* 2015), these species may respond to humans as any prey responds to its

420   predators (i.e., with avoidance and/or reductions in foraging behavior). Indeed, these novel

421   experiments have demonstrated that both large carnivores and mesocarnivores respond fearfully

422   to perceived human presence, resulting in reduced feeding time at baits or kill sites (Clinchy *et*

423   *al.* 2016; Smith *et al.* 2017), and that these responses can scale up to affect wildlife behavior and

424   predator-prey interactions at the landscape level (Suraci *et al.* 2019). The role of humans as

425   sources of perceived risk for wildlife has important conservation implications given the steady

426   expansion of human presence into wildlife habitat (Venter *et al.* 2016), and is thus likely to

427   remain a key focus of camera trap experiments.

428   The ability of camera trap-based experiments to isolate specific disturbance types in their

429   impacts on free-living predators and prey lends itself to several important future directions in

430   understanding the effects of global change on wildlife behavior. For instance, recent evidence

431   suggests that noise pollution (e.g., from vehicle traffic or industrial activity) can interfere with

432   the hunting abilities of auditory predators such as bats and owls (Siemers & Schaub 2011;

433   Senzaki *et al.* 2016). Current studies that control the intensity (amplitude, duration) of noise

434   pollution in an experimental context (Kleist *et al.* 2018; Mulholland *et al.* 2018) could be

435   expanded to identify mechanisms for observed physiological and demographic responses to

436   noise by deploying camera traps to quantify the severity of noise-induced foraging reductions in

437   free-living predators. Similarly, artificial light at night may substantially alter the behavior of

438   visual predators or crypsis-dependent prey (Longcore & Rich 2004), and could readily be

439   manipulated in the presence of camera traps to quantify effects on, e.g., prey foraging behavior

440   or predator hunting success. Data from observational camera trap studies have demonstrated that

441   anthropogenic disturbance affects the diel activity patterns of wildlife on a global scale (Gaynor

442   *et al.* 2018), including in response to reintroduced (Tambling *et al.* 2015) or invasive predators

443   (Bogdan, Jůnek, & Vymyslická 2016). Experimentally pairing camera traps with specific

444   disturbance types (e.g., light, noise pollution, human or other predator cues) may help identify

445   and mitigate the primary drivers of such impacts on wildlife activity.

446   Human-induced changes in animal behavior and interactions are a global phenomenon,

447   and global camera trap datasets are currently leading to new insights about biodiversity loss and

448   conservation (Beaudrot *et al.* 2016). Calls for the standardization of camera trap protocols and

449   data sharing have been made to increase opportunities for understanding anthropogenic

450   influences on key predator-prey interactions (Steenweg *et al.* 2017). We support similar

451   standardization of data collected from camera trap experiments around the world. For example,

452   playback experiments that use the same decibel range, collect standard measures of fleeing and

453   vigilance behavior, and maintain a similar distance between speaker and focal animal could be

454   compiled to compare the effects of different kinds of anthropogenic disturbances across a

455   species' range or to assess differential responses by various taxa to anthropogenic sound cues.

456   Here, at the leading edge of experimental camera trap studies, standardization of protocols will

457   promote longitudinal, comparative studies that capture the diversity of anthropogenic

458   environmental changes impacting wildlife populations.

459

460   **Challenges to Implementing Experimental Camera Trap Research**

461   While the integration of camera traps with experimental methods can help to overcome key

462   issues associated with observational studies (e.g., by providing a mechanistic understanding of

463   predator or prey responses), there are nonetheless several important considerations that may

464   impact the feasibility of camera trap experiments and/or the interpretation of their results.

465   Cameras are imperfect detectors (i.e., not all animals present in the vicinity of a camera trap will

466   be detected), and thus all camera trap-based studies, including experiments, will be subject to

467   issues of detectability (Burton *et al.* 2015). This may present challenges in some experimental

468   studies if detectability differs between experimental treatments in ways that are not accounted for

469   in the analysis. It is worth noting, however, that the probability of detecting an animal on camera

470   is, at least in part, a function of that animal's behavior near the camera site (Neilson *et al.* 2018).

