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Antipredator response diminishes during periods of resource deficit for a large herbivore

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Abstract. The starvation-predation hypothesis predicts that, during resource shortages, prey forego antipredator behavior and forage as much as possible to avoid starvation, even when risk of predation is high. We tested this hypothesis using GPS locations collected simultaneously from moose (*Alces alces*) and wolves (*Canis lupus*) in the Greater Yellowstone Ecosystem of North America. We assessed shifts in the speed, displacement, and habitat selection of moose 24 h following encounter with wolves (0–1,500 m distance). We examined whether the strength of antipredator behaviors would weaken as winter progressed and the nutritional condition of moose declined. Moose responded to wolf encounters by increasing their rate of movement in early winter, but only within 500 m distance. Importantly, these responses attenuated as winter progressed. Moose did not avoid their preferred foraging habitat (riparian areas) following encounters with wolves at any distance, and instead they more strongly selected riparian areas, especially in early winter. Our findings support theoretical predictions that resource deficits should dampen prey antipredator behavior, and suggest that nutritional condition of prey may buffer against run-away risk effects in food webs involving large mammalian predators and prey.

Key words: bottom up; context dependence; moose; predation risk; predator avoidance; top down; ungulate; winter; wolf.

INTRODUCTION

Animals often weigh the decision to forage or reduce predation risk (i.e., the risk of being killed) to maximize survival (Abrams 1984, Lima and Dill 1990, Matassa et al. 2016). Antipredator behavior of prey manifests through some combination of altered habitat selection, increased vigilance, higher movement rates, and reduced

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foraging (Heithaus et al. 2007, Winnie and Creel 2007). Because they come at the expense of energy gain, such behaviors can reduce the nutritional state of prey, indirectly reducing fitness (i.e., "risk effects"; Preisser et al. 2005, Peckarsky et al. 2008, Boonstra 2013). Thus, contingencies in antipredator behavior, driven by environmental context, warrant more attention as ecologists work to understand how, when, and where prey respond to the risk of predation (Agrawal et al. 2007). Improved understanding of the drivers of antipredator behavior may illuminate ties between individual behavior and population performance.

The nutritional state of an animal can influence the strength of antipredator response (McNamara and Houston 1986, 1990). For example, animals experiencing resource deficits should avoid starvation by foraging as much as possible, even when predation risk is high. This is commonly known as the starvation-predation hypothesis, and has been supported across a wide variety of taxa, including tadpoles (Rana catesbeiana; Werner and Peacor 2003), wildebeest (Connochaetes taurinus; Sinclair and Arcese 1995), small mammals (Brown and Kotler 2004), and green sea turtles (Chelonia mydas; Heithaus et al. 2007). In particular, the starvation-predation hypothesis should be well supported in environments characterized by seasonal resource shortages. Ungulates in temperate latitudes experience nutritional deficits in winter due to senescence of forage and increasing snow accumulation (Parker et al. 2009), and therefore should temper antipredator responses as winter progresses to avoid starvation. Although the starvation-predation hypothesis predicts that antipredator behavior should lessen as prey condition deteriorates, empirical tests remain rare for wide-ranging predators and prey exposed to temporal variation in resource availability (but see Sinclair and Arcese 1995).

We tested the starvation-predation hypothesis by evaluating antipredator response of moose (Alces alces) to wolves (Canis lupus) in the Greater Yellowstone Ecosystem (GYE) during winter, a period of resource deficit. We expected antipredator response of moose to weaken from early to late winter, because nutritional condition of ungulates deteriorates as winter progresses (Parker et al. 2009, Monteith et al. 2013). Moose exposed to wolves in the GYE have experienced population declines (Vartanian 2011, Oates 2016), although the extent to which antipredator behavior could have contributed to risk effects and population decline is unclear. Trade-offs with starvation that reduce antipredator effects could strongly alter antipredator effects in large mammal systems, highlighting the need for an improved understanding of how resource limitation interacts with antipredator behavior.

Methods

Study area

We monitored moose from February 2005 to May 2010 in northwestern Wyoming (Fig. 1; 43.5202° N, 110.2206° W). The study area (approximately 1,050 km²) consisted mostly of public land, including portions of Grand Teton National Park and the Bridger-Teton National Forest (43.5202° N, 110.2206° W). During winter, moose occupied mainly riparian areas, containing dense and expansive willow (*Salix* spp.) patches interspersed with narrowleaf cottonwood (*Populus angustifolia*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmanni*),

blue spruce (*Picea pungens*), and subalpine fir (*Abies lasiocarpa*). Homogenous and mixed-forests of aspen (*Populus tremuloides*) and conifers occurred throughout the study area. The climate is characterized by short, dry summers and long, cold winters with relatively deep snow (annual snowfall 339.09 \pm 17.41 cm [mean \pm SE]).

