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Fear Effects on Pheasant Reproductive Ecology and a Curriculum to Teach Wildlife Habitat Selection

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FEAR EFFECTS ON PHEASANT REPRODUCTIVE ECOLOGY

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A CURRICULUM TO TEACH WILDLIFE HABITAT SELECTION

by

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Predation risk is an important source of selection that shapes prey density, distribution and abundance via direct effects of selective mortality and indirect effects of fear. The immediate impacts of predator consumption on prey population dynamics are widespread and well studied, and a growing body of research demonstrates substantial, immediate impacts of predator-induced fear (independent of prey mortality) on prey behavior, physiology and life-history expression. However, predation risk is often seasonally variable and while it is clear that consumption effects often carry over to influence prey population demography for years after predators have left the landscape, the temporal carry-over effects of fear on prey populations remain largely unexplored.

We assessed the effects of fall hunting activity by humans on female pheasant reproductive ecology the following spring. We were able to isolate the effects of fear from the selective implications of predation because hunter harvest is limited to males, though both sexes experience similar cues indicative of risk. We found fall hunter activity did not influence female body condition, survival, or nest site choice the following spring; however, females had elevated baseline corticosterone concentrations that were sensitive to body condition, such that birds in poorer condition had higher baseline corticosterone concentrations in high risk sites. Additionally, hunting activity reduced

egg size by 10%. Our results indicate that fear alone can impact prey physiology and reproductive investment after cues indicative of risk are gone.

In order to teach grade school students how sources of selection such as predation risk shape wildlife populations, we developed and taught a curriculum that demonstrates concepts of habitat selection through a hands-on outdoor activity using radio-telemetry equipment as well as an indoor game and discussion. Students learn how competing sources of selection such as food availability, access to mates, and predation risk together influence where animals choose to live. Here we contribute new evidence as to how prey populations are influenced by predator's past and a curriculum designed to educate and inspire the next generation of scientists to continue to explore how competing sources of selection shape wildlife population dynamics.

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Chapter 1: FEAR AND THE PHANTOMS OF PREDATORS PAST

Abstract:

Predator-prey interactions elicit shifts in prey behavior, physiology and life-history that can impact prey population dynamics and community structure to the same extent as prey consumption (Turner and Mittelbach 1990, Ripple and Beschta 2004). An emerging body of literature addressing the 'landscape of fear' shows substantial immediate impacts of fear on prey hormone concentrations, body condition, behavior and reproductive investment (Scheurien et al. 2001, Pressier et al. 2005, Stankowich and Blumstein 2005, Zanette et al. 2011). However, predation risk is temporally variable (Chesson 1978b, Erlinge et al. 1984, Lima and Bednekoff 1999), and although seasonal increases in prey mortality carry over to constrain prey abundance after predators have moved on (Krebs et al. 1995, Abrams 2000), it remains unknown for how long and to what extent the effects of fear carry over to impact prey populations. We assessed the temporal carry-over effects of human hunting on reproduction in female ring-necked pheasants. Because harvest is limited to males, but both sexes experience similar cues indicative of risk, we were able to isolate the effects of fear from the selective effects of predation. We found that although hunting did not have prolonged effects on female survival, body condition or nest site choice, females on heavily hunted sites had elevated baseline corticosterone concentrations that were more sensitive to body condition such that birds in poor condition had disproportionately higher corticosterone concentrations on high risk sites. Furthermore, hunter activity caused females to produce 10% smaller eggs. Our results indicate that fear alone can carry over to impact prey physiology and

reproductive investment after cues indicative of risk are gone, and that fear associated with episodes of heightened predation risk can have prolonged impacts on prey populations even in relatively safe environments.

INTRODUCTION

Predator-prey interactions are complex and dynamic relationships that shape the evolution and expression of prey behavior, morphology, physiology and life history (Abrams and Rowe 1996, Abrams 2000, Stankowich and Blumstein 2005). Although studies of predators and their prey have long focused on the lethal implications of predation (Elton 1942, Sinclaire 1989) there is increasing evidence that predators influence prey through more subtle indirect mechanisms that have equally important consequences for population and community dynamics (Turner and Mittelbach 1990, Magnhagen 1991, Ripple and Beschta 2004). Growing evidence suggests that fear (the perception of risk) is a significant ecological condition that strongly shapes prey distribution, density and abundance (Frid and Dill 2002, Creswell 2007, Brown et al. 2009, Hua et al. 2013) by mediating trade-offs with other sources of selection such as access to food, appropriate thermal conditions, or mates (Sinclaire and Arcese 1995, Brown 1999, Zanette et al. 2003, Laundré et al. 2010). For example, behavioral responses to predation risk, such as increased vigilance, increased fleeing distance, or moving to lower quality habitat, can reduce foraging rate and forage quality (Lima and Dill 1990, Creel et al. 2005, Hua et al. 2013) with potential long-term consequences for individuals and populations (Lima 1998a, Ripple and Beschta 2004, Valeix et al. 2009).

Moreover, fear can significantly alter prey physiology by affecting metabolic and hormonal pathways (Siegel 1980, Boonstra et al. 1998, Sapolsky et al. 2000) and in doing so modulate energy intake and storage to buffer energy debts caused by stressful stimuli (Sapolsky et al. 2000, Angelier et al. 2007). Field and laboratory research indicate that the immediate effects of fear trigger reallocation of energy reserves with cascading consequences to prey condition, survival, and reproductive investment (Scheurien et al. 2001, Pressier et al. 2005, Zanette et al. 2011). However, despite evidence of the immediate and chronic impacts of fear on prey populations, it is unclear how fear manifests to influence prey populations when the risk of predation is temporally variable (Sheriff et al. 2010). Are the costs of fear only immediate, or are there long-term carry-over effects of fear on prey populations?

Annual and seasonal fluxes in predation risk are common as both predator and prey populations and their behaviors shift in response to variation in environmental conditions and annual life cycles (Chesson 1978b, Heithaus and Dill 2002). Evidence suggests that heightened predation rates resulting in reduced prey numbers carry over to affect prey demography for generations after predation rates decline (Krebs et al. 1995, Sheriff et al. 2010). Unfortunately, the extent to which carry-over effects are due to selective predation removing a subset of the prey population, or fear alone impacting prey after predator numbers decline is largely unknown. Post-traumatic stress research in humans suggests that long-term implications of fear associated with stressful experiences often carry over to influence human behavior, and physiology years after returning to a safe environment (Helzer et al. 1987, Yehuda 2002). A single traumatic experience or repeated unpredictable stressors can cause increased anxiety, poorer performance in the

workplace and reduced fertility years after stressful stimuli have disappeared (Cohen 1980, Newton et al. 1999). However, in wildlife populations it is challenging to assess the effects of fear alone because it is nearly impossible to separate lethal and non-lethal effects. Predation shifts phenotypic expression within prey populations due to selective mortality as well as plastic phenotypic expression in survivors. For example, in risky environments the most vigilant individuals tend to have the highest survival rates (Lima 1987, Dehn 1990, Cowlishaw 1998), increasing the average vigilance of the population. At the same time, survivors, faced with a fearful environment likely express more extreme behaviors in high risk environments (Lima and Dill 1990, Brown 1999), further increasing the average vigilance measured in the population. Generally, in natural populations selective mortality and shifts in phenotypic expression of survivors due to fear alter traits within prey populations simultaneously and thus the effects of fear are difficult to measure in isolation. Indeed, the best evidence implicating the effects of fear on populations comes from manipulated predator-prey interactions in laboratories that render predators non-lethal or field experiments that provide prey with a single predator cue (e.g., playback, visual model) (Schmitz et al. 1997, Zanette et al. 2011, Handelsman et al. 2013) and none of have considered how fear manifest into the future.

To measure how and if fear (independent of mortality) has long term implications for prey physiology and behavior, we assessed the carry-over effects of heightened, fall predator activity (hunting by humans) on the spring reproductive ecology of female ring-necked pheasants (*Phasianus colchicus*). Hunting by humans elicits anti-predator response in target and non-target wildlife species, including shifts in behaviors, hormone concentrations and reproduction (Bshary 2001, Cromsigt et al. 2013) indicating that

hunting activities reliably alter the landscape of fear. Within our system, harvest of

pheasants is limited to males, but females are exposed to the landscape of fear induced by

hunters because males and females cohabitate. Therefore contact with hunters, and thus

the perception of risk, is not sex dependent, allowing us to measure the effects of fear

independent of the selective implications of mortality. Furthermore, hunting occurs from

October through January while reproduction is from April through July, providing a

temporal gap to assess the carry-over effects of fear on reproductive ecology. Numerous

behavioral, physiological and life-history traits shape reproductive ecology and various

traits trade-off with one another to mediate investment in offspring (Schluter et al. 1991,

Stearns 1992, Sinervo and Svensson 1998). To measure variation in pheasant

reproductive ecology despite the complex trade-offs between reproductive parameters,

we quantified a suite of traits including female corticosterone concentration and body

condition, clutch size, egg size, nest initiation date and nest site choice.

METHODS

STUDY AREA AND SPECIES

In 2012 and 2013, we studied pheasants in Hitchcock, Hayes and Red Willow

counties in Southwestern Nebraska (Fig.1). The Nebraska Game and Parks Commission

has designated the area as the Southwestern Focus on Pheasant Area of Nebraska, within

which the Commission will focus pheasant management and conservation efforts. The

area is dominated by agricultural fields but also includes rangelands and mixed grass

prairies enrolled in the Conservation Reserve Program (CRP). Mean annual rainfall is 22.6 inches and elevation ranges from 669 meters to 916 meters.

We studied female pheasant reproductive ecology on 12 CRP fields (30 - 126 hectares) characterized as mixed grass prairie and dominated by warm and cool season grasses interspersed with forbs and minimal woody vegetation (Fig. 1). Public hunting was permitted on half the sites ('high risk treatment'), while half were closed to public hunting and received minimal hunting pressure from private parties ('low risk treatment'). Selected sites were at least 2km apart to minimize movement between treatments as pheasants generally remain within a 2km radius home range (Smith et al. 1999). Because numerous ecological conditions in addition to fear can shape female reproductive expression (Wilbur et al. 1974, Ballinger 1977, Martin 1992, Mann et al. 2000), we measured a suite of ecological parameters within our study sites to ensure that differences beyond our treatment did not affect the behavioral, physiological, and life history traits we were interested in assessing. Because we were primarily interested in ensuring proper site selection we present those findings here.

