The influence of human activity on predator-prey interactions

Amy Van Scoyoc[1], Justine Smith[2], Kaitlyn Gaynor[3], Kristin Barker[1], and Justin Brashares[4]

[1]University of California Berkeley
[2]UC Davis
[3]University of California Santa Barbara
[4]University of California

February 22, 2024

Abstract

Despite growing evidence of widespread impacts of humans on the behavior of animals, our understanding of how humans reshape species interactions remains limited. Here, we present a framework that draws on key concepts from behavioral and community ecology to outline four primary pathways by which humans can alter predator-prey spatiotemporal overlap, which may have implications for predator diet, predation rates, population demography, and trophic cascades. We then demonstrate the testability of the hypotheses that emerge from our framework using temporal activity data for 178 predator-prey dyads from published camera trap studies to reveal patterns of human influence on predator-prey activity and overlap. Our framework and case study highlight current challenges, gaps, and advances in linking human-induced animal behavior change to predator-prey dynamics. By using a hypothesis-driven approach to estimate the potential for altered species interactions, we can better predict the ecological consequences of human activities on whole communities.

UNIVERSITY OF CALIFORNIA, BERKELEY

BERKELEY • DAVIS • IRVINE • LOS ANGELES • MERCED • RIVERSIDE • SAN DIEGO • SAN FRANCISCO • SANTA BARBARA • SANTA CRUZ

COLLEGE OF NATURAL RESOURCES
DEPARTMENT OF ENVIRONMENTAL SCIENCE, POLICY & MANAGEMENT
137 MULFORD HALL #3114
BERKELEY, CA 94720-3114

BERKELEY, CALIFORNIA 94720
TEL (510) 643-7430
FAX (510) 643-5438

Dr. Jonathan Chase
Synthesis Editor, Ecology Letters

March 18, 2022

Dear Dr. Chase:

On behalf of my co-authors, I am pleased to submit our manuscript entitled "*The influence of human activity on predator-prey interactions*" for consideration as a Synthesis article at *Ecology Letters*.

A recent and growing body of research has summarized the far-reaching impacts of human disturbance on animal behavior. Yet, our understanding of how responses of individual species to humans may alter interactions, such as competition and predation, remains unstructured and incomplete. In this synthesis, we address this gap by drawing together key concepts from behavioral and community ecology to construct a framework for conceptualizing how humans influence overlap between predators and prey to affect community-level dynamics. We further demonstrate how empirical data may be applied within this framework to reveal patterns among the responses of predator-prey dyads to humans.

We believe our manuscript is an ideal fit for *Ecology Letters* given that your journal has played a leading role in establishing the study of behaviorally mediated effects as a central and still-growing topic in ecological and conservation science. Our synthesis formalizes the pathways by which humans influence species interactions, situates existing predator-prey research in a common framework, and promotes testable hypotheses to catalyze new research.

No material in the paper has been published or submitted for publication elsewhere. We appreciate your consideration of our submission and hope you find it to be of interest to readers at *Ecology Letters*.

Sincerely,

Amy Van Scoyoc
Telephone: +1 631 327 4329
E-mail: avanscoyoc@berkeley.edu

Title: The influence of human activity on predator-prey interactions
Running title: Human alteration of predator-prey overlap

Authors:
Amy Van Scoyoc[1], Justine A. Smith[2], Kaitlyn M. Gaynor[3,4], Kristin Barker[1], Justin S. Brashares[1]

Affiliations:
[1] Department of Environmental Science, Policy, and Management, University of California, Berkeley, 130 Mulford Hall, Berkeley, CA, USA 94720
[2] Department of Wildlife, Fish, & Conservation Biology, University of California, Davis, 455 Crocker Lane, Davis, CA, USA 95616
[3] National Center for Ecological Analysis and Synthesis, University of California Santa Barbara, 1021 Anacapa St, Suite 300, Santa Barbara, CA, USA 93101
[4] Departments of Zoology & Botany, University of British Columbia, BC, Canada V6T 1Z4

Corresponding author:
Amy Van Scoyoc
Tel: +1 631-327-4329
E-mail: avanscoyoc@berkeley.edu

Co-author emails:
justinesmith@ucdavis.edu; gaynor@zoology.ubc.ca; kristinjbarker@gmail.com; brashares@berkeley.edu

Keywords: avoidance, attraction, predation, prey refugia, prey switching, spatiotemporal overlap, trophic cascades

Paper type: Synthesis

Content: 82 references; 2 figures; 1 supplementary information file;

Word count: abstract, 148 words; main text, 3336 words

Statement of authorship: AV developed the initial framework, figures, and wrote the first manuscript draft. AV, JAS, KMG, and KB conducted the literature review, and AV performed the data analysis. All authors contributed substantially to the framework, results, and manuscript revisions.

Data accessibility statement: The data sources that support the findings of this study are listed in the article and the Supporting Information file. The authors confirm that any data that was not available from published sources was used and cited with permission of the data's original authors. The data and code used to produce the figures in this manuscript is available on GitHub: https://github.com/avanscoyoc/human-predator-prey-overlap

Title: The influence of human activity on predator-prey interactions

Abstract

Despite growing evidence of widespread impacts of humans on the behavior of animals, our understanding of how humans reshape species interactions remains limited. Here, we present a framework that draws on key concepts from behavioral and community ecology to outline four primary pathways by which humans can alter predator-prey spatiotemporal overlap, which may have implications for predator diet, predation rates, population demography, and trophic cascades. We then demonstrate the testability of the hypotheses that emerge from our framework using temporal activity data for 178 predator-prey dyads from published camera trap studies to reveal patterns of human influence on predator-prey activity and overlap. Our framework and case study highlight current challenges, gaps, and advances in linking human-induced animal behavior change to predator-prey dynamics. By using a hypothesis-driven approach to estimate the potential for altered species interactions, we can better predict the ecological consequences of human activities on whole communities.

