# Towards a temporal ecology of wildlife populations and communities

By

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## Dissertation Abstract

Ecology is becoming a data-intensive science characterized by broad-scale and automated data collection, bringing new challenges and opportunities to the field. The overarching goal of this dissertation is to explore these challenges and opportunities with a focus on Snapshot Wisconsin, a volunteer-powered camera-trap network. The first two chapters discuss practicalities in applying Snapshot Wisconsin to wildlife management. **Chapter 1** reviews methods to estimate abundance of unmarked animal species from camera-trap data, while **Chapter 2** shows how camera-trap data can be combined with more traditional datastreams (harvest data). Beyond these practicalities, one of the most exciting aspects of the ecological data revolution is the opportunity to explore the role of time in underpinning ecological processes, an opportunity afforded by the increasingly fine temporal resolution of data collection. Time can be considered an ecological resource (i.e., a niche dimension) akin to spatial habitat or food resources. Just as other niche dimensions can be destroyed, altered, or improved by human activities, “temporal habitat” is changing in the Anthropocene. For example, the diel activity patterns (e.g., nocturnal vs. diurnal) of organisms have evolved as adaptations to fluctuations in abiotic conditions (e.g., light and temperature). Thus, flexibility in activity patterns might increase buffering capacity from extreme conditions presented by climate change, which is the focus of **Chapter 3** with reference to white-tailed deer *Odocoileus virginianus* and winter weather. Similarly, biotic context influences the activity timing of animals, and human disturbance may alter partitioning of space and time by communities. **Chapter 4** explores this possibility, and, considering 74 species pairs, documents that cameras in human-dominated landscapes detect pairs in more rapid succession, indicating that disturbance compresses spatiotemporal niche dimensions. Finally, many unknowns remain regarding the ecological effects of human-induced changes to the activity timing of species; **Chapter 5** proposes hypotheses to motivate future work and outlines possible approaches for doing so. In summary, this dissertation demonstrates how ecologists can capitalize on emerging datastreams and highlights future opportunities for temporal ecology.

## Dissertation Introduction

Ecologists have traditionally ventured afield to count, measure, tag, or otherwise observe organisms. That tradition is changing (Hampton et al. 2013; Farley et al. 2018; Nathan et al. 2022). As the data revolution continues to unfold, ecologists are trading their boots for keyboards and their binoculars for dataframes. This dissertation explores some of the challenges and opportunities facing ecology in light of the data revolution.

Ecology's data revolution is fueled by increasing automation and participation in data collection. Technology that would have been unimaginable to early ecologists, including satellite remote sensing (Turner et al. 2003; Tatem et al. 2008) and tags small enough to track insects over many kilometers (Knight et al. 2019) are now available and routinely used by ecologists. Along a similar timeline as the technological revolution, citizen science—the collection of data by volunteers—has blossomed and continues to expand the spatiotemporal domains over which ecologists can acquire data (Dickinson et al. 2010). However, automation and participation have played out primarily in separate arenas. A hybrid approach—in which many volunteers collect automated measurements—promises to propel ecology farther into its evolution as a data-intensive discipline. This dissertation exists thanks to just such an effort: Snapshot Wisconsin.

Snapshot Wisconsin is a regional wildlife-monitoring network powered by volunteers and orchestrated by the Wisconsin Department of Natural Resources (WDNR). The volunteers collect data with camera traps, which have emerged in the last several decades as one of the most important technologies with which to monitor wildlife, especially for cases in which animals cannot be captured or when multiple species are being studied (Burton et al. 2015). Camera traps provide a particularly rich source of data when they can be organized into networks that can monitor multiple locations continuously through time (Steenweg et al. 2017). Started in 2014 as a NASA-funded collaboration between the WDR and the University of Wisconsin-Madison, Snapshot Wisconsin has achieved this goal; at the current writing (April 2022), the project has accumulated >64 *million* photos from >2,000 camera locations (Townsend et al. 2021). In 2018, I joined this collaboration as a PhD student to explore the challenges and opportunities of applying Snapshot Wisconsin data to wildlife management efforts and ecological questions.

The first two dissertation chapters are practical, intended the address the question of *"How do we use Snapshot Wisconsin data to inform wildlife science?"* **Chapter 1** (Gilbert et al. 2021b) is a practitioner's guide to the possible methods to estimate abundance of unmarked (not individually recognizable) wildlife populations based on camera-trap data. The essential summary is that, while multiple methods exist, no single method is a "silver bullet", meaning that practitioners should proceed cautiously in estimating abundance of unmarked wildlife populations. **Chapter 2** (Gilbert et al. 2021a) describes how an emerging datastream (camera-traps) can be integrated with an existing datastream (harvest records). The most important message of this paper is that, while it is appealing to leverage all possible data sources, it is important to formally address disparities (e.g., in spatial resolution) among datasets when trying to integrate them (Pacifici et al. 2019; Zipkin et al. 2021).

The final three chapters are unified in their exploration of time as ecological currency of interest in light of the data revolution. In particular, collection of data at ever-finer temporal resolution allows researchers to pursue questions that would be intractable under traditional, non-automated forms of data collection. To be clear, time has been of interest to ecologists from the birth of ecology as a disciple—seminal studies of population dynamics and vegetation succession, for example, focused explicitly on ecological processes through time (Clements 1916; Elton & Nicholson 1942). However, time has lagged behind space in research attention (Post 2019). In fact, while "spatial ecology" has emerged as something of a discipline (I frequently hear researchers define themselves as "spatial ecologists"), "temporal ecology" seems like a rather foreign term (Wolkovich et al. 2014; Post 2019; Yang 2020). As a simple demonstration, the search term "spatial ecology" returned 2,144 results on Web of Science on 6 April 2022, while the term "temporal ecology" returned only 67. As reflected in the latter three dissertation chapters, I believe ecology is on a trajectory of considering time a resource and/or a driver of ecological processes, rather than a mere nuisance variable or subscript (Kronfeld-Schor & Dayan 2003; Post 2019).

**Chapter 3** (Gilbert et al. 2022) encourages a view of time as a refugium—a shelter—from environmental stressors. Refugia are typically conceptualized as places to which organisms can retreat during stressful times (e.g., glacial periods over long timescales or heatwaves over short timescales; Hannah et al. 2014). However, especially for short-term stressors, strategically timing essential activities may help organisms reduce their exposure to stressful conditions (van der Vinne et al. 2019). One such stressor is variable winter weather. Wisconsin winters—legendary for their harshness—are changing. Snow cover is declining while average temperatures are rising; however, cold air outbreaks (the proverbial "polar vortex") are driving occasional extreme cold waves (Cohen et al. 2018; Thompson et al. 2021). Considering the white-tailed deer (*Odocoileus virginianus*), the third chapter quantifies changes in deer activity in time as well as over space in response to daily weather fluctuations—a goal enabled by many cameras operating continuously through time. We found that deer become more day-active and less night- and dawn-active during anomalously cold days, which we interpret as behavioral flexibility to track the warmest portion of the diel cycle.

**Chapter 4** (in review) evaluates how the partitioning of space and time by wildlife communities is changed by human disturbance. Space and time are two of the essential dimensions of the niche; species must cooccur in space and time to compete or otherwise interact (Suraci et al. in press). However, it is not clear how humans affect the sharing of space and time by wildlife communities. There is evidence from multiple systems that human disturbance compresses the time (Gaynor et al. 2018) and space (Tucker et al. 2018) available for species to share. However, it is also possible that human disturbance may expand the space and time available for communities to partition by, for example, providing resource subsidies or excluding apex predators (Estes et al. 2011; Oro et al. 2013). In this chapter, we used data from Snapshot Wisconsin to evaluate spatiotemporal cooccurrence of 74 pairs of wildlife species and also used spatiotemporal cooccurrence to create species networks for each camera site. Nearly all species pairs showed greater spatiotemporal cooccurrence in disturbed landscapes; in addition, the species networks in disturbed areas were more densely connected in disturbed landscapes. These results indicate that human disturbance, beyond altering the species and stage in nature's play, may also essentially rewrite the script of how species interact by altering how they partition time and space.

**Chapter 5** (in preparation) outlines research opportunities for ecologists to explore the ecological effects of shifts in activity timing in response to human disturbance. It is not clear whether activity-timing shifts in response to human-mediated stressors (e.g., climate change, urbanization) are adaptive (Lamb et al. 2020) or represent ecological traps (Robertson et al. 2013), or whether these shifts have ramifications at multiple levels of biological organization (Wilson et al. 2020). To motivate future work, we present hypotheses regarding the ecological effects of human-mediated shifts in activity timing; for example, we hypothesize that the effects of activity-timing shifts show macroecological patterns due to latitudinal gradients in photoperiod seasonality (Huffeldt 2020) and organismal physiological tolerances (Janzen 1967). We also review considerations for researchers seeking to pursue such hypotheses, for example encouraging researchers to link activity timing to other parameters (Wilson et al. 2020) and to evaluate intraspecific variation in activity timing (Hertel et al. 2017). As technology improves, ecologists will be better equipped to understand how animals respond to altered "timescapes" and how those responses affect ecological processes.

This dissertation highlights the diversity of objectives that can be achieved when automation and mass participation of data collection are combined. As the first two chapters demonstrate, camera-trap networks—alone or in tandem with other datastreams—can generate data to map species occurrence or abundance, key state variables for managing wildlife populations. Beyond such population-level applications, because such networks collect data at fine spatiotemporal resolution, it is possible to pursue behavioral questions (typically pursued at local scales) at landscape or regional scales. In addition, since cameras monitor multiple species simultaneously, they can inform questions pertaining to multispecies and community ecology questions. In my view, some of the most exciting opportunities afforded by such camera trap networks relate to time. At a technical level, the continuous form of data collection is driving an evolution from discrete-time modeling frameworks developed for surveys by field researchers (MacKenzie et al. 2002) to continuous-time analyses (Emmet et al. 2021). On a more conceptual level, I believe that these trends in data collection will elevate time to the level of space in research attention. This dissertation chapters focus on daily activity timing and spatiotemporal partitioning, but other temporal applications (e.g., phenology) are viable as well. I look forward to watching these trends and seeing how continued advances in technology and participation will shape the field of ecology.

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**Chapter 1: Abundance estimation of unmarked animals based on camera-trap data**

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**Abstract**

The rapid improvement of camera traps in recent decades has revolutionized biodiversity monitoring. Despite clear applications in conservation science, camera traps have seldom been used to model the abundance of unmarked animal populations. We sought  to summarize the challenges facing abundance estimation of unmarked animals, compile an overview of existing analytical frameworks, and provide guidance for practitioners seeking a suitable method. When a camera records multiple detections of an unmarked animal, one cannot determine whether the images represent multiple mobile individuals or a single individual repeatedly entering the camera viewshed. Furthermore, animal movement obfuscates a clear definition of the sampling area and, as a result, the area to which an abundance estimate corresponds. Recognizing these challenges, we identified 6 analytical approaches and reviewed 927 camera-trap studies published from 2014 to 2019 to assess the use and prevalence of each method. Only about 5% of the studies used any of the abundance-estimation methods we identified. Most of these studies estimated local abundance or covariate relationships rather than predicting abundance or density over broader areas. Next, for each analytical approach, we compiled the data requirements, assumptions, advantages, and disadvantages to help practitioners navigate the landscape of abundance estimation methods. When

seeking an appropriate method, practitioners should evaluate the life history of the focal taxa, carefully define the area of the sampling frame, and consider what types of data collection are possible. The challenge of estimating abundance of unmarked animal populations persists; although multiple methods exist, no one method is optimal for camera-trap data under all circumstances. As analytical frameworks continue to evolve and abundance estimation of unmarked animals becomes increasingly common, camera traps will become even more important for informing conservation decision-making.

## Introduction

Biodiversity loss is accelerating as humans exert greater pressure on natural ecosystems (Vitousek et al. 1997; Butchart et al. 2010). In response to biodiversity loss, patterns and changes in population abundance and density are critical metrics for guiding conservation decision-making (Mace et al. 2008). Traditional abundance estimation methods are challenging to implement because they usually require capturing and marking animals. In recent decades, camera traps have emerged as a valuable tool to monitor animal populations and represent a possible alternative to traditionally intensive methods (Fig. 1) (O'Connell et al. 2011; Burton et al. 2015; Wearn & Glover-Kapfer 2019). Researchers around the world have used camera traps for diverse analytical goals, including behavior, occupancy, and species richness (Burton et al. 2015). To date, however, camera-trap studies that estimated abundance focused almost exclusively on marked (individually distinguishable) animals (Fig. 1). As a result, estimating the abundance of unmarked animal populations remains a significant challenge and represents a key frontier for camera trapping.

We had 3 goals with this review: describe the challenges facing abundance estimation of unmarked populations; review current methods for estimating animal abundance with data from camera traps, with a focus on the data requirements, assumptions, advantages, and disadvantages of each method; and highlight considerations for practitioners designing studies to model the abundance of unmarked animals with camera-trap data.

### ***Challenges of individual identity, animal movement, and space***

Many traditional methods of abundance estimation require marked individuals (Borchers et al. 2002; Williams et al. 2002). Camera-trap data can be used in these frameworks in rare cases when individuals are identifiable by pelage pattern or natural marks such as scars (Karanth & Nichols 1998; Jimenez et al. 2017). However, distinguishing individuals in images or marking animals is often not feasible (but see Schneider et al. [2019] for review of emerging computer vision methods to distinguish unmarked individuals from images). Consequently, multiple detections of an unmarked animal at a camera could represent multiple mobile individuals or a single relatively sedentary individual. In addition, a camera will not always detect an animal that is present; therefore, an abundance estimator must disentangle the multiple-mobile versus single-sedentary problem while correcting for animals present but not detected.

Abundance requires reference to space to be meaningful, either by reporting the area to which an abundance estimate corresponds (e.g., we estimated an abundance of 10 squirrels in the 5 $km^2$ reserve) or by estimating population density (e.g., we estimated a density of 2 squirrels/$km^2$). However, the effective sampling area of a camera—the area a camera samples given how far detected animals move—is generally unknown because animal movement information is usually unknown (Fig. 2). Consequently, the sampling frame—the broader study area about which one wishes to make inference—is generally also unknown (Fig. 2). Various methods address the challenge of space in one of three ways. First, some methods estimate abundance at camera locations without any reference to space, meaning one must assign the estimate to an arbitrary area (Fig. 2a). Second, some methods estimate abundance within an area explicitly defined in the model by accounting for where and when animals are detected (Fig. 2B). Third, some methods estimate density within the collective viewsheds of cameras, which are assumed to be representative of the sampling frame (Fig. 2C-E). Depending on the method, the viewshed is defined as either the area within which animals can be detected by a camera's motion sensor (detection viewshed) or the total area photographed by a camera (total viewshed).

***Methods to estimate abundance or density from camera-trap data***

*Recent use of 6 analytical frameworks*

We reviewed the data requirements, assumptions, sampling requirements, extensions, advantages, and disadvantages of the following methods: site-structured models (including *N*-mixture and Royle-Nichols models), unmarked spatial capture-recapture, random encounter model, time-to-event model, space-to-event and instantaneous sampling models, and distance sampling (Table 1). We assembled this list of methods as an exhaustive list of abundance estimation methods that do not require identification of individuals.

We completed a literature review to assess the relative prevalence of the reviewed methods in published camera-trap studies. We used Web of Science to search for papers published from 2014 to 2019. We used the following search terms: (*camera trap** OR *remote camera**) AND (*wildlife* OR *mammal** OR *bird**) (Burton et al. 2015). We completed the search on 2 May 2019 and reviewed the returned 1,150 papers. We omitted studies that did not use camera traps, were exclusively review articles, or were purely methodological (e.g., software development). We reviewed the 927 papers that satisfied these criteria and noted whether the study used any of the methods we reviewed and whether the population studied was unmarked. For studies that used the methods we reviewed, we noted the inferential goal of the study (estimating abundance or density or both, quantifying covariate relationships, predicting abundance or density or both at unsampled locations). Furthermore, we evaluated whether each study listed or evaluated model assumptions. We classified a study as having evaluated assumptions if it deployed cameras in such a way to satisfy model assumptions, modified analyses to test or account for possible assumption violation, or discussed possible assumption violation and implications for interpretation.

Fifty-one studies (5.5%) used the methods we reviewed for estimating abundance (Fig. 1). Of the 876 (94.5%) other studies, the most frequent analytical focuses were indices of relative abundance (310, 35.4%), behavior (304; 34.8%), occupancy (181; 20.7%), and species richness (178; 20.3%). Indices of relative abundance based on detection rate were the default analytical option for many practitioners (Sollmann et al. 2013b; Burton et al. 2015). Of the 51 studies in which the methods we identified were used, 22 (43%) used the Royle-Nichols model, 14 (27%) the random encounter model, 13 (25%) *N*-mixture models, and 4 (8%) unmarked spatial capture-recapture. The former three methods were the earliest to appear in the literature (2003, 2008, and 2004, respectively); thus, their prevalence in our sample is unsurprising. We did not capture any studies that used distance sampling methods, the time-to-event model, the space-to-event model, or the instantaneous sampling model, beyond the publications that introduced these methods. The majority (39; 76%) of studies using the reviewed methods reported abundance or density, fewer studies (21; 41%) reported covariate relationships, and only 3 (6%) predicted abundance over a broader area. Finally, 28 (55%) of the studies listed model assumptions, and 23 (45%) evaluated assumption violations in some way.

*Site-structured models*

Site-structured models use replicated survey periods at independent locations (i.e., sites) to jointly model ecological and observational processes (Kéry & Royle 2015). These models estimate abundance at each camera location, but because animals move beyond the detection viewshed, the effective sampling area of each camera location is some larger unknown region (Fig. 2A). Under the umbrella of site-structured models, the Royle-Nichols (RN) model (Royle & Nichols 2003) requires binary detection-nondetection data (whether or not a species is present in any photos during each replicate survey period), whereas *N*-mixture models (Royle 2004) require count data (number of animals present in photos during each replicate survey period).

Both models assume population closure of the site (no individuals enter or leave the population via birth, immigration, death, or emigration); equal detection probability for all individuals; no false-positive detections (i.e., misidentifications or double counting of individuals); and independent detections of individual animals at a camera (Table 1) (Royle & Nichols 2003; Royle 2004). Practically speaking, the latter assumption implies that once an animal is detected by a camera, it is not any more likely to be detected during subsequent replicate survey periods. Site-structured models do not require random camera placement, meaning that cameras can be placed on trails or baited. However, cameras should be spaced far enough apart that individuals are not detected at multiple cameras to ensure there is no overlap in the effective sampling areas of cameras. Either method can be extended to jointly analyze data for multiple species (Yamaura et al. 2011, 2012) or open populations (Dail & Madsen 2011; Rossman et al. 2016). The *N*-mixture model can be extended to accommodate correlated detections (Martin et al. 2011). The RN does not perform well for common species because the binary detection histories will be saturated with 1s and therefore contain little information. In such cases, count data used with *N*-mixture models is preferable (Kéry & Royle 2015; Dénes et al. 2015).

Site-structured models have the advantage of quantifying spatial variation in abundance as a function of covariates. However, site-structured models have the major disadvantage that the effective sampling area of cameras is unknown (Fig. 2) (Kéry & Royle 2015). Consequently, predicting abundance (based on covariate patterns) across the remainder of the sampling frame or beyond is difficult and can only be done by arbitrarily defining predictive grid cell sizes (Fig. 2A). Finally, site-structured models are sensitive to assumption violations (Barker et al. 2018; Knape et al. 2018; Link et al. 2018; Duarte et al. 2018). For example, Link et al. (2018) demonstrated that minor closure violation cause biased abundance estimates that cannot be detected with goodness-of-fit checks. These limitations suggest that, unless their assumptions can be verified, site-structured models should be treated as indices of relative abundance.

*Unmarked spatial capture-recapture (USCR)*

USCR is part of the spatial capture-recapture family of models, which estimate density by considering when and where animals are detected within an array of detectors (Fig. 2B) (Royle et al. 2014). Unlike traditional forms of spatial capture-recapture that require marked animals, USCR treats the individual identities of animals as latent variables (Chandler & Royle 2013; Royle et al. 2014). Unmarked spatial capture-recapture estimates density by modeling the number and distribution of animal activity centers as a realization of a spatial point process within the state space, an explicit region of inference defined within the model (Fig. 2B) (Royle et al. 2014). These models require spatially correlated detection data—meaning that individual animals must be detected at multiple cameras—to make inference about the number and locations of the activity centers (Chandler & Royle 2013; Ramsey et al. 2015).

With USCR, one assumes that activity centers of individuals do not move, that activity centers exhibit no attraction or repulsion, that animals will be detected less frequently as the distance between their activity centers and a camera increases, and that the sampling frame contains all of the activity centers of animals detected by cameras (Chandler & Royle 2013). Unlike site-structured models that require cameras to be independent, USCR requires arrays of cameras spaced such that individuals are detected at multiple cameras, although the counts at individual cameras are assumed to be independent from one sampling occasion to the next (Table 1 & Fig. 2B) Chandler & Royle 2013).

The ability to estimate abundance within a clearly defined area is an advantage of USCR. While the basic formulation of USCR does not accommodate spatial variation in density, Evans and Rittenhouse (2018) extended USCR to quantify spatial variation in density as a function of covariates, although further research is warranted to corroborate the robustness of such an approach. A disadvantage of USCR is that it is computationally expensive and restricted to Bayesian frameworks, which may be a barrier for some practitioners (Royle et al. 2014). Furthermore, USCR produces highly imprecise density estimates (Royle et al. 2014; Augustine et al. 2019) and is sensitive to choice of priors on σ, a parameter that can be interpreted as the spatial scale over which a camera detects an individual (Sun et al. 2014; Burgar et al. 2018). Finally, USCR is sensitive to assumption violations; density estimates will be biased if animal density and camera spacing relative to animal movement fall beyond a narrow range of values (Ramsey et al. 2015; Augustine et al. 2019).

*Random encounter model (REM)*

The REM treats individual animals like ideal gas particles and estimate density within the collective detection viewsheds of a camera array (Fig. 2C). The REM estimates density from encounter rates (number of photographs from cameras per unit time), animal movement speed, and the camera's detection viewshed, which consists of the radius of the effective detection zone and the horizontal angle of view (Rowcliffe et al. 2008).

Importantly, the REM assumes that cameras are placed randomly relative to animal movement, meaning that cameras should be randomly deployed within habitat classes proportional to their use by animals and not target features that attract animals (e.g., trails). The model assumes population closure of the sampling frame and that individual animals move independently of one another; for species that travel in groups, average group size is required (Rowcliffe et al. 2008). Finally, the REM assumes that individual photos represent independent contacts between an animal and a camera (Table 1) (Rowcliffe et al. 2008).

An advantage of the REM is that it estimates density for a clearly defined area—the collective viewshed of cameras. However, extrapolating to the abundance for the sampling frame is problematic because the sampling frame must be arbitrarily defined unless the study targets a region with impermeable boundaries (e.g., an island [Fig. 2C]). A further disadvantage of the REM is that it requires data that are difficult to measure, specifically animal movement speed (requiring telemetry or intensive observations of behavior) and detection viewshed (requiring measurement of detection zone in the field calibrated to species of different sizes). Another disadvantage is that the REM does not allow inference about spatial variation in density, thus inhibiting covariate-driven prediction of density beyond the sampling frame. Finally, assumption violations, particularly nonrandom camera placement relative to animals, leads to biased estimates. For example, Cusack et al. (2015) used the REM to estimate African lion (*Panthera leo*) density and found that cameras placed beneath shade trees (which attracted lions) led to biased estimates compared to a comprehensive population census. They overcame the bias by discarding daytime data and using only nighttime data when lions exhibited less attraction to trees (Cusack et al. 2015). The REM has recently been extended to the random encounter and staying time (REST) model, which does not require animal movement data. Instead, the model relies on staying time, which is the amount of time an animal remains within the viewshed (Nakashima et al. 2018). Staying time can be measured either from videos or consecutive photos (Nakashima et al. 2018). The REST model accommodates spatial variation in density as a function of environmental covariates (Nakashima et al. 2020). These advances suggest that the REST model may replace the REM in terms of feasibility and utility, though the same assumptions and sampling design considerations apply (Nakashima et al. 2018).

*Time-to-event model (TTE)*

The TTE uses detection rate and animal movement data to estimate density within the collective detection viewshed of cameras (Table 1; Fig. 2C) (Moeller et al. 2018). Specifically, the TTE model uses the time (defined as the number of sampling periods) until the first detection of an animal within a longer sampling occasion (which can start at an arbitrary moment) to estimate density (Moeller et al. 2018).

The TTE assumes population closure of the sampling frame, that camera locations are random relative to animals, and that animal detections are independent both in space (e.g., once an animal is detected at one camera, it is not any more likely to be detected by a neighboring camera) and time (e.g., an animal will not linger in front of a camera). Finally, in its current formulation, the TTE model assumes that detection is perfect.

Unlike the REM, the TTE has the advantage of accommodating spatial variation in abundance across cameras with covariates (Moeller et al. 2018), which enables predictive modeling across the remainder of the sampling frame. However, the TTE has the disadvantage of relying upon restrictive assumptions. In particular, perfect detection is rarely a valid assumption for motion-triggered cameras. The TTE also relies heavily upon the assumption that animals are distributed according to a Poisson process; any consequences of violating this fundamental assumption have yet to be demonstrated. Additionally, while the density estimate clearly corresponds to the collective viewsheds of individual cameras, inference about the sampling frame requires arbitrary definition of the sampling frame's area. For example, Moeller et al. (2018) defined the sampling frame of their empirical example as a 2-km buffer around GPS fixes of an elk (*Cervus canadensis*) herd. In real-world applications, practitioners seldom have GPS-marked animals to define a biologically meaningful sampling frame. Moreover, placing a buffer around GPS points can be problematic and is analogous to defining the effective sampling area of cameras with site-structured methods. Generally, the difficulty of defining a sampling frame hampers predictive modeling of density beyond the sampling frame. Finally, simulations by Moeller et al. (2018) suggest the TTE is negatively biased, particularly for slow-moving species.

*Space-to-event model (STE) and instantaneous sampling model (IS)*

The STE model is an extension of the TTE model in which time-lapse photos are used. Cameras must be programed to take photos at predefined times, regardless of whether an animal is present (Fig. 2D). The IS is an extension of the STE that uses counts of animals in view of each time-lapse photo (Moeller et al. 2018).

Both methods share the assumptions of the TTE model; however, the assumption of perfect detection is likely more tenable with time-lapse photos. Additionally, the STE and IS rely upon the total viewshed (in a time-lapse photo, an animal may be detected beyond the distance at which it would trigger the motion sensor), meaning the viewshed must be measured based on the maximum distance at which animals can be identified, likely with the help of natural landmarks (Moeller et al. 2018). The STE estimates density from space (the number of cameras) until the first animal detection at a given moment in time (Moeller et al. 2018).

The STE and IS have the advantage of not requiring animal movement data; density estimates are independent of animal movement because each sampling occasion is a snapshot moment in time. An additional advantage is that simulations demonstrate that the STE and IS are unbiased and seem robust to some variation in movement rate and population density (Moeller et al. 2018). A major disadvantage is that time-lapse photos may make few or no detections of rare species, disqualifying STE and IS as options for such species. Additionally, neither STE or the IS model can accommodate heterogeneity in abundance across cameras. Therefore, predicting abundance (within the sampling frame and beyond) is problematic. Finally, as with the TTE model, while the density estimate clearly corresponds to the collective viewsheds of cameras, making inference about the abundance of the sampling frame relies heavily upon design considerations.

*Distance sampling (DS)*

Distance sampling is a well-developed class of methods for estimating population density (Buckland et al. 2001). Broadly, DS involves surveying transects or points, estimating the distance to detected animals, and fitting a detection function to the estimated distances, which allows the number of undetected animals to be estimated (Buckland et al. 2001; Borchers et al. 2002). Unlike traditional DS surveys in which observers move relative to animals, camera-based DS surveys involve stationary detectors that survey moving animals (Howe et al. 2017). The Howe et al. (2017) formulation of DS requires measurement of each camera’s detection viewshed, a calibrated measurement of the distance to the detected animal in each photo, and a measure of temporal sampling effort across all cameras (Fig. 2E) (Hofmeester et al. 2017; Howe et al. 2017).

With DS, one assumes that detectors are randomly located relative to animals, animals at distance 0 are perfectly detected, animals are detected at their initial location, distances are measured accurately, and detections are independent events in space and time (Table 1) (Buckland et al. 2001). Camera traps must representatively sample the focal landscape and not target trails or other features that attract animals (Buckland et al. 2001; Howe et al. 2017).

Like several other methods (Fig. 2C-E), DS has the advantage of estimating density within a clearly defined area (the collective camera viewsheds), although making inference about the sampling frame requires strong assumptions about sampling design. Distance sampling has the disadvantage of requiring data that may be difficult to collect (viewshed, distances). The Howe et al. (2017) formulation of DS does not permit inference about spatial variation in density, either within one camera array or across a sampling frame encompassing multiple arrays (Kéry & Royle 2015). Consequently, predictive mapping of abundance within or beyond the sampling frame based on covariate models is not possible. Hierarchical distance sampling permits modeling spatial variation in abundance as a function of covariates, but hierarchical DS has yet to be implemented with camera traps (Kéry & Royle 2015). Finally, DS is unbiased only when the study species is active and available for detection; researchers must account for the target taxon's activity pattern and censor times when animals are not active or available (Howe et al. 2017; Cappelle et al. 2019).

## ***Practitioner considerations***

Over the past 15 years, several methods have emerged to model abundance of unmarked animals from camera trap data. The intricacies of each method and the inconsistencies among them can be overwhelming for practitioners. Therefore, we compiled a series of considerations to guide practitioners to the method most appropriate for their application (Fig. 3).

### *Defining the focal species*

Although camera traps offer the opportunity of broad-spectrum monitoring of multiple species simultaneously (Burgar et al. 2019; Wearn & Glover-Kapfer 2019), interspecific variation in life-history traits renders multispecies abundance estimation problematic. When planning a study, researchers should select a focal species (or a group of species with similar traits) and use knowledge of its life history to inform study design. First, how much space does an individual use over the time frame of the study? One can find home-range estimates and movement behavior in the literature for many species. Such information is helpful for defining a sampling frame or determining the proper spacing of cameras. For instance, site-structured models assume that camera locations are independent, meaning that individual animals should not be detected by multiple cameras. One could space cameras at least twice the diameter of an animal's home range apart to ensure that individuals are not detected by multiple cameras.

Second, how does the species use features of the landscape? Several of the methods (Table 1, Fig. 2C-E) require cameras to be located randomly relative to animal distributions. If a species uses forest 75% of the time and prairie 25% of the time, randomly selecting camera locations without stratifying proportional to habitat use will result in nonrandom camera positions relative to animals.