Landscape-Scale Habitat Availability

Land-use practices clearly alter the resources and communities individuals are exposed to and thus affect behaviors, and life history expression (Aguilar and Galetto 2004, Fraterrigo et al. 2006, Jorgensen 2012). We quantified land-use (mixed grass prairie, rangeland, woodland, riparian area and type of agricultural field) within a 2-kilometer radius of study sites, an area that encompasses the average pheasant home range size (Smith et al. 1999). We limited land-use assessments to sites where we studied

birds in a given year and thus assessed three sites in both 2012 and 2013 and nine sites in only 2012 or 2013. We found no differences in the multitude of land-use practices employed between treatments ($F_{1,12} \leq 3.859$, $p \geq .073$).

Vegetation Available within Study Sites

Vegetation composition and structure can influence multiple sources of selection that shape avian reproductive strategies including food availability and predation risk (Martin 1993, Wilson et al. 1999, Whittingham and Evans 2004, Denno et al. 2005). We evaluated whether vegetation differed between high and low risk sites by assessing vegetation at randomly generated points within each study site that we generated in GIS using a spatially balanced sampling design (2 – 7 points per site; Martin 1997, Stevens and Olsen 2004). At each point we measured vegetation height and litter depth at three locations (1m, 3m, and 5m from the sampling point) in each cardinal direction and estimasted percent cover for: green vegetation, warm and cool season grasses, forbs, woody vegetation (greater than and less than 1.5m), crop, litter and bare ground within a 5m radius (Martin 1997). We used mixed models (R, nlme package) to assess to differences in available vegetation between high and low risk sites and included year, study site and point as random effects in the model (Pinheiro et al. 2014, R Core Team). We found no differences in any vegetative parameters measured between treatments ($F_{1,12} \leq 3.347$, $p \geq 0.092$).

Food Availability within Study Sites

Food availability can mediate female reproduction by constraining intrinsic

energetic reserves available for investment in offspring (Ballinger 1977, Daan et al. 1989,

Siikamaki 1998, Brown 1999). Because invertebrates comprise a large proportion of

female diet during the breeding season (Hill 1985) we measured relative invertebrate

abundance across our study sites from early May through June in 2013 via pitfall traps

and sweep net sampling at the same random points where we assessed vegetative

composition. We constructed an array of 4 pitfall traps at each point and placed traps 1 m

from points in each cardinal direction. Pitfall traps remained open for 48 hours.

Immediately prior to collecting pitfall trap samples we conducted sweep net sampling (1

sweep per step) along 2 perpendicular 30m transects, beginning 15 meters from each

point (Hill 1985, Fischer et al. 1996, Koricheva et al. 2000). All invertebrate samples

were frozen within 8 hours after collection and later counted and categorized into size

classes (<1-5mm, $\geq$ 5-10mm, and > 10mm). We included in the analysis the eight study

sites on which birds survived through the 2013 breeding season. We used mixed models

(R, nlme package) to assess to differences in relative invertebrate abundance between

high and low risk sites and included study site and sampling point as nested random

effects in the model (Pinheiro et al. 2014). We found no difference in relative invertebrate

abundance between treatments ($F_{1,6} = 2.44$, $p = 0.170$).

Access to Mates

The abundance of males in a pheasant population can increase intersexual

competition for resources (Mateos 1998) and affect female access to mates (Emlen and

Oring 1977, Crowley et al. 1991), both of which can mediate female condition, survival, and reproductive investment (Clutton-Brock 1998, Leturque and Rousset 2004). We estimated male abundance at each study site by recording the number of male calls detected within a two-minute sampling period each week. Surveys were conducted between thirty minutes prior to sunrise and 10am from mid-April through mid-June, the timeframes during which male calling rates peak (Kozicky 1952). We used mixed models (R, nlme package) to assess to differences in aural survey results between high and low risk sites and included year and study site as random effects in the model (Pinheiro et al. 2014, R Core Team). We found no difference in male abundance estimates between treatments ($F_{1,12} = 0.003$ p = 0.955).

CAPTURE AND HANDLING TECHNIQUES

We captured female pheasants prior to the breeding season in 2012 and 2013 via nightlighting (Labisky 1986) and equipped each with a 30-g necklace radio transmitter (ATS Series A4000) to track movement, survival and to locate nesting attempts. We extracted blood samples (~150µl) from the brachial vein with heparinized microcapillary tubes within 3 minutes of capture and again 20 minutes after capture to assess total baseline and peak CORT concentrations. Blood samples were stored on ice in small coolers for no more than 9 hours before being centrifuged and frozen for future analysis. We measured body mass with a 2.7-kg spring scale accurate to 2 g (CC1 Scale Co. Inc. model HS-6) and tarsus length with a digital caliper accurate to .01 mm (Carrera Precisions 0-150mm digital caliper, model CHICO14).

CORTICOSTERONE CONCENTRATION

CORT is a hormone that reallocates energy reserves in response to stressful stimuli (Sapolsky et al. 2000). Increased CORT concentrations facilitate anti-predator behavior and often constrain reproductive investment (Wingfield and Sapolsky 2003). To assess whether CORT concentration potentially mediated carry-over effects of hunter activity on female reproductive strategies we bled birds (see above) and measured total baseline and peak CORT concentration in female pheasant plasma samples ranging from $10 - 46$ µl (average 32 µl) via Enzyme Immunoassay (Enzo Life Sciences ADI-901-097) (Wada et al. 2007, Schoech et al. 2013). We tested for optimal sample dilution across a range of baseline and peak sample dilutions (1:20, 1:40, 1:60, 1:80) and diluted all samples at 1:40, as all test samples fell within the standard curve of optical density (assay accuracy averaged 0.145 ng / ml, Standard Error: .057) .We ran all samples in duplicate, including tests and analyses.

BODY CONDITION

Anti-predator response to perceived predation risk often mediates prey body condition and consequently prey reproductive investment (Lima 1986, Hik 1995, Scheuerlein et al. 2001). We calculated body condition (M_c) as a scaled mass index of capture date and tarsus size. We used capture date to scale mass because mass was positively correlated with capture date ($F_{1,55} = 20.85$, $p < 0.0001$) reflecting the increase in weight gain common as animals exit the winter. We corrected mass for capture date with the following formula $M_c = M_i * [C_o/C_i]^b_{OLS}$ where M_i and C_i are the mass and

capture date of the individual, C_o is the population mean capture date and $^b{}_{OLS}$, the

scaling exponent, the slope (Ordinary Least Squares) of the regression of the natural log

of mass by the natural log of capture Julian date for all individuals in the population (Peig

and Green 2009). Since we were ultimately interested in the relative body condition for a

given size, we then corrected this new mass estimate against tarsus size following the

same procedure, using the standardized major axis slope ($F_{1,55}$ = 1.517, p = 0.223, slope =

2.119) (Peig and Green 2009).

REPRODUCTIVE INVESTMENT

Adult predation risk can shift how individuals allocate energy to reproduction by

altering reproductive trade-offs between investment in parent and investment in offspring

as well as between current and future reproduction (Magnhagen 1991, Roff 2001,

Wingfield and Sapolsky 2003, Lima 2009). It has long been recognized that fear can alter

the trade-offs inherent in reproduction by constraining prey investment in offspring when

risky conditions limit access to resources or alter physiological pathways (Sapolsky et al.

2000, Pressier et al. 2005). However, it is increasingly apparent that some shifts in

reproductive investment are adaptive responses of prey evolved to maximize lifetime

reproduction in risky environments (Sih 1994, Reznick et al. 2000, Peluc et al. 2008).

Short-lived species, for example, increase reproductive investment in response to adult

predation risk, while longer lived species reduce investment or forego reproduction

altogether to ensure survival and future reproduction (Stearns 1992, Candolin 1998,

Heithaus et al. 2008).   Because the evolutionary and ecological implications of altering

reproductive investment are extreme (Boyd et al. 1995, Rodd and Reznick 1997, Saether

and Bakke 2000), it is necessary to understand whether changes in reproductive strategies represent an adaptive response or a physiological constraint.

We assessed reproductive investment by female pheasants based on clutch investment. We located nests using radio-telemetry, or opportunistically when we found nests of unmarked females within our study sites. We flushed hens from nests, recorded clutch size and measured eggs (length and width) from complete clutches with a digital caliper accurate to .01mm (Carrera Precisions 0-150mm digital caliper, model CHICO14). We confirmed clutches were complete by ensuring that clutch size remained constant for at least two consecutive days (pheasants lay one egg per day). Additionally, we determined incubation stage for at least three eggs per clutch by floating eggs (Westerkov 1950). We calculated egg volume using the following formula $V = K_V$ (LW^2), where V is volume, K_V is a volume coefficient developed for pheasant eggs (Hoyt 1979), L is egg length and W is egg width (Hoyt 1979). We then compared average egg volume between nests on high and low risk sites.

NEST SITE CHOICE

Nest site choice can mediate sources of selection that shape adult breeding behaviors, physiology and life history expression (Martin 1995). Variation in reproductive strategies within species is largely explained by variation in food availability and predation risk, two sources of selection that breeding birds can mediate via nest site choice (Martin 1987, Martin 1995, Fontaine and Martin 2006a). It is possible that fall hunter activity carries over to influence a female's perception of risk, and thus nest site choice the following spring, leading females to shift territories to safer nesting

habitats (Fontaine and Martin 2006b, Hua et al. 2013), or by altering nest site choice to maximize safety within a risky environment either for her offspring or herself (Eggers et al. 2006, Schmidt et al. 2006, Chalfoun and Martin 2009). We quantified nest site decisions by measuring vegetation composition and structure within 5 meters of nest sites and at random points within each study site (see above). Additionally, we estimated visual obstruction from each cardinal direction by photographing a 1m x 1m white board at the nest site (following Limb et al. 2007). We processed images in the open source image program GNU Image Manipulation Program® to calculate the percentage of the board obstructed by vegetation (following Jorgensen et al. 2013). We averaged the four visual obstruction values to attain a single value for each nest.