Keywords: avoidance, attraction, predation, prey refugia, prey switching, spatiotemporal overlap, trophic cascades

Introduction

Human activity has vastly altered animal behavior, often triggering cascading effects on ecosystems (Guiden et al. 2019; Wilson et al. 2020). Yet, complex behavioral responses between multiple players (i.e., predators, prey, competitors) frequently confound our understanding of the relationship between changes in animal behavior and broader ecological outcomes, such as predator diet, predation rate, population demography, competitive exclusion and trophic cascades. Although the effects of humans on species interactions, particularly predation, may influence wildlife coexistence and persistence within human-modified environments (Gaynor et al. 2021), existing understanding of these dynamics is largely anecdotal or context-specific (Wilson et al. 2020). Formally recognizing the role of humans in predator-prey interactions is necessary to inform data collection on species interactions and to anticipate the effects of growing anthropogenic disturbance on wild animals (Mumma et al. 2018; Sinclair et al. 2003).

The field of behavioral ecology has long demonstrated that predators and prey influence each other's spatial distributions (Brown et al., 1999; MacArthur & Pianka, 1966) in a behavioral response race, whereby predators seek to encounter prey while prey seek to avoid predators (Lima & Dill 1990; Sih 1984). Considerable research has established that contextual factors (e.g., patch size, habitat complexity, resources, and species traits) can give an advantage to either player in the predator-prey response race (Fretwell 1972; Laundré 2010; Luttbeg et al. 2020; Schmidt & Kuijper 2015; Sih 1998; Smith et al. 2019a). These conceptual models have allowed ecologists to predict changes to the consumptive (e.g., predation) and non-consumptive (e.g., risk effects) dynamics of ecological communities. However, although classic behavioral response models have been extended to communities with multiple predators (Sih et al. 1998) and changing landscapes (Miller & Schmitz 2019), surprisingly few models have been broadened to describe how human activity influences the contest between predator and prey.

Predicting how human-induced behavior change will affect species interactions is complex, because animal responses to humans are rarely uniform. Many wild animals avoid humans by changing patterns of movement, activity, or consumption (Gaynor et al. 2018; Smith et al. 2015; Tucker et al. 2018), whereas others preferentially use human-dominated areas to gain resources or safety (Berger 2007; Geffroy et al. 2015; Newsome & Van Eeden 2017). Accounting for this variation in animal responses could be key to predicting shifts in predation and potential cascading trophic effects (Kuijper et al. 2016; Yovovich et al. 2021). Each player's (i.e., predator or prey) response to humans can vastly influence the ecological outcome. For example, if a predator avoids human activity but its prey does not, predator and prey may encounter each other less often (Berger 2007; Rogala et al. 2011), possibly reducing predation and/or non-consumptive effects. Alternatively, if both predator and prey perceive human activity as a threat, mutual avoidance of humans may force prey and predator to share space and time. The loss of spatiotemporal refuges that previously stabilized predator-prey coexistence (Schoener 1974; Shamoon et al. 2018), may lead to the increase of predation and its non-consumptive effects.

Here, we present a unifying framework that draws on theory and empirical literature to conceptualize the multiple pathways by which human activity can reshape the overlap between predators and prey. As a proof of concept, we review the literature to evaluate evidence for each pathway in terrestrial mammal predator-prey dyads, and conduct an analysis to test how human activity influenced predator-prey temporal overlap. Further, we highlight current challenges, gaps, and advances in linking animal behavior changes to predator-prey interactions and ecological dynamics in human-modified systems. Our goal is to provide a testable framework that allows researchers to evaluate hypotheses and assess the potential for human-altered species interactions.

A framework for understanding predator-prey responses to human activity

Humans are dominant actors in ecological communities around the world and can alter the behavior of animals by amplifying or dampening perceptions of risk (Gaynor et al. 2019; Geffroy et al. 2020; Hammond et al. 2020; Sih et al. 2011) and foraging opportunities (Geffroy et al. 2015; Newsome et al. 2015; Newsome & Van Eeden 2017), thus reshaping risk-foraging trade-offs. Both human presence and habitat modification (e.g, urbanization, deforestation, agricultural expansion, energy development), which we collectively refer to as 'human activity' henceforth, produce sensory stimuli that can be directly perceived as a threat or benefit (e.g., smell, sound, light, movement; Ditmer et al. 2021; Francis & Barber 2013). Animals may also associate human disturbance with increased foraging opportunities (e.g., garbage, agriculture) (Newsome et al. 2015). In response to these trade-offs, animals can adjust their spatial distribution or temporal activity along a continuum of attraction to avoidance to humans. If individuals in a given animal population consistently alter their spatial and/or temporal distribution, we might expect reverberating impacts on closely interacting species (Muhly et al. 2011; Wilson et al. 2020).

Examining how predators and their prey simultaneously respond to human activity along an avoidance-attraction continuum reveals four primary pathways by which humans can alter predator-prey spatiotemporal overlap (hereafter, 'overlap') (**Fig. 1**). These pathways have the potential to tip the behavioral response race in favor of either player and influence the consumptive or non-consumptive effects of predation on ecosystems. Although linking predator-prey overlap to predation requires evaluating the full predation sequence (i.e., the encounter, pursuit, and successful capture of prey) (Guiden et al. 2019; Lima & Dill, 1990; Suraci et al. 2022), a predator and prey first must occupy the same space at the same time for an encounter to occur. We reduce this complexity to consider overlap a necessary precursor to any predator-prey encounter (Prugh et al. 2019). Human activity can also change the densities of both predator and prey species through non-behavioral pathways (e.g., direct mortality, habitat degradation), with additional potential consequences for their interactions, but here we focus on behaviorally-mediated effects of humans on predators and prey.

Human activity increases predator-prey overlap

There are two pathways through which human activity can increase the overlap between a predator and its prey, potentially tipping the behavioral response race in favor of the predator. First, **mutual attraction** to human activity (*i.e.,* synanthropy) may increase predator-prey encounter rates **(Fig. 1 quadrant I)**. For example, the attraction of black bears (*Ursus americanus*) to human food led to increased predation of mutually attracted red-backed voles (*Clethrionomys gapperi*) feeding nearby (Morris 2005). Second, **mutual avoidance** of human activity may cause a predator and prey to increase overlap to avoid a shared perceived risk **(Fig. 1 quadrant III)**. For instance, in Manas National Park, India, tigers (*Panthera tigris*) and ungulate prey constrained their spatiotemporal activity to avoid humans in the park, thus increasing overlap with one another (Lakhar et al. 2020).

