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L. S. Wszola (https://orcid.org/0000-0002-2660-2048) ✉ (lyndsie.wszola@huskers.unl.edu), E. F. Stuber and J. J. Fontaine, Nebraska Cooperative Fish & Wildlife Research Unit, School of Natural Resources, Univ. of Nebraska-Lincoln, 420 Hardin Hall, 3310 Holdrege Street, Lincoln, NE 68583, USA. – C. J. Chizinski, School of Natural Resources, Univ. of Nebraska-Lincoln, Lincoln, NE, USA. – J. J. Lusk, Nebraska Game and Parks Commission, Lincoln, Nebraska, USA.

A growing body of evidence suggests that hunter effort varies temporally and spatially, affecting game populations in unexpected ways. We set out to identify sources of variation in the spatial distribution of hunter effort by ring-necked pheasant *Phasianus colchicus* hunters during two time periods representing different spatial decisions: where to access a hunting location at the start of a hunt and where to hunt within it for the duration of the hunt. Pheasant hunters used direct and indirect information about the availability and accessibility of pheasants to make spatial decisions throughout their hunts, but the sources of information used at the beginning of hunts differed from those used for the duration of hunts. Hunter access point effort at the start of hunts was positively associated with proximity to public access signs and declined near marked safety zones around occupied structures and livestock, indicating that hunters responded to the spatial distribution and information content of public access infrastructure. Hunter effort within fields for the duration of hunts was positively related to predicted pheasant habitat use and negatively associated with correlates of physical exertion and increasing distance from field edges. Our findings indicate that hunters in the field are making spatial decisions in response to information about public land access, their own physical state, and perceived opportunity to encounter pheasants. Our results further suggest managers may be able to optimize public lands for wildlife habitat and recreational value without imposing new regulations by managing the information provided to hunters.

Keywords: anthropogenic predation risk, landscape of fear, pheasant hunters, social–ecological systems

Wildlife managers use regulations to control the effects of hunting on wildlife populations (Sinclair et al. 2006, Dirzo et al. 2014), but a growing body of evidence suggests that variation in hunter behavior within regulatory boundaries may profoundly affect ecological and even evolutionary dynamics of wildlife populations (Allendorf et al. 2008, Darimont et al. 2009). Harvest preferences, for example, can influence the direction of physical and behavioral selection in game populations (e.g. reduced ungulate antler size; Allendorf and Hard 2009). Wildlife managers cognizant of the selective effects of hunting (Pigeon et al. 2016) are increasingly managing game populations to mitigate harvest-induced selection (e.g. quality deer management, Turner et al. 2016), but hunting can influence game animal physiology and behavior even when hunters are not consciously seeking to harvest a desirable phenotype.

For gamebirds in particular, there is growing evidence that harvest patterns traditionally perceived to be random can actually increase mortality among individuals who might otherwise have the highest fitness, creating unexpected changes in population structure (Asmyhr et al. 2012). Unintentionally, selective harvest of red grouse *Lagopus lagopus scotica*, for example, can strengthen cyclic population dynamics and raise the risk of stochastic extinction (Bunnefeld et al. 2009, 2011). Similarly, hunting of ring-necked pheasants *Phasianus colchicus* imposes a selective pressure against boldness, a phenotype often associated with traits important to pheasants such as fecundity and foraging ability (Biro and Stamps 2008, Madden and Whiteside 2014, Madden et al. 2018). Moreover, hunting may drive unexpected outcomes even for unharvested individuals, as space use (Messinger 2015) and other behaviors such as foraging (McGrath et al. 2018) are often affected by the presence of hunters on the landscape. Population-scale responses to the distribution of risk imposed by hunters may create landscape-scale patterns of prey distribution and behavior, with prey concentrated away from spaces and times of intense hunting pressure, likely with fitness consequences (Wirsing et al. 2008, Madin et al. 2011, Lone et al. 2015).

Given the potential for hunters to impose unexpected ecological and evolutionary pressures on game populations, there is a need to understand the decisions that create the landscape of risk for game animals. Like other animals, hunters use information when choosing spaces in which to hunt (Decker et al. 1980, Larson et al. 2014). Previous work has suggested that hunter movement may be influenced by prey abundance, the location of a starting point, or cues associated with previous hunting success (Brøseth and Pedersen 2000, Kaltenborn and Andersen 2009, Lande et al. 2010, Lone et al. 2014). Outdoor recreationists may also consider physical difficulty when choosing among recreational opportunities and make tradeoffs between the perceived quality and physical costs of an outdoor recreation experience (Merrill and Graefe 1998, Lee et al. 2007, Ólafsdóttir and Runnström 2013).