FEMALE SURVIVAL

For ground nesting birds, female depredation during the breeding season can significantly impact populations (Magnhagen 1991); therefore, adult predation risk likely alters reproductive expression such that females are more risk adverse when the perception of risk is high (Lima 1998b). We evaluated whether fall hunting activities carried over to reduce female exposure to natural predators during the breeding season by monitoring female status (alive or dead) approximately every 3-4 days throughout the breeding season and conduced a known-fate survival analysis in Program Mark (White and Burnham 1999).

STATISTICAL ANALYSES

We used linear mixed models to determine the parameter(s) that accounted for variation in all our response variables (except for nest site choice and female survival see below) (R package lattice and nlme) (Pinheiro et al. 2014, R Core Team 2014; Deepayan, 2008, R Core Team 2013). We excluded non-significant variables and interactions from trial models. All reproductive investment and landscape-scale nest site choice analyses were limited to first nesting attempts within a given year as nesting attempt clearly alters reproductive investment (Murphy 1986, Perrins and McCleery 1989, Decker et al. 2012). In order to test for differences in nest site choice between treatments we used non-metric multi-dimensional scaling and the envfit function in R package vegan, which utilizes 999 permutations of the data (Oksanen et al. 2013, R Core Team 2013). We assessed the effects of hunter activity on the proportion of females that moved off mixed grass prairie sites to nest in adjacent fields using a Fischer's Exact Test (FET) because of small sample size (Upton 1992).

To assess female survival during the breeding season we conducted a known-fate survival analysis in Program Mark (White and Burnham 1999, Cooch and White 2014) and calculated weekly survival estimates as well as survival estimates for the duration of the breeding season for females in both treatments (Cooch and White 2014). We limited our analysis to female survival through the breeding season within the year of capture because only one bird survived to a second breeding season. Because we knew the fate of each female in the analysis (we never had birds that were censored due to disappearance), we assumed all females to be alive within a given week if we recorded them alive in a subsequent week (Cooch and White 2014). Only females that survived at least two weeks

after capture were included in the model to eliminate the potential effects of capture and handling on survival (Winterstein et al. 2001). We regressed weekly survival probabilities against Julian date in order to assess female survival throughout the breeding season and compared survival probability across the entire breeding season between high and low risk sites using a paired t-test.

RESULTS

HEN REPRODUCTION AND PHYSIOLOGY

We captured and radio-collared 126 female pheasants (high risk: 46, low risk: 80), assessed baseline plasma CORT of 24 (high risk: 11, low risk: 13), peak plasma CORT of 36 (high risk: 15, low risk: 21), body condition for 59 (low risk: 34, high risk: 23), and found and monitored 21 first nest attempts (high risk: 12, low risk: 9) (Table 1).

<u>Corticosterone Concentration</u>

One female, captured during a second capture event within the same season exhibited a significantly higher baseline CORT concentration (over 7 times higher) than females caught on the first visit. From the remaining baseline CORT concentrations, we visually identified five outliers, over three times higher than reported baseline CORT concentrations for gallinaceous birds (Beuving and Vonder 1978, Chloupek et al. 2009, Voslarova 2011) and significantly higher than all other baseline CORT concentrations we assessed ($F_{1,27} = 106.10$, $p < 0.001$). We therefore eliminated the six outliers from the analysis. Capture date, time and temperature did not influence baseline, peak CORT

concentrations, or the CORT stress response (peak – baseline) (baseline: $F_{1,22} \leq 1.189$, p ≥ 0.287; peak: $F_{1,37} \leq 0.549$, p $= 0.463$; CORT stress response: $F_{1,22} \leq 0.526$, p ≥ 0.476).

Baseline CORT concentration was higher on high risk sites across years (Fig. 2b; $F_{1,22} = 4.189$ p $= 0.053$) and in 2013 ($F_{1,11} = 6.63$ p $= 0.026$) but not in 2012 ($F_{1,9} = 0.127$ p $= 0.730$). However, the three-way interaction between hunting pressure and year did not predict baseline CORT concentration ($F_{3,20} = 1.965$ p $= 0.152$). The interaction between hunting pressure and body condition predicted female baseline CORT concentration (Fig. 3; $F_{2,19} = 7.653$, p $= 0.004$). Both peak CORT ($F_{1,20} = 4.86$, p $= 0.04$) and the difference between baseline and peak CORT ($F_{1,33} = 5.5151$, p $= 0.03$) negatively correlated with body condition, however neither differed between treatments (Fig. 2c; peak: $F_{1,37} = 0.013$, p $= 0.909$; stress response: $F_{1,22} = 0.012$, p $= 0.913$) or predicted clutch size (baseline: F $\leq$ 0.933, p ≥ 0.371), egg size (baseline: F ≤ 1.789, p ≥ 0.230) or lay date (F ≤ 1.358, p $\geq$ 0.288).

Body Condition

Body condition did not differ between treatments, whether assessed in all measured females (Fig. 2a; $F_{1,55} = 0.071$, p $= 0.79$), potential breeders (females that survived until the last lay date of a first nesting attempt we recorded in each year) ($F_{1,21} = 0.123$, p $= 0.72$) or the hens for whom we assessed reproductive investment ($F_{1,13} = 0.672$, p $= 0.427$). Body condition was negatively correlated with lay date ($F_{1,12} = 4.803$, p $= 0.05$) and differed among years (mean 2012: 1016.31g, mean 2013: 875.68g, $F_{1,55} = 34.25$, p < 0.0001), but year effects did not interact with the treatment for any subset of hens we considered (F ≤ 2.919, p ≥ 0.126).

Reproductive Investment

Hens on high risk sites produced smaller eggs than hens on low risk sites (Fig. 2e. $F_{1,19} = 6.275$, p = 0.022), but clutch size (Fig. 2f; $F_{1,19} = 0.026$, p = 0.874) and lay date (Fig. 2g; $F_{1,19} = 0.6418$, p = 0.433) did not differ between treatments. Variance in egg size within clutches did not differ between treatments ($F_{1,19} = 0.204$, p = .657). Clutch size was negatively correlated with nest initiation date ($F_{1,19} = 5.99$, p = .024), however nest initiation date did not predict egg size ($F_{1,19} = 0.020$, p = .890) and body condition did not predict clutch size or egg size ($F \leq .356$, $p \geq 0.5619$). Females initiated nests significantly later in 2013 (mean lay date 2012: April 28, mean lay date 2013: May 17; $F_{1,19} = 10.72$, p = 0.004), but there was no difference in egg size or clutch size between years (egg size: $F_{1,19} = 0.001$, p = 0.977; clutch size: $F_{1,19} = 0.123$, p = 0.729).

NEST SITE CHOICE

The number of females that moved off mixed grass sites to nest in alternative surrounding habitats (crop fields, weeds and rangeland) did not differ between treatments (p = 0.09, FET) nor did the distance traveled from capture site to nest site ($F_{1,14} = 2.313$, p = 0.151). There was no significant difference in nest site vegetative composition between treatments whether assessed across all nests ($r^2 = 0.072$, p = 0.129) or assessed across only nests within grassland study sites ($r^2 = 0.042$, p = 0.544). However, nests on grassland sites (across treatments) had significantly different vegetative composition than nests off grassland sites (Fig. 4b; $r^2 = 0.509$, p = 0.001) and only females from high risk

sites moved off grassland sites to nest. Nesting year was not significant in any of the above models.

FEMALE SURVIVAL

Weekly survival probability declined throughout the breeding season from March to mid-July ($F_{1,21}$ = 11.64, p = 0.003), but the probability that female's survive the breeding season did not differ between treatments (Fig. 2d; $t_{1,52}$ = 1.281, p = 0.206)

DISCUSSION

It is increasingly apparent that prey live in a landscape of fear (Lima and Dill 1990, Lima 1998a, Ripple et al. 2014). However, our results showing that fear alters prey physiology and maternal investment in eggs months after the indicators of risk have passed present some of the first evidence within natural populations that risk per se has long-term implications for prey life-history expression. Predation risk is a significant source of selection shaping reproduction across taxa (Frasier and Gilliam 1992, Stibor 1992, Creel et al. 2007), and the effects of predation on avian reproductive decisions is an especially well-studied example (Lima 1987, Zanette et al. 2003, Lima 2009); however, studies of the impacts of predation risk on avian reproduction have limited their assessment to the breeding season (Lima 2009, Bonnington et al. 2013, Hua et al. 2014). Our data suggest that traditional examinations of reproductive ecology could be missing a significant source of selection, especially within systems where seasonal variability in predation risk is high.

In our system, hunting imposed seasonal variation in predation risk, but there are many natural systems in which predation risk may vary among seasons or even years. For

example, a plethora of migratory predators such as raptors generate ephemeral landscapes of fear for prey along their migratory routes. While assessments of breeding performance of prey populations traditionally focus on breeding season conditions and carry-over effects of lethal predation events on prey population demography (Krebs et al. 1995, Abrams 2000), our data suggest that the ephemeral risk generated by migratory predators throughout their preys' non-breeding seasons may carry over to influence reproductive ecology and explain variance in reproductive parameters not attributable to breeding conditions or prey mortality. In addition, migratory prey populations experience heightened episodes of risk as predator communities differ between the numerous locations prey utilize throughout their annual cycle. Throughout the 450 km annual migration of wildebeest in the Serengeti, for example, there is temporally and spatially pointed predation risk (Berger 2004, Grant et al. 2013) that may influence reproductive strategies months and hundreds of kilometers later; however, to date this source of variation in reproductive expression is largely overlooked beyond consideration of the potential energetic constraints imposed by behavioral trade-offs (e.g., Moore et al. 2005). Here we demonstrate that independent of their current energetic state, female pheasants invest less in eggs when they have experienced fear in their past.