471   Responses to light and noise emitted by camera traps vary among individual animals, as some

472   may preferentially avoid camera trap sites while others are more likely to investigate, but this has

473   not been shown to produce significant differences in outcomes (Meek *et al.* 2016a). Thus, when

474   other environmental variables are adequately controlled for, changes in detection rates between

475   experimental treatments (e.g., lower detection rates of prey during predator treatments) can

476   actually serve as a response variable in camera trap studies (e.g., Suraci *et al.* 2019a; see also

477   Table 2). Low detectability may also lead to issues with data acquisition rates for studies in

478   which target species are particularly rare or cryptic, or when detectability differs substantially

479   among target species. In such cases, the use of attractants or placement of cameras along known

480   travel routes may help to increase detection rates but, of course, must be balanced against the

481   potential effects on animal behavior.

482   As illustrated by many of the research examples described above, combining camera

483   traps with the experimental presentation of risk cues is an increasingly common approach to

484   assessing the mechanisms and costs of prey responses to predation risk. However, despite their

485   broad utility, interpretation of camera trap experiments with predator cues requires careful

486   attention to the magnitude of the cue and whether cue type and intensity match the objectives of

487   the study (Prugh *et al.* 2019). Without such consideration, predator cue experiments risk

488   exposing animals to cue levels that do not correspond to those experienced by wild populations,

489   complicating inference to natural systems. Researchers pairing camera traps with predator cues

490   should make clear whether their objective is to mimic the magnitude of naturally occurring

491   predator cues, demonstrate the potential for animals to respond to specific cues types, or quantify

492   responses to an immediate and isolated predator encounter. Quantifying and replicating the

493   amount and combination of predator cues that prey actually experience in nature remains a key

494   challenge for predator-prey ecology in general, and thus care is required when integrating

495   predator cues into camera trap studies.

496   A related issue is the possibility that animals will habituate to experimental manipulations

497   given that, for instance, experimentally presented predator cues are dissociated from actual

498   predation risk. In general, predator cue field experiments will likely be most successful when

499   conducted in environments in which the prey actually co-occur with the predator of interest. In

500   such situations, interactions between predator and prey outside of the context of the experiment

501   may help to reinforce the perceived risk from the experimentally presented cue. Additionally,

502   there are several measures researchers can take to minimize the effects of habituation in camera

503   trap-based field experiments. When animals can be targeted individually, researchers can take

504   steps to only expose individuals to a treatment once during a study (e.g. Smith *et al*. 2017), or to

505   limit the total number of exposures and separate them by long time periods to minimize

506   opportunities for learning. Previous field experiments deploying predator cues over protracted

507   periods (e.g., several weeks) have used multiple cue types, random presentation of cues, and

508   regular movement of cues sources across the landscape to minimize the effects of habituation

509   (e.g., Zanette *et al.* 2011, Suraci *et al.* 2019a). The onset or intensity of habituation can in some

510   cases be estimated directly from camera trap data by measuring changes in behavioral response

511   variables (e.g., proportion of images in which prey exhibit vigilance) over time (Suraci *et al.*

512   2016). Habituation to experimental cues can also be a conservation or management concern, as it

513   may reduce anti-predator behaviours when prey encounter real cues. Habituation is a critical

514   consideration for all studies presenting predator or prey cues to animals, and researchers should

515   consider conducting pilot studies to determine the appropriate amount of treatment exposure to

516   minimize habituation.

517   For many species, direct observations of predator-prey interactions in nature are

518   exceedingly rare and thus difficult and costly to study. A key advantage of integrating camera

519   traps with experimental methods is that the occurrence of such predator-prey interactions can be

520   substantially increased by manipulating or simulating the presence of either predator or prey,

521   thus avoiding the logistical challenges of detecting actual interactions in the wild. Such

522   experimental approaches nonetheless come with their own suite of logistical challenges, which

523   must be considered when planning camera trap experiments. Experimental manipulations may

524   need to be checked regularly (e.g., daily, weekly) to ensure that experimental equipment is

525   working and to refresh baits or olfactory cues. Experiments that are conducted over large spatial

526   scales can therefore demand extensive labor to maintain. Studies that directly manipulate the

527   presence of predators or prey (e.g., through removals, additions, or exclosures) will also require

528   substantial financial and labor commitments to conduct trapping or maintain fencing, and for

529   monitoring to ensure that density manipulations were successful. Furthermore, camera vandalism

530   and theft can add considerable cost, incentivizing sub-optimal camera placement (Meek *et al.*

531   2016b). As with any study, these potential logistical challenges associated with camera trap

532   experiments must be weighed against the potential benefits when planning fieldwork.