Human activity decreases predator-prey overlap

There are two pathways by which human activity can decrease the overlap between a predator and its prey, potentially tipping the behavioral response race in favor of prey. First, predators may avoid human activity while prey do not, creating a spatial or temporal **prey refuge** (**Fig. 1 quadrant IV;** Berger 2007; Muhly et al. 2011). Prey refuges (also called 'human shields') occur in environments where the absence of large predators for fear of people allows prey species to reduce their anti-predator behavior (Shannon et al. 2014) or selectively use human-modified habitats that predators avoid (Gaynor et al. 2022). Second, prey may avoid human activity while predators do not (Fleming & Bateman 2018). This case may entail **prey switching** (**Fig. 1 quadrant II**), whereby predators either select different prey (*e.g.* synanthropic or domestic prey) or benefit from using human subsidies (*e.g.*, garbage, agriculture) in areas of high human activity, affording human-avoidant prey a refuge (Murdoch 1969; Murdoch & Oaten 1975; Newsome et al. 2015). For instance, in Maharashtra, India, 87% of leopard (*Panthera pardus*) diet in human-dominated areas consisted of domestic animals, reducing consumption of wild species (Athreya et al. 2016).

Human activity does not alter predator-prey overlap

Human activity may have no clear effect on the overlap among predators and prey, obscuring "winners" or "losers" in the predator-prey behavioral response race. This condition is likely to emerge when neither ecological player responds to human activity. Such lack of response could indicate at least four underlying mechanisms (Smith et al. 2021) including, but not limited to, high tolerance thresholds for human activity, perception of humans as non-threatening, intrinsic or extrinsic constraints on behavioral adjustments, and temporary transitions between avoidance and attraction. A true lack of response can only be measured when an animal does not alter its behavior despite consistency in the density of competitors, predators, and resources across a human-use gradient. Because community composition also generally varies with anthropogenic disturbances (Ordeñana et al. 2010), fully characterizing the conditions underlying non-response to humans may require additional non-observational approaches, such as experiments (e.g., Suraci et al. 2019) or simulations (e.g., Thompson et al. 2018).

Case study: Measuring human influence on predator-prey temporal overlap

Our framework formalizes four pathways for how human activity may alter predator-prey overlap, yet, it remains imperative to test support for these proposed hypotheses. As a proof of concept, we evaluated hypothesis support from a literature review of studies that measured temporal activity and overlap of predators and prey at paired settings of high and low human use (see **Supplementary Information**). We limited our analysis to terrestrial mammals with a body mass >1kg in line with recent research suggesting that medium and large-bodied terrestrial mammals exhibit varied responses to human activity (Frey et al. 2020; Suraci et al. 2021). We focused our review on published camera trap studies reporting predator-prey temporal overlap, given that the temporal dimension is often overlooked, easily standardized, and eliminates confounding lethal or density effects that may influence spatial indices.

Overall, we identified 178 predator-prey dyads from 19 camera trap studies, spanning five continents and including forest, savanna, shrubland, and desert ecosystems (see **Supplementary Information**). We examined evidence for each of the four behavioral response pathways (mutual avoidance, mutual attraction, prey refuge, and prey switching) by quantifying changes in the diurnal activity ratio (i.e., proportion of time active when humans were most active) between paired settings of low and high human use for each predator and associated prey

(**Fig. 2a**). Then, to evaluate how altered activity patterns affected the degree of temporal overlap between predator-prey dyads, we measured the difference in temporal overlap for each dyad between paired settings of high and low human use (**Fig. 2b**). Ultimately, testing our framework empirically revealed that predator-prey dyads exhibited responses for all four predicted pathways, but that these response pathways may have more nuanced overlap outcomes than previously appreciated.

We found that predators and prey altered their diel activity in areas of high vs. low human use, in patterns that reflected all four behavioral response pathways (**Fig. 2a**). Surprisingly, congruent activity shifts (i.e., mutual attraction to or avoidance of human activity) did not consistently increase temporal overlap between predator-prey dyads, nor did temporal overlap decrease among all predator-prey dyads exhibiting opposite activity shifts (**Fig. 2b**). Our analysis revealed several predator-prey dyads that exhibited opposite diel responses to high human activity (i.e., prey refugia or prey switching; one ecological player becomes more nocturnal while the other becomes more diurnal) and increased overlap with one another at high human activity (**Fig. 2b**). For instance, although black-tailed jackrabbits (*Lepus californicus*) decreased diurnal activity and their predator bobcat (*Lynx rufus*) increased diurnal activity at sites of high human use, these activity pattern shifts ultimately resulted in higher temporal overlap between the two species (see **Supplementary Information;** Baker & Leburg 2018). This finding reveals an alternative outcome, whereby human-avoidant prey tolerate high overlap with a predator rather than tolerate high human activity (also see Zbyryt et al. 2018). Thus, hypothesis testing within our framework can highlight potential risk tradeoffs among predators, prey, and humans.

Our analyses also revealed that some predator-prey dyads exhibited similar diel responses to human activity (i.e., mutual avoidance or mutual attraction; both predator and prey become more diurnal or nocturnal) yet decreased overlap with one another, divergent from predictions of our framework (**Fig. 2b**). This finding may reveal maintenance of temporal partitioning between predators and prey at a fine scale, despite human-induced activity shifts (Ferreiro-Arias et al. 2021). In such cases, maintaining fine-scale spatiotemporal partitioning with both natural and human predators could come at the cost of altered stress and fecundity (Tuomainen & Candolin 2011) or increased overlap among competitors (Smith et al. 2018; Manlick & Pauli 2020; Sévêque et al. 2020). Ecological outcomes for these scenarios might include increased intraspecific competition (Carter et al. 2015; Wang et al. 2015) and resource limitation (Muhly et al. 2011), rather than increased predation encounter risk, as key drivers of population dynamics.