Third, roughly how common is the species? For a common species, methods requiring random camera placement or time-lapse photos may be appropriate, whereas a rare species may require nonrandom camera placement or bait to even be detected (Moeller et al. 2018).

Finally, multispecies abundance estimation requires careful study design to be well founded. For example, Rich et al. (2019) estimated densities of seven marked species by employing a hybrid sampling design: half of the cameras were placed systematically with wide spacing (thus permitting density estimation for wide-ranging species) and the other half were placed randomly within the same area (thus falling within a range of distances of the systematic cameras, permitting density estimation for smaller-ranging species). For multiple unmarked species with different movement behavior, one could perhaps subset camera locations to account for differences among species, but the bottom line is that no single survey design is optimal for all species (Rich et al. 2019).

*Defining the focal area*

Prior to selecting a method, practitioners should consider the size of the study area relative to animal movement. For example, if 50 cameras are available and the sampling frame is small (e.g., a 5-$km^2$ reserve for a medium-bodied mammal), site-structured models are not appropriate because animals will surely be detected by multiple cameras. Instead, STE or DS approaches may be better choices, or USCR if the extent of animal movement is contained by the sampling frame (Fig. 3; Table 1). However, if the sampling frame is an entire province (e.g., 5,000 $km^2$), a site-structured approach is an option because cameras can be placed at distances greater than the distances moved by individual animals. Practitioners should also consider whether predicting abundance within areas not sampled by cameras should be an objective of their study. Prediction requires quantifying spatial variation in abundance as a function of covariates, which cannot be accommodated by all methods (Table 1).

*Sufficiency of relative abundance*

Given the pitfalls of abundance estimation, researchers should evaluate their objectives to determine whether an index of relative abundance is a viable alternative to estimating absolute abundance (Fig. 3) (Yoccoz et al. 2001). An index of relative abundance can be any variable that strongly correlates with absolute abundance (Johnson 2008). Relative abundance can be a helpful state variable to guide management and conservation efforts, particularly when estimating species-environment relationships are the primary objective rather than estimating population size. For example, if relative abundance of an animal is highest in prairies with low amounts of woody vegetation, then conservation strategies should focus on reversing shrub encroachment. However, relative abundance should be avoided when absolute abundance is required (e.g., evaluating endangered species recovery).

In the world of camera trapping, indices of relative abundance are usually based on detection rate (e.g., number of detection events/100 trap days) and are widely used in the camera trap literature (Rovero & Marshall 2009; Burton et al. 2015). Indices based on detection rate should be applied and interpreted judiciously, since they confound abundance and animal movement (Broadley et al. 2019). As such, abundance indices based on detection rate are premised on strong assumptions that movement behavior does not change over space or time (Sollmann et al. 2013b; Broadley et al. 2019). Ideally, researchers should calibrate detection rates—preferably to abundance estimates from independent methods—rather than blithely adopting them as replacements for abundance (Rovero & Marshall 2009; Sollmann et al. 2013b). Beyond detection rates, any of the methods we reviewed can be considered indices if their assumptions are violated. Even as indices, these methods provide advantages over indices based on detection rate. One can, for example, partially account for the observation process by using a model that includes detection probability (Sollmann et al. 2013b; Dénes et al. 2015). If one suspects that assumptions are violated, we recommend reporting the possible violations and reporting results as relative rather than absolute abundance (Fig. 3).

*Marking individuals*

Abundance estimation methods that draw upon the identity of individuals are the gold standard. Traditional methods require that all individuals captured be identifiable to individual (Borchers et al. 2002; Royle et al. 2014), but emerging methods accommodate partially marked samples (Royle et al. 2014). This could be the case when only a few animals within a population are marked or when only a subset of individuals can be identified from natural markings in photos (Fig. 3). The most promising methods for partially marked populations are spatial mark-resight models, an extension of the unmarked spatial capture-recapture method presented above (Chandler & Royle 2013). Simulations demonstrate that increasing numbers of marked individuals increases the accuracy and precision of parameter estimates (Chandler & Royle 2013). A further extension of spatial mark-resight models accommodate partially identifiable individuals (e.g., individuals that can be classified into categories such as sex or age group; Augustine et al. 2019). Such categorical marks can increase the reliability and precision of parameter estimates (Augustine et al. 2019).

Marking animals opens the possibility to using integrated population models, which combine demographic data (e.g. telemetry or mark-recapture) with detection data in a single model (Schaub & Abadi 2011; Sollmann et al. 2013a; Zipkin & Saunders 2018).

*Collection of ancillary data*

If marking animals is not feasible, practitioners should evaluate the types of ancillary data that can be collected (Fig. 3). The three major forms of ancillary data for use in the various methods are animal movement, distance to detected animal, and area of camera viewshed (Fig. 2). Animal movement is required for the random-encounter and the time-to-event models. Barring intensive behavioral observations or movement data gleaned from the literature (Rowcliffe et al. 2008), animal movement data requires placing radio or GPS tags on animals, tantamount to marking individuals. If animals must be marked to collect movement data, spatial mark-resight approaches are preferable to the REM and TTE models. Distance to detected animals is required for use with distance sampling. Collecting this information requires either placing distance markers in the field (Hofmeester et al. 2017) or extracting distance ex situ from calibrated reference photos (Caravaggi et al. 2016). Finally, the area of camera viewsheds is required for several methods (Fig. 2). In practice, viewsheds are challenging to measure because a camera's effective detection distance will vary based on vegetation surrounding the camera, weather conditions, and the size of the animal triggering the sensor (Manzo et al. 2012). Finding ways to automate measurements to detected animals and the area of camera viewsheds would be a fruitful way to increase the feasibility of models requiring these ancillary data.

***Validating methods via simulations and empirical comparisons***

Multiple unmarked abundance estimation methods exist and many more will surely emerge. Therefore, a crucial question for practitioners is, which method can be trusted to provide accurate abundance estimates and under what conditions? We therefore suggest a set of simulation studies to evaluate the performance methods under common conditions and comparisons of multiple methods in empirical settings.

While each method has been evaluated individually with simulations, comparison of the methods under a common simulation has not been performed. Such a simulation would begin by placing a known number of animals moving about a virtual landscape. Multiple animal movement processes (e.g., random walk versus Brownian motion) should be evaluated, and multiple species should be simulated that show different movement speeds, home range sizes, and grouping behaviors (Quaglietta & Porto 2019). Moreover, the landscape should incorporate some level of environmental heterogeneity—at least, binary habitat and nonhabitat classes—that influences the position of simulated animals (Sciaini et al. 2018). Next, cameras should be simulated under different sampling scenarios (e.g., systematic or random), varying the number and spacing of cameras. Contacts between animals and the cameras would provide data with which to evaluate the models. Ideally, such simulations could be encapsulated in a program (e.g., an R package) that would accommodate new methods as they emerge and provide practitioners with the ability to compare the performance of methods under conditions relevant to their studies.

Simulations are helpful but must be accompanied by rigorous empirical testing to establish the validity of unmarked abundance estimates in real systems. Although it is possible to simulate multiple types of animal movement in virtual landscapes, it is difficult to know which, if any, of the types accurately represent animals moving through real landscapes. Several empirical comparisons of unmarked methods exist and provide insight into the performance of multiple methods in common systems (Doran-Myers 2018; Burgar et al. 2018; Ruprecht et al. 2020). However, we suggest that further empirical comparisons would be valuable for identifying systems or conditions where abundance estimates from different methods diverge. Because some of the unmarked methods have incompatible sampling requirements, researchers should select two or more methods with similar sampling requirements and compare the abundance estimates that each provides. Such efforts should be paired with simulations that are fine-tuned to the focal system and species to evaluate the veracity of the simulations described above.

### ***Conclusion***

Camera trapping has transformed biodiversity monitoring and continues to grow in popularity. However, abundance estimation of unmarked populations remains a salient frontier for camera trap studies; few researchers (about 5% over the last 5 years) even attempted to estimate absolute abundance of unmarked populations. Several analytical frameworks have been developed to do just that, but each has a unique set of limitations and disadvantages. Ultimately, the analytical approaches face the same challenges and share certain assumptions (e.g., all assume population closure in their basic formulations), but each method addresses the problems of density estimation with unique data and sampling requirements. As a result, data collected for one modeling method will likely not be compatible with another. In general, a given framework addresses the challenges by either collecting more information or making more assumptions. Ancillary data directly address the challenges but can be difficult to collect. Conversely, approaches that rely on assumptions require less data but potentially sacrifice accuracy, precision, and applicability to real systems. We urge practitioners to proceed with caution when making inference about the abundance of unmarked populations. First and foremost, we emphasize that practitioners should design studies with careful attention to the life history of the focal species and the size of the study area. When possible, we encourage practitioners to seek opportunities to mark individuals or reframe their objectives to target relative abundance, being cautious to address the implicit assumptions that underlie even the most basic of indices. Regardless of the method chosen, we urge practitioners to report the assumptions that are made in their analyses and try to evaluate the consequences of violating them. We call for simulation studies to validate the methods under common conditions and further empirical comparisons of the methods in real systems. As the analytical frameworks for camera trap data continue to evolve, cameras will become even more vital to conservation decision-making.

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Table 1. Summary of the output, design considerations, data requirements, and assumptions for each method.

| | | **Site-structured** Kéry & Royle (2015) | **Unmarked SCR** Chandler & Royle (2013) | **REM** Rowcliff et al. (2008) | **TTE** Moeller et al. (2018) | **STE, IS** Moeller et al. (2018) | **DS** Howe et al. (2017) |
|---|---|---|---|---|---|---|---|
| Output | Spatial variation in abundance | X | X | | X | | |
| | Estimate corresponds to known area | | X | | | | |
| | Estimate corresponds to collective viewshed of cameras and is extrapolated to sampling frame | | | X | X | X | X |
| Design | Individuals should not be detected by multiple cameras | X | | | | | |
| | Cameras random relative to animals | | | X | X | X | X |
| | Must censor data to include times only when animals are active | | | X | | | X |
| Data | Area of viewshed | | | X | X | X | X |
| | Animal movement | | | X | X | | |
| | Distance to animal | | | | | | X |
| | Time-lapse photos | | | | | X | |
| Assumption | Closure | X | X | X | X | X | X |
| | No false positive detections | X | X | X | X | X | X |
| | No false negative detections | | | | X | X | |
| | Independent detections | X | X | X | X | X | X |
| | Activity centers do not move | | X | | | | |
| | Animals not attracted or repelled to each other | | X | X | | | |
| | Fewer detections as distance between activity centers and camera increases | | X | | | | |
| | Animals at distance 0 perfectly detected | | | | | | X |
| | Animals detected at initial location | | | | | | X |
| | Distances measured accurately | | | | | | X |

**Figures**

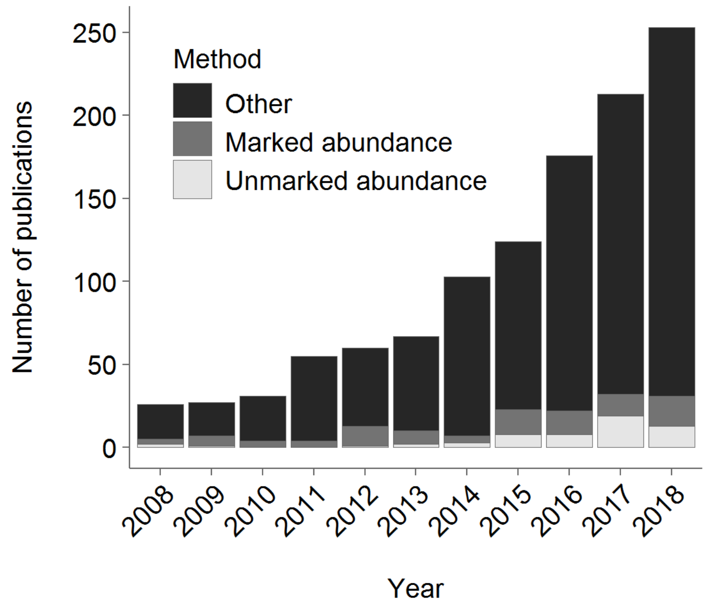
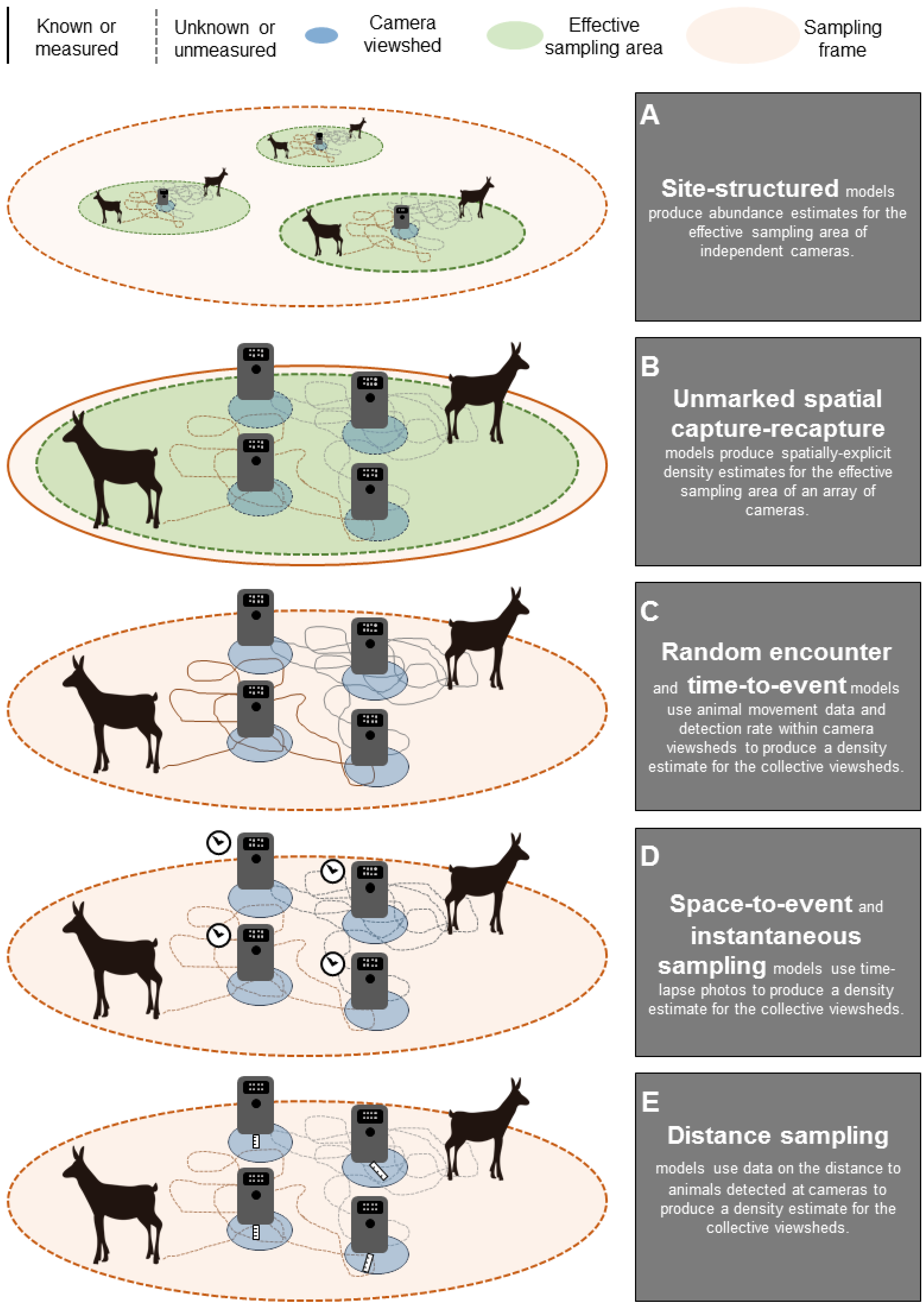
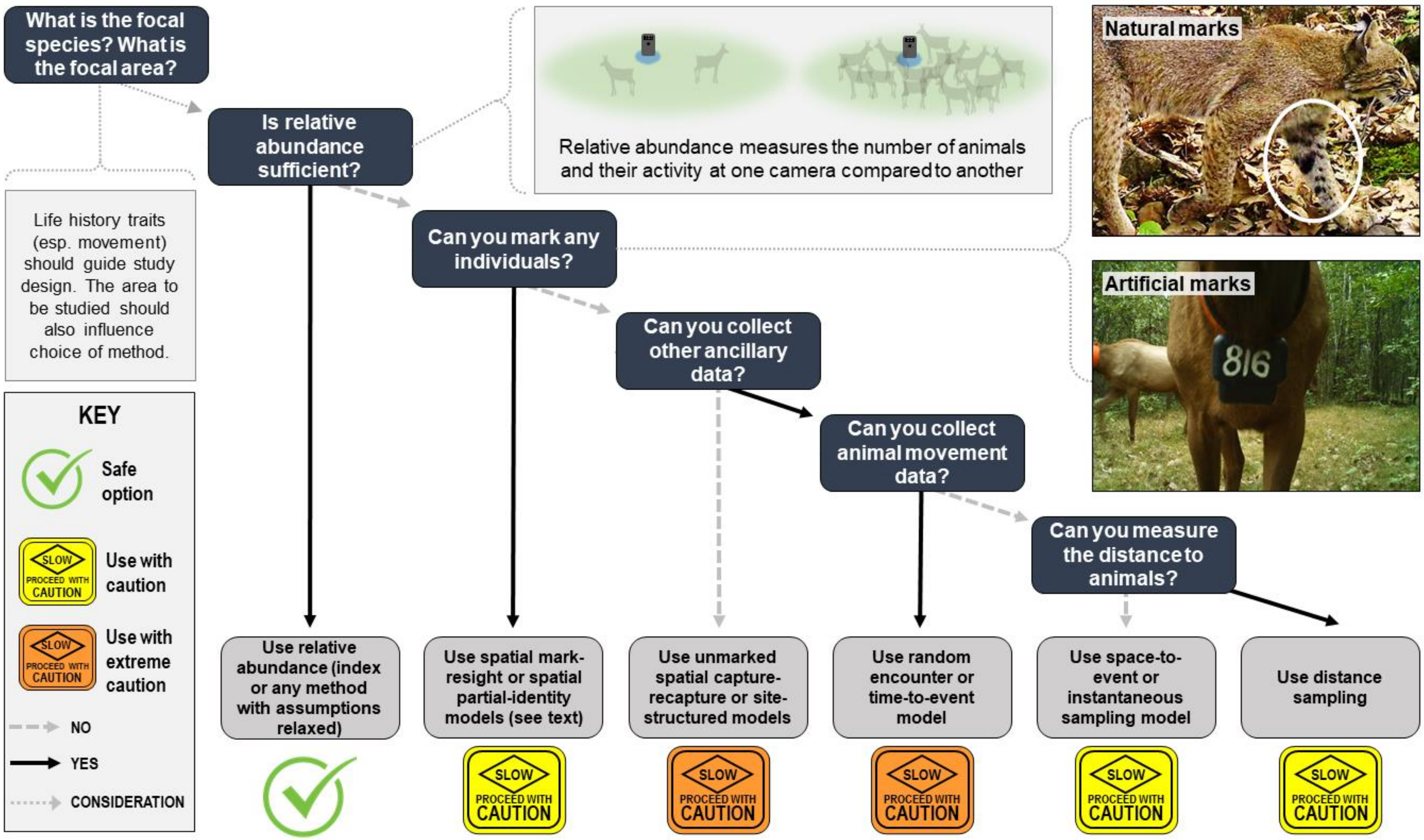



Figure 1. The number of peer-reviewed publications using camera traps has increased rapidly over the last decade. However, the number of studies using abundance estimation methods has lagged behind other applications of camera traps. In particular, the number of studies applying unmarked abundance estimation methods has been increasing only over the last five years. The studies were sampled with *(camera trap* OR remote camera*) AND (wildlife OR mammal* OR bird*)* search terms on Web of Science and filtered to include only empirical field studies.



Known or measured
Unknown or unmeasured
Camera viewshed
Effective sampling area
Sampling frame
A
Site-structured models produce abundance estimates for the effective sampling area of independent cameras.
B
Unmarked spatial capture-recapture models produce spatially-explicit density estimates for the effective sampling area of an array of cameras.
C
Random encounter and time-to-event models use animal movement data and detection rate within camera viewsheds to produce a density estimate for the collective viewsheds.
D
Space-to-event and instantaneous sampling models use time-lapse photos to produce a density estimate for the collective viewsheds.
E
Distance sampling models use data on the distance to animals detected at cameras to produce a density estimate for the collective viewsheds.

Figure 2. Design and data considerations for the methods covered in this review. In (A), the *effective sampling areas* for individual cameras are functions of animal movement and survey length and therefore unknown. In (B), what we show as the *sampling frame* is the prescribed state-space for the spatial process generating the activity centers of individuals. In (C-E), the effective sampling area of a camera is defined as the camera's viewshed, and the camera locations are assumed to be representative of the sampling frame. In (D), the clock symbols represent the need for time-lapse photos, and in (E), the ruler symbols represent the need for distances to detected animals to be measured.



What is the focal species? What is the focal area?
Life history traits (esp. movement) should guide study design. The area to be studied should also influence choice of method.
Is relative abundance sufficient?
Relative abundance measures the number of animals and their activity at one camera compared to another
Can you mark any individuals?
Natural marks
Artificial marks
816
Can you collect other ancillary data?
Can you collect animal movement data?
Can you measure the distance to animals?
Use relative abundance (index or any method with assumptions relaxed)
Use spatial mark-resight or spatial partial-identity models (see text)
Use unmarked spatial capture-recapture or site-structured models
Use random encounter or time-to-event model
Use space-to-event or instantaneous sampling model
Use distance sampling
SLOW
PROCEED WITH
CAUTION
KEY
Safe option
Use with caution
Use with extreme caution
NO
YES
CONSIDERATION

Figure 3. Decision tree for recommended practices of abundance estimation of unmarked populations. Knowledge of the study area and the life history of the focal species should be leading considerations when designing a study. If alternative state variables can be used to achieve objectives, practitioners should pursue those. If marking any individuals (either by natural or artificial marks) is an option, practitioners should explore spatial mark-resight models. If using the methods covered in this review to estimate absolute abundance (rather than relative abundance), practitioners should proceed with caution and carefully evaluate the degree to which assumptions are violated.

**Chapter 2: Integrating harvest and camera trap data in species distribution models**

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**Abstract**

Wildlife managers need reliable information on species distributions (i.e. patterns of occurrence and abundance) to make effective decisions. Historically, managers have relied on harvest records (collected at broad spatial extents but coarse resolution) to monitor wildlife populations. However, emerging citizen-science datastreams can potentially supplement harvest-based monitoring by providing fine-resolution data that permit identification of species-environment relationships needed to predict occurrence and abundance. We combined harvest records and citizen-science camera-trap data in integrated species distribution models (iSDMs) to estimate species-environment relationships and distribution patterns of six wildlife species in Wisconsin, USA. We expected that iSDMs would more precisely estimate species-environment relationships and predict spatial abundance patterns intermediate between camera- and harvest-only SDMs. We also conducted simulations to explore the consequences of incomplete knowledge of harvest effort for estimates of abundance and species-environment relationships. Integrated models produced more precise species-environment relationships than camera-only models in 53% of the relationships we tested; all harvest-only models failed to converge. Moreover, integrated and camera-only models showed low agreement (mean: 19.67%) in identifying abundance “hotspots” but considerably higher agreement (mean: 45.17%) in identifying abundance “cold spots”. Our simulations showed that abundance patterns estimated by iSDMs may suffer from imprecision if harvest effort is poorly measured. We recommend that harvest records be collected at finer spatial resolutions and be paired with in-depth effort reporting. Our work demonstrates the potential for integrating an existing datastream (harvest records) with an emerging one (citizen-science camera-trap monitoring) for modeling species distributions and providing support for wildlife management decisions.

**Keywords:** citizen science; data fusion; hierarchical modeling; joint-likelihood; jurisdictional observation network; species-environment relationships; wildlife management

## Introduction

Effective wildlife management requires knowing where focal species are and are not found. Thus, managers often predict spatial occurrence and abundance patterns based on ***species-environment relationships***, or correlations between environmental variables (e.g., land cover) and detection or count data (Elith et al. 2006; MacKenzie et al. 2018). Agencies (i.e., federal, state and/or provincial wildlife management organizations) typically manage wildlife over broad spatial extents (Fig. S1) that are impractical to sample comprehensively, and thus available datasets are typically at resolutions too coarse to inform species-environment relationships at local scales (Bauder et al.

2020). However, many potential management actions (e.g., habitat manipulations, translocations) are local-scale phenomena, necessitating information about species distributions at fine resolutions to guide decisions (Moilanen et al. 2005; Wiens & Bachelet 2010). *Therefore, wildlife managers should develop ways to use data that can be feasibly collected over broad spatial extents but can inform local-scale decisions.*

Historically, many agencies have used harvest data to monitor wildlife populations. Harvest data typically exist at broad extent (e.g., entire provinces) but at coarse resolution (counties or management units; Fig. S1). Agencies can use these data (in addition to age and sex ratios of harvested animals) in population reconstruction models to infer population size or trends within management units (Ryder 2018; Allen et al. 2018). While this approach has been instrumental, harvest data have largely not been used to infer species-environment relationships (and subsequently, fine-resolution occurrence or abundance patterns; (Bauder et al. 2020). Knowledge of fine-resolution species distributions is important for targeted management actions such as resolving human-wildlife conflict. Therefore, managers need additional datasets and methods to quantify species-environment relationships, thus complementing harvest-based methods.

In recent years, citizen science has become a powerful datastream to quantify species-environment relationships (Dickinson et al. 2010). Recognizing the promise of citizen science, many agencies have launched citizen-science based monitoring programs (Townsend et al. 2020; Lasky et al. 2021). In particular, recent years have seen the emergence of ***jurisdictional observation networks (JONs)***, agency-coordinated efforts to collect ecological data at fine resolutions over broad spatial extents, often via passive sensors that are maintained by citizen scientists (Townsend et al. 2020). Passive sensors such as camera traps can effectively monitor diverse taxa while minimizing skill or effort biases associated with human observations (Burton et al. 2015; Wearn & Glover-Kapfer 2019). However, JONs may not totally replace harvest-based wildlife monitoring. For example, JONs may rarely detect low-prevalence species; with few detections, fitting models and producing informative species-environment relationships is difficult. Ideally, managers should draw upon the strengths of both data sources to produce the best possible predictions of occurrence and abundance to guide decisions.

Harvest and camera-trap data are fundamentally observations of the same underlying ecological process: the distribution of animals in space. Reconciling differences between the datastreams within a single analysis is challenging (Pacifici et al. 2019), but ***integrated species distribution models*** (***iSDMs***; Isaac et al., 2020; Miller et al., 2019; Zipkin et al., 2019) provide a means to combine all available data to estimate species-environment relationships, thus informing species occurrence and abundance at fine resolution over broad spatial extents (Fig. 1A). Previous analyses have suggested that iSDMs generally reduce uncertainty in species-environment relationships, all within a single, streamlined approach (Fletcher et al. 2016; Koshkina et al. 2017; Miller et al. 2019; Isaac et al. 2020). However, the possibility of harvest data contributing to species distribution modeling has been largely overlooked (but see Bauder et al., 2020).

We applied iSDMs uniting JON camera-trap data and harvest records for six wildlife species representing a spectrum of prevalence in Wisconsin, USA (Fig. 1A-B). For comparison, we also developed camera-only and harvest-only SDMs (Fig. 1A). We hypothesized that iSDMs would produce more precise species-environment relationships than camera- and harvest-only models (Fig. 1C). In addition, we expected that iSDMs would capture spatial patterns of abundance intermediate to those predicted by individual data sources (Fig. 1D). Finally, we conducted a simulation study to evaluate the consequences of incomplete knowledge of harvest effort for estimates of abundance patterns and species-environment relationships.

## Methods

### *Species*

We focused on six wildlife species: wild turkey (*Meleagris gallopavo*; hereafter “turkey”), black bear (*Ursus americanus*; hereafter “bear”), river otter (*Lontra canadensis*; hereafter “otter”), fisher (*Pekania pennanti*), bobcat (*Lynx rufus*), and white-tailed deer (*Odocoileus virginianus*; hereafter “deer”). We chose these species because they are readily detected by cameras, their harvest is tracked by the Wisconsin Department of Natural Resources (WDNR), each is of management interest, and they represent a spectrum of prevalence (Fig. 1B).

***Camera data***

Our primary datastream was Snapshot Wisconsin, a JON operated by the WDNR (Fig. 2; Townsend et al., 2020). Snapshot Wisconsin has the dual goals of providing data to support wildlife management and increasing public engagement in wildlife science. The program relies on volunteers to host camera traps and classify images.

The WDNR solicits volunteers to host camera traps within US Public Land Survey System quarter-townships (spatial resolution, 4.8 x 4.8 km), which serve as sampling units for Snapshot Wisconsin. In an effort to maximize spatial coverage of the project, the WDNR prioritizes applicants from unoccupied cells. The WDNR provides each host with a Bushnell Trophy Cam (Overland Park, Kansas) with fixed settings such that the cameras record a 3-image sequence when triggered, with a 15-second gap between triggers. The hosts deploy their camera within their assigned quarter-township, typically on private land. They place their cameras along wildlife trails or water features at least 100 m from major roads or buildings. Hosts mount their camera 0.75-0.9 m from the ground and 3-4.5 m from the target, positioning the camera such that it aims the target at a diagonal angle and faces north to avoid false triggers from sunrise or sunset. Bait or lures are not used. Finally, hosts are instructed to clear vegetation between the camera and the target that may obstruct detection of animals. The hosts check their cameras every 1-3 months and upload the images to a web repository. Image classification takes three forms: *1)* individual classifications by camera hosts, *2)* consensus-based classification by volunteers on the Zooniverse crowdsourcing platform, *3)* and expert classification of subsets of images to quantify accuracy of volunteer classifications (Anhalt-

Depies et al., in prep). Since launching in 2016, Snapshot Wisconsin has generated >50 million photos from >2,000 cameras.

We derived binary detection histories from the camera data to use in our analysis. First, we deleted photos if critical information (camera coordinates or date-time data) were missing or clearly wrong. We reviewed triggers classified as fisher or otter due to the relatively low classification accuracy for these species and updated the triggers' classification based upon review. Classification accuracy for the other species is sufficiently high (>98%; Anhalt-Depies in prep.; Clare et al., 2019) that we judged *post hoc* review unnecessary. Next, we defined the temporal extent of sampling and length of replicate sampling occasion for each species (Fig. 2). We focused on one year (2018) of data since our objective was to develop proof-of-concept models combining camera and harvest data. We defined a unique temporal extent for each species to restrict the camera data to times during which population closure was most likely, i.e., after reproduction but prior to the harvest season (Fig. 2). We defined the length of the replicate sampling occasions to be 7 days for the less-prevalent species and 1 day for the most common species (Fig. 2). We assigned NA values in the detection histories to cameras that were not active on particular sampling occasions. For each species, we filtered cameras that were active for at least two sampling occasions, though for turkey we filtered cameras that were active for all sampling occasions due to convergence issues in exploratory analyses. Number of camera locations for each species ranged from 524 (turkey) to 1439 (otter; Fig. 2). For each species, the median number of sampling occasions with active cameras was 8 (otter), 10 (fisher), 9 (bobcat), 31 (turkey), 9 (bear), and 15 (deer), respectively.

