HABITAT AND SITE SELECTION OF PHEASANTS AND THEIR HUNTERS

DURING THE HUNTING SEASON

by

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Predator-prey interactions are dynamic and complex with implications for predators, prey, and entire ecological communities. Though predation has obvious mortality costs for prey, equally strong non-consumptive impacts of predation have been the focus of recent studies. Not only are prey affected by their predators through both consumption and fear of predation, but predators are driven by selection to respond to prey behavior. Here, we show how habitat decisions made by highly mobile predators and prey are dynamically linked. In our study system, recreational hunters (predators) make decisions about where to hunt based on a variety of resources (potential prey abundance, proximity to home) and we show that hunters preferentially select hunting locations where the density of primary habitat for their prey, the Ring-necked Pheasant (*Phasianus clochicus*), is greatest despite other resources (roads, towns). Targeted habitat selection by hunters as well as distinct periods of prey availability due to regulated hunting seasons create a spatially and temporally variable environment of predation risk in which prey are capable of responding. Female pheasants increased their home range size and shifted the center of their core home range in response to high risk at the onset of the hunting season. However, these responses diminished over time. Male mortality during the first few weeks of the hunting season further confirmed the short-term impacts

of high hunting pressure early in the season, though this effect diminishes over time with hunting having compensatory mortality effects on pheasant populations by the close of the hunting season. Our data demonstrate factors influencing both predator and prey habitat decisions and give a more holistic view of a predator-prey interaction with implications for wildlife managers concerned with maintaining healthy populations of both predator and prey.

DEDICATION

To my brother, Zach, and my best friend, Rooster, young lives that ended much too soon.

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CHAPTER 1: HABITAT SELECTION AND THE INFLUENCE OF FEAR

Abstract:

Predation has obvious consumptive impacts on prey populations through direct mortality, however the non-consumptive impacts of fear on prey populations is less understood, largely due to the difficulty of separating consumption from fear. Using a unique study system where regulations prohibit the harvest of female Ring-necked Pheasants (*Phasianus colchicus*), we were able to separate the consumptive and non-consumptive impacts of predation risk allowing us to present some of the first evidence of fear impacts on a wild prey population exposed to lethal predators. Furthermore, predation risk varies spatially by site and temporally by season in this system, allowing us to assess how spatial and temporal variation in predation risk manifests in prey habitat decisions at multiple ecological scales. We found an initial behavioral response to predation risk, independent of the selective effects of mortality, at a macro-habitat scale, with females on high risk sites increasing their home range size and shifting the center of their core home range, while females on low risk sites, and all males, showed no change in home-range formation with the onset of the hunting season. However, the long-term effect of predation risk disappears over time with female home range size returning to pre-hunting season levels by the end of the hunting season. Behavioral responses at the micro-habitat scale were less conclusive as limited sample sizes due to mortality prohibit us from drawing strong inferences. Finally, though there does appear to be an initial behavioral response to hunting pressure at the macro-habitat scale and hunting activity appears to be additive during the first several weeks of the hunting season, survival between the high and low risk sites does not differ for males or females, suggesting the

impacts of predation, both direct and indirect, to overall survival in this system is compensatory. Our findings not only provide evidence of fear effects on a wild prey population, but provide wildlife managers with a more holistic perspective of hunter impacts on a wild game population with implications for managing the species into the future.

INTRODUCTION

Habitat decisions have profound implications for individuals, and ultimately shape population and community dynamics (Fretwell and Lucas 1970, Rosenzweig 1991, Holmes et al. 1996, Morales et al. 2010). Resource limitation, predation, competition, and unfavorable climate all influence habitat decisions (MacArthur and Levins 1964, Whitham 1978, Jorde et al. 1984, Gilliam and Fraser 1987, Binckley and Resetarits 2005); however, sources of selection are not static, rather they vary in space and time with implications for how individuals select appropriate habitats (Orian and Wittenberger 1991, Johnson et al. 2001, Heithaus and Dill 2006). Additionally, sources of selection drive habitat decisions across a range of spatial and temporal scales, with individuals and even species showing response at one scale, but not others (Orian and Wittenberger 1991, Johnson et al. 2001, Turner and Montgomery 2003). Spatial and temporal variation in predation risk is an important ecological condition that influences a variety of behaviors, including habitat decisions (Creel et al. 2005, Fontaine and Martin 2006, Valeix et al. 2009). Across taxa there is clear evidence that individuals are found disproportionately in habitats that limit exposure to predators (reviewed by Lima and Dill 1990, Lima 1998); however, most studies assessing habitat decisions in response to predation risk have treated risk as either spatially explicit, associating discrete locations with static measures of long-term risk (risky places hypothesis, i.e., Hebblewhite et al. 2002, Frid et al. 2008), or temporally explicit, measuring response at one particular time (i.e., risky times hypothesis, Lima and Dill 1990, Lima 1998). Few studies have evaluated behavioral decisions in response to both spatial and temporal variation in risk (e.g. risk allocation

hypothesis, Lima and Bednekoff 1999), and those that do often reach novel conclusions (Sih and McCarthy 2002, Creel and Winnie 2005, Creel et al. 2008, Tolon et al. 2009).

The inclusion of spatial and temporal variation in predation risk is imperative for understanding how predators shape prey communities (Creel and Winnie 2005), but understanding how predators influence where prey are found is further complicated by the complexities inherent in risk. Although predation risk is indicative of the probability of encounter, detection, and capture of prey by predators (Lima and Dill 1990), the effects of risk on prey populations are further reaching. An emerging body of research suggests that fear (the perception of predation risk) is a significant ecological condition that alters habitat use, time allocation, species distribution, population growth, and species interactions (Sih 1987, Lima and Dill 1990, Lima 1998, Frid and Dill 2002, Cresswell 2008, Laundré et al. 2010) even in the absence of actual mortality (Schmitz 1998, Zanette et al. 2011). However, despite the potential importance of fear in shaping habitat decisions, in most systems it remains unclear the extent to which differential selection via consumption at the population level, versus phenotypic shifts in behavior driven by fear at the individual level, actually shape observed shifts in prey populations. Do we fail to find individuals using high risk environments because they have been depredated or because they are expressing risk adverse phenotypes (fig. 1-1)?

Unfortunately, separating the effects of consumption from fear is difficult in wild populations as they are inherently linked. Most studies that have successfully isolated fear effects have done so in laboratory settings by experimentally modifying predators so they are unable to consume prey (Schmitz 1998, Nelson et al. 2004), or in the wild by presenting prey with select predator cues (e.g., chemical, auditory) in the absence of the

predators themselves (Lima 1998, Zanette et al. 2011). Though capable of providing some insight on the relative effects of consumptive predation and fear, the laboratory and manipulative nature of these experiments lack important features of predator-prey dynamics found in natural environments. The absence of predators capable of consumption results in prey populations that receive no feedback—positive or negative— from the expression of anti-predator responses. However, feedback from predator-experienced conspecifics in the presence of predators enhances anti-predator responses even in naïve prey (Kelley et al. 2003). In experimental systems where prey do not observe conspecific mortality or experience injury from exposure to a predator presenting actual predation risk, prey receive no such feedback and are unable to optimize anti-predator behavior (Kelley et al. 2003). Additionally, wild prey are presented with a suite of cues indicative of predator presence (e.g., chemical, visual, auditory; Smith and Belk 2001). However, for obvious logistical reasons, laboratory and field experiments tend to focus on a subset of potential cues, limiting our understanding of how prey respond in natural settings when presented with a full range of predator cues. If we are truly to understand the relative importance of fear in shaping the habitat decisions of prey independent of mortality, we must separate the consumptive effects of predation from the effects of fear. Moreover, if we are to ensure that prey habitat decisions are indicative of the sources of selection acting through fear, we must measure prey decisions under conditions that incorporate spatial and temporal variation in a variety of cues indicative of risk and measure responses at multiple ecological scales.

To isolate the fear effects of predation in a wild population, we assessed habitat decisions of wild Ring-necked Pheasants (*Phasianus clochicus*) in response to spatial and

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temporal variation in recreational hunting activity by humans. Human hunters illicit similar anti-predator responses as those prompted by natural predators (Frid and Dill 2002, Proffitt et al. 2009), likely because human hunters search for prey in a similar manner, and are often accompanied by domestic dogs who strongly mimic the appearance and actions of natural predators, making pheasant hunting an appropriate system for understanding predator-prey dynamics. Importantly, however, while recreational hunting represents a consumptive predation risk for male pheasants, females only experience the non-consumptive fear effects associated with predation because although females cohabitate with males, harvest is limited to males. Females therefore receive feedback and reinforcement for the expression of anti-predator responses in the presence of recreational hunters, but females only experience the fear effects of predation as their harvest is prohibited, allowing us to isolate actual predation risk from fear. Moreover, our study system allows us to test spatial and temporal variation in predation risk simultaneously as hunting pressure (risk) varies spatially among fields and temporally through regulated hunting seasons and variation in hunting pressure within the hunting season.

METHODS

STUDY SPECIES

The Ring-necked Pheasant is a non-native upland game bird that is an economically and culturally important species coveted by recreational hunters in the central Great Plains of the United States. Pheasants are hunted in the fall and winter months by hunters on foot who are typically accompanied by dogs, and birds are primarily harvested with shotguns

as they are flushed from vegetation. Pheasants are sexually dimorphic, and as such sexes

can be discriminated in the field, with hunters permitted to harvest males only. Pheasants

make an excellent study species to separate consumptive impacts of hunting (imposed on

males only) from fear effects (experienced by males and females) because harvest is

legally restricted to males, but both sexes are exposed to the multitude of cues that are

indicative of risk.

STUDY AREA AND SITES

Our study took place on ten privately owned sites in Hitchcock and Hayes counties in

Southwestern Nebraska ranging in size from 29 to 155 hectares. All study sites were

enrolled in the Conservation Reserve Program (CRP) and dominated by warm and cool

season grasses with interspersed forbaceous vegetation and minimal woody components.

All sites were surrounded by a matrix of habitats including agricultural lands

(predominately dry-land winter wheat and milo and irrigated corn and soybeans),

rangeland pastures, and other CRP grasslands. Five sites were open to public access

hunting and received relatively high levels of hunting pressure ('high risk'), while access

to the remaining five sites was restricted to hunters granted permission by the landowner

and received relatively little to no hunting pressure ('low risk') (fig. 1-2).

ASSESSMENT OF HUNTING PRESSURE

We used remote cameras to document hunting pressure through daily hunter

detections at each study site. We placed cameras (Mountrie model M880, Bushnell

Trophy Cam) at fixed, elevated locations in an arrangement and manner that maximized

visualization of the site and minimized overlap in the field of view of each camera.

Cameras were mounted at a height and the field of view was such that individuals were not identifiable; however, blaze orange worn by most hunters was readily visible. Cameras were programmed to take one photograph every five minutes during legal hunting hours (30 minutes before sunrise and after sunset) each day for the duration of the 98-day pheasant hunting season (last weekend in October - 31 January) for the 2012-2013 and 2013-2014 hunting seasons. Each photograph was visually inspected for hunter presence and the date, time, and site of photographs were recorded. Hunter detections (present or absent) were summarized each day of the 98-day hunting season by calculating the mean hunter detections on high risk and low risk sites during each study year. We tested for differences in mean hunter detections between risk groups using linear mixed-effects models using package "lme4" (Bates et al. 2014) in Program R (version 3.1.2, R Development Core Team 2014). Risk group and hunting season date were incorporated as independent variables with year as a random effect.

PHEASANT CAPTURE

We captured pheasants via nightlighting (Labisky 1968) from 12 - 28 September 2012 and 10 September - 13 October 2013, and fitted each bird with a 22- or 26-gram (<5% pheasant body mass, Kenward 2001) necklace style VHF radio transmitter (Model #A4070, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) or a 20-gram combination GPS/radio necklace style transmitter (GiPSy 4, Technosmart, Rome, Italy, Advanced Telemetry Systems). Each individual was also marked with a uniquely numbered aluminum leg band for subsequent identification (via nightlighting or hunter harvest) in the event of radio collar loss or malfunction.

RADIO TRIANGULATION

We recorded movements of individual radio-tagged pheasants 3-7 days per week during approximately 1 October - 15 December via radio telemetry using truck-mounted, null-peak antenna systems (Brinkman et al. 2002, Gilsdorf et al. 2008). To reflect the full range of distinct habitats required by pheasants in the course of a day, we located pheasants during foraging (1-hr before sunrise to 2-hr after sunrise and 2-hr before sunset to 1-hr after sunset), loafing (2-hr after sunrise to 2-hr before sunset), and roosting (1-hr after sunset to 1-hr before sunrise). To obtain each location, a minimum of three bearings were taken within a 20-minute period to minimize biases and error associated with bird movement (Kenward 2001). Estimated location as well as associated error ellipses (calculated based on maximum likelihood estimations; Lenth 1981) were processed in the field using on-board computers and Location of a Signal (LOAS) software (Ecological Software Solutions, LLC, Hegymagas, Hungary, Version 4.0). Bearing sets with error ellipses >2000 m^2 were discarded or additional bearings were taken until error ellipse size was <2000 m^2 for daytime locations (foraging and loafing locations) and <1000 m^2 for nighttime (roosting) locations. Higher precision for roost sites was desired as roost sites were re-located in the field for vegetative assessment.

HABITAT DECISIONS

The primary factors limiting pheasant survival, and influencing body condition during the non-breeding season—when pheasants are exposed to recreational hunting activity—are the availability of winter cover and food resources (Gates and Hale 1974, Gatti et al. 1989). Our objective was to evaluate the role of fear in shaping habitat decisions of

pheasants at two spatial scales: Macro-habitat (home range formation) and micro-habitat (roost site selection). It is reasonable to expect that fear may shape prey behaviors differently at different scales and as such, evaluating habitat decisions at multiple scales allows us to evaluate the full range of potential fear impacts (Orian and Wittenberger 1991, Lima and Zollner 1996, Hebblewhite and Merrill 2009).

Macro-habitat

A home range—the spatial representation of the area an individual occupies while carrying out activities needed to survive and reproduce—represents a dynamic and plastic habitat decision that individuals make while considering multiple trade-offs (Morris 1992, Hebblewhite and Merrill 2009). Numerous sources of selection, including resource limitation, predation, competition, and unfavorable climate all interact to influence home range size and location (Tufto et al. 1996, Anderson et al. 2005). Maintaining a home range is re-enforced by increased efficiency and speed in conducting fitness-enhancing activities such as foraging, predator avoidance and escape, and mate location and reproduction (Stamps 1995). However, home range formation must be fluid with individuals continuously weighing and assessing changes in various sources of selection over both space and time, and adjusting home ranges accordingly. Here, we are interested in the role of fear in shaping pheasant home range size and location. Changes in home range size and location allow us to assess the effects of both spatial (low and high risk sites) and temporal (prior to and during the hunting season) variation in predation risk. Moreover, because home range formation occurs at the individual level, we can use measures of home range size and shifts in core 50% home range center over space and

time to evaluate and separate the fear effects of predation risk from mortality effects by

evaluating both female (fear only) and male (fear and mortality) responses to spatial and

temporal variation in predation risk.