Linking predator-prey overlap to ecological outcomes

Our framework (**Fig. 1**) provides testable hypotheses regarding the influence of humans on predator-prey behavior and overlap. Researchers might apply this framework to empirical data to draw conclusions about what additional empirical work must be done to identify the mechanisms that drive these patterns. Taken together, these concepts, as well as a few key considerations and emerging empirical methods, can help researchers link human-altered predator-prey overlap to ecological outcomes including predator diet, predation rates, competitive exclusion, trophic interactions.

A key consideration in linking predator-prey overlap to ecological outcomes is that altered overlap of dyads may not predict the distribution of predation events (Suraci et al. 2022). Prey might continue to avoid predators at fine scales, maintaining spatiotemporal partitioning despite high overlap. In such cases, non-consumptive effects (i.e., stress that leads to lower fecundity) may emerge if prey employ energetically costly anti-predator behaviors to avoid both humans and predators (Frid & Dill 2002; Soudijn et al. 2020). Pairing multi-species behavioral studies with demographic or physiological studies will be needed to determine whether consumptive or non-consumptive effects of predation change as a result of human-altered predator-prey overlap (e.g., Zbyryt et al. 2018).

Measuring human impacts on animal responses at the appropriate scale can also be key to accurately identifying ecological outcomes of behavioral shifts. Conceivably, predators and prey may respond to different human stimuli (including various auditory, olfactory, and visual cues), and at different scales. This can lead to situations where one species may be attracted to human activity at a broad spatial scale (for example, to forage on anthropogenic food sources), but both predator and prey avoid humans at fine spatial scales (e.g., Rogala et al. 2011). When possible, studies that measure animal behavior across spatiotemporal scales will be most informative. When this is not feasible, researchers might consider how the goal of the study and the ecology of the system correspond to tradeoffs associated with choosing various sampling designs (e.g., see Steidl & Powell 2006).

Comprehensive assessments of human influence on predator-prey interactions consider both spatial and temporal dimensions of predator-prey overlap, because prey may avoid predators in one dimension (i.e., space or time) despite high overlap in another dimension. If human activity increases predator-prey overlap in space, prey may still safely exploit risky places by foraging during predator downtimes (Beauchamp 2007). Methods like GPS telemetry and camera trapping facilitate inference on both spatial and temporal distribution simultaneously. Furthermore, using indices that simultaneously estimate predator-prey overlap in space and time, such as occupancy models with a continuous-time detection process (Kellner et al. 2022) or Bayesian time-dependent observation models (Ait Kaci Azzou et al. 2021), can avoid these issues and provide more accurate estimates of human impact on encounter probabilities. Applying our proposed framework to such inferences would provide a rigorous test of how humans influence predator-prey outcomes across dimensions.

As humans modify the contest between predators and prey, complex feedbacks among multiple players can obscure the true mechanisms driving an observed pattern. Human activity can influence each ecological player, while predator and prey simultaneously influence each other. As a result, it is often difficult to disentangle, for instance, whether a prey refuge pattern is the consequence of (a) prey attraction to human activity, or (b) prey exploitation of a predator-free zone. To resolve these types of uncertainty, researchers may consider using additional controlled experiments to further isolate and test the hypothesized drivers of an observed response to human activity (e.g., Sarmento & Berger 2017).

While our framework explicitly considers predator-prey relationships as dyads, rarely are predators and prey in obligate pairings. Human activity may influence prey choice, for example when predators have multiple prey, or reshape multi-predator effects on prey with more than one predator (Sih et al. 1998). To advance predictions of how human activity will affect species interactions, it will be beneficial to apply this framework to combinations of predators, prey, and competitors (Mills & Harris 2020). One promising avenue of research lies in comparing how humans alter predator-prey activity and overlap in diverse versus simplified food webs (e.g., see Sévêque et al. 2020). Researchers can deploy these research designs to identify whether predators, prey, competitors, or human disturbance are driving the predominant patterns of dietary preference and predation rate.

Future research might also consider how human influence on predator-prey overlap, encounter, or predation, is linked to the functional traits (e.g., body size, hunting mode, circadian rhythm) of each interactor (see **Supplementary Information**). For instance, nocturnal prey may outperform diurnal human-avoidant predators forced to hunt at night, limiting encounter risk despite high overlap between predator and prey (Beauchamp 2007). One successful approach to clarifying whether altered overlap results in altered predation is using multispecies camera trap studies in tandem with diet composition studies (e.g., Smith et al. 2018). Pairing camera and diet data can allow researchers to connect overlap to predation non-invasively, avoiding the more costly and effort-intensive research designs that use GPS telemetry clusters and animal necropsy data to estimate predation.

In certain cases, human influence on predator-prey overlap may be temporary and without lasting consequences for ecological communities. For instance, if predators and prey habituate to human activity over time (Blumstein 2016), encounter rates may be maintained, and the predator-prey response race may continue unaltered by humans. Yet in this case, the rise of human-wildlife conflict and use of lethal or non-lethal deterrents may in turn affect animal behavior and predator-prey overlap (Manlick & Pauli 2020). Researchers can use iterative experiments that measure how multiple ecological players habituate or sensitize to human disturbance (e.g., Uchida & Blumstein 2021) to better capture which of the four possible human-induced response pathways predict shifts in encounter risk over time.

Identifying thresholds of human activity that alter animal behavior will be key to drawing useful inference from human impact studies and improving our understanding of when altered interactions may have reverberating impacts across ecosystems. Examples of such studies include comparison of animal response to motorized versus non-motorized recreation (Larson et al. 2016), leashed versus unleashed domestic dogs (Reed & Merenlender 2011), exurban versus suburban development (Merenlender et al., 2009; Smith et al. 2019b), dense versus dispersed oil development (Sawyer et al. 2020), and the influence of human presence versus the human footprint (Nickel et al. 2020; Suraci et al. 2021). Such measurements can aid in creating specific guidelines for human activity near wildlife. Ultimately, these research designs will help anticipate how predators and prey respond to humans in rapidly changing landscapes.