### ***Harvest data***

The WDNR regulates harvest within species-specific management zones (Fig. S1). However, the WDNR tracks annual harvest per county, which represent smaller areas than management zones for most species (Fig. S1). Therefore, we used the number of animals harvested within each county in 2018 as our second source of data (Fig. 2). Clearly, the number of animals harvested within a given county is a function of not only abundance but also of harvest effort. Therefore, we gleaned measures of harvest effort from the WDNR's 2018 harvest reports (WDNR 2020) to be used as a bias term in the iSDMs (Fig. S2). Measures of harvest effort were based either on *1)* the number of harvest authorizations per management unit or *2)* metrics of harvest effort derived from WDNR hunter and trapper surveys. We were able to recover effort data at the county level for only two species (deer and bobcat); for the other species, we used information collected for larger management zones and assigned each zone's effort values to the counties whose centroids fell in that zone (Fig. S1, S2). We scaled the effort values to fall between 0 and 1. For more details on harvest effort data, please see Supplemental Information.

***Modeling framework***

*Overview*

Species distribution models create a statistical description of species occurrence and/or abundance, which are latent variables (i.e., cannot be directly observed). Therefore, SDMs use environmental predictors to characterize the distribution of interest and model uncertainty about observing the latent state via an observation submodel (Fig. 1A). Integrating multiple datastreams faces a fundamental challenge: different datastreams may arise from distinct sampling and observation processes (Fletcher et al. 2019). iSDMs address this challenge via datastream-specific observation submodels that inform a common ecological model (Fig. 1A).

Our two data sources represent detection-nondetection data (camera) and count data (harvest). To yoke these two distinct data currencies, we invoke a spatial point process as a unifying framework that generates both data types (Miller et al. 2019; Isaac et al. 2020). The expected abundance ($\lambda$) of the point process determines both whether a species occurs within some area as well as the true abundance ($N$) of the species within the same area. We consider space discrete and focus inference on expected abundance within grid cells (5 x 5 km resolution for 5 species and 10 x 10 km resolution for bears). Expected abundance $\lambda$ is a shared parameter in both submodels (i.e., both data sources provide information about $\lambda$). Below, we use index *i* to reference cells within the prediction grid, index *j* to reference cameras, index *k* to reference sampling occasions, and index *c* to reference counties.

*Model for latent state*

We used a Royle-Nichols model (Royle & Nichols 2003), which estimates abundance $N$ via heterogeneity in detection-nondetection data. We modeled expected abundance $\lambda$ as a function of environmental predictors and sampled the latent abundance state $N$:

$$log(\lambda_i) = \boldsymbol{\beta X_i} + \theta_i \quad \text{Eqn. 1}$$

$$N_i \sim Poisson(\lambda_i) \quad \text{Eqn. 2}$$

Where $\lambda_i$ is the expected abundance within the $i^{th}$ grid cell, $\boldsymbol{\beta}$ is a vector of regression coefficients, $\boldsymbol{X_i}$ is the design matrix of environmental predictors for the $i^{th}$ grid cell, and $\theta_i$ is a spatial random effect for the $i^{th}$ grid cell. We used weakly informative $\sim Normal(0, 2)$ priors—which are more robust to transformation than commonly used $\sim Normal(0, 100)$ priors—for the regression coefficients $\boldsymbol{\beta}$ (Hobbs & Hooten 2015; Banner et al. 2020). We used a conditional autoregressive (CAR) prior for the spatial random effect $\theta_i$, which acts as a cell-specific intercept by treating the random effect of the $i^{th}$ grid cell as conditional on the magnitude of neighbors' random effects as well as the strength of spatial dependence (Banerjee et al. 2015; Hoef et al. 2018). We used a $\sim Gamma(1, 1)$ hyperprior for the scalar precision of the CAR prior (Hoef et al. 2018).

For each species, we defined a parsimonious set of environmental predictors (i.e., $\boldsymbol{X_i}$ in Eqn. 1) that we hypothesized would drive its distribution; thus, different species had different predictors (Table 1, Table S1). Because our goal was to compare results from iSDMs and individual-datastream SDMs (Fig. 1A), we defined a single global model rather than conducting multi-model inference. The covariates included percent canopy and impervious cover from the 2016 National Land Cover Database (Dewitz 2019), mean annual temperature from WorldClim (Fick & Hijmans 2017), edge density between forest and open land cover types from the 2018 MODIS land cover product (Friedl & Sulla-Menashe 2019), and stream density from a shapefile of rivers and streams (ESRI, 2020; Fig. S3). Several other candidate predictors were omitted due to high (Pearson's | *r* | > 0.7) correlations with the other predictors (Dormann et al., 2013). We quantified mean values of the predictors within 5 x 5 km (5 species) and 8.5 x 8.5 km (bear) grid cells to roughly match the space use of each species (Schank et al., 2019; Supplemental Information).

*Camera submodel*

Observational submodels are conditional on the latent state. In the case of the Royle-Nichols model, the submodel describes the probability of detecting an animal, *given abundance of the species at the location* (Royle & Nichols 2003). We allowed detection probability to vary by camera and sampling occasion via covariates and random effects.

$$Y_{1jk} \sim Bernoulli(p_{jk}) \quad \text{Eqn. 3}$$

$$p_{jk} = 1 - (1 - r_{jk})^{N_j} \quad \text{Eqn. 4}$$

$$logit(r_{jk}) = \boldsymbol{\alpha X_{jk}} + \varepsilon_{jk} \quad \text{Eqn. 5}$$

Where $Y_{1jk}$ is a binary indicator of whether the focal species was detected at the $j^{th}$ camera during the $k^{th}$ sampling occasion, $p_{jk}$ is the per-camera detection probability at the $j^{th}$ camera during the $k^{th}$ sampling occasion, $N_j$ is abundance within the grid cell containing the $j^{th}$ camera, and $r_{jk}$ is per-individual detection probability at the $j^{th}$ camera during the $k^{th}$ sampling occasion. In Eqn. 5, $\boldsymbol{\alpha}$ is a coefficient vector, $\boldsymbol{X_{jk}}$ is the corresponding design matrix of detection predictors, and $\varepsilon_{jk}$ is a camera- and sampling occasion-level random effect. We used percent canopy cover within the 30 x 30 m grid cell containing each camera (reasoning that forest structure may correlate with animal detectability), ordinal date, camera height, and distance to the targeted trail as detection predictors (Table 1, Supplemental Information). We used ~Logistic(0, 1) priors for $\boldsymbol{\alpha}$ (Banner et al., 2020) and a ~Normal(0, σ) prior for $\varepsilon_{jk}$, where σ is a hyperprior modeled with a ~Gamma(1, 2) distribution.

*Harvest submodel*

The harvest data exists at a coarser spatial resolution than the camera data and environmental predictors (Pacifici et al. 2019). Such a misalignment of spatial resolution between data sources can lead to severe biases if not addressed (Banerjee et al. 2015; Pacifici et al. 2019). Therefore, we defined county-level expected abundance to be a linear function of the sum of fine-resolution expected abundances within a given county; that is, we induce a formal statistical change-of-support to reconcile the spatial misalignment between the point-level camera observations and the areal harvest counts to make inference at the grid cell resolution described above (Pacifici et al. 2019).

$$\log(\lambda County_c) = \gamma_0 + \gamma_1 \log\left(\sum_{i=c1}^{n=c2} \lambda_i\right) \quad \text{Eqn. 6}$$

$$Harvest_c \sim Poisson(effort_c * \lambda County_c) \quad \text{Eqn. 7}$$

Where $\lambda County_c$ is expected abundance for the *c^th^* county, $\gamma_0$ and $\gamma_1$ are the intercept and slope, respectively, of the equation scaling fine-resolution expected abundance to county-resolution expected abundance, and c1 and c2 index the first and last cells, respectively, to fall within county *c.* We used ~$Normal(0, 2)$ priors for $\gamma_0$ and $\gamma_1$. Importantly, this scaling equation implies that county-level abundance need not be a simple sum of grid-level abundances, thus accommodating issues such as different sampling exposure of grid-level and county-level subpopulations or suboptimal grid resolution selection. Finally, $Harvest_c$ and $effort_c$ are the harvest count and effort data for the $c^{th}$ county.

*Model evaluation*

We compared results for three models: an integrated model with submodels for both data sources (*integrated*), a model with a camera submodel only (*camera-only*), and a model with a harvest submodel only (*harvest-only*). Discriminating among these models is a challenge, since model-ranking methods (e.g., AIC) are not appropriate for use with models that contain different sets of observations (Isaac et al. 2020). Moreover, because the species' true distributions are unknown, we cannot evaluate which model provides more accurate results. Consequently, we compared estimates of species-environment relationships and expected abundance from the three models and conducted a simulation study (see next section) to evaluate possible biases.

We compared the precision of species-environment relationships (i.e., the coefficient vector $\boldsymbol{\beta}$ from Eqn. 1) estimated by the three models (Fig. 1B). The variance of a coefficient represents uncertainty about the relationship between a predictor and expected abundance. While a coefficient's variance is not indicative of model fit or performance *per se*, we reasoned that practitioners want models that reduce uncertainty in species-environment relationships as much as possible (Graves et al. 2012; Milner-Gulland & Shea 2017; Nicol et al. 2019).

In addition, we compared patterns of expected abundance (i.e., $\lambda_i$ in Eqn. 1) and occurrence probability $\psi_i$ (converted from expected abundance $\lambda_i$) predicted by the three models to evaluate how the models might provide different information in a management context. For both expected abundance and occurrence, we computed Pearson's correlation coefficient *r* for all cells across the entire state. For expected abundance, we compared areas that each model predicted to have the lowest and highest expected abundance, reasoning that areas of rarity and high abundance are both of management significance. To do so, for each model, we selected grid cells within the 90$^{th}$ and 10$^{th}$ percentiles for $\lambda_i$. We then mapped these cells to evaluate levels of agreement between models about areas predicted to have the lowest and highest expected abundance. We define "agreement" as the proportion of overlapping 10$^{th}$ or 90$^{th}$ percentile cells between multiple models.

We ran all models in the R package NIMBLE 0.8.0 (de Valpine et al. 2017; R Core Team 2021). We ran three Markov Chain Monte Carlo (MCMC) chains and assessed convergence via visual inspection of traceplots and the Gelman-Rubin diagnostic $\hat{R}$ (considering parameters with $\hat{R} \leq$ 1.1 to be converged; Brooks and Gelman, 1998). We ran chains until they converged or reached 100,000 iterations, at which point we declared the model unconverged.

### *Simulation study*

The goal of the simulation study was to evaluate the consequences of incomplete knowledge of harvest effort for estimates of expected abundance $\lambda_i$ and species-environment relationships. For a low- and a high-prevalence "pseudospecies", we ran a camera-only, a harvest-only, and two integrated models with mediocre and quality effort data, respectively (thus for a total of 8 simulation scenarios, each of which we replicated 100 times). We created a grid of 1,296 fine-resolution cells nested within 36 coarse-resolution cells (i.e., each coarse cell contained 36 fine cells; Fig. 3). This roughly corresponds to the resolution misalignment in our empirical data; for the bear model, each county contained an average of 30 cells, and for the other species, each county contained an average of 85 cells. For both pseudospecies, we generated fine-cell expected abundance $\lambda_i$ as a function of the grid's x- and y-coordinates, as follows:

$$\log(\lambda_i) = \beta_0 + \beta_1 x_i + \beta_2 y_i + \varepsilon_i \quad \text{Eqn. 8}$$

Where $\beta_0$ is the average expected abundance, fixed to 0 for the low-prevalence pseudospecies and 1 for the high-prevalence pseudospecies. $\beta_1$ and $\beta_2$ are species-environment relationships; we fixed the values of these coefficients at -0.5 and 1.25, respectively, which roughly matches the magnitude of the species-environment relationships estimated in our empirical application. Finally, $x_i$ and $y_i$ are the x- and y-coordinates (minima and maxima of -1 and 1, respectively) of the cell's center, and $\varepsilon_i$ is cell-specific noise drawn from a ~Normal(0, 0.1) distribution. We intended the low-prevalence pseudospecies (median $\lambda_i$ = 0.98, IQR 0.53–1.87) to represent the less prevalent species in our dataset (e.g., fisher; Fig. 1) and the high-prevalence pseudospecies (median $\lambda_i$ = 2.66, IQR 1.45–5.10) to represent the more prevalent species in our dataset (e.g., turkey; Fig. 1). We sampled abundance $N_i$ from a Poisson distribution (Fig. 3a). Finally, we randomly selected 15% of the fine cells to survey and generated 15 replicate surveys by sampling a binomial distribution, fixing per-individual detection probability at 0.1 (Fig. 3b). In our empirical data, the average percentage of fine cells surveyed (across species) was 14% and the average number of replicate surveys (across species) was 13.67. Additionally, exploratory analyses suggested that per-individual detection probabilities for most of the species considered were comparably low.

We calculated coarse cell abundance $N_c$ as the sum of fine-cell abundances $N_i$ nested within each coarse cell (Fig. 3c). We assigned each coarse cell a random per-individual harvest probability between 0 and 0.5 (Fig. 3d) and sampled harvest counts from a binomial distribution (Fig. 3e). The varying per-individual harvest probability represents variable harvest effort (and consequently, varying proportions of the coarse-cell population harvested) in different counties. For the integrated models, we evaluated “mediocre” and “quality” effort scenarios in which county-level effort was modestly ($r$ = 0.46) and strongly ($r$ = 0.94) correlated with county-level harvest probability (Fig. 3f). For the harvest-only model, we included the quality-level effort data. All models included each cell’s x- and y-coordinates as predictors as well as an intercept. We ran all models for 20,000 MCMC iterations in NIMBLE (de Valpine et al. 2017) and discarded all but the final 1,000 iterations as burn-in. We evaluated model performance in all scenarios by *1)* calculating the relative bias of expected abundance $\lambda_i$, *2)* calculating the standard deviation of estimated expected abundance $\lambda_i$, *3)* and assessing accuracy and precision of the species-environment relationships in Eqn. 8. Please see Supplemental Information for code to run the simulation.

## Results

### ***Species-environment relationships***

We estimated 15 species-environment relationships (2-3 predictors for each of 6 species; Table 1). Harvest-only models failed to converge. Thus, we only report results from integrated and camera-only models. Integrated models produced more precise species-environment relationships for 8 (53%) of the relationships (Fig. 4). The signs of relationships estimated by the two models for a species were always the same (Fig. 4). However, in three cases (stream density for otter and edge density for turkey and deer), the integrated model estimated a relationship that did not overlap zero, while the camera-only model estimated a relationship that did overlap zero (Fig. 4). Conversely, in two cases (percent canopy for bear and mean annual temperature for turkey), the camera-only model estimated a relationship that did not overlap zero, whereas the integrated model produced a relationship that overlapped zero (Fig. 4).

Regarding species prevalence and species-environment relationships, trends predicted in Fig. 1B partly emerged. As predicted, the most precise relationships were estimated for deer, the most prevalent species (Fig. 1B, Fig. 4). However, the least precise relationships were *not* for the least prevalent species (e.g., otter coefficients were more precise than bear coefficients).

### *Patterns of expected abundance and occurrence*

Integrated and camera-only models generally did not identify the same abundance hotspots. Bobcat and turkey showed the highest (40%) and lowest (3%) levels of agreement, respectively, about high-abundance areas (Fig. 5). In contrast, four species showed higher levels of agreement about abundance cold spots, with otter and deer being the exceptions (Fig. S4). Bear showed the highest agreement about low-abundance areas (82%), while otter showed the lowest (10%; Fig. S4). The strongest correlation between expected abundances predicted by the two models was for bobcat (0.80) and weakest for otter (0.12; Table S2). With expected abundance translated to occurrence, the integrated and camera-only models predicted similar spatial patterns of occurrence for most species (Fig. 6). Correlations between occurrence predicted by the two models was slightly stronger than the abundance correlations except for deer (Fig. 6, Table S2). Notably, while bear expected abundance predicted by the two models was only modestly correlated (0.58), bear occurrence correlation between the two models was strong (0.87; Fig. 6).

### *Simulation study*

The camera-only and integrated models produced estimates of expected abundance $\lambda_i$ with limited bias (< 5%); the harvest-only model produced highly biased results (Fig. 7). For the high-abundance pseudospecies, the “quality effort” integrated model produced less biased (-1%) estimates than the “mediocre effort” integrated model (-5%; Fig. 7). In addition, the integrated models produced more precise estimates than the camera-only model, and the “quality effort” scenario produced more precise estimates than the “mediocre effort” scenario (Fig. 7).

The camera-only and integrated models identified the true species-environment relationships; the harvest-only estimates were extremely imprecise and overlapped zero (Fig. S5). In all but one case ($\beta_2$ from the integrated model with mediocre effort for the high-prevalence pseudospecies), the integrated models produced more precise estimates of species-environment relationships than the camera-only model(Fig. S5). The two effort scenarios in integrated models produced species-environment relationships with similar levels of precision (Fig. S5).

## Discussion

Integrated models produced more precise species-environment relationships than camera-only models in a narrow majority of cases, and harvest-only models failed to converge (Fig. 4). The fact that harvest-only models did not converge suggests that harvest data alone cannot be used to inform species distributions at fine resolution and in turn guide local-scale management efforts (Bauder et al. 2020). Simulations corroborated this idea, as the harvest-only model produced extremely biased and imprecise estimates of expected abundance and species-environment relationships (Fig. 7, Fig. S5). Taken together, these results suggest that harvest records should be supplemented with fine-resolution data to inform local-scale management. Cameras represent a good supplementary datastream because they provide occurrence data at an exact point in space, which facilitates the identification of species-environment relationships.

Our results suggest that camera networks can benefit from the integration of harvest data, particularly if high-quality harvest effort data is available. Assuming quality effort data is available, the information added by harvest can generate more precise species-environment relationships; for rare or difficult-to-detect species, the added information may make all the difference between an informative species-environment relationship and a relationship too imprecise to support management decisions. We note that a JON on the scale of Snapshot Wisconsin is not required to redeem harvest records for fine-resolution inference; for example, even 30-100 strategically-placed cameras paired with harvest data would likely permit identification of species-environment relationships (Kays et al. 2020; Simmonds et al. 2020). Emerging fine-resolution datastreams and iSDMs provide managers with the option to co-opt existing, coarse-resolution datasets to make fine-resolution predictions of species distributions. These predictions, in turn, can be used to guide local-scale management actions such as identifying areas for human-wildlife conflict resolution.

We found low agreement in areas predicted to be abundance hotspots by the integrated and camera-only models. While it is difficult to judge which model better predicts the latent species distribution, the fact that two models show low agreement is still informative for decision-makers. Because agencies must make management decisions with incomplete information, managers should draw upon multiple sources of data to navigate decisions. For example, agencies occasionally reconfigure management zones based on perceived abundance. Low agreement about high-abundance regions between models might reduce managers' confidence in delineating new management zones, whereas high agreement would provide robust justification for such management decisions. Managers might target low-agreement regions with fine-resolution sampling to help resolve uncertainty in estimates of species distributions. In other words, managers can use integrated and single-datastream analyses to cross-check each other when facing management decisions.

### ***Recommendations for wildlife management agencies***

*Enhance effort reporting.* As demonstrated by our simulation study, high-quality effort data can help improve the precision (and in some cases, accuracy) of estimates of species-environment relationships and expected abundance (Pacifici et al. 2019). Our simulations suggest that poor effort information can lead to particularly misleading results for high-abundance species (Fig. 7). In our empirical application, we had harvest effort data at the scale of harvest records (the county) for only two species, making it difficult to separate variation in the harvest counts that arise due to the ecological process (the species' distribution) versus the observational process (hunting effort). We suggest that agencies expand programs to track harvest effort data. While implementing mandatory effort reporting would be logistically challenging and potentially face pushback from hunters (Kilpatrick et al. 2005; Schmidt & Chapman 2014), such information would increase the value of harvest records as a form of distribution data.

*Track harvest at finer spatial resolution*. Agencies commonly monitor wildlife species within taxon-specific jurisdictional units that cover vast areas (Fig. S1). While it is desirable to tailor unit delineations to match the system of interest, we suggest that tracking harvest at finer resolution would increase the value of these data for distribution modeling (Bauder et al. 2020). One possible solution would be to adopt a single system of finer-resolution jurisdictional units. In particular, effort reporting would be simplified for hunters and trappers if these records were collected within units that are readily recognized by the public (e.g., counties or townships), rather than species-specific management units. Implementing such changes would require considerable agency resources and likely be difficult given the idiosyncratic governance structure for each species, but we suggest it could enhance the quality of harvest records.

*Expand taxonomic resolution*. One of the appealing aspects of cameras is that they represent a means to conduct broad-spectrum monitoring of multiple species simultaneously (Burton et al. 2015). In contrast, agencies often do not track harvest of all game species. For example, in Wisconsin, harvest is regulated but not tracked at resolution finer than the state level for a number of species, including snowshoe hare (*Lepatius americanus*) and ruffed grouse (*Bonasa umbellus*). Harvest records for such taxa could enhance camera-based efforts to monitor these species (Townsend et al. 2020). While expanding harvest record-keeping would be a logistical challenge, we emphasize that it would provide information that could improve predictions of species distributions, which is an appealing prospect because the aforementioned species are declining in the region and considered vulnerable to climate change (Wilson et al. 2019; Shipley et al. 2019).

### *Conclusion*

We highlight the potential of integrating emerging datastreams with pre-existing forms of ecological data. Camera traps and harvest records are not the only data types that fit within this framework; for example, acoustic monitoring datastreams from JONs could be combined with coarser-resolution bird atlas data. In addition, the iSDM framework is flexible and can accommodate alternate submodels for cases in which researchers collect fine-resolution count (rather than detection-nondetection) data. Our simulation study underscores the need for quality information on effort for the coarser-resolution data. Our application demonstrates that integrated models can provide more precise species-environment relationships and may identify different spatial patterns of occurrence and abundance from individual-datastream models. We highlight that multiple sources of data can be used to cross-check each other and bolster management decisions. We anticipate that integrated approaches to species distribution modeling will continue to grow and encourage practitioners to tailor existing forms of data collection to accommodate emerging datastreams from observation networks.

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**Tables**

Table 1. Variables used to predict expected abundance (Environmental predictors) and per-individual detection probability (Detection predictors) for each species. Please see Table S1 for a detailed justification of the environmental predictors used.

| Species | Environmental predictors | Detection predictors |
|---|---|---|
| otter | canopy cover, impervious cover, stream density | local canopy, date, $date^2$, camera height, target distance |
| fisher | canopy cover, impervious cover | local canopy, date, $date^2$, camera height, target distance |
| bobcat | canopy cover, impervious cover | local canopy, date, $date^2$, camera height, target distance |
| turkey | mean annual temperature, impervious cover, forest-open edge | local canopy, camera height, target distance |
| bear | canopy cover, impervious cover | local canopy, date, $date^2$, camera height, target distance |
| deer | mean annual temperature, impervious cover, forest-open edge | local canopy, date, camera height, target distance |

**Figures**

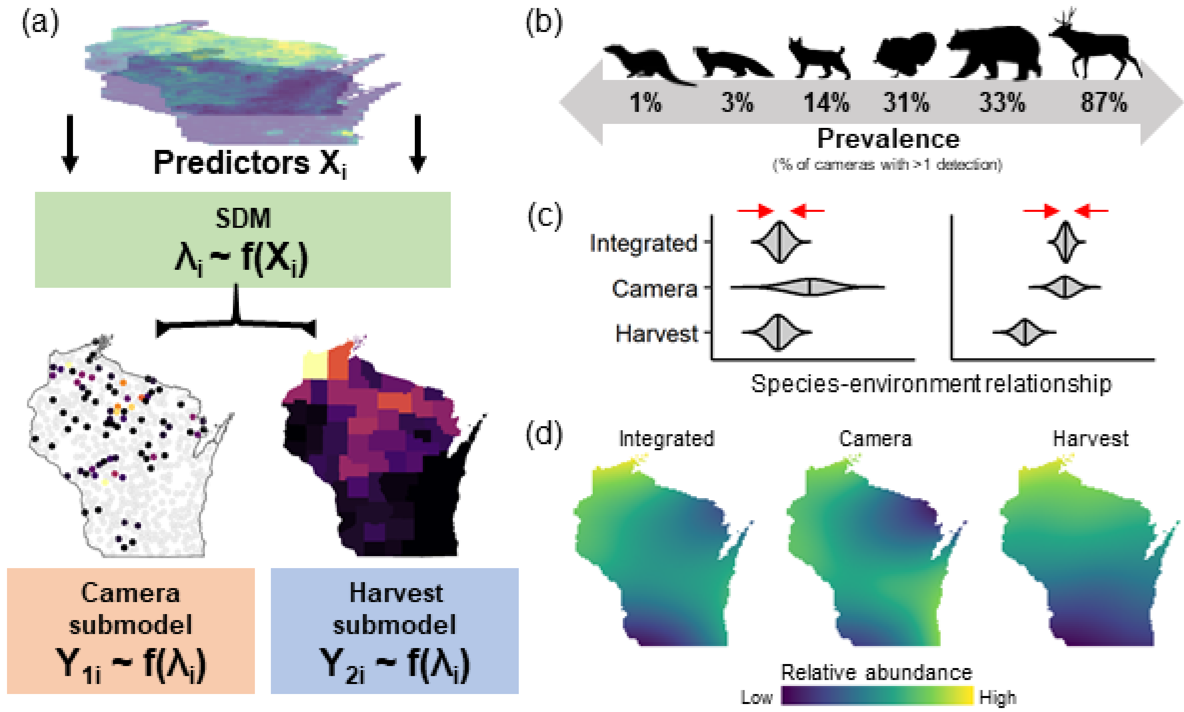


Figure 1. (a) The iSDM framework with separate submodels for camera-trap data and harvest data (adapted from Miller et al. 2019); the camera- and harvest-only models contain submodels for only the camera and harvest data, respectively. (b) Focal species prevalence, defined as the percent of cameras that detected a species. From left to right, the silhouettes represent otter, fisher, bobcat, turkey, bear, and deer. (c) We predicted that integrated models would more precisely estimate species-environment relationships and that variance shrinking would be contingent upon species prevalence (left, low prevalence; right, high prevalence). (d) We predicted that harvest- and camera-only models would produce slightly different spatial patterns of abundance and that the patterns predicted by integrated models would be intermediate.

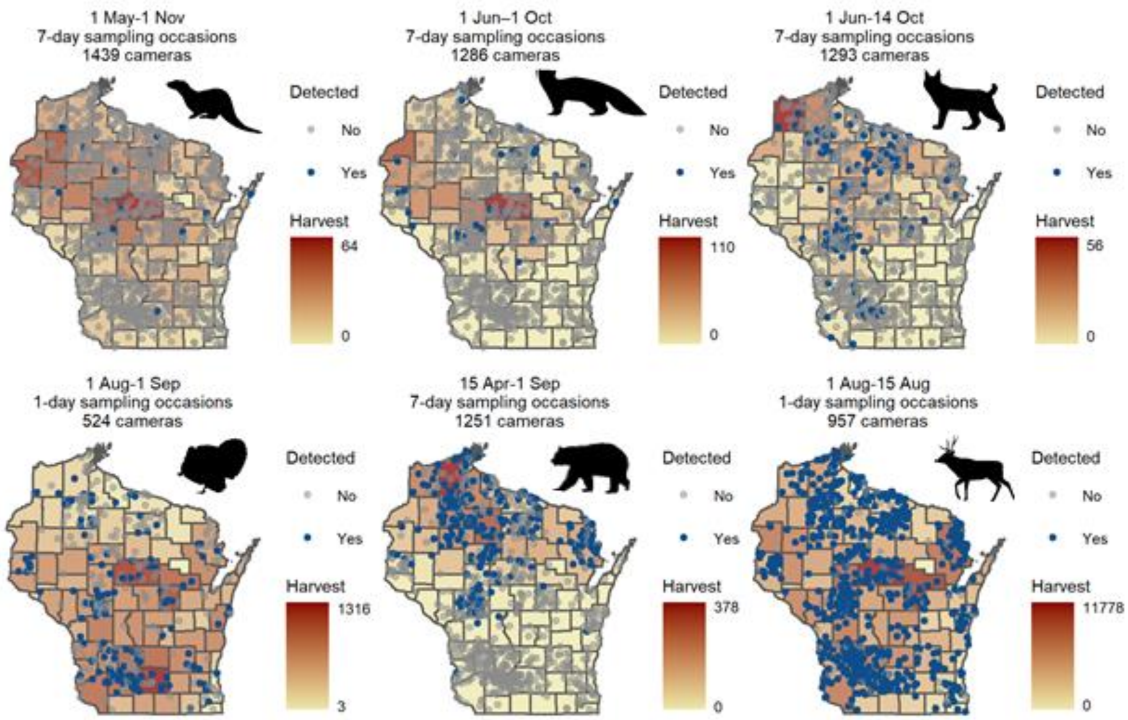


Figure 2. Data used in analysis: county-level harvest (fill) and camera-trap detection records (points; translucent gray points represent cameras that never detected the species). The temporal extent, length of replicate sampling occasions, and number of locations for the camera data are shown above the map for each species.