Home range assessment

Radio locations recorded prior to the onset of hunting season (1 October - 25

October, referred to as "pre-hunting season" hereafter) were separated from those

recorded during the hunting season and serve as the before impact control within each

risk group (low and high hunting pressure sites). Previous research (Stokes 1968, Leif

2003), as well as the current study (fig. 1-3a), shows that pheasant hunting pressure is not

constant over the hunting season with the majority of hunter effort and hunter harvest

occurring within the first few weeks of the hunting season. Given the change in hunting

behavior it is reasonable to expect pheasant behavior early in the hunting season to differ

from that later in the season when hunting pressure is substantially lower. Therefore, we

divided radio telemetry locations recorded during the hunting season into "early-" and

"late-" hunting seasons according to *a priori* predictions of pheasant response to temporal

variation in hunting pressure. The early-hunting season (27 October - 23 November)

represents an immediate behavioral response to hunting pressure whereas the late-hunting

season (24 November - 15 December) allows us to determine if immediate behavioral

responses continue given a reduction in predation risk as the hunting season progresses.

Home range size

We used radio locations from each daily period (foraging, loafing, roosting) in the

quantification of 95% home ranges and calculation of centers for core 50% home ranges

for each individual during each season (pre-, early-, and late-hunting seasons). Home

ranges were estimated using fixed kernel utilization distributions (Van Winkle 1975,

Worton 1989, Powell 2000, Calenge 2011) calculated using the "adehabitatHR" package

(Calenge 2006) in Program R (version 3.1.2, R Development Core Team 2014) with

smoothing parameter h_{ref}. We calculated kernel utilization distributions because they

provide a more accurate representation of space-use by individuals by using the complete

distribution of locations unlike more traditional home range estimators, such as minimum

convex polygons (MCP) that are largely dependent on the outermost set of locations.

Kernel utilization distributions take into consideration the density of re-locations giving a

more accurate assessment of the relative importance of various portions of an individual's

home range and are less sensitive to outliers (Kernohan et al. 2001). Individuals with

fewer than 10 radio-locations during a given season were excluded from analysis for that

season to reduce errors in home range estimation associated with small sample sizes.

Still, division of data into distinct "seasons" resulted in estimates that were generated

using fewer than the recommended number of relocations (10-25 versus 30-50, Seaman

and Powell 1996, Seaman et al. 1999); however, estimates include a broad suite of

potential movements allowing us to assess immediate changes in home range size that

would be less evident over longer time-frames. We tested for differences in home range

size between risk groups (high and low) and across seasons (pre-, early-, and late-) for

male and female pheasants using mixed effects models using package "lme4" (Bates et

al. 2014) in Program R (version 3.1.2, R Development Core Team 2014). Risk group and

hunting season were incorporated as independent variables with site and year as random

effects.

Micro-habitat

Nightly roost site selection is crucial for providing pheasants safety from predators and thermal protection in the face of harsh weather conditions (Walsberg and King 1980, Warner and David 1982), and thus represents an important microhabitat decision. In our study system, CRP grasslands are the primary source of vegetative cover for predator concealment and thermoregulation (Messinger pers obs.), but CRP grasslands permitting public access hunting also present increased predation risk. If predation risk drives trade-offs in roost site selection, we expect pheasants to occupy roost sites in areas with less risk in the form of hunting pressure, but potentially poorer thermal cover (i.e. adjacent pasture and crop lands) in an effort to reduce predation risk. Alternatively, if thermoregulation were the primary determinant of roost site selection, we would expect pheasants to remain in risker locations despite potential predation costs in favor of higher-quality thermal cover. This trade-off between thermoregulation and predation risk influences microclimate selection in a variety of taxa (Wiebe and Martin 1998, Pitt 1999, Carr and Lima 2012). Our objective was to determine if fear alters the trade-offs inherent in roost site selection. Furthermore, our study design allows us to assess the influences of fear on microhabitat-scale decisions by assessing roost sites used by radio-collared pheasants given spatial (high and low risk sites) and temporal (pre-, early-, and late-hunting seasons) variation in predation risk.

We used GPS coordinates of estimated roost site locations, which were acquired via radio-telemetry (see above), to navigate to actual roost sites in the field within several days of the pheasant occupying the roost, approaching the roost during day-light hours when roosts are un-occupied. We systematically searched the area surrounding the

estimated coordinates until the presence of fecal matter and feathers confirmed a roost

location (Klimstra and Ziccardi 1963). To assess microhabitat vegetation characteristics,

we established a 5-m radius plot centered on the roost site and recorded vegetation cover

(percentage warm season grass, cool season grass, forbaceous, bare ground, and litter)

using ocular estimation (following BBIRD grassland sampling protocol,

http://umt.edu/bbird/). We tested for the effects of risk group and season on roost site

vegetation characteristics for each sex with a permutational multivariate analysis of

variance (PERMANOVA) using distance matrices (Adonis) in package "vegan"

(Oksanen et al. 2013) in Program R (version 3.1.2, R Development Core Team 2014).

Because we were unable to measure roost sites for every individual during each sampling

period, our dataset included repeated measurements for some, but not all, individuals.

Due to low overall sample sizes, multiple measurements for any one individual had the

potential to bias our findings. To account for such bias, we sub-sampled the dataset,

randomly selecting one roost per season per individual for inclusion in the Adonis

analysis. Furthermore, we bootstrapped the Adonis analysis 1000 times, incorporating a

new random sample of roost sites for each iteration. We extracted the median F and p

values along with the lower 25% and upper 75% confidence bounds for reporting.

SURVIVAL

Hunting pressure has obvious mortality implications for male pheasants; however,

less obvious are survival implications for both males and females resulting from

behavioral modifications in response to fear alone. Site fidelity has important benefits

(Stamps 1995), and increased movement or shifts in core home range areas and

microhabitats can have survival implications (Gatti et al. 1989, Thompson and Fritzell

1989). To assess potential survival implications associated with the fear effects of hunting, we evaluated daily survival rates of male and female pheasants using a generalized linear modeling approach that relies on Akaike's Information Criterion (AIC) model selection. We developed a candidate model set (see table 1-2 for full model set) describing relationships predicted *a priori* to impact pheasant survival including sex (male or female) and risk group ('high' or 'low' risk). Additionally, because we predicted survival to vary over time given changes in weather conditions and fluctuations in risk associated with the hunting season, we included variations of time trends, modeling linear (time), quadratic (time^2), and non-linear (time^3) time trends on survival. To improve our sample set, and thus model inference, we chose a nest-survival model because such models allow individuals to be added to the population and monitored at independent intervals, an approach that suited our 'ragged' type of telemetry monitoring data (Williams et al. 2002). We used the nest survival module in package "RMark" (Laake 2013) in Program R (version 3.1.2, R Development Core Team 2014) using the logit link function to evaluate daily survival rates of adult pheasants prior to and during the hunting season. To limit bias associated with handling-induced mortality only individuals that survived seven or more days after initial capture were included in the analysis. We developed a single model that included both years and estimated daily survival over a 106-day period from 1 September - 15 December. Individuals surviving the 2012 hunting season that were alive 1 September 2013 were included in the analysis twice (n=5), once for each year.

RESULTS

HUNTING PRESSURE

There was a significant effect of risk group (0.02 hunter detections per day per site on low risk sites compared to 0.09 hunter detections per day per site) and hunting season date on mean hunter detections, with hunter detections declining with hunting season date on high risk sites (fig. 1-3a; risk group: $F_{1,386}=54.02$, p<0.001; hunting season date: $F_{1,386}=26.66$, p<0.001; risk group*hunting season date: $F_{1,386}=15.55$, p<0.001).

CAPTURE

We captured and radio-collared 226 pheasants (99 male, 127 female) in 2012 and 2013. Not all individuals captured were equipped with radio-collars for reasons including failure to meet minimum weight requirements, collar distribution protocol (high vs. low risk sites), injuries sustained during capture, and escape during handling.

HABITAT DECISIONS

Macro-habitat

Female pheasants exposed to high hunting pressure increased home range size at the onset of the pheasant hunting season, but home range sizes late in the hunting season were similar to pre-hunting season home range sizes on high risk sites (fig. 1-4a; season: $F_{2,184}=5.60$, p<0.01; risk group*season: $F_{2,184}=5.82$, p<0.01). Male home range size was not influenced by risk group or season and remained constant in size prior to and during the hunting season (fig. 1-4c and d; risk group: $F_{2,6}=0.01$, p=0.91; season: $F_{2,142}=1.97$, p=0.14; risk group*season: $F_{2,142}=0.38$, p=0.68). Females on high risk sites demonstrated significant shifts in home range center, but home ranges did not shift in response to

hunting season (fig. 1-5a; risk group: $F_{1,6}=9.44$, p<0.02; season: $F_{1,92}=2.35$, p=0.13; risk group*season: $F_{1,92}=2.38$, p=0.13). Males showed no change in home range center across risk groups and seasons (fig. 1-5c and d; risk group: $F_{1,8}=0.30$, p=0.60; season: $F_{1,77}=1.21$ p=0.27; risk group*season: $F_{1,77}=0.05$, p=0.83).

Micro-habitat

Neither risk group nor season had significant effects on female roost site vegetative characteristics (risk group: $F_{1,131}=3.05$ lower 25% CI=1.99 upper 95% CI=4.36, p=0.034 lower 25% CI=0.109 upper 95% CI=0.007; season: $F_{2,131}=1.10$ lower 25% CI=0.72 upper 95% CI=1.57, p=0.366 lower 25% CI=0.667 upper 95% CI=0.142; risk group*season: $F_{2,131}=0.93$ lower 25% CI=0.57 upper 95% CI=1.40, p=0.486 lower 25% CI=0.785 upper 95% CI=0.239); however, risk group did have a significant effect on male roost site vegetative characteristics (risk group: $F_{1,82}=4.23$ lower 25% CI=3.06 upper 95% CI=5.45, p=0.005 lower 25% CI=0.021 upper 95% CI=0.002; season: $F_{2,82}=1.59$ lower 25% CI=1.04 upper 95% CI=2.29, p=0.127 lower 25% CI=0.393 upper 95% CI=0.034; risk group*season: $F_{2,82}=1.91$ lower 25% CI=1.34 upper 95% CI=2.60, p=0.056 lower 25% CI=0.211 upper 95% CI=0.02).

SURVIVAL

We evaluated the survival of 188 pheasants (table 1-1). Models incorporating sex received substantial support; the best-supported model included only the effect of sex ($AIC_c=836.33$, $w_i=0.35$) with the proportion of females surviving the 106-day evaluation period estimated at 0.61 (se=0.05, lower 95% CI=0.50, upper 95% CI=0.71) compared to 0.42 for males (se=0.06, lower 95% CI=0.31, upper 95% CI=0.53). The model containing

sex and a linear time trend received considerable support (AIC$_c$=838.19, w_i=0.14) and the

combined weight of the sex and sex + time models was 0.49. There was little support for

models that included risk group or quadratic or non-linear time trends (table 1-2).

DISCUSSION

Predation is an important driver of behavior in prey species (reviewed by Lima

and Dill 1990); however, the extent to which the fear of predation alone alters prey

behavior in wild populations is still largely unknown due to the difficulty of separating

the effects of fear from those of mortality (but see Schmitz 1998, Preisser et al. 2005,

Zanette 2011). Ours is one of the first investigations to evaluate the extent to which fear

alone influences habitat decisions in a wild prey population. By assessing behavioral

responses of male and female pheasants to predation risk in the form of recreational

hunting, we have a better understanding of the extent to which differential selection due

to consumption at the population level, and phenotypic shifts in behaviors driven by fear

at the individual level, shape the changes in prey behavior we see at the population level.

Additionally, by considering both spatial and temporal variation in predation risk and

evaluating prey habitat decisions at multiple scales, we were able to obtain a more

holistic understanding of the impacts predators impose on their prey.

FEAR EFFECTS ON HABITAT DECISIONS

Hunting pressure had no effect on male pheasant home range size (fig. 1-4c and

d) or location (fig. 1-5c and d). No change in macro-habitat use by male pheasants could

indicate pheasants have limited behavioral plasticity in macro-habitat decisions in

response to hunting activities; however, female pheasants on high risk, but not low risk,

sites increased their home range size by over four times that of females on low risk sites during the early hunting season (fig. 1-4a and b) and shifted their core home range centers nearly 1000 m between the pre- and late-hunting seasons (fig. 1-5a). Moreover, females exposed to high hunting pressure were highly sensitive to temporal variation in predation risk as their initial response to the onset of the hunting season was quickly reversed, returning to pre-hunting season sizes once hunting pressure subsided (fig. 1-4a). The variability in individual female responses to onset of hunting season (fig. 1-4a) further demonstrates the plasticity of pheasant movements in response to predation risk and also highlights the breadth of phenotypic strategies expressed by individuals in response to fear. Even though mean home range size increased by 342% from the pre- to early-hunting seasons for females on high risk sites, individual female home range sizes varied greatly. Changes in home range size for females on high risk sites ranged from a 77% decrease to a 5234% increase. This indicates that fear effects manifest individually and responses to fear are likely a complex process unique to each individual as trade-offs inherent in home range adjustments are likely sensitive to a range of factors including an individual's age, past experiences, body condition, familiarity with the surrounding landscape (Tufto et al. 1996), and maybe most importantly predator encounter rate (Lima and Bednekoff 1998). Still the apparent sensitivity to both spatial and temporal variation in predation risk by female pheasants suggests that hunting is an important ecological component of shaping the landscape of fear in harvested populations, with clear implications for macro-habitat use, and supports the use of prey movements as a metric of fear effects on prey populations as others have demonstrated (Lima and Dill 1990, Norrdahl and Korpimaki 1998, Willems and Hill 2009, Lone et al. 2015).

The dramatic response by female pheasants to the fear imposed by hunting suggests that home range formation is highly plastic in response to spatial and temporal variation in predation risk and begs the question of why we failed to see a response in males? There are obviously important differences between male and female pheasants, and we cannot rule out the possibility that home range formation is a sex dependent trait, as may be indicated by the difference in home range size between males and females (fig. 1-4). Pheasants are polygamous, which has obvious implications for home range formation during the breeding season (Burger 1966, Whiteside and Guthery 1983), but the ornate plumage of males also puts them at greater risk of mortality (Slagsvold et al. 1995), likely affecting their anti-predator response. While changes in home range size or location may have advantages for cryptic females by allowing them to 'escape' high risk environments, the same behavior may have inherently greater risk for males. Increased movement, as demonstrated by female pheasants at the onset of the hunting season, is associated with increased predation risk in a variety of taxa (Azevedo-Ramos et al. 1992, Ciuti et al. 2012) and may act similarly in affecting harvest rates of exploited species (Ciuti et al. 2012, Lone et al. 2015). For males, which are much more obvious in their habitats, increasing movement through home range expansion or re-location may be a particularly riskier behavior (Slagsvold et al. 1995, Stuart-Fox et al. 2003) and may necessitate an alternative strategy. Indeed, given the dramatic temporal shifts in risk on the landscape (fig. 1-3a), a 'wait-and-see' approach may have inherent advantages for individuals that survive the initial onset of hunting season, as risk quickly dissipated, returning to near pre-hunting season levels in a matter of weeks.