Concluding remarks

Behavioral ecology is increasingly recognized as a valuable aspect of population and ecosystem management (Gaynor et al. 2021), yet complex behavioral interactions among predators, prey, and humans (Kuijper et al. 2016) challenge the application of theory to practical solutions. Nonetheless, understanding species interactions remains key to the coexistence and persistence of wildlife, and ecosystem function, in human-modified systems. For example, anthropogenic effects on prey may sometimes need to be minimized before predator recovery and predator-prey interactions can be restored (Lahkar et al. 2020). Unfortunately, the daunting task of studying or modeling complex behavioral feedbacks among players in this ecological game has deterred progress in understanding the ecology of landscapes characterized by high human activity. Investment in models that explain how humans modify species interactions, rather than solely species richness or abundance, is critical to fundamental ecology and the implementation of science-based management and conservation practice. Adopting our framework can help researchers identify patterns of human influence on strongly interacting species and test possible mechanisms driving broader ecological outcomes.

Acknowledgements

We thank the researchers who graciously shared data with us, making the insights of this synthesis possible. We are grateful to the Brashares and Middleton lab groups for their encouragement and comments on the early versions of this idea. AV was supported by an NSF Graduate Research Fellowship and the Mary M. Yang & H. William Kuni Environmental Stewardship Fund.

Conflict of interest

The authors have no conflicts of interest to declare.

References

Ait Kaci Azzou, S., Singer, L., Aebischer, T., Caduff, M., Wolf, B., & Wegmann, D. (2021). A sparse observation model to quantify species distributions and their overlap in space and time. *Ecography*, 44(6), 928–940.

Athreya, V., Odden, M., Linnell, J. D. C., Krishnaswamy, J., & Karanth, K. U. (2016). A cat among the dogs: leopard Panthera pardus diet in a human-dominated landscape in western Maharashtra, India. *Oryx*, 50(1), 156–162.

Baker, A. D., & Leberg, P. L. (2018). Impacts of human recreation on carnivores in protected areas. *PloS ONE*, 13(4), e0195436.

Beauchamp, G. (2007). Exploring the role of vision in social foraging: what happens to group size, vigilance, spacing, aggression and habitat use in birds and mammals that forage at night. *Biol. Rev.*, 82(3), 511–525.

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.*, 3(6), 620–623.

Blumstein, D. T. (2016). Habituation and sensitization: new thoughts about old ideas. *Anim. Behav.*, 120, 255–262.

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.*, 80(2), 385–399.

Carter, N., Jasny, M., Gurung, B., & Liu, J. (2015). Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. *Glob. Ecol. Conserv.*, 3, 149–162.

DeWitt, T. J., Sih, A., & Wilson, D. S. (1998). Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.*, 13(2), 77-81.

Ditmer, M. A., Stoner, D. C., Francis, C. D., Barber, J. R., Forester, J. D., Choate, D. M. et al. (2021). Artificial nightlight alters the predator–prey dynamics of an apex carnivore. *Ecography*, 44(2), 149-161.

Ferreiro-Arias, I., Isla, J., Jordano, P., & Benítez-López, A. (2021). Fine-scale coexistence between Mediterranean mesocarnivores is mediated by spatial, temporal, and trophic resource partitioning. *Ecol. Evo.*, 11(22), 15520-15533.

Fleming, P. A., & Bateman, P. W. (2018). Novel predation opportunities in anthropogenic landscapes. *Anim. Behav.*, 138, 145-155.

Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Front. Ecol. Environ.*, 11(6), 305-313.

Fretwell, S. D. (1972). Theory of habitat distribution. In: *Populations in a Seasonal Environment*, Princeton Univ. Press, Princeton, NJ, pp. 79–114.

Frey, S., Volpe, J. P., Heim, N. A., Paczkowski, J., & Fisher, J. T. (2020). Move to nocturnality not a universal trend in carnivore species on disturbed landscapes. *Oikos*, 129(8), 1128–1140.

Frid, A., & Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Cons. Ecol.*, *6*(1), 11–27.

Gates, J. E., & Gysel, L. W. (1978). Avian nest dispersion and fledging success in field-forest ecotones. *Ecology*, *59*(5), 871–883.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*. 360(6394), 1232-1235.

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of fear: spatial patterns of risk perception and response. *Trends Ecol. Evol.*, 34(4), 355–368.

Gaynor, K. M., Cherry, M. J., Gilbert, S. L., Kohl, M. T., Larson, C. L., Newsome, T. M. et. al. (2021). An applied ecology of fear framework: linking theory to conservation practice. *Anim. Conserv.*, 24(3), 308–321.

Gaynor, K. M., McInturff, A., & Brashares, J. S. (2022). Contrasting patterns of risk from human and non-human predators shape temporal activity of prey. *J. Anim. Ecol.*, 91(1), 46–60.

Geffroy, B., Samia, D. S. M., Bessa, E., & Blumstein, D. T. (2015). How Nature-Based Tourism Might Increase Prey Vulnerability to Predators. *Trends Ecol. Evol.*, 30(12), 755–765.

Geffroy, B., Sadoul, B., Putman, B. J., Berger-Tal, O., Garamszegi, L. Z., Møller, A. P. et al. (2020). Evolutionary dynamics in the Anthropocene: Life history and intensity of human contact shape antipredator responses. *PLoS Biol.*, 18(9), e3000818.

Gorini, L., Linnell, J. D. C., May, R., Panzacchi, M., Boitani, L., Odden, M. et al. (2012). Habitat heterogeneity and mammalian predator-prey interactions. *Mamm. Rev.*, 42(1), 55–77.

Guiden, P. W., Bartel, S. L., Byer, N. W., Shipley, A. A., & Orrock, J. L. (2019). Predator–Prey Interactions in the Anthropocene: Reconciling Multiple Aspects of Novelty. *Trends Ecol. Evol.*, 34(7), 616–627.