533

534   **Conclusion**

535   The study of predator-prey interactions has undergone a renaissance in recent decades largely

536   due to the ability of camera traps to monitor free-living predators and prey in their natural habitat

537   over large spatial scales. Combining camera traps with experimental methods may provide the

538   next major advance in predator-prey ecology by isolating the drivers of animal behavior and thus

539   clarifying the mechanisms behind observed spatiotemporal patterns of predator and prey activity.

540   Such approaches have already begun to make substantial contributions to our understanding of

541   how prey detect, recognize, and respond to their predators (including humans; see Table 1).

542   Experimental investigations of the factors influencing the predator side of the predator-prey

543   game – i.e., predator detection and selection of prey or the rate and success of predator attacks –

544   have progressed more slowly, highlighting an important area for future research. In addition to

545   the opportunity that camera trap-based experiments provide to bring rigorous tests of

546   fundamental predator-prey theory out of the laboratory and into the field, these methods are also

547   poised to play a crucial role in applied ecology and conservation by allowing researchers to

548   quantify the relative impact of multiple anthropogenic disturbance types on wildlife. While

549   experimental camera trap studies remain rare, the relatively rapid uptake of this approach over

550   the last five years (Fig. 1, inset) suggests this will become an increasingly common component

551   of the ecologist's toolkit, with the potential to substantially increase our understanding of

552   predator-prey dynamics in natural systems.

553   Extensions of the work reviewed here include examining the interactions between

554   predator-prey pairs and other trophic levels (e.g. scavengers, resources, or intraguild predators)

555   and integrating experimental studies with longitudinal camera trap surveys. For example, a

556   growing literature on applications of experimental camera trap techniques to link predation risk,

557   prey behavior, and resource biomass has begun to investigate the mechanisms of trait-mediated

558   trophic cascades (e.g. Suraci *et al.* 2016, Atkins *et al.* 2019). At the global scale, extensive use of

559   food provisioning at camera traps has allowed for analyses of relationships within scavenger

560   communities (e.g. Sebastián-González *et al.* 2019). Similar experimental techniques that evaluate

561   the mechanisms underlying predator-prey interactions should be expanded to understand broader

562   patterns in population and community dynamics.

563

564   **Authors' Contributions**

565   All authors conceived of the study, contributed to the systematic review, and edited the

566   manuscript. JAS, JPS, JSH, KMG, CBK, MSP, and LB developed the conceptual framing and

567   wrote the manuscript. JAS, JPS, and JSH made the figures. JPS and JAS the developed the

568   proposed experimental design. JAS led the systematic review.

569

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575

576   **Data Accessibility**

577   All data have been made available in Appendix 1.

578

579   **References**

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861   **Figure Legends**

862   Figure 1. Distribution and number of experimental and observational camera trap (CT) studies on

863   predators and/or prey by continent. Observational studies included in the inset figure include all

864   predator-prey camera trap papers mentioning either *abundance*, *activity*, *density*, or *occupancy*.

865   Methods for literature search in Appendix 1. Bar height represents the number of studies [totals:

866   Africa (45), Asia (80), Europe (34), North America (88), Oceania (39), South America (46)].

867   Studies that contain more than one of the five examined keywords or have authors from multiple

868   regions may contribute to multiple bars. Data include studies published before January 2020.

869

870   Figure 2. Examples of measurements used to quantify predator-prey interactions in experimental

871   camera trap studies. (a) Taxidermied animal mounts used to determine the effect of aposematic

872   coloration and body shape on mammalian predator recognition of and response to potential prey

873   (treatment type: simulated prey cue). (b) Playback experiments used to test puma fear of humans

874   and synanthropic species (e.g. domestic dogs, shown here; treatment type: simulated risk cue).