A major reason why research has failed to address carry-over effects of fear is because it is extremely challenging to separate the effects of differential predator-induced mortality on prey populations from the effects of fear after episodes of risk have passed. In natural populations, it is likely that all prey perceive risk while predators simultaneously remove a subset of the prey population. Thus, within a prey population it is generally not possible to tease apart the effects of fear from differential selection that

may ultimately alter the prey phenotypes present in the population through genetic rather than plastic phenotypic mechanisms (Chesson 1978a, Reznick 1982, Quinn and Kinnison 1999). For example, in one of the best assessments of the potential carryover effects of fear, Sheriff et al. (2010) demonstrate that elevated CORT concentrations in snowshoe hare (*Lepus americanus*) populations are maintained several years after lynx (*Lynx canadensis)* populations have crashed. Although the authors argue that the high CORT levels are indicative of fear having long-term phenotypic effects, it is also reasonable that differential depredation by lynx altered the underlying genetic structure of the hare population such that individuals with innately higher CORT levels survived the predation bottleneck. In this case it is difficult to differentiate whether phenotypic expression is moving along the reaction norm, or whether the reaction norm has altogether shifted. By eliminating the selective effects of predation on the population we definitively demonstrate that fear alone carries over to alter prey breeding ecology months after the cues indicative of risk have left the landscape. Our data showing no differences between treatments in other sources of selection (i.e., habitat and food availability, and access to mates) and no difference in female CORT levels, egg size or nest site choice between years suggests that differences in female reproductive ecology between treatments was due to hunting pressure intensity. Furthermore, our assessments of temporal carry-over effects of fear on reproductive ecology are likely conservative, considering a subset of females that experienced heavy hunting pressure may have moved to low risk sites during the hunting season. In our analysis, we assumed that females captured after the hunting season on low risk sites experienced minimal hunting pressure, but some females moved from high to low risk sites during the hunting season (Messinger and Fontaine,

unpublished data). If in fact a subset of females we categorized as low risk, experienced a high risk environment, it is likely that any females categorized incorrectly reduced our effect size, indicating the potential strength of fear in shaping long-term phenotypic expression.

FEMALE PHYSIOLGOICAL CONDITION

Females on high risk sites had elevated baseline CORT months after the hunting season. Steroid hormones such as CORT coordinate various physiological responses to environmental stressors that shunt intrinsic resources to mediate deleterious impacts of stressors on animal survival, often at the expense of reproduction (Sapolsky et al. 2000). That we found no differences in body condition between treatments suggests that elevated baseline CORT concentrations on high risk sites likely corresponded with increased foraging to compensate for reduced condition imposed by altered behaviors expressed during the hunting season (Fontaine, unpublished data).

We also found, as have many others (Kitaysky et al. 1999, Romero and Wikelski 2001, Bókony et al. 2009), that body condition was negatively correlated with baseline CORT concentrations. Body condition can modulate adrenocortid responses to stressors including CORT (McEwen and Wingfield 2003) such that individuals in better body condition have lower CORT concentrations. However, fear appears to alter the relationship between condition and CORT by making baseline CORT levels more sensitive to body conditions in high risk environments. Elevated CORT is known to alter a variety of behaviors, many of which are presumed adaptive responses to predation risk or the food limitation imposed by predation risk (Sapolsky et al. 2000, Wingfield 2003);

however, our data suggests that chronic exposure to fear may disrupt this relationship with unknown consequences. The interaction between body condition, predation risk, and CORT suggest that chronic fear alters the physiological condition necessary to impose an emergency life history strategy (Wingfield et al. 1998, Wingfield 2003). Moreover, that we found individuals maintaining an emergency life history strategy months after their exposure to predation risk had passed indicates the potential importance of temporally variable predation risk in shaping life history expression. Humans exposed to temporally variable stressors express behaviors (i.e., heighten awareness) that while adaptive at the time of the stressor can be maladaptive in normal societal situations (i.e., insomnia) (Cohen 1980, Vgontzas et al. 1998, Staal 2004). We might expect similar maladaptive consequences of fear in animals if emergency life history strategies are maintained after the risk of predation has passed.

FEMALE INVESTMENT IN OFFSPRING

Although elevated glucocorticoid concentrations often correspond with reduced reproductive effort, fear did not appear to affect which females bred or their respective clutch size. That clutch size did not differ between treatments confirms the well-documented relationship between clutch size and female body condition (Meijer et al. 1988, Erikstad et al. 1993, Bêty et al. 2003) as body condition of breeders did not differ between risky environments and safe environments. We did, however, find that females on high risk sites produced smaller eggs and showed greater variation in nest site choice despite no difference in body conditions or food availability, suggesting that elevated baseline CORT concentrations may have mediated maternal investment in eggs and

habitat decisions. Still it is unclear whether CORT was the causal factor that drove either reproductive decision or whether it acted as a physiological constraint or alternatively, facilitated adaptive benefits of alternative nest sites and reduced egg size in high risk environments (Fox and Czesak 2000, Fontaine and Martin 2006a). Nest site choice has obvious implications for female (Martin 1995, Amat and Masero 2004) and offspring (Martin and Roper 1988, Wesolowski 2002, Forstmeier and Weiss 2004) survival. That we saw that a subset of females exposed to fear chose significantly different nest sites by nesting outside of traditional grassland nesting habitats suggests that females on high risk sites are searching more diligently for nest sites that reduce risk (Schimidt et al. 2006). Indeed, the reduction in egg size also may have been an attempt to reduce risk via nest site decisions, as smaller eggs require smaller nests, which may reduce nest predation (Biancucci and Martin 2010).

Unfortunately, the effects of egg size on the development and fitness of precocial young remains equivocal as do the benefits of smaller eggs in high risk environments (Williams 1994, Smith et al. 1995, Christians 2002, Pelayo and Clark 2003). Reducing egg size may reduce the overall incubation period (Worth 1940, Rahn and Ahr 1974) and potentially nest attentiveness patterns (Hanssen et al. 2002), reproductive traits that have the potential to mediate predation risk (Montgomerie and Weatherhead 1988, Persson and Göransson 1999, Martin et al. 2000). We found, as have many others (Ainley and DeMaster 1980, Shine 1980), a distinct decline in female survival during the nesting period suggesting that females are especially vulnerable to adult predation risk while nesting and are therefore likely sensitive to any additional perception of risk. If the assessment of predation risk from the fall continues to invoke an emergency life history

strategy as we suggest, then it is reasonable that females may reduce egg size as a means to reduce risk to themselves by limiting the overall incubation period and movement around the nest (Bernardo 1996, Olofsson et al. 2009). Alternatively, if females were incapable of differentiating between adult and nest predation risk, the reduction in egg size may indicate a bet-hedging strategy whereby females reduced investment in a particular nest as a means to facilitate renesting in high risk environments (Cunnington and Brooks 1996, Love et al. 2005). No matter the mechanism, it is becoming increasingly apparent that egg size is a sensitive indicator of avian assessment of predation risk (Fontaine and Martin 2006b, Olofsson et al. 2009). Females can adjust egg size by marginal increments while continuously assessing environmental conditions and adjusting egg size throughout the laying period. In contrast, shifts in clutch size increase or reduce reproductive investment by a minimum of one egg, a large proportion of total pheasant clutch investment. Thus, in response to perceived predation risk, changes in egg size allow for more conservative bet-hedging, a strategy life-history would predict for a short-lived species like the ring-necked pheasant that generally only lives to breed once (Stearns 1992).

Reproductive strategies of short-lived species tend to be less malleable to ensure reproductive success within an individual's minimal life-time breeding opportunities, whereas reproductive strategies of relatively long-lived species are generally more sensitive to adult predation risk as individuals sacrifice current reproduction for future breeding opportunities (Stearns 1992, Ghalambor and Martin 2000). Here we show that perceived risk can affect the reproductive ecology of a species on the fast end of the life-history spectrum months after the fear has passed. That mere phantoms of predators past

can reduce reproductive investment in a short-lived species suggests that the carry-over

effects of predation risk on reproductive ecology are likely widespread across the life-

history spectrum.

POTENTIAL FITNESS IMPLICATIONS OF TEMPORAL

CARRY-OVER EFFECTS OF FEAR

If past conditions do not predict the current breeding environment and

reproductive decisions are being made independent of a physiological constraint, it seems

likely that the responses of females to the phantoms of predators past are maladaptive.

Hunter activity poses no threat to nesting pheasants, though the effects of fall hunter

activity on female physiology persist through the spring potentially acting as the

mechanism that alters female breeding decisions (i.e., reduced egg size). If adult

predation risk during the breeding season was in fact higher on high risk sites, it may be

beneficial for females to maintain elevated baseline CORT concentrations that facilitate

anti-predator response (Wingfield and Sapolsky 2003). However, breeding conditions did

not differ between treatments, suggesting that elevated baseline CORT levels and reduced

egg size are maladaptive strategies triggered by cues that are no longer relevant to

breeding success in current conditions. Presumably, organisms that evolved in a system

with predictable temporal variability in predation risk would evolve flexible life-history

strategies that reduce the probability of mortality in risky environments and increase

reproductive investment in safe environments, though empirical evidence is scarce (Lima

and Dill 1990, Ghalambor and Martin 2002, Eggers et al. 2005). It is possible that

variation in predation risk coupled with minimal predictability in temporal patterns of

risk generate conservative strategies that mitigate potential fitness costs (mortality) and maximize fitness-benefits within a range of unpredictable environmental conditions (Hopper 1999, Beaumont et al. 2009). Conservative responses to adult predation risk are common, likely because the cost associated with overestimating adult risk and reducing reproductive investment unnecessarily is relatively limited (reduced fecundity) compared to the costs associated with underestimating risk to maintain reproductive investment in a high risk environment (mortality) (Van Buskirk and Arioli 2002, Pressier et al. 2005).