Large carnivores in the study area included gray wolves and cougars (*Puma concolor*), with grizzly (brown) bears (*Ursus arctos*) and American black bears (*U. americanus*) emerging from dens typically in mid to late April. Elk were the most common ungulate in the study area (Appendix S1: Fig. S1a). Other ungulates during winter included bison (*Bison bison*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*).

Collaring of moose and wolves

We captured a total of 51 adult (>2.5 yr) female moose in January–March from 2005 to 2009 (details in Becker 2008, Vartanian 2011). We fit each individual with a GPS collar containing store-on-board technology (TGW-3700, Telonics, Mesa, Arizona, USA); the GPSfix intervals were hourly from 2005 to 2007, and every three hours from 2008 to 2010. We omitted all moose that died within two weeks of capture (n = 3) from analyses. We used all locations from winter ranges, determined using net-squared displacement calculations (Appendix S1) from GPS fixes (Bunnefeld et al. 2011).

From 2005 to 2010, we captured wolves (n = 20 individuals from six packs) largely via helicopter darting during winter, and fitted them with GPS Argos collars. GPS collars acquired locations every three or six hours, depending on the transmitter. We omitted locations that were clearly erroneous or characteristic of dispersing individuals. Based on our knowledge of pack hierarchy, we used locations from the GPS-collared wolf (n = 14) in each pack that best represented pack-level movement and territory use. We justified using one wolf to represent pack-level movement because cohesiveness is high during winter (Benson and Patterson 2015).

Encounters

We tested antipredator response of moose on winter range by comparing their movement rates and habitat selection 24 h before and after potential encounters with wolves. We defined encounters as occasions in which moose and wolves were within 1.5 km of each other. We binned encounters into three distance categories: 0 to 500 m (hereafter, 500 m), 500 m to 1 km (hereafter, 1 km), and 1 km to 1.5 km (hereafter, 1.5 km; Appendix S1: Fig. S2; Table S1). We assumed that moose were unlikely to detect wolves beyond 1.5 km, based on aerial behavioral observations of moose to wolf presence in other studies (Mech et al. 2015). To identify



FIG. 1. Study area in the Greater Yellowstone Ecosystem, with locations of moose on winter range (December–April), and wolf pack territorial use (colored polygons) estimated from 95% dynamic Brownian bridge movement models. Overlapping pack territories of Teton and Antelope are not shown.

encounters, we intersected the GPS fix time and coordinates of wolves and moose. We set a time buffer around each GPS fix of each species to detect all encounters occurring within 70 minutes of the GPS fix times of moose. For 24 h before and after encounters, we measured speed (meters traveled between successive locations divided by elapsed time) and total distance traveled (displacement) of each moose. To maintain sampling independence and to allow movement rates and displacement of moose to return to pre-encounter levels, we omitted successive encounters that occurred within 48 h. Additionally, we required that the wolf was further away from the moose than the distance category at which the encounter occurred for 48 h prior to the hour at which the encounter occurred. For example, if an encounter occurred at 600 m and a GPS-collared wolf approached within 600 m over the next 48 h, we omitted the first 600-m encounter, and retained the encounter with the closest distance category to the moose (Appendix S1: Fig. S2).

Modeling approach

We used a mixed-effects model framework to assess shifts in speed and displacement of moose in response to wolf encounters. For each distance category, we constructed models to assess change in movement speed and displacement in the 24 h post-encounter relative to the entire 24 h prior, as a paired analysis. Speed (log-transformed) between locations and displacement (log-transformed; i.e., total distance traveled before and after encounter) were dependent variables, and 24 h before (locations coded as 0) and after (locations coded as 1) each encounter was the independent variable. To reduce pseudoreplication in sampling before and after an encounter, we identified each encounter as a random intercept. To assess whether antipredator response (i.e., speed, displacement) attenuated as winter progressed, we tested an interaction term of before and after the encounter with day of year (hereafter, DOY). Although female moose with juveniles are likely to be more

cautious of predators compared to those without juveniles (White and Berger 2001, Dussault et al. 2005), our limited sample size of moose with juveniles (n = 12encounters from three moose) precluded a rigorous test of antipredator response.

