The Hunter’s Pulse: Non-target consumer use, hunter participation, and prey behavior shift in reference to hunter bait sites

A DISSERTATION
SUBMITTED TO THE FACULTY OF THE
UNIVERSITY OF MINNESOTA
BY

ELLEN MARIE CANDLER
IN PARTIAL FULFILLMENT OF THE REQUERIMENTS
FOR THE DEGREE OF
THE DOCTOR OF PHILOSOPHY

Advised by
Joseph Bump

December 2021

Acknowledgements

John Donne said that “no [wo]man is an island.” No person is truly unaffecting or acts alone. Science is no different and neither is this dissertation. I have put the effort into bringing this research into one compete work, but I did not, could not, and would not have wanted to do it alone. If this past year has taught me anything, it’s that the joy of science is in the people that you work with.

First, I want to thank my advisor Dr. Joseph Bump for supporting and encouraging my interests to develop research questions that are motivating to me. I’ve known Joseph for over a decade now, first as an undergraduate student at Michigan Tech University and now as a PhD student at the University of Minnesota. Over this decade, Joe has demonstrated what it means to be an effective and inspirational teacher and mentor.

I want to thank those that helped and encouraged me in writing my dissertation. I especially want to thank my committee members Todd Arnold, David Fulton, and Julia Ponder for their support and review of this dissertation as well as the continued interest in my future career and research interests. Thank you also to Julia Leone and Anna Peschel for keeping me on track and being encouraging voices.

Thank you also to the Conservation Science graduate program and all the students that I have interacted with over my years at the University of Minnesota in classes and at happy hours. A special thanks to my lab and honorary lab mates: Roger Faust, Aaron Morris, Tyler Obermoller, Lala Odock, Jordan Pruszenski, Tom Gable, Quinn Harrison, Jack Rabe, Nicole Tatton. Thanks also to post-docs Bill Severud and Stotra Chakrabarti

for helping me develop my research and supporting me in transitioning into and out of graduate school.

Thank you to the many undergraduate students that helped make this research possible. Without the assistance in the field and in the lab, this research would not be possible.

I particularly want to thank my parents. I was very privileged growing up with parents that encouraged and supported my interest in the outdoors and wildlife, helped me through college, and supported me through years of field positions. Without their help, getting to this point would have been nearly impossible.

Finally, I want to thank my husband Mike. He encouraged me through field positions and my PhD. Mike moved back to Houghton with me then on to the Twin Cities so that I could pursue and continue my studies. I want to thank him for being my sounding board, mental health support, and putting up with bear bait slurry in the garage. Without him I'm not sure I could have made it as far as I have.

Dedication

To my daughter Rose.

I hope my work encourages you to ask all the questions that come to you
and inspires you to work for the good in
whatever field motivates you.

Abstract

The hunting hypothesis emphasizes the importance that hunting has had on the development of the human species. Anthropologists often credit hunting with tool development, increased meat eating, and larger brain size (Domínguez-Rodrigo 2002). One such tool, or method, that hunters developed was the use of bait to attract animals to an ideal hunting location. This centuries old method is even recognized as one possible reason for animals domestication (Svizzero 2016). Today this hunting method is used around the world to lure animals away from places such as farm fields, increase herd size or supplement feed in winter, or for the original purpose, hunting (Litvaitis and Kane 1994, Smith 2001, Putman and Staines 2004).

Baiting for the purpose of hunting is controversial among the wildlife managers, the public, and hunters alike (Peyton 1989, Dunkley and Cattet 2003). It challenges the hunting ethic of fair chase that values the pursuit of an animal and emphasizes the fairness of the capture and kill (Morris 2013). Conversely, the idea of an ethical shot stresses a quick kill with minimal suffering (Stokke et al. 2018). Hunting over bait increases the possibility of an ethical shot and increases the likelihood of harvesting an animal.

Though baiting has proven to be an effective method for attracting target species to bait for the purpose of hunting, it does not come without consequences to the bait consumers. For example, black bears in Wisconsin that frequent bait often limit hibernation time to maximize bait consumption (Kirby et al. 2019). This results in shorter telomere length consequently impacting cellular aging (Kirby et al. 2019). Impacts and

visitation of non-target species to bait is less known, however. In this dissertation, I focus on three aspects of hunter bait: non-target species use of black bear bait (chapter 1 and 2), gray wolf (*Canis lupus*) olfactory cue impacts on white-tailed deer (*Odocoileus virginianus*) behavior at deer hunter bait (chapter 3), and wolf space use shifts in relation to black bear hunter bait (chapter 4).

In Chapter 1, I focus on non-target species use of black bear bait in the Upper Peninsula (UP) of Michigan. Baiting for bears in the United States, and in particular Michigan, is a common practice used to attract bears to a central location and create a good shooting opportunity. Hunters often use a recipe of pastries, fruits, grains, and meat products to create an enticing slurry to attract bears. This formula is not only likely to attract bears, but also non-target species that find the bait attractive. Though research has looked into nontarget species use of white-tailed deer bait, the extent of visitation by nontarget species to black bear bait sites is unknown (Bowman et al. 2015). To fill this research gap, I carried out a study using remote cameras and pseudo black bear bait sites to record nontarget species use of black bear bait. I collected data at 21 pseudo bear bait sites in the Baraga Hunting Unit in the UP of Michigan over the course of six weeks in August and September 2016 collecting 8,642 pictures. Using a paired *t*-test, I evaluated black bear and carnivore non-target species use of hunter bait sites before and during the hunting season. I found that black bears reduce their daily visitation during hunting season while all other carnivore species increase their visitation. I also used a nonparametric kernel density estimation procedure to compare diel activity of the same species between the two time periods and found that black bears become more nocturnal during the hunting season while most other carnivores maintain their diel activity between both time periods.

In Chapter 2, I demonstrate the potential of observations from remote cameras that hunters use at their bear bait sites and report via hunter surveys to be an effective method to monitor multiple species. Monitoring wildlife is essential for wildlife managers to understand population trends and adjust management plans. As technology advances, new wildlife monitoring techniques come on board and enable managers and researcher to better understand many aspects of wildlife populations. Remote cameras are one such technology that has enabled researchers to better understand the occupancy as well as spatial and temporal patterns of different species (Wang et al. 2015, O'Malley et al. 2018, Candler et al. 2019). As remote cameras become increasingly more affordable, the public has become increasingly interested in using them to peer into the lives of wildlife that share their spaces (Lasky et al. 2021). Hunters, in particular, have become interested in using remote cameras to investigate the species that are walking their hunting trails or visiting their bait sites. As hunter use of remote cameras become more widespread, more data are being collected, but currently those data are going unrecorded by researchers. In this chapter, I demonstrate how hunter surveys, commonly used to collect target species harvest and hunter satisfaction data, can be an effective tool for collecting hunter recorded remote camera images for multiple species. I collaborated with the Michigan Department of Natural Resource (DNR) to add questions to the annual Michigan Black Bear Hunter Survey regarding hunter remote camera use as well as animals they see at their bait sites. I compare remote camera image results from pseudo

black bear hunter bait sites in fall of 2016 to remote camera observation from hunters reported via hunter surveys in the same hunting unit over the same time. I also test the effectiveness of these reports to be and index for multiple species by comparing them to gray wolf survey, mustelid (Mustelidae) trapping, and deer hunter harvest reports from 2016-2018. Using a Fisher exact test, I found that hunter reports are a useful tool for reporting remote camera images for four of the six species observed. Additionally, using Pearson's correlation coefficients and simple linear regression models, I found that these hunter reported remote camera images have great potential to be an effective way of indexing multiple species.

In Chapter 3, I illustrate the behavioral effect that a predator has on a naïve and an experienced prey population at hunter bait. For similar reasons to bear baiting, hunters use bait to attract deer to a central location to create a good shooting opportunity. However, deer are not the only species attracted to deer hunter bait (Bowman et al. 2015). Other species, such as wolves, have been recorded visiting hunter bait, even scent marking (Ruid et al. 2009, USFWS: Q and A's about Gray Wolf Biology 2011, Bowman et al. 2015). These olfactory cues left by wolves are likely to impact the intended bait target, deer, by changing their vigilance behavior or time spent at the bait site (Melchiors and Leslie 1985, Kuijper et al. 2013, Chamaillé-Jammes et al. 2014, Wikenros et al. 2015, Sahlén et al. 2016). However, research has demonstrated that *naïve* prey do not maintain an innate threat sensing ability when it comes to extirpated predators (Berger et al. 2001). Therefore, we would expect deer would not change their behavior around bait visited by wolves in areas where wolves have been extirpated and remain absent, such as

the Lower Peninsula (LP) of Michigan. However, in areas where wolves are established, such as the UP of Michigan, we would expect deer to be more vigilant and spend less time at bait that has been visited by wolves. In this chapter, I experimentally test the behavioral reaction of deer to wolf urine at deer hunter bait sites for both wolf savvy and wolf naïve white-tailed deer populations in Michigan. In September to November 2018, I constructed 30 deer bait sites between the UP and LP and used a before, after, control, impact (BACI) design with three treatment types (water, lemon juice, or wolf urine). Using remote cameras, I recorded white-tailed deer images and evaluated deer behavioral metrics and diel patterns before and after treatment, among treatments, and between the UP and LP. By analyzing 213,264 images and comparing the difference in behavioral metrics before and after treatment, I found that wolf urine had little effect on deer behavior in either area. However, when vegetation cover was compared to vigilance intensity using generalized linear models, a significant pattern emerged in the UP where wolves are present, but not in the LP, where they are absent. This indicates that vegetative obscurement, not predator olfactory cues, have more impact on savvy deer population vigilance.

In Chapter 4, I consider the impacts that a predictable hunter food source has on the movement of a predator. Predator-prey systems are rarely simple systems with a single predator and single prey. Looking at predator-prey interactions through this simple lens will produce an incomplete picture of the ecosystem process. A complete understanding of predator-prey interactions requires consideration of all consumers and prey or other food in the ecosystem, including consideration of scavenged food sources such as anthropogenic food. Anthropogenic subsidies can act as an alternative food source, taking pressure off other prey species (Baruch-Mordo et al. 2014, Ciucci et al. 2020). Alternatively, it can increase pressure on prey by improving predator fitness (Robb et al. 2008, Oro et al. 2013, Plaza and Lambertucci 2017). Before the effects that these anthropogenic inputs have on predator-prey systems can be understood, the extent of use by predators needs to be understood. In this chapter, I focus on wolf movement shifts in relation to black bear hunter bait in the Greater Voyagers Ecosystem (GVE). I conduct a preliminary analysis of six GPS collared wolves in the GVE and their recursion movements in relation to black bear hunter bait sites, homesites, and other site types for the baiting and hunting time periods in the GVE from 2017-2019. Using student's t-test and a nonparametric kernel density estimation procedure, I found that black bear bait sites are returned to often during the baiting and hunting periods, but that visitation becomes shorter and more nocturnal during the hunting season.

For the remainder of this dissertation, I will use ‘we’ instead of ‘I’ to reflect that multiple people made this work possible. The first chapter of this dissertation is published in *Human–Wildlife Interactions* (Candler et al. 2019) and Chapter 2 is in published in *Conservation Science and Practice* (Candler et al. 2021).

Table of Contents

Chapter 1: Who takes the bait? Non-target species use of bear hunter bait sites

Chapter 2: Untrapped potential: do bear hunter cameras accurately index non-target species?

Chapter 3: Exploitative competition between wolves and humans: How does perceived wolf presence affect naïve and experienced deer behavior at hunter bait sites?

Chapter 4: Recursion patterns of wolves in relation to bear hunter bait sites in the Greater Voyagers Ecosystem, Minnesota, USA

List of Tables

Chapter 1

Chapter 2

Chapter 4

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

CHAPTER 1

Who takes the bait? Non-target species use of bear hunter bait sites

Copyright by Berryman Institute. Candler, E. M., Severud, W. J., and Bump, J.K. 2019. Who takes the bait? Non-target species use of bear hunter bait sites. Human–Wildlife Interactions. 13(1), 14. https://digitalcommons.usu.edu/hwi/vol13/iss1/14/

SYNOPSIS

Although hunting bears (*Ursus* spp.) over baits is legal in many countries, states, and provinces, the practice remains controversial topic among wildlife managers, hunting groups, and the general public. The baits used to attract bears may also provide a pulsed resource on the landscape that can be used by other wildlife species, particularly carnivores. To determine what other species might use bear bait sites, we constructed, and monitored 21 bear bait sites using camera traps from August–October 2016 in the western Upper Peninsula of Michigan, USA. The site mimicked typical American black bear (*U. americanus*) hunter bait sites. We tested recorded changes in carnivore visitation before and during hunting season using paired t-test and analyzed carnivore temporal shifts between the 2 periods using a non-parametric kernel density estimation procedure. We analyzed 7,915 images, of which 81.9% were non-target species. Bear daily visitation at the bait sites was reduced by 49.3% during hunting season while non-target carnivore visitation increased by 33%. Bears also increased their nocturnal activity by 22.4% during the legal hunting season while other carnivore species maintained their diel patterns. Because of the high rates of non-target species use of the bear hunter bait sites,

there is a potential for disease spread and conflict with hunters. Managers could evaluate the potential impacts on target and non-target species when establishing hunter bait regulations.

INTRODUCTION

Resource pulses, such as seed mast events (e.g., *Quercus* spp.) and postspawning salmon (Salmonidae) carcass concentrations, are infrequent, large, and ephemeral events of increased food availability for generalist consumers (Yang et al. 2010). These pulses are ubiquitous across the globe, bridge ecosystem boundaries, and have the potential to impact communities for years after depletion (Holt 2008, Yang et al. 2008). Many species have likely evolved with the ability to take advantage and even anticipate naturally occurring resource pulses (Boutin et al. 2006, Gamelon et al. 2017). Anthropogenic resource pulses represent a special case that are similarly universal and may have comparable impacts on communities as naturally occurring resource pulses (Oro et al. 2013). However, human-provided resource pulses may differ temporally, spatially, and compositionally from naturally occurring resource pulses, which in turn may cause various effects on consumers and communities (Wilmers et al. 2003, Newsome et al. 2015).

Discerning how natural and anthropogenic resource pulses diverge is necessary to understand the ecological effects of human activities. Natural resource pulses likely have positive and negative impacts on consumer vital rates, such as fecundity and survival (Ostfeld and Keesing 2000, Newsome et al. 2015, Gamelon et al. 2017). Similarly, human-provided food has been linked to earlier reproductive age and higher litter sizes for consumer species (Rogers 1987, Beckmann and Lackey 2008, Kavčič et al. 2015). Pulses of human-provided food are likely to have similar effects as natural pulses (Holt 2008, Yang et al. 2008, 2010).

Alternatively, human presence and composition of anthropogenic pulses may cause a different impact on consumer species than natural pulses. For example, if consumer species detect higher risk associated with anthropogenic pulses, they may temporally shift their feeding behavior (Baruch-Mordo et al. 2014). Coyotes (*Canis latrans*) showed such a response to risk in suburban environments, where they shifted to nocturnal prey, forcing common gray foxes (*Urocyon cinereoargenteus*) to consume more diurnal prey species (Smith et al. 2018). This result is consistent with risk allocation hypothesis that predicts that species will respond to temporal variation in risk by changing their behavior (Lima and Bednekoff 1999).

Hunter bait sites are an example of an understudied anthropogenic resource pulse. Although hunting over baits is legal in many countries, states, and provinces, the practice remains controversial topic among wildlife managers, hunting groups, and the general public (Peyton 1989, Dunkley and Cattet 2003). The baits are used to increase hunter success and are provided on the landscape for a regulated time before and during a hunting season (Bowman et al. 2015). Baits are typically placed in predictable locations aimed to attract target species.

In Michigan, USA, white-tailed deer (*Odocoileus virginianus*) and American black bear (*Ursus americanus*; bear) are both commonly baited and hunted species. It is permitted to bait both species with corn (*Zea mays*), fruit and vegetables, but bears can also be attracted using meat, fish products, and baked goods (Michigan Department of Natural Resources [MI DNR] 2017). Though bait intended for bears is effective at attracting black bears, unintended use by non-target species is unknown. The goal of this study was to investigate non-target species use of black bear bait sites across a typical hunting season. We initiated this study because bait sites have been implicated in exacerbating human-wildlife conflicts (Bump et al. 2013). We assessed species visitation and diel patterns at bait sites across the 'baiting only' period before hunting season (~August 10–September 9) and through the 'baiting and hunting' period that follows (~September 10–24; (MI DNR 2017). We expected visitation by non-target carnivores would be higher while baiting only occurred than while baiting and hunting because of increased human presence. Because bears generally experience hyperphagia during the hunting season (late summer to early autumn), we expected bears would maintain high visitation rates to bait sites (Hristienko and McDonald 2007). Similar to research on hunted black bear, brown bear (*U. arctos*), white-tailed deer, and coyote, we expected that visitation at bait sites would shift to a more nocturnal pattern in response to more diurnal human presence on the landscape during hunting (Kilgo et al. 1998, Kitchen et al. 2000, Ordiz et al. 2012).

METHODS

Study Area. We conducted this study in the western Upper Peninsula (UP) of Michigan, USA (Figure 1). Our study area was within the Baraga bear hunting unit where ~1,166 bear hunting permits were purchased annually from 2013–2016 (4-year mean;

(Frawley 2017*a*). Nearly 65.5% (419,178 ha) of the total study area (640,271 ha) was publicly available hunting land. Further hunting likely occurred on private lands. Additionally, in the Baraga hunting unit ~94% of individual hunters and 99% of hunting guides use bait to attract bears (Frawley 2017*a*). We established bait sites across the Baraga hunting unit at locations where non-target species densities were similar, e.g., gray wolf (*C. lupus*) abundance (O'Neil et al. 2017).

Land cover consisted of deciduous forests (53%), wetlands (1%), mixed forest (17%), conifer forest (17%), open water (2%), grassland and herbaceous (6%), and developed areas (4%; Homer et al. 2015). From August 1, 2016 to October 26, 2016, 11 weather stations throughout the study area recorded a mean daily precipitation of 0.43 cm (National Oceanic and Atmospheric Administration 2018 [NOAA]). Temperatures ranged from −3.89˚ C to 32.22˚ C with a mean temperature of 12.59˚ C (NOAA 2018).

Sample Design. We used camera-trap surveys to monitor bear and non-target species use of hunter bait sites from August 1, 2016 to October 26, 2016. No baiting occurred for 9 days preceding the legal bear baiting (August 10–October 26) and hunting (September 10–October 26) season to establish baseline conditions. We established an adjusted systematic design that allowed for full coverage of the study area and scaled placement of the sampling units to avoid detection overlap (O'Connell et al. 2010, Sun et al. 2014, Niedballa et al. 2015).

To minimize photographing the same individual among sites, we scaled our sampling units based on the mammal species with the largest home range we expected to observe, i.e., gray wolf (Sun et al. 2014, Niedballa et al. 2015). Because our study area included public land (national and state forests), commercial forest land, and Michigan Technological University-owned land, we determined the available lands were bear hunting was legal within the hunting unit (MI DNR 2017).

To mimic bear hunters, we selected sites within 500 m water. Once in the field, we adjusted placement at some locations based on characteristics bear hunters use to increase chances of bears encountering bait, such as along linear features (trails or roads) and under moderate cover. We also created a circular buffer with a radius of 6.1 km resulting in an area of 11,654 ha around each point to mimic the average size of a wolf's home range regionally (Beyer et al. 2006).

At each site, we deployed 1 camera (Reconyx Hyperfire series, Holmen, WI) 0.5–0.8 meters above ground directed toward the bait site (Burton et al. 2012, Bowman et al. 2015, Lesmeister et al. 2015, Stirnemann et al. 2015). We programmed the cameras to take 2 consecutive motion-activated pictures with a 5-minute delay. With each image date, time, and temperature were recorded (Bowman et al. 2015). We further classified each photo as obtained during daylight or nighttime hours. During August 1–9, the site remained un-baited while the camera recorded images to establish baseline conditions.

On August 10 we constructed a bait site 2–3 m from cameras to provide a maximum field of view focal length to obtain readable images of each site. To reduce images without animal subjects (e.g., false triggers), we removed vegetation likely to activate the camera. Twice a week from August 10 to August 26, the sites were re-baited with a mixture of food that replicated a typical Michigan bear hunter's bait (a combination of meat products such as dog and cat food, cafeteria leftovers, imitation maple syrup, fryer grease, pie filling, pastries, and Bruin Buster predator lure [James Valley Scents, Mellette, SD, USA]). Bait was consistent across sites but varied each baiting occasion depending on bait availability, similar to hunter baiting efforts. From September 2 to 24, we re-baited each site weekly, similar to bear hunter behavior (Frawley 2017*a*). Based on long term bear hunter survey data, we concluded baiting September 24, the historical date when most UP bear hunters harvested bears and subsequently ceased baiting (Frawley 2017*a*). Cameras remained at sites through the end of hunting season (October 26) to assess species visitation post-baiting.

Data analysis. We eliminated images containing no animals or blurred/unidentifiable images. Because each detection typically recorded 2 images, we only analyzed 1 image from the pair. For each image, we recorded species present and number to calculate total number of detections, e.g., an image with one raccoon (*Procyon lotor*) counts as single detection and an image with two raccoons as two detections. These data indicate use of hunter bait sites rather than estimations of abundance of individuals.

To determine if there was a difference in visitation between the period before hunting (August 10–September 9) and during hunting (September 10–24; baiting occurred during both periods), we determined the mean daily detection rate for different species or taxa (e.g., Mustelidae; *Martes pennanti*, *M. americana*, and *Mustela* spp.) from 100 bootstrapped samples in each period. We compared bootstrap samples using a paired t-test, testing for difference in means and accepting statistical significance at $P < 0.05$. We also calculated a 95% confidence interval for each species or species group to better understand the effect size of the change.

We analyzed temporal activity of species based on detections before and during bear hunting season. We used a non-parametric kernel density estimation procedure to examine whether species altered activity patterns between these 2 periods (Wang et al. 2015). First, we converted times to radians then used a kernel density estimator to create a probability density distribution for each species between periods (Ridout and Linkie 2009). We then calculated an overlap term ($\hat{\Delta}$) that ranged from 0 to 1 and indicated the proportion of temporal overlap shared between periods (Wang et al. 2015). We would expect that if $\hat{\Delta}$ were high, there would be no temporal shift from before hunting to during hunting. Ridout and Linkie (2009) compared 3 methods for estimating $\hat{\Delta}$ and suggested using $\hat{\Delta}_4$ with a smoothing parameter of 1 for samples sizes > 50 and $\hat{\Delta}_1$ with a smoothing parameter of 1.25 for sample sizes < 50. We used $\hat{\Delta}_4$ to estimate overlap for bears, mustelids, raccoons, and the combined Carnivora because our sample sizes were > 50 (Meredith and Ridout 2018). For red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*) and coyote, we used $\hat{\Delta}_1$ to estimate overlap because one species count from each period comparison was > 50 (Meredith and Ridout 2018). Statistical analysis was conducted using the overlap package (Wang et al. 2015, Meredith and Ridout 2018) in R (R Development Core Team, 2013). To calculate how bears changed their nocturnal activity between the two periods, we quantified the difference between the areas under the activity curves for the nocturnal time before hunting and the nocturnal time during hunting.

To test for significance of temporal change for each species, we applied Watson's U2 statistic employed in the CircStats package (Lund and Agostinelli 2012, Lashley et al.

2018). This test calculates the probability that the 2 samples are homogeneous (i.e., that the 2 time periods have the same distribution). It tests the null hypothesis that there is no difference in the distribution of times of detection before hunting and during hunting (Lund and Agostinelli 2012). If a species significantly changed its diel pattern, we expected a Watson's U2 statistic greater than the critical value (0.19 for an α value of 0.05) and $P < 0.05$.

RESULTS

We obtained 8,642 images; 727 were of domestic species or humans and not included in analyses. Of the remaining 7,915 images, we calculated 12,070 individual animal detections (Table 1). Most of the images were raccoons (69.8%), followed by bears (18.1%) and mustelids (6.4%). More of the detections at sites (81.9%; Table 1) were of non-target species (~21). We also assumed some degree of consumption by carnivores because all were photographed in at least some images eating bait.

During the nine-day pre-baiting period, we detected bears, raccoons, deer, 1 moose, 1 mustelid, and 1 snowshoe hare (*Lepus americanus*) totaling 40 detections resulting in a mean daily (24 hr) number of detections (+ standard deviation [SD]) of 0.09 + 0.06 and accounting for only 0.33% of all detections throughout the entire study. For the entire study period, the mean daily number of detections (+SD) for raccoons was greater than any other species (5.02 + 5.48), followed by bears (1.60 + 1.95), and mustelids (0.52 + 0.55). Mean daily detection for all species remained constant before hunting and during hunting (Table 2). However, carnivore daily mean detections declined by 0.40 (± 0.11), due to reduced visitation by bears.