Our system represents an artificial shift in risk, with which pheasants did not evolve. Novel environmental variation likely increases the probability of maladaptive carry-over effects in response to environmental cues, as rapid environmental change precludes the evolution of life-history strategies in tandem with historically predictable fluctuations in sources of selection (Robertson and Hutto 2006). Anthropogenic and climate change also alter landscapes of fear altering the spatial and temporal patterns of risk (Sanford 1999, Gilg et al. 2009, Harley 2011) and introducing novel predators to naïve prey communities (Ripple and Beschta 2003, Blackburn et al. 2004). On Isle-Royale winter snow accumulation related to rapid climate change explained inter-annual variation in wolf-moose dynamics and consequently moose predation risk across 40 years: more snow caused wolves to hunt in larger packs leading to increased moose mortality (Post et al. 1999). Within the same population, human-introduced canine parvovirus caused a decline in wolf populations in the 1980's and a corresponding reduction in predation risk for moose (Wilmers et al. 2006). Generally, ecologists assess the impacts of rapid environmental change by quantifying the environmental cues and an organism's response within a given timeframe. Our data suggest that we may be missing

causal relationships between novel environmental cues and an organism's fitness parameters as seasonal environmental variation increases and humans introduce cues to the landscape with which prey have not evolved.

MANAGEMENT IMPLICATIONS

Ring-necked pheasants are a culturally and economically important species throughout the Great Plains, providing hunting opportunities for sportsmen and conservation funds via hunting permit sales for state wildlife management agencies (Erickson 1973, Dahlgren 1988, Bangsund et al. 2004). Over the past thirty years, various organizations, professionals, and wildlife enthusiasts have invested considerable resources to increase pheasant populations and bolster hunter participation and success (Rogers 2002, Bangsund et al. 2004). Unfortunately, current pheasant populations and hunter harvest rates are a small fraction of those a half a century ago (Taylor et al. 1978, Dalgren 1988, Suchy et al. 1991, Perkins et al. 1997). Moreover, the impacts of current management strategies are unclear. For example, pheasant harvest management has changed little over the last forty years and remains focused on maintaining viable female populations by excluding females from harvest. The direct impacts of harvest on pheasant populations may be negligible because few males are required to ensure mating opportunities for all females (Alcock 2009); however, critical to the success of the current management paradigm is the assumption that hunting does not impact female reproduction. Our research provides the first evidence that challenges the current management paradigm and suggests that independent of hunter harvest, fear associated

with hunter activity in the fall carries over to impact female reproductive ecology the following spring, with potential, but unverified demographic consequences.

To develop more effective pheasant management strategies, it is necessary to understand how hunter activity mediates female reproductive ecology across a continuum of hunting pressure and the demographic consequences for future generations. We assessed the carry-over effects of fall hunter activity on female reproduction across two treatments: relatively high hunting pressure and minimal hunting pressure. Our data suggest that the effects of fall hunter activity carry over to elevate spring female baseline CORT concentration and reduce egg size. However, the nature of the relationship between hunting intensity and the degree of carry-over effects on female reproductive ecology remains unknown. While it is reasonable that a threshold of hunting pressure exists, under which there are minimal effects of fear on female reproduction this assumption remains untested here or in any study of game management to date. Evaluating the threshold of hunting pressure that initiates impacts to pheasant reproduction or any game species can inform managers to more effectively maximize hunter satisfaction while minimizing impacts on female reproduction (Fig. 5).

Moreover, the implications of elevated baseline CORT levels and reduced egg size for pheasant demography remain unclear. Baseline CORT levels and egg size may impact nest and adult survival during the breeding season (Olofsson et al. 2009, Rubolini et al. 2005, Blomqvist et al. 1997), and potentially mediate offspring fitness immediately (Christians 2002) or across generations (Sheriff et al. 2010). Understanding the relative impact of shifts in reproductive ecology on pheasant demography are necessary to completely inform management decisions. For example, if demographic consequences

are severe, conservative hunter regulations may be necessary to limit impacts of hunter activity on pheasant population growth. Alternatively, if demographic consequences are minimal, permitting high hunting pressure and/or opening more locations to public hunting may improve hunter participation with minimal impact on pheasant population growth. Clarifying how to maximize hunter participation and success as well as pheasant population growth will help to afford more pheasant hunting opportunities to sportsmen, an important cultural activity that connects hunters and bird enthusiasts with the natural landscape and facilitates conservation efforts.

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TABLES AND FIGURES

Table 1. Summary of parameters of female condition and female investment in offspring each year across treatments including sample sizes, means and standard errors.

| Parameter	Hunting Pressure	Year	Sample Size	Mean	Standard Error
Baseline CORT (ng/ml)	Low	2012	7	3.54	0.67
	High	2012	4	3.93	0.57
	Low	2013	6	2.6	0.35
	High	2013	7	4.75	0.65
Peak CORT (ng/ml)	Low	2012	10	36.90	4.88
	High	2012	6	32.90	7.10
	Low	2013	11	37.02	3.56
	High	2013	9	39.02	4.57
Body Condition $(M_i = M_i * [C_o/C_i]^b)$	Low	2012	15	993.56	29.26
	High	2012	6	1073.19	25.66
	Low	2013	19	869.53	15.94
	High	2013	17	882.56	17.09
Clutch Size	Low	2012	5	11.80	1.58
	High	2012	8	11.50	1.75
	Low	2013	4	10.5	0.83
	High	2013	4	11.5	1.03
Egg Size (mm^3 x 10^3)	Low	2012	5	24.25	0.63
	High	2012	8	21.80	0.58
	Low	2013	4	23.13	0.45
	High	2013	4	22.40	0.76
Survival (weekly survival probability)	Low	2012	11	0.10	0.73
	High	2012	7	< 0.001	< 0.001
	Low	2013	18	0.11	0.16
	High	2013	18	0.46	0.12
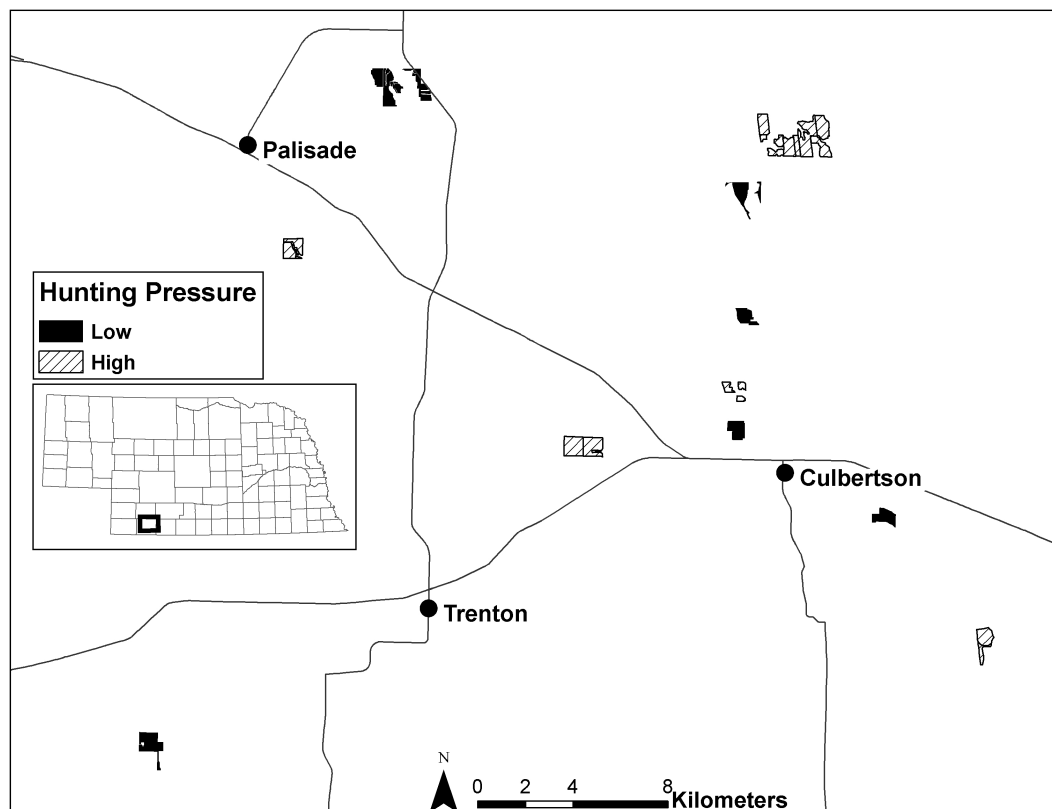
Figure 1. Map of study sites in southwestern Nebraska including six sites that received high hunting pressure and six sites that received low hunting pressure.
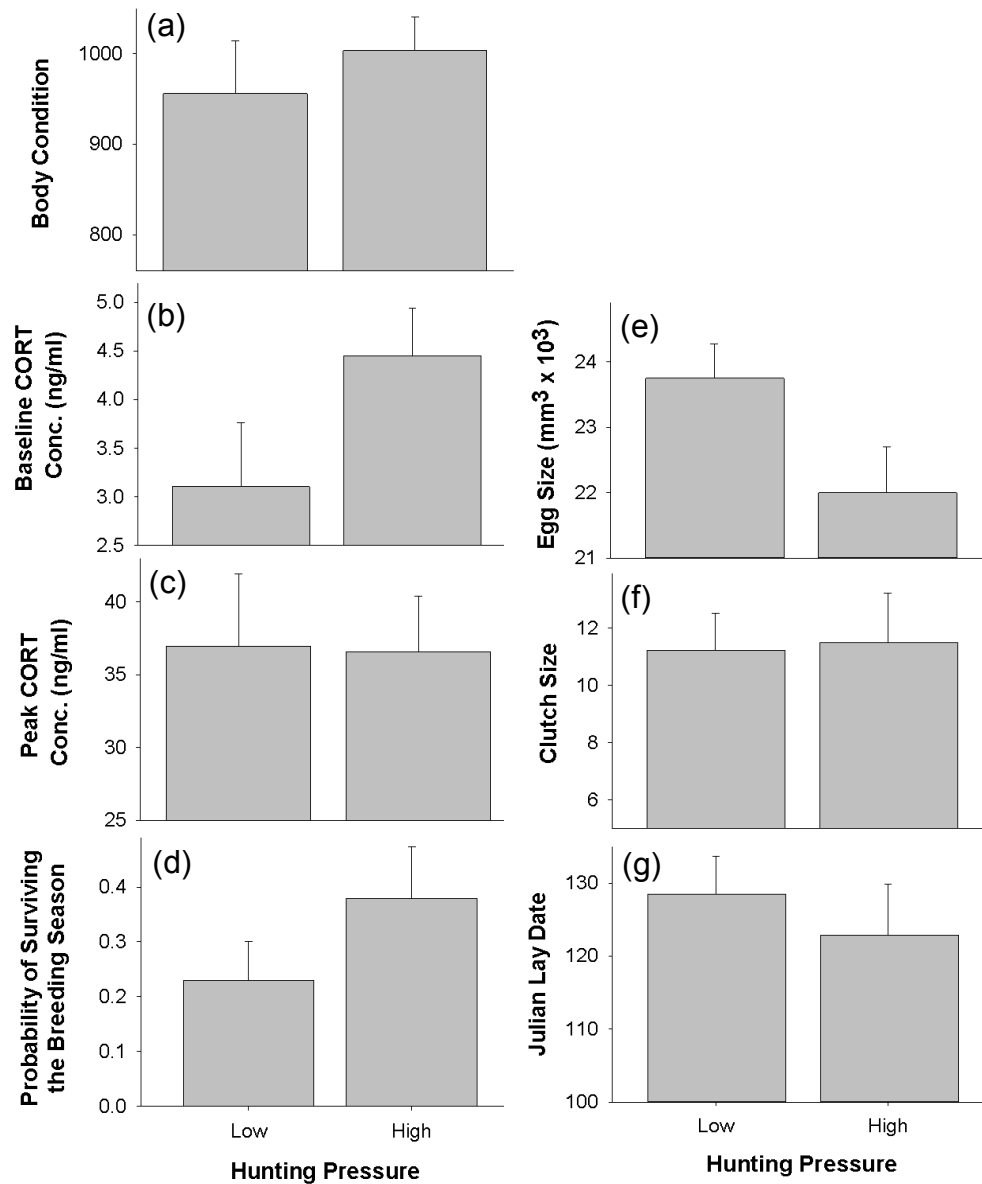
Figure 2 Perceived predation risk carried over to influence spring baseline CORT concentration and egg size, but none of the other parameters of adult condition or reproductive investment. Females on sites with high hunting pressure (a) had similar body condition*, (b) higher baseline CORT concentrations, (c) similar peak CORT concentrations, (d) similar survival probability, (e) laid smaller eggs, (f) had similar clutch sizes, (g) and had similar nest initiation dates.