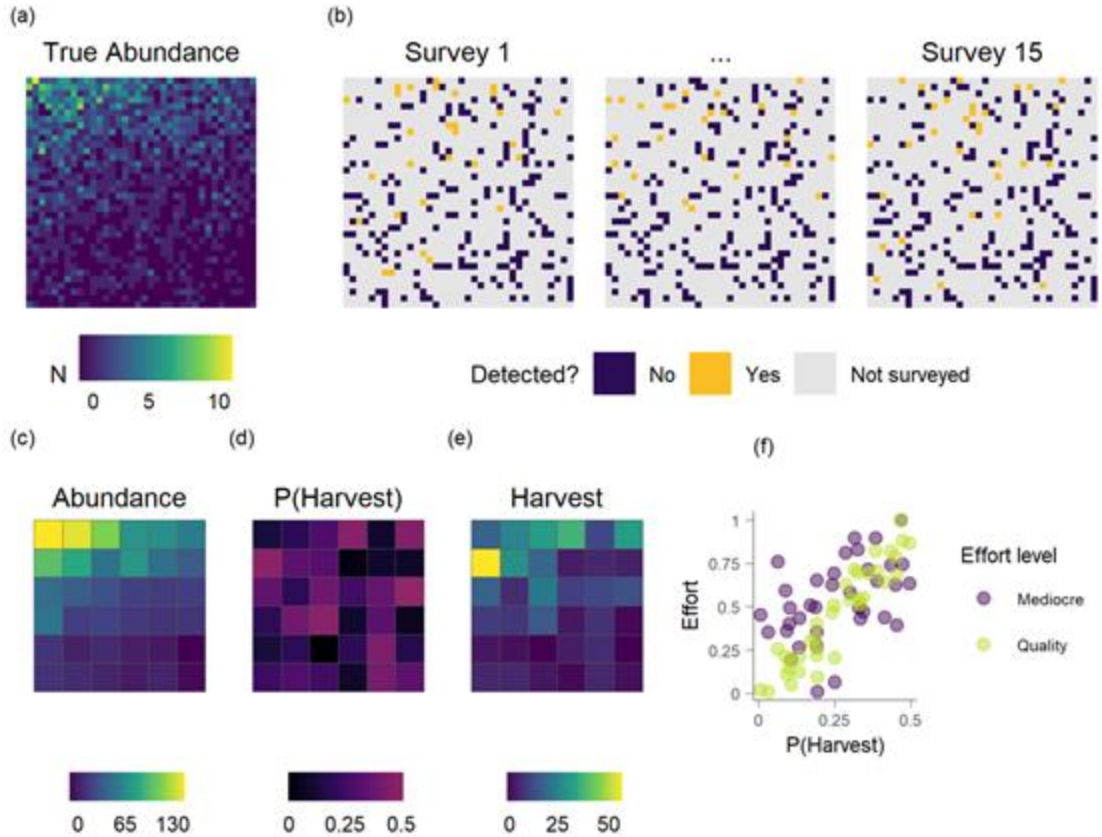


Figure 3. Setup of simulation study to evaluate the effects of incomplete knowledge of harvest effort. In (a), fine-resolution abundance is highest in the upper left part of the landscape; (b) shows 3 of the 15 replicate fine-resolution surveys in which 15% of the cells were surveyed to produce detection-nondetection data. Each coarse-resolution cell contained 36 fine cells (c), and probability of harvest varied among the coarse cells (d) such that the harvest counts (e) were imperfect representations of underlying coarse-resolution abundance. Finally, we evaluated integrated models with varying quality of effort data (f).

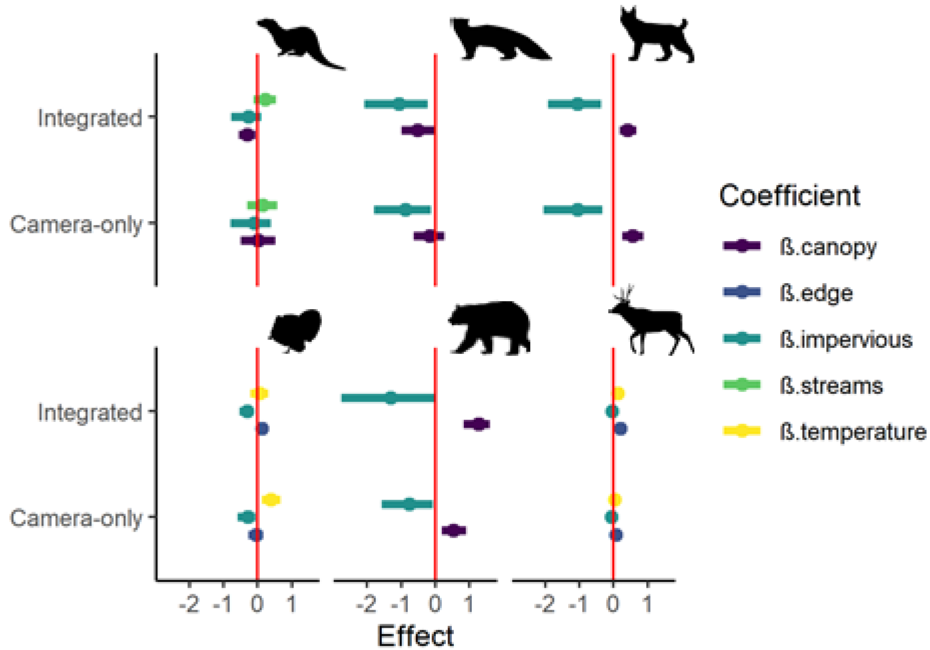


Figure 4. Posterior distributions of species-environment relationships. Harvest-only results omitted because models did not converge. The points and bars represent the coefficients' posterior means and 95% credible intervals, respectively. The dashed red lines represent no relationship between the predictor and expected abundance.

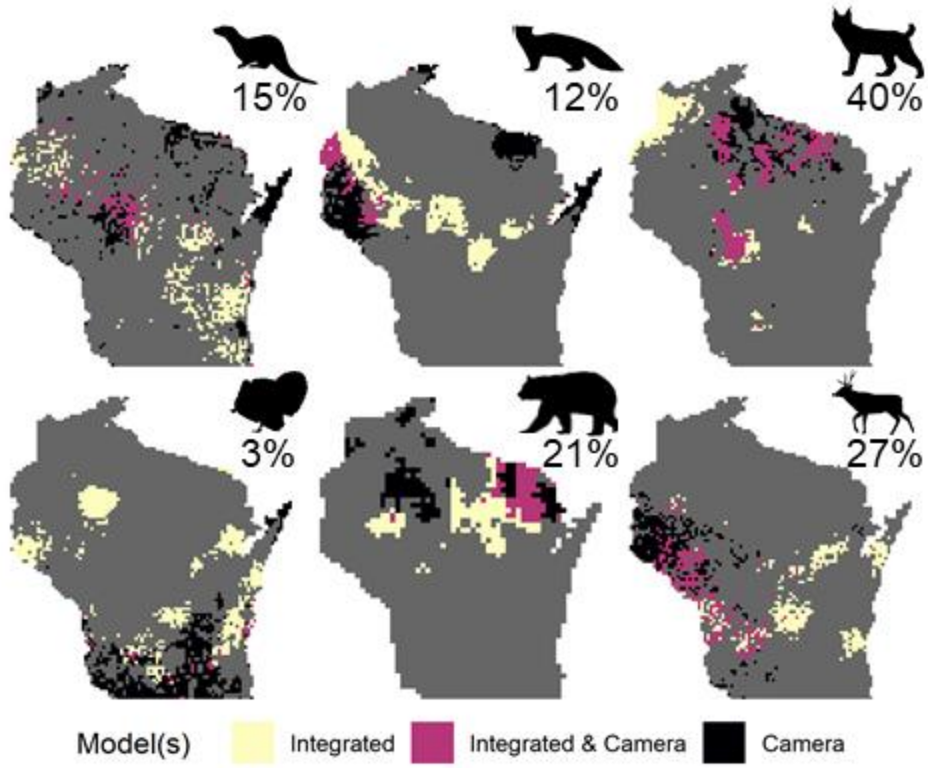


Figure 5. Regions of highest expected abundance (90th percentile) as predicted by the camera-only and integrated models. Areas where the two models agree are shown in purple; the percent agreement is displayed under the silhouette of each species.

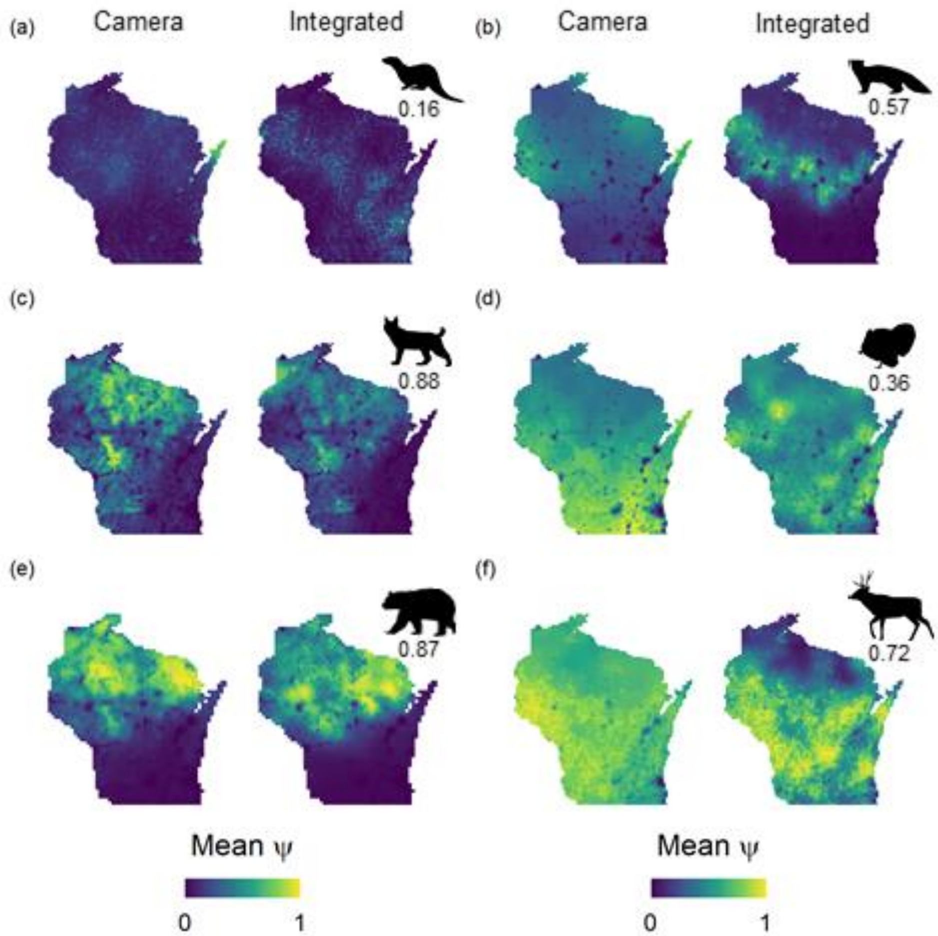


Figure 6. Occurrence probability (mean) for the six focal species from integrated and camera-only models (harvest-only results omitted due to convergence issues). Occurrence probabilities are scaled to have minima and maxima of 0 and 1, respectively, to facilitate comparisons. The numbers beneath the species silhouettes are the correlations between occurrence values predicted by the two models.

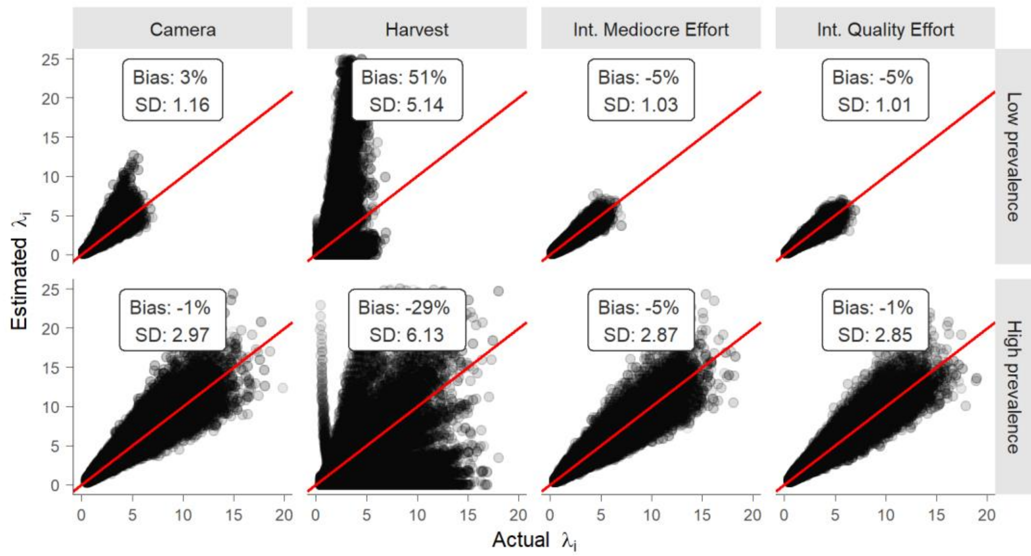


Figure 7. Bias and precision of estimates of expected abundance λ from 8 simulation scenarios. The red lines show the 1:1 relationship between estimated and actual expected abundance, "Bias" is the relative bias of estimated expected abundance, and SD is the standard deviation of estimated expected abundance. Rows represent a low- and high-prevalence "pseudospecies"; the columns represent camera-only, harvest-only, and integrated models with mediocre and quality effort information, respectively.

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**Chapter 3: Behavioral flexibility facilitates use of spatial and temporal refugia during variable winter weather**

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**Abstract**

In North America, winters are becoming more variable such that warm and cold extremes are increasingly common. Refugia (in time or space) can reduce the exposure animals experience to extreme temperatures. However, animals must be able to adjust their behavior to capitalize on refugia. Our goal was to identify the behavioral mechanisms that grant access to refugia in time and space, focusing on a northern ungulate (white-tailed deer, *Odocoileus virginianus*) as a model. We drew upon an extensive camera-trap network in Wisconsin, USA, over two winters that experienced both warm and cold extremes. To understand use of temporal refugia, we modeled deer activity (at daily resolution) during night, dawn, day, and dusk as a function of weather predictors. To understand use of spatial refugia, we modeled deer activity at camera locations (at daily resolution) as a function of landscape characteristics, weather conditions, and landscape-weather interactions. During anomalously cold temperatures, deer became more diurnal; conversely, on anomalously warm days, deer were more nocturnal. Deer were more active in conifer-dominated landscapes on cold days. Conversely, during warm extremes, deer increased activity in deciduous-dominated landscapes. Finally, deer showed multiple modes of behavioral flexibility (activity in time as well as space) and demonstrated stronger responses to temperature anomalies later in the winter, suggesting that the effects of extreme events are dependent upon their seasonal timing. Behavioral shifts presumably reduce exposure to extremes and may render species more resilient to increasingly variable winter climates.

**Keywords**

climate change, diel activity patterns, extreme weather, habitat selection, occupancy modeling, phenotypic plasticity, refugia

## Introduction

The global climate is warming and becoming more variable (Rahmstorf & Coumou 2011; IPCC 2013). Such variation—particularly extreme weather events—pushes the limits of adaptation for many species (Post 2013; Latimer & Zuckerberg 2019). Overall, winters in the northern hemisphere are trending milder (Schwartz et al. 2006; IPCC 2013), but weakening and wobbling of the jet stream is increasing the incidence of cold extremes (Cohen et al., 2018). As a result, many regions are seeing juxtapositions of anomalously cold and warm temperatures within single winter seasons (Casson et al. 2019). Such variation—by exposing organisms to cold extremes—may force animals to retain adaptations related to cold tolerance and limit their adaptive capacity to warming trends (Post 2013).

Behavioral flexibility can be a key defense against short-term perturbations such as warming trends and extreme events (Wong & Candolin 2015; Beever et al. 2017; van de Pol et al. 2017; Fey et al. 2019). Indeed, behavioral thermoregulation is ubiquitous in the animal kingdom, with organisms as diverse as insects (May 1979; Huey & Pascual 2009; Abram et al. 2017), fish (Armstrong et al. 2013), lizards (Muñoz & Losos 2018), and humans (Schlader et al. 2010) shifting their behaviors to ameliorate thermal stress. By changing their behavior, animals can capitalize on **refugia**, or conditions that reduce exposure to stressors and thus facilitate energy conservation (Scheffers et al. 2014; Levy et al. 2019; Morelli et al. 2020). ***Importantly, refugia may exist in time or space.***

Certain times during the 24-hour cycle may serve as refugia that buffer individuals from extreme conditions. According to the **temporal refugia hypothesis**, animals shift their **activity in time** to reduce exposure to stressors. While many factors structure a species' activity timing (e.g., light-gathering capacity of eyes, predation risk; Hut et al., 2012; Kronfeld-Schor & Dayan, 2003), extreme weather can induce altered activity timing (van der Vinne et al. 2019). For example, van der Vinne et al. (2014) exposed mice (*Mus musculus*) to cold conditions and observed shifts to daytime activity in the normally nocturnal mice (van der Vinne et al. 2014). Similarly, cold temperatures induce daytime activity in normally crepuscular *Drosophila* flies (Dubruille & Emery 2008; Huey & Pascual 2009).

Landscape features such as dense forest (Kearney et al. 2009; De Frenne et al. 2021), topographic relief (Suggitt et al. 2018), and burrows (Riddell et al. 2021) create refugia that reduce exposure to stressors; the **spatial refugia hypothesis** predicts that animals shift their activity in space to take advantage of these refugia. For example, Moore et al. (2018) discovered that the burrows used by the desert lizard *Liopholis kintorei* buffer temperatures by as much as 40 °C as compared to surface temperatures (Moore et al. 2018). Similarly, Shipley et al. (2019) found that individual ruffed grouse (*Bonasa umbellus*) roosting in snow burrows experienced less cold-associated stress than individuals that roosted on the ground or in trees (Shipley et al. 2019).

High-latitude winters are energetically demanding, and behavioral flexibility may be crucial to withstanding winter's thermal and energetic challenges (Kronfeld-Schor & Dayan 2003; Hall & Chalfoun 2019). During cold extremes, animals can minimize heat loss by allocating activity to daytime or using refugia habitats that are thermally buffered relative to the surrounding landscape (Scheffers et al. 2014; van der Vinne et al. 2014, 2019). Winter warm extremes relax thermal constraints and allow animals to use times and habitats that would be inhospitable under colder temperatures (Cohen et al., 2021). An animal's body condition (e.g., fat reserves)—which likely underpins decisions to change its behavior—varies over the course of a winter, generally deteriorating in groups like ungulates but potentially improving in taxa such as scavengers (Kautz et al., 2020; Mattisson et al., 2016). Thus, behavioral shifts in response to extreme winter weather are likely contingent upon *when* extreme weather occurs. However, it is poorly known how animals modify their activity in time and space relative to extreme winter weather, particularly in the context of routine seasonal shifts in behavior (Maxwell et al. 2019).

**Here, we investigate the behavioral mechanisms that grant animals access to refugia in time and space.** Our goals were to 1) establish how animals shift temporal and spatial activity relative to daily and seasonal weather conditions, and 2) assess these behaviors during warm and cold extremes. We addressed these points using two winters of data from a network of camera traps operated by volunteers in Wisconsin, USA. We focused on a northern ungulate, the white-tailed deer (*Odocoileus virginianus)*, which represents an ideal model because the northern extent of their range is limited by winter severity (Kautz et al. 2020), and behavioral flexibility is presumably an important mechanism underpinning their occurrence in high-latitude regions (Dawe & Boutin 2016).

Following the temporal refugia hypothesis, we predicted that deer would increase their daytime activity under anomalously cold temperatures and as winter progresses (Fig. 1). Similarly, during anomalously warm days and earlier in the winter, we predicted that deer would be active primarily during dawn, dusk, and night, which are generally considered to be the times of peak deer activity under typical circumstances (i.e., when animals are not exposed to thermal stress; Hewitt, 2011). Under the spatial refugia hypothesis, we predicted that, as the winter progresses and during anomalously cold days, deer would anchor their activity around refugia habitats (e.g., coniferous forests, which trap infrared radiation emitted from Earth's surface and intercept snow, resulting in shallower accumulation that is easier for deer to traverse; DelGiudice et al., 2013). On anomalously warm days, we predicted that deer would be less likely to use refugia habitats and more likely to use non-sheltered but nutritionally rewarding habitats (e.g., waste grain in open croplands; Fig. 1).

## Methods

### *Camera trap data*

We obtained time-stamped detections of deer from Snapshot Wisconsin, an extensive network of >2,000 camera traps maintained by community (citizen) scientists and overseen by the Wisconsin Department of Natural Resources (WDNR; Townsend et al., 2021). Since its launch in 2016, Snapshot Wisconsin has gathered >55 million photos. Snapshot Wisconsin uses United

States quarter-townships (23 $km^2$) as survey units and prioritizes prospective camera hosts from unoccupied quarter-townships to maximize survey coverage across the state of Wisconsin, with exceptions for denser placement of cameras to monitor local elk (*Cervus canadensis*) herds and deer populations in hotspots for chronic wasting disease (Fig. S1). The WDNR mails a Bushnell Trophy Cam (Overland Park, KS) to camera hosts, who place the cameras—without bait or lures—along wildlife trails or water features (within 3-5 m of the targeted feature) and at least 100 m from buildings or major roads. Hosts mount their camera 0.75-0.9 m from the ground, position the camera such that it faces north to avoid false triggers from sunrise or sunset, and trim any vegetation between the camera and the target to maximize the detectability of animals (Rovero & Zimmerman 2016). Finally, hosts check on their cameras every 1–3 months to replace batteries and retrieve photos, which they upload to a WDNR server.

Photo classification takes three forms: classification on a WDNR interface by camera hosts, crowd-sourced classification on the Zooniverse platform, and expert classification (generally by WDNR scientists; Townsend et al., 2021). Verification against expert classification has demonstrated that host and crowd-sourced classification of photos containing deer is >99% accurate (Clare et al. 2019; Townsend et al. 2021). To isolate the core of the winter, we focused on the period 15 December–10 March in the winters of 2017–2018 and 2018–2019.

### *Weather and landscape data*

We used three dynamic (daily) weather predictors. First, we obtained daily temperature anomalies from Daymet, a gridded product (1 $km^2$ resolution) created by interpolating observations from weather stations (Thornton et al. 2016). We calculated the anomalies as the difference between each day's minimum temperature and the 1980-2019 average minimum temperature for that location and ordinal date. Second, we used snow depth from SNODAS, a gridded product (1 $km^2$ resolution) derived from satellite sensors and weather stations (NOHRSC 2004). Third, we calculated a cumulative winter severity index, defined here as the cumulative sum of days between 1 December and 30 April with temperature less than -17.8 °C and/or snow depth greater than 38 cm, which approximates a snow depth which severely impairs deer movement (DelGiudice et al. 2002; Kautz et al. 2020). As a cumulative metric, winter severity increased over the winter and was highest in northern Wisconsin, which generally experiences colder temperatures and deeper snow than southern Wisconsin (Fig. S2). Winter severity correlated strongly with ordinal date ($r > 0.9$); thus, we used it both as a measure of winter severity as well as progress through the season. Finally, in addition to these dynamic weather predictors, we identified cold and warm extremes so that we could qualitatively compare model predictions from extreme days to non-extreme days, defining extremes as the coldest and warmest 5% of days calculated from statewide averages of the temperature anomalies.

We used four landscape predictors (Fig. S3) that were static over the course of the study. We measured the landscape predictors within a 1-km buffer around camera locations, which approximates the "scale-of-effect" at which predictors are most strongly associated with deer occurrence (Hewitt 2011; Jackson & Fahrig 2015). First, we calculated topographic relief (hereafter "relief") as the standard deviation of a digital elevation model with 30 x 30 m resolution (USGS 2019). We anticipated that topographic relief would correlate with refugia, since topographic variation drives microclimate diversity, some of which may buffer against thermal extremes (Dobrowski 2011; Suggitt et al. 2018). Second, we calculated percent coniferous forest as the proportion of coniferous and mixed forest classes from Wiscland 2, a 30 x 30 m land cover product derived from Landsat imagery and comparable to the National Land Cover Database in terms of classification accuracy (WDNR 2016). We expected coniferous forest to represent refugia that would buffer against wind, cold, or snow (Scheffers et al. 2014; De Frenne et al. 2021). Indeed, previous work has indicated that deer at northern latitudes congregate in conifer stands during the winter, presumably to reduce exposure to cold temperatures, deep snow (which impedes movement), and predation risk (Van Deelen et al. 1998; Hewitt 2011; DelGiudice et al. 2013; Kautz et al. 2020). We included the mixed forest class because we assumed that deer might use individual or small patches of conifers embedded within deciduous forest as refugia (De Frenne et al. 2021). Third, we calculated percent deciduous forest from Wiscland 2 (WDNR 2016). We predicted deciduous forests would serve as refugia, albeit less effective ones than coniferous forest, since deciduous trees intercept less snow and wind than conifers (De Frenne et al. 2021). Finally, we calculated percent open habitat as the proportion of cropland or grassland cover classes from Wiscland 2 (WDNR 2016). We expected open habitat to contain high-quality forage (i.e., waste grain; Hewitt, 2011) but provide no buffering against wind, cold, or snow.

### ***Temporal refugia analysis***

The goal of the temporal refugia analysis was to determine how deer allocate activity to night, dawn, day, and dusk periods relative to daily and seasonal weather conditions. The response variables were the proportions of activity during night, dawn, day, and dusk periods of each day (Fig. 2). To measure this response, we first estimated daily activity curves with a nonparametric kernel density function from the *activity* R package (Rowcliffe et al. 2014), pooling deer detections from all cameras on a given day. From these activity curves, we calculated the proportion of activity occurring during night, dawn, day, and dusk periods. We defined each period using the *suncalc* R package (Thieurmel & Elmarhraoui 2019) and converted detection times and period endpoints to solar time to correct for seasonal and geographic variation in daylength (Vazquez et al. 2019).

We used beta regression (Douma & Weedon 2019) to model the activity proportions as a function of weather predictors. We developed five candidate models incorporating non-collinear combinations of the predictors; high correlation ($r$ > 0.9) prevented us from including winter severity and snow depth together in any model (Table 1; Dormann et al., 2013). We included temperature anomaly-snow and temperature anomaly-winter severity interactions in the models that included more than one predictor (Table 1). Finally, we included a random effect for year (Table 1). We ran all models in the R package NIMBLE (de Valpine et al. 2017) and ranked the candidate models with the Watanabe-Akaike information criterion (Watanabe 2013). For data, code, and details, please see (Gilbert et al. 2021).

### *Spatial refugia analysis*

The goal of the spatial refugia analysis was to evaluate how deer changed their activity levels over space relative to daily and seasonal weather conditions. We used occupancy models (MacKenzie et al. 2018), which distinguish an ecological state that cannot be directly observed (here, whether or not deer activity occurs at a location on a given day) from the process of imperfectly observing the ecological state (whether or not a camera detects deer activity, given that deer activity occurs). To do so, occupancy models require repeated surveys at fixed locations (making inference about the observational process via detection/non-detection patterns in the replicate surveys) and can accommodate predictors at the ecological and/or observational levels in the model to describe patterns in occurrence and detectability, respectively (MacKenzie et al. 2018). To make inference about occurrence of deer activity at daily resolution, we divided each day into three 8-hour replicate surveys (between 00:00-08:00, 08:00-16:00, and 16:00-00:00 hrs, respectively) and recorded whether or not each camera detected deer during each 8-hour survey on each day during the two winters.

We interpret the ecological state as “occurrence of deer activity at cameras” instead of “occurrence” or “occupancy” (MacKenzie et al. 2018; Steenweg et al. 2018) because we wished to make inference at a daily scale, in contrast to more common use of occupancy models to make inference about occurrence of a species over some longer duration such as a breeding season (MacKenzie et al., 2018). Because deer occupy fairly static winter home ranges over the scope of analysis (Nelson 1995; Van Deelen et al. 1998), we reason that daily variation in estimated deer occurrence correlates with overall activity levels within home ranges (versus broader habitat selection; Johnson, 1980).

We modeled the daily probability of deer activity (the ecological level of the model) as a function of the four landscape predictors, two weather predictors (temperature anomaly and winter severity; we omitted snow depth due to strong correlation with winter severity), and landscape–weather interactions. We included quadratic terms for coniferous forest, deciduous forest, and open habitat because we anticipated that deer activity would be most strongly associated with intermediate levels of these landscape patterns (Hewitt 2011). In addition to the predictors, we included a random intercept for year and a spatial random effect (Crainiceanu et al. 2005). The spatial random effect accounts for the location of the cameras and captures unmodeled broad-scale patterns in deer activity.

We modeled detection probability (the observational level of the model; MacKenzie et al., 2018) with a binary predictor indicating whether or not a replicate survey period was during the day (i.e., 08:00-16:00 hrs) and random effects of site and year. We ran all models in the R package NIMBLE (de Valpine et al. 2017). After fitting, we plotted the predicted probability of deer activity at representative cameras and inspected the activity dynamics relative to the extreme days. For details and code, please see Supporting Information.

## Results

Over the two focal winters (2017-2018 and 2018-2019), Snapshot Wisconsin accumulated 195,481 deer detections from 2,028 cameras (Fig. S1). We identified nine cold extremes and nine warm extremes during the two winters. The minimum temperatures during the cold extremes ranged from -35.3 to -24.9 °C (or 19.9 to 13.8 °C colder than 1980-2019 averages, respectively), while the daily minimum temperatures during warm extremes ranged from -6.4 to -0.67 °C (or 9.8 to 12.7 °C warmer than 1980-2019 averages). Three and six of the cold and warm extremes occurred during

2017-2018, while six and three cold and warm extremes occurred during 2018-2019. Cold extremes occurred during December (3), January (3), Feburary (1), March (2), while warm extremes were concentrated in January (7), with single warm extremes falling in December and February.

***Temporal refugia***

Deer altered their activity timing in response to both daily and seasonal weather conditions (Figs. 2-3). The top-ranked model for night, dawn, and day activity included both temperature anomaly and either snow depth or winter severity (Table 1). Under anomalously cold temperatures and deeper snow, deer became more day-active and less dawn- and night-active (Fig. 3). Deer became less night- and dawn-active and more day-active over both winters (Fig. 2) and as winter severity increased (Figs. 3, S4). Finally, deer became more day-active on cold days under severe winter conditions than on similarly cold days under mild winter conditions (Fig. S4). Notably, deer did not alter their dusk activity relative to weather conditions (Fig. 3).

During cold extremes, dawn activity was lower than seasonal averages (Fig. S5). In most cases, daytime activity during cold extremes was higher than seasonal averages (Fig. S5). On the coldest day (31 January 2019 with an average minimum temperature of -35 °C), deer showed the lowest and highest proportions of dawn and daytime activity, respectively (Fig. S5). During warm extremes, deer reallocated daytime activity to the night and dawn, while dusk activity was not dramatically different from seasonal averages (Fig. S5).

***Spatial refugia***

Deer adjusted their activity in space relative to daily and especially seasonal weather conditions (Fig. 4). First, deer activity was higher in landscapes with more topographic relief, particularly as winter severity increased (Fig. 4). Second, deer were generally more active in landscapes with intermediate levels of coniferous forest; during cold anomalies, deer were more likely to be active in landscapes with greater proportions of coniferous forest (Fig. 4). Under severe winter conditions, deer activity was lower but remained greatest in landscapes with intermediate levels of coniferous forest (Figs. 4, S6). Third, deer showed highest levels of activity in landscapes with intermediate levels of deciduous forest (Figs. 4, S6) but reduced activity in deciduous-dominated landscapes during cold extremes and under severe winter conditions (Fig. 4). Finally, deer activity was highest in landscapes with intermediate levels of open habitat and did not change according to daily temperature anomaly (Figs. 4, S6). Conversely, under high winter severity, deer activity was generally lower (but still highest at intermediate levels of open habitat), particularly in landscapes dominated by open habitat (Figs. 4, S6).