Black bear mean daily number of detections was reduced by 1.33 (± 0.11) between the 2 periods (Table 2). In contrast, all other carnivore species that were recorded more than 20 times, which excluded gray wolf and bobcat (*Lynx rufus*), increased visitation during the hunting period (Table 2, Figure 2). Though detections were low between the two periods, 7 and 1 for wolves and bobcats respectively, wolves were not recorded once hunting started while bobcats were not recorded until after hunting started. Though there was a significant overall increase regionally, this increase was not uniform across all bait sites. For example, at 1 site we detected 3 mustelids both before and during hunting, at another we detected 3 before hunting and 14 during, and yet at another detection was 5 before hunting and 1 during. As a group, carnivore species changed their diel activity to be slightly more nocturnal from before hunting to during hunting ($\hat{\Delta}_4 = 0.93$, U2 = 0.58; Figure 3), though this is largely driven by bear shifts. Bears altered their behavior more dramatically and tended to visit at nocturnal times during hunting ($\hat{\Delta}_4 = 0.73$, U2 = 2.74; Figure 3). We observed a 22.4% increase in nocturnal activity during hunting for bears. Conversely, mustelids, red fox, coyote, and skunks maintained their diel pattern between both periods ($P < 0.001$; Figure 3). Wolves were only detected before hunting, but overall detections were low, i.e., 9 detections across 3 sites (Figure 2). Additionally, few bobcats were detected and only during and after hunting (i.e., 3 detections across 2 sites; Figure 2, Figure 4).

DISCUSSION

Our results indicated that overall non-target species use of bait stations was higher than bear use. Most of the non-target species are opportunistic omnivores (e.g., raccoons, skunks, and coyotes) while some are predominantly herbivores (e.g., snowshoe hares and squirrels [Sciuridae]). The variety of consumers visiting bait sites was possibly a result of the variety of bait types used (Figure 4). Mean daily visitation and total number of detections during the pre-baiting period was very low indicating that bear bait was an important attractant to consumers.

Although many hunters in the Northern Great Lakes region have reported wolves at bear bait sites (Ruid et al. 2009), we detected few and none once hunting started (Figure 2). Our bait was similar to a typical bear hunter's bait, but ingredients used may not have been as desirable to wolves as other bait types commonly used by bear hunters (e.g., meat).

As expected, bear visitation shifted to a more nocturnal pattern during hunting season (Figure 3). An overall increase in nocturnal and diurnal activity has been observed in unhunted bear populations consistent with hyperphagia in autumn (Garshelis and Pelton 1980, Hwang and Garshelis 2007). However, we recorded a decrease in diurnal activity at bait sites with a shift to nocturnal activity (Figure 3).

Hunted bears in Virginia and brown bears in Sweden demonstrated similar trends during hunting season (Bridges et al. 2004, Ordiz et al. 2012). This shift is also evident in populations that experience periodic high human activity, such as increased hiking and angling, that may pose no direct threat to bears (Gunther 1990, MacHutchon et al. 1998, Olson et al. 1998, Kaczensky et al. 2006). However, human activity in our study area was high before hunting in the form of baiting and bear dog (*Canis familaris*) training efforts (hunting bears with the assistance of dogs is also permitted in Michigan; MI DNR 2017), which has been suggested as a reason for temporal shifts in hunted Virginia black bear populations (Bridges et al. 2004). Therefore, the shift we observed may be a response to active hunting of bears (Erb et al. 2012). Consistent with risk allocation theory, bears are likely shifting their activity patterns to less risky nocturnal visitation to avoid human hunters (Lima and Bednekoff 1999). How black bears detect the difference between the baiting only period (August 10-September 9) and the baiting and hunting period (September 10–24) remains unexplained.

Because bears experience hyperphagia before and during hunting season, we expected that detection rates at bait sites would remain high (Hristienko and McDonald 2007). We observed that bears not only shifted to nocturnal visitations, but also reduced their visitation overall by 49.28% (Figure 2). Though we did not actively hunt our bait sites, bears may have perceived a higher risk at bait. Previous research has reported the bears spatially shift away from unpaved roads used by hunters in the UP during hunting season (Stillfried et al. 2015). Bears may avoid bait sites during hunting season and instead target less risky, natural foods available during the fall (Gray et al. 2004, Kirby et al. 2017). The regional bear food index for 2016 was within normal conditions for (Garshelis and Tri 2017). In a low mast year, we may not observe a reduction in visitation as bears might compensate for lower natural food availability and continue to target bait sites (Oro et al. 2013).

Counter to our expectations, all other carnivore species that we detected more than 20 times increased their visitation to bait sites during hunting season (Figure 2). Though bears may not usually pose a threat, smaller carnivore species may yield bait sites to the much larger predator (Briffa and Sneddon 2007). However, non-target carnivores, with the exception of raccoons, did not alter their temporal patterns from before hunting to during hunting, indicating that they did not temporally avoid bears (Figure 3). The shift in activity patterns by raccoons from earlier to later in the morning might indicate that they are avoiding bears, who shifted from late morning to early morning hours (Figure 3).

The consumption of bait by opportunistic species may not only affect those consumer species, but may impact the broader mesopredator community (Figure 4). Similar to effects of natural resource pulses, consumption of bait may affect vital rates of consumers. For instance, bears that consume bait have increased fecundity and higher litter sizes (Gray et al. 2004, Kavčič et al. 2015, Kirby et al. 2017). These effects are likely to occur in non-target consumers as well. Additionally, consumers may experience higher densities than would naturally occur (Oro et al. 2013). As opportunistic species are the primary consumers of bear bait, their populations might benefit the most. Individuals disproportionally affected as a result of a poor food year, particularly young, inexperienced, or individuals in poor condition, will be positively affected by consumption of bait (Oro et al. 2013).

Though bait may have positive impacts on populations of opportunistic species, bait might also create an ecological trap for species at lower trophic levels (Morris 2005, Cortés-Avizanda et al. 2009). We recorded several rodent species, and snowshoe hares at bear bait sites, all of which are prey of mustelids, coyotes, and red foxes. Presence of both predators and their prey at bait sites may increase encounters and therefore predation risk for prey. Research in urban environments has shown that food subsidies to predators reduced their need to hunt, decoupling the predator-prey relationship (Rodewald et al. 2011). Additional research is needed to investigate if bear bait negatively impacts some non-target prey species.

Encounter competition among consumer species might also be exacerbated at bait sites (Schoener 1983). Larger-bodied species are likely to win an encounter, therefore having a higher resource holding potential (Briffa and Sneddon 2007). Encounter competition may explain why non-target carnivore species limited their mean daily visitation to bait sites, avoiding competition with bears and increasing their visitation when bear visitation was reduced. However, during hunting, species of similar sizes (i.e., red foxes and raccoons) increased their daily visitation to bait sites making the outcome of an encounter less predictable (Allen et al. 2016). We regularly observed raccoons and red foxes as well as raccoons and skunks at bait sites together (Figure 5). Bear bait creates a foraging arena, aggregating and possibly increasing encounter competition between non-target consumers (Ahrens et al. 2012, Allen et al. 2016).

Bear baiting is a common practice in North America, occurring in 11 of the 27 states in the United States and 10 of the 13 provinces and territories in Canada where black bear hunting is permitted (black bear hunting is not permitted in Mexico). Although bear baiting might have positive effects on non-target species, some of these benefits may manifest as negative community-level impacts (Wilmers et al. 2003, Bump et al. 2013, Oro et al. 2013, Newsome et al. 2015, Kirby et al. 2017). In addition to inter- and intra-specific conflict at bait sites, human-wildlife conflict might be exacerbated. For example, wolf/hunting dog conflicts may be positively related with bear bait duration on the landscape (Bump et al. 2013). Chronic wasting disease (CWD) was recently documented in the UP (Michigan Department of Natural Resources 2018*a*) and, perhaps non-intuitively, we recorded deer visiting bear bait sites. This has management implication because, in areas with CWD, deer baiting is typically banned (Michigan Department of Natural Resources 2018*b*).

Research of white-tailed deer at hunter bait sites shows that concentrated deer are more likely to spread diseases such as CWD and bovine tuberculosis (Thompson et al. 2008). Aggregation of species at bear bait sites, such as raccoons and skunks, also provides opportunity for the spread of diseases (e.g., rabies) that are transmitted through contact (Houle et al. 2011).

MANAGEMENT IMPLICATIONS

This research demonstrated that bear bait attracts several nontarget species whose resource need and feeding activity directly competes with the intention of hunters to use the bait to attract bears exclusively. Managers could consider that the amount, type, method, and duration of baiting is likely to affect what and how species use bait when considering regulations pertaining to bait use. Additionally, the aggregation of individuals and different species at bear bait sites increases the potential for disease spread.

ACKNOWLEDGEMENTS

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. 00039218. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. This research was also supported by grants from the National Science Foundation to J. K. Bump (NSF ID#1545611, NSF ID#1556676). We thank D. E. Beyer with the Michigan Department of Natural Resources for project support. We thank M. J. Candler, J. M. and B. A. Beller, C. M. Boucher, S. A. T. Beckley, V. M. Engler, S. K. Olds, J. R. Curtis, and M. R. Wappes for field assistance and image analysis. We would also like to thank Suomi Home Bakery & Restaurant, Granton Inn, Wheeler's Restaurant, and Michigan Technological University Dining Service for support. Comments provide by C. Lackey, HWI Associate Editor and two anonymous reviewers greatly improved our paper.

CHAPTER 2

Untrapped potential: do bear hunter cameras accurately index non-target species?

Copyright by Society of Conservation Biology. Candler, E. M., Severud, W. J., Beyer, D. E. Jr., Frawley, B., and Bump, J.K., 2021. Untrapped potential: do bear hunter cameras accurately index non-target species? Conservation Science and Practice. e570. https://conbio.onlinelibrary.wiley.com/doi/full/10.1111/csp2.570

SYNOPSIS

Remote camera use by hunters offers the potential to collect citizen-derived data on multiple species using hunter surveys, but the effectiveness of this approach is untested. We examine whether observations from remote cameras that hunters use at their black bear (*Ursus americanus*) bait sites and reported via hunter surveys are an effective method to monitor species. We compared data collected from pseudo-bear bait sites established for this study to hunter established bear bait site observations from the same study area. We also quantified observations reported on hunter surveys as a landscape index alternative to white-tailed deer (*Odocoileus virginianus*) hunter indices, gray wolf (*Canis lupus*) surveys, and mustelid (Mustelidae) trapper indices. We did not detect a difference in hunter reported camera observations versus our observations for four of the six species recorded at pseudo-bear bait sites. Hunters were over nine times more likely to report photographing wolves and nearly one third as likely to report photographing mustelids. We observed a relationship between trapper survey-derived

mustelid indices and the camera-derived index, but not for deer or wolves. Foremost, these results emphasize the need to further evaluate the utility of remote camera data derived from hunters. The widespread use of remote cameras by hunters, the low-cost of hunter surveys, and the potential to collect accurate community composition and occurrence/presence indices, points to the value of adding questions to hunter surveys regarding multiple species of interest.

INTRODUCTION

Monitoring wildlife populations is essential to effective species conservation. As monitoring methods and technology improve, our understanding of animal distributions and resource use becomes more comprehensive. This is especially true for remote cameras, which have proven to be an effective tool for occupancy as well as spatial, and temporal, patterns of multiple species (Wang et al. 2015, O'Malley et al. 2018, Candler et al. 2019). Remote cameras have also proven effective in characterizing species use of black bear (*Ursus americanus*) and white-tailed deer (*Odocoileus virginianus*) hunter bait sites (Bowman et al. 2015, Candler et al. 2019). Experimental or observational bait sites across management jurisdictions (i.e., hunting unit, a state) would provide the most control over potentially confounding variables (e.g., density of camera sites, distribution) when examining species at bait sites. The logistics and cost of such studies, however, can be restrictive or prohibitive to researchers.

Hunter surveys may offer a method to overcome these challenges (Mahard et al. 2016, Crum et al. 2017). In many states, hunters are surveyed yearly to assess hunter participation, success, and satisfaction (Frawley 2019*a*, Duda et al. 2020, Wyoming Game and Fish Department 2021). Adding survey questions regarding non-target species that hunters observe at their bait sites can help managers understand species presence at and use of bait sites at larger scales. As remote cameras have become more affordable, hunters have begun to use them to record animals that travel certain trails or frequent bait sites. Similar to their use in conservation research, hunters use cameras to identify individuals, understand local occurrence, and track the diel cycles of animals (Roland and Slauson 2008).

To test the effectiveness of hunter surveys as an approach to estimate species' presence at, and likely use of, hunter bait sites, we compared data from pseudo-bear bait sites in Michigan, USA to responses from the annual Michigan Black Bear Hunter Survey. The survey included questions regarding remote camera use and the species that hunters recorded at their bait sites. We expected that the proportion of cameras at our pseudo-bear bait sites that recorded various species at bear bait sites would be equal to the proportion of hunter-reported observations of the same species at their bait sites for the same geographic areas.

We also assessed the effectiveness of camera observations reported on hunter surveys as an index for gray wolves (*Canis lupus*), white-tailed deer, and mustelid species, such as American marten (*Martes americana*) and fisher (*Pekania pennanti*), at the landscape scale, i.e., in different counties in Michigan's Upper Peninsula (hereafter UP; Fig 1). Counties are the finest scale that hunting reports are recorded for all species and frequently the scale of wildlife management and conservation within states. We predicted that the proportion of hunter-reported observations of each species or family (camera index) in each county would be positively correlated to independent data from the Michigan Department of Natural Resources (MI DNR) on wolves (bi-annual surveys), white-tailed deer (harvest reports), and mustelids (trapper reports).

METHODS

Study Area. We analyzed hunter survey and abundance data across the entire UP of Michigan, USA, but conducted our camera trap observations in the western UP within the Baraga bear hunting unit encompassing our pseudo-bear bait sites (Fig 1). In 2016, bear hunters purchased 1,135 permits for the Baraga hunting unit and ~97% of hunters used bait to attract bears (Frawley 2017*a*).

The UP (~44,123 km^2) was primarily deciduous forest (33%), wetlands (32%), and evergreen forest (10%) (Homer et al. 2015). Elevation ranges from approximately 156–603 m. In 2016, 2017, and 2018, an estimated 96%, 97%, and 97% of bear hunters in the entire UP (4,758, 4,862, and 4,725 permits sold, respectively) used bait (i.e. artificial food sources) to attract bears, respectively (Frawley 2017*a*, 2018*a*, 2019*a*).

Field Observations. During 1 Aug–26 Oct 2016, we conducted camera trap surveys to determine non-target species occurrence at bear hunter bait sites. We selected 21 sites within the Baraga hunting unit that matched characteristics used by bear hunters, such as proximity to water and tertiary roads. These sites were created at locations where non-target species' densities were similar among sites (e.g., gray wolf density; O'Neil 2017). Sites were located on public lands open to hunting (i.e. National and State Forest and commercial forest lands; Fig 1). At each site, we deployed 1 camera (Reconyx

Hyperfire series, Holmen, WI). We programmed each camera to take 2 consecutive pictures once triggered , with a five minute delay between trigger events (Bowman et al. 2015, Candler et al. 2019).

After camera sites were established (1 Aug 2016), we constructed bait sites at all 21 camera locations 2–3 meters from each camera on 10 Aug 2016, the first day that legal baiting is allowed. We baited each site with a mixture of food that replicated a typical Michigan bear hunter's bait (a combination of pie filling, pastries, meat products such as dog and cat food, imitation maple syrup, cafeteria leftovers, fryer grease, and Bruin Buster predator lure [James Valley Scents, Mellette, SD, USA]). Bait content varied across baiting occasions but was consistent among sites for each baiting instance (Candler et al. 2019). We baited twice a week until 26 Aug 2016 when we switched to baiting once a week to mimic bear hunter behavior (Frawley 2017*a*).

We subset photos that were recorded from the time baiting started (10 Aug 2016) to the time most hunters harvest a bear and retrieve their cameras (24 Sep 2016; Frawley 2017). This time period was when hunters were most likely to record species at their bait sites. For each camera we determined if a photo recorded a bear, coyote (*C. latrans*), deer, bobcat (*Lynx rufus*), wolf, or mustelid during the 46-day period in order to directly compare species observed at pseudo-bear bait sites with data from questions in the hunter survey.

Hunter Survey. In 2016 we worked with the MI DNR to add 2 questions to the Michigan Black Bear Hunter Survey asking hunters to indicate whether they used bait and a remote camera and, if so, what species were recorded (bear, coyote, deer, bobcat, wolf, or marten and/or fisher) at their bait sites (marten and fisher were later combined into a "mustelid" group for analysis; Appendix A). The MI DNR provided bear hunters the option to report using an online survey. In addition to voluntary respondents, a random sample of hunters who purchased a bear harvest license were mailed the same survey (Frawley 2017*a*).

Data Analysis

Observational Comparison. To compare the survey data to the field observations, we subset statewide survey data to include only responses from hunters who baited, used a remote camera, and hunted in the Baraga bear management unit (BMU) in the western UP in the area that overlapped with our study site. We eliminated observations from hunters who hunted only in Keweenaw County as we did not have camera traps north of Portage Canal. We restricted our sample to observations reported from a single county to ensure observations were correctly assigned geographically since some hunters reported hunting in 2 or 3 counties, but observations were not assigned to each county in such cases.

We calculated proportions of each species at pseudo-bear bait sites and hunter-reported observations to evaluate frequency of occurrence differences between the two groups. We compared the difference in proportions between the number of observational cameras that recorded a species at least once and the number of hunters that reported species using Fisher's exact test ($\alpha = 0.05$; Ramsey and Schafer 2002). This test indicates the odds that a given species will be recorded by cameras at hunter vs. pseudo-bear bait sites, a 1 indicating that the odds, for either method, are equal. The confidence interval produced is asymmetrical since the distribution of the odds ratio is from 0 to infinity. This simple, yet robust, comparison is an effective test (Zar 1999) between the proportions of species reported by hunters and those recorded at pseudo-bear bait sites.

Camera index analysis. To compare the MI DNR reports (i.e., deer hunter and mustelid trapping reports) and wolf survey results to hunter observations recorded in the black bear hunter survey, we also restricted our sample to observations from hunters that hunted in a single county. We included observations from each of the 15 Michigan UP counties to compare them to wolf survey data and deer and mustelid harvest densities. We determined the yearly density of wolves as well as harvest indices for deer and mustelids in each UP county using data provided by the 2016 and 2018 MI DNR wolf survey results, the 2016–2018 Michigan Deer Harvest Survey Reports, and the 2016–2018 Michigan Furbearer Harvest Surveys, respectively (Frawley 2017*b*, 2018*b*, 2019*b*, *c*, *d*, 2020). We used counties as our unit of comparison because it is the smallest common unit between the black bear hunter, deer hunter, and mustelid trapping surveys, and it also matches the scale of wildlife management for many states. We calculated harvest indices for mustelids and deer for each county by dividing the total number of mustelids trapped or deer harvested in each county by the total area of the county. We removed Isle Royale National Park from the area of Keweenaw County because no hunting or trapping occurred on the island. Wolf survey units (WSU) do not directly correspond to county boundaries (i.e. some counties are entirely within a single WSU and some counties cross WSU boundaries). We were interested in how hunter camera trap data might reflect landscape-level wolf occurrence, so we derived county-level wolf densities based upon a weighted average of WSU values and area within each county. While mustelid and deer harvest reports covered the entire UP annually, only 40% of WSUs were surveyed in both 2016 and 2018 which resulted in gaps in the UP where wolves were not surveyed. For counties that did not have full coverage, we applied the index estimates for the surveyed areas to the entire county. Because wolf populations in the UP appear to be stable, estimating county density from WSUs is robust despite minimal survey effort in some counties (O'Neil 2017).

We calculated a camera index for each county by dividing the number of hunters who baited and reported the detection of a given species by the total number of hunters who baited and used a camera within each respective county (Appendix A). We examined the relationship between camera index and county-level wolf density estimates, white-tailed deer harvest indices, and mustelid harvest indices using Pearson's correlation coefficients ($\alpha = 0.05$). We also fit simple linear regression models to the data to examine the relationship between harvest indices among counties and the camera index. We accounted for human presence at hunter bait sites in all models by incorporating bear hunter effort days as an additional explanatory variable. This variable was derived from the Michigan Black Bear Hunter Surveys (Frawley 2017*a*, 2018*a*, 2019*a*).

RESULTS

Observational comparison. Of the total number of hunters who baited in the observational study area, 69% of them used remote cameras. After subsetting survey data to include bear hunters who used a remote camera while hunting exclusively within the boundaries of our study area in the Baraga BMU, we analyzed 221 of 474 hunter reports.

Our observational cameras at pseudo-bear bait sites recorded the same species as those reported by hunters (Table 1). The likelihood of hunters reporting that they observed wolves was 9.41 (95% CI: 1.44–397.14) times greater than at our pseudo-bear bait sites. Hunters were less likely to observe mustelids (0.31 95% CI: 0.09–0.88; Table 1). We did not detect a difference between any other species recorded by either method (Table 1).

Camera index analysis. In the UP overall, 76% of 3,100 surveyed hunters in 2016, 76% of 3,181 surveyed hunters in 2017, and 80% of 3,238 surveyed hunters in 2018 that used bait also used remote cameras. The camera index across counties was positively, but weakly, correlated to the harvest density indices of mustelids (*Pearson's R* = 0.415, P = 0.005) and deer (*Pearson's R* = 0.329, P = 0.027) in each county, but was not correlated for wolves (*Pearson's R* = 0.077, P = 0.687). A relationship between camera index and independent MI DNR indices was significant for mustelids (R^2 = 0.267, P = 0.002) when including bear hunter effort as an explanatory variable (Fig 2). We did not, however, detect a relationship between camera index and wolf (R^2 = 0.061, P = 0.430) or deer (R^2 = 0.124, P = 0.063) indices across UP counties (Fig 2).

DISCUSSION

While some states (e.g., Iowa, Wisconsin, and Minnesota) use hunter observations to monitor trends in wildlife populations, these methods can be biased by hunter presence and be incomplete because they only incorporate the time that a hunter is making observations (i.e. daylight hours; Lohr 2017; Harms et al. 2018; Obermoller et al. 2018). Other studies have used hunter surveys to glean information about non-target species observed by hunters as well (e.g. Mahard et al. 2016, Caruso et al. 2017, Crum et al.

2017), but to our knowledge, this is the first comparison of hunter reports to a field study using the same method (i.e., remote cameras deployed at bait sites). Overall, this study highlights the potential effectiveness, as well as some of the opportunities and limitations of using hunter remote camera photographs as a surrogate or additional method for camera trap-based monitoring and field studies for multiple species. In particular, data from surveys of hunters who use cameras are potentially useful in species distribution and occupancy modeling (e.g., presence only approaches), but not widely applicable to assessing population trends depending on the species.

As predicted, the observational comparison produced statistically similar results, for 4 of 6 species at the county scale. The two methods differed in the proportion of sites that recorded wolves and mustelids at bait sites, with hunters detecting wolves in more of their photos and mustelids in fewer than we did at our pseudo-bear bait sites. Because we could not confirm correct identification of species by hunters, there may be some misidentification between similar-looking species such as wolves and coyotes. Additionally, people often over report species that they perceive to cause more human-wildlife conflict, which may be wolves in this case (Ruid et al. 2009, Bump et al. 2013, Caruso et al. 2017). In the Great Lakes states, hunters have a low tolerance for wolves as they consider them a threat to hunting and safety (Hogberg et al. 2016, Vucetich et al. 2017). In addition, unlike the bordering state of Wisconsin, Michigan does not compensate for bear dogs that may have been killed by wolves (Bump et al. 2013). This lack of compensation may lead to additional disdain for wolves by bear hunters (Treves et al. 2009). This underlying intolerance may affect a hunter’s decision or inclination to identify a canid as a wolf if they are uncertain of its identity (Caruso et al. 2017). For example, if only 16 of 221 hunters misidentified coyotes as wolves, which is easily plausible, the proportions would not be significantly different between hunter reported observations and our pseudo-bear bait sites observations in our analysis. This potential to misidentify species may also partially explain the lack of correlation between the camera index and wolf density across the UP.

In addition to misidentification, human presence and time spent at bait may affect the species that are recorded by hunters vs. ones recorded at the pseudo-bear bait sites. We only visited experimental sites for the purpose of baiting, while hunters visited bait sites for baiting and hunting. The increased presence of humans at the bait site may have deterred mustelids from visiting the bait (Powell 1993) and explain the difference in mustelid observations between the two methods. If increased presence of humans deterred mustelids, then the pseudo-bear bait sites may have overestimated true visitation.

The comparison between hunter survey data (camera index) and other indices is additional evidence for the utility and untapped potential of hunter surveys in non-target species monitoring; it is worth exploring this approach further. As we expected, the mustelid harvest index was positively correlated with the hunter-derived camera index across the UP. Though hunters reported photographing fewer mustelids than expected in the previous analysis, the trend demonstrated in the correlation between camera index and harvest index is valuable as relative change over time is often of interest in wildlife management and conservation. Additionally, underreporting of mustelids by hunters provides a conservative index estimate that can alert managers to reduced numbers before a real problem arises. Differentiating between fisher and martin in the analysis would also be more informative to managers. Our assessment could be improved to better account for variation in species density across counties (Fig 2). In the future, camera index predictions may be improved by including habitat variables such as cover type and by gathering camera effort data (i.e. the number of days a camera is deployed), and number of cameras used per hunter from the hunter survey. These would likely be an important descriptive variable in modeling species indices, would be more appropriate than simply hunter effort as estimators of human presence at bait sites, and could be easily added to hunter surveys. With advancements in online surveys, hunters could also upload images that could be used to create detection histories. Such additions would also allow managers to possibly develop occupancy models to detect changes in occupancy and possibly estimate abundance (e.g. integrated population models), particularly at bait sites that are consistently baited every year. This technique is not possible with data that is currently available (Royle and Nichols 2003, Ahrestani et al. 2013, Zipkin and Saunders 2018).