*Body condition was calculated by correcting mass for capture date using the following formula: $M_i = M_i * [C_o/C_i]^b$ where M_i and C_i are the mass and capture date of the individual, C_o is the population mean capture date and ^{b}, the slope of the regression of LN(mass) by LN(capture Julian date) for all individuals in the population. The calculation was repeated in order to correct the newly calculated mass by tarsus length ($M_i = M_i * [T_o/T_i]^b$) (Peig and Green 2009).
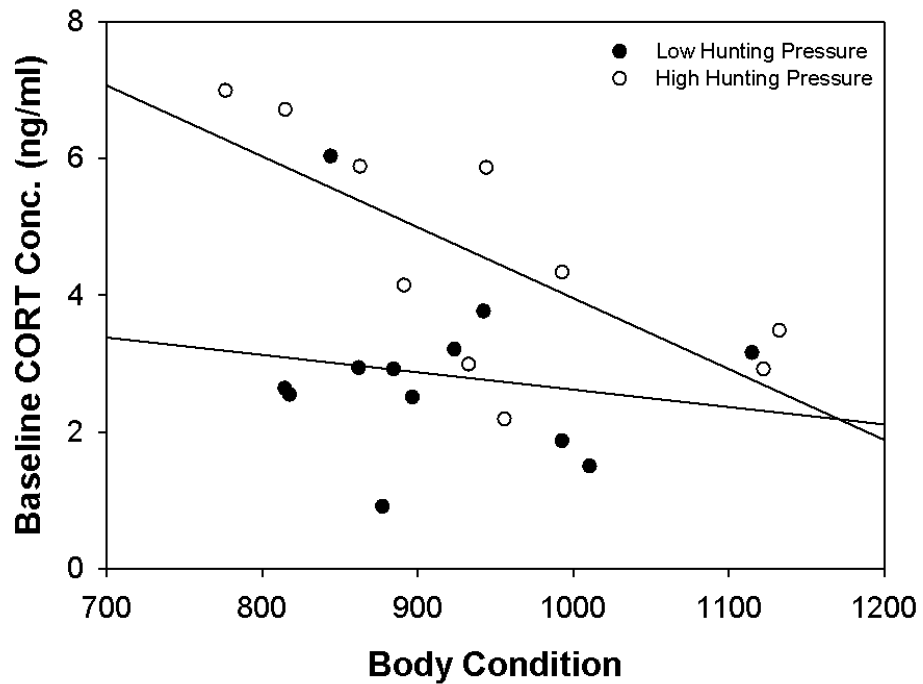
Figure 3 Females on high risk sites had higher baseline CORT concentrations that were more sensitive to body condition*, such that females in poorer condition had higher baseline CORT concentrations.

*Body condition was calculated by correcting mass for capture date using the following formula: $M_i = M_i * [C_o/C_i]^b$ where M_i and C_i are the mass and capture date of the individual, C_o is the population mean capture date and ^{b}, the slope of the regression of LN(mass) by LN(capture Julian date) for all individuals in the population. The calculation was repeated in order to correct the newly calculated mass by tarsus length ($M_i = M_i * [T_o/T_i]^b$) (Peig and Green 2009).
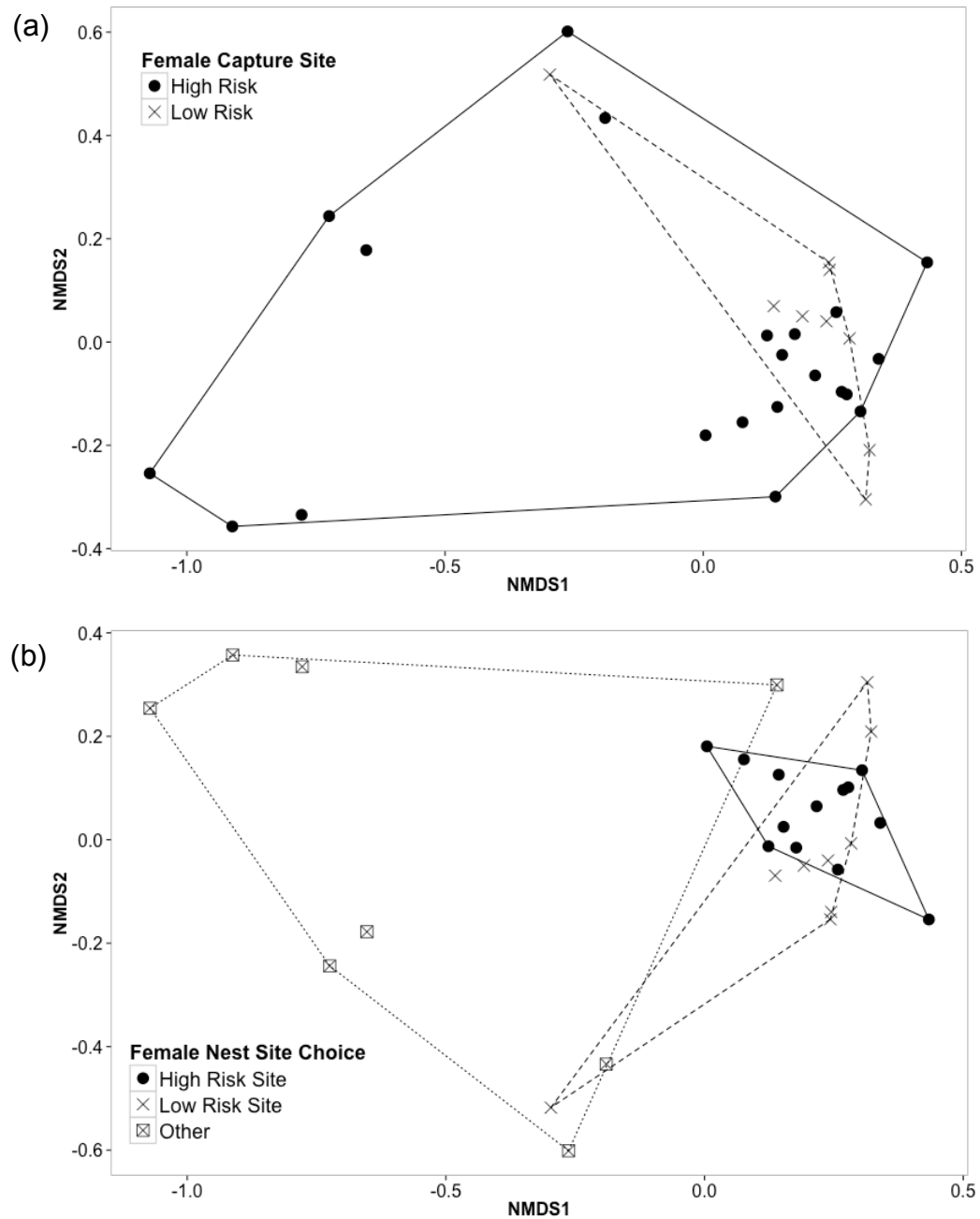
Figure 4 (a) Effects of hunter activity did not cause significant differences in nest vegetative composition or structure. (b) For hens that nested within mixed grass prairie study sites, nest site choice did not differ between treatments ('High Risk Site' and 'Low Risk Site' polygons). A subset of females from high risk sites moved off grassland sites to nest. Nests off grassland site ('Other' polygon) had different vegetative characteristics. The above graphics represents non-metric multi-dimensional scaling (NMDS) ordination of characteristics of nest site vegetation composition and structure including percent cover of the following: green vegetation (AG), warm season grass (WS), cool season grass (CS), warm and cool season grass combined (Grass), Forb, Crop, Litter and bare ground (BG) as well as litter depth (LD), maximum vegetation height (MH) and visual obstruction (VOS).
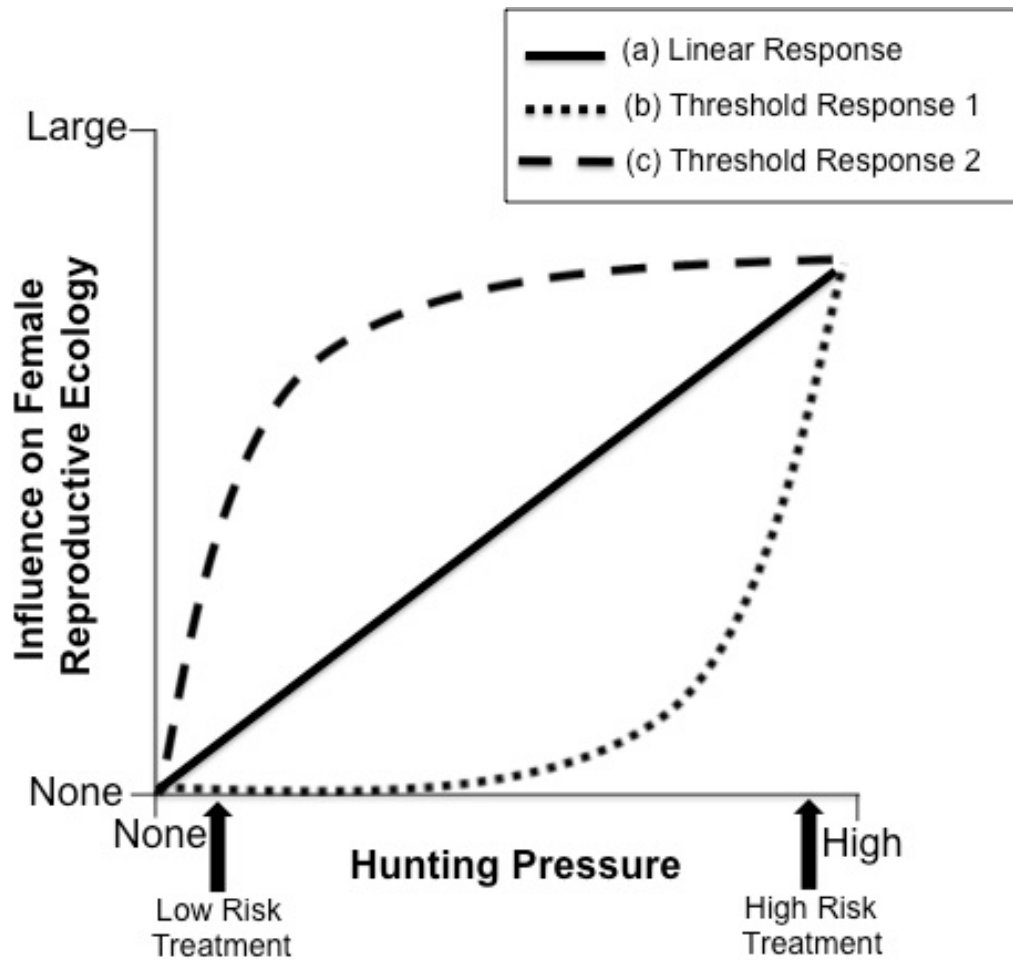
Figure 5. Theoretical graph representing potential responses of female reproductive ecology to hunting pressure intensity. Arrows represent estimated hunting pressure of the experimental treatments. Differences in hunting pressure between experimental treatments maximized the effect size, but do not allow for identification of the conditions under which hunting initiates responses in pheasant populations. Ultimately, the shape of the curve will determine the conditions that would favor management consideration of hunting pressure in regulating pheasant hunting pressure. If the curve is linear (a), then management decisions can be made based on the relative capacity of the population to cope with incremental impacts of hunting; however, if the curve is a threshold (b, c) the location of the threshold has obvious implications for the population and ultimately management decisions.