Antipredator responses of ungulates include not only movement rates and displacement, but also shift in habitat selection (Creel et al. 2005, Middleton et al. 2013, Ford et al. 2014, Donadio and Buskirk 2016, Ng'weno et al. 2017). During winter, wolves search for prey in or near predictable habitats to increase encounter probability (McPhee et al. 2012). We assessed whether habitat selection of moose changed 24 h after encounters with wolves using a land cover raster (30-m spatial resolution) for Teton County (Cogan and Johnson 2013). During winter, moose are obligate browsers, and consume few species of woody plants (Houston 1967; J. M. Vartanian, unpublished data). In our study area during winter, moose diet consists of 59% \pm 0.04% (mean \pm SE) willow (Salix spp.), $22\% \pm 0.04\%$ conifer (Abies spp., Pinus spp.), and $15\% \pm 0.01\%$ deciduous trees (*Populus* spp., Betula spp.; J. M. Vartanian, unpublished data); therefore, we calculated distance to vegetation classes deemed important to moose: riparian vegetation (i.e., stands dominated by Salix spp.), conifer, and aspen.

We analyzed habitat selection of moose with a use-vs.availability design at the third-order scale (Johnson 1980) 24 h before and after wolf encounters with generalized linear mixed-effects models (GLMMs). We fit binomial GLMMs with the logit link function, and used each encounter as a random intercept. For all GLMMs of habitat selection, we defined third-order availability by estimating a kernel Brownian bridge (Horne et al. 2007) contour at the 99% level from the 48 h of locations (24 h before and 24 h after an encounter). Within the extent of the kernel contour, we extracted distance to habitat type from the "used" locations, as well as from randomly sampled ("available") locations, and ensured that each encounter had ≥ 100 random locations to minimize bias (Northrup et al. 2013). In each distance category, we tested for relative change in habitat selection of riparian, conifer, and aspen forests after the encounter by interacting moose response (before = 0, after = 1; main effect) with distance to each habitat type. To ease the interpretation of habitat use post-encounter relative to time of year (e.g., DOY \times distance to riparian \times response), we binned encounters into early (<DOY 60) vs. late (> DOY 60) winter. We then fit GLMMs separately for each time period to determine if habitat shifts in response to wolf encounters were different in early vs. late winter. We allowed covariates to be in the same model if the Pearson correlation coefficient between the pair was <0.5. We checked global models for each distance category without the interaction of response (i.e., only main effects of distance to habitat type) to ensure directions of covariates (positive vs. negative) were

consistent. We inspected Variance Inflation Factors (VIFs) for covariates and retained them if VIFs in the global model were <3.0. We interpreted covariates with 95% bootstrapped (500 simulations) confidence intervals that did not overlap zero as significant. We used R version 3.3.0 (R Core Team 2016) for all data extraction and analyses.

RESULTS

We detected 120 unique encounters among 25 individual moose and six wolf packs (Appendix S1: Table S1). Neither speed nor displacement of moose increased significantly following wolf encounters for any distance category when we did not account for DOY. However, when we incorporated DOY into GLMMs as an interaction term, moose increased speed and displacement within the 500-m distance category during early winter, gradually diminishing as winter progressed (Fig. 2a, b; Appendix S1: Table S1). Sample size for encounters in the 500-m category during early winter (January–February) was limited (n = 3); therefore, we combined observations between 0 and 1 km (n = 22) to avoid type II error and the result did not change ($\beta = -0.01$; 95% CI: -0.01, -0.0002).

When evaluating habitat selection following wolf encounters for early vs. late winter, we grouped encounters (n = 22) between 0 and 1 km due to limited sample size of early-winter encounters within the 500-m distance category (n = 3). We found that moose more strongly selected riparian habitat during early winter following encounters within 1 km, but habitat selection did not change during late winter (Fig. 2c, d; Appendix S1: Table S2).

DISCUSSION

Our findings support the starvation-predation hypothesis, in which resource-limited prev are predicted to be less responsive to predation risk and should forage in riskier places or times to avoid starvation (McNamara and Houston 1990). In early winter, when moose are presumed to be in relatively good condition (Parker et al. 2009), movement rates increased following wolf encounters, but only at close proximity (\leq 500 m). In late winter, when moose are presumed to be in relatively poor condition, movement rates (speed and displacement) did not change following encounters. Although individual estimates of nutritional condition during winter were unavailable, previous work in the study area (Becker et al. 2010) and elsewhere (Parker et al. 2005, Cook et al. 2013, Monteith et al. 2013) support our key assumption that body condition in moose, and other ungulates, declines sharply as winter progresses. The unwillingness of moose to abandon preferred habitats following encounters with wolves adds further support



FIG. 2. Predicted relationships 24 h before (gray lines) and after (black lines) moose encounters with wolves from the 500-m distance category (0-500 m), with 95% CIs (shaded for before encounters; dashed lines for after encounters) of (a) speed (m/s) and (b) displacement (m), both with an interaction term of before and after the encounter with day of year (hereafter, DOY) during winter in northwest Wyoming from 2005 to 2010; panels c and d show relative probability of selection of riparian habitat during early (<DOY 60) and late (>DOY 60) winter, respectively.

for the predation-starvation hypothesis. Moose did not avoid their preferred foraging habitat (riparian) following encounters with wolves and, in early winter, they more strongly selected riparian areas. Predators can strongly shape the antipredator behaviors of their prey (Creel et al. 2005), with the potential for risk effects and even trophic cascades (Donadio and Buskirk 2016). Our findings suggest that the risk of starvation has the potential to dampen or altogether negate the demographic effects of antipredator behavior and its community-level consequences.