Contrary to our expectations, we did not find a significant correlation between wolf density and camera index. This finding may be due to misidentification of wolves, as suggested above, but may also be a result of the gaps in wolf density estimates and the method we used to estimate density. Only two years of data are presented here, so it would be inappropriate to make assumptions about trends. As more data are collected across years, more detailed analysis could compare camera index to counties that have more complete wolf surveys.

Although some of the variation in the white-tailed deer index was captured by camera index it varied greatly among years (including year as an interaction variable would be inappropriate as there are too few samples per year in the current data set). This high variability may be reflective of the behavior of deer around bear hunter bait. At our pseudo-bear bait sites for instance, we observed deer, but they were often passing through the area and may not have been attracted to bear bait like mustelids (Holinda et al. 2020, Ribeiro and Bianchi 2020). Additionally, the deer index derived from hunter harvest data was dominated by a single sex (males) while cameras captured either sex. Adding an additional question to the hunter survey asking for number of antlered and antlerless deer recorded would make this comparison more appropriate. To gain a better understanding of deer activity or abundance using information derived from hunter cameras, it may be more beneficial to use camera index information from deer hunter survey results instead of bear hunter survey results. The MI DNR has recognized the potential in collecting these data and has since added similar questions to the Michigan Deer Harvest Survey Report (Frawley 2019c, Frawley 2020a).

While caution should be used when developing indices, they show potential to be useful in identifying population and landscape level responses to management decisions or environmental changes (Letnic et al. 2011, Cooper et al. 2012, Mahard et al. 2016). With improvement to the camera index models (e.g. inclusion of habitat and camera effort as well as additional years of collection to better understand annual variation) the hunter-derived camera index could be an additional tool for the DNR to detect variation in some species' trends at the county level. As hunters become accustomed to camera-trap related questions and surveys increasingly become electronic (e.g., web and app based), additional details may be collected such as images of species per unit time (e.g., day, week, etc.) and identification of individuals for use in mark-recapture methods as is done with some species (Jhala et al. 2011, Alonso et al. 2015, Moore et al. 2020). For example, deer identified via antler formation and ear notches, American martens identified from their ventral patches, and other species identified using tags from other studies (e.g. collared wolves) can be used in mark-recapture analyses (Jordan et al. 2011, Sirén et al. 2016, Macaulay et al. 2020). Collection of such metrics would expand the utility of camera data from presence, composition, and range metrics to more robust relative abundance measures. Additionally, camera-trap derived indices may have the potential to fill in gaps between years that more rigorous field work is conducted or between survey years (O'Brien et al. 2010). This approach may be most useful to detect changes in species' relative occurrence, range, or density if the species is intensely surveyed infrequently or not at all (O'Brien et al. 2010).

Though our analysis shows potential for using hunter-supplied information, it is not recommended as a stand-alone tool. Outside factors are likely to affect the interpretation of species distributions and relative densities from year to year. For example, in food-poor years, some species may use bait or move more often and be recorded at a higher rate than in good-food years (McCall et al. 2013, Oro et al. 2013). This increase in bait use may inaccurately indicate an increase in relative density for some species. Additionally, if bait type or quantity regulations change within the area of observation, species visitation to bait are also likely to change. Wildlife managers may also consider additional metrics, such as food availability and bait regulation changes, when interpreting hunter reports at bait sites.

Hunter harvest numbers have long been used as a proxy for species population trends and relative densities (Brand and Keith 1979, Rolandsen et al. 2011). These hunter proxies, derived from hunter reports, are often biased by hunting regulations and hunter preference. With the advancement and adoption of remote camera technology by hunters, additional information is incidentally being collected. Other studies have employed hunter citizen scientists to record observation or sign of a single species encountered while hunting (Cooper et al. 2012, Mahard et al. 2016, Crum et al. 2017). Our analysis shows that adding questions related to remote cameras to hunter surveys is likely an effective and relatively inexpensive way to collect information on numerous, but not all, species across a large scale. Additionally, the reported hunter observations are likely more representative than harvest indices as remote camera images are not restricted by harvest regulations (e.g., age or sex restrictions) or hunter's harvest preferences (e.g., antler-point restrictions imposed on deer). Information from hunter reports can be used to identify non-target species using bait sites, which has the potential to serve as an index of relative occurrence of species in different management areas. The MI DNR has recognized the utility of including these questions on surveys and expanded their use beyond black bear hunter survey to now include the white-tailed deer hunter survey. Additionally, hunter surveys may act as a monitoring tool for rare or recovering species (e.g. lynx or cougar) that hunters might observe on their remote cameras. Additional research on the relationship between the abundance of hunter-captured presence data and estimates of species occupancy, density, and abundance, particularly with capture-mark-recapture methods, is warranted, which highlights the utility of adding remote camera related questions to hunter surveys.

MANAGEMENT IMPLICATIONS

Hunter surveys offer an effective, wide reaching, and relatively inexpensive way to collect data about hunter activity and species trends. Additionally, hunters are increasingly using remote cameras to monitor their hunting sites and inevitably record numerous wildlife species. This immense volume of camera data to monitor wildlife is a resource that has yet to be accessed to its full potential. We suggest that managers consider including questions regarding remote camera use and non-target species, particularly species that require high-cost resources to monitor, on hunter surveys. Though the indices reported in this analysis require additional exploration to improve their utility, the inexpensive nature of adding these questions to hunter surveys as well as the popularity of remote cameras with hunters makes adding these questions a management opportunity to examine. Adding these questions now will ensure a larger pool of data to incorporate once indices are refined.

ACKNOWLEDGEMENTS

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. 00039218. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. This research was also supported by grants from the National Science Foundation to J. K.

Bump (NSF ID#1545611, NSF ID#1556676). We thank M. J. Candler, J. M. Beller and B. A. Beller, C. M. Boucher, S. Beckley, V. M. Engler, S. Olds, J. R. Curtis, and M. Wappes for field assistance and image analysis. We would also like to thank Suomi Home Bakery & Restaurant, Granton Inn, Wheeler’s Restaurant, and Michigan Technological University Dining Service for support.

CHAPTER 3

Exploitative competition between wolves and humans: How does perceived wolf presence affect naïve and experienced deer behavior at hunter bait sites?

SYNOPSIS

As predators are reintroduced and expand to their historic ranges, their prey species must exhibit innate predator sensing abilities or quickly learn to respond to predator threats. These prey responses are likely to manifest as increased vigilance, shift in diel activity, or reduced time spent at certain sites, including feeding sites. This shift in activity may make hunting more difficult for other predators, particularly human hunters. To determine the effect that an expanding gray wolf (*Canis lupus*) population may have on white-tailed deer (*Odocoileus virginianus*) and the ability to hunt them, we constructed 15 deer hunter bait sites both in areas with wolf savvy and wolf naïve deer populations. Using a before, after, control, experiment (BACI) design, we treated sites with wolf urine, a novel scent (lemon juice), and a control (distilled water) and used remote cameras to observe deer behavior, diel activity, and abundance from September 21, 2018 to November 10, 2018 in the Upper (wolves present) and Lower (wolves absent) Peninsulas (UP and LP respectively) of Michigan, USA. We tested for a difference in predator response metrics before and after treatments were applied and analyzed deer temporal shifts before and after treatment using nonparametric kernel density estimation. We also used a generalized linear model to examine the effect that vegetation cover has on vigilance intensity of deer. We analyzed 213,264 images from both the UP and LP.

The wolf urine treatment did not have a statistically significant effect on predator response metrics except for a slight increase in group size where wolves are present and a decrease in vigilance intensity where wolves are absent. We observed a noticeable difference in the overall diel pattern between areas with and without wolves and detected significant shifts in diel activity of deer in both areas before and after treatment but did not detect a consistent directional pattern to these shifts. Deer vigilance intensity was not greatly affected by treatment type, but we did observe a significant correlation between vegetation cover and vigilance intensity in areas with wolves but did not detect this same pattern in areas without wolves. These results indicate that habitat variables affect white-tailed deer response to predators more than indirect olfactory predator cues at hunter bait sites in predator savvy populations. Whereas in predator naïve white-tailed deer populations, responses to predators were virtually nonexistent or not detectable. Predator presence may negatively impact hunting success in areas with established predator populations (i.e. exploitative competition may occur), but hunters may avoid these impacts by selecting for favorable habitat characteristics.

INTRODUCTION

Optimally foraging animals behave to maximize their energy gained from foraging and minimize energy loss in efforts to obtain food or avoid risk of predation (Emlen 1966, MacArthur and Pianka 1966, Sih 1980). Studies suggest that, in order to reduce the risk of predation, animals may avoid high risk areas even if there is an abundance of food (Edwards 1983, Ripple and Beschta 2004, Kuijper et al. 2013).

Similarly, the predation risk allocation hypothesis suggests that temporal variation in predation risk severity will affect foraging and vigilance behavior in prey species (Lima and Bednekoff 1999). This hypothesis further suggests that in areas where the frequency of risk is high and prolonged, prey species have little choice but to decrease anti-predator behaviors (such as vigilance) in order to feed.

Prey species can detect predation risk through auditory, visual, tactile, or olfactory (i.e., smell) stimuli. The first three detection methods indicate a high predator risk situation while the fourth indicates that a predator *is* or *was* present. Olfactory perceived risk to prey may be low or high depending on the intensity of the scent (Kats and Dill 1998). For example, ungulates are known to elicit intense vigilance behaviors or limit duration of feeding in presence of predator odors (Melchiors and Leslie 1985, Kuijper et al. 2013, Chamaillé-Jammes et al. 2014, Wikenros et al. 2015, Sahlén et al. 2016). This behavior is important to consider when trying to understand highly valued and hunted ungulate species such as white-tailed deer (*Odocoileus virginianus*).

Whether or not white-tailed deer increase vigilance behaviors or adjust feeding in presence of predator odors at hunter-provided food sites is an important question for recreational hunters and wildlife managers. Gray wolf (*Canis lupus*) occurrence at these bait sites may increase the perception that there are fewer deer, or it is more difficult to hunt deer where wolves exist if deer exhibit a strong avoidance response to wolf cues at bait sites (Pedersen et al. 2019, Grima et al. 2021). However, the answer to whether wolves make hunting deer more difficult is unknown and thus managers are unable to address these concerns.

Questions regarding predator presence at hunter bait is important to hunters across the US. White-tailed deer hunters in 21 states are allowed to use bait piles to attract deer to a central location. In Michigan, hunters bait deer with either corn or fruits and vegetables. The presence of this bait on the landscape is not only effective in attracting white-tailed deer, but also other non-target species such as raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), turkeys (*Meleagris gallopavo*), and squirrels (*Sciuridae spp*.; Lambert and Demarais 2001, Campbell et al. 2013, Bowman et al. 2015). Wolves, a top predator of deer in the Upper Peninsula (UP) of Michigan, have also been recorded at deer bait sites, sometimes even scent marking the area (Ruid et al. 2009, USFWS: Q and A's about Gray Wolf Biology 2011).

Although deer behavioral change in response to predator odors may occur at some bait sites, the naivety of some deer may mean that they will not react to the presence of an unknown predator scent. For example, in areas where wolves and grizzly bears had been extirpated, moose did not exhibit predator avoidance, while those that had been exposed to both predators did (Berger et al. 2001). This ungulate research suggests that deer in predator-free areas will not display or have diminished behavioral change to predator cues and, consequently, exhibit a different response to the food subsidy at bait sites than deer that have been exposed to predators. This may be particularly true for deer in the Lower Peninsula (LP) of Michigan where wolves have been absent since the mid-1800s (Gray Wolf Recovery in Minnesota, Wisconsin, and Michigan 2011). In contrast, deer in the UP that have been exposed to a re-established wolf population that has been re-established since the mid-2010s may demonstrate more predator avoidance (O'Neil et al. 2017)

We tested the risk allocation hypothesis by examining the perceived effect of wolf presence on naïve versus experienced deer behavior at hunter bait sites. We tested for a difference in response among deer in the UP of Michigan, where deer have coexisted with wolves since the early 1990s and deer in Michigan's LP where wolves have been functionally absent since the mid-1800. We expected that while there would not be a response in naïve deer (LP deer; no wolf population) to the presence of wolf scent (urine), deer that experience wolf predation (UP) would increase their group size, the intensity of vigilance, and occur less often at bait sites with wolf cues (scent). Additionally, we expected that experienced deer would adjust their activity patterns to avoid active-wolf hours, while wolves in the LP (naïve) would not make such adjustments.

METHODS

Study Area. We conducted the study in Michigan's UP and LP from September 21, 2018 to November 10, 2018. The UP study area was entirely contained in the Hiawatha National Forest. Bait sites in the LP study area were all located in Mackinaw State Forest of Michigan, but the study area was interspersed with private agriculture, forestland, and roads. The UP study sites' landcover was evergreen (5 sites), woody wetland (3 sites), grassland (3 sites), deciduous (2 sites), and mixed forest (2 sites) while the LP study sites were deciduous (6 sites), scrub/shrub (4 sites), grassland (3 sites), and evergreen (2 sites; Homer et al. 2015).

While Gray wolves (*Canis lupus*) were eradicated from Michigan in the mid 1900s, they have successfully recolonized and established as the main predator of white-tailed deer (*Odocoileus virginianus*) in the UP (O'Neil et al. 2017, DNR - Wolf Biology and Identification 2018). Wolves in the Lower Peninsula remain functionally absent even though wolves or wolf/coyote hybrids have been detected rarely (Freedman 2019).

Study Design. We established 30 deer bait sites between the two study areas, 15 in the UP and 15 in the LP (Figure 1). In an effort to mimic recreational hunters, sites were selected based on deer hunting desirability such as habitat openness and/or proximity to a deer trail (Peterson 2015). Per hunter suggestion, we established each site at least one km away from the nearest bait site to avoid scent detection by deer between sites (Winke 2012).

We deployed one remote camera (Reconyx Hyperfire series or Cuddeback E) on a tree 4 meters from the center of the bait site. Each camera was programmed to take 5 burst images with no delay between triggers to record the number of deer present, their posture, sex (if possible to determine), and presence/absence of fawn(s). We replaced batteries and SD cards weekly.

We used a six-week BACI design for the experimental treatment of both areas with one week preceding the six-week period to establish a baseline condition of deer visitation to the bait sites. We baited each site with two gallons of corn spread in a 10 by 10-foot square per the Michigan deer baiting regulations MI DNR 2018*b*). For the duration of the study, all sites were baited each week in order to maintain two gallons of corn on the ground and to mimic actual hunter behavior. For the first three weeks

(September 28-October 20), we baited sites, recorded deer occurrence and behavior via remote cameras with no treatments applied. The following three weeks we continued to bait and record deer after treating sites with three scents. In each area, UP and LP, five sites were treated each with wolf urine (experimental treatment), lemon juice (novel scent), and distilled water (control). We assigned site treatment randomly (Wikenros et al. 2015, Atkins et al. 2016). When we treated sites in the field, we visited all control sites in an area first followed by the novel scent sites and finally experimental sites to minimize cross-site spread of scents. We also used different treatment application tools (i.e. pipets and buckets) for each treatment type. At each site, we applied 10 mL of the given treatment (experimental, novel, or control) by dripping it from a pipet onto the bait site. This was done to mimic the scent marking of two wolves (Peters and Mech 1975).

We also recorded predator hiding potential (horizontal cover) at each site to account for site specific differences in the risk of predation. We used a 2 m cover pole with 20 sections, each 10 cm long, to measure predator hiding potential at each site (Kuijper et al. 2014, Severud et al. 2019). From the center of each bait pile, we measured the vertical cover in each cardinal direction. One person held the cover pole 10-meters from the center of the bait pile while the other took a picture of the cover pole from a 1-meter high pole at the center of the bait pile intended to mimic a deer visual height (Severud et al. 2019). We conducted this procedure twice during the study, once at the beginning and once when treatment started, to account for change in hiding potential with loss of leaves later in the year. For each of the 20 (10 cm) sections on the 2 m cover pole, we estimated obscurement to the nearest 25 percent (Severud et al. 2019). We calculated a single mean and standard error value for each site and each measurement time (beginning and middle of study).

Analysis.

Photo analysis. Images were tagged in batches using the DigiKam photo editing software (Niedballa et al. 2016). Each batch was defined by any set of images taken within 5 minutes of the prior image. In each batch, for deer only, we recorded if young were present, labeled all sexes present, and tallied a total count. For individual pictures within batches, we recorded behaviors (i.e. fighting, nursing, etc.). We also labeled batches for different species that were captured at site visits. We analyzed each image for vigilance by indicating the number of deer in the image with their head above their shoulders (Figure 2; Flagel et al. 2016, Schuttler et al. 2017).

Treatment Impact. We explored the impact of different treatments in the two areas (UP and LP) on the number of deer at each site, proportion of group that is vigilant, and the number of visits made to the site. In order to account for the paired nature of our treatment design, we first averaged the variable values for each site individually and calculated a difference in values before and during treatment application. We then averaged across all sites within a given treatment. We also calculated a vigilance intensity metric using equation 1. This metric includes both group vigilance and event time.

$$I = \frac{\sum \frac{v}{g}}{e}$$

(Eq 1)

Where *I* is the vigilance intensity metric for a given event, *v* is the number of deer vigilant in a single image, *g* is the group size in a single image, and *e* is the total time of the event. Hence, vigilance intensity simply standardizes individual vigilance across group sizes and time spent in front of the camera. Similar to the previous analysis, we calculated a difference in vigilance intensity before and after treatment for each treatment type in each area.

Diel activity. To analyze possible temporal variability in the use of bait sites in the UP and LP before and after treatment, we used a nonparametric kernel density estimation procedure (Wang et al. 2015, Prugh et al. 2019). We converted times to radians and used a kernel density estimator to create a probability density distribution for each before or after period (Ridout and Linkie 2009). We calculated the proportion of temporal overlap shared between the two treatment periods for each treatment in each area (Wang et al. 2015). We used a $\hat{\Delta}_4$ with a smoothing parameter of 1 since our sample size for all analyses was greater than 50. We conducted this analysis using the overlap package (Wang et al. 2015, Meredith and Ridout 2018) in R (R Development Core Team 2013).

We applied Watson's U2 statistic with the CircStats package to test for homogeneity between the two samples of interest (i.e. detect a statistically significant shift in the diel pattern before and after treatment; Lund and Agostinelli 2012, Lashley et al. 2018). If deer significantly shifted their temporal pattern between the two treatment periods, we expected to see Watson's U2 statistic greater than the critical value (0.19 for an α value of 0.05) and $P < 0.05$. We expected that, in the UP, we would not see a shift in temporal visitation by deer at the control and lemon treated sites (high $\hat{\Delta}_4$, $U2 \leq 0.19$) but we would see a shift to more nocturnal activity at the wolf scent sites (lower $\hat{\Delta}_4$, U2>0.19; Kohl et al. 2018). In the LP, we expected that we would not see a significant shift in any treatment sites since deer in the LP are ostensibly naïve to wolf predation.

Vegetation Cover analysis. We used generalized linear models to examine the relationship between vigilance intensity (Eq 1) and vegetation cover (i.e. predator hiding potential; Fležar et al. 2019, Prugh et al. 2019). First, we fit models using pooled data from both the UP and LP. We tested additive and interactive models by including before and after treatment application, area (UP or LP), treatment type since all may affect overall vigilance intensity of deer (Eq 1). Next, we fit models using data from the UP and LP, separately. The model variations included before and after treatment application and treatment type. Finally, we fit models to examine the relationship between vigilance intensity (Eq 1) and vegetation cover at each treatment type within both the UP and LP before and after treatment.

RESULTS

We obtained 286,436 images over seven weeks. After removing images taken during the pre-experimental, baseline week and images that did not contain deer, we had 213,264 images for analysis with 85,675 images taken in the LP and 127,589 images taken in the UP.

When we compared the images taken before and after treatment application, we found an increase in group size at wolf urine treated sites in the UP, an increase in the number of visits at both lemon and control treated sites in the UP, and a decrease in the proportion of the group that was vigilant at lemon treated sites in the LP (Figure 3). We also found a decrease in vigilance intensity by deer at wolf urine treated sites in the LP (Figure 3). We did not find a significant change before and after treatments for any other treatment sites in either areas for the four response variables, i.e., the proportion of group that is vigilant, group size, number of visits, and vigilance intensity (Figure 3).

Deer changed their diel activity in both areas and all treatment types from before to after treatment application. We did not detect a consistent directional pattern in the temporal shifts that we observed. However, we did see a noticeable difference between the UP and LP diel patterns where the deer in the UP tended to reduce activity between 6:00 and 18:00 both before and after treatment application while the deer in the LP did not have a consistent inactivity period (Figure 4).

Deer vigilance intensity increased significantly with an increase in vegetation cover in the UP but not in the LP (Figure 5). Though vigilance intensity did not increase with vegetation cover in the LP, the base vigilance intensity (model intercepts) increased significantly after all treatment applications (S1).

DISCUSSION

The recolonization of predators to their native ranges where they have been absent for decades raises questions about the response naïve prey will have once predators return, particularly in prey populations valued and pursued by human hunters. We investigated the difference in naïve and experienced prey responses at food rich hunter bait sites as well as the effects of simulated predator presence at these sites. We did not find a significant effect of wolf scent cue on deer vigilance, number of visits, or vigilance intensity in the UP, but did detect a slight increase in group size, though the difference was not ecologically meaningful (significant increase was less than half of one deer). Though we used a small amount of wolf urine at wolf urine treated sites, similar findings have been documented in populations of deer in the Netherlands and Poland where little evidence was found for effects of predator scents in both predator savvy and predator naive prey populations even when three times the volume of wolf urine is used (van Ginkel et al. 2019*b*). This lack of reaction to wolf scent cues in both areas may also be a result of decreasing response overtime to the wolf urine as it degrades (Bytheway et al. 2013, Kuijper et al. 2013, Wikenros et al. 2015). Introducing cues that indicate immediate wolf proximity, such as howling or visual, will likely produce different results (Liley and Creel 2008, van Ginkel et al. 2019*b*).

We also saw a significant shift in diel patterns at all sites before and after treatment, but there was no consistent pattern to the shift in activity for most treatment sites. However, deer at sites treated with wolf scent in the UP reduced their visitation in the evening hours. This finding is similar to other research that suggests that ungulate prey shift their activity to avoid more risky times (Gehr et al. 2018, Kohl et al. 2018). For example, deer in Minnesota demonstrated a more diurnal pattern when wolf urine was applied to avoid the riskier crepuscular times when wolves tend to hunt (Palmer et al. 2021). It is also noteworthy that before and after treatment application for the UP sites, all show a decrease in activity at bait sites between 6:00 and 18:00, while the LP sites have inconsistent patterns at all sites before and after treatment application. This suggests that deer in the UP are avoiding peak wolf activity/hunting hours regardless of cues at sites while LP deer do not have as large of a inactivity period, likely because they do not have experience with wolf predation (S2; Kohl et al. 2018).

We found that vigilance intensity (Eq 1) does vary based on vegetation cover where wolves are established. Since UP deer are ostensibly familiar with wolf predation, it may be that the increase in vegetation cover, representing more predator hiding potential and more difficult escape routes, causes an increase in deer vigilance intensity regardless of olfactory cues at the site (Wikenros et al. 2015, Dellinger et al. 2019, van Ginkel et al. 2019*a*). Research comparing white-tailed deer and mule deer (*Odocoileus hemionus*) in Oregon's expanding wolf range found that white-tailed deer do not avoid areas with wolves but do favor areas with less dense vegetation that facilitates an easy escape since they rely on flight and early detection of predators (Dellinger et al. 2019). Alternatively, mule deer avoided areas where wolves were present altogether since they rely on a stotting gait that is advantageous in uneven areas with more obstacles. Our findings further highlight the importance of considering prey escape strategies and habitat characteristics along with direct predation cues (Wikenros et al. 2015, Dellinger et al. 2019).

Though vegetation cover did not have a significant effect at LP sites, deer at wolf urine treated sites did demonstrate higher baseline vigilance intensity after treatment was applied though it did not vary across vegetation cover. This would appear to show that naïve deer demonstrate an innate fear of wolves (Chamaillé-Jammes et al. 2014). However, when the novel scent (lemon) and control sites were assessed in the same context, we saw a similar pattern indicating that something other than predator scent is affecting starting vigilance later in the study. Since the second half of the study was conducted during archery hunting season, this shift in vigilance may indicate a response to increased human presence (Benhaiem et al. 2008). Research in Poland found that red deer (*Cervus elaphus*) demonstrated heightened vigilance during hunting season at times hunters were likely pursuing them (Proudman et al. 2020). This vigilance shift may also be related to an increase in mating behavior (Schuttler et al. 2017). We did not see the same pattern in the UP wolf urine treated sites, however (S1).