875   (c) Giving-up density (GUD) experiments used to measure red fox food-safety trade-offs in

876   response to predator scent (treatment type: simulated prey cue). (d) Salmon stocking used to

877   measure size-specific predation rates (treatment type: prey subsidy/addition). Figures adapted

878   from: (a) Hunter (2009); (b) Suraci *et al.* (2019b); (c) Haswell *et al.* (2018) ; and (d) Miyamoto,

879   Squires, & Araki (2017) (photo from published article).

880

881   Figure 3. Illustration of the proposed study design for integrating camera traps (CT) and

882   experimental methods to test the Risk Allocation Hypothesis (RAH). The RAH addresses a

883   perennial question in predator-prey ecology, i.e. how prey balance foraging and safety to

884   optimize anti-predator behavior. (**a**) Spatial layout of the proposed experiment. Each

885   experimental replicate consists of three grids of playback speakers broadcasting predator

886   vocalizations at varying intensity (here 20, 40, and 60% of the time). Camera traps and GUDs or

887   feeding stations (yellow boxes) are deployed systematically across each grid to monitor prey

888   vigilance/foraging. The inset in each grid illustrates the set schedule of predator cue presentation,

889   allowing prey to predict risky vs. safe periods (playbacks on = high risk, playbacks off = low

890   risk; Ferrari *et al.* 2009). Under the "classic" formulation of the RAH (based on proportion of

891   time a prey animal spends at risk), prey foraging intensity is measured during both risky and safe

892   periods at each level of overall predation risk. The same design can be used to test the risky

893   times vs. risky places hypothesis (see text for details) by deploying motion-sensitive playback

894   systems (Suraci *et al.* 2017) at camera traps/feeding stations to simulate immediate predator

895   encounters (risky times) against varying backgrounds (risky places). (**b**) Expected results of both

896   the "classic" RAH formulation (left panel, adapted from Lima & Bednekoff 1999) and the risky

897   times vs. risky places formulation (right panel). In the left panel, average time spent vigilant is

898   compared both between risky (playbacks on) and safe (playbacks off) periods and across overall

899   risk levels. In the right panel, responsiveness to an immediate predator encounter is compared

900   between background levels of predation risk.