Although we cannot rule out the possibility that home range formation is a sex dependent trait, it seems unlikely that the degree of behavioral plasticity in home range expression would differ significantly between males and females because in the fall individuals of both sexes are primarily limited by the same ecological requirements (e.g., access to food and thermal cover; Gates and Hale 1974, Gatti et al. 1989) which presumably fluctuate independent of pheasant gender. Indeed, considering trade-offs between sources of selection, the response of males to predation risk may be expected to be stronger than females as males are dominant over females and therefore potentially less limited in other resources (Burger 1966). An alternative explanation for our failure to find a response in males may be that our approach to measure responses to predation risk and mortality within a population masks the inherent interaction between behavioral plasticity at the individual level and selective mortality at the population level. The extreme variation among individual females, but not males, in response to the increased predation risk highlights this possibility. Although there were substantial differences between high and low risk sites in hunter detections (fig. 1-3a), hunter movements within sites ultimately determines encounter rates on high risk sites for individual pheasants. Females that failed to demonstrate shifts in home range location or size may have simply occupied safer locations (i.e., lower predator encounter rates) within high risk sites. Assuming the same pattern holds true, males on high risk sites that survived the onset of the hunting season may have simply had limited encounters with hunters and thus no need to alter home ranges, whereas those that may have shifted home range size or location were harvested and thus not included in our sample. In this case, differential selection imposed by predation may have masked the effects of fear on the population if

we were to only consider the implications for males (fig. 1-1e). Unfortunately, because of the high rates of mortality in the male population during the period when behavioral responses by females were greatest, we were unable to track the reaction norms of individual males with enough power to test this possibility.

Though we failed to find a shift in male pheasant home range formation in response to the onset of hunting season we did find roost site characteristics for males were significantly different between low and high risk sites. That we failed to find a seasonal effect may imply that there were inherent vegetative differences between our high and low risk sites; however, the lack of a difference in roost site selection for females and that a post hoc analysis (Adonis) of pre-hunting season roost sites revealed no significant effect of risk group (male: $F_{1,29}=0.88$, p $=0.465$; female: $F_{1,50}=2.46$, p$=0.056$) suggests that the differences between low and high risk sites in roost site selection is due to differences in hunting pressure. Creation of high and low risk groupings includes the notion of place as well as time (i.e. high risk group is only high risk after the onset of hunting season), and unfortunately the limitations of our analytical approach (Adonis) does not allow us to assign site as a random effect and cleanly separate the implications of time and place. Still, that risk group was no longer significant in our post hoc analysis leads us to conclude that time (the onset of hunting season) and not place (site) is driving the difference between high and low risk groups for males in our analysis.

Like our assessment of macro-habitat decisions, our findings of the effects of hunting on micro-habitat decisions revealed clear differences between males and females requiring us to consider what might differ between the sexes or our assessment of their

response. Unlike the shifts we saw in home range formation, the changes we saw in roost

site selection were manifested by the sex that experienced the consequences of fear and

mortality. Such a finding makes it less likely that our assessment of roost site selection is

biased by trade-offs between individual behaviors and population level mortality, as in

this case we would expect individual and population attributes to act additively to have

maximum impact on the male population. Rather, that females did not shift roost site

selection while males did may indicate that predation only manifests to affect micro-

habitat selection through differential mortality, not fear. However, such a definitive

statement again assumes that males and females respond to fear through the same anti-

predator strategy. That both sexes respond to predation risk, but at different spatial scales

may suggest that fear is scale dependent. Consideration of how selection agents act

across ecological scale is increasingly identified as important for understanding species

ecology (Turner et al. 2001, Cunningham and Johnson 2006), including pheasants

(Jorgensen et al. 2014; Simonsen 2015). Female pheasant body size is small and females

have smaller home ranges (fig. 1-4), suggesting that they may be more sensitive to local

habitat conditions (i.e., safe roost sites; Fisher et al. 2011). That paradoxically females

respond to fear on the landscape by altering home range formation and not roost site

selection may indicate that in a smaller home range 'safe' roost sites are limiting. As

such, females are forced to move and given the hierarchical nature of habitat selection

(Hutto 1985) presumably establish new home ranges in safer landscapes where 'safe'

roost sites are not limiting and thus we find no difference in roost site selection before

and after the onset of hunting season. The larger home ranges of male pheasants in this

case may actually buffer against the presumably high costs of moving because there are

more roost site opportunities allowing males to presumably select 'safe' roost sites within their current home range.

Still, it would not be surprising if roost site selection is insensitive to the landscape of fear imposed by hunting pressure, as pheasants typically select and occupy roosts after hunters have left for the day. A roost site may therefore be used despite the risk associated with its location within a high risk site if the assessment of risk must be timed with the decision process (i.e., encountering predators when habitat decisions are made; Lima and Dill 1990) or if there are additional benefits that outweigh the possible costs of encountering a hunter the following morning. So if fear is not the mechanism, our findings suggest that differential mortality is driving the change in male roost site selection we measured in our population. Pheasants may be particularly vulnerable to hunting-induced mortality at roost sites, as vigilance early in the morning while still in a sleep state is likely reduced (Lima et al. 2005), and therefore individuals may have reduced response times and subsequently limited ability to express behaviors (i.e., running versus flying) that reduce exposure to mortality (Lima et al. 2005). However, that we measured shifts in roost site selection in response to hunting pressure indicates that a subset of the population is predisposed to mortality, presumably because they roost in habitats where hunters prefer to hunt. If hunters differentially search for pheasants in particular micro-habitats (Broseth and Pedersen 2000, Lone et al. 2014), then the relative safety of the micro-habitat, not the macro-habitat (site), would be the primary determinant of roost site selection. Although there are a multitude of studies that have examined micro-habitat decisions for upland game birds (Francis 1968, Patten et al. 2005, Hovick et al. 2014), few have addressed trade-off among alternative sources of

selection and predation risk (but see Hiller and Guthery 2005, Tirpack et al. 2005), and to our knowledge no study has examined how hunting pressure manifests at a the micro-habitat level to shape the landscape of fear. Our findings suggest that such trade-offs not only exist, but that hunting may alter how trade-offs between various sources of selection are represented within the population; however, we caution that sample sizes for male roosts within each risk group during the late-hunting season were small and may ultimately limit our inference (table 1-1).

We see clear evidence for a fear response to predation risk in our female pheasant population as they expand and shift their home range in response to hunters on the landscape. However, this response is less evident in our population of males who also experience mortality. For males, is difficult to determine whether observed differences between the sexes in macro-habitat selection and between risk groups in micro-habitat selection are sex determinant or if they are indeed a response to predation risk. In order to truly understand what is driving these findings, experimental manipulation of the male population would be necessary and is beyond the scope of the current study.

FEAR EFFECTS ON SURVIVAL

Changes in behavior, such as those demonstrated through macro-habitat decisions of the pheasants in our study, likely do not come without costs. Costs may manifest subtly through reduced body condition (Hik 1995, Scheuerlein et al. 2001) or lowered reproductive investment (Zanette et al. 2011, Laskowski 2014), but the ultimate cost an individual stands to pay if predation risk is not mitigated is an increased risk of mortality. As predicted, male mortality on high risk sites sharply increases at the onset of the

hunting season with almost half of the total male mortality taking place during the first 5 days of the hunting season (fig. 1-3b). In contrast, 95% of radio-collared males on low risk sites survived the same time interval. Because we determined cause of death when we recovered each radio-collar, we were able to confirm that 27% of males collared on high risk sites died as a direct result of hunter harvest with another 3% being fatally injured, but un-recovered by hunters. Our daily survival rates showed a clear difference in survival between the sexes, with over 60% of females surviving compared with just over 40% of males. However, we did not find any significant effect of risk group on daily survival rates. The most likely reason for this finding is because risk groups encompass components of both space and time that our modeling approach was unable to separate. Additionally, hunting pressure is highly variable, with no hunting pressure prior to the hunting season on both high and low risk sites, and heavy hunting pressure on high risk sites (mostly in the first 7 days) that quickly declines to near low risk site levels by the end of the study period. This variation in hunting pressure makes it difficult for a linear-regression modeling approach, such as the nest survival module in program MARK, to detect survival differences between discrete risk groups. A more robust modeling approach might include measures of risk (hunting pressure) experienced by each individual on each day in the modeling period, allowing the model to better assess declines in survival with more fine-scale fluctuations in hunting pressure. Although we found no significant differences in survival between risk groups or seasons, home range expansion and relocation that was observed by female pheasants may have more subtle, non-lethal consequences that may add up to have significant long-term effects (i.e., reproductive investment; Laskowski 2014).

MANAGEMENT IMPLICATIONS

Pheasants are an economically and culturally important species coveted by recreational hunters throughout the central Great Plains of the United States. Upland game bird hunters contribute significantly to local economies through hunting equipment purchases, hunting trip expenditures such as hotel, food, and fuel, and through hunting license sales that are an important source of income for state wildlife management agencies (IAFWA 2002). Conservation programs, such as the Focus on Pheasants Program initiated in 2001 in Nebraska, aim to conserve upland game bird habitat as well as opportunities for sportsmen who pursue them. The findings of our research have many practical implications for wildlife managers who aim to maintain healthy pheasant and hunter populations.

The number of breeding females is the primary determinate of pheasant productivity (Jarvis and Simpson 1978); thus, pheasant harvest is generally restricted to males to ensure adequate female populations. Breeding ratios as extreme as 1 male to every 10 females are sufficient to maintain and even increase pheasant populations under appropriate breeding conditions (Shick 1947, Ball 1950), allowing for significant harvest and ensuring hunter satisfaction. By assuming that limiting harvest to males has no effect on pheasant populations, management has failed to consider the potential indirect impacts of hunting on female pheasant survival and reproduction. Our results are clear evidence of the fear impacts of hunting pressure on female pheasant behavior as demonstrated through shifts in macro-habitat decisions at the onset of hunting season. Moreover, even if females survive the hunting season, additional costs may manifest as females reduce

reproductive investment and shift nesting locations off optimal CRP grasslands
(Laskowski 2014).

The strong and prolonged response of females to hunting activities both during
the hunting season and lasting into the breeding season suggests that prime nesting
habitats should be protected from heavy hunting pressure. For wildlife managers this may
mean restricting hunting all-together on a sub-set of sites each year to shelter some
females from the fear effects of hunting we have quantified. It is apparent that
maintaining a patchy landscape in terms of hunting pressure may be important for
minimizing fear effects and thus reproductive and survival costs. For instance, pheasants
on one low pressure hunting site in our study were often found foraging in a nearby small
grain field where public access hunting was permitted. Anecdotally, this site received
heavy hunting pressure; however, movements and survival of these birds were no
different than others on other low hunting pressure sites. This suggests that refuge
habitats providing safe roosting and loafing habitats near high risk habitats (i.e.,
patchiness of high and low risk habitats on the landscape scale) may be enough to off-set
the immediate effects of fear from hunting on pheasant behavior (home range size and
shift in core home range center) as well as the carry-over effects of fear on breeding
behavior (nest site selection and egg size investment).

Another finding from our research important to wildlife managers was the trend
toward compensatory mortality observed in survival probabilities for male and female
pheasants in our study. Ours is one of the first studies to document compensatory
mortality in this well-studied game bird. Previous research has indicated hunting
activities are at least partially additive with maximum sustainable harvest (yields) ranging

from 20-50% (Newton 1998). Morality rates (combined hunting and natural) during the

hunting season in our study were 30% for females and were similar between high and

low hunting pressure sites. Mortality for males on high hunting pressure sites at the close

of the hunting season was 55% whereas mortality for males on low hunting pressure sites

was 40%. Although we see mortality differences in males between low and high risk sites

at the close of the hunting season, we have reason to suspect that this trend is driven

largely by just a few harvests late in the season and decreasing sample sizes caused these

harvests to appear as if survival differences exist between high and low risk sites late in

the season. We suspect however that male survival between low and high risk "catches

up" and again becomes compensatory shortly after the hunting season as breeding male

"crow" counts conducted in the spring on the identical sites indicated there was no

difference in male abundance between high and low risk sites (Laskowski 2014). This

suggests that the costs of harvest, and the survival costs of fear, are both compensatory in

this population. Still, harvest is fairly low in our population (hunter harvest during our

study accounted for about 34% of total mortality of males on high risk sites) so it is

difficult to say whether the compensatory costs we documented would hold true if

harvest was increased to 50% or more. Indeed, the threshold over which harvest is no

longer compensatory for this species is wide-ranging, varying significantly by region and

between years (Newton 1998). Moreover, most of the work concerning pheasant harvest

and the impacts of harvest on population dynamics are focused on 'healthy' populations.

For logistical reasons it is clearly easier to obtain adequate samples to assess survival

when populations are high, as is often seen in favorable habitat conditions. However, as

the landscape is increasingly less supportive of pheasants (Taylor et al. 1978, Warner

1994, Rodgers 1999, Peterjohn 2003, Jorgensen et al. 2014) the potential impacts of harvest, both direct and indirect, are increasingly unknown. For example, although a sex ratio of 1:10 may be adequate when populations are high (Shick 1947, Ball 1950), the costs of finding a mate are likely confounded by population size irrespective of sex ratio (Taber 1949, Mateos 1998). As such harvest rates may have nonlinear effects on population demographics through increased female search effort for mates (Mateos 1998). In wildlife management, few account for such indirect mortality effects as a result of fear despite the obvious implications in the establishment of regulations such as bag limits and season lengths. As we move forward, and populations, both harvested and un-harvested, are increasingly challenged by anthropogenic impacts to the environment, it behooves managers to consider the potential indirect impacts of management actions, especially harvest, on wildlife populations.

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TABLES AND FIGURES

Table 1- 1. Summary of sample sizes, means, and standard errors of variables used to assess pheasant habitat decisions (macro- and micro-) prior to and during the hunting season by risk group, hunting season, and sex.