Some of our findings support the predator risk allocation hypothesis by showing a shift in activity to a less risky feeding time for prey that experience a pause in predation pressure (Lima and Bednekoff 1999, Kohl et al. 2018). This hypothesis may also explain the lack of difference in vigilance detected in the UP deer population in relation to the wolf urine treatment. Since this population is under a more consistent predation pressure from wolves and frequent wolf cues, they may demonstrate a lack of vigilance especially at food rich site such as hunter bait sites, in order to take advantage of the food source as quickly as possible. They are also likely, as we observed, to show more vigilance intensity in areas with higher predation potential, such as high vegetation cover (Dellinger et al. 2019).

Finally, this study adds more evidence in highlighting the importance of considering both spatial and temporal factors when understanding predator effects on experienced versus naïve prey (Moll et al. 2017, Kohl et al. 2018, Dellinger et al. 2019, Gaynor et al. 2019). Past research has suggested that naïve prey do not maintain the innate ability to react to predator olfactory cues but do have the ability to learn and adjust to predators within one generation (Berger et al. 2001, Steindler et al. 2020). Though olfactory cues did not have a significant effect on most variables we investigated, we do see a strong effect depending on habitat.

The recreational hunting tradition of baiting is controversial inside and outside the hunting community. This method increases the opportunity for a shot and more immediate kill but also creates a predictable food source that concentrates deer and deer scent, which in turn attracts wolves. As large predators continue to recolonize their former ranges, they will inevitably come into contact with human hunters. This research on the effect of predator recolonization on the hunting of naïve and experienced prey can shed light on the impact a predator has on a predator savvy and predator naïve prey population as it relates to hunting.

ACKNOWLEDGEMENTS

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. 00039218. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. This research was also supported by grants from the National Science Foundation to J. K. Bump (NSF ID#1545611, NSF ID#1556676). We thank M. Dean, K. Rajski, and A. Schubel for field assistance.

CHAPTER 4

Recursion patterns of wolves in relation to bear hunter bait sites in the Greater Voyagers Ecosystem, Minnesota, USA

SYNOPSIS

Considering the use of anthropogenic food sources by top carnivore species is important when studying consumers in otherwise natural systems. Human food used to bait black bear (*Ursus americanus*) by hunters is one such source commonly visited by nontarget species including gray wolves (*Canis lupus*). To better understand the recursion behavior of wolves in relation to bear hunter bait sites, we calculated revisitation to homesites, bear bait sites, and other cluster sites (e.g. kills, bed sites) for 6 GPS collared wolves from mid-July to mid-October for 2017, 2018, and 2019 in the Greater Voyagers Ecosystem, Minnesota, USA. Cluster site types were confirmed in the field. Revisitations, time of visitations, and time spent at sites were calculated by counting the number of times a wolf entered, observing entrance times, and calculating how long wolves stayed at a bait or within a homesite radius respectively. As we predicted, wolves revisited bait sites more than other site types, but not more than homesites. Wolves also spent more time at homesites than all other site types. While wolves spent more time at bait sites during the bait only, pre-hunt period, they reduced their time spent at bait sites and increased their time spent at other sites types during the bear hunting season. Wolves also shifted bait site visits to a more nocturnal pattern during the bear hunting season. This research highlights the need to incorporate hunter provided foods into food web analysis. Though

limited in wolf sample size, it indicates a pattern of wolf use of bear hunter bait that should be assessed further.

INTRODUCTION

Understanding the relationship of predators and their prey is a central theme in ecology and essential to the understanding of ecosystem function. Often predator-prey relationships are more complicated than consumptive effects and include non-consumptive responses (Wikenros et al. 2015, Gehr et al. 2018, Kohl et al. 2018). For example, consistent with the predator sensitive foraging hypothesis, European roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) have been shown to reduce visitation to feeding sites when presented with fresh Eurasian lynx (*lynx lynx*) scat, which in turn reduces time that they are able to feed (Anson et al. 2013, Wikenros et al. 2015). Additionally, the predator stress hypothesis posits that predators can elevate specific hormones in prey that increase vigilance but also negatively affect fecundity and individual health (Boonstra et al. 1998, Clinchy et al. 2004, Anson et al. 2013). All of these effects are altered by the predator hunting mode, habitat cover options, and density and diversity of both predators and prey in ecosystems (Wikenros et al. 2015, Kohl et al. 2018).

Since real world systems are often more complex than a simple one predator, one prey scenario, making inferences about a predator-prey system by simply accounting for one predator and one prey will often mask the true ecological processes at play. When more prey species are available, prey switching can take place (Garrott et al. 2007). For example, gray wolves (*Canis lupus*) in Prince Albert National Park, Saskatchewan practiced prey switching between larger ungulates such as plains bison (*Bison bison bison*), moose(*Alces alces*), and elk (*Cervus canadensis*) in the summer and the smaller white-tailed deer (*Odocoileus virginianus*) in the winter (Shave et al. 2020). Prey switching can result in a more stable predator population since a second prey species can fill gaps when the first prey species is at low densities or is more difficult to hunt (Davis 1957). Additionally, the subsidized and more stable predator populations can result in apparent competition between prey species causing potential issues for rare or small prey populations (Holt et al. 1994, Gibson 2006, Latham et al. 2013, Wittmer et al. 2013).

Anthropogenic food inputs also add another layer of complexity to the understanding of foraging and predator-prey interactions. They can often mimic an alternative prey source for predators, acting as a buffer when natural (i.e. not human provided) foraging options are limited (Baruch-Mordo et al. 2014). Similar to natural prey, anthropogenic food subsidies can positively impact the survival and fecundity of consumers, which in turn can have a negative impact on alternative prey species (Robb et al. 2008, Oro et al. 2013, Plaza and Lambertucci 2017). Alternatively, anthropogenic food subsidies can take pressure off alternative prey species (Ciucci et al. 2020). Additionally, anthropogenic food can have negative impacts on some consumer species. For example, hibernation, a process shown to slow cellular aging in black bear (*Ursus americanus*), is reduced in individuals that regularly use human provided foods (Kirby et al. 2019). This added complexity of anthropogenic food subsidies in otherwise complex natural systems highlights the importance of understanding different anthropogenic inputs and their impacts on consumer species.

One common anthropogenic subsidy is hunter provided food or bait, particularly black bear hunter bait. Black bear baiting is a common practice throughout the United states and Canada, occurring in 11 states and 10 provinces. Bear bait often consist of high calorie foods such as baked goods, bacon, syrups, and grease (Kirby et al. 2017). Because bait placement is regulated by hunting season, the occurrence of bait on the landscape is predictable in time, thus creating the possibility for species to remember this input and change their space use behavior seasonally (Vercauteren and Hygnstrom 1998, Darimont and Reimchen 2002, Noser and Byrne 2007). Additionally, hunters often reuse the same bait site year to year making the subsidy predictable spatially as well. Recent research has shown high use of bear hunter bait sites by non-target species (Candler et al. 2019). However, the extent to which some species may alter their behavior and change their space use in response to bear hunter bait sites is unknown.

To better understand the implication of the bait hunters place for black bears on a predator-prey system, we first have to understand if, when, and how often consumers use the alternative anthropogenic food source. To begin to understand this, we investigated one non-target species, the grey wolf, based on field observations indicating that wolves visited bait sites. The goal of this study was to investigate the revisitation, or recursion, of wolves to known bait sites in Northern Minnesota. We assessed recursions of GPS-collared wolves to known bear bait sites and homesites for a month prior to baiting (mid-July –August) and during baiting (September 1 – mid-October). We expected that wolves would revisit black bear hunter bait sites over the duration of baiting and more often than other site types (e.g., kill sites), as sites are regularly replenished, but that revisitation would not be as regular as homesite revisitation. Additionally, we expected that wolves would spend the most amount of time at homesites, but that time spent at homesites would decrease during hunting season. We also expected that wolves would spend more time at bait sites than other site types but that they would decrease time spent at bait sites during hunting season (September 1 through mid-October) when compared to a bait only period (mid-August through August 31). Finally, we expected that wolves would revisit bait sites primarily at night to avoid interactions with humans that are likely to visit the same site.

METHODS

Study Area. This study was conducted in collaboration with the Greater Voyagers Wolf Project, which takes place in the Greater Voyagers Ecosystem (GVE). The GVE contains Voyagers National Park and as well as a mix of national, state, and commercial forests (Gable et al. 2020). The GVE is dominated by dense forest and several lakes and wetlands (Figure 1; Gable et al. 2021). Wolf populations in the GVE has sustained a dense wolf population (35–45 wolves/km^2) for more than 30 year (Gable et al. 2016). Wolves in this study area primary feed on white-tailed deer, snowshoe hare (Lepus americanus), and beavers (Castor canadensis; Thomas D. Gable et al. 2018*a*).

The bear and wolf range in Minnesota overlap substantially across Minnesota (Figure 1). Bear baiting is permitted throughout the entire black bear range with the exception of the Boundary Waters Canoe Area Wilderness making bear bait available across nearly all of the wolf range in Minnesota.

Minnesota bear hunters are permitted to establish three bear bait sites at a time during the baiting and hunting/baiting season (mid-August–August 31 and September 1–mid-October respectively; Minnesota Department of Natural Resources [MN DNR] 2017, 2018, 2019) Hunters are allowed to use anything, including candy, pastries, and cured pork, but excluding bones and animal carcasses, in any amount to attract black bears to their desired hunting location (MN DNR 2020).

Data collection. Between 2017 and 2019, wolves in this analysis were captured using foothold traps and cable restraints. They were fitted them with 20-min-fix-interval GPS collars (Gable et al. 2021). Researchers searched clusters of GPS locations from the collared wolves from April–November to identify predation events but also recorded other reasons for clusters, such as visits to a bear hunter bait site (Gable et al. 2021). A cluster was defined as ≥2 consecutive locations within a 200-m radius (Gable et al. 2018*c*). We used 6 collared wolves from 4 different packs in this analysis, 2 females and 4 males.

We subset the GPS locations to include only locations recorded one month prior to the start of bear baiting through the bear baiting and hunting periods. These dates varied slightly among years but were roughly mid-July through mid-October. After sub-setting the data, remaining locations were matched with searched cluster information to determine site type (homesite, bait site, and other visits) as well as dates that those sites were used. For example, locations were not defined as bait sites unless they were visited after the start of the legal baiting date for each year. Similarly, field crews confirmed dates that homesites were abandoned so locations were reassigned site type (e.g. bait or other) designation if the location occurred after the abandonment date. Homesites were defined as the den site or rendezvous site associated with each wolf. We defined any point within 200 meters of a homesite as being associated with that homesite since most homesites in the GVE were generally <15ha (Gable et al. 2018*b*). Points that were within 200m of located bait sites were also considered visits to that bait site.

Analysis. For this analysis, we combined all 6 wolves into one dataset. We used the recuse package in R (R Development Core Team 2013) to calculate revisitation to homesites, bear hunter bait sites, and other sites (including bed sites, travel routes, and kill or scavenging sites; Bracis et al. 2018). Revisitations are calculated by counting the number of times an animal occurs within a defined circle (200-m radius) around a GPS location. We removed any sites that were revisited fewer than 5 times to account for chance revisits (e.g., walking the same trail). Using the same R package, we calculated total time spent at each site type (homes site, bait sites, both homesite and bait site, and other) by summing the time spent within the site area for all visits (Bracis et al. 2018).

We used student's t-test to test for a difference between the number of revisits by site type (bait vs. homesite and bait site vs. other sites) for the whole study period (mid-July through mid-October). We also used students t-test to test for a difference between the number of revisits for bait sites in the bait only period and the bait/hunting periods. Using the same site type comparisons, we used the student's t-test to compare time spent at each site.

We compared the diel activity patterns between homesite and bait sites as well as between bait sites and other site types for the overall study period (mid-July through mid-October). We also compared the diel activity patterns for the bait (Mid-August through August 31) and hunt (September 1 through mid-October) periods for bait sites and homesites. We looked at these comparisons using a nonparametric kernel density estimation procedure (Wang et al. 2015, Prugh et al. 2019). Using the overlap package in R (R Development Core Team 2013), we converted times to radians and used a kernel density estimator to create a probability density distribution for each site type or study period (Ridout and Linkie 2009, Wang et al. 2015, Meredith and Ridout 2018). We calculated the proportion of temporal overlap shared between each of the two comparisons and used a $\hat{\Delta}_4$ overlap estimator with a smoothing parameter of 1 since our sample size for all analyses was greater than 50 (Ridout and Linkie 2009, Meredith and Ridout 2018).

To test for a significant difference (i.e. not homogeneity between each of the two comparisons) we used the Watson's U2 statistic with the CircStats package (Lund and Agostinelli 2012, Lashley et al. 2018). If wolves shifted their diel activity at either of the two site types or during the two time periods, we expected to see Watson's U2 statistic greater than the critical value (0.19 for an α value of 0.05) and $P < 0.05$.

RESULTS

We found a significant difference between the number of revisits at bait vs. homesites and bait sites vs other sites throughout the entire study period (Table 1; Figure 2). Homesite revisits reduced over time as wolves abandoned den and rendezvous sites

(Figure 3). Alternatively, revisits to bait sites and other site types did not change over time (Figure 3).

Though bait site revisits did not change between the baiting only and hunting/baiting periods, the time that wolves spent at bait sites decreased during the hunting/baiting periods (Table 1). This was also the case for homesites. Alternatively, other site types had an increase in time spent by wolves (Figure 3).

We found a significant difference for all diel pattern comparisons we analyzed. Though we found a significant difference between bait site and other site type over the whole study period, it appears that wolves visit both site types throughout the day (Figure 4 B). Alternatively, wolves tended to visit homesite more often during the day (Figure 4 A). During the bait only period, wolves tended to visit bait sites throughout the day but reduced visitation around 18:00. During the hunting season, wolves tended to reduce bait site visitation during the day and visit more often at night (Figure 4 C). Though our other analysis showed that wolves reduced revisitation to homesites as the bear hunting season progresses, when they did visit homesites during the bait only period, their visitation were higher during the day, but visitation occurred throughout the full 24-hours. Alternatively, during the hunting and baiting period, wolves visited homesites exclusively between 12:00 and 18:00 (Figure 4 D).

DISCUSSION

Our results indicate that wolves are indeed finding and revisiting black bear hunter bait sites in the GVE. Since bear hunters are regularly replenishing bait sites, wolves are likely returning to these sites often to take advantage of the predictable food whereas other sites (e.g. kill sites) are not as predictable and therefore are ostensibly revisited less often. Wolves will take advantage of, and change their space use, in response to anthropogenic resources within their home ranges (Carmichael et al. 2001, Alexander et al. 2006). Opportunistic species, such as wolves, will even reduce the size of their home range in response to anthropogenic food source (Bino et al. 2010, Šálek et al. 2015, Petroelje et al. 2019)

The amount of time spent at locations also varied among site types and between baiting and hunting periods. Since hunters likely only visited bait sites during the baiting period to replenish their sites, wolves may not have been deterred by human presence as consistently. In contrast, during the hunting period, human hunters are likely spending more time actively hunting at or close to their bait sites. Hunter bait is not only revisited multiple times throughout the hunting season, but often year to year (Zedrosser et al. 2013). This makes these sites a predictable, but risky food source. This human presence may be the reason we detected a reduction in time spent by wolves at bear bait sites during hunting season (Theuerkauf et al. 2003*a*, Kusak et al. 2005).

Another possibility is that wolves are spending less time at bear bait sites during hunting season because other, less risky food becomes available and is a preferred alternative. For example, when a hunter harvests a bear or deer in the GVE, they often field dress the animal by removing the internal organs, or offal. This cools the animal down quickly and prevents the meat from spoiling. This offal is often left afield and made available to scavengers such as wolves. Though closely associated with humans, this highly nutritious food source is often quickly found and consumed by wolves and other scavengers (Ruth et al. 2003, Wilmers et al. 2003, Lafferty et al. 2016, Gable et al. 2018*a*). Offal sites are very unlikely to be revisited by hunters, making them less risky for wolves to spend time when compared to bear bait sites that are revisited often throughout the season and years. This may also explain the increase in time spent at other site types during hunting season.

Although it may be that wolves are “prey switching” from bait sites to offal, many of the bear offal piles are likely located at, or within the 200-meter halo, of the bear bait pile. Time spent at these offal locations would appear as revisitations to the associated bait sites in our analysis, not other site types. In contrast, deer offal left from archery hunters is likely spatially separate from bear bait sites and would register as other site types in our analysis. However, time spent at deer offal sites is likely to be limited as they are small and often discovered and consumed quickly by multiple scavengers (Jennelle et al. 2009, Gomo et al. 2017). Including location data from additional wolves over more years will likely bring more clarity to the decrease in time spent at bait sites and an increase in time spent at other sites during the bear hunting season.

While we did detect a shift to a more nocturnal visitation pattern of wolves to bear bait sites during the hunting season, contrary to our expectations, we did not detect this same pattern during the bait only period. Other research has shown that wolves tend to be more active in the dawn and dusk hours when their prey is also active (Theuerkauf et al. 2003*b*, Kohl et al. 2018). However, if wolves are consuming a food source that is stationary and available throughout the day, their diel scavenging pattern may not have crepuscular peaks. Again, because hunters are not actively hunting their bait sites during the bait only period, the daytime hours may be relatively less risky for wolves to visit whereas the presence of hunters at bear bait sites during the hunting season is likely to influence wolf activity to nocturnal hours (Chavez and Gese 2006).

Though we detected recursion patterns of wolves to bait sites, including additional wolves in future analyses will enable us to investigate more detailed questions about wolf movement ecology in the context of bear baiting. Further research with additional wolves could shed light on behavioral differences between sexes or potential bear bait pack specialization (Manlick and Newsome 2021). Wolf packs have been documented specializing on bison, salmon, and beavers (Darimont and Reimchen 2002, MacNulty et al. 2014, Gable and Windels 2018). This specialization may impact things such as wolf pack movement patterns. For example, packs of wolves in British Columbia that specialize on caribou (*Rangifer tarandus*) migrate with the herd whereas other packs that specialize on moose (*Alces alces*) are territorial (Carmichael et al. 2001). Additionally, pack size is strongly corelated with prey risk resulting in smaller packs associated with less risky prey (Barber-Meyer et al. 2016). This specialization will also certainly affect the prey being targeted as well as those that escape predation. As humans continue to expand, they may be creating more dietary niches and increased specialization within species (Manlick and Newsome 2021). Understanding if there is a difference in bear bait specialization among packs in the GVE will help us better understand how hunter bait affects prey and how that impact may among packs.

In addition to more wolves, a more detailed understanding of homesites shape and size could bring the comparison of homesite vs. bait site revisitation into greater focus. In this analysis, we grouped den site and rendezvous site into one category. Additionally, the shape that we used to define homesites was a 200-meter circle, which is almost certainly an approximation of the actual area that was used by wolves. Both of these homesite criteria are oversimplifications of homesite use and may be underestimating or overestimating wolf use of the sites.

Finally, future analysis should explore wolf recursion behavior throughout the year rather than time periods in the late summer and early fall only. Employing a periodicity analysis such as a Fourier and wavelet analyses can better show when select areas (i.e., bear bait sites) are being used throughout the year and with more temporal detail (Riotte-Lambert et al. 2013). These analyses would enable us to investigate weekly, daily, or even hourly changes to wolf recursion behavior rather than look at collar data in large blocks of time (i.e., bait vs. hunting periods).

With additional data and analyses highlighted above, we can start to understand how this anthropogenic food source may be impacting the food web. The late summer and early fall in northern Minnesota are typically the most difficult time for wolves to capture prey such as white-tailed deer, since deer are at their most fit (Nelson and Mech 1986). The addition of anthropogenic resources, such as black bear hunter bait, may buffer wolves from lower survival that would take place in the absence of humans (Baruch-Mordo et al. 2014). If bear bait is indeed positively affecting wolf survival, prey species may see a negative impact after bait is once again absent and wolves turn to an alternative prey source. (Robb et al. 2008, Oro et al. 2013, Plaza and Lambertucci 2017).

Anthropogenic food subsidies are a known attractant to non-target species and can have both positive and negative impacts on individual consumer species as well as the food web (Rodewald et al. 2011, Gutgesell et al. 2020, Brunk et al. 2021). Leaving anthropogenic food resources, such as hunter bait, out of food web analysis leaves out an important piece of the puzzle. This research has confirmed the continual use of black bear hunter bait by wolves and demonstrates the impact it has on wolf space use and movement. Future research should consider similar seasonal anthropogenic foods into consumer research.

ACKNOWLEDGEMENTS

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. 00039218. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. This research was also supported by grants from the National Science Foundation to J. K. Bump (NSF ID#1545611, NSF ID#1556676). We thank T. Gable and the Voyageurs Wolf Project for sharing wolf collar data and S. Rettler for bear bait location data. Thank you also to S. Barber-Meyer and D. Mech for question development and additional data that can be used to continue this analysis.

ILLUSTRATIONS

Chapter 1

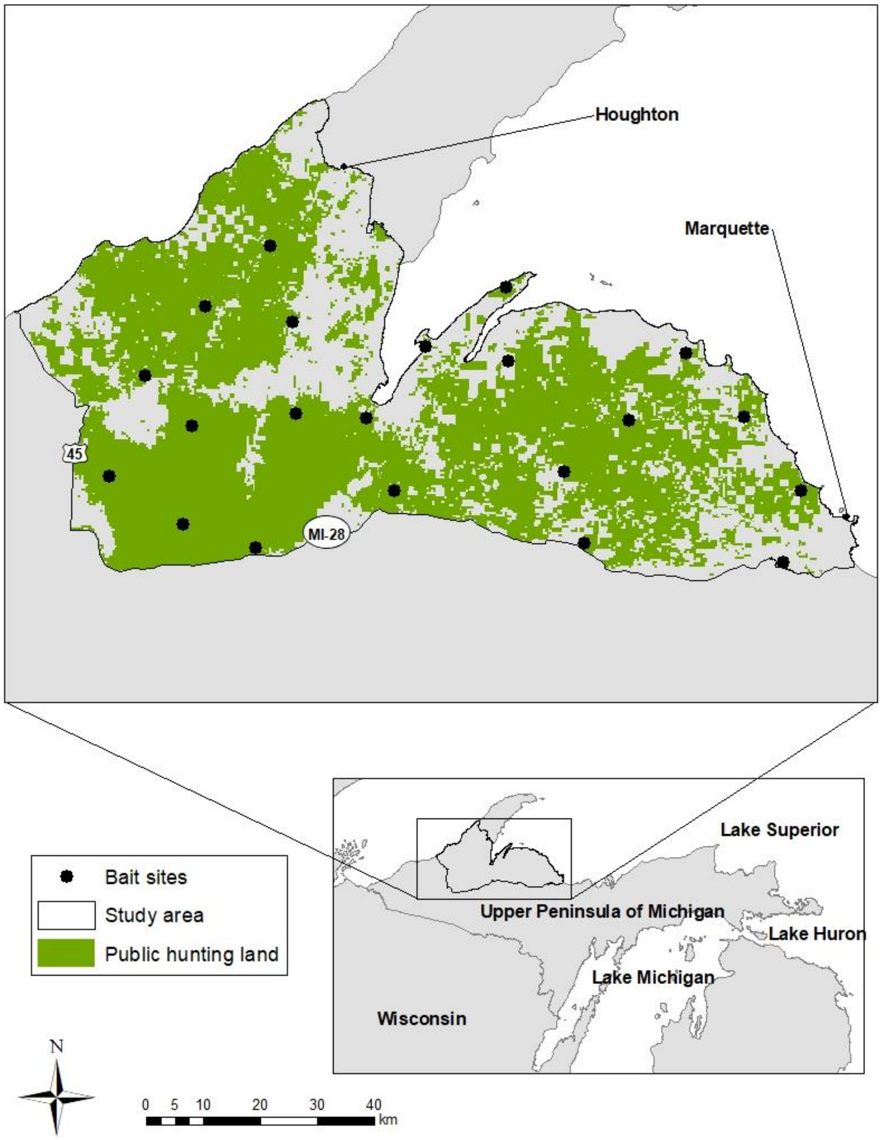


Figure 1. Locations of 21 black bear (Ursus americanus) bait sites with camera traps August to October 2016 in the western Upper Peninsula of Michigan, USA. The Baraga hunting unit includes land east of U.S. Hwy 45 and north of Michigan State Hwy 28.

Table 1. Camera-trap detections of all species at bear (*Ursus americanus*) hunter bait sites, Western Upper Peninsula, MI, USA, August–October 2016. Total number of detections (column 2) are the number of animals in photographs (many images had multiple individuals) taken throughout the study with duplicate photos removed. Percent (column 3) is the percent of total detections attributed to each species or taxonomic group.