Considered holistically, probability of deer activity dropped gradually over the course of the winter across the state (Fig. 5) but dropped most drastically in deciduous- and open-dominated landscapes in northern Wisconsin (Fig. 5a). This model prediction was driven by the strong negative effect of winter severity as well as its interactions with the landscape predictors (Figs. 4, S6). In contrast, daily temperature anomaly alone showed only a weak negative effect on spatial activity (Figs. 5a, S6). Finally, temperature anomaly and winter severity interacted (Fig. S6) such that deer showed idiosyncratic responses to temperature extremes over time and space (Fig. 5b-c). For example, a major mid-winter cold wave in 2018-2019 seemed to accelerate the season-long decline in deer activity, but the effect was most pronounced in northern Wisconsin (Fig. 5c).

## Discussion

We documented behavioral flexibility in the use of temporal and spatial refugia by a northern ungulate in response to extreme temperatures and seasonality. During cold extremes and late in the winter, deer were more day-active and less dawn- and night-active; conversely, on warm days and early in the winter, deer were relatively more active at night. Similarly, deer were more active in landscapes with abundant coniferous forests during cold extremes and in landscapes with abundant topographic relief late in the winter. These results suggest that behavior might be key in adapting to increasing climatic variability and the greater likelihood of extreme weather. Importantly, such behavioral flexibility allows animals to access refugia in time (Levy et al. 2019) and space (Scheffers et al. 2014); understanding how animals use such refugia is crucial to predicting the consequences of warming trends and extreme events.

### ***Temporal refugia***

We found support for the temporal refugia hypothesis (Hut et al. 2012; van der Vinne et al. 2014), which posits that animals may shift activity in time to reduce exposure to stressors. Under cold conditions, energetic stress likely overwhelms other factors—for example, predation—that are fundamental in shaping a species' activity patterns (Oates et al. 2019). Night and dawn are typically the coldest portion of the 24-hr cycle, and thus deer can conserve energy by restricting activity during these periods and allocating activity to the day, which is consistently the warmest portion of the 24-hr cycle. Similarly, energy balance optimization explains the seasonal trends of increased daytime and reduced nighttime activity (Fig. 2). As an animal's condition deteriorates over the winter, the temporal refugia hypothesis asserts that it should be active during times that are the energetically least costly. In contrast, warm extremes relax thermal constraints and release animals to structure their activity budgets in response to other constraints. For example, with thermal constraints relaxed, increased predation risk during day and night may coerce an animal to concentrate activity during dawn and dusk (Kohl et al. 2018).

While activity timing flexibility has attracted attention as a potential mechanism for "behavioral rescue" from climate change (Fey et al. 2019; Levy et al. 2019; Bonebrake et al. 2020; Veldhuis et al. 2020), most studies have focused on activity timing flexibility as an antidote to warming trends, not extremes, and particularly not cold extremes (Maxwell et al. 2019). Importantly, time is a resource (Kronfeld-Schor & Dayan 2003) that can be partitioned and used as a refugium (Kohl et al. 2018; Levy et al. 2019; Riddell et al. 2021), but only when animals can dynamically adjust their activity budgets.

***Spatial refugia***

We found some support for the spatial refugia hypothesis, which predicts that animals adjust activity in space to reduce exposure to stressors. For example, deer were more active in landscapes with abundant topographic relief or coniferous forests under severe winter conditions and during cold extremes, respectively (Fig. 4). Topographic relief has been linked to microclimate diversity (via processes such as ridges blocking wind or south-facing slopes gaining greater solar radiation; Suggitt et al., 2018), while coniferous forests create warmer and more stable winter microclimates and shallower snow accumulation than other forms of land cover (De Frenne et al. 2021). Strikingly, winter severity had a strong negative effect on deer spatial activity, meaning that cameras in high-severity areas (e.g., northern Wisconsin late in the winter; Fig. S2) were far less likely to detect deer than cameras in milder areas (e.g., southern Wisconsin; Fig. 5c). This strong effect of winter severity is likely an artefact of reduced movement and stronger anchoring to specific refugia habitats (e.g., conifer stands), which would result in fewer detections at cameras. Importantly, deer may show such behavior not only to reduce exposure to energetic stress (cold temperatures) but also to reduce predation risk, since the shallower snow in conifer stands facilitates escape from wolf predation (DelGiudice et al. 2013).

The spatial refugia hypothesis implies that, when a stressor is relaxed, animals are free to use habitats that would otherwise be inhospitable (Fig. 1). Consistent with this idea, we documented that deer were more active in open landscapes under low winter severity (Figs. 4, S6). In the context of thermal energetics, using open habitats is high risk (elevated exposure to thermal stress; De Frenne et al., 2021) but high reward (waste grain can rapidly balance energy deficits; Fowler et al., 2020). Open habitat showed a stronger interaction with winter severity than temperature anomaly (Figs. 4, S6), indicating that factors such as snow depth and energetic condition constrain deer activity in open habitats more so than temperature.

***Resilience to increasing climatic variability***

Behavioral flexibility lays the groundwork for resilience to greater climatic variation, including extreme events (Beever et al. 2017). The behavioral flexibility that we observed indicates that, on the whole, large mammals such as deer may be able to withstand cold extremes by seeking refugia in time and space. Large body size and activity timing flexibility have been identified as the two traits that most strongly predict a species' ability to respond to climate change (McCain & King 2014). Ungulates exhibit both of these traits. Nevertheless, in northern regions, deer non-hunting mortality is highest during the winter due to starvation and increased predation (DelGiudice et al. 2002; Weiskopf et al. 2019). Indeed, energetic stress may dampen antipredator behavior (the so-called starvation-predation tradeoff), since cold and starving animals often prioritize obtaining food at the expense of avoiding predators (McNamara et al. 2016; Oates et al. 2019). Thus, cold extremes pose a particularly dire survival challenge if they occur during the late winter. In both the temporal and spatial refugia analyses, we found temperature-winter severity interactions that indicate deer show stronger behavioral responses to daily temperature under severe versus mild winter conditions (Figs. S4, S6). Thus, animals may display multiple modes of behavioral flexibility in response to acute stressors, depending upon seasonal context.

Winter warm extremes are a respite from thermal stress and provide the opportunity to forage in habitats such as croplands, which are high risk in terms of potential cold exposure but high reward in nutritional payoff. However, the opportunity afforded by warm extremes is contingent on existing conditions, particularly snow cover. A single anomalously warm day following deep snow accumulation will offer poor foraging opportunities because most ungulates are reluctant to move through deep snow (Hewitt 2011). Moreover, warm extremes may exacerbate snow conditions; freeze-thaw and rain-on-snow events create dense, crusty snow, which impairs movement and foraging for ungulates (Robinson & Merrill 2012) and may make them more vulnerable to predators (Kautz et al. 2020). The stronger interaction between open habitat and winter severity versus temperature anomaly supports the idea that seasonal conditions may constrain behavioral flexibility in space use. In addition, warm extremes may have other deleterious effects including heat stress (Sherwood & Huber 2010) due to physiological adaptations to cold (e.g., thick pelage; Hewitt, 2011) or increased disease transmission (Cohen et al., 2020; Weiskopf et al., 2019). Thus, warm extremes likely enhance energetic condition and thus predator avoidance (Oates et al. 2019; Weiskopf et al. 2019) but do not necessarily represent a “free lunch” for cold-adapted organisms.

Ultimately, because this study is observational, there remains a need to link behavioral flexibility to fitness metrics and direct measures of energy expenditure to determine whether such flexibility can indeed promote resilience to winter temperature extremes. Doing so would necessitate continuous monitoring of the physiological condition or survival of individuals in different landscapes as they experience extreme events (Latimer & Zuckerberg 2019; Lamb et al. 2020). In particular, a natural experiment in which researchers deploy “physiologgers” (which record variables such as heart rate, blood oxygen content, or breathing frequency; Hawkes et al., 2021) on animals in landscapes with low and high refugia potential—or on animals confined to areas without refugia—would elucidate the efficacy of behavioral flexibility for modulating energy expenditure. In addition, future research should explore the community- and ecosystem-level consequences of such behavioral flexibility. For example, by shifting activity in space and time, do ungulates increase (or decrease) their exposure to predation risk (Kohl et al. 2018) or exert greater browsing pressure on plant communities (Alverson et al. 1988)? Finally, behavioral flexibility should inform management and conservation efforts under climate change; for example, management efforts could focus on maintaining microclimate diversity to buffer organisms against cold extremes (Keppel & Wardell-Johnson 2012; Woods et al. 2015) or mitigating increases in wildlife-vehicle collisions due to increased animal activity during warm extremes and winters with reduced snow cover (Thompson et al. 2021; Raynor et al. 2021). In conclusion, spatial and temporal refugia are key to withstanding extreme events, and species (such as deer) which show the behavioral flexibility necessary to access these refugia will likely be more resilient than those that do not.

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**Tables**

Table 1. Candidate models for the proportion of activity during each period as a function of weather predictors. In the Night, Dawn, Day, and Dusk columns, the “X” denotes the top model.

| Predictors | Night | Dawn | Day | Dusk |
|---|---|---|---|---|
| Temp. anomaly + Winter severity + Temp. anomaly* Winter severity | X | | X | |
| Temp. anomaly + Snow depth + Temp. anomaly * Snow depth | | X | | |
| Temp. anomaly | | | | |
| Snow depth | | | | |
| Winter severity | | | | X |

**Figures**

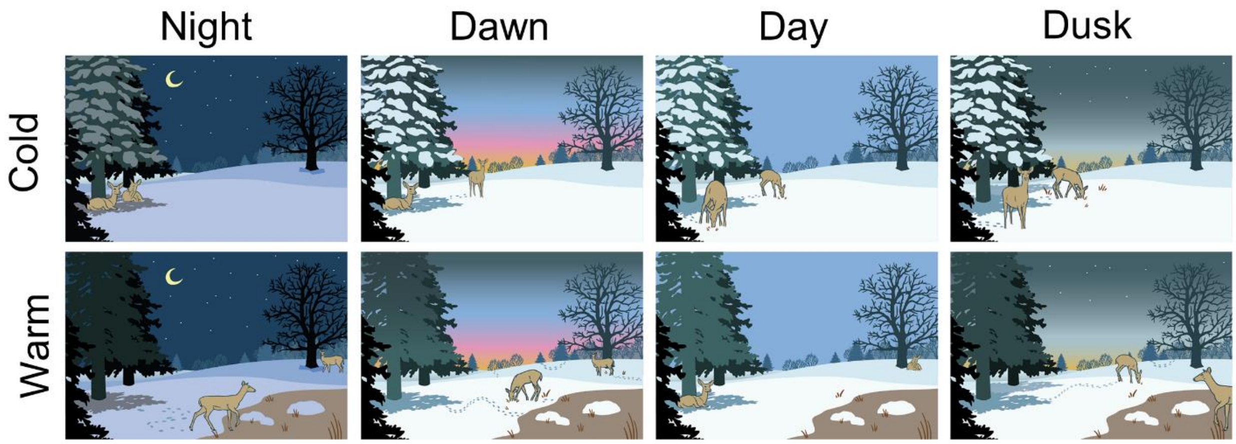


Figure 1. Predicted behavioral flexibility in response to cold and warm extremes. During cold extremes (top row), we predict that deer become more diurnal, move less, and show stronger anchoring to refugia habitats such as coniferous forest. During warm extremes (bottom row), we predict that deer become more nocturnal and crepuscular, move more, and are more likely to use open habitats.

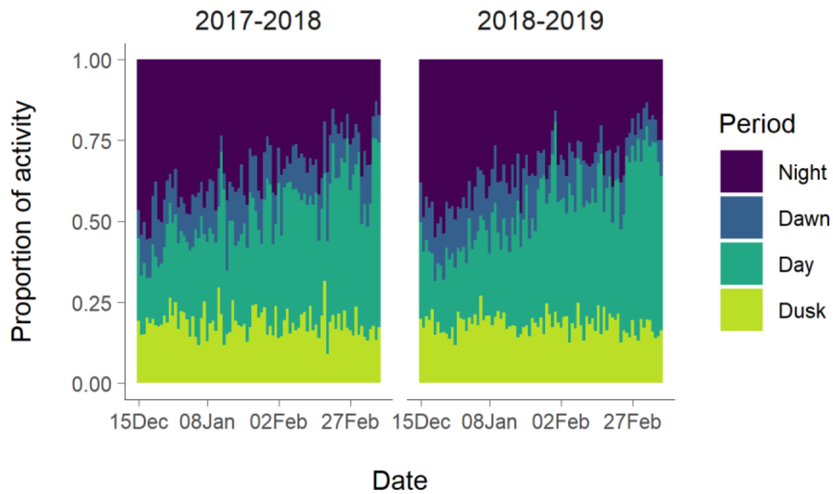


Figure 2. Proportions of deer activity falling within night, dawn, day, and dusk periods over two winters. Note the decrease in nighttime activity and increase in daytime activity as the winter progresses. Dusk activity is relatively stable whereas dawn activity is less common and highly variable.

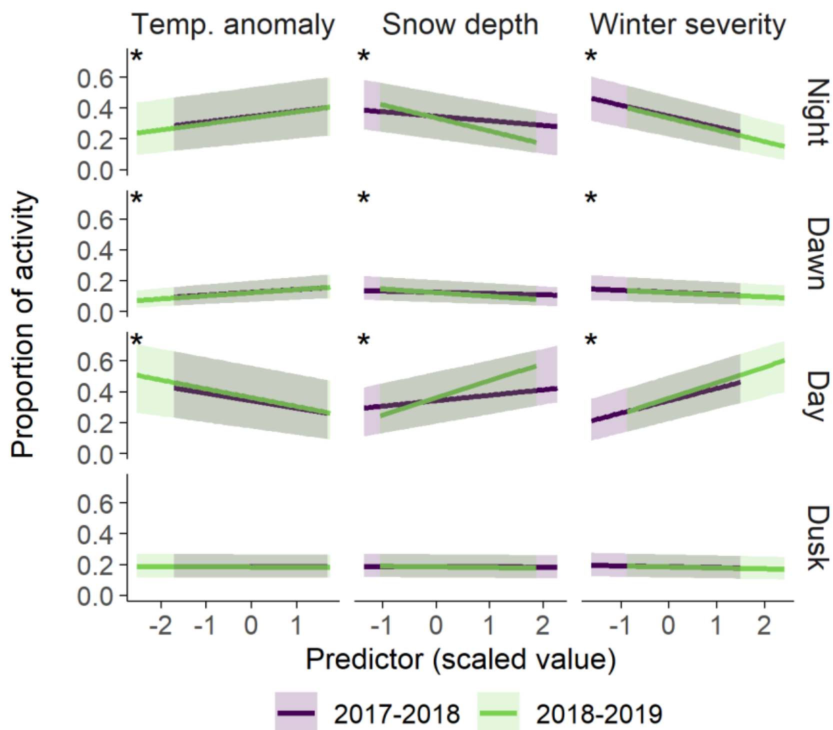


Figure 3. Relationships between weather predictors and proportion of deer activity during night, dawn, day, and dusk (univariate models; see Table 1). Asterisks denote significant relationships (i.e., the 95% credible interval of the slope excluded zero). Deer showed more daytime and less dawn and night activity, respectively, under cold temperatures, deep snow, and severe winter conditions. Note also that deer did not change dusk activity relative to weather predictors.

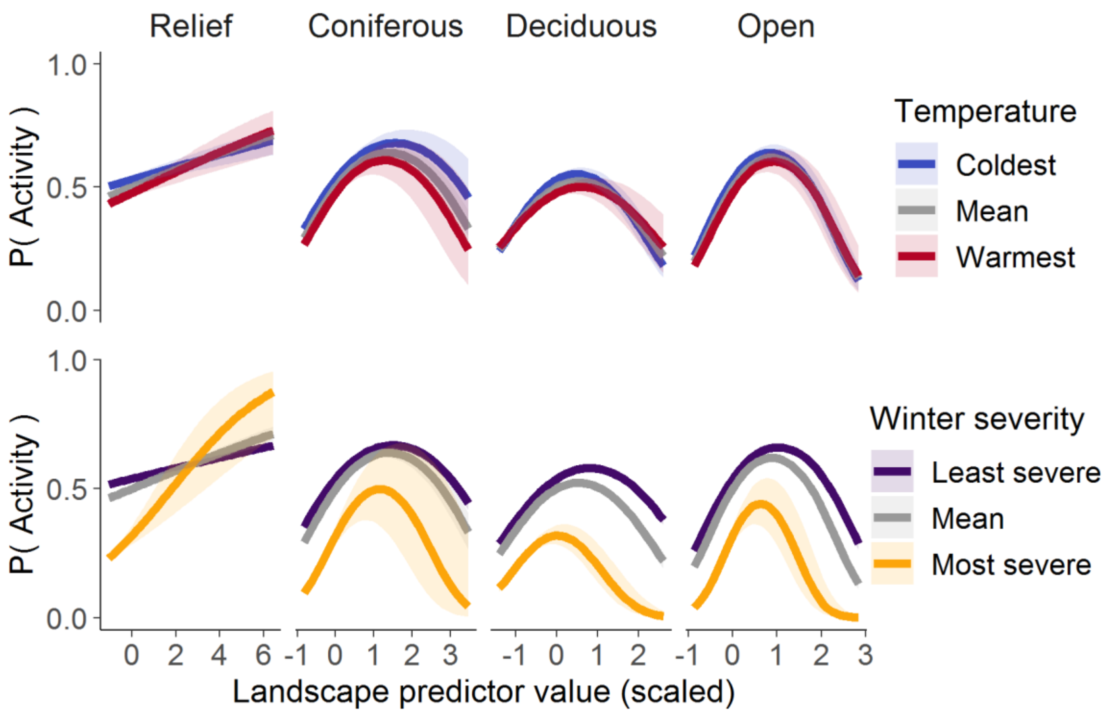


Figure 4. Partial effect plots showing weather-mediated shifts in associations between deer activity and landscape patterns. Lines represent means and shaded areas represent 95% credible intervals. During cold extremes, deer were slightly more active in conifer-dominated landscapes. Under high cumulative winter severity, deer were generally much less active, with highest activity occurring in landscapes with abundant topographic relief and intermediate levels of coniferous forest, deciduous forest, and/or open habitat.

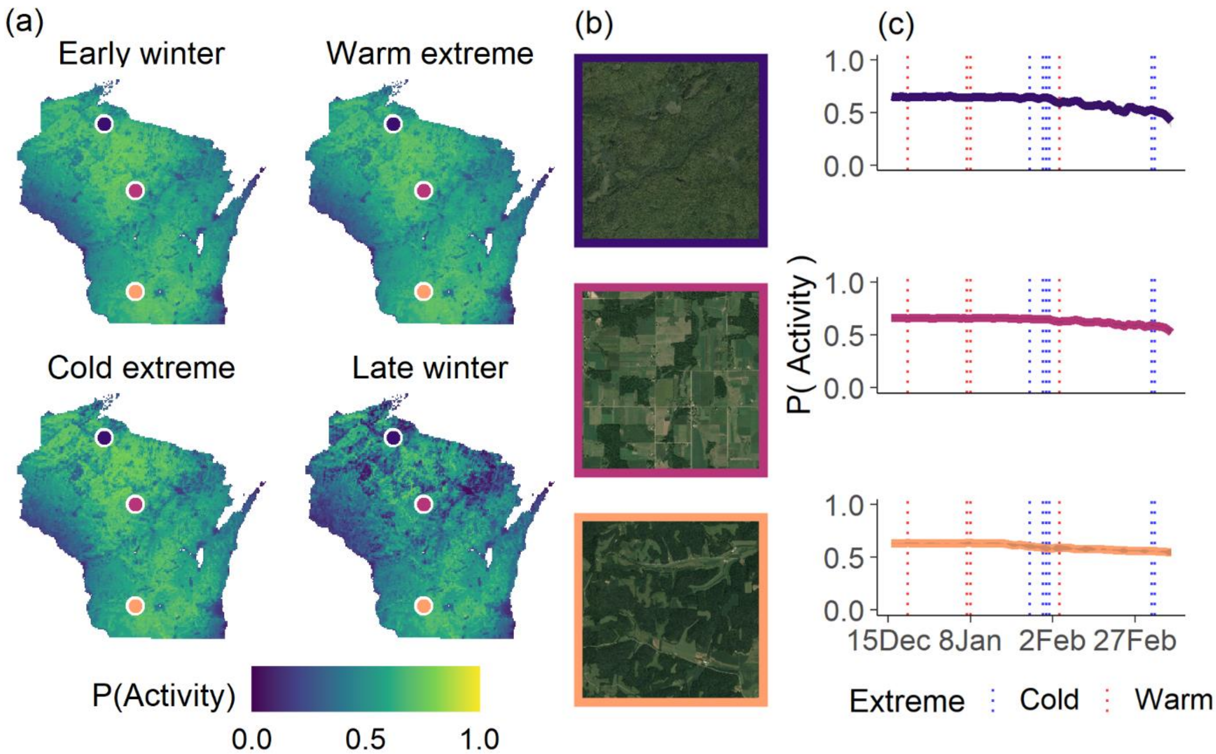


Figure 5. (a) Predicted deer activity for early winter (15 December 2018), a warm extreme (8 January 2019), a cold extreme (31 January 2019), and late winter (10 March 2019). (b) Three representative landscapes: the northern landscape (purple) is densely forested (60% deciduous, 21% coniferous); the middle landscape (maroon) is flat and dominated by open habitat (68%) with limited deciduous (18%) and coniferous (5%) forest; the southern landscape (gold) is a forest-agriculture mosaic (68% deciduous, 30% open) with abundant topographic relief. (c) Predicted deer activity dynamics for the three landscapes over the winter of 2018-2019. Note the larger decline in deer activity over the winter in the northern landscape as well as a slight kink in all the lines corresponding to a major mid-winter cold wave.

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**Chapter 4: Human disturbance compresses the spatiotemporal niche**

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**Abstract**

Human disturbance may fundamentally alter not only the actors in ecological communities but also the way they interact, a prospect that remains poorly understood. Thus, we investigated whether human disturbance compresses or expands the space and time—key niche dimensions—partitioned by animal communities. Using 4 years of data from >2,000 camera traps across a human disturbance gradient in Wisconsin, USA, we measured spatiotemporal co-occurrence (the time between successive detections at cameras) for 74 species pairs and created species networks based off spatiotemporal co-occurrence at each camera. Cameras detected species pairs in more rapid succession (by ~2 days) in disturbed landscapes than cameras in the least-disturbed landscapes. In parallel, cameras detected denser species networks, comprised of greater proportions of low-antagonism pairs, in disturbed landscapes. These findings suggest that many biotic interactions—from mutualisms to predation—are likely to be compressed in disturbed landscapes, with possible far-reaching ecological effects.

## Introduction

Humans alter the proverbial ecological theater (Hutchinson 1965) in several ways. First, humans mediate species extirpations and colonizations, thus reshuffling the actors in a given ecological play (McKinney & Lockwood 1999). Second, via disturbances like climate and land-cover change, humans reshape the stage upon which the play occurs (Song et al. 2018; IPCC 2021). And finally, human disturbance may affect *how the remaining actors interact*, in essence rewriting the script of nature’s play (Smith et al. 2015; Suraci et al. 2019; Wilson et al. 2020). However, we lack a comprehensive understanding of the implications of human disturbance for species interactions (El-Sabaawi 2018; Wilson et al. 2020).

Space and time are central niche dimensions that influence the degree to which species interact. Species compete for space and must be somewhat proximate in order to interact (Tilman 1994). Similarly, time is an ecological resource for which species compete (Kronfeld-Schor & Dayan 2003), and species that co-occur temporally (at either seasonal or daily scales) should interact more frequently (Post 2019; Yang 2020). Human disturbance likely alters the space and time that can be shared by animal communities but it is not clear whether such disturbances generally compress or expand the spatiotemporal dimensions of the niche (Sévêque et al. 2020).

Human disturbance may compress the space and time that can be partitioned by co-occurring species (Parsons et al. 2019; Sévêque et al. 2020). For example, mammals move shorter distances (using less space; Tucker et al. 2018) and become more nocturnal (using less time; Gaynor et al. 2018) in human-disturbed areas, a trend that emerges across diverse taxa. With less space and time available, it is possible that co-occurring species may be competing for compressed niche space in human-dominated areas (Manlick & Pauli 2020).

Alternatively, humans may expand the space and time to be partitioned by communities (Moll et al. 2021). Humans may expand the time available for species by, for example, excluding competitors or predators and thus opening a broader temporal niche for other species (Suraci et al.

2019). Additionally, humans can expand the space available for species by either building infrastructure that serves as habitat (Moll et al. 2021) or by providing subsidies (e.g., trash or crops; Oro et al. 2013) which may reduce the space needs of competitors or predators (Fischer et al. 2012; Newsome et al. 2015; El-Sabaawi 2018; Sévêque et al. 2020).

Our goals were to evaluate 1) the effects of human disturbance on spatiotemporal co-occurrence between species pairs, 2) whether these effects vary among pairs with low, medium, or high antagonism levels (ranked according to their probability of lethal encounter), and 3) implications of human disturbance for the broader network of species. We offer two competing hypotheses. First, the compression hypothesis posits that human disturbance compresses the space and time available to animals, leading to greater spatiotemporal co-occurrence between species pairs—and ultimately, more compact species networks—in disturbed environments (Fig. 1a,b). Second, the expansion hypothesis posits that human disturbance expands the space and time available to animals, leading to less frequent spatiotemporal co-occurrence of pairs—and ultimately, less dense species networks—in disturbed environments (Fig. 1a,b). Regarding the second goal, we hypothesized that predators or dominant competitors are more likely to be excluded by human disturbance (Estes et al. 2011), leading predation or competition to be dampened or decoupled in human-disturbed areas (Fischer et al. 2012). Thus, we predicted that antagonistic pairs would more likely follow the expansion hypothesis and that their spatiotemporal co-occurrence would show a comparatively stronger relationship to human disturbance than non-antagonistic pairs (Fig. 1a). We evaluated these hypotheses with data from an extensive camera-trapping network in Wisconsin, USA (Fig. S1), performing analyses on 74 species pairs and species networks (using the time between detections of species pairs as an index of spatiotemporal co-occurrence) across a gradient of human disturbance, as quantified by a composite metric of agricultural, urbanization, resource extraction, and other data layers on anthropogenic landscape modification.

## Materials and Methods

*Camera-trap data: Snapshot Wisconsin*

We obtained time-stamped animal detections linked to precise spatial locations from Snapshot Wisconsin, a regional camera-trap network powered by citizen science (Townsend et al. 2021). Operated by the Wisconsin Department of Natural Resources (WDNR) in collaboration with thousands of volunteers, the program launched in 2016 and has since gathered >60 million photos from >2,000 camera traps. Snapshot Wisconsin uses quarter-townships (4.8 x 4.8 km resolution) as sampling units, prioritizing prospective camera hosts from unoccupied cells to maximize the project's coverage. The WDNR provides each host with a Bushnell Trophy Cam (Overland Park, KS) with pre-programmed settings to record 3-image sequences when triggered, with 15-second gaps between successive sequences. Hosts place their cameras—without bait or lures—along wildlife trails or water features and at least 100 m from buildings or major roads. The hosts mount cameras 0.75–0.9 m from the ground and 3–5 m from the target, preferably aiming the camera north to avoid false triggers from sunrise or sunset. Finally, hosts clear vegetation between the camera and the targeted feature to maximize animal detectability. Hosts visit their cameras every 1–3 months to replace batteries and retrieve photos, which they upload to a WDNR server. The image-classification workflow consists of 1) classification by camera hosts, 2) consensus classification by additional volunteers, and 3) expert classification by WDNR scientists to quantify the accuracy of volunteer classifications (Clare et al. 2019).

*Processing Snapshot Wisconsin data*

We used the time between detections of species pairs as a measure of spatiotemporal co-occurrence. This quantity measures—for a fixed location—the temporal spacing between species (Karanth et al. 2017; Niedballa et al. 2019). Recent simulations have demonstrated that this approach is a robust way to detect spatiotemporal avoidance or aggregation between species pairs (Niedballa et al. 2019). Approaches that consider co-occurrence in space *and* time are necessary to evaluate the influence of human disturbance on interacting species, because strictly spatial or temporal approaches may be uninformative if species can avoid each other in time or space, respectively (Frey et al. 2017; Suraci et al. In press).

We considered data from 2017–2021 and defined 3-month seasons during summer (1 June–31 August) and winter (1 December–28 February). We chose 3 months to avoid major shifts in community composition at camera sites. We differentiated summer and winter because many species show behavioral differences (e.g., reduced movement) between the two seasons.

We employed three filtering rules to calculate the time between detections of species pairs. First, we defined a sample of eligible cameras. To be eligible, a camera had to be active during at least one of the 3-month periods and needed to have >99% of its photos classified. Second, we defined a list of eligible species as those with >95% classification accuracy (calculated by comparing volunteer and expert classifications; Clare et al. 2019), thus omitting inaccurately classified species and retaining 18 species (16 mammals and 2 birds; Table S1). Third, we developed a list of eligible species pairs. Capitalizing on the fact that camera traps monitor many species simultaneously, we included all pairs that were co-detected at ≥50 cameras, which removed pairs that exhibited limited range overlap. We then calculated the time (in minutes) between successive detections of a given pair at each camera. Finally, we filtered the responses to limit inference to successive detections within 30 days of each other, reasoning that such a time scale is relevant to species interactions because scent can linger for weeks (Apfelbach et al. 2005) and animals may show altered behavior for days to weeks after traumatic encounters with predators (Zanette et al. 2019). Ultimately, we prepared data from 74 species pairs (out of 153 possible pairs from the 18 species considered; Table S2).

*Antagonism ranking of pairs*

We ranked the "antagonism level" of each species pair, conceptualized as the chance of a lethal encounter between species in the pair. Such an approach precludes classifying pairs into non-exclusive interaction categories; for example, the red fox (*Vulpes vulpes*)—coyote (*Canis latrans*) interaction could be classified as either competition or predation (Newsome & Ripple 2015; Moll et al. 2018). We ranked each pair as showing a low, medium, or high chance of interspecific killing using a combination of two rules and subjective classification.