901

902　**Figures**

903　Figure 1.
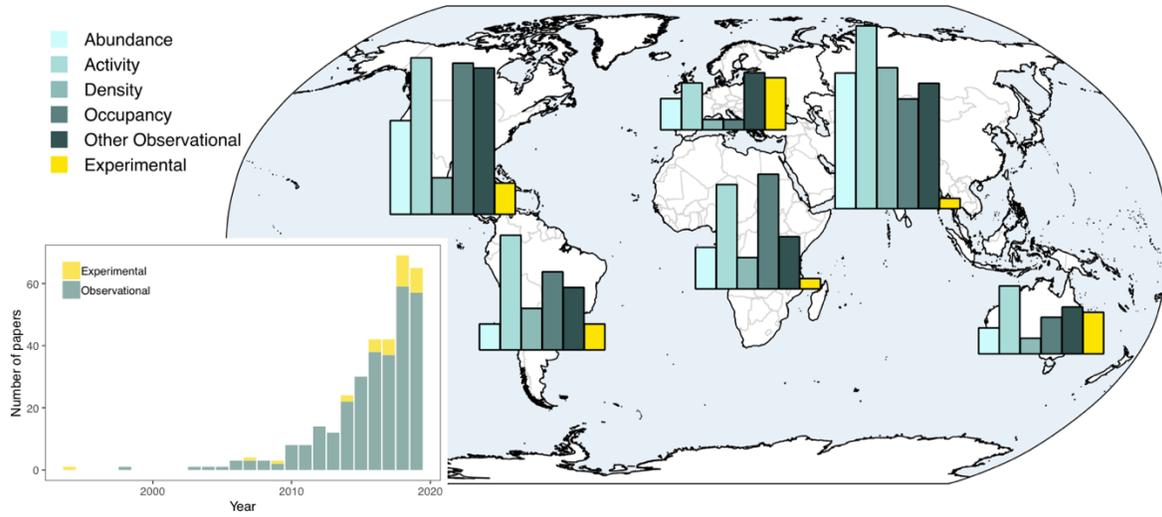
904

905   Figure 2.

906

907   Figure 3.

a

b

"Classic" RAH

Risky times vs. risky places

908
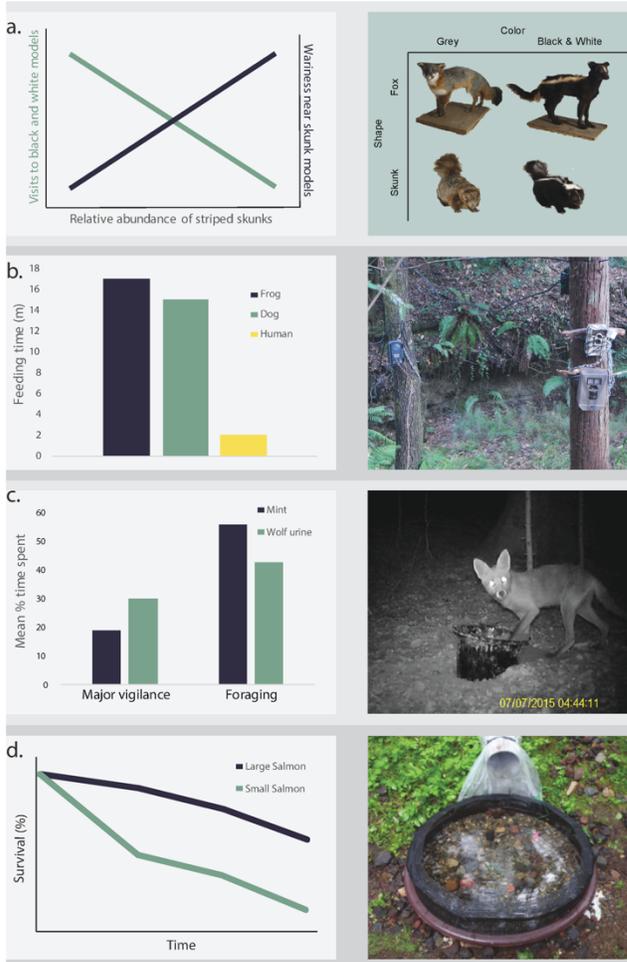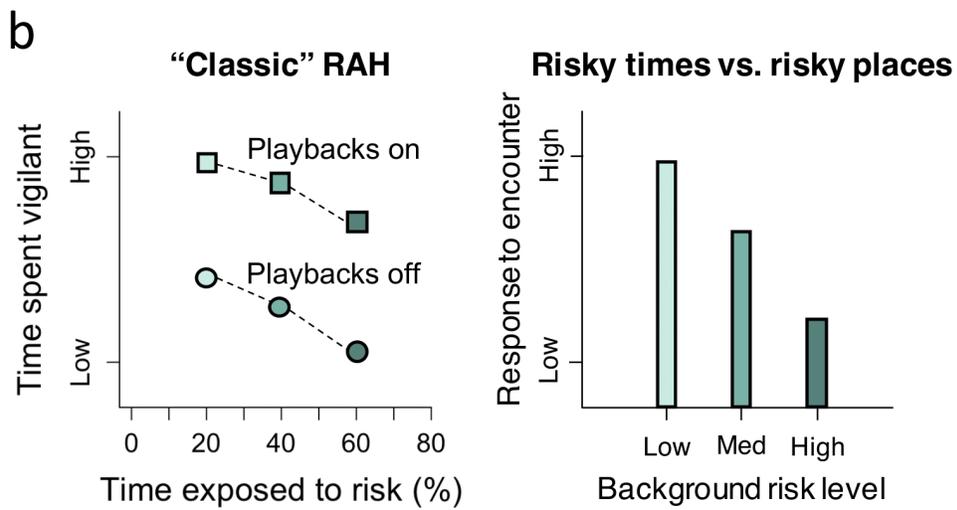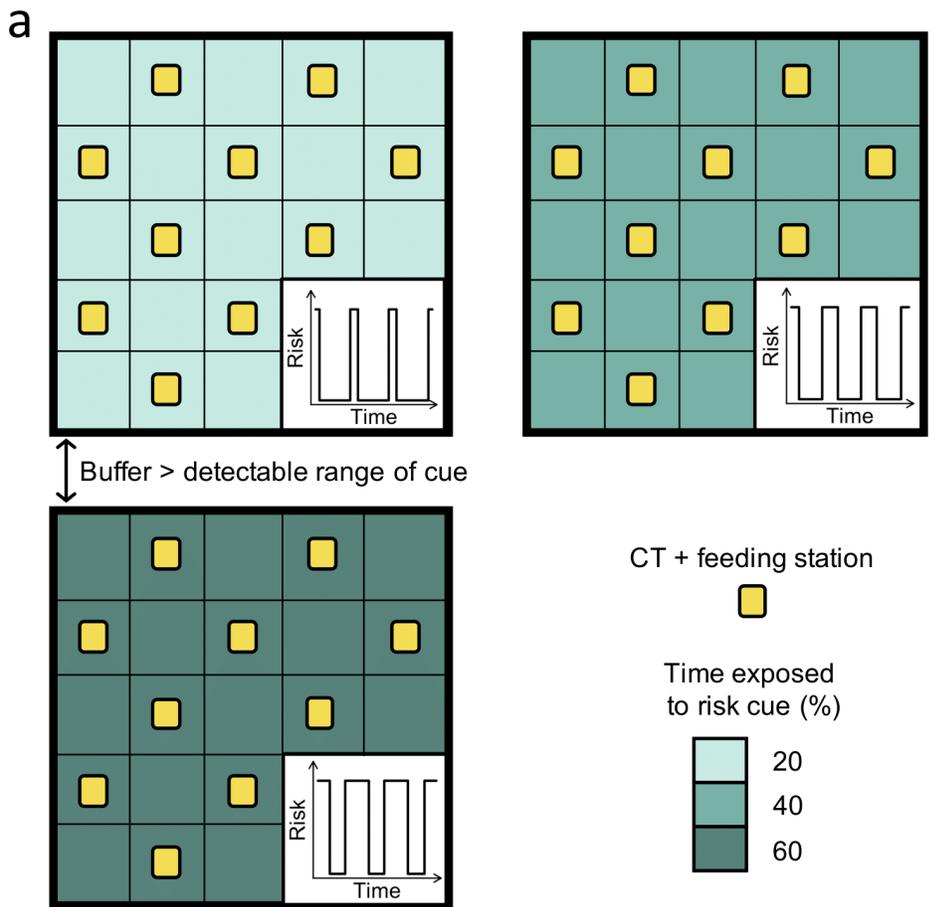
909 **Tables**