Hammond, T. T., Ortiz-Jimenez, C. A., & Smith, J. E. (2020). Anthropogenic change alters ecological relationships via interactive changes in stress physiology and behavior within and among organisms. *Integr. Comp. Biol.*, 60(1), 57–69.

Hill, J. E., DeVault, T. L., Wang, G., & Belant, J. L. (2020). Anthropogenic mortality in mammals increases with the human footprint. *Front. Ecol. Environ.*, 18(1), 13–18.

Kellner, K. F., Parsons, A. W., Kays, R., Millspaugh, J. J., & Rota, C. T. (2022). A Two-Species Occupancy Model with a Continuous-Time Detection Process Reveals Spatial and Temporal Interactions. *J. Agric. Biol. Environ. Stat.*, 1–18.

Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K. et al. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proc. R. Soc. B: Biol. Sci.*, 283(1841), 20161625.

Lahkar, D., Ahmed, M. F., Begum, R. H., Das, S. K., & Harihar, A. (2020). Responses of a wild ungulate assemblage to anthropogenic influences in Manas National Park, India. *Biol. Conserv.*, 243, 108425.

Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS ONE*, 11(12), e0167259.

Laundré, J. W. (2010). Behavioral response races, predator--prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology*, *91*(10), 2995–3007.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canad. J. Zool.*, 68(4), 619–640.

Luttbeg, B., Hammond, J. I., Brodin, T., & Sih, A. (2020). Predator hunting modes and predator--prey space games. *Ethology*, 126(4), 476–485.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *Am. Nat.*, 100(916), 603–609.

Manlick, P. J., & Pauli, J. N. (2020). Human disturbance increases trophic niche overlap in terrestrial carnivore communities. *Proc. Nat. Acad. Sci.*, 117(43), 26842–26848.

Merenlender, A. M., Reed, S. E., & Heise, K. L. (2009). Exurban development influences woodland bird composition. *Landsc. Urban Plan.*, 92(3-4), 255–263.

Miller, J.R.B. & Schmitz, O.J. (2019). Landscape of fear and human-predator coexistence: Applying spatial predator-prey interaction theory to understand and reduce carnivore-livestock conflict. *Biol. Conserv.*, 236, 464–473.

Mills, K. L., & Harris, N. C. (2020). Humans disrupt access to prey for large African carnivores. *ELife*, 9, e60690.

Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L. et al. (2017). The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *J. Anim. Ecol.*, 86(4), 749–765.

Morris, D. W. (2005). Paradoxical avoidance of enriched habitats: have we failed to appreciate omnivores? *Ecology*, 86(10), 2568–2577.

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., & Musiani, M. (2011). Human activity helps prey win the predator-prey space race. *PLoS ONE*, 6(3), e17050.

Mumma, M. A., Gillingham, M. P., Parker, K. L., Johnson, C. J., & Watters, M. (2018). Predation risk for boreal woodland caribou in human-modified landscapes: evidence of wolf spatial responses independent of apparent competition. *Biol. Conserv.*, 228, 215–223.

Murdoch, W. W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.*, 39, 335–354.

Murdoch, W. W., & Oaten, A. (1975). Predation and population stability. *Adv. Ecol. Res.*, 9, 1–131.

Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J. et al. (2015). The ecological effects of providing resource subsidies to predators. *Glob. Ecol. Biogeogr.*, 24(1), 1–11.

Newsome, T. M., & Van Eeden, L. M. (2017). The effects of food waste on wildlife and humans. *Sustainability*, 9(7), 1269.

Nickel, B. A., Suraci, J. P., Allen, M. L. & Wilmers, C. C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biol. Conserv.*, 241, 108383.

Ordeñana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., Siudyla, S. et al. (2010). Effects of urbanization on carnivore species distribution and richness. *J. Mammal.*, 91(6), 1322-1331.

Prugh, L. R., Sivy, K. J., Mahoney, P. J., Ganz, T. R., Ditmer, M. A., van de Kerk, M. et al. (2019). Designing studies of predation risk for improved inference in carnivore-ungulate systems. *Biol. Conserv.*, 232, 194–207.

Reed, S. E., & Merenlender, A. M. (2011). Effects of management of domestic dogs and recreation on carnivores in protected areas in northern California. *Conserv. Biol.*, 25(3), 504–513.

Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A., Coleshill, J., & Musiani, M. (2011). Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. *Ecol. Soc.,* 16(3), 16–40.

Sarmento, W. M., & Berger, J. (2017). Human visitation limits the utility of protected areas as ecological baselines. *Biol. Conserv.*, 212, 316–326.

Sawyer, H., Lambert, M. S., & Merkle, J. A. (2020). Migratory disturbance thresholds with mule deer and energy development. *J. Wildl. Manage.*, 84(5), 930–937.

Schmidt, K., & Kuijper, D. P. J. (2015). A “death trap” in the landscape of fear. *Mamm. Res.*, 60(4), 275–284.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, 185(4145), 27–39.

Sévêque, A., Gentle, L. K., López-Bao, J. V, Yarnell, R. W., & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biol. Rev.*, 95(6), 1689–1705.

Shamoon, H., Maor, R., Saltz, D., & Dayan, T. (2018). Increased mammal nocturnality in agricultural landscapes results in fragmentation due to cascading effects. *Biol. Conserv.*, 226, 32–41.

Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS One*, 9(4), e94630.

Sih, A. (1984). The behavioral response race between predator and prey. *Am. Nat.*, 123(1), 143–150.

Sih, A., Englund, G. and Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.*, 13, 350–355.

Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.*, 4(2), 367–387.

Sinclair, A. R. E., Mduma, S., & Brashares, J. S. (2003). Patterns of predation in a diverse predator-prey system. *Nature*, 425(6955), 288–290.

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proc. R. Soc. B: Biol. Sci.*, 282(1802), 20142711.

Smith, J. A., Thomas, A. C., Levi, T., Wang, Y., & Wilmers, C. C. (2018). Human activity reduces niche partitioning among three widespread mesocarnivores. *Oikos*, 127(6), 890–901.

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., Bidder, O. R., & Middleton, A. D. (2019a). Habitat complexity mediates the predator–prey space race. *Ecology*, 100(7), e02724.