Chapter 2: USING WILDLIFE TRACKING EQUIPMENT TO TEACH

ANIMAL HABITAT SELECTION

Abstract:

Habitat selection is the process by which animals choose where to live. By selecting locations or 'habitats' with many benefits (e.g., food, shelter, mates) and few costs (e.g., predation), animals improve their ability to survive and reproduce. Biologists track animal movement using radio telemetry technology to study habitat selection so they can better provide species with habitats that promote population growth. We present a curricula in which students locate "animals" (transmitters) using radio telemetry equipment and apply math skills (use of fractions and percentages) to assess their animal's habitat selection by comparing the availability of habitat types with the proportion of 'animals' found in each habitat type.

INTRODUCTION

Animals depend upon their environment (habitat) for the resources necessary to survive and reproduce. Unfortunately, habitat loss is a primary driver of wildlife declines. In order to conserve threatened wildlife species, biologists investigate which habitats promote population growth by observing where animals choose to live (habitat selection). Animals select habitats that provide benefits such as food and mates, and avoid habitats with high costs such as a lot of predators. Maximizing benefits and minimizing costs facilitates survival and reproduction for each individual and collectively drives population growth and stability. Biologists study wildlife habitat selection by locating

animals using radio-telemetry, technology designed to track animal movement by securing a transmitter to an animal and using a receiver to determine the transmitter's approximate location. Habitats that animals use more often than expected by the habitat's availability are defined as preferred habitats, generally areas with lower cost-benefit ratios than alternative available habitats (Table 1). Conservation efforts create and restore preferred habitats for animals to provide individuals with resources that boost population growth. For example, conservation efforts to help declining least tern populations (a small bird) in California involved creating new artificial beaches closed to people where humans could not inadvertently step on and destroy nests. Terns nested on the new beaches and their chicks hatched successfully (Powell and Collier 2000).

Radio Telemetry

How wildlife radio telemetry works: Animals are equipped with a transmitter secured as a necklace, a backpack, or inserted under the skin (Fig. 1a). Using a receiver with an antenna, biologists listen for a transmitter's unique frequency (Fig. 1b). When the receiver is tuned to the appropriate frequency it emits a beep when close to the transmitter. The beeps grow louder as the antenna on the receiver is pointed toward or gets closer to the transmitter, allowing the user to estimate the location of the transmitter by listening for changes in the volume of the beeps.

Applications: The first large-scale radio-telemetry project tracked grizzly bears in Yellowstone National Park and biologists found that even though garbage dumps covered

a small percentage of the park, bears spent a great deal of time at dumps, benefiting from easy access to large quantities of food (Fig. 2; McCullough 1986).

METHODS

We propose a curricula to teach students about habitat selection through a hands-on, outdoor activity in which students use radio telemetry equipment to locate 'animals' and assess habitat preference using mathematical skills. Teaching habitat selection meets many national teaching standard requirements (Table 2). The activity is suited for students in grade levels 5-12 and requires 45-60 minutes outdoors with an additional 45-60 minutes of discussion.

MATERIALS

Two decks of playing cards

Telemetry equipment:

- receivers

- handheld yagi antennas

- cords (to connect each antenna to a receiver)

- transmitters

State wildlife agencies (see additional resources) have telemetry equipment, which is often readily available for educational purposes. We recommend asking for a brief tutorial similar to the demonstration described below before borrowing equipment.

ACTIVITY PREPARATION

Choose an animal, real or fictional.

Create a map of the habitats in the outdoor classroom (Fig. 3) and record for your own notes their approximate proportions.

Select the number of transmitters you will hide in each habitat in order to exemplify habitat preference, avoidance and no preference / avoidance (Table 3a). Preference: Hide most transmitters in the 'preferred' habitat, which should comprise a small percentage of the outdoor classroom. The percentage of transmitters in this habitat should be greater than the percentage of the classroom this habitat covers. Avoidance: Hide few transmitters in the 'avoided' habitat which should cover more than 30% of the area. The percentage of transmitters in this habitat should be less than the percentage of the classroom this habitat covers. No Preference / Avoidance: Choose a habitat the animal will neither prefer nor avoid. The percentage of transmitters in this habitat should be equal to the percentage of the classroom this habitat covers.

Write transmitter frequencies on paper that students will carry during the activity. Hide transmitters. Remove magnets attached to transmitters to activate them. Place transmitters within 200 meters of where students will begin to ensure students can recover them. Conceal transmitters so students must use telemetry equipment to locate them.

Assemble telemetry equipment. Each group of 2 - 3 students will need a receiver, an antenna and a cord to connect them. Unfold antennas to resemble the photograph and

tighten screws to secure them. Connect one end of the cord to the receiver and the other end to the antenna.

Mark the dials and switches the students will use (on/off, frequency, volume and gain (signal strength), as there will likely be additional dials and switches that are not necessary.

PROCEDURE FOR STUDENT ENGAGEMENT

Step 1: What is habitat?

Encourage students to brainstorm the definition of habitat. Ask them for examples of their habitat (e.g., town, school, house, room). Ask students what habitats are available to wild animals (e.g., trees, grass, rocks, rainforest, mountains, ocean).

Step 2: What is habitat availability?

Ask students what habitats are available in the outdoor classroom.

Step 3: Telemetry Introduction:

Provide a brief introduction about how wildlife biologists track animal movement and determine where animals live using radio telemetry (refer to 'Introduction to Radio Telemetry' and 'Additional Resources').

Step 4: Telemetry Equipment Demonstration:

Outside, place a transmitter 30-100 meters away and tune the receiver to the transmitter's frequency. Demonstrate how to determine the direction of the transmitter by

pointing the antenna in one direction for 1-3 seconds and listening to the beeps (Fig. 1b).