Elk are the primary prey of wolves in the GYE and, following encounters with wolves, are more vigilant (Liley and Creel 2008), shift habitat selection toward (presumably safer) coniferous stands (Fortin et al. 2005), and increase movement rates within 5 km of wolves throughout the year (Proffitt et al. 2009). In contrast, moose increased movement rates in response to wolves only during early winter, and did not shift from preferred habitats. Riparian habitat, which is structurally complex in the study area, may have served as some combination of food resources and refuge from wolves, despite the predictability of moose occurrence in these areas. Further, compared with elk in the GYE, moose were less sensitive to the spatial proximity of wolves, only responding at distances up to 500 m, whereas elk increased movements when wolves approached within 1 km distance (Middleton et al. 2013). These findings are consistent with predictions made by Creel (2011) that large-bodied prey should exhibit muted responses to predators (e.g., responding only at short distances), because perceived predation risk should be inversely related to body size. Further, compared with elk, moose are more likely to stand their ground when approached by wolves (Mech et al. 2015), a pattern also found in bison (MacNulty et al. 2014). Although moose may be generally less responsive to predation risk from wolves, our detection of a heightened behavioral response during early winter suggests that antipredator behavior is dynamic within and among species of ungulates.

Shifts in resource availability are fundamental to assess the direction and strength of antipredator behavior (Preisser et al. 2009). Seasonal resource shortages characterize temperate (Parker et al. 2009) and tropical ecosystems (Owen-Smith 2008), suggesting that statedependent antipredator responses should be widespread. Our findings integrate antipredator responses with a long history of work on starvation-predation trade-offs (Abrams 1984, Brown 1992, Ovadia and Schmitz 2002), suggesting that nutritional condition of prey may buffer against run-away risk effects in large mammal systems. For example, when prey populations are below carrying capacity (K) and resources are abundant, risk effects may be relatively strong; however, as populations approach K, consumptive effects of predation are likely to outplay risk effects as prey take risks to avoid starvation.

Several caveats of our study are warranted. We did not collect data on vigilance, which may reduce forage intake along with increased movement rates. In addition to predation risk, other factors could influence habitat selection throughout winter. For example, we did not test the influence of accumulating snow on habitat selection, which may bury preferred forage for moose in riparian areas as winter progresses. Thus, individuals may seek lower quality (but more accessible) forage in other habitats (Van Beest et al. 2010), possibly explaining the lack of selection for riparian areas in late winter after wolf encounters (Appendix S1: Table S2). Additionally, the temporal resolution of our GPS collars (fixes every 1-3 h) was likely too coarse to detect all encounters between collared moose and wolves, which could have been more acute and persistent through winter than we report (Creel et al. 2013). Regardless, we were still able to detect differences in movement rates and habitat selection predicted by the

starvation-predation hypothesis. Although the locomotive cost of accumulating snow likely contributed to lower movement rates of moose during late winter, our paired analysis accounted for relative changes in movement as winter progressed (Appendix S1: Fig. S3). Thus, increasing snow depths could have contributed to dampening antipredator movements if they increased the relative costs of such movements at a given point in winter. These circumstances, as well as our record of observed encounters from start to end of winter (Appendix S1: Fig. S4), suggest that our results provide both a meaningful characterization of antipredator behavior of moose during winter, and a rigorous test of the starvation-predation hypothesis.

Wolves can alter the behavior of their prey through predation risk (Fortin et al. 2005, Liley and Creel 2008), and numerous studies have advanced our knowledge of mechanisms of predation risk and risk effects across taxa (Lima and Dill 1990, Werner and Peacor 2003, Peckarsky et al. 2008, Schmitz 2008, Fortin et al. 2015). Although wolves and elk have been the focus of antipredator research in the GYE, moose have largely been overlooked, despite their strong influence on shrub communities (Brandner et al. 1990, Berger et al. 2001). Our work suggests that the impact of herbivory in the GYE, and the extent to which it is reduced by predation risk, is more dynamic than currently appreciated. In multi-prey systems, speciesor population-specific factors such as body size, diet specialization (Creel et al. 2014), and resource limitation (Owen-Smith 2008) are likely to interact to mediate the strength of antipredator responses across prey taxa, leading to outcomes of species interactions that are complex and difficult to predict. Therefore, we caution against generalizations of predators inducing ecosystem-level changes through fear, especially in multi-prey systems.

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