First, we ranked pairs in which neither species was a carnivore as having a low chance of interspecific killing (Prugh & Sivy 2020). Second, if both species in a pair were carnivores (classifying the opossum *Didelphis virginiana* as a carnivore due to its similar functional role to carnivores such as striped skunk *Mephitis mephitis* and raccoon *Procyon lotor*; Wang et al. 2015), we assigned the pair's rank according to relative body mass (Donadio & Buskirk 2006; Jones et al. 2009). If one species was much larger than the other (>10x mass), we ranked the pair as having a medium chance of a lethal encounter, since large carnivores tend to ignore much smaller carnivores (Donadio & Buskirk 2006; Prugh & Sivy 2020). We also assigned a medium rank to carnivore pairs with similar body masses (within a factor of 2), since encounters are too mutually risky for either species to initiate attack (Donadio & Buskirk 2006). Finally, if the larger species was 2–10x larger than the smaller one, we assigned a high chance of a lethal encounter (Donadio & Buskirk 2006).

For pairs in which one species was a carnivore and the other was not, we ranked the pair according to whether we expected low (e.g., raccoon and cottontail *Sylvilagus floridanus*), medium (rare or opportunistic predation, e.g., bear *Ursus americanus* and cottontail), or high chance (archetypical predator-prey relationships, e.g., deer *Odocoileus virginianus* and wolf *Canis lupus*) of a lethal encounter between them. We classified 44% of the pairs with the two rules and the remaining 56% subjectively. All told, we classified 42%, 31%, and 27% of pairs as having low, medium, and high chance of lethal encounter, respectively (Table S2).

*Human disturbance data*

We used the global human modification layer created by Conservation Science Partners as a measure of human disturbance (Kennedy et al. 2019). It is a composite metric of 13 anthropogenic stressors, including human population density, agriculture, transportation infrastructure, and energy production (Kennedy et al. 2019). The data layers used to compute the composite metric had a median date of 2016. The metric is based on both the spatial extent and expected intensity of impact of each stressor and ranges from 0 (no human disturbance) to 1 (highest human disturbance), with a spatial resolution of 1 km (Fig. S1). We calculated mean human disturbance within 5 km of camera locations; we chose this buffer size because it encapsulates the space use of most of the species considered over the temporal scope (≤3 months) of camera sampling.

*Pair analysis*

We used a Bayesian hierarchical model (McElreath 2020) to evaluate the association between human disturbance (the predictor) and the observed time between detections of species pairs (the response). We modeled the response with a gamma distribution, treating the expected value (μ) as a function of human disturbance (x) and antagonism (z) predictors with a log link. We allowed the intercept and the human disturbance term to vary among species pairs, and, within pairs, among seasons (i.e., as random effects). We incorporated the antagonism ranking of the pairs (an ordered categorical variable) as a monotonic effect such that the antagonism rankings were not assumed to act as continuous variables (Bürkner & Charpentier 2020; McElreath 2020). Finally, to evaluate whether pairs with different levels of antagonism showed different relationships to human disturbance, we included interactions between the human disturbance and antagonism predictors.

In Eqn. 1 below, *i* indexes camera, *j* indexes observation, *p* indexes species pair, and *s* indexes season (summer, winter). $\mu_{ij}$ is the expected value of the $j^{th}$ observation at the $i^{th}$ camera, $x_i$

is the human disturbance in the landscape surrounding the $i^{th}$ camera, and $z_j$ is the antagonism ranking for the pair representing the $j^{th}$ observation.

$$log(\mu_{ij}) = \beta_{0[p,s]} + \beta_{1[p,s]}x_i + \beta_3 \sum_{k=1}^{z_j} \zeta_{1k} + \beta_4 x_i \sum_{k=1}^{z_j} \zeta_{2k} \text{ Eqn. 1}$$

$\beta_{0[p,s]}$ is the intercept and $\beta_{1[p,s]}$ is the slope for the human disturbance predictor. The $_{[p,s]}$ index indicates that the intercept and slope parameters are permitted to vary among species pairs—and, within pairs, among seasons (as random effects; Table 1). We treated the random effects as draws from a common distribution; thus, for each of these parameters, in addition to the pair- and season-specific parameter (i.e., $\beta_{0[p,s]}$ and $\beta_{1[p,s]}$), we estimated a pair-level parameter ($\beta_{0[p]}, \beta_{1[p]}$) and a "global" parameter ($\beta_0$, $\beta_1$). We used standard weakly informative priors for the "global" parameters and the variance components of the hyperpriors (McElreath 2020).

In Eqn. 1, the monotonic effect of antagonism ranking is $\beta_3 \sum_{k=1}^{z_j} \zeta_{1k}$, comprised of parameters $\beta_3$ (the expected difference between the high- and low-antagonism rankings) and $\zeta_1$, a simplex (a vector of proportions that sum to one) that describes the expected difference between sequential categories as a proportion of the overall difference $\beta_3$ (Bürkner & Charpentier 2020). The final term in Eqn. 1 is the interactions between human disturbance and antagonism ranking.

*Network analysis*

We constructed species networks for each camera site and 3-month period, considering species as nodes and linking a given pair if the camera detected the pair within 30 days of each other. We used the R package *network* (Butts 2008) and calculated 1) network density, defined as the proportion of the total possible linkages observed in the network, and 2) the proportions of each network's links representing pairs with low, medium, and high probabilities of lethal encounter. We modeled the relationship between network density and network proportions of each antagonism ranking (the responses) and human disturbance (the predictor) as well as season (summer, winter) and disturbance–season interactions (Eqn. 2). We modeled the responses with zero–one inflated beta distributions (since all responses were proportions that could take on values of zero or one; Douma & Weedon 2019), treating the expected value φ as a function of predictors with a logit link:

$$logit(\varphi_i) = \alpha_0 + \alpha_1 x_i + \alpha_2 season + \alpha_3 season * x_i \quad \text{Eqn. 2}$$

*Software*

We ran all models in the R package *brms* (Bürkner 2017; R Core Team 2021) using three Markov chain Monte Carlo (MCMC) chains run for 4,000 iterations, discarding the initial 2,000 iterations as warm-up. We assessed convergence via visual inspection of MCMC traceplots and by checking that the Gelman-Rubin convergence statistic was <1.05 (Brooks & Gelman 1998). We evaluated model performance via posterior predictive checks to ensure the model provided valid predictions given the data used to fit the model (McElreath 2020). Finally, to evaluate the hypotheses, we simulated from the model's posterior to generate plots of the model's predictions and compute contrasts of the model's predictions for differing levels of human disturbance or pairs with different antagonism rankings.

## Results

*Sampling summary*

Camera-trapping sampling captured 789,130 photos of 18 focal species (16 mammals, 2 terrestrial birds; Table S1) from 2,095 locations over 322,294 camera-days of effort. From these photos, we calculated 197,254 time-between-detections for 74 species pairs, ranging from a minimum of 127 (raccoon *Procyon lotor* – wolf *Canis lupus*) to a maximum of 28,927 (deer *Odocoileus virginianus* – raccoon) per pair. For complete sample size information, please see Table S2.

*Pair analysis*

*Overall responses to disturbance*

Averaged across pairs, cameras detected species in more rapid succession (i.e., greater spatiotemporal co-occurrence) in disturbed landscapes (Fig. 2). Compared to the most disturbed landscapes, cameras in the least-disturbed landscapes showed 1.52 [0.96, 2.02], 2.00 [1.39, 2.61], and 2.07 [1.03, 3.09] days longer between detections of low-, medium-, and high-antagonism pairs, respectively (mean and 95% credible intervals; Fig. 2, Fig. S2). Antagonistic pairs showed less spatiotemporal co-occurrence than less antagonistic pairs (Fig. 2); at average values of human disturbance, high-antagonism pairs showed 0.30 [0.01, 0.91] and 1.69 [0.99, 2.39] days longer between detections than medium- and low-antagonism pairs, respectively (Fig. 2, Fig. S3), while medium-antagonism pairs showed 1.29 [0.74, 2.04] days longer between detections than low-antagonism pairs (Fig. 2, Fig. S3). However, there was limited evidence of a statistical interaction between antagonism ranking and human disturbance, which indicates that, while intercepts varied according to antagonism ranking, the slopes of the relationships between spatiotemporal co-occurrence and human disturbance were similar across antagonism rankings (Fig. 2).

*Pair-level responses to disturbance*

All pairs showed less time between detections in disturbed landscapes (Fig. 3). The strength of this trend varied among pairs. For example, 69/74 (93%) and 34/74 (46%) of the pairs showed reduced time between detections in disturbed landscapes with 68% and 95% probability, respectively (Fig. 3). Most of the variation among pairs was driven by the intercept; the standard deviation among pair-level intercepts was 0.23 [0.18, 0.29], while the standard deviation among pair-level slopes for the human disturbance term was 0.04 [0.00, 0.07] (Fig. S4).

*Pair-season level responses to disturbance.*

Most pairs showed minor seasonal variation in predicted time between detections (Fig. S5). Only 16 and 7 pairs showed differences by season with 68% and 95% probability, respectively (Fig. S5). All considered, 44/70 (63%) of pairs trended towards more extreme associations between human disturbance and detection time during the winter, while 26/70 (37%) trended towards more extreme associations between human disturbance and detection time during the summer (Fig. S5). Seasonal variation in intercepts within pairs was smaller than variation among pairs; for example, the standard deviation among pair-season intercepts was 62.8% [124%, 10.8%] smaller than the standard deviation among pair-level intercepts (Fig. S4). However, the opposite was true for the human disturbance slopes: the standard deviation of pair-season slopes was 29.3% larger [50.8% smaller, 94.5% larger] than the standard deviation among pair-level intercepts.

*Network analysis*

Species networks showed a greater proportion of possible connections between pairs (i.e., greater network density) in landscapes disturbed by humans (Fig. 5a, b). In the network density model, the human disturbance term had a strong positive effect (posterior mean = 0.18, 95% CI [0.15, 0.21]). Season did not have an apparent effect (posterior mean = 0.00, 95% CI [-0.05, 0.05]) and interacted with human disturbance (posterior mean = 0.03, 95% CI [-0.01, 0.07]) such that human disturbance had a slightly stronger association with network density in the winter (Fig. 5b).

Species networks in disturbed landscapes were on average composed of greater proportions of low-antagonism pairs, particularly in the summer (Fig. 5c). The difference in the proportion of the network composed of low-antagonism pairs between low- and high-disturbance landscapes was 0.19 (95% CI [ 0.17, 0.21]) in summer and 0.11 (95% CI [0.08, 0.14]) in winter. In contrast, species networks in disturbed landscapes were generally composed of smaller proportions of medium- and high-antagonism pairs (Fig. 5c). The difference in the proportion of the network composed of medium-antagonism pairs between low- and high-disturbance landscapes was 0.17 (95% CI [ 0.16, 0.20]) in summer and 0.12 (95% CI [0.10, 0.14]) in winter. Finally, for high-antagonism pairs, the difference was 0.06 (95% CI [0.04, 0.08]) in summer and 0.14 (95% CI [0.12, 0.16]) in winter.

## Discussion

We observed near-universal reductions in time between detections of pairs in disturbed landscapes, a result that supports the compression hypothesis and indicates that human disturbance may rewire species interactions. Our results also indicate that all interaction types—from mutualisms to predation—may be compressed by disturbance (Fig. 2). However, compared to high- and medium-antagonism pairs, low-antagonism pairs were detected in more rapid succession across all levels of human disturbance (i.e., intercepts differed according to antagonism ranking but slopes did not; Fig. 2), suggesting that predator avoidance behavior is maintained even in disturbed landscapes (Gallo et al. 2019). Finally, species networks in disturbed landscapes were more densely connected and composed of greater proportions of low-antagonism pairs than those in less disturbed landscapes, indicating that compression of the spatiotemporal niche scales to altered species interaction networks.

What mechanisms underlie the observed compression pattern? We suggest three non-mutually exclusive mechanisms: fear of humans, reductions in extent of spatial habitat, and human-mediated increases in abundance. First, humans may function as apex predators and cause animals to use less space and/or time in disturbed landscapes (Smith et al. 2017; Tucker et al. 2018; Gaynor et al. 2018; Suraci et al. 2019). Second, disturbance may reduce the amount of space available for partitioning independent of fear-motivated effects. For example, impervious surfaces or agricultural fields may function as barriers (Forman & Alexander 1998), restricting animals within smaller areas and thereby leading to more frequent encounters (Parsons et al. 2019). Finally, human disturbance may amplify species abundance (e.g., by provision of resource subsidies; Newsome et al. 2015; Manlick & Pauli 2020), leading to more frequent interspecific encounters (Poisot et al. 2015). Because humans may restrict the space and time available for animals while simultaneously providing resource subsidies, an intriguing possibility is that total niche volume might be conserved even while the spatiotemporal dimensions of the niche are compressed. The mechanisms driving spatiotemporal compression likely vary according to traits of the species forming a pair. For example, human-disturbed landscapes favor smaller, less carnivorous, and faster-reproducing taxa (Suraci et al. 2021). Extrapolating the body size principle from Carnivora (Donadio & Buskirk 2006), large mammals (i.e., closer in size to humans) might be more likely to display fear-motivated changes in their use of space and time in disturbed landscapes due to greater perceived chance of conflict with humans (Carter & Linnell 2016).

Human-mediated compression of spatiotemporal niche partitioning may have far-reaching ecological consequences (Wilson et al. 2020). Assuming shorter time between detections corresponds to more frequent encounters between pairs, our model predicts that high-antagonism pairs would encounter each other 6 more times (95% CI [3, 10]) within high-disturbance landscapes compared to low-disturbance landscapes over a 3-month period (Figure S6). For individual animals, exposure to antagonistic heterospecifics elevates stress levels (Sheriff et al. 2009) and can reduce body condition or even survival (MacLeod et al. 2018). Such individual-level effects can scale up to affect population-level processes (Creel et al. 2007; Sheriff et al. 2009). For example, Zanette et al. (2011) exposed nesting Song Sparrows (*Melospiza melodia*) to predator cues (vocalizations) while concurrently eliminating direct predation and found that perceived predation risk reduced fecundity by 40% (Zanette et al. 2011). At the community level, compression of spatiotemporal niche partitioning would seem to amplify interactions such as predation and competition, but many studies suggest a decline in predation rates in disturbed landscapes (Kozlov et al. 2017; El-Sabaawi 2018), possibly due to human subsidies or exclusion of apex predators in favor of more omnivorous mesocarnivores (Fischer et al. 2012). Beyond predation, such compression could lead to increased disease transmission; previous work suggests that directly transmitted wildlife diseases are more frequent in urban areas (Brearley et al. 2013). Finally, at the ecosystem level, compression of spatiotemporal niche partitioning might have rippling effects to processes such as nutrient flows (El-Sabaawi 2018; Wilson et al. 2020). Several studies suggest conflicting ecosystem-level effects of human disturbance; for example, Kozlov et al. (2017) documented decreased insect herbivory in urban settings (likely due to greater predation pressure from birds; Kozlov et al. 2017), while Suraci *et al.* (2019) found that rodent consumption of seeds increased when a simulated human cue (voice playbacks) suppressed predator activity (Suraci et al. 2019). Such ecosystem-level effects are notoriously difficult to document but seem likely if disturbance restructures the composition of species networks (Piovia-Scott et al. 2017).

It is clear that humans alter the stage and actors of nature's play, but human disturbance may also change how those remaining actors interact. By jointly considering space and time, we provide a comprehensive evaluation of how human activities might rewrite the script of nature's play. Since biodiversity conservation should encompass not only populations but also the functions and interactions of species (Valiente-Banuet et al. 2015), understanding the implications of human-mediated spatiotemporal niche compression is a pressing need for conservation biology. Thus, we encourage future work to explore the mechanisms driving the observed phenomenon and probe the multiscale ecological effects of this pattern (Wilson et al. 2020).

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**Data and materials availability:**

Raw Snapshot Wisconsin camera-trap data cannot be shared to protect the privacy of participants. However, processed data (with location information removed) and code to reproduce the results and figures are available on Github (https://bit.ly/3tMF2sw) and shall be archived on Dryad upon article acceptance. Human disturbance layer is freely available on Google Earth Engine (https://bit.ly/36HBwaF) and processed data is available at aforementioned GitHub repository.

**Figures and Tables**

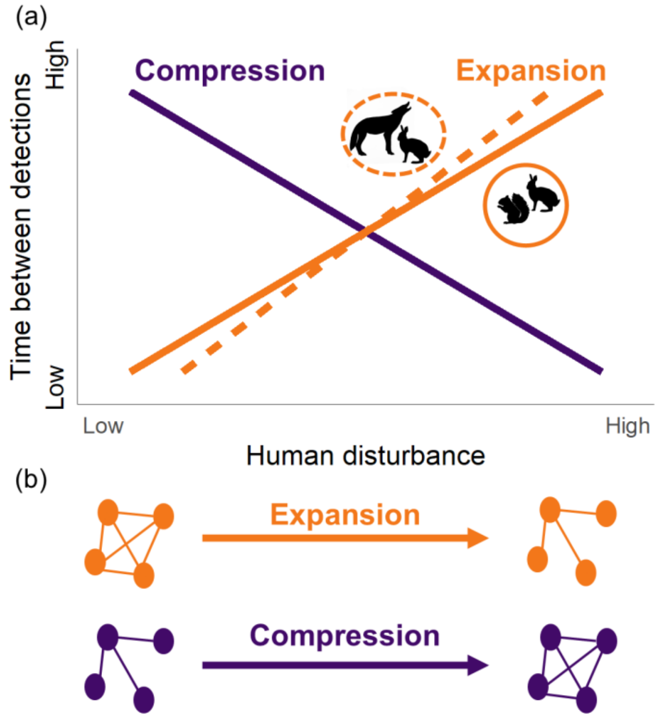


Figure 1. Competing hypotheses. (a) Relationships between human disturbance and time between successive detections of species pairs predicted by competing hypotheses of compression and expansion. The compression hypothesis predicts shorter times between successive detections of species pairs (a) and denser species networks (b) in disturbed landscapes, whereas the expansion hypothesis predicts the opposite. Further, we predicted that antagonistic pairs (dashed orange) would be more likely to follow the expansion hypothesis and show more extreme responses to human disturbance than less antagonistic pairs (solid orange).

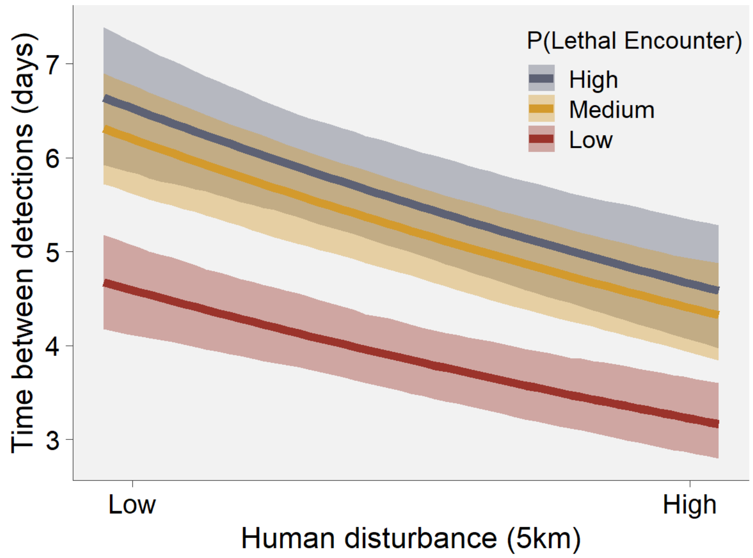


Figure. 2. Results across pairs. Cameras in disturbed landscapes detected species pairs in more rapid succession. Longer times between detections were observed for more antagonistic pairs, but the slopes of the relationships with human disturbance were similar across antagonism rankings. Lines and shaded areas represent means and 95% credible intervals.

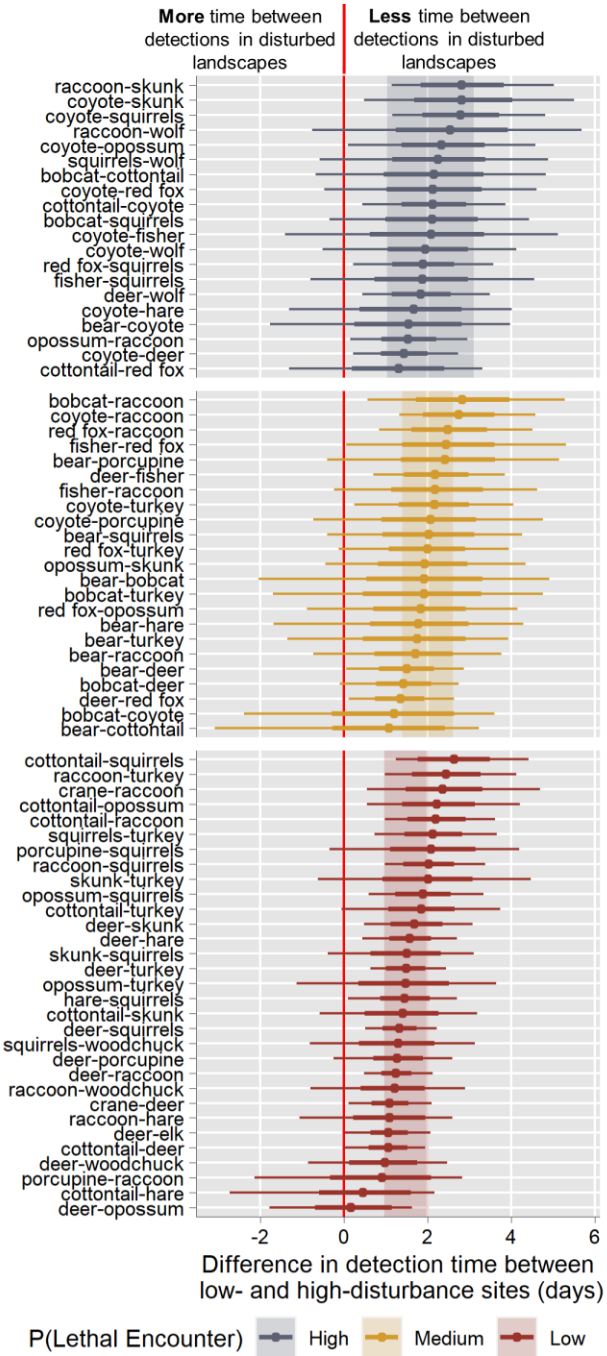


Figure. 3. Pair-level results. Difference in predicted time-between-detection (days) between the least- and most-disturbed landscapes from 1000 simulated draws from the model. Points are the means; thick and thin horizontal bars represent 68% and 95% credible intervals, respectively. The shaded rectangles represent the average difference (95% credible interval) across pairs for each antagonism ranking. Please reference Table S1 for the scientific names.

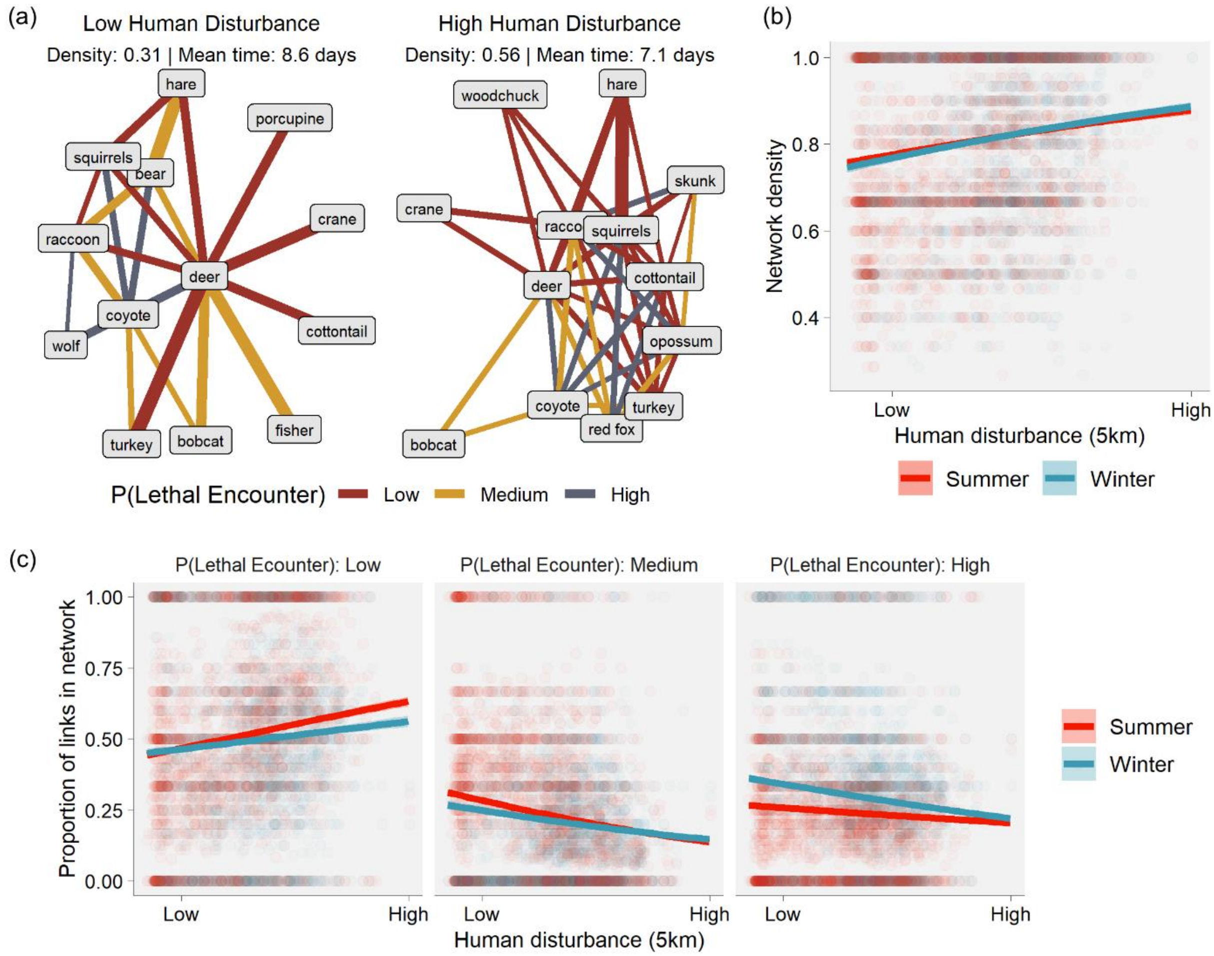


Figure 4. Network-level results. (a) Examples of species networks from camera-trap data, representing aggregated data from 5 of the least- and most-disturbed sites. Nodes are species and edges represent successive detections between species, colored to indicate antagonism and width representing average time between detections (thicker = less time). Density is the proportion of total possible pairs that are connected, and mean time is the average time between detections across pairs. (b) Species networks tended to be more dense in human-disturbed landscapes. (c) Network composition shifted over the human disturbance gradient; networks in disturbed landscapes showed a greater proportion of low-antagonism pairs and a smaller proportion of medium- and high-antagonism pairs. In (b) and (c), lines and shaded areas are means and 95% credible intervals.

Table 1. An example of the priors used to illustrate the varying effects by pair and season.

| Parameter | Prior | Parameter interpretation |
|---|---|---|
| $\beta_{1[p,s]}$ | ~ Normal($\beta_{1[p]}$, $\varepsilon_{\beta 1[p]}$) | Pair- and season-specific slope for human disturbance linear term |
| $\varepsilon_{\beta 1[p]}$ | ~ Exponential(1) | Standard deviation of season-specific slopes within a pair |
| $\beta_{1[p]}$ | ~ Normal($\beta_{1}$, $\varepsilon_{\beta 1}$) | Pair-specific slope for human disturbance linear term |
| $\varepsilon_{\beta 1}$ | ~ Exponential(1) | Standard deviation of pair-specific slopes |
| $\beta_{1}$ | ~ Normal(0, 1) | “Global” slope for human disturbance linear term |

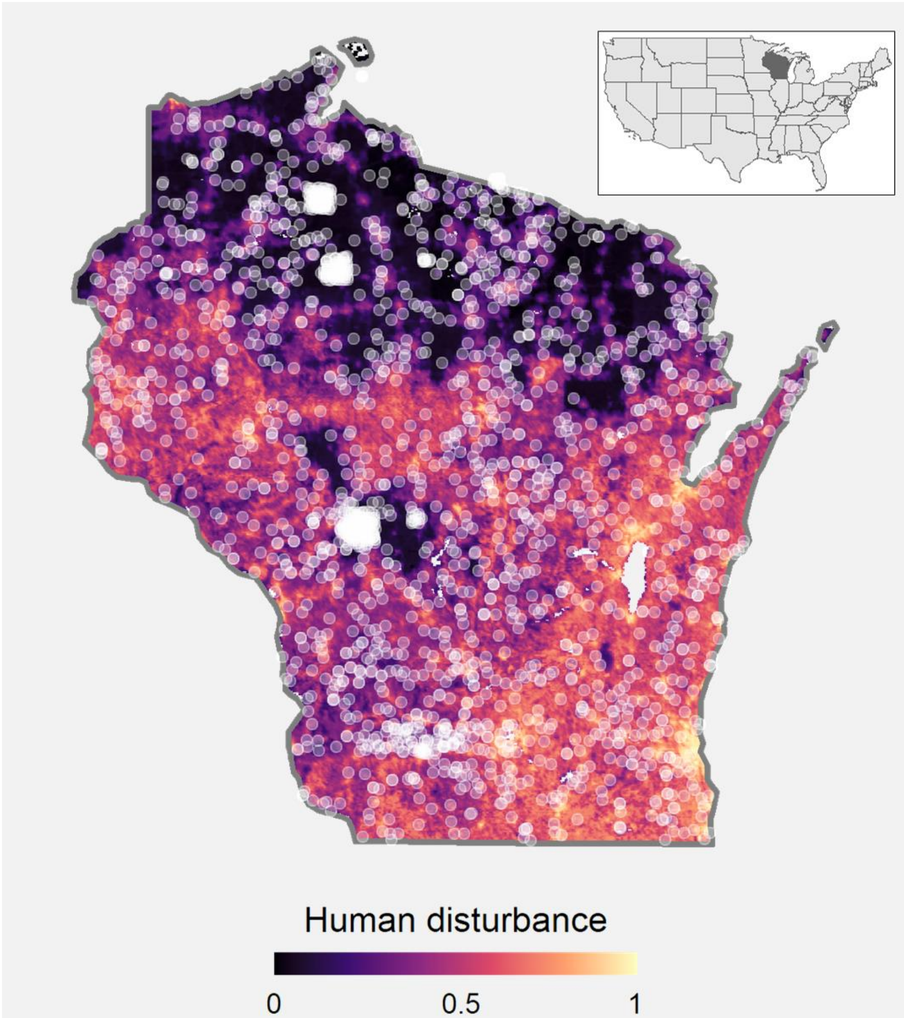


Figure. S1. Gradient of human disturbance in Wisconsin, USA, with camera-trap locations overlaid with white points.