Species and Taxonomic Groups	**Total Number of Detections**	**Percent**
Northern raccoon (*Procyon lotor*)*	8,427	69.82%
American black bear (*Ursus americanus*)*	2,185	18.10%
Mustelids (Mustelidae)*	768	6.36%
Striped skunk (*Mephitis mephitis*)*	215	1.78%
Unidentified small mammals	129	1.07%
Snowshoe hare (*Lepus americanus*)	114	0.94%
Red fox (*Vulpes vulpes*)*	92	0.76%
White-tailed deer (*Odocoileus virginianus*)	45	0.37%
Squirrel (*Sciurus* spp.)	29	0.24%
Coyote (*Canis latrans*)*	22	0.18%
Chipmunk (*Tamias* spp.)	11	0.09%
Gray wolf (*Canis lupus*)*	9	0.07%
Unidentified anuran	6	0.05%
Moose (*Alces alces*)	6	0.05%
Flying squirrel (*Glaucomys* spp.)	5	0.04%

Bobcat (*Lynx rufus*)*	3	0.02%
Common raven (*Corvus corax*)	2	0.02%
Wild turkey (*Meleagris gallopavo*)	1	0.01%
Turkey vulture (*Cathartes aura*)	1	0.01%
Total	**12,070**	

* Carnivore species

Table 2. Mean difference in daily number of detections before hunting season vs. during hunting season for taxa in the Western Upper Peninsula, MI, USA, August–October 2016 observed at black bear (*Ursus americanus*) hunter bait sites. Differences between the period before hunting and the period during hunting were significant if the 95% confidence interval did not include 0.

Taxon	**Mean difference**	**95% confidence interval**
All Species	−0.08	−0.17 to 0.01
Carnivores	−0.40	−0.52 to −0.29
Black bears	−1.33	−1.44 to −1.23
Mustelids	0.33	0.29 to 0.37
Raccoon	1.91	1.61 to 2.21
Skunk	0.38	0.36 to 0.40
Red fox	0.07	0.04 to 0.09
Coyote	0.04	0.03 to 0.04

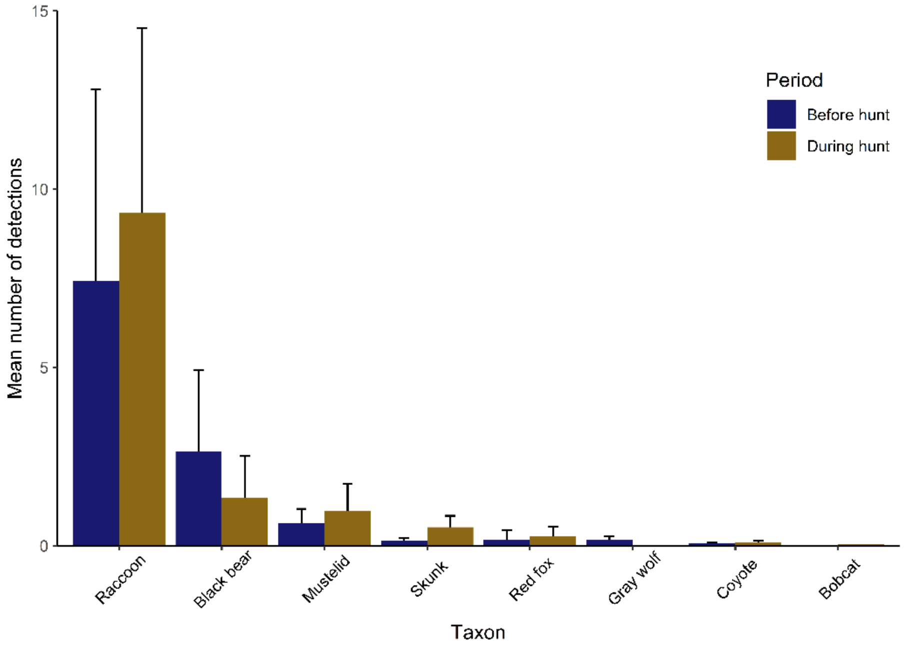


Figure 2. Mean (+ SD) daily number of camera-trap detections of taxa at black bear (*Ursus americanus*) hunter bait sites, Western Upper Peninsula of Michigan, USA, August–October 2016.

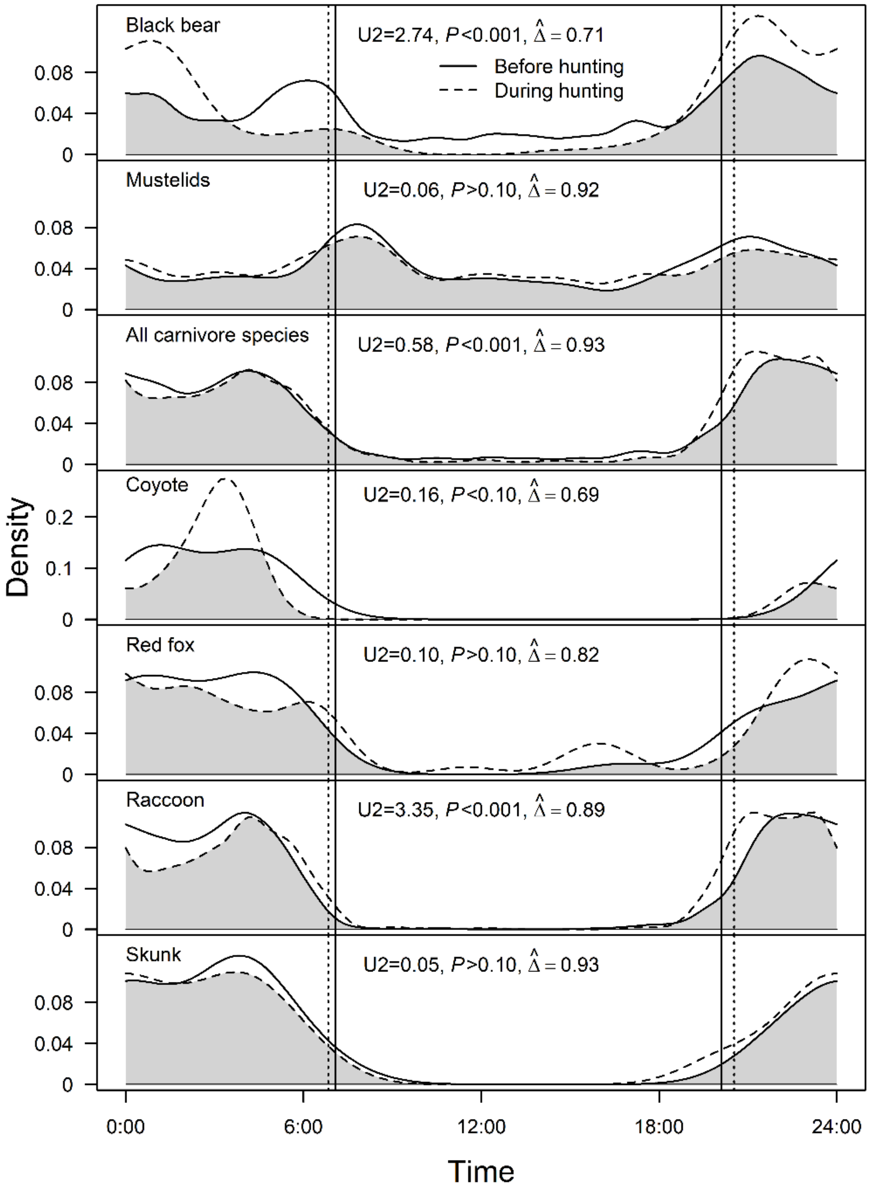


Figure 3. Temporal overlap for indicated species at black bear (*Ursus americanus*) hunter bait sites before hunting (solid line; August 10-September 9) and during hunting (dashed line; September 10–24) in the Western Upper Peninsula of Michigan, USA. Shaded area indicates the temporal overlap between the 2 time periods. Vertical lines

indicate start (~06:50 and ~7:04) and end (~20:32 and ~20:07) of shooting hours for September 10, 2016 (dotted) and September 24, 2016 (solid) respectively. The reported U2 statistic is compared with the test statistic U2 = 0.19.

Figure 4. Camera-trap detections of a black bear (*Ursus americanus*; A), a fisher (*Martes pennanti*, B), 5 raccoons (*Procyon lotor*, C), 2 bobcats (*Lynx rufus*, D) at black bear hunter bait sites Western Upper Peninsula, MI, USA, August–October 2016.

Figure 5. Camera-trap detections of red fox (*Vulpes vulpes*) and raccoons (*Procyon lotor)* demonstrating aggressive behavior (A) and sharing food (B), striped skunk (*Mephitis mephitis*) and raccoon displaying defensive behavior (C), and American marten (*Martes americana*), and raccoon (D) at black bear (*Ursus americanus*) hunter bait sites Western Upper Peninsula, MI, USA, August–October 2016.

Chapter 2

Table 1. Comparison of Species Recorded at Observational and Hunter Site. Total and proportion of pseudo-bear bait site cameras and black bear hunters who recorded each species in the western Upper Peninsula, MI, USA, August–October 2016 at black bear (*Ursus americanus*) hunter bait sites. The confidence interval is asymmetrical since the distribution of the odds ratio is from 0 to infinity. Significant differences between survey results and pseudo-bear bait site observations are indicated with an asterisk ($\alpha = 0.05$).

Taxonomic group	pseudo-bear bait sites	Survey	Observational proportion	Survey proportion	Odds ratio	95% confidence interval	***P***
Black bear	20	200	0.95	0.90	0.48	0.01–3.31	0.703
Coyote	3	51	0.14	0.23	1.80	0.49–9.89	0.426
White-tailed deer	6	68	0.29	0.31	1.11	0.39–3.65	1.000
Bobcat	1	5	0.05	0.02	0.46	0.05–22.98	0.423
Gray wolf	1	71	0.05	0.32	9.41	1.44–397.14	0.006*
Mustelid	15	96	0.71	0.43	0.31	0.09–0.88	0.020*
Total	21	221					

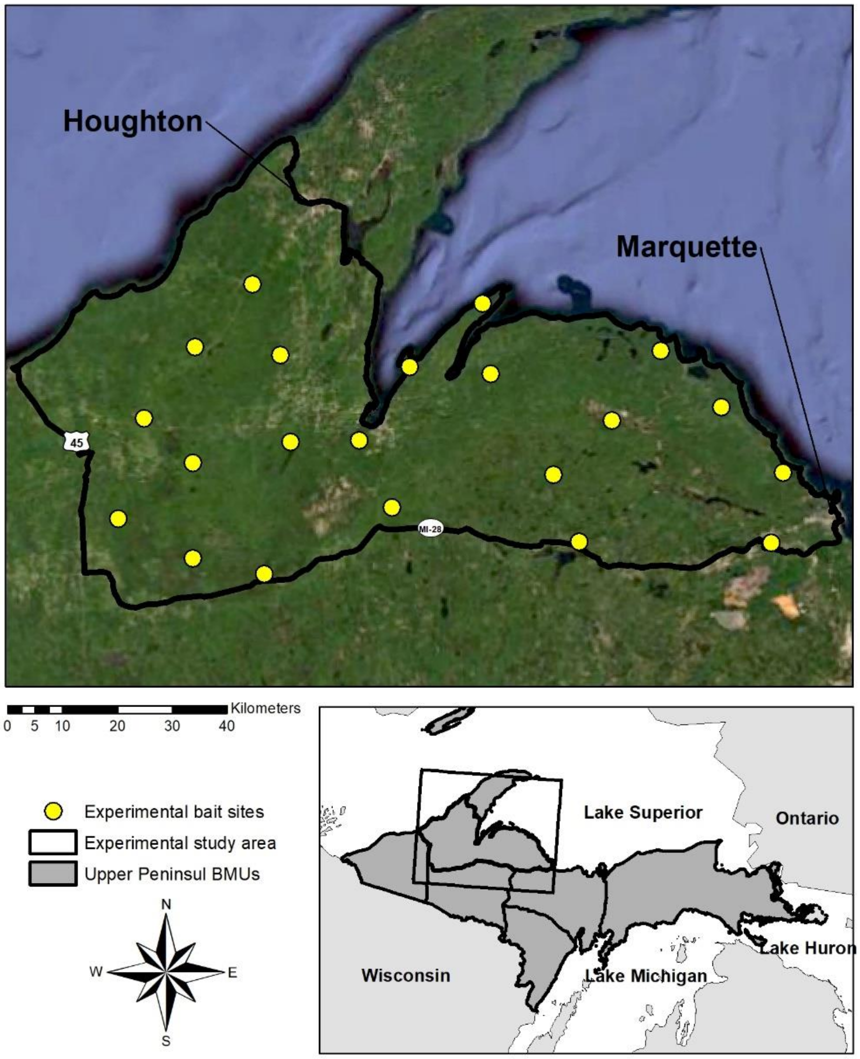


Figure 1. Pseudo-bear Bait Site Locations. Locations of 21 black bear (*Ursus americanus*) pseudo-bear bait sites with remote cameras deployed August–October 2016 in the Western Upper Peninsula (UP) of Michigan, USA. The study site was located in the Baraga hunting unit, which includes land east of US highway 45 and north of Michigan State Highway 28. The bottom map indicates bear management units in the UP.

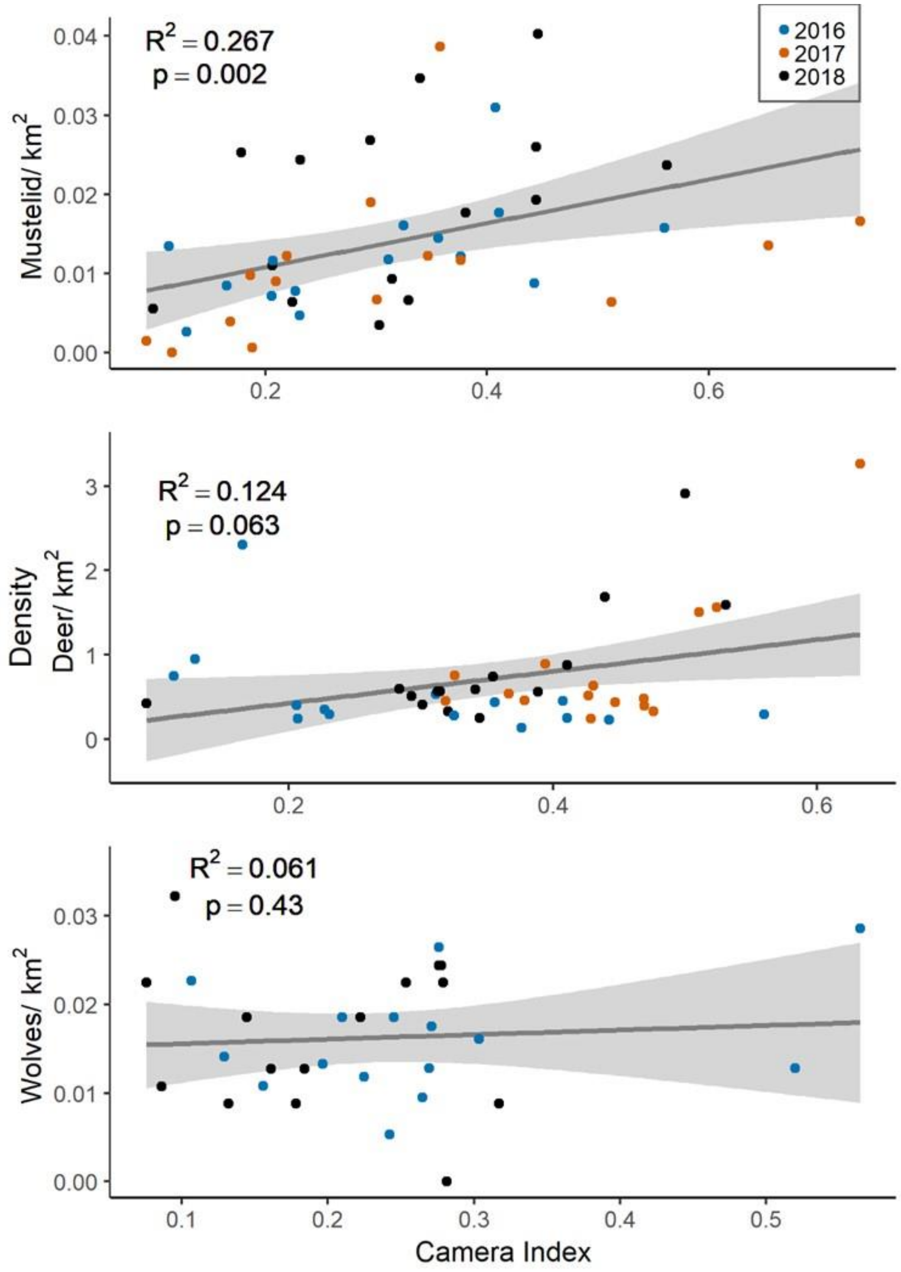


Figure 2. Camera Index and Michigan Department of Natural Resources Harvest Reports. Relationship between camera index and mustelid (Mustelidae; top graph), white-tailed deer (*Odocoileus virginianus*; middle graph), and gray wolf (*Canis lupus*; bottom graph) density indices in the Upper Peninsula of Michigan, USA August–

September 2016 (blue), 2017 (orange), and 2018 (black). Each dot represents one county in one year. Dotted lines and model statistics represent the simple linear model that includes bear hunter effort as an explanatory variable.

Chapter 3

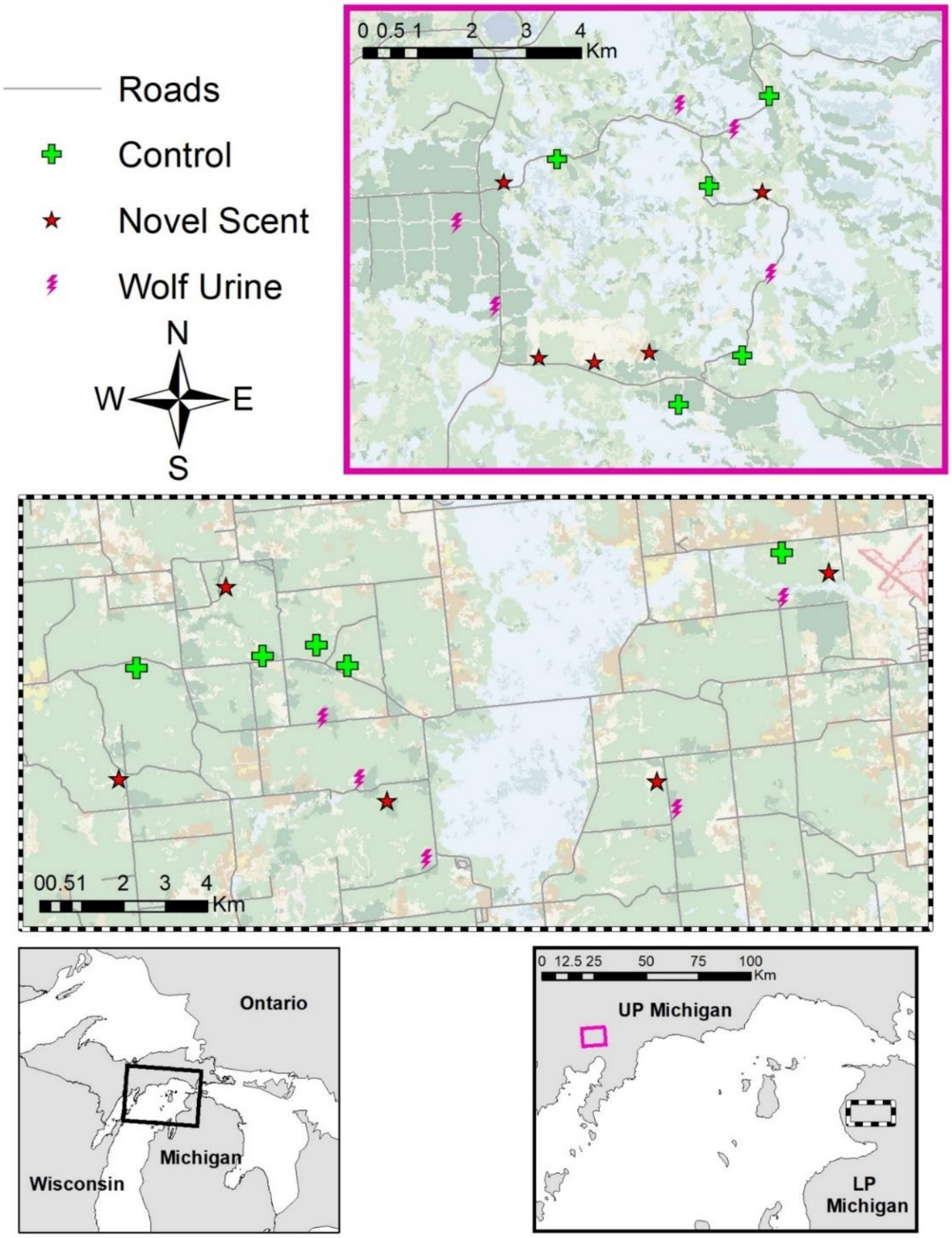


Figure 1. Location of 30 experimental deer bait sites with camera traps September to November 2018 in Michigan, USA. The top inset map (sold magenta line) indicates the 15 sites in the Upper Peninsula and the lower inset map (black dashed line) indicates the

15 sites in the Lower Peninsula. The different symbols indicate the different treatments assigned to each site.

Figure 2. Camera-trap detections of white-tailed deer (*Odocoileus virginianus*) at simulated deer hunter bait sits. These images indicate vigilance (A) and non-vigilance (B) behavior.

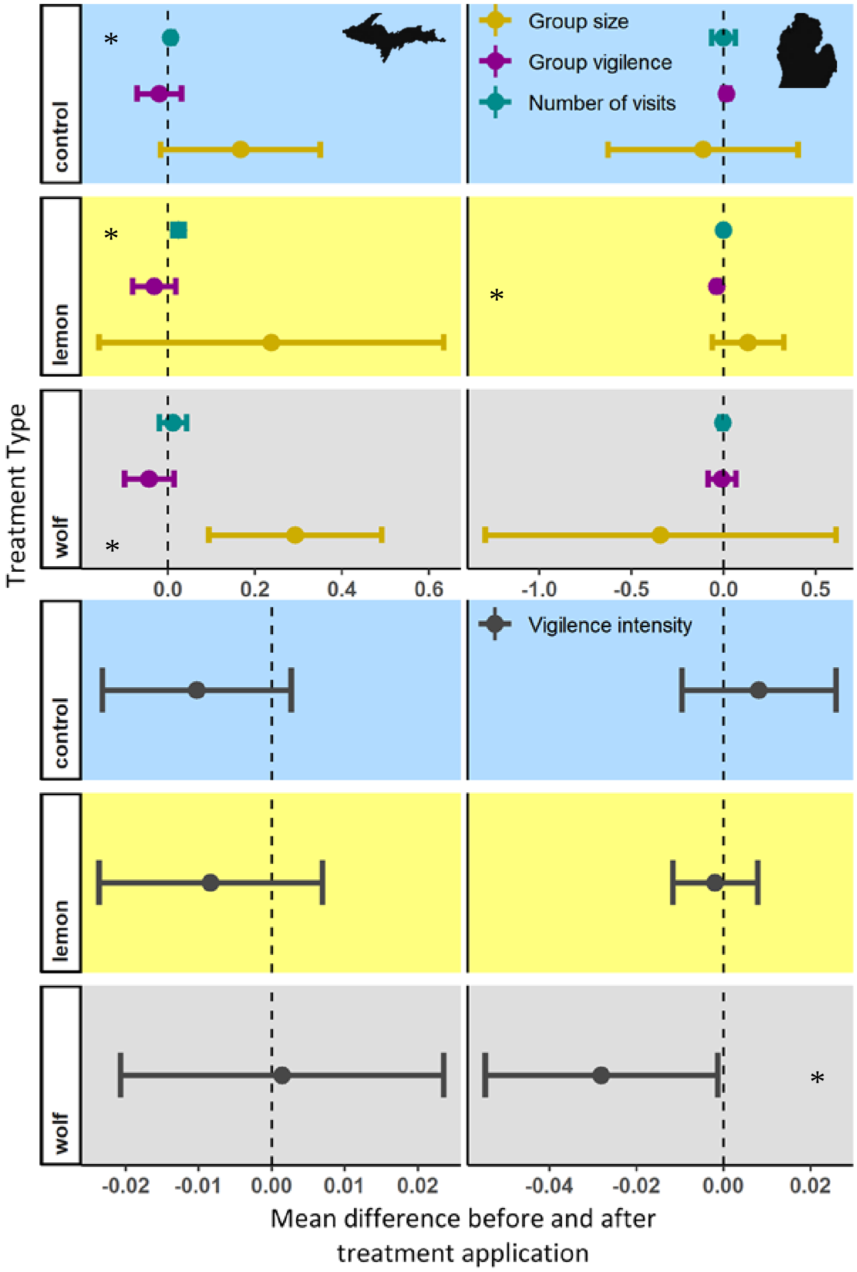


Figure 3. Difference in group size, group vigilance, number in the group that is vigilant, and vigilance intensity (sum of proportion of group vigilant in each event divided by total time of event) before treatment period and during treatment period. Symbols indicate the mean of sites and error bars indicate the 95% confidence interval. Blue shading

represents the control sites (water), yellow indicates the novel scent sites (lemon), and gray indicates the wolf urine treated sites. Asterix indicates $*p < 0.05$.