Whereas hunter habitat decisions are path-dependent, meaning that a decision at one step constrains decisions at all succeeding steps, the social and ecological cues considered, and the direction and strength of relationships, may change as a hunt progresses. Conclusions drawn about decisions observed at any one point in the hunt may therefore be misleading and limit the applicability of inferences about hunter behavior. Because the choice of a starting location can constrain hunter movements, we must examine both how hunters choose where to begin their hunts, and how they navigate through space for the duration of their hunts (Lima and Bednekoff 1999, Lima 2002). Herein, we use Nebraska ring-necked pheasant hunters to identify sources of social and ecological variation in hunter effort during two periods of the hunting trip: at access points at the start of a hunt, and within fields for the duration of a hunt. We define access points as the spaces comprising the perimeter of a hunting site and consider the area within a site to include the access points as well as the space they enclose. Our objectives were to assess:

1. How the spatial distribution and information content of public access infrastructure affected the spatial distribution of hunter effort among access points at the start of hunts, and
2. How prey distribution cues and physical exertion costs affected the spatial distribution of hunter effort within public access hunting sites for the duration of hunts.

Material and methods

Study system

Ring-necked pheasants are a historically popular and economically important gamebird across much of the United States. In Nebraska, pheasant hunting begins in late October and extends through the end of January (Nebraska Game and Parks Commission [NGPC] 2016). Walking through fields, most often accompanied by dogs (approximately 89% of the time in this system; Wszola et al unpubl.), hunters attempt to flush birds from vegetation and shoot males in flight (Supplementary video). In contrast to European driven hunts, where some hunters act as stationary shooters and other hunters drive pheasants toward the shooters, hunters in this system primarily move through fields behind dogs in groups averaging two hunters in size (Wszola et al. unpubl.). Pheasants in this system often flush well in front of both pointing and flushing dogs, so hunters must be prepared to shoot at any time. Although harvest is limited to males per regulation (NGPC 2016), female pheasants regularly encounter hunters.

To assess how variation in social and ecological features of hunting sites affect hunter spatial decisions, we monitored pheasant hunter movement within seven public access sites in Hitchcock and Hayes counties in southwest Nebraska, USA. Pheasant populations respond to variation in landscape structure and predation risk at multiple spatial scales, resulting in significant spatial variation in pheasant abundance and habitat use among and within sites (Jorgensen et al. 2014, Simonsen and Fontaine 2016, Stuber et al. 2017). The region is characterized by a semi-arid steppe climate and marks the transition between tallgrass and shortgrass prairie on the North American Great Plains. The elevation is approximately 800 m above sea level, and the region receives on average 57 cm of precipitation per year (National Oceanic and Atmospheric Administration 2018). Hunting parties in the region harvest pheasants on approximately 34% of hunting trips, and parties who harvest any pheasants most often harvest two (Wszola et al. unpubl.).

All sites consisted of fields enrolled in the federal Conservation Reserve Program and open to public hunting as part of NGPC's Open Fields and Waters (OFW) public access program (Lucas 2013). While vegetation characteristics like height and functional group composition varied between sites, all sites were characterized by some combination of native prairie grasses and forbs. Sites differed in area (24–183 hectares), public access infrastructure, and pheasant abundance, with all sites embedded in a matrix of privately owned rangeland and small grain agriculture. One site surveyed in 2015 was not re-enrolled in the OFW program during the 2016 field season, so we selected a similar replacement site, resulting in five sites with two years of data each, and two sites with one year of data each. All hunters arrived at sites in vehicles, parked their vehicles at a location of their choosing on the interface of the field and the road, and proceeded into fields on foot from a location of their choosing on the perimeter of the site.