Smith, J. A., Duane, T. P., & Wilmers, C. C. (2019b). Moving through the matrix: promoting permeability for large carnivores in a human-dominated landscape. *Landsc. Urban Plan.*, 183, 50–58.

Smith, J. A., Gaynor, K. M., & Suraci, J. P. (2021). Mismatch Between Risk and Response May Amplify Lethal and Non-lethal Effects of Humans on Wild Animal Populations. *Front. Ecol. Evol.*, 9, 140.

Soudijn, F. H., van Kooten, T., Slabbekoorn, H., & de Roos, A. M. (2020). Population-level effects of acoustic disturbance in Atlantic cod: a size-structured analysis based on energy budgets. *Proc. R. Soc. B*, 287(1929), 20200490.

Stankowich, T. (2008). Ungulate flight responses to human disturbance: a review and meta-analysis. *Biol. Conserv.*, *141*(9), 2159–2173.

Steidl, R. J., & Powell, B. F. (2006). Assessing the effects of human activities on wildlife. *The George Wright Forum*, 23(2), 50–58.

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol. Lett.*, 22(10), 1578-1586.

Suraci, J. P., Gaynor, K. M., Allen, M. L., Alexander, P., Brashares, J. S., Cendejas-Zarelli, S. et al. (2021). Disturbance type and species life history predict mammal responses to humans. *Global Change Biol.*, 27, 3718–3731.

Suraci, J. P., Smith, J. A., Chamaillé-Jammes, S., Gaynor, K. M., Jones, M., Luttbeg, B. et al. (2022). Beyond spatial overlap: harnessing new technologies to resolve the complexities of predator–prey interactions. *Oikos*, e09004.

Thompson, P. L., MacLennan, M. M., & Vinebrooke, R. D. (2018). Species interactions cause non-additive effects of multiple environmental stressors on communities. *Ecosphere*, 9(11), e02518.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C. et al. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359(6374), 466–469.

Tuomainen, U., & Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biol. Rev.*, 86(3), 640-657.

Uchida, K., & Blumstein, D. T. (2021). Habituation or sensitization? Long-term responses of yellow-bellied marmots to human disturbance. *Behav. Ecol.*, 32(4), 668–678.

Wang, Y., Allen, M. L., & Wilmers, C. C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biol. Conserv.*, 190, 23–33.

Wilson, M. W., Ridlon, A. D., Gaynor, K. M., Gaines, S. D., Stier, A. C., & Halpern, B. S. (2020). Ecological impacts of human-induced animal behaviour change. *Ecol. Lett.*, 23(10), 1522-1536.

Yovovich, V., Thomsen, M., & Wilmers, C. C. (2021). Pumas' fear of humans precipitates changes in plant architecture. *Ecosphere*, 12(1), e03309.

Zbyryt, A., Bubnicki, J. W., Kuijper, D. P., Dehnhard, M., Churski, M., & Schmidt, K. (2018). Do wild ungulates experience higher stress with humans than with large carnivores? *Behav. Ecol.*, 29(1), 19–30.

Fig. 1. Humans can alter predator and prey behavior, spatiotemporal overlap, and encounter probability via four major pathways: mutual attraction, mutual avoidance, prey refuge, and prey switching. Predator (y-axis) and prey (x-axis) respond to human activity along a continuum of attraction to avoidance. Similar responses of predator and prey to human activity are predicted to result in increased predator-prey overlap and encounter probability, whereas opposite responses are predicted to reduce overlap and potential encounters.

Fig. 2. Human influence on predator-prey temporal activity and overlap based on review of camera trap studies between paired settings of low and high human use. (a) Humans altered diel activity in mammal predator-prey dyads via four major pathways: mutual attraction, mutual avoidance, prey refuge, and prey switching. Lines reflect the relative magnitude and direction of diel activity response toward nocturnality (-1) or diurnality (1) for each predator-prey dyad at paired settings of low and high human use (n = 178 predator-prey dyads, 19 studies). (b) Change in predator-prey temporal overlap between settings of low and high human use did not vary predictably with predator-prey activity responses (n = 167 predator-prey dyads, 16 studies). Similar predator-prey responses (i.e., prey refuge, prey switching) to humans did not result in increased overlap between dyads, likewise opposite predator-prey responses (i.e., mutual attraction, mutual avoidance) to humans did not result in decreased overlap between dyads as predicted. Black dots represent change in temporal overlap for each dyad. Red error bars represent estimated marginal means and ± 95% confidence interval.