	Hunting Pressure	Hunting Season	Sex	Sample Size (n)	Mean	Standard Error
	High	Pre	Male	32	167.59	33.41
	Low	Pre	Male	35	165.70	30.98
	High	Pre	Female	33	100.46	14.29
	Low	Pre	Female	32	130.10	41.33
Macro-habitat	High	Early	Male	21	210.19	38.22
	Low	Early	Male	29	168.25	32.52
Home Range Size	High	Early	Female	40	442.09	125.18
(hectares)	Low	Early	Female	33	108.04	19.61
	High	Late	Male	19	133.54	21.85
	Low	Late	Male	21	119.94	21.12
	High	Late	Female	33	84.50	8.94
	Low	Late	Female	27	95.08	14.28
	High	Pre to Early	Male	20	349.95	101.47
	Low	Pre to Early	Male	28	269.74	53.80
	High	Pre to Early	Female	29	484.28	110.71
Macro-habitat	Low	Pre to Early	Female	28	188.62	83.50
	High	Early to Late	Male	19	212.32	51.10
Shift in Home	Low	Early to Late	Male	21	152.92	30.03
Range Center	High	Early to Late	Female	33	537.60	176.38
(m)	Low	Early to Late	Female	27	152.86	31.17
	High	Pre to Late	Male	18	442.47	143.82
	Low	Pre to Late	Male	20	319.61	71.77
	High	Pre to Late	Female	23	930.08	278.25
	Low	Pre to Late	Female	22	182.35	40.89
	High	Pre	Male	17		
	Low	Pre	Male	20		
	High	Pre	Female	31		
	Low	Pre	Female	21		
Micro-habitat	High	Early	Male	12		
	Low	Early	Male	22		
Roost Site	High	Early	Female	27		
characteristics	Low	Early	Female	24		
	High	Late	Male	9		
	Low	Late	Male	8		
	High	Late	Female	18		
	Low	Late	Female	16		
	High		Male	41		
Survival	Low		Male	43		
	High		Female	54		
	Low		Female	50		

Table 1- 2. Summary of model selection results for survival of adult pheasants prior to and during the hunting season using a nest survival approach with Akaike information criterion corrected for small sample sizes (AIC_c) and ΔAIC_c values.

Model (S~)	K	AIC_c	ΔAIC_c	w_i
sex	**2**	**836.33**	**0.00**	**0.35**
sex + time	**3**	**838.19**	**1.86**	**0.14**
sex + time + risk group	4	838.74	2.41	0.10
sex * time	3	839.30	2.97	0.08
sex * time^3	3	839.84	3.51	0.06
(.)	1	840.17	3.84	0.05
sex * time^2	3	840.21	3.88	0.05
sex * risk group	5	840.87	4.54	0.04
time^3	2	840.98	4.65	0.03
risk group	2	840.99	4.66	0.03
time^2	2	841.89	5.56	0.02
time	2	842.11	5.78	0.02
sex * risk group * time	5	842.82	6.50	0.01
sex * risk group * time^3	5	843.76	7.43	0.01
sex * risk group * time^2	5	844.15	7.82	0.01

Notes: Models are ranked by ascending ΔAIC_c; w_i is the model weight and k is the number of parameters. Factors included sex, risk group, linear (time), quadratic (time^2) and non-linear (time^3) time trends, and constant daily survival (.). Models in bold are the most supported models ($\Delta AIC_c < 2$).

Predators illicit consumptive and non-consumptive effects on prey populations. However, it is often difficult to determine whether observed trait expression in a prey population is due to differential selection via consumptive effects (mortality) at the population level or phenotypic modification driven by non-consumptive effects (fear) at the individual level.
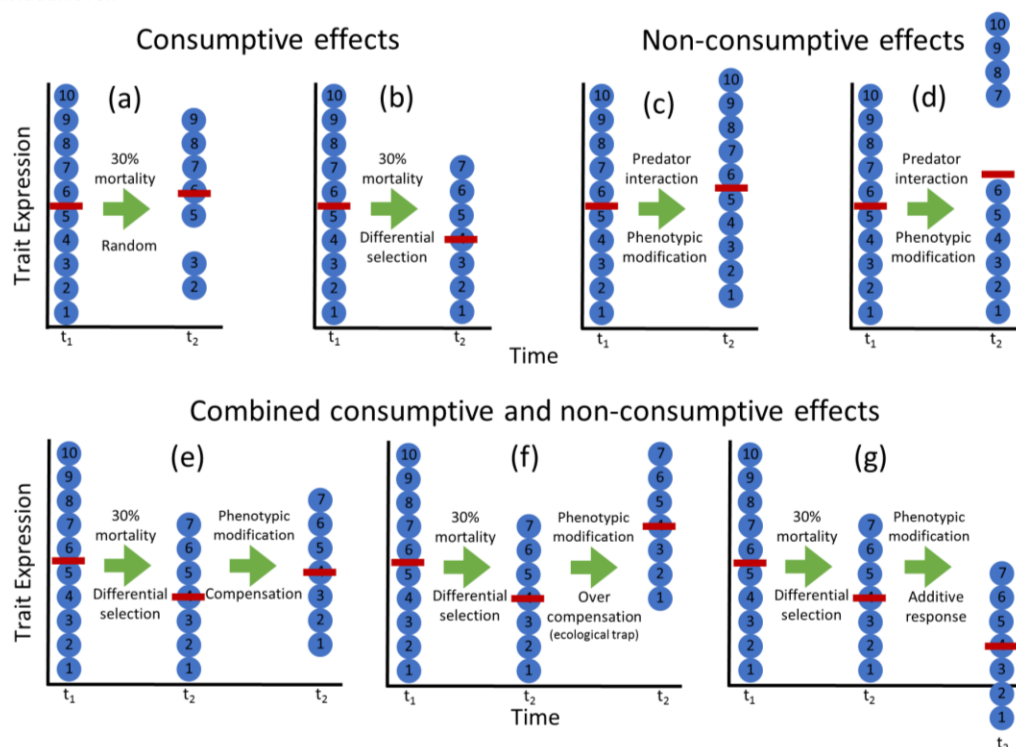
Consider a prey population that exhibits heterogeneous expression of a given trait (individuals numbered 1-10 in figures a-e above). The prey population interacts with predators between time 1 (t_1) and time 2 (t_2). The red bar represents the mean trait expression of the population.

When the consumptive and non-consumptive effects on trait expression are considered independently, there are several potential explanations for any observed shifts in mean trait expression of the population. Under consumptive predation that occurs randomly, where all individuals regardless of their magnitude of trait expression have an equal probability of experiencing mortality due to predation, there is no significant change in mean trait expression of the population from t_1 to t_2 (a). However under differential selection where specific trait expression increases an individual's probability of mortality, mean trait expression for the population shifts away from the trait expression that has a higher probability of mortality due to the non-random removal of those individuals from the population (b). However, the non-consumptive effects of predation can also shift mean trait expression of a population without removing individuals. One example is a shift in trait expression by all individuals in the population, each moving in the same direction and at the same magnitude (c). Alternatively, trait expression may dictate the magnitude of phenotypic shifts in expression with some individuals responding stronger than others at t_2 based on trait expression at t_1 (d).

Although consumptive and non-consumptive predation effects on trait expression can be considered independently, in most systems these effects co-occur (e-g). The simultaneous occurrence of consumptive and non-consumptive effects on wild populations creates challenges for interpreting observed shifts in mean trait expression at the population level. For example, consumptive and non-consumptive effects may cause trait expression to shift in opposite directions with differential selection shifting the population mean in one direction and phenotypic modification at the individual level shifting the population mean in the opposite direction through compensation, masking consumptive and non-consumptive effects on trait expression at the population level (e). Alternatively, shifts in trait expression may be observed even when consumptive and non-consumptive effects shift in opposite directions, were individuals increase expression of a given trait even though it is selected against in what is termed an ecological trap (f). Finally, shifts in trait expression in response to consumptive and non-consumptive predation risk may be complimentary, with differential selection at the population level and phenotypic modification at the individual level shifting the mean trait expression of the population in a similar direction with an additive response to predation.

Figure 1- 1. The consequences of consumptive and non-consumptive predation effects on trait expression in prey populations.
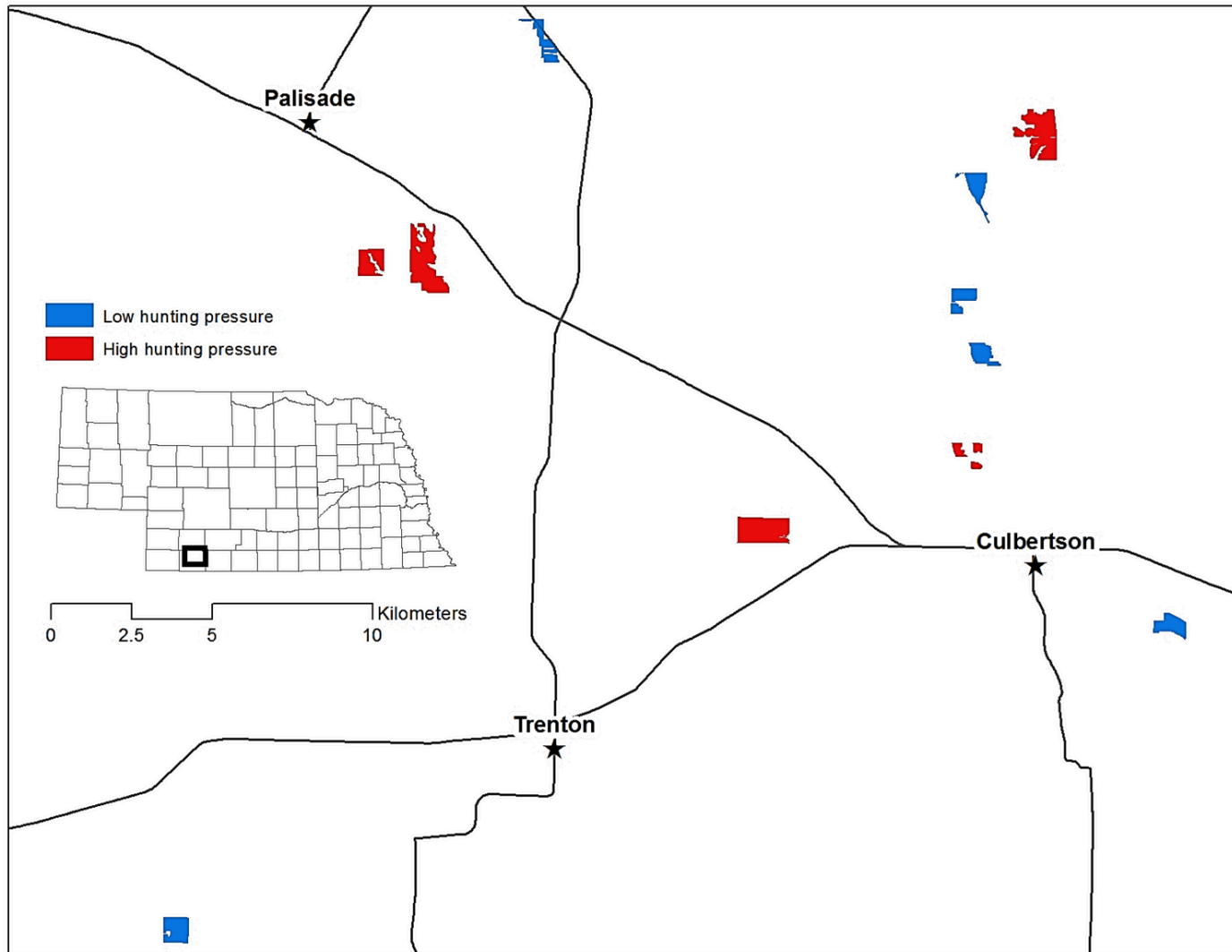
Figure 1- 2. Southwest Nebraska study area and study sites.
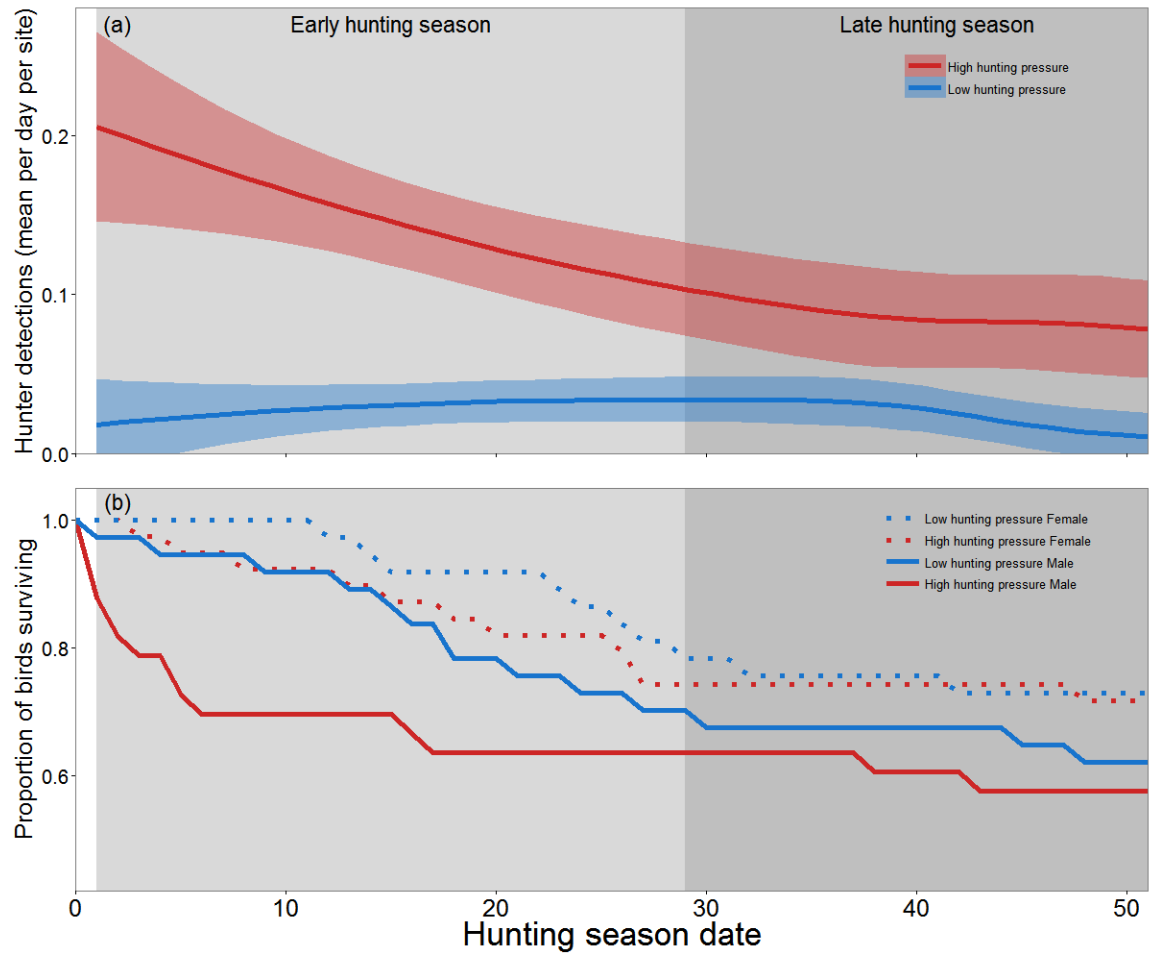
Figure 1- 3. As predicted, hunting pressure and pheasant population size decline as the hunting season progresses. Hunting pressure on high pressure sites (red line, a) declines steeply early in the hunting season (light gray shaded region), leveling off during the late hunting season (dark gray shaded region). Hunting pressure is represented by fit lines generated using loess smoothing of the mean number of hunter detections per day per site. Colored regions around the lines represent the standard error surrounding the mean hunter detections per day within each risk group. The population of male pheasants on high pressure sites declines sharply at the on-set of the hunting season (solid red line, b), but declined at a similar rate to that of both sets of female pheasants (dotted red and blue lines, b) on low pressure sites (solid blue line). Changes in population size are illustrated by the proportion of radio-collared individuals surviving the first 51 days of the 98-day hunting season (when intensive radio-tracking and survival monitoring took place).
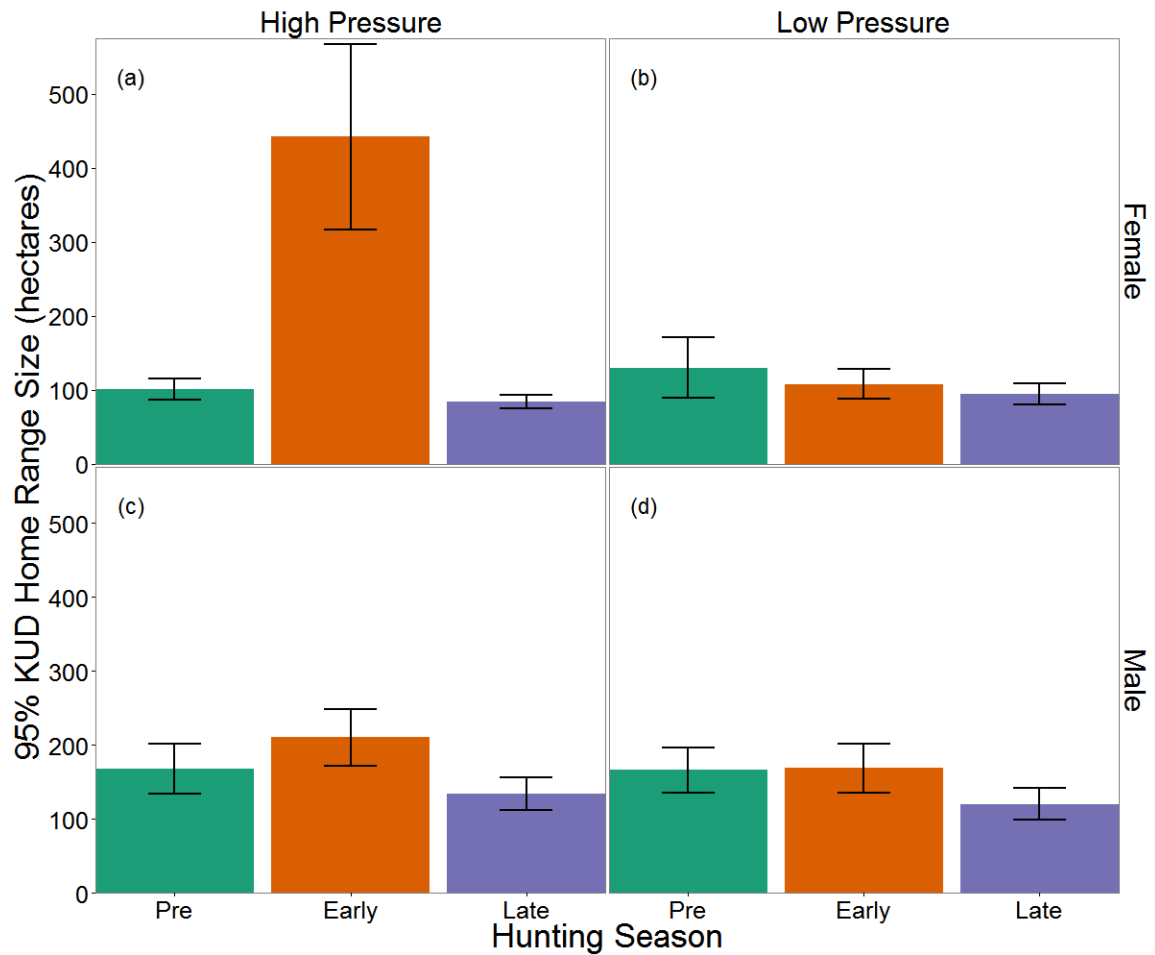
Figure 1- 4. Female, but not male, pheasants responded to the onset of the hunting season by changing their home range size. Perceived predation risk increased female home range size during the early hunting season (a) while females on low pressure sites (b) had similar home range sizes prior to and throughout the hunting season. Males on low and high pressure sites showed no change in home range size prior to and during the hunting season (c) and (d).
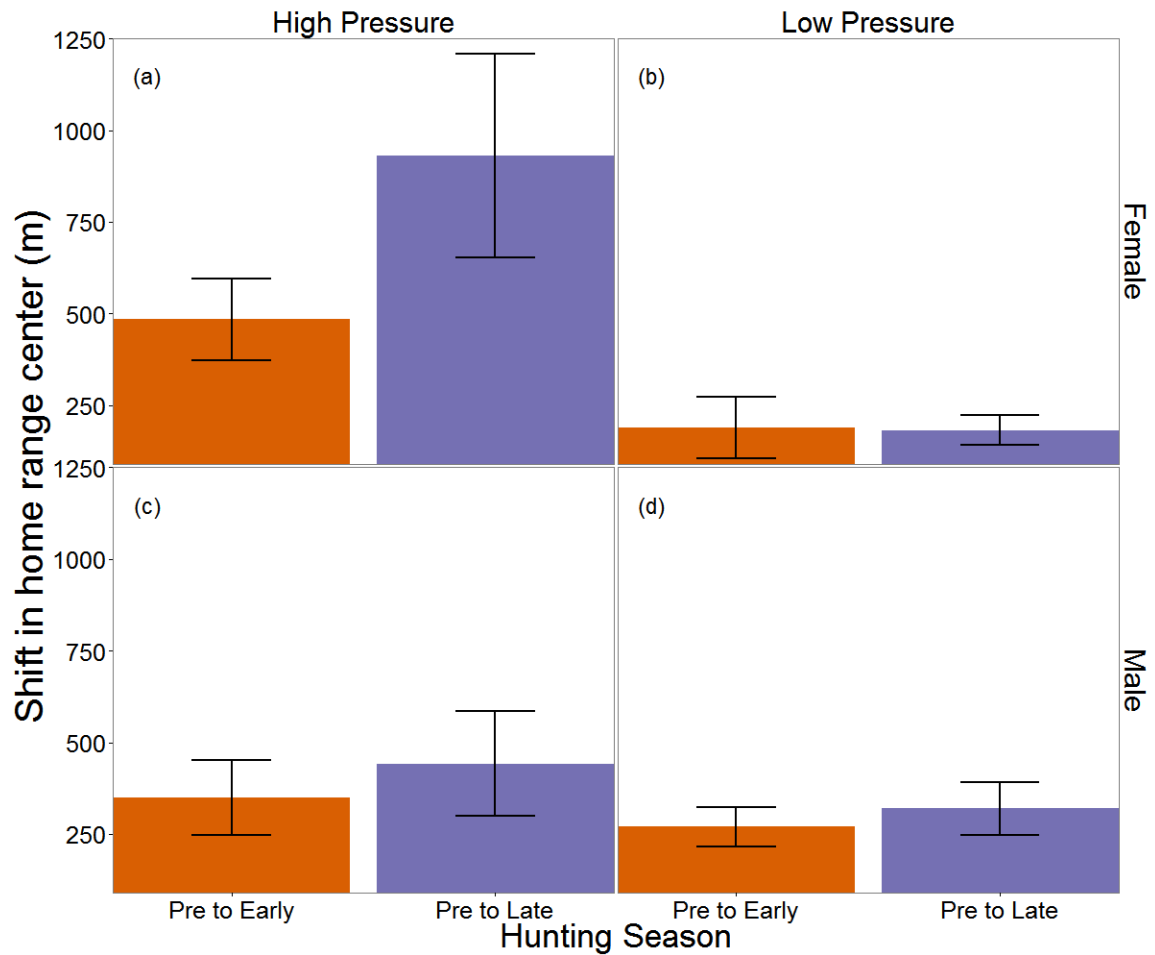
Figure 1- 5. Female, but not male, pheasants responded to the onset of the hunting season by changing the location of their home range. Perceived predation risk shifted centers of core home ranges of females who experienced high hunting pressure (a). Females on low pressure sites (b) and males on high (c) and low pressure sites (d) saw no change in home range center over the course of the hunting season.