GPS track collection

We assessed sources of variation in hunter access point effort at the start of hunts and among all quadrats for the duration of hunts by collecting GPS tracks from hunter volunteers. Hunter volunteers were actively recruited through informational fliers posted at local businesses, social media outlets operated by NGPC, and the Nebraska Fish and Game Association online forum (<www.nefga.org/forum>). Additionally, observers waited at fields and recruited hunters at the start of their hunts. We collected hunter movement data from 30 min before sunrise to 30 min after sunset, during the 2015 (31 October 2015–31 January 2016) and 2016 (29 October 2016–31 January 2017) pheasant hunting seasons. Because the vast majority of hunting activity occurs within the first two months of the season (Gruber et al. 2019), we concentrated our effort from opening day until

mid-December (15 December 2015 and 22 December 2016). For safety reasons, we did not collect data during the rifle deer season (14–22 November 2015 and 12–20 November 2016), or when precipitation rendered roads impassable, but pheasant hunter activity during these times was negligible (Gruber et al. 2019), reducing the potential for bias in our sampling effort. Because a significant proportion of the year's pheasant hunting activity occurs on opening weekend, we increased survey effort from opening day (the last Saturday in October) through the following Monday, positioning eight observers at the six sites from 30 min before sunrise to 30 min after sunset. Larger (100 + ha) sites were sampled by two observers concurrently. After opening weekend, sites were surveyed seven days a week by two observers in six-hour blocks, from 06:00 to 12:00 and from 12:00 to 18:00, or 30 min after sunset. Each site was surveyed approximately four times per week. Because more hunting activity occurs on weekends than weekdays, we randomized our sampling schedule each week to ensure that sites received an equal amount of survey effort on weekends.

Observers deployed one GPS unit (Garmin Forerunner 225 integrated heart rate monitor/GPS) to one member of the party chosen at random from the subset of individuals in the party who expressed their willingness to carry the GPS. Per institutional human subjects policy (IRB no. 20151015692EP), only parties with at least one individual over the age of 19 were included in the study and no individually identifiable information was collected. Hunters were instructed to begin recording data when they began their hunt or passed inside the field boundaries, and to stop recording data when they finished their hunt or left the field boundaries. The GPS units collected track points and heart rate measurements at a rate of approximately 8 locations per minute.

We quantified spatial variation in hunter effort by dividing study sites into one-hectare quadrats using the 'Fishnet' function in QGIS (QGIS ver. 2.18), resulting in a total of 392, 1-ha quadrats. Because the study sites were irregularly shaped, the fishnet procedure also produced 271 quadrats with area <1 ha. We therefore scaled hunter effort by quadrat area in all subsequent analyses. Because we quantified effort as the amount of time hunters spent in quadrats, we divided the number of GPS detections per hectare per study year by eight, the average number of detections per minute. The dependent variable in all subsequent analyses was thus the number of hunting minutes per hectare.

Access point effort

Defining access points

A hunter's decision of where to enter a site constrains subsequent decisions and influences the overall pattern of interactions with game populations (Mecozzi and Guthery 2008). We therefore examined social and ecological causes of variation in access point effort in addition to habitat decisions made for the duration of the hunting trip. Because hunters may legally enter the field from whatever perimeter location they choose, we defined access points as all study quadrats adjacent (110 m or less) to a field edge. We defined the 'start' of a hunt as the first two minutes of activity recorded within the boundaries of a study site. Two minutes approximates the time it takes an average adult to traverse a 1-ha study quadrat traveling in a straight, 100-m line (Knoblauch et al. 1996).

Public access infrastructure

Hunter starting location decisions may be influenced by the distribution of public access infrastructure. Hunters on foot may make increased use of the spaces near roads because roads reduce the time and physical difficulty of accessing a space (Stedman et al. 2004). Additionally, hunters on foot are subject to laws and norms regulating their behavior (Sigmon 2004, NGPC 2016). Infrastructure such as 'hunting permitted' signs and trails signal to hunters that a space may be legally hunted, whereas 'no hunting' signs indicate that a space is not legally available.

We extracted the locations of county roads and highways using the U.S. Census Bureau road layer, and digitized unmapped roads from satellite images in Google Earth. Our definition of roads included numbered county roads and trails created by agricultural activity at the edges of the study sites (Supplementary material maps). We identified and recorded with a handheld GPS unit the locations of all signs, including bright yellow public access signs and signs marking the 200-yard radius safety zone around occupied structures and livestock. We assigned each quadrat a distance to road value by calculating the minimum Euclidean distance from any point in the quadrat to any road. We then calculated minimum Euclidean distance to a yellow 'hunting permitted' access sign from each quadrat and classified the quadrat as either included in or adjacent to a safety zone, or not included in or adjacent to a safety zone.