910 Table 1. A conceptual guide for designing camera trap studies to address themes in predator-prey

911 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	*Zöttl et al. 2013 (prey: meerkat)
			Predator playback	Auditory	*Clinchy et al. 2016 (prey: European badger) *Smith et al. 2017 (prey: puma) *Suraci et al. 2016a (prey: raccoon)
			Predator scent	Olfactory	Carthey and Banks 2018 (prey: black rat)

					Kuijper et al. 2014 (prey: red deer)
					Sahlen et al. 2016 (prey: fallow deer)
			Habitat riskiness	Any	Farnworth et al. 2018 (prey: weta spp.) Fležar et al. 2019 (prey: impala, warthog)
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)
Prey subsidy/addition	Attack rates Hunting behavior Prey selection State-dependent predation	Predator	Bait, food supplements, or prey proxy (e.g. artificial nests)	Presence	Dahl et al. 2019 (predator: raccoon dog) Gruebler 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 et al. 2017 (prey: woodlark) Luna et al. 2018 (prey: red-tailed tropicbird)

					Miyamoto et al. 2018 (prey: Masu salmon)
Risk elimination	Attack rates Risk perception Survival	Prey	Predator removal or exclosures	Presence	Hirsch et al. 2014 (prey: *Azteca* ant) Oppel et al. 2014 (prey: St. Helena plover) van Veen et al. 2017 (prey: Jamaican rock iguana)
Prey food subsidy	Encounter risk Risk perception	Prey	Baiting Giving-up densities	Presence	Esparza-Carlos et al. 2018 (prey: collared peccary)

912   * Not identified by systematic review

913   Table 2. A guide for identifying and measuring response variables in experimental camera trap

914   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. 2015 (prey: European ungulates)
		Total time (# photos, duration in video) spent at a camera site	Fležar et al. 2019 (prey: African ungulates) Garvey et al. 2016 (prey: small mammalian predators)
Feeding behavior	Risk perception; Predator detection	Visitation to or time spent at feeding stations (including GUDS)	Carthey and Banks 2018 (prey: black rat) *Suraci et al. 2019a (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 et al. 2019a (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 et al. 2019b (prey: puma)

		Time (# photos, duration in video) spent approaching and/or sniffing a predator odor cue	*Bytheway et al. 2018 (prey: black rats) Garvey et al. 2016 (prey: small mammalian predators)
Investigation	Predator recognition		
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. 2017 (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 behavior	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)

915   * Not identified by systematic review