CHAPTER 2: PUBLIC HUNTING LANDS AS NETWORKS

Abstract:

Recreational hunting has both strong cultural connections for hunters as well as substantial economic benefits for rural communities and state wildlife agencies. Declining hunter populations and limited availability of accessible hunting lands has spurred state agencies to create programs aimed at increasing hunting opportunities. Though these programs have seen success, managers understand little about how hunters select individual hunting sites and move across networks of concentrated hunting opportunities. We combined information collected during in-person interviews of Ring-necked Pheasant hunters in Southwestern Nebraska and the principles of network theory in a novel approach to assess factors driving hunter site selection and movement. Additionally, we identify key hunting sites and their characteristics based on *a priori* predictions of factors influencing hunter site selection (habitat, opportunity, ease of access, and proximity to amenities). We found that habitat, specifically Conservation Reserve Program (CRP) grasslands, plays a profound role both locally and regionally in driving pheasant hunter movements and site selection. Additionally, hunters appear to select high-quality habitat even when it takes them farther from amenities and access is more difficult. This suggests that pheasant hunters are searching for hunting locations that are potentially 'wilder'. By identifying key hunting sites and factors driving their selection, wildlife managers are better equipped to use patterns in hunter decision making

to not only create better hunting opportunities for sportsmen and economic growth in rural areas, but to mitigate hunter impacts on wildlife populations.

INTRODUCTION

Hunter and angler participation is a crucial component of wildlife and fisheries management in the United States because it provides a method for, and economic support of, management actions (Arlinghaus and Cooke 2009, Sharp and Wollscheid 2009). As such, aging hunter and angler populations and trends indicating decreasing participation in hunting and fishing are cause for concern for state agencies charged with managing and conserving wildlife and fish populations (USFWS 1991, USFWS 1996, USFWS 2001, USFWS 2006, Pergams and Zaradic 2008, USFWS 2011). Unfortunately, as society becomes more urban and landscapes increasingly fragmented, wildlife and fish habitat, and thus opportunity for hunters and anglers, becomes increasingly scarce and more difficult for the public to access (Foley et al. 2005, Leu et al. 2008, Vrtiska et al. 2013). As the lack of suitable places to recreate is cited as a primary reason why people stop participating in outdoor recreation (Mehmood et al. 2003, Miller and Vaske 2003), many state fish and wildlife agencies have partnered with private landowners to provide public access on privately-owned lands in an effort to increase participation in recreational activities. Though public access programs are generally thought to be well-received, managers understand little about if and how hunters and anglers use the properties enrolled in access programs, why they use specific areas, and how the

availability and distribution of properties in the landscape affect use and movements of sportsmen. Given the limited funds available to support public access programs, it is important for managers to understand how hunters and anglers use public lands when deciding if and when to enroll additional properties. Moreover, understanding the movements of hunters and anglers is important for determining how game populations are affected by harvest and sportsmen behavior.

Hunters and anglers are highly mobile and make rapidly changing day-to-day, hour-by-hour decisions about when and where to hunt and fish (Carpenter and Brock 2004, Martin and Pope 2011). As such, they can choose to recreate at multiple sites in a given month, week, or even day. Properties made available for hunting or fishing are traditionally viewed independently and managed as separate and discrete entities (Carpenter and Brock 2004, Martin and Pope 2011). Recently however, managers have begun to look beyond the individual site to view fishing—and to a lesser degree hunting—locations as components of larger, regional networks where individual sites are linked and interdependent with management at one location influencing use at a neighboring location (Hunt 2005, Martin and Pope 2011, Martin 2013). Understanding the use and relationships of regional recreation networks provides policy insight into the effectiveness of creating large networks of accessible hunting and fishing lands as well as insights for managers in the placement of future public access lands, allowing for the best use of limited conservation dollars.

Network theory provides a unique approach of evaluating public access sites as part of a larger, regional system of interconnected and interdependent components. The study of networks and network structure is widely explored in mathematics, and computer science and social science (Milgram 1967, Watts and Strogatz 1998, Strogatz 2001, Newman 2003); however, ecological application of network theory has taken longer to develop (Urban and Keitt 2001, Newman 2003, Krause et al. 2007, Bodin and Norberg 2007). In particular, the use of network theory in natural resource management is underutilized despite the potential to influence how management is conducted. Wildlife and fisheries managers work at the human-wildlife interface, managing populations for consumptive (hunting and angling) and non-consumptive (wildlife watching) uses, as well as for the overall persistence and sustainability in the face of increased human influence on habitat quality and accessibility (Foley et al. 2005, Leu et al. 2008). Thus, managers often incorporate sociological and ecological theory to help predict and mitigate human impacts on natural populations. By integrating theory and methodology from network applications, natural resource managers may discover a powerful tool useful in an array of management decisions, including how best to develop public access programs. Our objectives are to 1) document hunter movement within a region of concentrated hunting opportunity, and 2) construct a recreational hunter network utilizing network theory and methodology and describe patterns in hunter movement over the region to inform management decisions.

METHODS

STUDY AREA AND SITES

National declines in pheasant populations, and subsequently hunters, are of

concern to state wildlife agencies because small game hunting is traditionally an

important avenue of hunter recruitment and can account for a considerable proportion of

annual revenue for wildlife management (USFWS 2011). Unfortunately, enrollment in

the Conservation Reserve Program (CRP), an important habitat for pheasants and

consequently hunting habitat for sportsmen, is declining as CRP lands are put back into

crop production and drought conditions have put further pressure on remaining CRP

lands for livestock feed (Wright and Wimberly 2013). Concerned by the decline of CRP

acres, managers and policy makers have begun to focus on programs for maintaining and

increasing wildlife habitat and accessible hunting lands in an agriculturally dominated

landscape by soliciting cooperation from private landowners. Included in the 2008 Farm

Bill, the Voluntary Public Access and Habitat Incentive Program (VPA-HIP) was aimed

at helping state agencies improve public access for hunting while improving habitat

conditions for wildlife. As a result, thousands of acres of CRP grasslands are now

accessible to the public for hunting and thousands of acres of productive farmland are

managed with wildlife conservation in mind. Individual states have also initiated similar

programs aimed at providing public hunting access to private lands.

Located in the heart of the central Great Plains, Nebraska is over 97% privately

owned (NWI 1995), making public hunting access an important concern for the Nebraska

Game and Parks Commission. In 2002, the Nebraska Game and Parks Commission in partnership with Pheasants Forever and the United States Department of Agriculture initiated the Open Fields and Waters Program, a statewide program aimed at maximizing hunting opportunities by enrolling private lands into public access hunting. Unfortunately, despite the successful enrollment of nearly 1 million acres annually, little is known about how hunters are choosing to use or move among and between public access sites. These insights stand to provide managers and policy-makers critical information needed to strategically enroll public access hunting sites in the future, promoting maximum use by hunters.

The Southwest Focus on Pheasants area (SWFOP), established in 2010, is one of several focal areas designated by the Nebraska Game and Parks Commission for intensive enrollment in the Open Fields and Water Program. In 2012, the SWFOP encompassed 3,800 km^2 in southwest Nebraska, USA, including all of Hitchcock County a large portion of Hayes County and portions of Red Willow and Frontier counties. Within the focus area between 30 and 75 contracts are issued annually in the Open Fields and Water Program encompassing nearly 69.54 km^2 of private lands in open-access hunting programs.