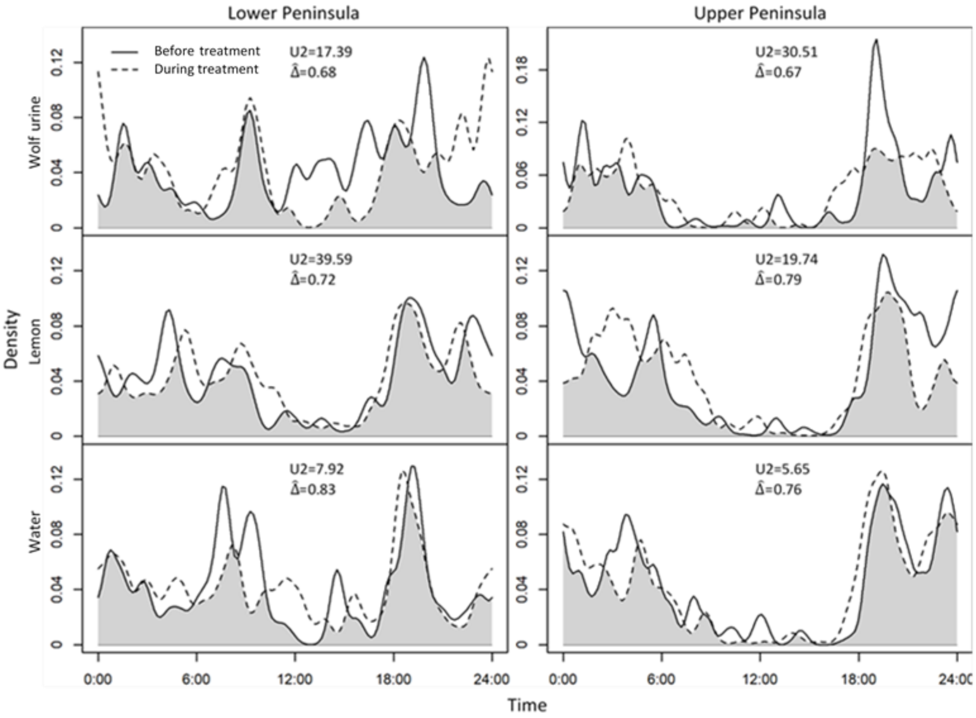


Figure 4. Temporal overlap for indicated area and treatment at white-tailed deer (*Odocoileus virginianus*) hunter bait sites before treatment (solid line) and during treatment application (dashed line) in the Upper Peninsula and Lower Peninsula of Michigan, USA. Shaded area indicates the temporal overlap between the 2 periods. The reported U2 statistic is compared with the test statistic U2 = 0.19.

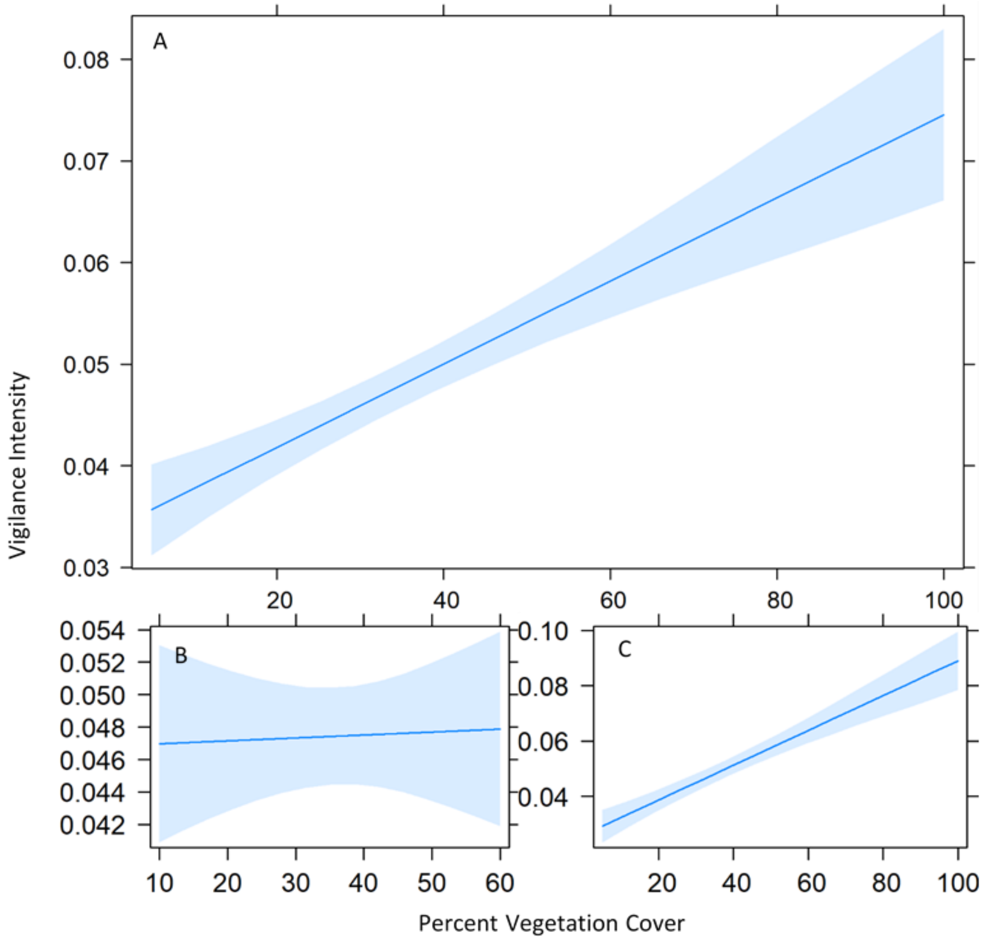


Figure 5. Effects graph showing the predicted vigilance intensity (sum of proportion of group vigilant in each event divided by total time of event) by percent vegetation cover for both areas, all treatment sites, and across the whole study period (A); all treatment sites and across the whole study in the Lower Peninsula of Michigan, USA (B); and all treatment sites and across the whole study in the Upper Peninsula of Michigan, USA (C).

Chapter 4

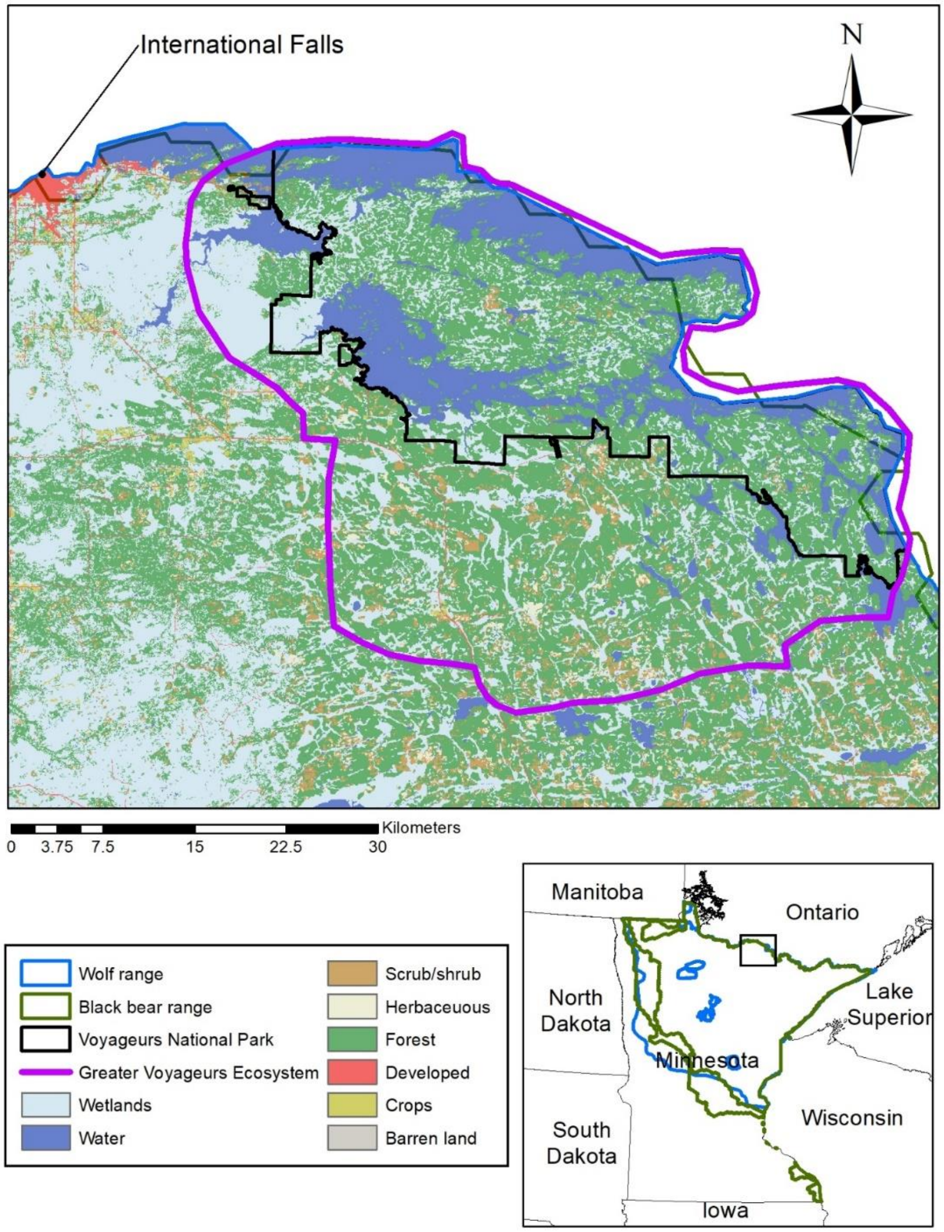


Figure 1. Voyagers Wolf Project study area Minnesota, USA. The solid magenta line indicates the Greater Voyagers Ecosystem, and the black line indicates Voyagers

National Park boundary. The inset map indicates the wolf and bear range in Minnesota, USA.

Table 1. Mean number of revisits and time spent (hours) by site and period type by gray wolves (*Canis lupus*) in the Greater Voyagers Ecosystem, Minnesota, USA from mid-July to mid-October for 2017, 2018, and 2019. The confidence interval indicates the 95% confidence interval of the mean difference for each given comparison. Differences between each site type were significant if the 95% confidence interval did not include 0 (significance indicated with an asterisk).

	Site type	**Period**	**Mean**	**95% Confidence interval**
number of revisits	home	overall	43.72	26.98 to 29.32*
	bait		15.58	
number of revisits	bait	overall	15.58	−3.66 to −2.78*
	other		12.36	
number of revisits	bait	bait	15.75	−0.50 to 1.16
		hunt/bait	15.42	
number of revisits	homesite	bait	38.32	38.32 to 8.71*
		hunt/bait	8.71	
number of revisits	other	bait	11.84	−0.75 to 0.00
		hunt/bait	12.22	
Time spent	home	overall	4.03	1.87 to 2.33*
	bait		1.93	
Time spent	bait	overall	1.93	0.44 to 0.63*
	other		2.46	
Time spent	bait	bait	2.40	0.76 to 1.07*
		hunt/bait	1.49	
Time spent	homesite	bait	2.95	0.34 to 1.44*
		hunt/bait	2.06	
Time spent	other	bait	2.13	−0.58 to −0.30*
		hunt/bait	2.57	

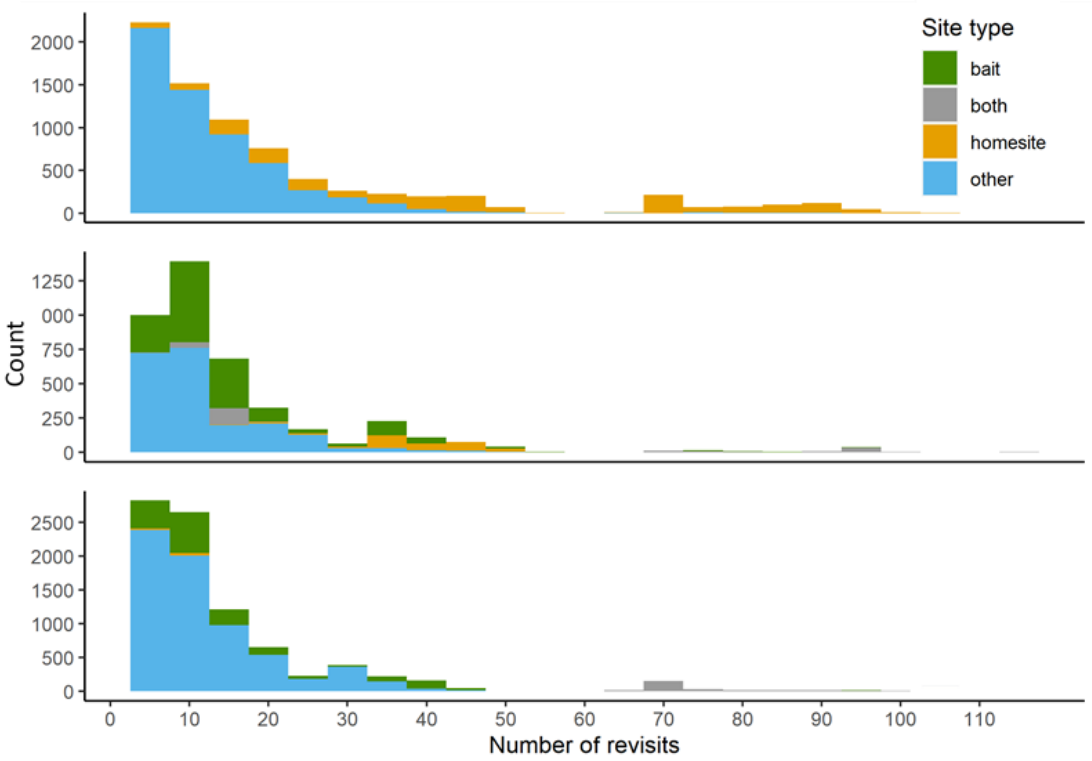


Figure 2. Histogram indicating the number of times locations were revisited by wolves (*Canis lupus*) in the Greater Voyagers Ecosystem for the pre-bait (top graph), bait only (middle graph), and bait and hunting periods (bottom graph) from mid-July to mid-October for 2017, 2018, and 2019. The different colors indicate black bear (*Ursus americanus*) hunter bait sites, both bait and homesites, homesites, and other site types.

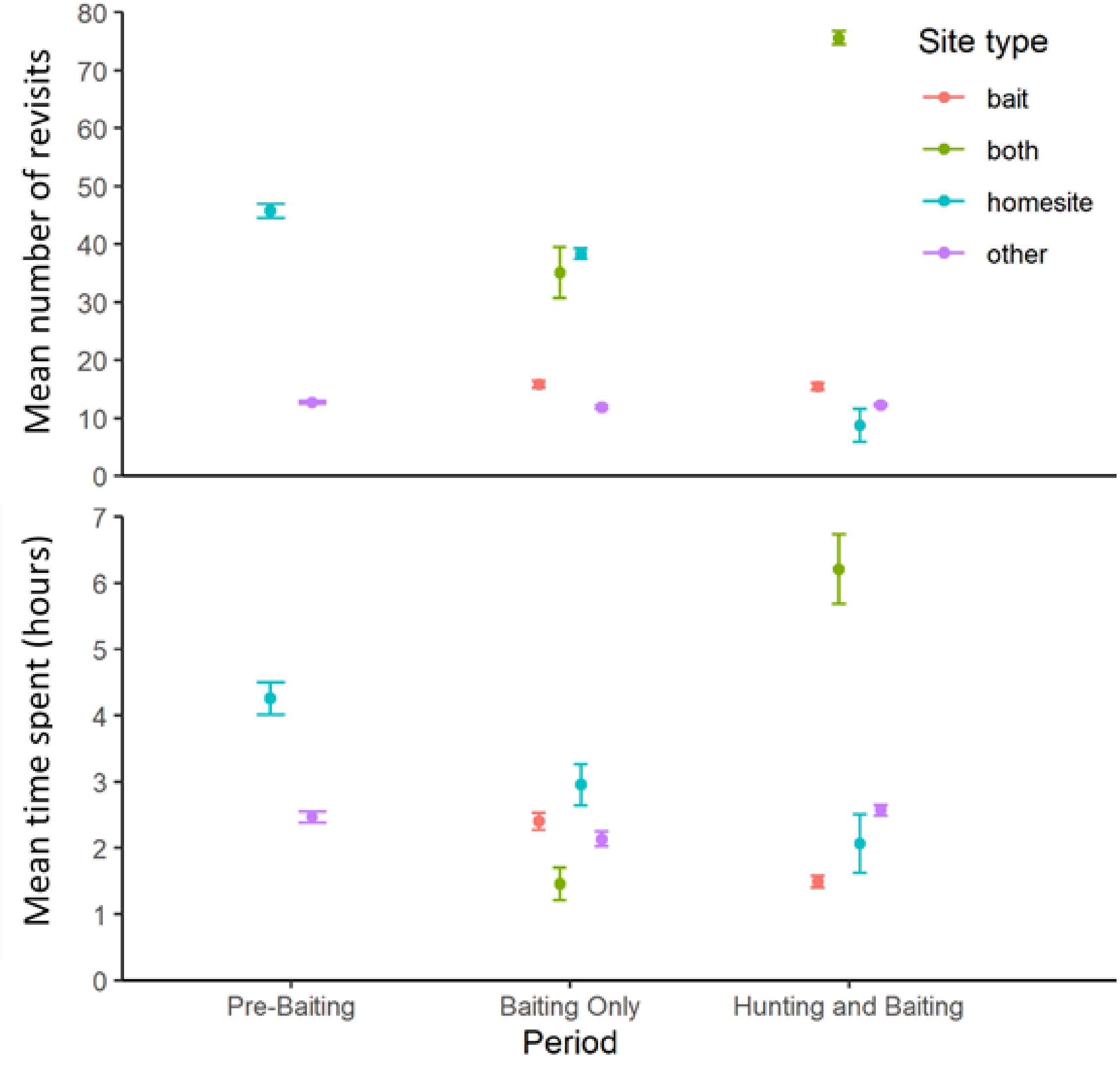


Figure 3. Gray wolf (*Canis lupus*) mean number of revisits (top) and mean time spent (hours; bottom) at different site types for three different periods in the Greater Voyagers Ecosystem from mid-July to mid-October for 2017, 2018, and 2019. Error bars indicate a standard deviation.

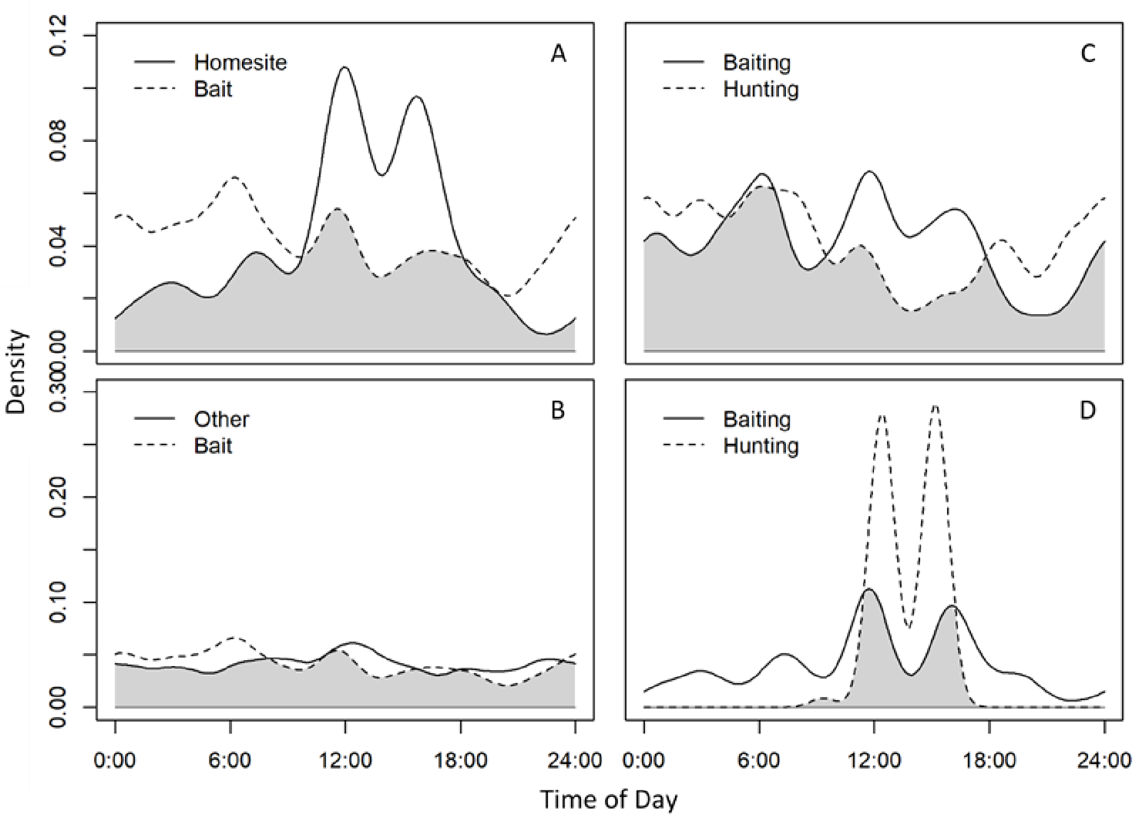


Figure 4. Gray wolf (*Canis lupus*) temporal overlap between visitations to black bear (*Ursus americanus*) hunter bait sites and homesites (A) and between bear bait sites and other sites (B) from mid-July to mid-October 2017, 2018, and 2019 in the Greater Voyagers Ecosystem. Panels C and D represent the temporal overlap between the baiting and hunting periods for bait sites and homesites respectively. Shaded area indicates the temporal overlap between the 2 time periods or site types.

BIBLIOGRAPHY

Ahrens, R. N. M., C. J. Walters, and V. Christensen. 2012. Foraging arena theory. Fish and Fisheries 13:41–59.

Ahrestani, F. S., M. Hebblewhite, and E. Post. 2013. The importance of observation versus process error in analyses of global ungulate populations. Scientific Reports 3:1–10.

Alexander, S. M., T. B. Logan, and P. C. Paquet. 2006. Spatio-temporal co-occurrence of cougars (Felis concolor), wolves (Canis lupus) and their prey during winter: a comparison of two analytical methods. Journal of Biogeography 33:2001–2012.

Allen, M. L., C. Wilmers, M. L. Elbroch, J. M. Golla, and H. U. Wittmer. 2016. The importance of motivation, weapons, and foul odors in driving encounter competition in carnivores. Ecology 97:1905–1912.

Alonso, R. S., B. T. McClintock, L. M. Lyren, E. E. Boydston, and K. R. Crooks. 2015. Mark-recapture and mark-resight methods for estimating abundance with remote cameras: a carnivore case study. PLOS ONE 10:e0123032.

Anson, J. R., C. R. Dickman, R. Boonstra, and T. S. Jessop. 2013. Stress Triangle: Do Introduced Predators Exert Indirect Costs on Native Predators and Prey? PLOS ONE 8:e60916.

Atkins, R., D. T. Blumstein, K. E. Moseby, R. West, M. Hyatt, and M. Letnic. 2016. Deep evolutionary experience explains mammalian responses to predators. Behavioral Ecology and Sociobiology 70:1755–1763.

Barber-Meyer, S. M., L. D. Mech, W. E. Newton, and B. L. Borg. 2016. Differential wolf-pack-size persistence and the role of risk when hunting dangerous prey. Behaviour 153:1473–1487.

Baruch-Mordo, S., K. R. Wilson, D. L. Lewis, J. Broderick, J. S. Mao, and S. W. Breck. 2014. Stochasticity in natural forage production affects use of urban areas by black bears: implications to management of human-bear conflicts. PLOS ONE 9:e85122.

Beckmann, J. P., and C. W. Lackey. 2008. Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. Human-Wildlife Conflicts 2:168–174.

Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. J. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour 76:611–618.

Berger, J., J. E. Swenson, and I.-L. Persson. 2001. Recolonizing Carnivores and Naïve Prey: Conservation Lessons from Pleistocene Extinctions. Science 291:1036–1039.

Beyer, D. E., T. Hogrefe, R. B. Peyton, P. Bull, J. P. Burroughs, and P. Lederle. 2006. Review of social and biological science relevant to wolf management in Michigan. Michigan Department of Natural Resources, Michigan, USA.

Bino, G., A. Dolev, D. Yosha, A. Guter, R. King, D. Saltz, and S. Kark. 2010. Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. Journal of Applied Ecology 47:1262–1271.

Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The Impact of Predator-Induced Stress on the Snowshoe Hare Cycle. Ecological Monographs 68:371–394.

Boutin, S., L. A. Wauters, A. G. McAdam, M. M. Humphries, G. Tosi, and A. A. Dhondt. 2006. Anticipatory reproduction and population growth in seed predators. Science 314:1928–1930.

Bowman, B., J. L. Belant, D. E. Beyer, and D. Martel. 2015. Characterizing nontarget species use at bait sites for white-tailed deer. Human - Wildlife Interactions 9:110–118.

Bracis, C., K. L. Bildstein, and T. Mueller. 2018. Revisitation analysis uncovers spatio-temporal patterns in animal movement data. Ecography 41:1801–1811.