Hunter effort within fields

Smoothing heart rates

Hunters may make tradeoffs between visit quality and physical exertion (Stedman et al. 2004). We thus assessed the relationship between hunter heart rate, a well-established correlate of physical exertion, and hunter effort in study quadrats (Tanaka et al. 2001). To quantify the variation in physical exertion within public access hunting sites, we created kernel-smoothed estimates for each quadrat of variation in individual heart rate throughout a pheasant hunting trip. Because individual hunters had different resting heart rates, we scaled each heart rate observation as a percent of the minimum observed during that trip. We used the 'smooth' function in the R package SpatStat (Baddeley et al. 2018) to interpolate scaled heart rate estimates over an observation window defined by the study sites, plus a 200-m buffer to minimize edge effects. We selected our smoothing bandwidth using mean-squared error cross validation and used Diggle's improved edge correction to prevent a negative bias at the edges of the observation window (Diggle 1985, 2010, Berman and Diggle 1989, Baddeley et al. 2015).

Pheasant distribution

Hunters presumably make habitat decisions in response to the expected and actual distribution of prey within a field. For example, a hunter may use a space where they expect to find pheasants given their perceptions of habitat quality or other cues. Because pheasant habitat use may affect

hunter effort, we monitored the locations of pheasants within the same fields where we collected GPS tracks. As part of an ongoing study of pheasant ecology, we captured male and female pheasants by nightlighting. Pheasants with mass exceeding 500 g were fitted with a 22-g necklace-style A4060 VHF transmitters (Advanced Telemetry Systems, Isanti, MN) transmitting a standard 40 ppm signal with an 8-h, 80 ppm mortality circuit. Pheasant locations were estimated 3–4 times per week via vehicle-based telemetry from 1 September (two months prior to the hunting season) to 31 January (the last day of the hunting season). We rendered locations in the field using LOAS (Location of a Signal – Ecological Software Solutions LLC). If a location estimate did not converge or if its error ellipse exceeded 0.1 ha, we collected additional bearings to reduce the size of the error ellipse. If the error ellipse could not be reduced to <0.1 ha, we excluded the location from the analysis.

In addition to VHF telemetry, we also fit a subset of females with Lotek PinPoint 450 GPS tags packaged with TW51 VHF transmitters, broadcasting at 40 ppm with a 12-h mortality circuit transmitting at 80 ppm. The combined unit weighed <30 g, and was only placed on birds with mass exceeding 600 g. The GPS tags were programmed to collect points at scheduled intervals from 15 October to 31 January. To prevent temporal auto-correlation we subsampled the combined vector of GPS and VHF locations to one location per pheasant per day.

To assess the effect of within-field pheasant habitat use on hunter effort, we used the 'density' function in the R package spatstat across observation windows defined by the site boundaries (Baddeley et al. 2018) to create kernel-smoothed estimates of pheasant detection intensity in each quadrat for each year (Baddeley et al. 2015). The measure of pheasant intensity used in all subsequent analyses was thus smoothed pheasant detections per hectare. We selected our smoothing bandwidth using a likelihood Cox point process and applied a Diggle edge correction to control for negative bias at window edges (Diggle 1985, 2010).

Vegetation structure

Features of the vegetation community such as tall grass or forbs can provide cues of pheasant habitat quality, but may also increase the physical difficulty of moving through a space. We thus quantified variation in vegetation height within the study sites to assess whether variation in the vegetation community affected hunter effort by recording vegetation height from September to December in 2015 and 2016 (Jorgensen et al. 2013). Because vegetation characteristics on the study sites are highly repeatable across years, we also included vegetation measurements collected from September to December 2014 as part of a pilot study. We surveyed vegetation at an intensity of 1.24 points per hectare using the Breeding Bird Protocol (Martin et al. 1997). We characterized variation in vegetation height across study sites by creating a smoothed estimate for each quadrat, as described above. We selected the smoothing bandwidth using likelihood cross validation assuming an inhomogeneous Poisson process, allowing the smoothing algorithm to adaptively adjust the smoothing bandwidth in a non-random point pattern, and used Diggle's improved edge correction to prevent negative bias at window edges (Diggle 1985, 2010).