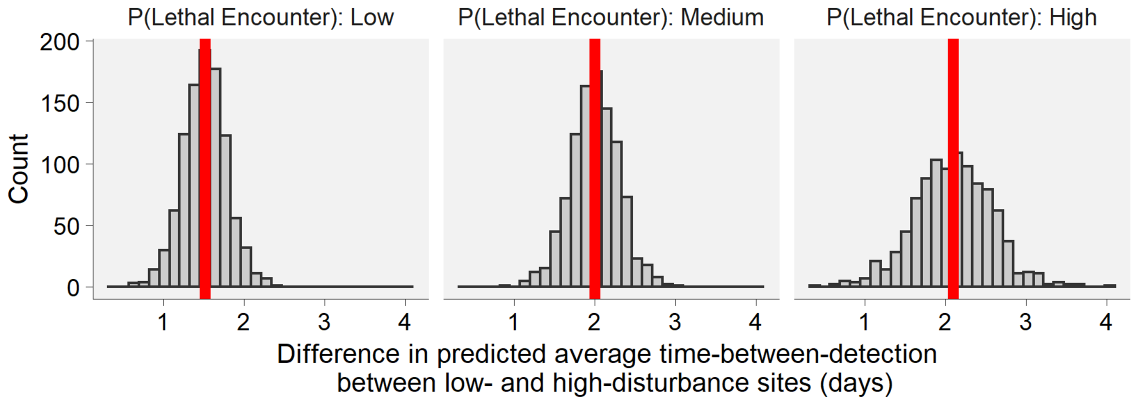


Figure S2. Contrast between predicted time-between-detection for low- and high-disturbance sites at each antagonism level, calculated from 1000 simulated draws from the model. Red line represents the median.

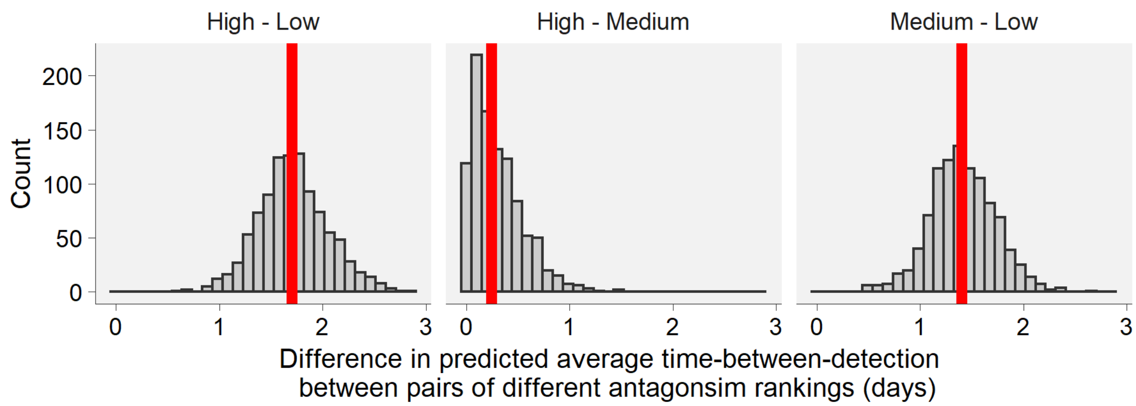


Figure S3. Contrast between predicted time-between-detection for pairs of differing antagonism rankings at average levels of human disturbance, calculated from 1000 simulated draws from the model. Red line represents the median.

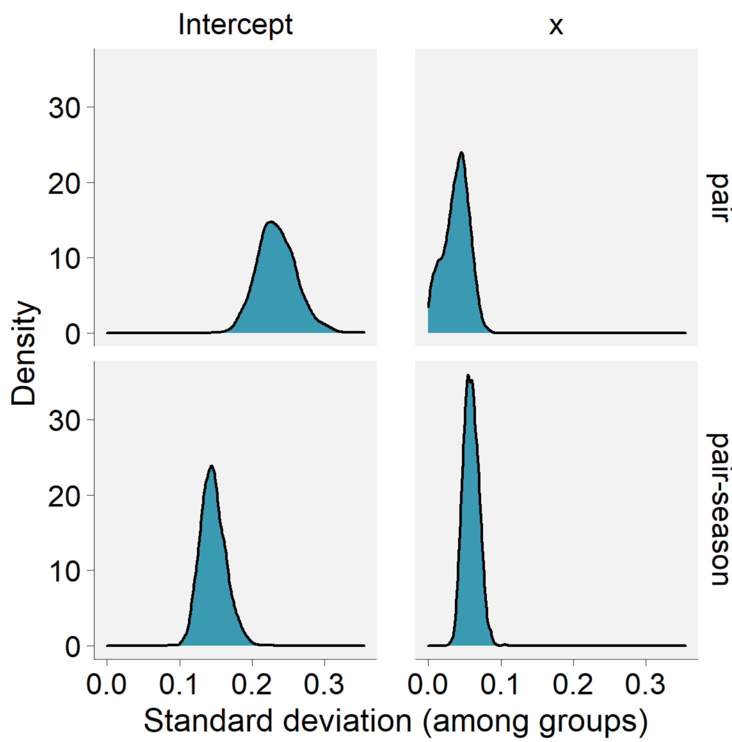


Figure S4. Posterior distributions of standard deviations of varying parameters (intercept and human disturbance slope) among model levels. Note 1) the greater magnitude of variation in intercepts than among slopes and 2) the greater variation in intercepts among pairs than within pairs between seasons.

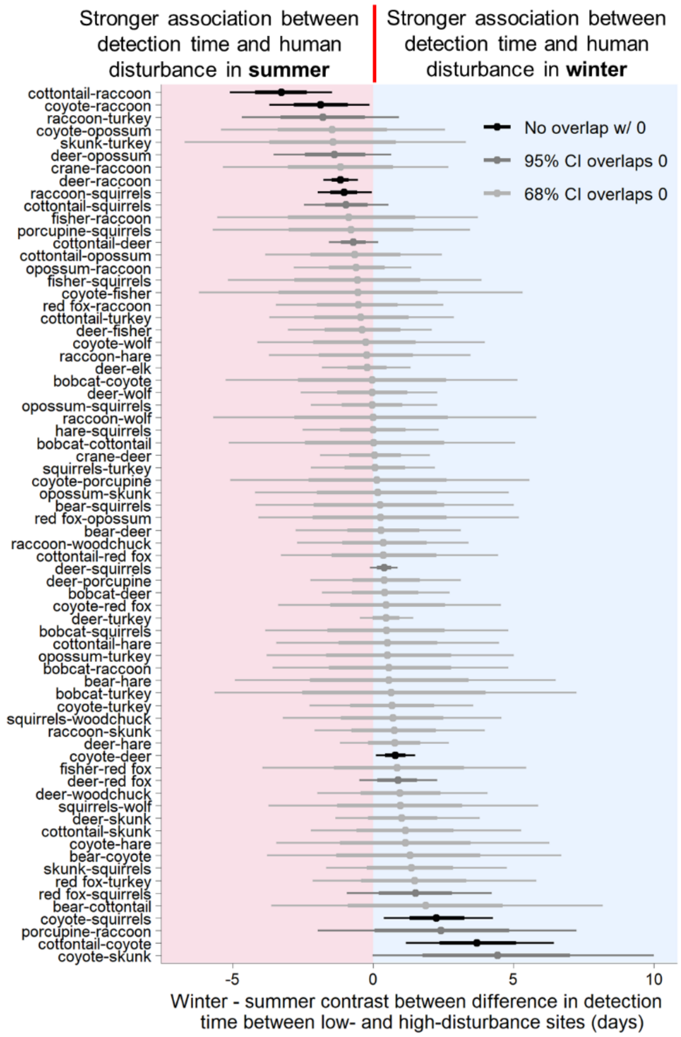


Figure S5. Seasonal variation in the predicted relationship between human disturbance and temporal spacing of detections. Blue region corresponds to stronger association in the winter, while red region corresponds to stronger association in the summer. Points represent means of contrasts and thick and thin bars represent 68% and 95% credible intervals. Shading indicates whether 95% (black) or 68% (dark grey) credible intervals omit zero, or whether 68% credible interval overlaps zero (light grey).

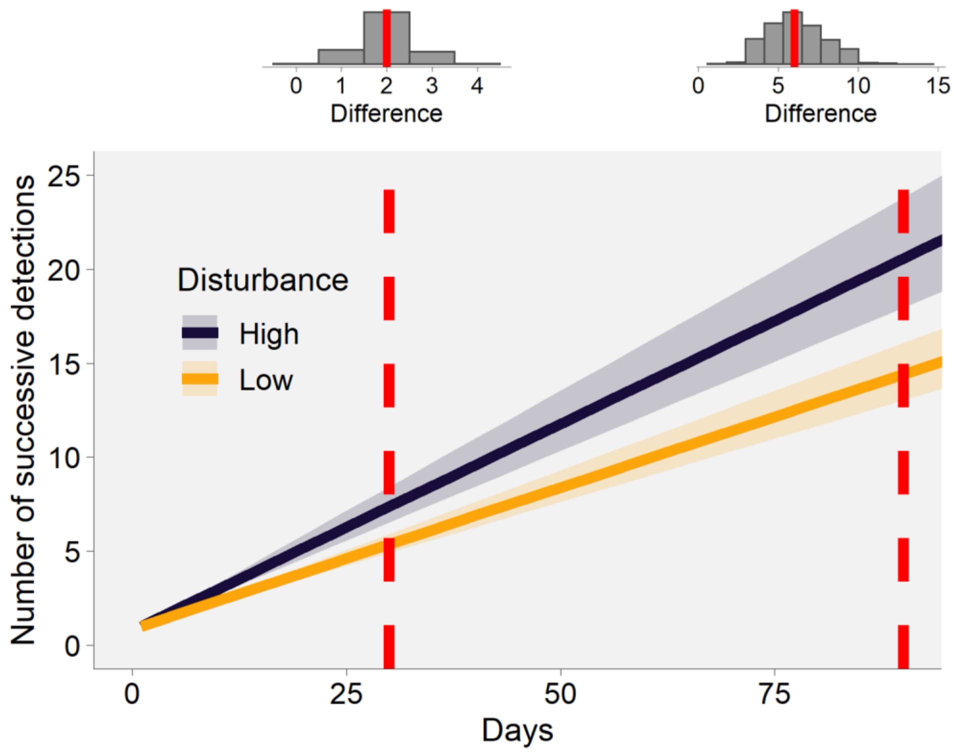


Figure S6. Possible consequences of spatiotemporal compression for species encounters. Using 1000 simulated draws for the most antagonistic pairs at the sites with highest and lowest levels of disturbance, respectively, we calculated how many successive detections (species encounters) would accumulate over the course of a three-month period. Here, the high disturbance site is estimated to have 6 more encounters (95% CI [3, 10]) by the end of the 3-month period than the low-disturbance site. Histograms show distribution of differences in the number of successive detections between low- and high-disturbance landscapes at 30 and 90 days, respectively.

Table S1. Taxa considered in the analysis.

| Common name | Scientific name | Order |
|---|---|---|
| bear | *Ursus americanus* | Carnivora |
| bobcat | *Lynx rufus* | Carnivora |
| cottontail | *Sylvilagus floridanus* | Lagomorpha |
| coyote | *Canis latrans* | Carnivora |
| deer | *Odocoileus virginianus* | Artiodactyla |
| elk | *Cervus elaphus* | Artiodactyla |
| fisher | *Pekania pennanti* | Carnivora |
| opossum | *Didelphis virginiana* | Didelphimorphia |
| porcupine | *Erethizon dorsatum* | Rodentia |
| raccoon | *Procyon lotor* | Carnivora |
| red fox | *Vulpes vulpes* | Carnivora |
| crane | *Antigone canadensis* | Gruiformes |
| skunk | *Mephitis mephitis* | Carnivora |
| hare | *Lepus americanus* | Lagomorpha |
| squirrel sp. | *Tamias*, *Sciurus,* or *Glaucomys* sp. | Rodentia |
| turkey | *Meleagris gallopavo* | Galliformes |
| wolf | *Canis lupus* | Carnivora |

| | | |
|---|---|---|
| woodchuck | *Marmota monax* | Rodentia |

Table S2. Sample sizes for each of the pairs included in the analysis. N refers to the total number of observed times between successive detections of the pair, and N site represents the number of unique sites for each pair. Antagonism is the ranked probability of lethal encounter between the species comprising the pair.

| Pair | N | N Site | Antagonism |
|---|---|---|---|
| deer-raccoon | 28,927 | 1,317 | Low |
| deer-squirrel | 25,950 | 1,303 | Low |
| coyote-deer | 17,377 | 1,430 | High |
| raccoon-squirrel | 14,819 | 861 | Low |
| deer-turkey | 12,491 | 1,073 | Low |
| cottontail-deer | 7,898 | 638 | Low |
| coyote-raccoon | 7,099 | 836 | Medium |
| coyote-squirrel | 5,857 | 787 | High |
| cottontail-squirrel | 5,170 | 464 | Low |
| raccoon-turkey | 4,830 | 632 | Low |
| cottontail-raccoon | 4,810 | 437 | Low |
| bear-deer | 3,941 | 650 | Medium |
| deer-red fox | 3,779 | 507 | Medium |
| opossum-raccoon | 3,685 | 358 | High |
| squirrel-turkey | 3,602 | 535 | Low |
| deer-opossum | 3,571 | 421 | Low |
| coyote-turkey | 3,174 | 560 | Medium |
| opossum-squirrel | 2,962 | 322 | Low |
| cottontail-coyote | 2,821 | 387 | High |
| red fox-squirrel | 1,917 | 340 | High |
| bobcat-deer | 1,832 | 479 | Medium |
| red fox-raccoon | 1,832 | 306 | Medium |
| deer-snowshoe hare | 1,446 | 191 | Low |

| | | | |
|---|---|---|---|
| coyote-opossum | 1,351 | 243 | High |
| cottontail-opossum | 1,332 | 188 | Low |
| sandhill crane-deer | 1,284 | 128 | Low |
| cottontail-turkey | 1,281 | 251 | Low |
| deer-skunk | 1,163 | 296 | Low |
| bear-raccoon | 1,039 | 244 | Medium |
| opossum-turkey | 974 | 187 | Low |
| bear-coyote | 902 | 256 | High |
| coyote-red fox | 895 | 270 | High |
| raccoon-skunk | 876 | 214 | High |
| deer-fisher | 864 | 240 | Medium |
| bobcat-coyote | 810 | 269 | Medium |
| deer-wolf | 804 | 226 | High |
| bobcat-raccoon | 798 | 230 | Medium |
| deer-porcupine | 790 | 191 | Low |
| snowshoe hare-squirrel | 674 | 115 | Low |
| skunk-squirrel | 664 | 181 | Low |
| bobcat-squirrel | 642 | 228 | High |
| bear-squirrel | 614 | 196 | Medium |
| red fox-turkey | 581 | 157 | Medium |
| deer-elk | 571 | 81 | Low |
| bear-turkey | 551 | 177 | Medium |
| cottontail-red fox | 521 | 139 | High |
| coyote-skunk | 479 | 147 | High |
| bobcat-turkey | 413 | 139 | Medium |
| fisher-squirrel | 391 | 132 | High |
| porcupine-raccoon | 341 | 93 | Low |

| | | | |
|---|---|---|---|
| coyote-snowshoe hare | 338 | 92 | High |
| fisher-raccoon | 336 | 107 | Medium |
| skunk-turkey | 334 | 103 | Low |
| bobcat-cottontail | 332 | 102 | High |
| raccoon-snowshoe hare | 332 | 74 | Low |
| coyote-fisher | 297 | 117 | High |
| bear-bobcat | 291 | 95 | Medium |
| cottontail-skunk | 268 | 84 | Low |
| porcupine-squirrel | 268 | 88 | Low |
| coyote-wolf | 267 | 94 | High |
| bear-cottontail | 264 | 79 | Medium |
| sandhill crane-raccoon | 260 | 71 | Low |
| red fox-opossum | 252 | 73 | Medium |
| raccoon-woodchuck | 231 | 64 | Low |
| opossum-skunk | 225 | 65 | Medium |
| bear-snowshoe hare | 224 | 61 | Medium |
| deer-woodchuck | 209 | 75 | Low |
| cottontail-snowshoe hare | 207 | 55 | Low |
| coyote-porcupine | 200 | 81 | Medium |
| squirrel-woodchuck | 188 | 51 | Low |
| bear-porcupine | 148 | 70 | Medium |
| fisher-red fox | 133 | 54 | Medium |
| squirrel-wolf | 128 | 66 | High |
| raccoon-wolf | 127 | 61 | High |

**Chapter 5: Activity timing in the Anthropocene**

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**Abstract**

Circadian activity rhythms are a ubiquitous feature of life, and many animals alter their activity rhythms in response to anthropogenic disturbances. However, we lack an understanding of the ecological effects of these altered activity rhythms. Therefore, we suggest three hypotheses to motivate future research: that activity-timing mismatch underpins ecological effects, that the duration and timing of disturbance determine the effects of activity-timing shifts, and that effects vary latitudinally due to gradients in abiotic and biotic constraints. Finally, we synthesis considerations for future research such as integrating data from site-based (e.g., camera traps) and individual-based

(e.g., accelerometers) sensors. Behavioral change—like altered activity rhythms—is a hallmark of the Anthropocene, and understanding the implications of these changes is a major need.

**Keywords** behavioral plasticity, chronobiology, circadian rhythms, global change

**Introduction**

Time is an essential currency of life: finding food, avoiding predators, and reproducing require being active at the right time. Animals have evolved ***activity rhythms*** in response to environmental conditions (e.g., light levels, temperature) that vary dramatically over the 24-hour cycle (Yerushalmi & Green 2009; Helm et al. 2017). These activity rhythms arise from biological clocks, which are entrained by stimuli such as light, temperature, and species interactions (Kuhlman et al. 2018). Human activities are modifying many of these stimuli, and thus an important research goal is determining whether animals change their activity rhythms in accordance with these altered stimuli and whether such shifts are adaptative (Lamb et al. 2020) or represent ecological traps (Robertson et al. 2013). In addition to its fundamental role in shaping individual fitness and population persistence, activity timing underpins the ecological interactions that characterize communities and modify ecosystems. Competition, predation, infection, parasitism, and mutualisms all depend upon multiple organisms behaving in a particular way at a particular time.

Humans drive myriad environmental changes, which—alone or in concert—may induce activity-timing shifts of free-living animals (Fig. 1; Kronfeld-Schor et al. 2017). For example, some wildlife species perceive humans as apex predators, leading to fear-motivated shifts in activity rhythms; many mammal species, for instance, become more nocturnal in human-disturbed settings (cf. Gaynor et al. 2018; Frey et al. 2020). Human-induced climate change may also drive activity-timing shifts; for example, diurnal species may shift to greater proportions of nocturnal activity to escape rising daytime temperatures (Levy et al. 2019). Humans also generate light pollution (Gaston et al. 2017; Gaston 2018), which may disturb the sleep of diurnal organisms (Raap et al. 2015) and lead them to be active later and earlier in the evening and morning, respectively (Da Silva et al. 2015; Gaston et al. 2017), while compressing the activity duration of nocturnal animals (Gaston et al. 2017). Importantly, these various human-altered stimuli often co-occur and may interact to produce complex behavioral and ecological responses (Robertson et al. 2013; Côté et al. 2016; Wilson et al. 2021).

The consequences of activity-timing shifts have the potential to ripple across multiple levels of biological organization—from individuals to ecosystems (Fig. 1; Wilson et al. 2020). For individuals, shifting activity to novel times can have profound (and detrimental) effects on physiology, as evidenced by the impaired immunity and other health problems of humans who “live against the clock” and work night shifts (Vyas et al. 2012; Loef et al. 2019). At population levels, activity-rhythm shifts might dampen recruitment if an individual’s foraging or vigilance is impaired by being active at unnatural times (Creel et al. 2007). At community levels, activity-rhythm shifts could result in novel species interactions or result in dampened or amplified competition, predation, or disease transmission (Wilson et al. 2020). Finally, at an ecosystem level, activity-timing shifts could result in altered nutrient flows if altered species interactions disrupt processes such as herbivory (El-Sabaawi 2018). While such effects are difficult to document—particularly at broader (e.g., ecosystem) scales of organization (Gaynor et al. 2018; Wilson et al. 2020)—opportunities are expanding as technologies and sampling approaches continue to improve.

Opportunities to explore the ***ecological effects*** (here, we use “ecological effects” to encapsulate effects at all levels of organization) of activity timing are expanding with continued advances in technologies and sampling approaches that allow ecologists to characterize activity rhythms over ever-increasing spatiotemporal extents and resolutions. Ever-improving technologies like GPS tags (Kays et al. 2015), camera traps (Burton et al. 2015), and accelerometers (Brown et al. 2013)—along with citizen science observations—provide researchers with time-stamped behavior data at previously untenable scales. Considering these technological advances and growing interest in understanding behavioral responses to global change, our objectives are to **1)** offer testable hypotheses regarding the ecological effects of human-mediated activity-timing shifts, **2)** briefly summarize activity-timing research via a literature review, and **3)** synthesize research considerations that will advance our ability to make inference about the ecological effects of activity-timing responses to global change.

## Ecological effects of activity-timing shifts: testable hypotheses and predictions

To motivate future work, we offer three testable hypotheses (Fig. 2) and predictions regarding the ecological effects of activity-time shifts.

**Hypothesis 1. Ecological effects of activity-timing shifts arise via activity-timing mismatch** (Fig. 2). Activity-timing mismatch occurs when individuals or species respond to stressors differently, reducing the activity-rhythm overlap between conspecifics or heterospecifics (Renner & Zohner 2018). Drawing an analogy to phenological mismatch, such activity-timing mismatches may have effects at organismal (Reed et al. 2013), population (Simmonds et al. 2020), community (Post 2019), or ecosystem levels of organization (Beard et al. 2019). We offer predictions for population- and ecosystem-level effects below.

For populations, we predict that activity-timing mismatches of sexually-selected behaviors have negative effects on demographic rates (Wong & Candolin 2015). For example, imagine a scenario in which male birds in urban settings commence singing earlier in the morning to avoid acoustic masking from traffic noise (Barber et al. 2010; Dorado-Correa et al. 2016). In such a scenario, if female birds commence activity in response to light levels—not sound—the decoupled activity timing between males and females may result in fewer successful pairings and thus reduced recruitment (Habib et al. 2007; Wong & Candolin 2015).

For ecosystems, we predict that activity-timing mismatch between predators and prey is most likely to influence processes such as nutrient flows (Beard et al. 2019). Such mismatches benefit one party but not the other (in contrast to mutualistic interactions, in which both parties will suffer from the mismatch) and thus should not be evolutionarily stable (Renner & Zohner 2018). While they persist, such mismatches may affect nutrient flows if predators switch to different food sources (Deacy et al. 2017) or if the temporal release from predation risk allows the prey to increase herbivory rates (Kohl et al. 2018; Beard et al. 2019).

**Hypothesis 2. Activity-timing responses to disturbance depend upon the timing as well as the duration of disturbance** (Fig. 2). Time can be conceptualized as a habitat that is used by organisms (Kronfeld-Schor & Dayan 2003; Post 2019). In the same way that disturbances to spatial habitat can be described as habitat loss (i.e., amount of habitat, agnostic of its configuration; Fahrig 2013, 2017) or habitat fragmentation (i.e., habitat amount with an explicit focus of its configuration; Fletcher et al. 2018b, a), it is pertinent to ask whether the fragmentation of temporal habitat—independent of temporal habitat loss—matters in determining activity-timing responses. For example, would one hour of artificial light exposure induce a stronger behavioral response during twilight periods or during the middle of the night (Gaston et al. 2017)? We predict that disturbances that overlap with sensitive behaviors (e.g., foraging, mate signaling) are more likely to precipitate ecological effects of activity-timing shifts. Moreover, we predict that longer durations of disturbance induce more extreme activity-timing shifts and therefore larger ecological effects.

**Hypothesis 3. Ecological effects of activity-timing shifts vary latitudinally due to gradients in biotic and abiotic constraints** (Fig. 2). Interacting species partition time as a resource (Kronfeld-Schor & Dayan 2003), and since low latitudes generally host more species-rich communities, these tropical communities likely partition time in a more granular fashion than temperature communities (Fig. 2). Similarly, photoperiod and temperature show much less seasonal variation at low latitudes than at high latitudes (Post 2019; Huffeldt 2020), and subsequently tropical species may be more sensitive to abiotic constraints (i.e., adaptation to a narrower range of conditions; Janzen 1967; Freeman et al. 2021). Thus, activity-timing shifts in tropical settings may expose organisms to relatively more novel abiotic conditions (Spence & Tingley 2020), which may produce additional or unexpected behavioral responses (Robertson et al. 2013). Therefore, we predict that activity-timing shifts have larger ecological effects at lower latitudes under the assumption that activity-timing mismatches are more likely due to tighter temporal partitioning and greater chance of exposure to novel abiotic conditions.

**Review: characteristics of activity-timing research**

In an effort to characterize the current state of activity-timing research, we conducted a literature review (see Supplementary materials for search terms and review methodology) and reviewed 1,024 studies (Gilbert et al. 2021) that measured the activity rhythms of animals under natural conditions. This research goal has rapidly grown over the last two decades (Fig. 3a), and most studies (65%) focused on mammals or teleost fish (Fig. 3b). Aquatic studies dominated until about 2015, after which terrestrial studies became more prevalent (Fig. 3c). In addition, the spatial extent of activity-rhythm studies has increased. In 2000, about 75% of the studies focused on areas roughly 1 $km^2$ in size (Fig. 3d), but by 2020, that proportion had dropped below 50% and most studies focused on areas at least 100 $km^2$ in size (Fig. 3d). Simultaneously, the temporal extent of studies has grown (Fig. 3e). In 2000, the three-year mean of study duration was 4.7 months; by 2020, the three-year mean had risen to 19.7 months (Fig. 3e). In addition, the temporal resolution of activity-rhythm studies has increased such that, by 2020, nearly 50% of studies used continuous-time analyses (versus categorical day–night comparisons; Fig. 3f). Data collection has also changed; studies using direct observation have steadily declined over the last 30 years, while studies using tags (GPS, radio, and RFID tags considered collectively), acoustic recorders, and especially camera traps have increased (Fig. 3g). Finally, the focus of studies has shifted; descriptive studies (in which the objective is simply to estimate a given taxon's activity rhythm) have declined, while those using activity rhythms to inform species interactions are increasing (Fig. 3h). The preponderance of studies with descriptive or species interaction objectives suggests that, to date, most activity-rhythm studies have explored ecological processes at population and community levels.

**Synthesis: considerations for activity timing research**

Opportunities are expanding to study activity timing, which can be an important behavioral response to human-induced change (Wilson et al. 2020). Activity timing may also provide important information for conservation (Blumstein & Fernández-Juricic 2010), as management actions can be coordinated with times when critical animal behaviors occur. Thus, we synthesize several considerations for researchers undertaking activity-timing investigations (Fig. 4). Clearly, implementing all of the considerations is not practical for all studies, but any of these considerations—alone or in combination with others—would advance activity timing research.

**1. Link activity-timing shifts to other parameters**

In our first hypothesis, we suggest that any ecological effects of activity-timing shifts arise primarily via activity-timing mismatches. While researchers often document such shifts and mismatches (Frey et al. 2017; Gaynor et al. 2018), assessing the biological meaningfulness of such mismatches is difficult without additional data on the possible ecological consequences of such shifts (Wilson et al. 2020). Thus, we encourage researchers to link activity-timing shifts to physiological, demographic, or trophic parameters (Fig. 4a). Only 9% of studies in our sample attempted to do so, and this proportion was consistent through time (Fig. 3l).

Perhaps the most direct way to evaluate the consequences of activity-timing shifts is to measure individual condition or survival. For example, Guiden and Orrock (2020) discovered that rodents that shifted to daytime activity in the winter significantly reduced heat loss. As another example, Lamb *et al.* (2020) demonstrated that more-nocturnal brown bears showed reduced mortality risk in urban areas. While logistically challenging, measuring condition (e.g., body mass, stress metabolites) or survival in free-living animals would allow researchers to evaluate the consequences of activity-timing shifts for individuals (Fig. 1b).

Beyond individual-level consequences, we encourage researchers to seek ways to link population-, community-, and ecosystem-level parameters to activity-timing shifts (Fig. 1b). Researchers often compare the activity rhythms of co-occurring species to make inference about species interactions (Frey et al. 2017; Lashley et al. 2018) but rarely link observed activity rhythms to parameters such as predation rates to truly evaluate the consequences of activity-timing overlap for community processes. Activity-timing shifts may also influence processes at higher levels of organization (Hertel et al. 2017; Gaynor et al. 2018). For example, Suraci *et al.* (2019) found such community- and ecosystem-level consequences; carnivores avoided human cues spatially and increased nocturnal activity, releasing rodents from predation risk and resulting in greater rates of seed consumption (Fig. 1b). Finally, activity-timing research may provide insight into disease dynamics since direct contact is necessary for agents to infect hosts (Greggor et al. 2016). Activity timing may be an important mechanism that allows animals to “social distance” in time, thus reducing infection risk (Butler & Behringer 2021). For example, changes in mammal activity timing (due to habitat alteration or fear of humans; Gaynor *et al.* 2018; Guiden and Orrock 2019) and climatic shifts conducive to tick activity (Burtis et al. 2016) could, alone or in concert, drive changes in the encounter rate between humans and ticks infected with the bacterium *Borrellia burgdorferi*, a key parameter in Lyme disease risk.

## 2. Intraspecific variation in activity timing

Hypothesis 1 predicts that activity-timing mismatches of sexually-selected behaviors have negative effects on demographic rates. Investigation of such hypotheses necessitates data and inference on intraspecific variation in activity rhythms (Fig. 3b; Hertel et al. 2017). Intraspecific behavioral diversity can be vast (Bolnick et al. 2003; Des Roches et al. 2018) and can facilitate adaptation to changing conditions (Miner et al. 2005) if certain behavioral types confer demographic benefits (Shipley et al. 2020). Moreover, intraspecific activity-timing inference may inform conservation practice by, for example, revealing which individuals or groups within populations that may face greater exposure to time-varying threats. Intraspecific factors such as age, sex, body size, or personality (Brehm et al. 2019) may be associated with activity-timing variation, which may confound population-level conclusions if unaccounted for. However, only 37% of studies accounted for intraspecific variation in activity rhythms, and this proportion has remained stable over the last 15 years (Fig. 3j).

Individual- or group-level variation in activity rhythms may yield insight into demographic processes (Fig. 1b). For example, Crawford *et al.* (2020) discovered that the activity rhythms of male, female, and nursery groups of white-tailed deer (*Odocoileus virginianus*) were similar in predator-free areas. However, under predation risk, nursery groups—but not adults—concentrated activity during predator downtimes. Such observations potentially shed light on the groups that are most vulnerable to predation. As another example, Hertel *et al.* (2017) found considerable individual variation in activity rhythms in a population of brown bears (*Ursus arctos*)—including greater nocturnality in young bears versus adults—but found no evidence that the variation was linked to survival. In contrast, Lamb *et al.* (2020) found that, in human-disturbed landscapes, young bears were more diurnal than adults and subsequently experienced greater mortality risk; such findings could help managers tailor conservation strategies optimized for intraspecific groups.