Brand, C. J., and L. B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. Journal of Wildlife Management 43:827–849.

Bridges, A. S., M. R. Vaughan, and S. Klenzendorf. 2004. Seasonal variation in American black bear *Ursus americanus* activity patterns: quantification via remote photography. Wildlife Biology 10:277–284.

Briffa, M., and L. U. Sneddon. 2007. Physiological constraints on contest behaviour. Functional Ecology 21:627–637.

Brunk, K. M., E. H. West, M. Z. Peery, and A. M. Pidgeon. 2021. Reducing anthropogenic subsidies can curb density of overabundant predators in protected areas. Biological Conservation 256:109081.

Bump, J. K., C. M. Murawski, L. M. Kartano, D. E. Jr. Beyer, and B. J. Roell. 2013. Bear-baiting may exacerbate wolf-hunting dog conflict. PLoS ONE 8:e61708.

Burton, A. C., M. K. Sam, C. Balangtaa, and J. S. Brashares. 2012. Hierarchical multi-species modeling of carnivore responses to hunting, habitat and prey in a West African protected area. PloS ONE 7:e38007.

Bytheway, J. P., A. J. R. Carthey, and P. B. Banks. 2013. Risk vs. reward: how predators and prey respond to aging olfactory cues. Behavioral Ecology and Sociobiology 67:715–725.

Campbell, T. A., J. A. Foster, M. J. Bodenchuk, J. D. Eisemann, L. Staples, and S. J. Lapidge. 2013. Effectiveness and target-specificity of a novel design of food dispenser to deliver a toxin to feral swine in the United States. International Journal of Pest Management 59:197–204.

Candler, E., W. Severud, and J. Bump. 2019. Who takes the bait? Non-target species use of bear hunter bait sites. Human–Wildlife Interactions 13:98–110.

Carmichael, L. E., J. A. Nagy, N. C. Larter, and C. Strobeck. 2001. Prey specialization may influence patterns of gene flow in wolves of the Canadian Northwest. Molecular Ecology 10:2787–2798.

Caruso, N., E. Luengos Vidal, M. Guerisoli, and M. Lucherini. 2017. Carnivore occurrence: do interview-based surveys produce unreliable results? Oryx 51:240–245.

Chamaillé-Jammes, S., H. Malcuit, S. L. Saout, and J.-L. Martin. 2014. Innate threat-sensitive foraging: black-tailed deer remain more fearful of wolf than of the less dangerous black bear even after 100 years of wolf absence. Oecologia 174:1151–1158.

Chavez, A. S., and E. M. Gese. 2006. Landscape Use and Movements of Wolves in Relation to Livestock in a Wildland-Agriculture Matrix. The Journal of Wildlife Management 70:1079–1086.

Ciucci, P., S. Mancinelli, L. Boitani, O. Gallo, and L. Grottoli. 2020. Anthropogenic food subsidies hinder the ecological role of wolves: Insights for conservation of apex predators in human-modified landscapes. Global Ecology and Conservation 21:e00841.

Clinchy, M., L. Zanette, R. Boonstra, J. C. Wingfield, and J. N. M. Smith. 2004. Balancing food and predator pressure induces chronic stress in songbirds. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:2473–2479.

Cooper, S. E., C. K. Nielsen, and P. T. McDonald. 2012. Landscape factors affecting relative abundance of gray foxes Urocyon cinereoargenteus at large scales in Illinois, USA. Wildlife Biology 18:366–373.

Cortés-Avizanda, A., M. Carrete, D. Serrano, and J. A. Donázar. 2009. Carcasses increase the probability of predation of ground-nesting birds: a caveat regarding the conservation value of vulture restaurants. Animal Conservation 12:85–88.

Crum, N. J., A. K. Fuller, C. S. Sutherland, E. J. Cooch, and J. Hurst. 2017. Estimating occupancy probability of moose using hunter survey data. Journal of Wildlife Management 81:521–534.

Darimont, C. T., and T. E. Reimchen. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. Canadian Journal of Zoology 80:1638–1642.

Davis, D. E. 1957. The Use of Food as a Buffer in a Predator-Prey System. Journal of Mammalogy 38:466–472.

Dellinger, J. A., C. R. Shores, A. Craig, M. R. Heithaus, W. J. Ripple, and A. J. Wirsing. 2019. Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves. Oecologia 189:487–500.

DNR - Wolf Biology and Identification. 2018. <https://www.michigan.gov/dnr/0,8817,7-350-79135_79218_79619-292026--,00.html>.

Domínguez-Rodrigo, M. 2002. Hunting and Scavenging by Early Humans: The State of the Debate. Journal of World Prehistory 16:1–54.

Duda, M. D., M. Jones, T. Beppler, S. J. Bissell, A. Center, A. Criscione, P. Doherty, G. L. Hughes, C. Gerken, and A. Lanier. 2020. Alabama hunter harvest annual report. Responsive Management National Office.

Dunkley, L., and M. R. L. Cattet. 2003. A comprehensive review of the ecological and human social effects of artificial feeding and baiting of wildlife. Canadian Cooperative Wildlife Health Center, Saskatoon, Saskatchewan.

Edwards, J. 1983. Diet shifts in moose due to predator avoidance. Oecologia 60:185–189.

Emlen, J. M. 1966. The Role of Time and Energy in Food Preference. The American Naturalist 100:611–617.

Erb, P. L., W. J. McShea, and R. P. Guralnick. 2012. Anthropogenic influences on macro-level mammal occupancy in the Appalachian Trail corridor. PloS ONE 7:e42574.

Flagel, D. G., G. E. Belovsky, and D. E. Beyer. 2016. Natural and experimental tests of trophic cascades: gray wolves and white-tailed deer in a Great Lakes forest. Oecologia 180:1183–1194.

Fležar, U., E. le Roux, G. I. H. Kerley, D. P. J. Kuijper, M. te Beest, D. J. Druce, D. Prinsloo, and J. P. G. M. Cromsigt. 2019. Simulated elephant-induced habitat changes can create dynamic landscapes of fear. Biological Conservation 237:267–279.

Frawley, B. J. 2017*a*. 2016 Michigan black bear hunter survey. Wildlife Division Report No. 3641, Michigan Department of Natural Resources, Michigan, USA.

Frawley, B. J. 2017*b*. Michigan Deer Harvest Survey Report 2016 Seasons. Wildlife Report No. 3639, Michigan Department of Natural Resources, Michigan, USA.

Frawley, B. J. 2018*a*. 2017 Michigan black bear hunter survey. Wildlife Division Report No. 3655, Michigan Department of Natural Resources, Michigan, USA.

Frawley, B. J. 2018*b*. Michigan Deer Harvest Survey Report 2017 Seasons. Wildlife Report No. 3656, Michigan Department of Natural Resources, Michigan, USA.

Frawley, B. J. 2019*a*. 2018 Michigan black bear hunter survey. Wildlife Division Report No. 3674, Michigan Department of Natural Resources, Michigan, USA.

Frawley, B. J. 2019*b*. 2016 Marten and Fisher Harvest Survey. Wildlife Division Report No. 3662, Michigan Department of Natural Resources, Michigan, USA.

Frawley, B. J. 2019*c*. 2017 Marten and Fisher Harvest Survey. Wildlife Division Report No. 3663, Michigan Department of Natural Resources, Michigan, USA.

Frawley, B. J. 2019*d*. Michigan Deer Harvest Survey Report 2018 Seasons. Wildlife Division Report No. 3973, Michigan Department of Natural Resources, Michigan, USA.

Frawley, B. J. 2020. 2018 Marten and Fisher Harvest Survey. Wildlife Division Report No. 3683, Michigan Department of Natural Resources, Michigan, USA.

Freedman, E. 2019. The debate is on: Will wolves move to Michigan's Lower Peninsula? | Bridge Michigan. <https://www.bridgemi.com/michigan-environment-watch/debate-will-wolves-move-michigans-lower-peninsula>.

Gable, T. D., A. T. Homkes, S. M. Johnson-Bice, S. K. Windels, and J. K. Bump. 2021. Wolves choose ambushing locations to counter and capitalize on the sensory abilities of their prey. J. Quinn, editor. Behavioral Ecology 32:339–348.

Gable, T. D., S. M. Johnson-Bice, A. T. Homkes, S. K. Windels, and J. K. Bump. 2020. Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers. Science Advances 6:eabc5439.

Gable, T. D., and S. K. Windels. 2018. Kill rates and predation rates of wolves on beavers: Kill and Predation Rates of Wolves on Beavers. The Journal of Wildlife Management 82:466–472.

Gable, T. D., S. K. Windels, J. G. Bruggink, and S. M. Barber-Meyer. 2018*a*. Weekly Summer Diet of Gray Wolves (Canis lupus) in Northeastern Minnesota. The American Midland Naturalist 179:15–27.

Gable, T. D., S. K. Windels, J. G. Bruggink, and A. T. Homkes. 2016. Where and how wolves (Canis lupus) kill beavers (Castor canadensis). PLOS ONE 11:e0165537.

Gable, T. D., S. K. Windels, and J. K. Bump. 2018*b*. Finding wolf homesites: improving the efficacy of howl surveys to study wolves. PeerJ 6:e5629.

Gable, T. D., S. K. Windels, and A. T. Homkes. 2018*c*. Do wolves hunt freshwater fish in spring as a food source? Mammalian Biology 91:30–33.

Gamelon, M., S. Focardi, E. Baubet, S. Brandt, B. Franzetti, F. Ronchi, S. Venner, B.-E. Sæther, and J.-M. Gaillard. 2017. Reproductive allocation in pulsed-resource environments: a comparative study in two populations of wild boar. Oecologia 183:1065–1076.

Garrott, R. A., J. E. Bruggeman, M. S. Becker, S. T. Kalinowski, and P. J. White. 2007. Evaluating Prey Switching in Wolf–Ungulate Systems. Ecological Applications 17:1588–1597.

Garshelis, D. L., and M. R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. Journal of Mammalogy 61:8–19.

Garshelis, D., and A. Tri. 2017. Status of Minnesota American black bears, 2016. Minnesota Department of Natural Resources, Minnesota, USA.

Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power, and J. S. Brashares. 2019. Landscapes of Fear: Spatial Patterns of Risk Perception and Response. Trends in Ecology & Evolution 34:355–368.

Gehr, B., E. J. Hofer, A. Ryser, E. Vimercati, K. Vogt, and L. F. Keller. 2018. Evidence for nonconsumptive effects from a large predator in an ungulate prey? Behavioral Ecology 29:724–735.

Gibson, L. 2006. The Role of Lethal Control in Managing the Effects of Apparent Competition on Endangered Prey Species. Wildlife Society Bulletin 34:1220–1224.

van Ginkel, H. A. L., D. P. J. Kuijper, J. Schotanus, and C. Smit. 2019*a*. Wolves and Tree Logs: Landscape-Scale and Fine-Scale Risk Factors Interactively Influence Tree Regeneration. Ecosystems 22:202–212.

van Ginkel, H. A. L., C. Smit, and D. P. J. Kuijper. 2019*b*. Behavioral response of naïve and non-naïve deer to wolf urine. PLOS ONE 14:e0223248.

Gomo, G., J. Mattisson, B. R. Hagen, P. F. Moa, and T. Willebrand. 2017. Scavenging on a pulsed resource: quality matters for corvids but density for mammals. BMC Ecology 17:1–9.

Gray, R. M., M. R. Vaughan, and S. L. McMullin. 2004. Feeding wild American black bears in Virginia: a survey of Virginia bear hunters, 1998–99. Ursus 15:188–196.

Gray Wolf Recovery in Minnesota, Wisconsin, and Michigan. 2011. U.S Fish and Wildlife Service-Wolf-Western Great Lakes. Government. <https://www.fws.gov/midwest/wolf/aboutwolves/r3wolfrec.htm>.

Grima, N., J. Brainard, and B. Fisher. 2021. Are wolves welcome? Hunters' attitudes towards wolves in Vermont, USA. Oryx 55:262–267.

Gunther, K. A. 1990. Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park. Pages 73–78 *in*. International Conference on Bear Research and Management. Volume 8.

Gutgesell, M., B. C. McMeans, M. M. Guzzo, V. deGroot, A. T. Fisk, T. B. Johnson, and K. S. McCann. 2020. Subsidy Accessibility Drives Asymmetric Food Web Responses. bioRxiv.

Harms, T. M., J. M. Coffey, and V. D. Evelsizer. 2018. Iowa bow hunter observation survey: 2018 summary.

Hogberg, J., A. Treves, B. Shaw, and L. Naughton-Treves. 2016. Changes in attitudes toward wolves before and after an inaugural public hunting and trapping season: early evidence from Wisconsin's wolf range. Environmental Conservation 43:45–55.

Holinda, D., J. M. Burgar, and A. C. Burton. 2020. Effects of scent lure on camera trap detections vary across mammalian predator and prey species. PLOS ONE 15:e0229055.

Holt, R. 2008. Theoretical perspectives on resource pulses. Ecology 89:671–681.

Holt, R. D., J. Grover, and D. Tilman. 1994. Simple Rules for Interspecific Dominance in Systems with Exploitative and Apparent Competition. The American Naturalist 144:741–771.

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. G. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States – representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Houle, M., D. Fortin, J. Mainguy, and P. Canac-Marquis. 2011. Landscape composition and structure influence the abundance of mesopredators: implications for the control of the raccoon (*Procyon lotor*) variant of rabies. Canadian Journal of Zoology 89:1107–1116.

Hristienko, H., and J. E. McDonald. 2007. Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. Ursus 18:72–88.

Hwang, M. H., and D. L. Garshelis. 2007. Activity patterns of Asiatic black bears (*Ursus thibetanus*) in the Central Mountains of Taiwan. Journal of Zoology 271:203–209.

Jennelle, C. S., M. D. Samuel, C. A. Nolden, and E. A. Berkley. 2009. Deer Carcass Decomposition and Potential Scavenger Exposure to Chronic Wasting Disease. The Journal of Wildlife Management 73:655–662.

Jhala, Y., Q. Qureshi, and R. Gopal. 2011. Can the abundance of tigers be assessed from their signs? Journal of Applied Ecology 48:14–24.

Jordan, M. J., R. H. Barrett, and K. L. Purcell. 2011. Camera trapping estimates of density and survival of fishers Martes pennanti. Wildlife Biology 17:266–276.

Kaczensky, P., D. Huber, F. Knauer, H. Roth, A. Wagner, and J. Kusak. 2006. Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. Journal of Zoology 269:474–485.

Kats, L. B., and L. M. Dill. 1998. The scent of death: Chemosensory assessment of predation risk by prey animals. Écoscience 5:361–394.

Kavčič, I., M. Adamič, P. Kaczensky, M. Krofel, M. Kobal, and K. Jerina. 2015. Fast food bears: brown bear diet in a human-dominated landscape with intensive supplemental feeding. Wildlife Biology 21:1–8.

Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the florida panther. Conservation Biology 12:1359–1364.

Kirby, R., H. E. Johnson, M. W. Alldredge, and J. N. Pauli. 2019. The cascading effects of human food on hibernation and cellular aging in free-ranging black bears. Scientific Reports 9:2197.

Kirby, R., D. M. MacFarland, and J. N. Pauli. 2017. Consumption of intentional food subsidies by a hunted carnivore. Journal of Wildlife Management 81:1161–1169.

Kitchen, A. M., E. M. Gese, and E. R. Schauster. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. Canadian Journal of Zoology 78:853–857.

Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. Ecological Monographs 0:1–15.

Kuijper, D. P. J., de Kleine C., Churski M., van Hooft P., Bubnicki J., and Jędrzejewska B. 2013. Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. Ecography 36:1263–1275.

Kuijper, D. P. J., M. Verwijmeren, M. Churski, A. Zbyryt, K. Schmidt, B. Jędrzejewska, and C. Smit. 2014. What Cues Do Ungulates Use to Assess Predation Risk in Dense Temperate Forests? PLOS ONE 9:e84607.

Kusak, J., A. M. Skrbinšek, and D. Huber. 2005. Home ranges, movements, and activity of wolves (Canis lupus) in the Dalmatian part of Dinarids, Croatia. European Journal of Wildlife Research 51:254–262.

Lafferty, D. J. R., Z. G. Loman, K. S. White, A. T. Morzillo, and J. L. Belant. 2016. Moose (Alces alces) hunters subsidize the scavenger community in Alaska. Polar Biology 39:639–647.

Lambert, B. C., and S. Demarais. 2001. Use of Supplemental Feed for Ungulates by Non-Target Species. The Southwestern Naturalist 46:118–121.

Lashley, M. A., M. V. Cove, M. C. Chitwood, G. Penido, B. Gardner, C. S. DePerno, and C. E. Moorman. 2018. Estimating wildlife activity curves: comparison of methods and sample size. Scientific Reports 8:1–11.

Lasky, M., A. Parsons, S. Schuttler, A. Mash, L. Larson, B. Norton, B. Pease, H. Boone, L. Gatens, and R. Kays. 2021. Candid Critters: Challenges and Solutions in a Large-Scale Citizen Science Camera Trap Project. Citizen Science: Theory and Practice 6.

<http://theoryandpractice.citizenscienceassociation.org/article/10.5334/cstp.343/>. Accessed 25 Aug 2021.

Latham, A. D. M., M. C. Latham, K. H. Knopff, M. Hebblewhite, and S. Boutin. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. Ecography 36:1276–1290.

Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern north America. Wildlife Monographs 191:1–61.

Letnic, M., A. Greenville, E. Denny, C. R. Dickman, M. Tischler, C. Gordon, and F. Koch. 2011. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? Global Ecology and Biogeography 20:343–353.

Liley, S., and S. Creel. 2008. What best explains vigilance in elk: characteristics of prey, predators, or the environment? Behavioral Ecology 19:245–254.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649–659.

Litvaitis, J. A., and D. M. Kane. 1994. Relationship of Hunting Technique and Hunter Selectivity to Composition of Black Bear Harvest. Wildlife Society Bulletin 22:604–606.

Lohr, J. R. 2017. Deer hunter wildlife survey 2017.

Lund, U., and C. Agostinelli. 2012. CircStats: Circular Statistics, from “Topics in circular Statistics” (2001).

MacArthur, R. H., and E. R. Pianka. 1966. On Optimal Use of a Patchy Environment. The American Naturalist 100:603–609.

Macaulay, L. T., R. Sollmann, and R. H. Barrett. 2020. Estimating deer populations using camera traps and natural marks. The Journal of Wildlife Management 84:301–310.

MacHutchon, A. G., S. Himmer, H. Davis, and M. Gallagher. 1998. Temporal and spatial activity patterns among coastal bear populations. Ursus 10:539–546.

MacNulty, D. R., A. Tallian, D. R. Stahler, and D. W. Smith. 2014. Influence of Group Size on the Success of Wolves Hunting Bison. PLOS ONE 9:e112884.

Mahard, T. J., J. A. Litvaitis, P. Tate, G. C. Reed, and D. J. A. Broman. 2016. An evaluation of hunter surveys to monitor relative abundance of bobcats. Wildlife Society Bulletin 40:224–232.

Manlick, P. J., and S. D. Newsome. 2021. Adaptive foraging in the Anthropocene: can individual diet specialization compensate for biotic homogenization? Frontiers in Ecology and the Environment.

McCall, B. S., M. S. Mitchell, M. K. Schwartz, J. Hayden, S. A. Cushman, P. Zager, and W. F. Kasworm. 2013. Combined use of mark-recapture and genetic analyses reveals response of a black bear population to changes in food productivity. The Journal of Wildlife Management 77:1572–1582.

Melchiors, M. A., and C. A. Leslie. 1985. Effectiveness of Predator Fecal Odors as Black-Tailed Deer Repellents. The Journal of Wildlife Management 49:358–362.

Meredith, M., and M. Ridout. 2018. overlap: Estimates of Coefficient of Overlapping for Animal Activity Patterns.

Michigan Department of Natural Resources. 2017. Michigan Hunting and Trapping Digest. Michigan, USA.

Michigan Department of Natural Resources. 2018*a*. Natural Resources Commission approves deer regulations related to chronic wasting disease. Michigan Department of Natural Resources, Michigan, USA.

Michigan Department of Natural Resources. 2018*b*. Michigan Hunting Digest. Michigan, USA.

Minnesota Department of Natural Resources. 2017. Minnesota Hunting and Trapping Regulations. Minnesota, USA.

Minnesota Department of Natural Resources. 2018. Minnesota Hunting and Trapping Regulations. Minnesota, USA.

Minnesota Department of Natural Resources. 2019. Minnesota Hunting and Trapping Regulations. Minnesota, USA.

Minnesota Department of Natural Resources. 2020. 2020 Bear Hunting Regulations. Minnesota, USA.

Moll, R. J., K. M. Redilla, T. Mudumba, A. B. Muneza, S. M. Gray, L. Abade, M. W. Hayward, J. J. Millspaugh, and R. A. Montgomery. 2017. The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. Journal of Animal Ecology 86:749–765.

Moore, H. A., J. L. Champney, J. A. Dunlop, L. E. Valentine, and D. G. Nimmo. 2020. Spot on: using camera traps to individually monitor one of the world’s largest lizards. Wildlife Research 47:326–337.

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

Morris, S. P. 2013. Challenging the Values of Hunting: Fair Chase, Game Playing, and Intrinsic Value. Environmental Ethics 35:295–311.

National Oceanic and Atmospheric Administration. 2018. National Weather Service Forecast Office Marquette, MI. <https://www.weather.gov/mqt/>.

Nelson, M. E., and L. D. Mech. 1986. Mortality of White-Tailed Deer in Northeastern Minnesota. The Journal of Wildlife Management 50:691–698.

Newsome, T. M., J. A. Dellinger, C. R. Pavey, W. J. Ripple, C. R. Shores, A. J. Wirsing, and C. R. Dickman. 2015. The ecological effects of providing resource subsidies to predators. Global Ecology and Biogeography 24:1–11.

Niedballa, J., R. Sollmann, A. Courtiol, and A. Wilting. 2016. camtrapR: an R package for efficient camera trap data management. Methods in Ecology and Evolution 7:1457–1462.

Niedballa, J., R. Sollmann, A. bin Mohamed, J. Bender, and A. Wilting. 2015. Defining habitat covariates in camera-trap based occupancy studies. Scientific Reports 5:1–10.

Noser, R., and R. W. Byrne. 2007. Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, Papio ursinus. Animal Behaviour 73:257–266.

Obermoller, T. R., A. S. Norton, and L. Cornicelli. 2018. 2018 Minnesota bowhunter observation survey report.

O'Brien, T. G., J. E. M. Baillie, L. Krueger, and M. Cuke. 2010. The wildlife picture index: monitoring top trophic levels. Animal Conservation 13:335–343.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth, editors. 2010. Camera traps in animal ecology: methods and analyses. Springer Science & Business Media, New York City, New York.

Olson, T. L., R. C. Squibb, and B. K. Gilbert. 1998. Brown bear diurnal activity and human use: a comparison of two salmon streams. Ursus 10:547–555.

O'Malley, C., L. M. Elbroch, P. E. Lendrum, and H. Quigley. 2018. Motion-triggered video cameras reveal spatial and temporal patterns of red fox foraging on carrion provided by mountain lions. PeerJ 6:e5324.

O'Neil, S. 2017. The spatial ecology of gray wolves in the Upper Peninsula of Michigan, 1994–2013. Open Access Dissertation, Michigan Technological University. <https://digitalcommons.mtu.edu/etdr/451>.

O'Neil, S. T., J. K. Bump, and D. E. Beyer. 2017. Spatially varying density dependence drives a shifting mosaic of survival in a recovering apex predator (*Canis lupus*). Ecology and Evolution 7:9518–9530.

Ordiz, A., O.-G. Støen, S. Sæbø, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they are being hunted? Biological Conservation 152:21–28.

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501–1514.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology & Evolution 15:232–237.

Palmer, M. S., C. Portales-Reyes, C. Potter, L. D. Mech, and F. Isbell. 2021. Behaviorally-mediated trophic cascade attenuated by prey use of risky places at safe times. Oecologia 195:235–248.

Pedersen, S., P. Angelstam, M. A. D. Ferguson, P. Wabakken, and T. Storaas. 2019. Impacts of wolves on rural economies from recreational small game hunting. European Journal of Wildlife Research 65:1–9.

Peters, R. P., and L. D. Mech. 1975. Scent-Marking in Wolves: Radio-tracking of wolf packs has provided definite evidence that olfactory sign is used for territory maintenance and may serve for other forms of communication within the pack as well. American Scientist 63:628–637.

Peterson, T. J. 2015. 5 Best Funnel & Pinch-Point Setups for Hunting Whitetails. Game & Fish. <https://www.gameandfishmag.com/editorial/5-best-funnel-pinch-point-setups-for-hunting-whitetails/191246>.

Petroelje, T. R., J. L. Belant, D. E. Beyer, and N. J. Svoboda. 2019. Subsidies from anthropogenic resources alter diet, activity, and ranging behavior of an apex predator (Canis lupus). Scientific Reports 9:1–9.

Peyton, B. 1989. A Profile of Michigan Bear Hunters and Bear Hunting Issues. Wildlife Society Bulletin (1973-2006) 17:463–470.