DATA COLLECTION

We conducted in-person interviews of hunting parties using public lands in the SWFOP during the 2012-2013 and 2013-2014 pheasant hunting seasons (last weekend in October - 31 January). Hunting parties were interviewed upon completion of hunting

activities at an individual property with one representative of the hunting party answering

all interview questions (fig. 2-2). The primary question of concern for this study

(question 2) asked hunting parties to identify on a map all publically accessible sites they

had visited that day (including the site of interview) in order to assess hunting site

selection and movement between hunting sites. In addition, we asked questions

pertaining to hunting party composition and hunting effort (questions 4-9), primary target

species abundance and harvest of pheasants (questions 10-12), hunter satisfaction

(question 13), and travel distance (question 14). Interview effort was focused during the

first several days of each hunting season and was dramatically reduced by day 51 of the

98-day hunting season; this interview effort followed the general pattern of hunting effort

in the study region (fig. 1-3a).

NETWORK CREATION AND CHARACTERISITCS

We created a matrix with hunting parties in rows and hunting sites in columns

from completed hunter interviews. Hunting sites were assessed at the section level with

all public hunting lands in a single square-mile section (259 hectares) representing one

hunting location. In the matrix, each individual section visited by an individual hunting

party was marked with a "1" in the cell corresponding to the specific hunting party–

hunting site pairing. All other sites not visited by the hunting party of interest, but by

other interviewed parties received a "0". Network analysis was completed using the

"igraph" package (Csardi and Nepusz 2006) in Program R (version 3.1.2, R Development

Core Team 2014). We used a weighted, bipartite projection to create a graph of our

hunting site matrix. In a bipartite projection, two distinct matrices are generated; in our

case, one representing hunting sites, the other hunting parties. Only the hunting site

matrix was used for the analyses hereafter. Hunting party movements (edges) connect

hunting sites (nodes) visited by hunting parties, and were weighted by the number of

hunting parties who connected a pair of nodes.

Community Structure

Identifying node groups or communities, in our case groups of publically

accessible properties, in a network is one way to describe large-scale patterns within the

network or patterns unique to specific nodes in the network. In our network, community

identification may allow us to evaluate patterns in hunting-site selection, distinguishing

spatial patterns or unique patterns in hunting site selection expressed by certain types of

hunting parties. Most community detection algorithms work to partition nodes based on

edge connections, grouping nodes such that modularity is maximized when there are

many edges within communities and only a few edges spanning between communities.

We used a modularity-based community detection algorithm known as "fast-and-greedy".

This algorithm functions by first identifying each node as a separate community, then

merging communities so that at each step, modularity is maximized.

Centrality

Measures of centrality are common network analysis tools and are used to identify

important nodes (i.e., individual properties in our case) within the network. We assessed

two measures of centrality, degree centrality and eigenvector centrality, for each node in

our hunting site network. Degree centrality evaluates the number of connections a particular node has to all other nodes in the network. Nodes with a large degree are the most connected. In our network, hunting sites with larger degrees represent sites important for drawing hunters into the network (i.e., to southwestern Nebraska). Providing hunting opportunities is important to wildlife managers and as such, identifying sites with a high degree allows managers to assess which sites draw in and disperse hunters to other hunting sites. Identifying high-degree sites also allows managers to describe patterns in hunter movement over the region based on common attributes. The second measure of centrality we assessed for each node was eigenvector centrality, which ranks each node in the network based on connections. High ranking nodes are those that are well-connected (high degree) themselves and are connected to other well-connected nodes. In our network, sites with high eigenvector centrality indicate "hotspots" that are both able to draw hunters in *and* connect them to other highly-desirable locations. By identifying and describing sites with high degree and eigenvector centrality, managers are better equipped to provide hunters with additional sites sharing characteristics with these preferred locations. Additionally, identifying these important sites in the network informs managers which sites should be preserved if sites should be eliminated from the network due to funding restrictions for example.

Factors driving hunting site selection

Southwest Nebraska is rich with public access hunting opportunities for sportsmen due to recent efforts to provide public hunting access on private lands. As

such, hunting parties have the opportunity to seek sites that meet certain criteria they look

for in a hunting experience. These criteria may be practical concerns of a hunting trip,

such as proximity of the location to a hunter's home, or may be more existential, such as

success at a given location for several years. Here, we propose there are several physical

attributes of individual hunting sites that influence whether a hunting party will select a

given site for their hunt and may be drivers of community structure and node centrality in

our network. Our *a priori* attributes included measures of habitat quality, hunting

opportunity, access to the site, and proximity of site to urban amenities.

Habitat

CRP grasslands are associated with high pheasant abundances (King and Savidge

1995, Delisle and Savidge 1997). In our study area, CRP grasslands are targeted by

wildlife managers for enrollment into public access programs because of the habitat they

provide. In addition, managers also target for enrollment working lands where farmers

are already performing wildlife friendly agricultural practices such as small grain stubble

fields managed for tall stubble or pastures where landowners have deferred grazing.

Although hunters have multiple types of habitat available to them for public access

hunting, we predicted *a priori* that pheasant hunters would prefer hunting sites enrolled in

CRP because of traditional hunting associations with these lands and the quality of

habitat and pheasant abundances associated with these lands. We evaluated the presence

of CRP at the local scale (square-mile section) for each node, assessing the proportion of

CRP (even if not pubically accessible) vs. other land use types. We also evaluated the

role of CRP at the landscape scale, assessing the proportion of CRP in all sections directly adjacent to and including the hunting site section (nine square-mile sections total), again including properties that may or may not be publically accessible. If hunting parties select CRP grasslands over other land use types for hunting, we would expect that nodes with a higher proportion of CRP at the local scale will also be those with the highest degree centrality. Given the heterogeneous landscape of the study area and the fact that agricultural lands also play a role in providing winter food and cover sources for pheasants as well as hunting opportunity for sportsmen, hunters likely consider the surrounding landscape when selecting a hunting location. In many cases, CRP may not be important at the local scale (i.e., hunting party selects a public access small grain field to hunt) but may be important at the landscape scale (i.e., small grain field was selected because it is nearby a CRP field not enrolled in any public access program). If CRP at the landscape scale is important to hunters, sites with a higher degree should have a higher proportion of CRP at the landscape scale. We assessed the proportion of CRP at the local and landscape scales using Geographic Information Systems (GIS) and the 2011 CRP data layer for our study area (Nebraska Game and Parks Commission).

Opportunity

We only interviewed hunters that accessed public properties for our study. However, the density and size of public access lands at both the local and landscape levels vary widely within the study region. We predicted *a priori* that hunters would seek hunting locations with a higher proportion of public access at both the local and

landscape scale. At the local scale, the proportion of public access gives some indication

of the size of site hunters prefer. At the landscape scale, the proportion of public access

indicates whether hunters find it important to hunt in "clusters" of public access lands,

allowing them to move from site to site within a hunting day most efficiently. We

assessed the proportion of public access at the local (one section) and landscape (nine

sections) scales using GIS and the 2013 public access atlas (Nebraska Game and Parks

Commission).

Ease of access

Ease of travel to hunting sites is a practical concern for hunters and one we

predicted *a priori* would influence hunting site selection with hunters selecting sites with

more available roads for parking and aiding travel between sites. We hypothesized sites

with more road access at the local scale (section) would have more connections (higher

degree) in the network. We assessed the linear kilometers of road at the local scale using

the Nebraska 2010 TIGER (Topologically Integrated Geographic Encoding and

Referencing) roads dataset from the U.S. Census Bureau in GIS.

Amenities

Pheasant hunting in Southwest Nebraska is not only popular with Nebraska

residents, but also attracts residents from neighboring states (Messinger unpublished

data). Proximity to local towns with lodging, restaurants, and fueling stations is important

in supporting the influx of out-of-town residents and non-resident hunters who often

make multi-day trips to the area. We predicted *a priori* that hunting sites closer to towns

with food, lodging, and fueling stations would be selected more often by hunters. In our

study area, towns providing these services were Stratton, Trenton, Culbertson, and

McCook. Palisade was the only other community providing some amenities for hunters,

but was not included as an amenity-providing location in this analysis because it lacks

both public food and lodging facilities. For each hunting site in the network, we

calculated the Euclidean (shortest straight-line) distance (km) to the nearest amenity-

providing community. Calculations were conducted using GIS with section centers

representing the site location for each node and the 2000 "Nebraska Populated Places"

data layer from the U.S. Geological Survey providing town center locations.

DATA ANALYSIS

To assess differences in factors influencing hunter site selection at the community

level, we tested whether there were differences between communities in habitat and

opportunity at the local and landscape scales, roads at the local scale, and proximity to

amenity-providing communities using Kruskal-Wallis tests in in Program R (version

3.1.2, R Development Core Team 2014). To assess whether habitat, opportunity, ease of

access and proximity to amenities influenced measures of centrality (degree and

eigenvector) in the hunting site network, we fit linear models in Program R (version

3.1.2, R Development Core Team 2014) using analysis of variance. Because CRP at the

local scale and CRP at the landscape acale are inherently correlated, and managers

actively seek CRP hunting lands for enrollment into the Open Fields and Waters

Program, we did not test for interactions between these variables as we expected *a priori* these variables to be related and add little to our overall understanding of the system.

RESULTS

HUNTING SITE NETWORK

We interviewed 117 parties who hunted 203 public access lands in the 2012-2013 and 2013-2014 pheasant hunting seasons. Of these sites, 53 were unique, resulting in a network with 53 nodes and 115 edges (hunter movements between hunting sites). Individual hunting parties hunted an average of 1.74 sites daily, with a range from one to six.

<u>Community Structure</u>

The fast-and-greedy community detection algorithm identified eight distinct communities in the network (table 2-1) with a modularity of 0.50. Hunting network communities do not appear to be spatially driven with communities containing nodes from various areas within the study region (fig. 2-3), except communities six, seven, and eight which only contained one node each. We did find significant differences between communities in the proportion of CRP (Kruskal-Wallis, χ^2=19.52, df=7, p=0.01) and public access at the landscape scale (Kruskal-Wallis, χ^2=16.26, df=7, p=0.02), as well as the distance from the nearest amenity-providing town (Kruskal-Wallis, χ^2=21.38, df=7, p=0.003). However, the proportion of CRP (Kruskal-Wallis, χ^2=10.03, df=7, p=0.19) and public access (Kruskal-Wallis, χ^2=6.89, df=7, p=0.44), as well as linear coverage of roads

(Kruskal-Wallis, χ^2=9.83, df=7, p=0.20) at the local scale did not differ between communities (fig. 2-7).

Degree Centrality

The proportion of CRP at the local scale positively predicted hunting site degree ($F_{1,35}$=17.94, p<0.001); however there were no significant influences of any of the other factors we measured (fig. 2-4).

Eigenvector Centrality

Proportion of CRP at the local ($F_{1,35}$=21.41, p<0.001) and landscape scales ($F_{1,35}$=35.99, p<0.001) as well as roads ($F_{1,35}$=5.27, p=0.03) and proximity to amenities ($F_{1,35}$=7.88, p=0.01) predicted eigenvector centrality of hunting sites. However, there was no significant influence of proportion of public access at the local or landscape scales on eigenvector centrality of hunting sites (fig. 2-6).

DISCUSSION

As participation in hunting and angling declines, and opportunities, particularly for hunters, become increasingly scarce due to habitat fragmentation and changing land use patterns, wildlife managers are ever more interested in novel strategies such as public access programs that aim to maintain healthy hunting and angling populations. However, mangers often lack crucial knowledge of how publically accessible lands are used by sportsmen. By understanding underlying factors driving hunter site selection, managers may be better equipped to use limited conservation funding to provide hunters with the best hunting opportunities into the future. Here, we used network analysis to visualize

hunting site selection and hunting party movements within a region of concentrated

opportunity in Southwestern Nebraska (fig. 2-1). Moreover, network analysis allowed us

to assess factors influencing hunting site selection, and identify the sites best at drawing

hunters into the network and distributing hunters over the network using quantitative

methods.

Through information collected from hunters in the field, we constructed a hunting

network that can be displayed spatially and overlaid with various background features

such as roads and land use that help illuminate factors influencing hunter site selection

and movement behavior throughout the region (figs. 2-3 and 2-5). We identified eight

distinct communities within the network. These communities largely overlapped with

several spanning across the entire network, and thus do not appear to have strong spatial

influence. Instead, it is likely that each of these communities is driven by hunter typology

rather than spatial predictors. For instance, hunting sites in community one had a high

proportion of CRP and public access at the landscape scale, but were some of the farthest

from amenity-providing towns. In contrast, community two was characterized by a

moderate proportion of CRP at the landscape scale, a relatively low proportion of public

access at the landscape scale, and included some of the closest sites to towns. Thus while

some hunters may find it worth their while to travel 'off-the-beaten-path' to sites with a

higher density of habitat and public access lands, others prefer to hunt sites with less

habitat closer to a home-base (town). Though many types of hunters spanning the entire

range of possible preferences likely exist, there were general trends apparent among all

communities in our network. First, although public access and CRP were important at the local scale, they did differ among communities at the landscape scale. Additionally, convenience features such as proximity to amenity-providing towns were different between communities, but not road density. By focusing on factors that distinguish communities of hunting sites from one another and targeting specific types of hunters through the sites they select, managers widen their ability to create meaningful hunting experiences for their constituents as well as better predict the movements and influences of hunters on wildlife populations.

In addition to identifying and describing hunting site communities in the network, we were also able to identify and describe the importance of individual sites in bringing hunters into the region and distributing hunters to other public access hunting sites. We found a significant positive relationship between the proportion of CRP at the local scale and node degree, indicating that pheasant hunters are directly or indirectly assessing the local availability of CRP (fig. 2-4). Although public access programs in Nebraska have recently expanded to include working lands such as small grain stubble fields and pasturelands, which did provide alternative hunting opportunities for sportsmen, it seems the most well-connected sites in our pheasant hunting network are still those with the highest proportion of CRP. Although the importance of CRP to pheasant hunters is not surprising, in an era of dwindling CRP acres, it is apparent that wildlife managers concerned with pheasant hunting participation and satisfaction must be concerned with maintaining the habitats hunters and likely pheasants prefer. Managers should work to

maintain sites with abundant CRP at the local scale if their goal is to provide hunters the types of hunting lands they desire.