Analysis

We assessed sources of variation in hunter access point effort (hunting minutes per hectare) during the first two minutes of each hunt and among all quadrats for the duration of hunts in the R statistical environment (ver. 3.5.2, <www.r-project.org>). We fit generalized linear mixed models (GLMM; Bolker et al. 2009) in package MCMCglmm (Hadfield 2012, 2018) using priors with mean 0 and large variance and log-normal error distributions to guarantee positivity of back-transformed predictions. We estimated parameter means and 95% credible intervals using 10 000 draws from the joint posterior distributions, confirmed convergence using trace plots and Gelman–Rubin scale reduction factors and assessed model fit by calculating mean absolute error (Brooks and Gelman 1998, Gelman and Su 2018). We visually examined residuals for autocorrelation and evaluated fixed effects for collinearity.

We fit one GLMM including nested random effects of quadrat and site to assess the conditional effects of public access infrastructure features (i.e. roads, access signs and safety zones) on the magnitude of hunter effort (hunting minutes per hectare) that access points received in the first two minutes of hunts. Fixed effects included the minimum distance from any point in the quadrat to a sign indicating that the site was open to hunting, minimum quadrat distance to road, a binary variable describing whether the quadrat was part of or adjacent to a safe zone around occupied structures or livestock, and study year.

We explored how the distribution of direct and indirect cues of pheasant distribution, as well as spatial variation in physical exertion, affected the number of hunting minutes per hectare received by habitat patches within public access hunting fields for the duration of hunts by fitting one generalized linear mixed model. As above, the model included a nested random effects of study site and quadrat. Fixed effects included smoothed pheasant detections per hectare, smoothed heart rate, smoothed vegetation height, and distance from field edge. We first tested for the possibility of quadratic relationships for heart rate and vegetation, but present the results of a linear-only model, as there was no evidence of quadratic relationships (data not shown).

Results

We recorded 132 geo-referenced heart rate tracks and tracked 241 pheasants in the 2015 and 2016 seasons. Hunters spent a mean (± SE) of 54.65 ± 2.76 min in a field. Access points received a mean of 0.59 ± 0.59 hunting minutes per hectare at the start of hunts, and quadrats received a mean of 8.12 ± 4.01 hunting minutes per hectare during the duration of hunts (Supplementary material maps). Of 663 unique quadrats surveyed, 109 received no receorded effort in either year. We recorded 1317 pheasant locations within the boundaries of the study sites and estimated a mean of 1.08 ± 0.05 pheasant detections per hectare per year, with a maximum pheasant observation intensity of 15.14 pheasant detections per hectare per year.

Hunter access point effort was negatively related to distance (m) from a public access sign (post. mean = −6.216 e-04, 2.5% CI = −8.206 e-04, 97.5% CI = −4.121 e-04;

Table 1. Posterior means and 95% credible intervals for the regression assessing sources of variation in hunter access point effort at public access hunting sites. Credible intervals that do not overlap zero are highlighted in bold.

	Posterior mean	2.5% CI	97.5% CI
Intercept (study year 2015, outside safe zone)	0.516	0.273	0.745
Study year 2016	−0.016	−0.095	0.063
Distance from sign (m)	−6.22 e-04	−8.21 e-04	−4.12 e-04
Within or adjacent to safety zone	−0.145	−0.267	−0.017
Distance from road	1.20 e-04	−8.19 e-05	3.33 e-04

Table 1, Fig. 1). Access points located in or adjacent to a marked 200-m radius safe zone around livestock or occupied structures received less effort than access points that were not part of a safe zone (post. mean = −0.145, 2.5% CI = −0.267, 97.5% CI = −0.017). Hunter access point effort was not associated with distance from roads (post. mean = 1.20 e-04, 2.5% CI = −8.19 e-05, 97.5% CI = 3.33 e-04). Mean absolute error was 1.00 for a range of [0, 47.62].

Within fields, the number of hunting minutes per hectare was positively related to pheasant detections per hectare (post. mean = 0.106, 2.5% CI = 0.073, 97.5% CI = 0.140; Table 2, Fig. 2), negatively associated with distance from field edge (post. mean = −0.004, 2.5% CI = −0.005, 97.5% CI = −0.003), heart rate (post. mean = −0.004, 2.5% CI = −0.008, 97.5% CI = 0.001), and vegetation height (post. mean = −0.006, 2.5% CI = −0.010, 97.5% CI = −0.002). Mean absolute error was 6.71 for a range of [0, 523.81].