Plaza, P. I., and S. A. Lambertucci. 2017. How are garbage dumps impacting vertebrate demography, health, and conservation? Global Ecology and Conservation 12:9–20.

Powell, R. A. 1993. The fisher : life history, ecology, and behavior. Second edition.

Proudman, N. J., M. Churski, J. W. Bubnicki, J.-Å. Nilsson, D. P. J. Kuijper, N. J. Proudman, M. Churski, J. W. Bubnicki, J.-Å. Nilsson, and D. P. J. Kuijper. 2020. Red deer allocate vigilance differently in response to spatio-temporal patterns of risk from human hunters and wolves. Wildlife Research 48:163–174.

Prugh, L. R., K. J. Sivy, P. J. Mahoney, T. R. Ganz, M. A. Ditmer, M. van de Kerk, S. L. Gilbert, and R. A. Montgomery. 2019. Designing studies of predation risk for improved inference in carnivore-ungulate systems. Biological Conservation 232:194–207.

Putman, R. J., and B. W. Staines. 2004. Supplementary winter feeding of wild red deer Cervus elaphus in Europe and North America: justifications, feeding practice and effectiveness. Mammal Review 34:285–306.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth: a course in methods of data analysis. Second.

Ribeiro, R. L. A., and R. C. Bianchi. 2020. Evaluation of bait use for mammal richness. Mammalia 84:26–33.

Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.

Riotte-Lambert, L., S. Benhamou, and S. Chamaillé-Jammes. 2013. Periodicity analysis of movement recursions. Journal of Theoretical Biology 317:238–243.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? BioScience 54:755–766.

Robb, G. N., McDonald Robbie A, Chamberlain Dan E, and Bearhop Stuart. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6:476–484.

Rodewald, A. D., L. J. Kearns, and D. P. Shustack. 2011. Anthropogenic resource subsidies decouple predator–prey relationships. Ecological Applications 21:936–943.

Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 97:3–72.

Roland, K. W., and K. M. Slauson. 2008. Remote cameras. Pages 110–140 *in*. Noninvasive Survey Methods for Carnivores.

Rolandsen, C. M., E. J. Solberg, I. Herfindal, B. V. Moorter, and B.-E. Sæther. 2011. Large-scale spatiotemporal variation in road mortality of moose: Is it all about population density? Ecosphere 2:1–12.

Royle, A. J., and J. D. Nichols. 2003. Estimating abundance from repeated presence–absence data or point counts. 84:777–790.

Ruid, D. B., W. J. Paul, B. J. Roell, A. P. Wydeven, R. C. Willging, R. L. Jurewicz, and D. H. Lonsway. 2009. Wolf–human conflicts and management in Minnesota, Wisconsin, and Michigan. Pages 279–295 *in*. Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, USA.

Ruth, T. K., D. W. Smith, M. A. Haroldson, P. C. Buotte, C. C. Schwartz, H. B. Quigley, S. Cherry, K. M. Murphy, D. Tyers, and K. Frey. 2003. Large-Carnivore Response to Recreational Big-Game Hunting along the Yellowstone National Park and Absaroka-Beartooth Wilderness Boundary. Wildlife Society Bulletin 31:1150–1161.

Sahlén, E., S. Noell, C. S. DePerno, J. Kindberg, G. Spong, and J. P. G. M. Cromsigt. 2016. Phantoms of the forest: legacy risk effects of a regionally extinct large carnivore. Ecology and Evolution 6:791–799.

Šálek, M., L. Drahníková, and E. Tkadlec. 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mammal Review 45:1–14.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122:240–285.

Schuttler, S. G., A. W. Parsons, T. D. Forrester, M. C. Baker, W. J. McShea, R. Costello, and R. Kays. 2017. Deer on the lookout: how hunting, hiking and coyotes affect white-tailed deer vigilance. Journal of Zoology 301:320–327.

Severud, W. J., G. D. DelGiudice, and T. R. Obermoller. 2019. Association of moose parturition and post-parturition habitat with calf survival. The Journal of Wildlife Management 83:175–183.

Shave, J. R., S. G. Cherry, A. E. Derocher, and D. Fortin. 2020. Seasonal and inter-annual variation in diet for gray wolves Canis lupus in Prince Albert National Park, Saskatchewan. Wildlife Biology 2020.

Sih, A. 1980. Optimal Behavior: Can Foragers Balance Two Conflicting Demands? Science 210:1041–1043.

Sirén, A. P. K., P. J. Pekins, P. L. Abdu, and M. J. Ducey. 2016. Identification and density estimation of American martens (Martes americana) using a novel camera-trap method. Diversity 8:3.

Smith, B. L. 2001. Winter Feeding of Elk in Western North America. The Journal of Wildlife Management 65:173–190.

Smith, J. A., A. C. Thomas, T. Levi, Y. Wang, and C. C. Wilmers. 2018. Human activity reduces niche partitioning among three widespread mesocarnivores. Oikos 127:890–901.

Steindler, L. A., D. T. Blumstein, R. West, K. E. Moseby, and M. Letnic. 2020. Exposure to a novel predator induces visual predator recognition by naïve prey. Behavioral Ecology and Sociobiology 74:102.

Stillfried, M., J. L. Belant, N. J. Svoboda, D. E. Beyer, and S. Kramer-Schadt. 2015. When top predators become prey: black bears alter movement behaviour in response to hunting pressure. Behavioural Processes 120:30–39.

Stirnemann, I., A. Mortelliti, P. Gibbons, and D. B. Lindenmayer. 2015. Fine-scale habitat heterogeneity influences occupancy in terrestrial mammals in a temperate region of Australia. PloS ONE 10:e0138681.

Stokke, S., J. M. Arnemo, S. Brainerd, A. Söderberg, M. Kraabøl, and B. Ytrehus. 2018. Defining animal welfare standards in hunting: body mass determines thresholds for incapacitation time and flight distance. Scientific Reports 8:1–13.

Sun, C. C., A. K. Fuller, and J. A. Royle. 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. PloS ONE 9:e88025.

Svizzero, S. 2016. Hunting Strategies with Cultivated Plants as Bait and the Prey Pathway to Animal Domestication. International Journal of Research in Sociology and Anthropology 2:53–68.

Theuerkauf, J., W. Jędrzejewski, K. Schmidt, and R. Gula. 2003*a*. Spatiotemporal Segregation of Wolves from Humans in the Białowieża Forest (Poland). The Journal of Wildlife Management 67:706–716.

Theuerkauf, J., W. Jędrzejewski, K. Schmidt, H. Okarma, I. Ruczyński, S. Śniezko, and R. Gula. 2003*b*. Daily Patterns and Duration of Wolf Activity in the Białowieza Forest, Poland. Journal of Mammalogy 84:243–253.

Thompson, A. K., M. D. Samuel, and T. R. Van Deelen. 2008. Alternative feeding strategies and potential disease transmission in Wisconsin white-tailed deer. Journal of Wildlife Management 72:416–421.

Treves, A., R. L. Jurewicz, L. Naughton-Treves, and D. S. Wilcove. 2009. The price of tolerance: wolf damage payments after recovery. Biodiversity and Conservation 18:4003–4021.

USFWS: Q and A’s about Gray Wolf Biology. 2011. <https://www.fws.gov/midwest/wolf/biology/wolfbiology.html>.

Vercauteren, K. C., and S. E. Hygnstrom. 1998. Effects of Agricultural Activities and Hunting on Home Ranges of Female White-Tailed Deer. The Journal of Wildlife Management 62:280–285.

Vucetich, J. A., J. T. Bruskotter, M. P. Nelson, R. O. Peterson, and J. K. Bump. 2017. Evaluating the principles of wildlife conservation: a case study of wolf (Canis lupus) hunting in Michigan, United States. Journal of Mammalogy 98:53–64.

Wang, Y., M. L. Allen, and C. C. Wilmers. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation 190:23–33.

Wikenros, C., D. P. J. Kuijper, R. Behnke, and K. Schmidt. 2015. Behavioural responses of ungulates to indirect cues of an ambush predator. Behaviour 152:1019–1040.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003. Resource dispersion and consumer dominance: scavenging at wolf-and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters 6:996–1003.

Winke, B. 2012. Can Deer Tell How Far Away a Source of an Odor Is? Petersen's Bowhunting. <https://www.bowhuntingmag.com/editorial/can-deer-tell-how-far-away-a-source-of-an-odor-is/309382>.

Wittmer, H. U., R. Serrouya, L. M. Elbroch, and A. J. Marshall. 2013. Conservation Strategies for Species Affected by Apparent Competition. Conservation Biology 27:254–260.

Wyoming Game and Fish Department. 2021. 2020 deer harvest report. Wyoming Game and Fish Department, Cheyenne, WY.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses. Ecology 89:621–634.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. Ecological Monographs 80:125–151.

Zar, J. H. 1999. Biostatistical analysis.

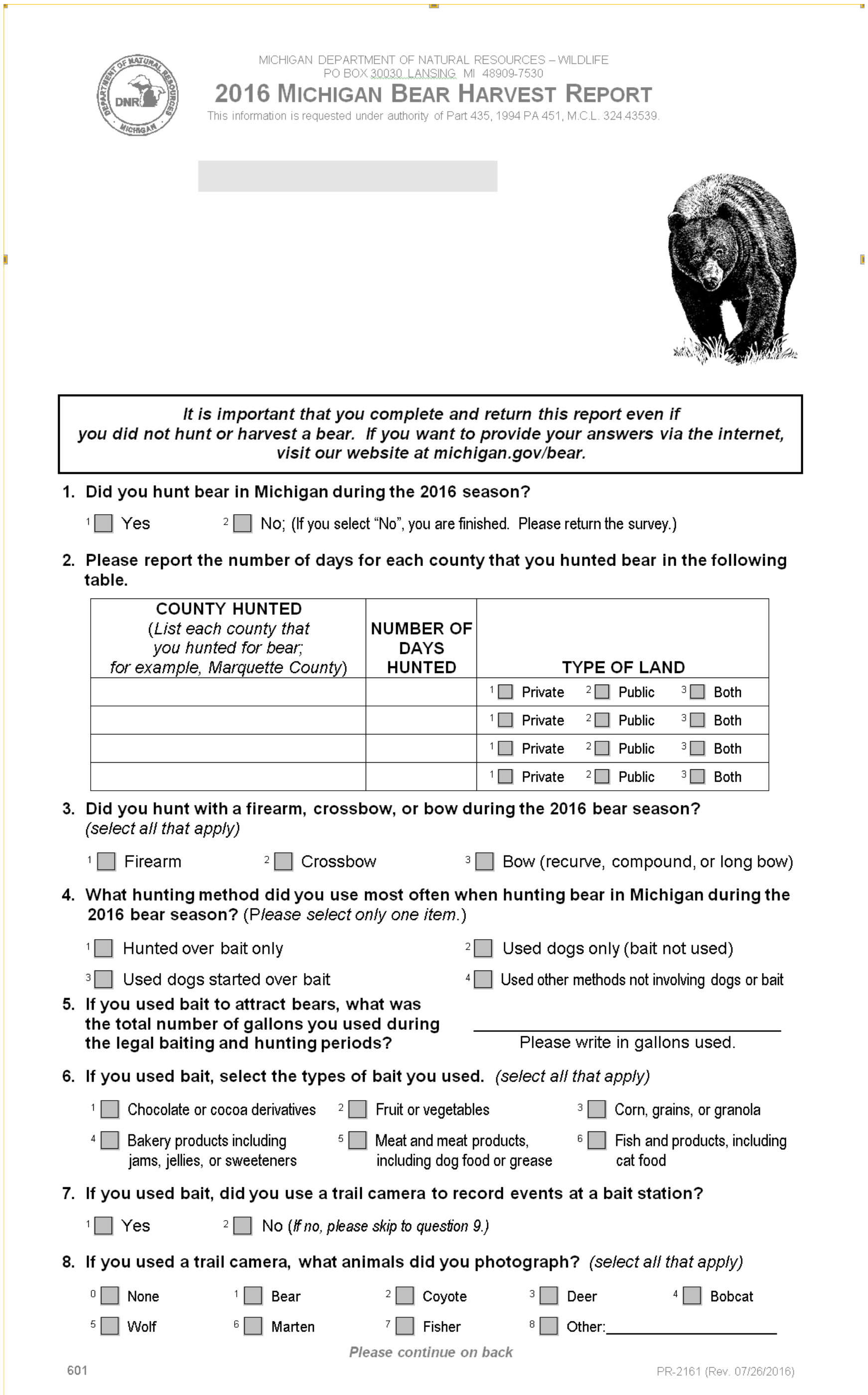
Zedrosser, A., J. Kindberg, and J. E. Swenson. 2013. Final report of bait hunting trials in Västerbotten, Norrbotten, and Dalarna counties, Sweden, 2010-2012. Scandinavian Brown Bear Research Project.

Zipkin, E. F., and S. P. Saunders. 2018. Synthesizing multiple data types for biological conservation using integrated population models. Biological Conservation 217:240–250.

Appendices

Chapter 2

Appendix A. 2016 MICHIGAN BLACK BEAR HUNTER SURVEY.



MICHIGAN DEPARTMENT OF NATURAL RESOURCES – WILDLIFE
PO BOX 30030 LANSING MI 48909-7530

2016 MICHIGAN BEAR HARVEST REPORT

This information is requested under authority of Part 435, 1994 PA 451, M.C.L. 324.43539.

It is important that you complete and return this report even if you did not hunt or harvest a bear. If you want to provide your answers via the internet, visit our website at michigan.gov/bear.

1. Did you hunt bear in Michigan during the 2016 season?

1 ☐ Yes 2 ☐ No; (If you select "No", you are finished. Please return the survey.)

2. Please report the number of days for each county that you hunted bear in the following table.

COUNTY HUNTED (*List each county that you hunted for bear; for example, Marquette County*)	**NUMBER OF DAYS HUNTED**	**TYPE OF LAND**
		1 ☐ Private 2 ☐ Public 3 ☐ Both
		1 ☐ Private 2 ☐ Public 3 ☐ Both
		1 ☐ Private 2 ☐ Public 3 ☐ Both
		1 ☐ Private 2 ☐ Public 3 ☐ Both

3. Did you hunt with a firearm, crossbow, or bow during the 2016 bear season? *(select all that apply)*

1 ☐ Firearm 2 ☐ Crossbow 3 ☐ Bow (recurve, compound, or long bow)

4. What hunting method did you use most often when hunting bear in Michigan during the 2016 bear season? (*Please select only one item.*)

1 ☐ Hunted over bait only
2 ☐ Used dogs only (bait not used)
3 ☐ Used dogs started over bait
4 ☐ Used other methods not involving dogs or bait

5. If you used bait to attract bears, what was the total number of gallons you used during the legal baiting and hunting periods? ____________________ Please write in gallons used.

6. If you used bait, select the types of bait you used. *(select all that apply)*

1 ☐ Chocolate or cocoa derivatives
2 ☐ Fruit or vegetables
3 ☐ Corn, grains, or granola
4 ☐ Bakery products including jams, jellies, or sweeteners
5 ☐ Meat and meat products, including dog food or grease
6 ☐ Fish and products, including cat food

7. If you used bait, did you use a trail camera to record events at a bait station?

1 ☐ Yes 2 ☐ No (*If no, please skip to question 9.*)

8. If you used a trail camera, what animals did you photograph? *(select all that apply)*

0 ☐ None 1 ☐ Bear 2 ☐ Coyote 3 ☐ Deer 4 ☐ Bobcat
5 ☐ Wolf 6 ☐ Marten 7 ☐ Fisher 8 ☐ Other:____________________

Please continue on back

601 PR-2161 (Rev. 07/26/2016)

9. **At any time during the 2016 season, did you hire a guide's service to hunt bear in Michigan?**

1 ☐ Yes 2 ☐ No (*If no, please skip to question 11.*)

10. **If yes, what hunting techniques were used most often by the guide?** (P*lease select only one item.*)

1 ☐ Hunted over bait only
2 ☐ Used dogs only (bait not used)
3 ☐ Used dogs started over bait
4 ☐ Used other methods not involving dogs or bait

11. **Did you kill a bear and place your harvest tag on it?**

1 ☐ Yes 2 ☐ No (*If no, please skip to question 13.*)

12. **If your harvest tag was put on a bear, please fill in the information below**

a. **What date was the bear harvested?**
(*please check [X] the box for the date of harvest*)

September 2016						
S	M	T	W	T	F	S
						10
11	12	13	14	15	16	17
18	19	20	21	22	23	24
25	26	27	28	29	30	

October 2016						
S	M	T	W	T	F	S
						1
2	3	4	5	6	7	8
9	10	11	12	13	14	15
16	17	18	19	20	21	22
23	24	25	26			

b. **What was the sex of the bear?**

1 ☐ Male 2 ☐ Female 3 ☐ Not sure

c. **In what county was it harvested?** ______________________
please write in county name

d. **On what type of land was the bear harvested?**

1 ☐ Private 2 ☐ Public

e. **What weapon was used to harvest bear?**

1 ☐ Firearm 2 ☐ Crossbow 3 ☐ Bow (recurve, compound, or long bow)

f. **What was the method of harvest?**

1 ☐ Taken over bait
2 ☐ Used dogs only (bait not used)
3 ☐ Used dogs started over bait
4 ☐ Used other methods not involving dogs or bait

g. **If you used a hunting guide, was your hunting guide responsible for your success in taking a bear?** (You can skip this question if you did not use a hunting guide.)

1 ☐ Yes 2 ☐ No 3 ☐ Not sure

13. **Did other hunters interfere with your bear hunting?** 1 ☐ Yes 2 ☐ No (*Skip to question 15.*)

14. **If you answered "yes" to the previous question, was the interference caused by other bear hunters?** 1 ☐ Yes 2 ☐ No

15. **How would you rate the following for your 2016 bear hunting season:**
(*Select one choice per item.*)

	Very Good	Good	Neutral	Poor	Very Poor	Not Applicable
a. Number of bear you saw.	1 ☐	2 ☐	3 ☐	4 ☐	5 ☐	6 ☐
b. Number of opportunities you had to take a bear.	1 ☐	2 ☐	3 ☐	4 ☐	5 ☐	6 ☐
c. Your overall bear hunting experience.	1 ☐	2 ☐	3 ☐	4 ☐	5 ☐	6 ☐

Return the completed report in the enclosed postage-paid envelope. Thanks for your help.

Chapter 3

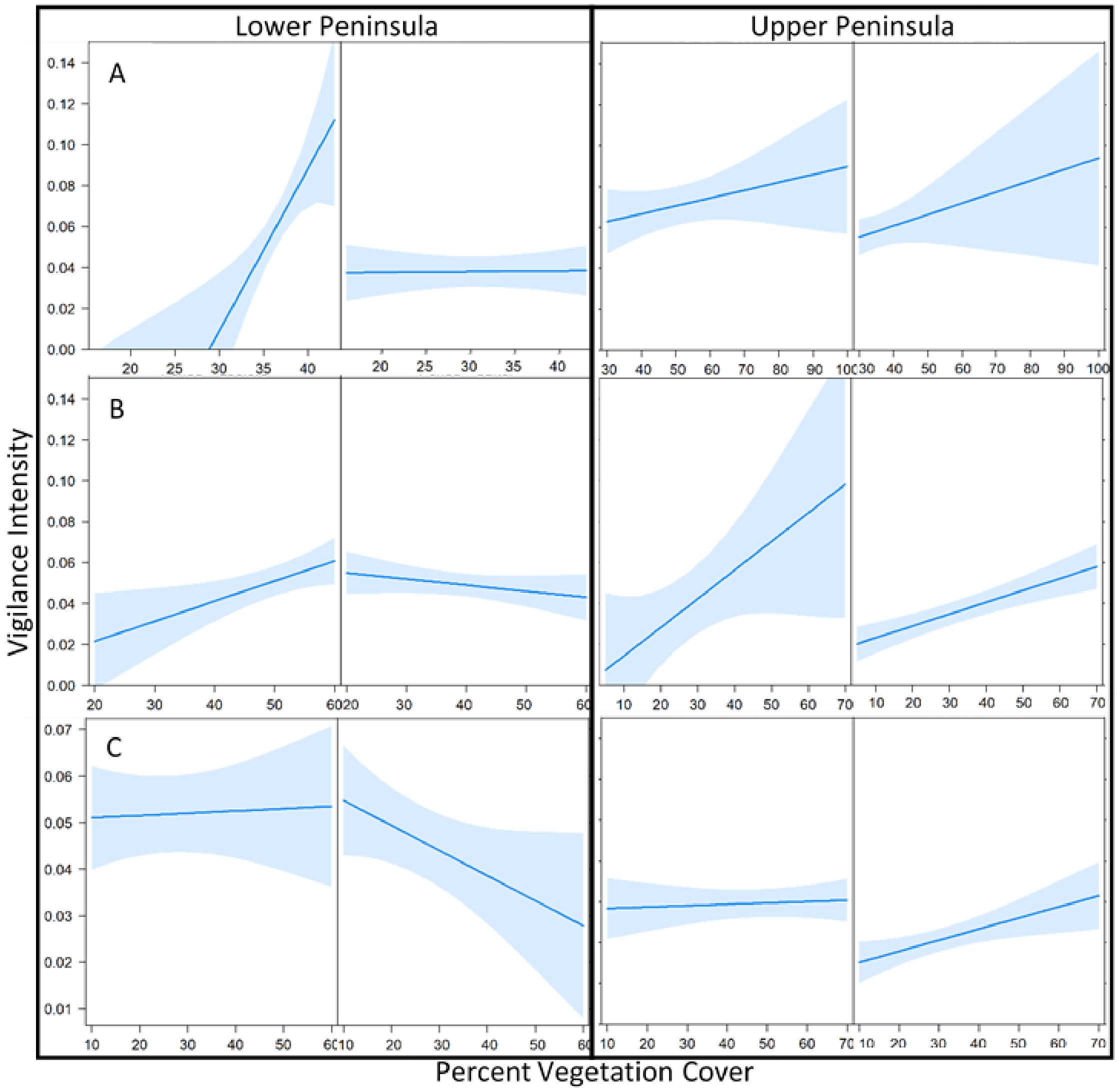
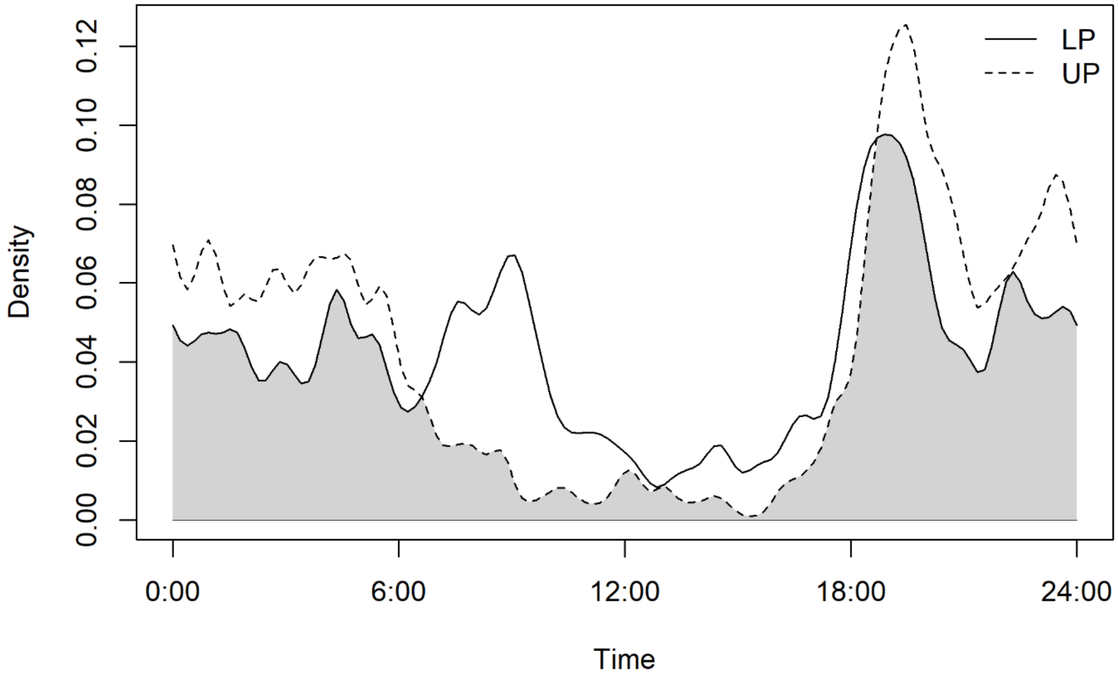


Fig S1. Obscurement cover effect on vigilance intensity. Effects graph showing the predicted vigilance intensity (sum of proportion of group vigilant in each event divided by total time of event) by percent vegetation cover for wolf urine (A), novel scent (lemon; B), and control (water; C) for the Lower and Upper Peninsula of Michigan, USA.



S2. Temporal overlap between deer visitation in the Upper and Lower Peninsula. Temporal overlap for white-tailed deer (*Odocoileus virginianus*) hunter bait sites for Lower Peninsula of Michigan, USA sites (solid line) and Upper Peninsula of Michigan, USA sites (dashed line). Shaded area indicates the temporal overlap between the 2 periods.