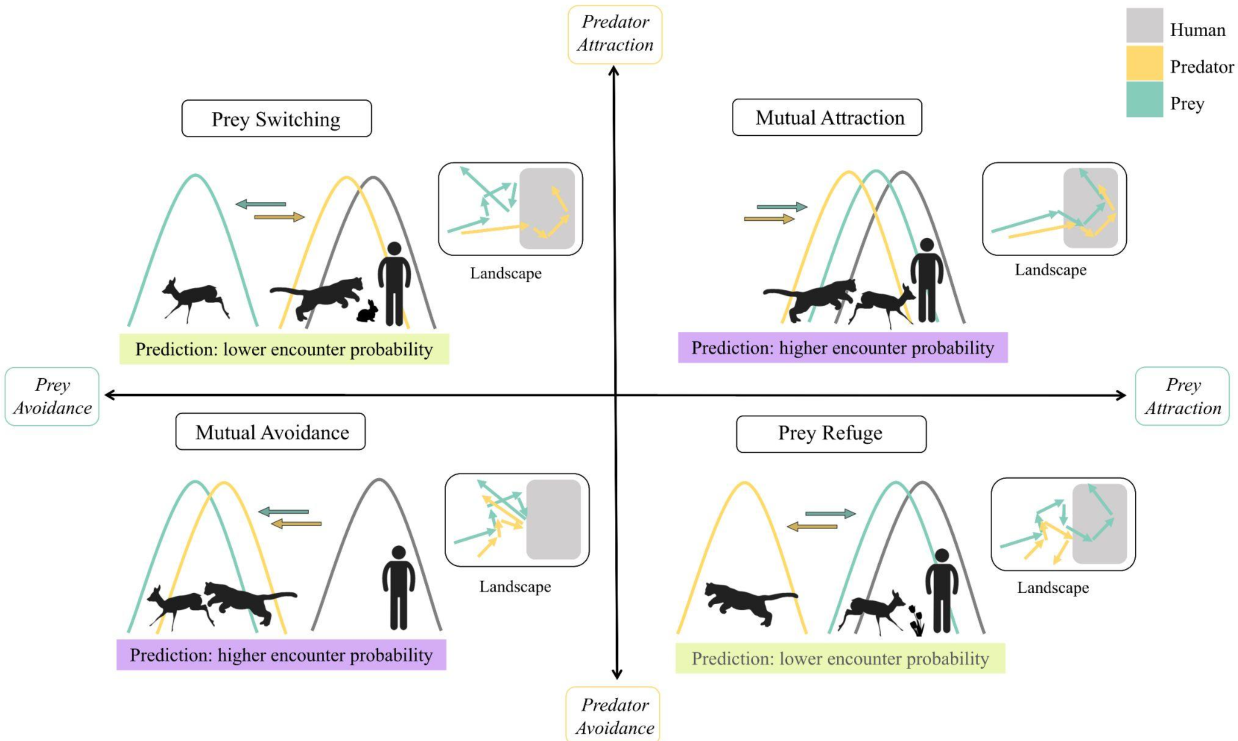

Fig. 1. Humans can alter predator and prey behavior, spatiotemporal overlap, and encounter probability via four major pathways: mutual attraction, mutual avoidance, prey refuge, and prey switching. Predator (y-axis) and prey (x-axis) respond to human activity along a continuum of attraction to avoidance. Similar responses of predator and prey to human activity are predicted to result in increased predator-prey overlap and encounter probability, whereas opposite responses are predicted to reduce overlap and potential encounters.

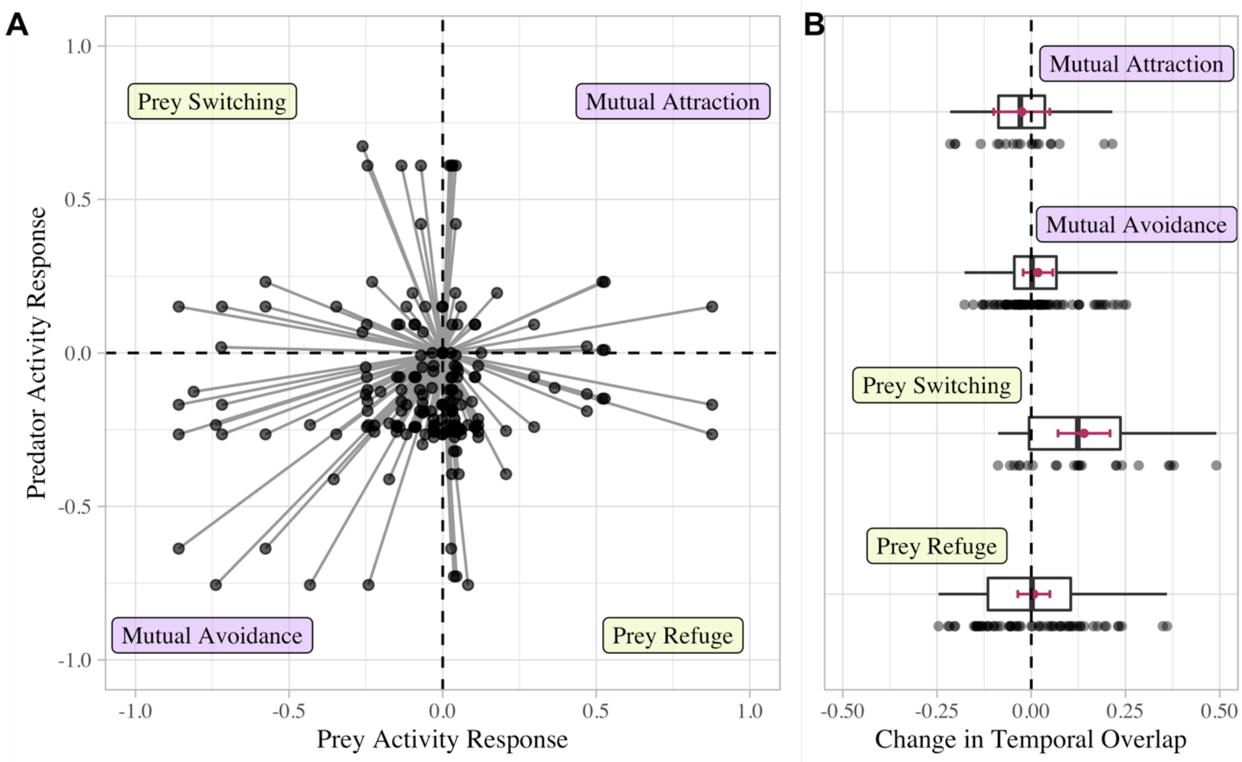

Fig. 2. Human influence on predator-prey temporal activity and overlap based on review of camera trap studies between paired settings of low and high human use. (a) Humans altered diel activity in mammal predator-prey dyads via four major pathways: mutual attraction, mutual avoidance, prey refuge, and prey switching. Lines reflect the relative magnitude and direction of diel activity response toward nocturnality (-1) or diurnality (1) for each predator-prey dyad at paired settings of low and high human use (n = 178 predator-prey dyads, 19 studies). (b) Change in predator-prey temporal overlap between settings of low and high human use did not vary predictably with predator-prey activity responses (n = 167 predator-prey dyads, 16 studies). Similar predator-prey responses (i.e., prey refuge, prey switching) to humans did not result in increased overlap between dyads, likewise opposite predator-prey responses (i.e., mutual attraction, mutual avoidance) to humans did not result in decreased overlap between dyads as predicted. Black dots represent change in temporal overlap for each dyad. Red error bars represent estimated marginal means and ± 95% confidence interval.