Discussion

Wildlife managers are increasingly working to mitigate unintended effects of hunting on game populations (Allendorf and Hard 2009, Proffitt et al. 2009, Turner et al. 2016, Leclerc et al. 2017). Herein, we provided an examination of the factors influencing where pheasant hunters began their hunts and what space they used for the duration of their hunts. Nebraska pheasant hunters responded to direct and indirect cues of public land access and pheasant distribution when accessing hunting locations and moving through fields during their hunts. Hunters made greater use of access points that provided cues of public land accessibility and avoided potential access points with prohibitions against hunting. During the rest of their hunts, hunters spent more time in spaces that were also more used by pheasants, and less time in spaces that required more exertion to access. Our finding that hunter habitat decisions incorporate information about prey availability and accessibility suggests that humans, like other animals, make tradeoffs between finding prey and incurring physical costs. Our results further suggest that wildlife managers may be able to make more informed tradeoffs between providing a quality hunting experience and minimizing unwanted effects on game populations by managing the information available to hunters.

Hunters moving through public access fields responded to direct and indirect cues of pheasant habitat use, but their behavior was constrained by their use of starting locations that provided cues of public land access. Our finding that hunter access point effort was not affected by proximity to roads is perhaps counter-intuitive, especially given previous evidence that roads affect hunter behavior (Trombulak and Frissel 2000, Havlick 2002, Bonnot et al. 2013). However, Nebraska differs from most other systems in which hunter movement behavior has been monitored (Stedman et al. 2004, Lone et al. 2014) in that the average distance of access points from roads is lower and more predictable. In contrast, the positive relationship between hunter effort and sign placement agrees with and expands upon previous evidence that hunters are sensitive to the distribution of access infrastructure (Stedman et al. 2004, Hunt 2005). Lower hunter effort in safety zones further

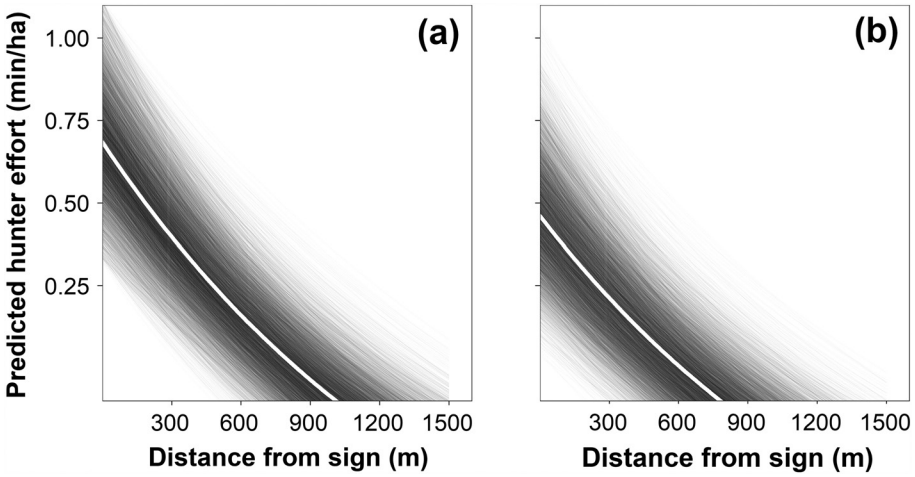

Figure 1. Pheasant hunter access point effort at public access hunting sites was negatively associated with increasing distance from public access hunting signs. Access points outside safety zones (a) received more use on average than did access points inside safety zones (b). White lines represent parameter means and black lines represent individual MCMC iterations within the 95% credible intervals.

Table 2. Posterior means and 95% credible intervals for the regression assessing sources of variation in hunter effort within public access hunting sites. Credible intervals that do not overlap zero are highlighted in bold.