Measuring intraspecific variation in activity timing is facilitated by individual identification; indeed, of the 386 studies in our sample that accounted for individual variation in activity rhythms, 273 (71%) used tagged animals (Fig. 3j). However, only 68.5% of studies that used tagged animals accounted for intraspecific variation in analysis, indicating that an important opportunity exists to further our understanding of intraspecific variation in activity rhythms. Finally, even for studies that cannot identify individuals, researchers can classify animals into demographic groups (age, sex, body size) that align with ecologically meaningful differences in activity rhythms (Crawford et al. 2020).

**3. Timing of specific behaviors rather than general activity rhythms**

Both Hypotheses 1 and 2 indicate that the timing of specific behaviors—rather than general activity—may matter in determining the ecological effects of activity-timing shifts (Fig. 2). However, the activity rhythms commonly estimated by researchers encompass all non-resting behaviors and thus represent a rather general behavioral metric. About a third of studies in the literature review estimated the timing of specific behaviors other than movement, and this proportion remained consistent over time (Fig. 3i).

General activity rhythms may be relatively uninformative about phenomena of interest if the timing of specific behaviors is decoupled from general activity peaks. For example, Ditmer et al. (2018) found that black bears (*Ursus americanus*) preferred to cross roads in the middle of the night even though bear activity typically peaks around dawn and dusk (Hertel et al. 2017). Similarly, using RFID tags, Hillemann *et al.* (2019) discovered that tit (*Paridae*) flocks were most vocal in the morning even though flock size grew over the course of the day, suggesting that the flocks calibrate vocalization timing to optimize the benefits of recruiting conspecifics and minimize the costs of attracting predators. We encourage researchers to measure the timing of specific behaviors that might confer fitness-related benefits (e.g., foraging, mate-signaling) or costs (e.g., crossing roads) over general activity rhythms (Fig. 4c). Such practice could increase the relevance of activity-timing research to conservation, since conservation objectives are frequently linked to specific behaviors (e.g., reproduction).

Measuring the timing of specific behaviors may require improvisation upon the sampling approaches that researchers commonly employ in activity-rhythm studies (Fig. 3g). For example, pairing tags with other animal-borne instruments (e.g., physiological monitors or video cameras) may permit researchers to better parse the timing of specific behaviors (Papastamatiou et al. 2018; Ditmer et al. 2018). Alternatively, researchers working with site-based sensors (e.g., camera traps) can catalogue specific behaviors and interactions if they target locations that anchor focal behaviors (e.g., carcasses to monitor the timing of scavenging or nests to understand the temporal dynamics of predation risk; Benson et al. 2010, Brown et al. 2015, Perrig et al. 2019).

**4. Integrating data from multiple types of sensors**

Investigating Hypotheses 1 and 2 would benefit from measuring the timing of specific behaviors and intraspecific variation in activity timing; as noted previously, making inference about such variables may require creative approaches to collecting and analyzing activity-timing data. In particular, such efforts might benefit from integrated modeling efforts that draw upon all available data sources to make inference (Fig. 4d; Zipkin et al. 2019; Isaac et al. 2020). Continued technological improvements such as GPS tags, camera traps, and acoustic recording devices are revolutionizing activity-timing research and replacing direct observation of animals (Fig. 3g); these technologies can broadly be classified as “site-based” sensors that sample fixed locations (e.g., camera traps) or “individual-based” sensors mounted to animals that record the movements and behaviors of individuals (e.g., GPS tags, accelerometers). We encourage researchers to develop analytical frameworks that combine data from site-based and individual-based sensors to improve activity-timing inference.

Site-based sensors are appealing because they can readily sample multiple landscapes without needing to capture animals. However, researchers often pool data from site-based sensors (generally to gain adequate sample sizes for common analyses; Lashley et al. 2018) and thereby lose information about spatiotemporal variation in activity rhythms (Frey et al. 2017). However, such methods (wrapped kernels) can be extended to accommodate spatiotemporal effects (Heaton & Gelfand 2012). In addition, activity rhythms represent an important source of variation in detectability of animals by site-based sensors. Consequently, we encourage researchers to “calibrate” their models to account for the activity rhythms of focal species. Models that jointly estimate activity rhythms and other parameters (e.g., occupancy or abundance; Guillera-Arroita et al. 2011, Borchers et al. 2014, Dorazio and Karanth 2017, Distiller et al. 2020) represent an important development but have seen limited application to date (see Azzou et al. 2021, Rivera et al. 2021 for the newest developments in this regard).

Studies employing individual-based sensors face different challenges and opportunities. Importantly, tags allow investigators to confidently identify individuals. Location data provide several activity measures (e.g., displacement between points), and several models can be used to infer spatiotemporal variation in these attributes (e.g., Buderman *et al.* 2016). Researchers are increasingly using multiple measurements to infer latent behavioral states using hidden Markov models (McClintock et al. 2020). A possible issue is that an algorithm classifies behavioral states, and consequently, the inferred behavioral states may differ statistically but not biologically (McClintock et al. 2020). Additional animal-borne datastreams (e.g., video cameras) are a promising way to better supervise behavioral classification (Papastamatiou et al. 2018).

Integration of site-based and individual-based sampling of activity rhythms may overcome limitations associated with each technique (*sensu* Isaac *et al.* 2020). Individual-based sensors provide reliable information regarding the individual performing behaviors (thus permitting inference about intraspecific variation in activity timing), and site-based observations may provide more complete information regarding the behavior being performed (thus permitting inference about specific behaviors). Moreover, models uniting these datastreams would permit inference regarding covariance between activity rhythms and conservation-relevant processes such as demography or habitat selection.

**5. Spatiotemporal variation in daily activity rhythms**

Hypothesis 3 suggests that the ecological effects of activity-timing shifts vary latitudinally due to gradients in biotic and abiotic variables. Addressing this hypothesis would require measuring activity rhythms at multiple locations and/or time periods displaying variation in biotic and abiotic variables. However, researchers often aggregate data from multiple locations or over long temporal scales and thus potentially lose information on spatiotemporal variation in activity timing (Ridout & Linkie 2009; Nouvellet et al. 2012). For example, about a quarter of studies estimated spatial variation in activity rhythms, though that proportion appears to be growing (Fig. 3k). Similarly, about a third of studies accounted for seasonal variation in activity rhythms (Fig. 3k). We encourage researchers to further explore the complementary roles of biotic and abiotic variables in driving activity-timing (Fig. 4e-f).

Biotic interactions are an important factor structuring the activity rhythms of species. Variation in predator space use or activity rhythms can create a heterogeneous risk landscape and drive variation in prey activity timing (Wirsing et al. 2021). For instance, Larranaga and Steingrímsson (2015) found that arctic charr (*Salvelinus alpinus*) in streams with limited shelter showed greater movement rates and round-the-clock activity (compared to charr with shelter access), presumably because the lack of shelter increased their perceived risk of predation. Similarly, Kohl *et al.* (2018) demonstrated that elk (*Cervus elaphus*) capitalize on risky habitats during downtimes in wolf (*Canis lupus*) activity. To truly evaluate the role of community richness in structuring activity rhythms and driving ecological effects of activity-timing shifts, researchers should move beyond pairwise comparisons (Montgomery et al. 2019) to try to determine whether more species-rich communities exhibit more granular temporal partitioning.

Abiotic context can also structure activity timing and presumably constrain activity-timing responses to various forms of human-induced environmental change. Many species show seasonal variation in activity rhythms due to relatively predictable fluctuations in day length, temperature, and precipitation (Bloch et al. 2013; Guiden & Orrock 2020). Within seasons, variation in temperature and precipitation can drive activity-timing shifts. For example, van der Vinne *et al.* (2014) showed that nocturnal mice (*Mus musculus*) switched to daytime activity under extremely cold temperatures, presumably to coordinate activity with the warmest part of the day to optimize energy conservation. Similarly, Payne *et al.* (2013) found that a diurnal fish (*Acanthopagrus australis*) shifted to nocturnal activity during rainfall, possibly to minimize predation risk. Finally, habitat structure and landscape context can modify abiotic factors (e.g., light levels, temperature) that drive activity timing. For example, Guiden and Orrock (2019) demonstrated that nocturnal mice (*Peromyscus leucopus*) became active earlier in habitats dominated by invasive shrubs (*Rhamnus cathartica*), which provide dense cover and reduce moonlight intensity at the forest floor.

Because both biotic and abiotic variables can structure activity rhythms and also covary latitudinally, disentangling the relative contributions of biotic (e.g., community richness) and abiotic (e.g., photoperiod) to any ecological effects of activity-timing shifts would benefit from a factorial design in which researchers compare activity-timing shifts and their consequences from species-rich and species-poor communities at multiple latitudes (thus controlling for broad gradients in abiotic variables such as photoperiod and climate). Ultimately, the increasing spatiotemporal extent and resolution of activity-rhythm studies (Fig. 3e-f)—and efforts to measure the relationship between activity timing and fitness (Fig. 4a)—will facilitate such factorial investigations, as future sampling will likely span large areas, multiple seasons, and capture responses to ephemeral conditions.

**6. Macroscale activity-timing investigations powered by emerging datastreams**

In Hypothesis 3, we suggest that the ecological effects of activity-timing shifts vary latitudinally (Fig. 2). Pursuing this hypothesis would require moving beyond local- and regional-scale investigations and collating activity-timing data over macroscales (Bennie et al. 2014). We encourage researchers to leverage datastreams such as broad-scale monitoring networks (e.g., NEON; Keller et al. 2008), distributed experiments, and citizen science (Fraser et al. 2013; Dornelas et al. 2019) to 1) describe macroecological patterns in activity rhythms, 2) describe community processes at broad scales, and 3) develop dynamic forecasts of animal activity to inform broad-scale conservation (Fig. 4g).

Describing macroscale patterns in activity rhythms is a growing research focus (Bennie et al. 2014; Bulla et al. 2016). Population-level descriptions of activity rhythms have historically been a common goal (Fig. 3h), but these studies typically focused on relatively small spatial regions (Fig. 3d). A pertinent question is whether activity rhythms of local populations scale up and match those of broader populations (Bulla et al. 2016). For example, Searfoss *et al.* (2020) analyzed recordings of chipping sparrows (*Spizella passerina*) from public repositories and discovered that—on a continental scale—chipping sparrows sing shorter songs before sunrise than after sunrise.

Emerging datastreams may facilitate the exploration of community processes at macroscales. For example, Lang *et al.* (2019) used eBird data to compare the activity rhythms of hawks on different continents. They discovered convergent daily hunting strategies across species, with differences according to prey type. Importantly, existing monitoring programs can retrofit their protocols to collect behavioral data (*sensu* Miller *et al.* 2017) or even implement experiments (Fraser et al. 2013) to gain a mechanistic understanding of species interactions, e.g. by instructing volunteers to simulate risk cues and record prey responses (Smith et al. 2020). Scaling up behavioral studies may help uncover the processes that form macroecological patterns; such mechanisms have been notoriously difficult to discover (Keith et al. 2012).

Finally, macroscale activity-timing data can potentially contribute to near-term forecasting (Dietze et al. 2018) of animal activity (Van Doren & Horton 2018). Importantly, many threats to animal populations (e.g., poaching, vehicle traffic, light pollution) are not static but rather pulsed (and often predictable) through time (Gavin et al. 2010). Identifying such threats—and quantifying animal exposure to them through time—can help pinpoint the optimal locations and times to concentrate conservation action (Horton et al. in press).

**Concluding remarks**

Researchers have long recognized the importance of time in animal behavior. In the current era of global change, humans are altering the "timescape" that is perceived by and available to organisms in multiple ways; thus, it is important to understand 1) whether activity-timing responses to human activity are adaptative or result in ecological traps and 2) ecological effects of activity-timing shifts. We hypothesize that ecological effects of activity-timing shifts arise via activity-timing mismatches between con- and heterospecifics, that the timing as well as duration of disturbance influences the ecological effects of activity-timing shifts, and that the ecological effects of activity-timing shifts vary latitudinally. We synthesize several considerations for researchers undertaking activity-timing work; for example, we encourage researchers to link activity-timing shifts to other parameters, measure intraspecific and spatiotemporal variation in activity timing, and attempt to measure the timing of specific behaviors in addition to general activity. Moreover, to complement the ever-increasing amount and resolution of data, we suggest that integrated behavior models combining location data from individual-based sensors and behavioral classifications from site-based sensors could provide improved activity-timing inferences. Finally, we highlight the opportunities afforded by citizen science, broad-scale networks, and distributed experiments to pursue activity-timing research over ever-expanding scales in time and space. Research implementing some of these considerations will advance our understanding of activity timing as a response to changing world and would potentially inform conservation planning such that actions can be calibrated to occur at the most effective times during the diel cycle.

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**Figures**

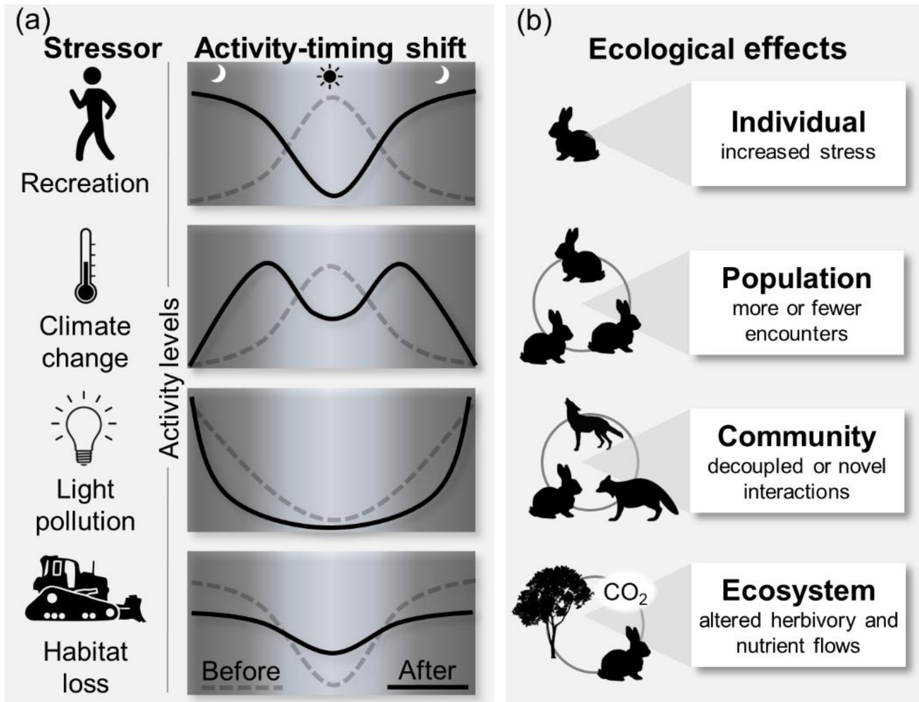


Figure 1. (a) Multiple forms of human-induced environmental change can induce activity-timing shifts in free-living animals. (b) These shifts are likely to have effects and multiple levels of biological organization.

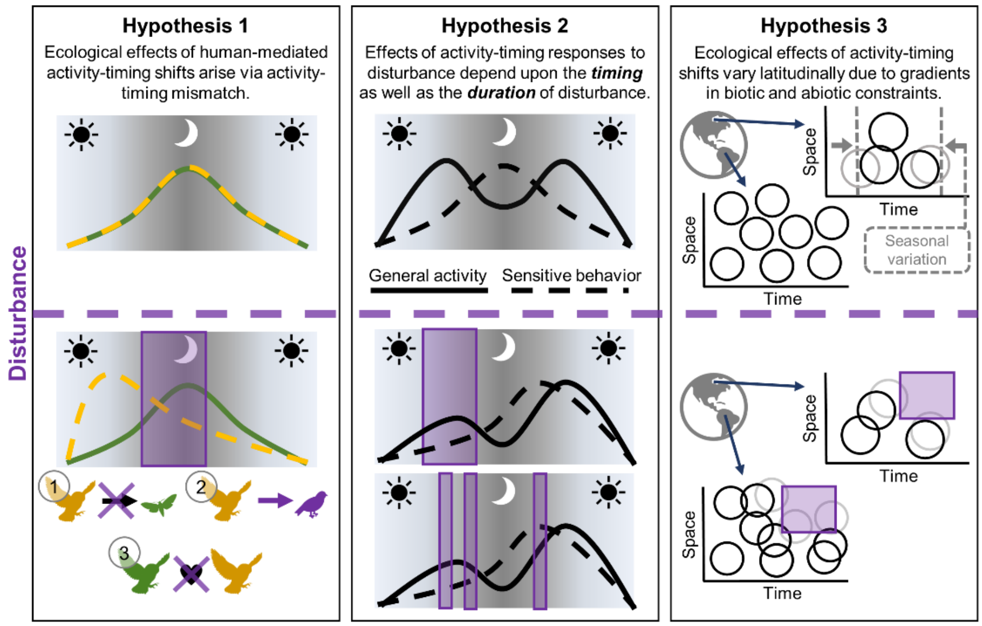


Figure 2. Hypotheses regarding the ecological effects of human-induced activity-timing shifts. In the first panel, activity-timing shifts of a predator in response to a disturbance (purple) result in 1) a decoupled predator–prey interaction, 2) a novel predator–prey interaction, and 3) activity-timing mismatches between sexes, dampening recruitment. In the second panel, the same amount of disturbance occurs but the bottom scenario is predicted to precipitate larger effects, since disturbance overlaps with a sensitive behavior. In the third panel, the spatiotemporal niches (circles) of species for high- and low-latitude sites shift in response to disturbance, and disturbances are predicted to precipitate larger effects due to greater species diversity and lack of adaptation to seasonal variation in photoperiod.

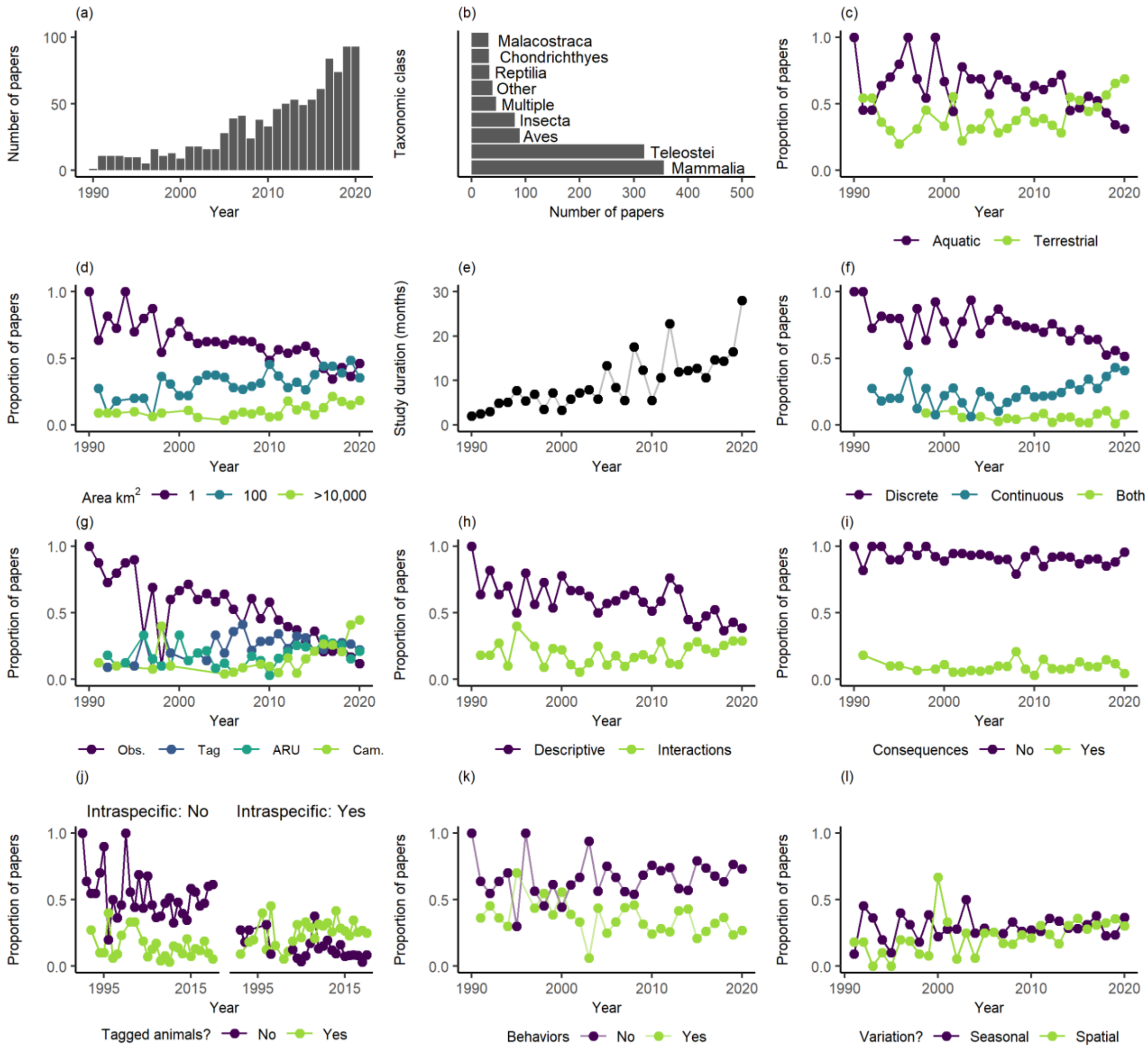


Figure 3. The number of studies measuring daily activity rhythms has increased in the last two decades (a). Mammals and teleost fish studies dominate (b), and terrestrial studies have recently overtaken aquatic ones (c). The spatial (d) and temporal extents (e) of studies are increasing, and continuous-time applications (f) are increasing. The proportion of studies collecting data by direct observation (Obs.) has dropped over the past 30 years; acoustic sensors (ARU) and cameras (Cam.) are increasing, while studies using tagged animals (Tag) have been stable (g). Papers with descriptive objectives are declining, while papers focusing on species interactions are increasing (h). Less than half of studies estimate the timing of specific behaviors (i), intraspecific variation in activity

timing (j; those that do mostly rely on tagged animals), or spatial or seasonal variation in activity rhythms (k). Few studies evaluate the consequences of activity-timing shifts (l).

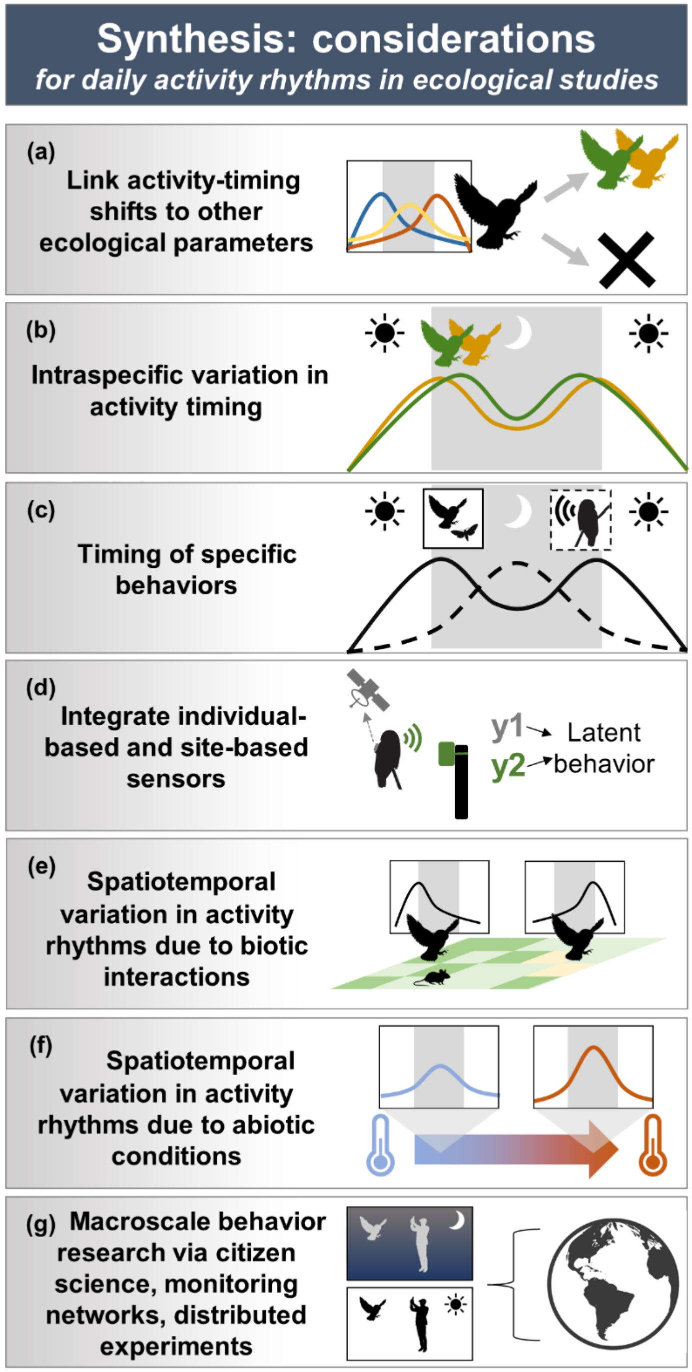


Figure 4. We encourage researchers to (a) link activity-timing shifts to other ecological (e.g., physiological, demographic) parameters, (b) estimate the timing of specific behaviors rather than general activity, (c) explore intraspecific variation in activity rhythms, (d) integrate data from individual-based and site-based sensors, (e) estimate spatiotemporal variation in activity timing due

to biotic interactions and (f) abiotic conditions, and (g) draw upon emerging broad-scale datastreams (e.g., citizen science, observation networks) to pursue questions at macroscales.

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# Dissertation Epilogue

The data revolution is reshaping ecology. My dissertation navigates the opportunities afforded by the one-of-a-kind camera-trapping network that is Snapshot Wisconsin. For several years, data from thousands of camera traps across the state have been pouring into WDNR servers. Broadly, the overarching goal of my dissertation is to showcase the insights that can be gained from such datastreams. The first two dissertation chapters have a practical focus and are intended to advise researchers on how they might use such datastreams. The latter three chapters explore temporal aspects of ecology and conservation, ideas born out of my reflections on the temporally continuous nature of data collection.

## A tension between Big Data and Deep Ecological Knowledge?

As a science, ecology is evolving to fill niches created by the data revolution, and part of that evolution is an increased emphasis on training early-career ecologists to be data-fluent. I am part of that trend, and I sometimes wonder whether I will be involved in fieldwork ever again (I predict not). I also cannot help but wonder if we (both ecologists collectively as a discipline, and myself individually) are missing something with the emphasis on ecology as a data-intensive science. Are more data always better? Put another way, in what scenarios will more data fail to provide the desired information? Alternatively, what can observing an individual animal in the field for several hours reveal that cannot be discerned from squinting at datapoints from 10,000 animals on a computer screen? There are not straightforward answers to these questions, but my first dissertation chapter indicates that, for a common goal in conservation biology (estimating population abundance), broad-scale passive monitoring cannot replace targeted studies with marked animals.

## Complementing camera traps with other datastreams

My dissertation is uniquely intertwined with Snapshot Wisconsin. It is worth reflecting on how the datastream shapes the dissertation. Camera traps have emerged as perhaps *the* premier way to monitor a certain guild of animals: those with medium-to-large body size (since small animals do not reliably trigger the sensors) and that are primarily terrestrial. Thus, camera traps can only monitor a fairly small fraction of the species occupying a given site. I anticipate that, as camera-trap networks continue to expand and mature, they will be complemented by other automated or semi-automated biodiversity data collection schemes. For example, autonomous recording units (ARUs) are seeing increased uptake in biodiversity monitoring and expand the taxonomic realms that can be monitored to birds, insects, bats, and even fish. I cannot help but speculate about farther-fetched advances in biodiversity monitoring that may occur within my lifetime. Will, for example, eDNA become so easy to sample and analyze that networks of volunteers can collect vast amounts of data on cryptic biodiversity like moths and millipedes and mosses? Only time will tell. In the meantime, however, I think it is important to give thought to how datastreams like Snapshot Wisconsin can be combined with other existing or emerging datastreams to inform biodiversity conservation. My second dissertation chapter illustrates how an emerging datastream (Snapshot Wisconsin) can be integrated with an existing one (harvest records) and highlights challenges facing such endeavors.

**Looking forward: the growth of temporal ecology**

Quite organically, many of my ideas during my PhD coalesced around time, a phenomenon undoubtedly sparked by the continuous nature of Snapshot Wisconsin’s data collection. Chapter 3, for example, encourages a view of certain times during the diel cycle acting as a refugia; we found that, in addition to changing their activity in space, deer shifted their activity timing in accordance with daily and seasonal weather conditions. Chapter 4 extends this thinking to a community level, encouraging a view of time as a resource that is shared by species, and demonstrates that human disturbance to landscapes is associated with compression of species along spatiotemporal dimensions. Chapter 5 reviews future research opportunities into the ecological effects of activity-timing shifts and highlights considerations for researchers pursuing these opportunities. More broadly, I have found myself repeatedly wondering whether patterns from spatial disciplines of ecology—like species–area relationships—have temporal counterparts. As with subdisciplines such as landscape ecology, I believe that temporal ecology will have to grapple with questions of scale, particularly given the uniquely cyclical nature of time. And finally, I wonder whether temporal conservation will gain prominence. Spatial mapping of conservation priorities has become common, and I think there is a need to complement these efforts with information on *when* conservation action should be prioritized to maximize benefits. The ongoing data revolution will facilitate these advances, particularly as automated monitoring networks operate over longer temporal extents (imagine what the Snapshot Wisconsin database will look like in 2035). I am eager to see whether temporal ecology will gain traction and experience formalization as a subdiscipline of ecology.

**Personal reflections on doing science**

It feels surreal to craft these final words of my dissertation. I have learned a lot in these four years, too much to easily express in a paragraph, but I thought I would conclude with my three favorite lessons from my PhD. The first is *"read regularly and broadly"*. Over and over again, I find that the best insights come from reading literature that falls beyond my wheelhouse and trying to establish connections to my work. The second is *"science before statistics"*. It is all too easy to be paralyzed by the constellation of potentially relevant methods to apply to data, or for an analysis to snowball to unmanageable proportions. The antidote is to clearly define the objectives of a study and the estimand(s) of interest, and to execute and communicate the analysis in as simple of a fashion as possible. Finally, the third is *"kindness is everything"*. Kind words and actions from colleagues have kept me afloat, and it is my goal to promote a culture of kindness to make science a more inclusive community. I am eager to continue learning and hope that my dissertation is a milestone, not a final destination, in my journey to explore the natural world.