We also measured Eigenvector centrality which allows us to assess a hunting site's ability to disperse hunters over the network. In our network, there was a cluster of sites with a high eigenvector centrality on the north-western edge of our spatial network (fig. 2-5, community one). Like our analysis of node degree, eigenvector centrality was positively associated with the local availability of CRP; however, eigenvector centrality was uniquely positively affected by the availability of CRP in the surrounding landscape, distance from the nearest town, and road density (fig. 2-6). Thus, the most important hunting locations in generating movements among alternative hunting sites are those located in regions with a high proportion of preferred hunting lands (CRP) but counter to our predictions, are also those farthest from a town and had the lowest road densities. Such a finding suggests that simply increasing access on CRP lands for hunters is likely not sufficient to ensure hunter participation. Hunters seemingly are interested in large complexes of suitable habitat that may allow for movement among potential hunting sites and are either willing to travel farther from amenities to reach these locations or actually seek areas of high habitat which are "off-the-beaten-path". For managers, this suggests that accessibility, at least in the context of road networks, and proximity to amenities is not a factor limiting hunter participation in open access hunting. Although eigenvector centrality provides a meaningful way to assess a hunting site's ability to distribute hunters over the network, very few sites in our network had high eigenvector centrality

and thus patterns drawn from our sample are highly skewed by just a few sites. Even so, the fact that so few sites are well-connected and connected to other well-connected sites indicates that although hunters do move about the region, there is wide variability in hunter movements from one site to another.

Here we demonstrate the capacity of network analysis as a tool to assist wildlife managers in evaluating hunter site selection and movement within a region of public access hunting opportunities. Like recent findings in fisheries management (Martin and Pope 2011, Martin 2013) we demonstrate that hunting sites likely do not function independently, but are linked with use at one hunting location related to use at another. Though we acknowledge that we have included only a small sub-set of factors likely influencing hunter site choice, mostly physical features, we hoped to demonstrate the ease with which hunter movement information can be used to further assess the efficacy of hunter access programs. Clearly, and certainly not surprisingly, CRP plays a profound role both locally and regionally in driving pheasant hunter movements and site selection. More surprisingly, however, is that despite the apparent need for amenities, even pheasant hunters, a group associated with agrarian landscapes, appear to be searching for hunting locations that are less accessible and potentially wilder. Such a finding underlies the connection between hunting and rural America and suggests the fragility between rural economies and hunting opportunities. Although sites within the study region represent a gradient of proximities to amenity-providing towns, no sites in our study region are particularly isolated, with the most isolated site only 23.5 km from the nearest

town. Within our study region it is likely we were unable to capture the threshold at which hunters trade habitat for amenities when selecting a hunting location. In other regions of the state where public hunting opportunities are concentrated, sites are located much farther from towns and access limited by sparse road networks. Study of hunting networks in these regions may further illuminate the extent to which hunters are willing to select habitat over amenities and access, and if that trade-off differs by hunter type (deer vs. pheasant, for instance). Regardless, in choosing locations for inclusion in open access programs, wildlife managers must be cognizant that use is influenced by habitat, but may be limited by suitable amenities and road access. Similarly, policy makers must realize that suitable networks of hunting properties represent a potential windfall for those willing to invest in rural economies, and that network analysis can help identify how to select properties to improve both opportunities for hunters and for small business. Indeed, although our analysis was limited to physical features, one of the strengths of a bipartite network analysis is that it can also be used to create a network of hunting parties and to identify groups or typologies of hunters and what distinguishes them. This type of network would allow for the incorporation of factors related to motivations, satisfaction, and demographics. Additionally, network analysis can be used to assess factors driving hunter site selection and predict changes in hunter movement and site use when hunting sites are added or dropped from the network. Ultimately, network analysis equips managers to provide hunters with the best possible hunting opportunities given the complex nature of hunter site selection and behavior.

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TABLES AND FIGURES

Table 2- 1. Summary of network communities, with number of hunting site members, mean degree, and mean eigenvector centrality.

Network Community	Nodes (count)	Mean degree centrality	Mean eigenvector centrality
1	10	5.1	0.48
2	16	5.4	0.13
3	12	4.6	0.12
4	10	3.5	0.09
5	2	1	0
6	1	0	0
7	1	0	0
8	1	0	0
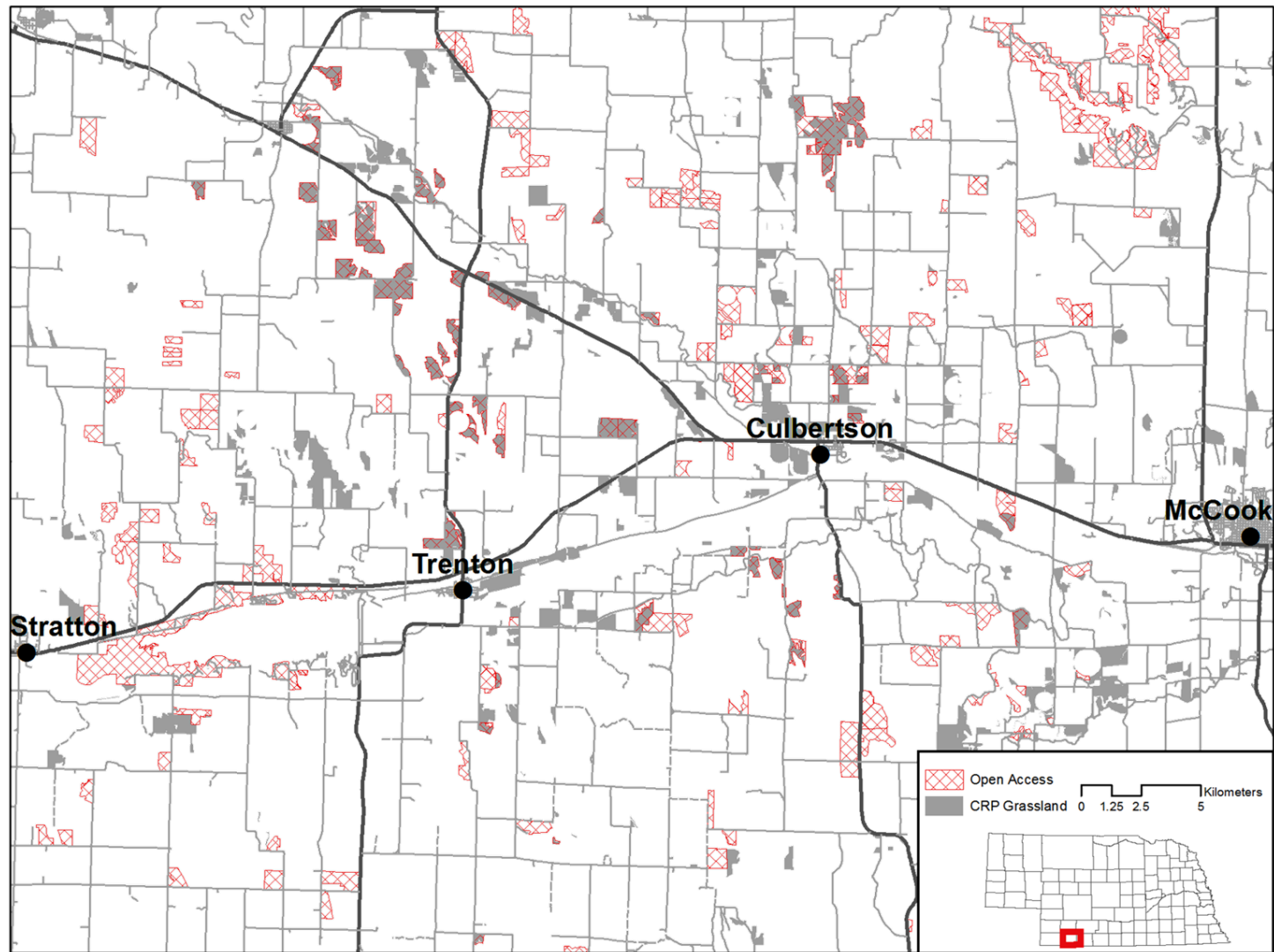
Figure 2- 1. Map of public access hunting lands within the Southwest Focus on Pheasants area in Southwestern Nebraska

Hunter Survey - Southwest Nebraska Upland Game Bird Focus Area

Script for in-person interview

Hi. My name is _____. I am an employee of the University of Nebraska and we are conducting a survey to learn more about upland game hunters and their experiences while hunting in the Southwest Focus on Pheasants area. We would like to ask you to participate in a 3-5 minute survey involving a few short questions about your hunting experience. There are no known risks involved in taking the survey and your participation is completely voluntary

1. Are you interested in taking our survey?
> *If "Yes", proceed with survey*
> *If "No", end survey*

2. Is this the first field/site your group visited/hunted today?
> **If "Yes", proceed with next question**
>
> **If "No", "We are trying to determine what types of areas hunters prefer to hunt. We would like to gather information on the order of hunting sites visited by hunters in a given day to assess the hunting quality in this area. What previous sites did you visit today before arriving at this site, did you hunt at each of these sites, and in what order did you visit these sites?**

3. Is your party finished hunting at this site today?
> *If "Yes", proceed with the interview*
> *If "No", thank the respondent and wish them "good luck" with their hunt*

4. How many people in your party were present, either hunting or doing other activities, in this field, today?

5. How many were actively hunting and are: Adult males, adult females, juvenile (18 years old or younger) males, juvenile females?

6. How much time was spent by each hunter actively hunting in this field, today?

7. How many dogs does your party have with you today?

8. How many dogs were with you in this field today?

9. How much total time was spent by each dog in this field today?

10. What is the primary species your party targeted at this site, today?

11. How many pheasants did your party see while hunting at this site today?

12. How many total pheasants did your party harvest on this site today?
> *If >0, would you allow me to measure and examine the crop contents of the pheasants you harvested in this field today?*

13. How satisfied were you with your hunt on this site today on a scale of 1 to 5 with 1 being not satisfied and 5 being very satisfied?

14. What is your home zip code?

15. Have you received our take-home survey anytime since September 1 of this year?
> *If "Yes", thank them for their time and end the interview*
> *If "No", proceed below:*

16. Would you like to participate in our take-home survey that asks more detailed questions about your hunting experience throughout the season? This survey should take you roughly 10 minutes to complete. Your participation is again, completely voluntary.
> *If "Yes", give them the mail in survey and instructions, end the interview*
> *If "No", end the interview*

Thank you for your time. Do you have any questions?

If you have any further question that come up or you feel I did not answer adequately feel free to contact lead project investigator, Joseph Fontaine at the Nebraska Cooperative Fish and Wildlife Research Unit (402-472-0339). Or if you have questions or concerns about your rights contact the University of Nebraska-Lincoln Institutional Review Board at (402) 472-6965.