	Posterior mean	2.5% CI	97.5% CI
Intercept (study year 2015)	2.810	2.155	3.503
Study year 2016	−0.126	−0.224	−0.033
Distance from edge (m)	−0.004	−0.005	−0.003
Vegetation height (cm)	−0.006	−0.010	−0.002
Heart rate (% of minimum)	−0.004	−0.008	−0.001
Pheasant detections per ha	0.106	0.073	0.140

suggests that hunters respond to legal and social pressures imposed by the information content of signage. Given the (perhaps unconscious) propensity of hunters to respond to simple cues like signage, our results suggest that managers may be able to shape hunter–prey interactions by managing cues of public land access. Managing hunter behavior is increasingly a priority for state and provincial game agencies (Festa-Bianchet et al. 2014) and one that may have particular importance in hunting systems like pheasant hunting where non-target members of the population experience unintended consequences.

Unfortunately, mitigating the unintended consequences of pheasant hunting is challenging because land-use change increasingly limits the area of land suitable for pheasant habitat and hunting. In the United States, CRP grasslands are a favored habitat of both pheasants and pheasant hunters (Anderson and David 1998, Hiller et al. 2015, Pabian et al. 2015), but CRP enrollment has steadily declined with negative consequences for pheasant populations and pheasant hunters (Ryan et al. 1998, Taylor et al. 2018). To offset the consequences for hunters, state agencies are under increasing pressure to provide hunter access to CRP by increasing landowner incentives in priority landscapes. Although ostensibly good for pheasant hunters, the consequences of fewer highly productive habitats receiving ever-increasing hunting pressure are less clear for pheasant populations. The habitat created by management is essential to ensuring that future generations can hunt wild pheasants, making the question of how to optimize public lands for wildlife habitat and recreational opportunity ever more pressing.

Our assessment of hunter movement indicates that hunters, like other predators, make tradeoffs between the costs and benefits associated with pursuing prey. Hunter effort increased closer to field edges, which hunters perceive to