Keep the volume set to medium / medium-high and adjust the gain (signal strength) so

that you can clearly hear the beeps while the receiver rests at waist height. Turn about 90

degrees and listen again. Repeat until you have turned a full circle, paying attention to

which direction the beeps are the loudest. If you can barely detect a signal, increase the

gain. If the signal is very loud in every direction, reduce the gain and try again. Walk

toward the transmitter, stopping to reduce the gain as you get closer. As you approach,

point the antenna toward the ground and then to the sky to determine the specific location

of the transmitter.

Step 5: Students Practice Locating Transmitters:

  Providing students an opportunity to practice with an example transmitter may

alleviate the need for one-on-one assistance during the activity.

Step 6: Students Locate Hidden Transmitters:

  Provide each group of students with frequencies written on paper of 1-2

transmitters they will locate. Ask students to remember the habitats where they find each

transmitter. After the students find all transmitters, gather inside.

Step 7: Introduce Card Game:

  Students play a card game throughout the activity (aces and face cards = 10

points, numbered cards = 5 points). All attempts to answer questions correctly are

rewarded with the opportunity to choose a card. Students accumulate points throughout the activity, which can be traded in for prizes or privileges.

Students will choose more face cards than numbered cards even though fewer face cards are available, just as their animal will choose preferred habitat more than expected by availability. Students choose face cards because more points provide more rewards, just as animals prefer habitats that provide food, mates, and protection from weather and predators. This analogy can help to clarify the meaning of habitat preference in step 9.

Step 8: Calculate Available Habitat:

Present the map and ask students to complete the first two columns of Table 3a. Questions to facilitate discussion include:

- Is there more of one habitat than another?

- Which habitat covers the most area?

- Does a certain habitat cover more or less than half of the area?

Work with students so that percentages of habitats add up to 100%.

Step 9: What is habitat use?

Invite students to share (and/or mark on the map) how many transmitters they found in each habitat and complete the third column of Table 3a. Ask students what percentage of transmitters they found in each habitat type to complete the fourth column of Table 3a. This is an opportunity for students to convert fractions to percentages. Questions to stimulate discussion include:

- Did your animal use all available habitats?

- What habitat did your animal use the most?

Step 10: What is habitat preference?

Ask students how they can distinguish habitat preference from habitat use. Encourage students to brainstorm the definition of preference. Refer to the card game and ask students to complete Table 3b to clarify what preference means. Discuss what habitat your animal prefers, avoids, or neither prefers nor avoids.

Step 11: Costs and benefits of habitat-use:

Ask students why their animal might choose its preferred habitat. Questions to facilitate discussion include:

- What resources do students use in their habitats? Do some places have more resources than others?

- What resources do they think are most valuable to wild animals and why?

- How might those resources help animal populations to grow?

- What resources are most valuable to animals and why?

Step: 12: Conservation:

Ask students what would happen if we cut all the trees down and paved all the grass. Animals with diminishing habitat may move, begin using other available habitats, or go extinct. Explain that radio-telemetry helps biologists know what habitats animals prefer so that biologists can work to provide those habitats for wildlife populations.

Step13: Points and Prizes:

Distribute rewards and/or award privileges.

MODIFICATIONS

Expand the activity*:* Use more than one kind of animal, each with different habitat

preferences.

Conduct only the indoor activity*:* Skip steps 3 - 6 and provide students with

animal locations on a map of available habitat.

CONCLUSION

Active-learning helps to engage students and teach abstract scientific concepts

(e.g., habitat selection) (Laws et al. 1999). Our outlined curriculum provides an

opportunity for students to act as biologists and collect data using wildlife tracking

equipment outdoors. Students develop critical thinking skills by assessing habitat

selection using their data. Additionally, students use math skills to calculate habitat

selection, integrating math and science material. We hope the outlined curriculum will

teach students how animals choose where to live and how habitat selection and

conservation efforts can affect individual animals and entire populations.

ADDITIONAL RESOURCES

Dr. Paul Krausman provides definitions associated with wildlife habitat selection

and discusses how knowledge of habitat selection guides wildlife conservation.

http://www.webpages.uidaho.edu/range456/readings/krausman.pdf

The following website lists state wildlife agencies and contact information

http://www.fws.gov/offices/statelinks.html

Advanced Telemetry Systems, a company that manufactures and sells wildlife tracking equipment provides a brief explanation of radio telemetry and photographs.

http://atstrack.com/Generic-58-Basics-of-Radio-Telemetry.aspx#three

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TALBES AND FIGURES

Table 1. Important Terminology and Associated Definitions

<u>Species</u>: A category of similar plants or animals capable of reproducing with one another

<u>Population</u>: A group of individuals of the same species living in close proximity

Habitat Selection

<u>Habitat</u>: An environmental area where an animal resides (e.g., sleeps, eats, rests, mates). Habitat includes resources that animals need to survive and reproduce (e.g., food, shelter, mates).

<u>Habitat Availability</u>: Environmental area(s) that an animal can access.

<u>Habitat Use</u>: Occurs when an animal resides in and uses resources in an environmental area.

<u>Habitat Selection</u>: How and why animals choose where to live among various habitats (e.g., trees, grass, rocks, ocean, desert, tundra).

<u>Habitat Preference</u>: An animal uses a habitat more than expected by the habitat's availability

<u>Habitat Avoidance</u>: An animal uses a habitat less than expected by the habitat's availability

<u>No Habitat Preference or Avoidance</u>: An animal uses a habitat according to the habitat's availalability.

Radio Telelmetry

<u>Wildlife Radio Telemetry</u>: A transmitter (on an animal) sends information via radio waves to a reciever that can be used to locate the animal.

<u>Radio Frequency</u>: Radio waves carry radio signals. Frequency refers to the form of the radio wave. Different radio frequencies can carry different signals, just the way car radios play different stations. In wildlife radio telemetry, each transmitter has a unique frequency across which it sends a signal.

<u>Yagi Antenna</u>: An antenna composed of several short rods mounted across a support rod that can be used to locate radio transmitters.

<u>Gain vs. Audio</u>: Two available adjustments on radio telemetry recievers. Gain refers to signal strength and audio refers to volume.

Table 2. Application of Education Standards

Life Science Content Standard C (NRC, 1996)

Grades 5 – 8:
Students should develop an understanding of:
- Structure and function in living systems
- Regulation and behavior
- Populations and ecosystems
- Diversity and adaptations of organisms

Grades 9 – 12:
Students should develop an understanding of:
- Interdependence of organisms
- Behavior of organisms

Core Ideas in the Life Sciences (NRC, 2011)

Core Idea LS2:
Ecosystems: Interactions, Energy and Dynamics
- Interdependent relationships in ecosystems
- Ecosystem dynamics, functioning and resilience
- Social interactions and group behavior

Table 3.

(a) Habitat availability, use and selection

Habitat Type	Availability (%)	Use (# trans)	Use (%)	Habitat Selection
Grass	50%	1	10%	Avoid
Tree	5%	7	50%	Prefer
Pavement	10%	1	10%	Neither Avoid / Prefer
Dirt	20%	2	20%	Neither Avoid / Prefer
Roof	10%	1	10%	Neither Avoid / Prefer

(b) Students prefer face cards

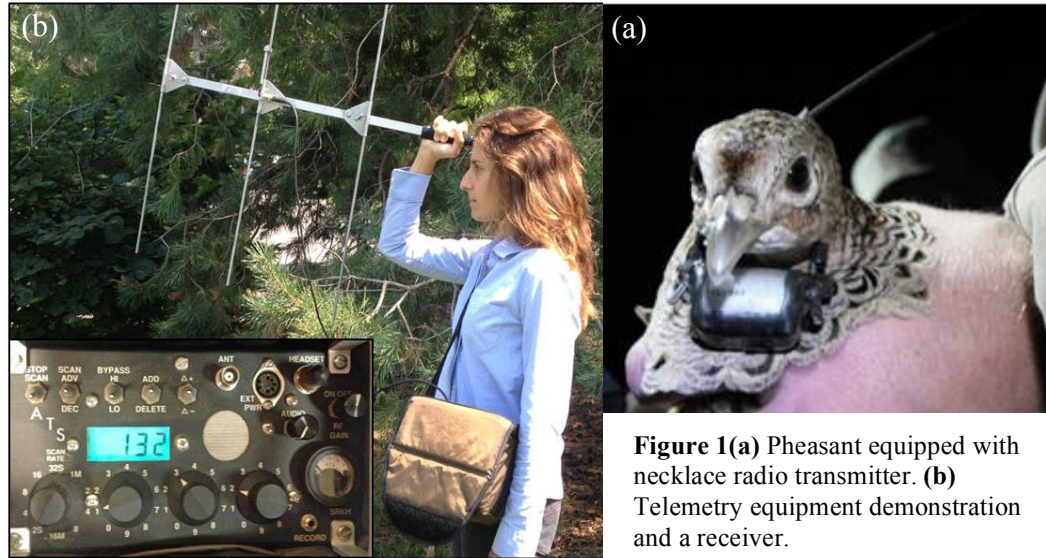| Card Type	# in Deck	# Picked Up
Face Cards	16	16
Numbered Cards	32	10

Figure 1(a) Pheasant equipped with necklace radio transmitter. **(b)** Telemetry equipment demonstration and a receiver.

Biologists Track Grizzly Bears in Yellowstone National Park

In 1959 Frank and John Craighead (biologists and brothers) began tracking grizzly bears using radio telemetry in Yellowstone National Park. At the time extremely close and dangerous human-bear encounters unnerved both managers and park visitors. The Craigheads developed methods to immobilize bears in order to equip them with radio transmitters. They applied sedative to a dart and with a gun, from a distance rendered bears unconscious. The Craighead's discovered that grizzlies regularly visited the park's open-pit garbage dumps to feed and consequently habituated to humans. The Craigheads identified and relocated "problem" bears and worked with the park to close open-pit garbage dumps and keep bears out of campsites and developed areas. Today, there are considerably fewer human-bear encounters in Yellowstone (McCullough 1986).

Figure 2.   Photograph courtesy of the Craighead Institute

Figure 3. The outdoor classroom: example map of habitat availability and transmitter locations