Figure 2- 2. Script reflecting questions asked of hunting parties during in-person hunter interviews.
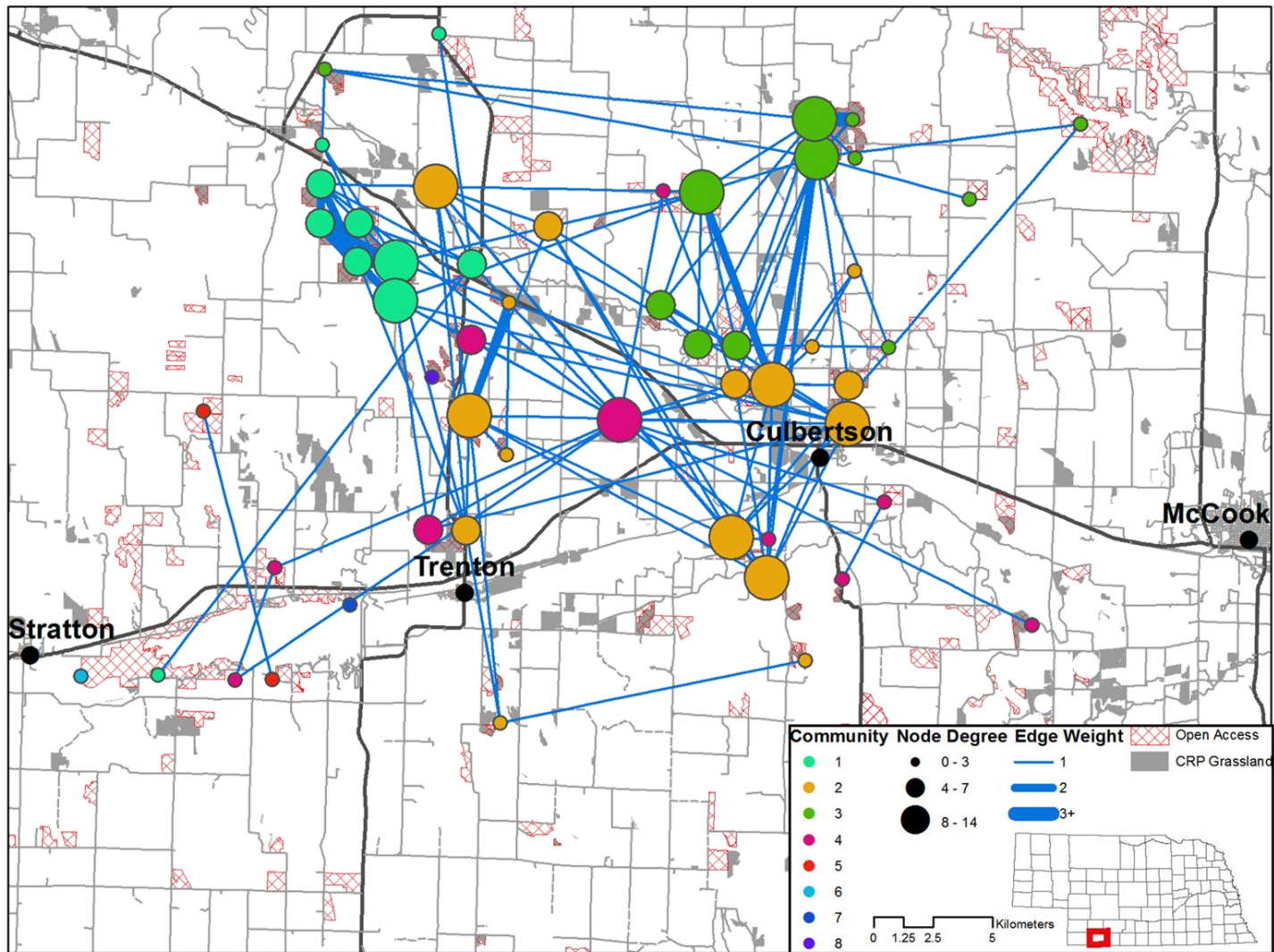
Figure 2- 3. Southwest Nebraska public lands pheasant hunting network with nodes shaded by community membership and sized proportionately to node degree. Edge thickness corresponds to the edge weight (the number of hunting parties moving between a pair of nodes).
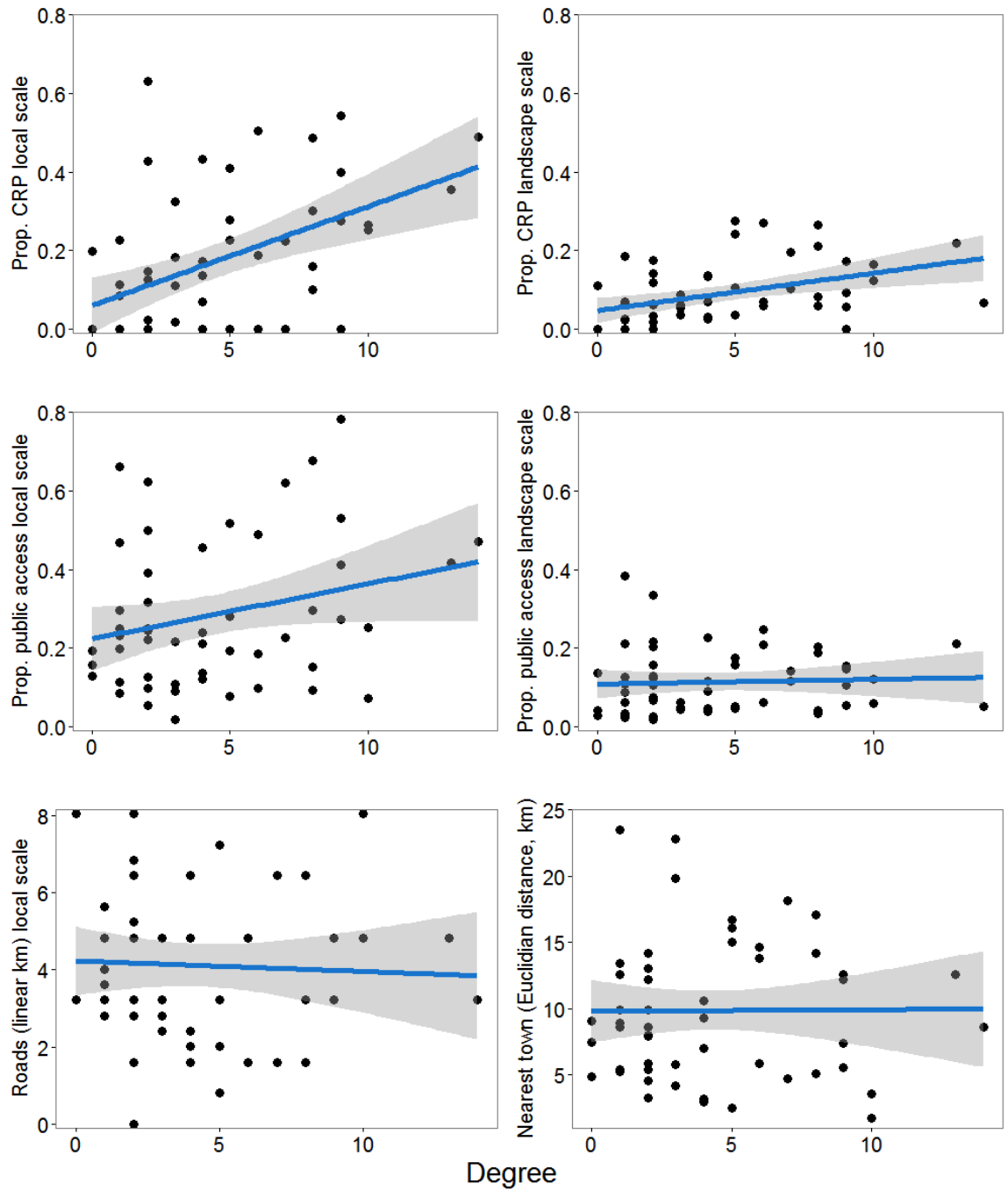
Figure 2- 4. Relationship between network node degree and spatial factors predicted *a priori* to influence hunter site selection. Loess (local polynomial regression) fit line (blue) and standard error (gray shaded region) show relationship to node degree.
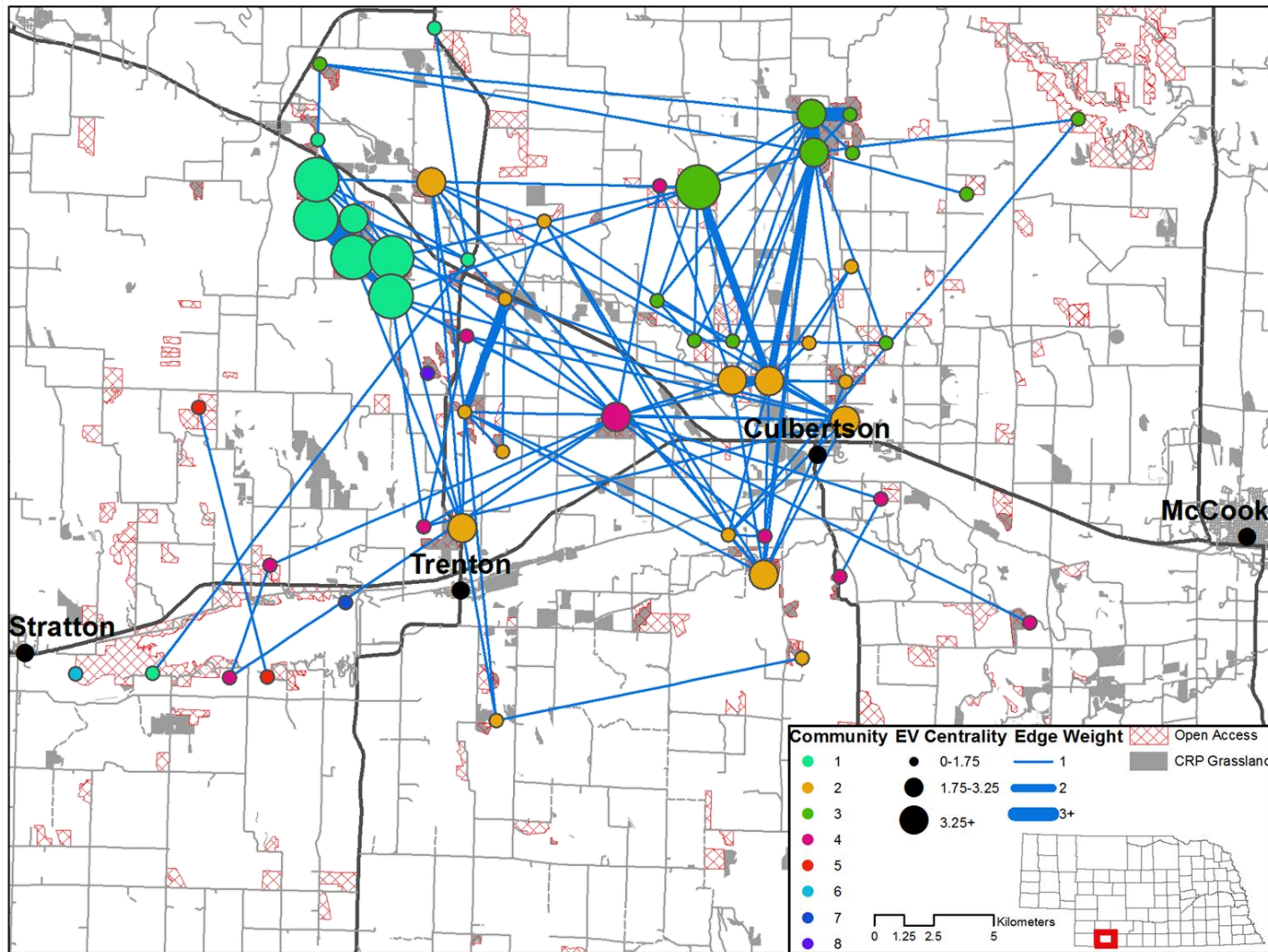
Figure 2- 5. Southwest Nebraska public lands pheasant hunting network with nodes shaded by community membership and sized proportionately to eigenvector centrality. Edge thickness corresponds to the edge weight (the number of hunting parties moving between a pair of nodes).
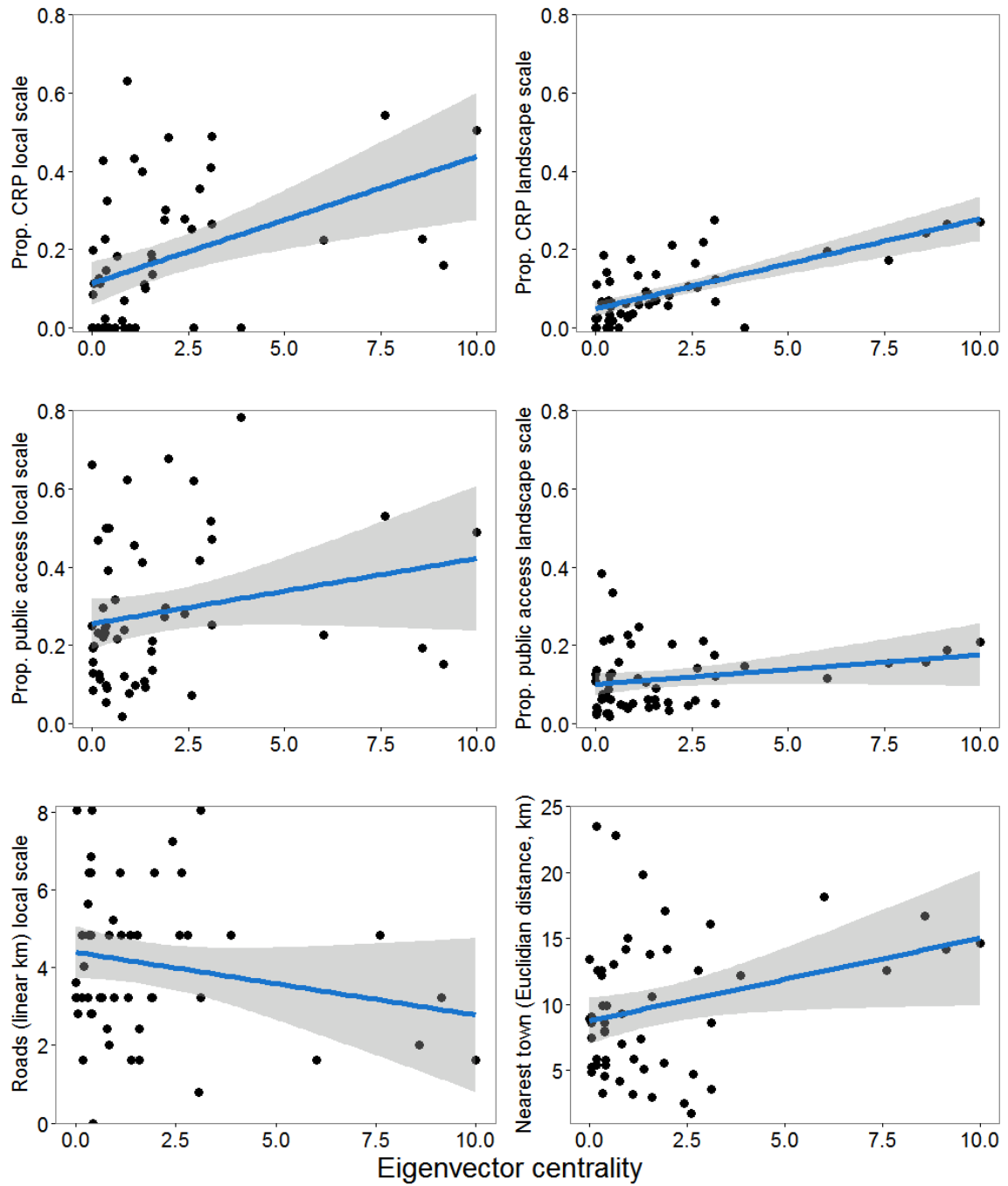
Figure 2- 6. Relationship between network node Eigenvector centrality and spatial factors predicted *a priori* to influence hunter site selection. Loess (local polynomial regression) fit line (blue) and standard error (gray shaded region) show relationship to Eigenvector centrality.
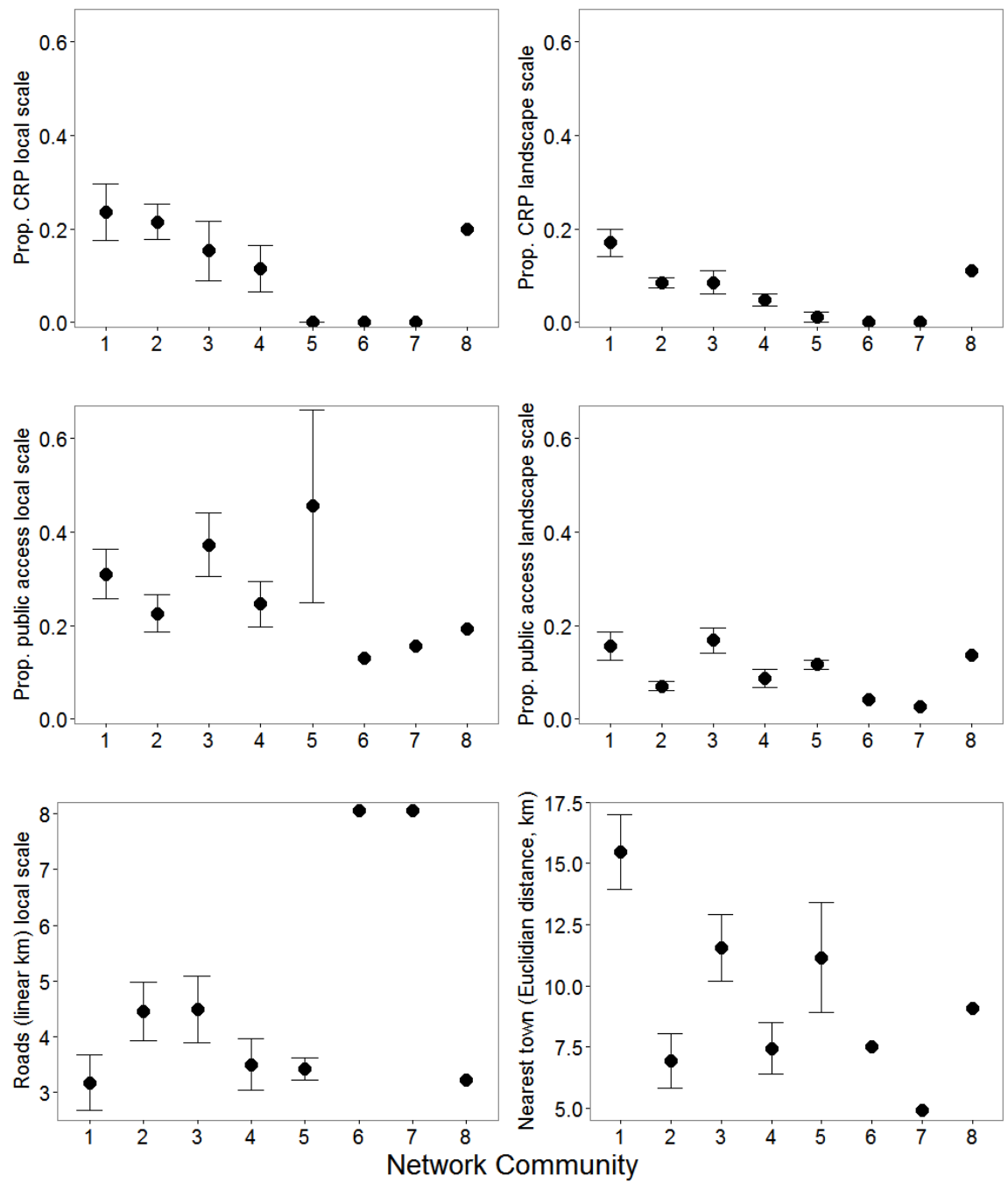
Figure 2- 7. Network community means and standard errors for each of the factors predicted *a priori* to influence hunter site selection.