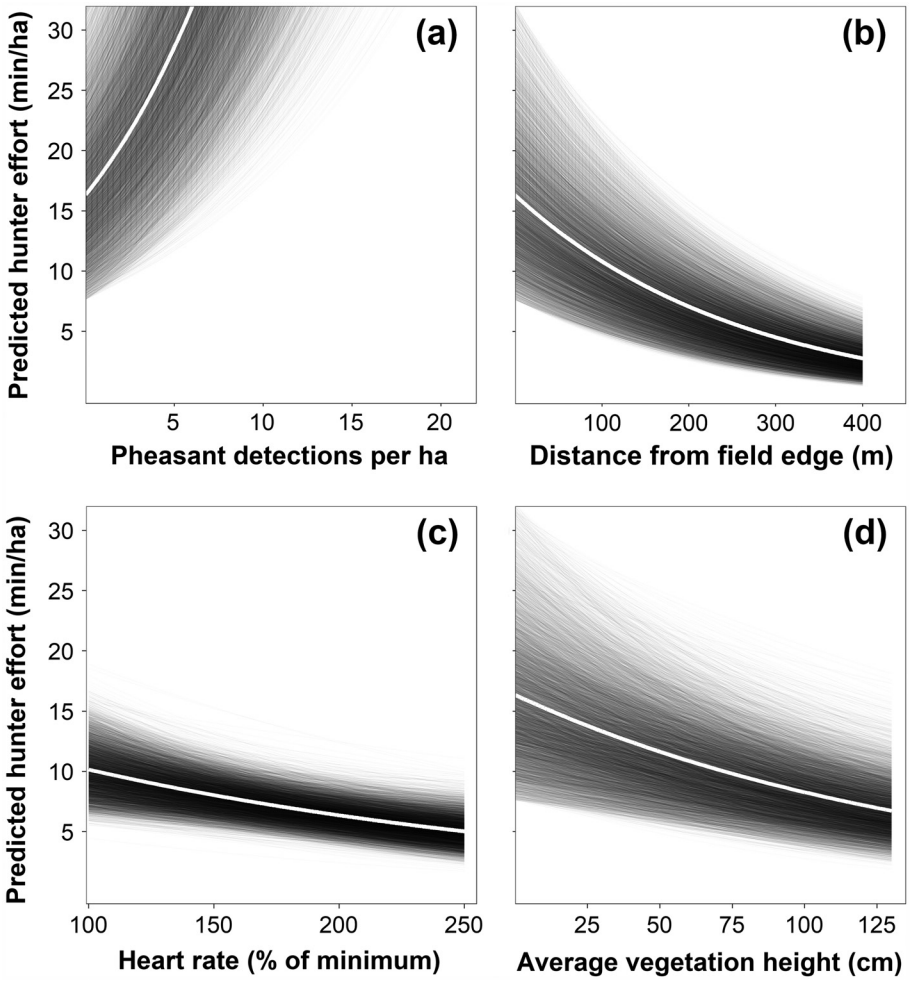

Figure 2. Pheasant hunter effort within public access sites was positively associated with pheasant detection intensity (a), and negatively associated with increasing distance from field edge (b), heart rate (c), and increasing vegetation height (d). White lines represent parameter means and black lines represent individual MCMC iterations within the 95% credible intervals.

provide resources for upland game birds. Hunters also spent more time in spaces that were also more used by pheasants, potentially reflecting their knowledge of pheasant habitat needs or even previous experience hunting the same locations. Still, pheasant habitat use may vary in space and time, requiring hunters to incorporate real-time information into their habitat decisions. As hunters are largely unable to detect pheasants directly, the correlation between pheasant habitat use and hunter effort likely reflects hunters tracking dogs that use olfactory cues to find pheasants (Furton 2001, Mecozzi and Guthery 2008, Richardson et al. 2008). Working as a team, hunters can direct dogs into regions within a field where they may expect to encounter pheasants based on previous experience or expectations (Hare and Tomasello 1999, Szetei et al. 2003) and then allow the dogs to direct them to specific locations, with hunters consequently spending more time in areas used by pheasants while searching for and potentially recovering birds.

That pheasant hunters appear to avoid areas with thick vegetation, a habitat type typically preferred by pheasants (Pauly et al. 2018), may speak to tradeoffs between prey availability and accessibility made by dogs and hunters. Beyond avoiding thick vegetation, hunters tended to avoid areas that were associated with increased heart rate. Decreased effort in spaces with tall vegetation or physically stressful conditions may indicate that pheasant hunters, like other predators, chose less physically costly spaces. Tall vegetation may additionally impede dog movement, disrupt olfactory cues, or reduce shooting ability, decreasing the likelihood that hunters following dogs and carrying shotguns will use spaces with taller vegetation. Although the vast majority of hunters in our system hunted with dogs, this is not necessarily representative of all upland gamebird hunting systems, as hunting dogs are expensive and time-consuming to train and care for. It could therefore be of great interest for future studies to compare the spatial behavior and effect on game populations of hunters with and without dogs. Ultimately, our findings underscore that hunter spatial decisions are an emergent outcome of information hunters bring to their hunts and information they process during the hunt.

Though hunters were more likely to use spaces most used by pheasants, areas of the study sites far from public access signs and field edges received little or even no recorded effort regardless of pheasant detection intensity (Supplementary maps). The tradeoffs hunters make between cues of prey availability and prey accessibility therefore suggest it may be possible to manage undesirable effects of hunting by 'nudging' hunters toward an optimal distribution of hunting pressure (Jolls et al. 1998, Thaler and Sunstein 2008). Specifically, it may be possible to create areas of refuge with lower hunting pressure within heavily used public lands by strategically placing public access infrastructure to draw hunting pressure away from more remote intended refuges. Managers of large public lands with multiple roads could strategically open and close roads to limit the spatial distribution of vehicle traffic and thus sway hunters toward entering public lands at certain points. Likewise, those managing portfolios of smaller temporary properties like those in our study could seek to enroll larger properties with rugged or more remote areas, or cluster signs on parts of the property they wish to receive greater effort. Such a nudge-based approach could be a valuable addition to a management toolbox because it can be deployed by individual managers using expert knowledge about their systems, without the need to impose potentially unpopular new regulations.

The distribution of hunting effort by Nebraska pheasant hunters reflects the distribution of multiple sources of information about pheasant availability and accessibility. As the amount of suitable land available to both pheasants and pheasant hunters decreases, it will become increasingly essential to optimize available land for habitat and recreational value. Strategic communication of public land accessibility and species–habitat relationships may nudge hunters toward ecologically optimal distributions of hunting pressure, increasing the habitat value of public lands while maintaining hunting opportunity.

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Supplementary material (the supplementary maps and video may be accessed at <https://osf.io/c7tfz/?view_only=570627ecdfa0495abcf2b1a55452b6a5>).

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