**LETTER**

## Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore

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### Abstract

Ecological theory predicts that the diffuse risk cues generated by wide-ranging, active predators should induce prey behavioural responses but not major, population- or community-level consequences. We evaluated the non-consumptive effects (NCEs) of an active predator, the grey wolf (*Canis lupus*), by simultaneously tracking wolves and the behaviour, body fat, and pregnancy of elk (*Cervus elaphus*), their primary prey in the Greater Yellowstone Ecosystem. When wolves approached within 1 km, elk increased their rates of movement, displacement and vigilance. Even in high-risk areas, however, these encounters occurred only once every 9 days. Ultimately, despite 20-fold variation in the frequency of encounters between wolves and individual elk, the risk of predation was not associated with elk body fat or pregnancy. Our findings suggest that the ecological consequences of actively hunting large carnivores, such as the wolf, are more likely transmitted by consumptive effects on prey survival than NCEs on prey behaviour.

### Keywords

Anti-predator behaviour, drought, elk, grey wolf, grizzly bear, non-consumptive effects, predation risk, predator hunting mode, ungulate, Yellowstone.

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## INTRODUCTION

As humans alter the global distribution and abundance of large carnivores, there is a pressing need to understand the full extent of these predators' influence on prey populations and ecosystems (Estes *et al.* 2011). The ecological consequences of predation can be transmitted not only by the killing and consumption of prey but also by changes in prey behaviour (Werner & Peacor 2003; Preisser *et al.* 2007). When predators alter prey foraging behaviour sufficiently to influence prey demography or patterns of plant growth, they are said to induce 'non-consumptive effects' (NCEs). While rapid advances in smaller scale experimental systems have documented strong and widespread NCEs (Werner & Peacor 2003; Preisser *et al.* 2007; Schmitz 2008), we still know little about the mechanics of risk effects on the vast landscapes occupied by large vertebrates.

Ecologists have recently uncovered several factors that can mediate the occurrence and strength of NCEs (Preisser *et al.* 2007, 2009; Schmitz 2008; Creel 2012). The hunting mode of the predator is key among them. Recent experimental (Schmitz 2008) and meta-analytic (Preisser *et al.* 2007) studies indicate that ambush predators produce stronger NCEs than active predators. Ambush predators are thought to generate point-source cues that prey can predictably associate with habitat features, whereas more widely ranging, active predators generate diffuse cues that leave prey with little information to justify chronic and costly anti-predator behaviours (Luttbeg & Schmitz

2000). A recent behavioural study of African ungulates supports this notion, revealing stronger responses to ambush predators such as lions (*Panthera leo*) than to active predators such as wild dogs (*Lycaon pictus*) (Thaker *et al.* 2011). Yet, few studies of large mammals have looked beyond behaviour to evaluate whether predator hunting mode shapes NCEs influencing prey nutrition and demography.

To date, our limited knowledge of population-level NCEs among large mammals has come from the wolves (*Canis lupus*) and elk (*Cervus elaphus*) of the Greater Yellowstone Ecosystem (GYE). The presence of wolves can cause elk to become vigilant (Liley & Creel 2007; Winnie & Creel 2007) and move into refuge habitat (Creel *et al.* 2005; Fortin *et al.* 2005), setting up a pathway for NCEs to operate. However, as a wide-ranging, active hunter, the wolf is not predicted to induce anti-predator behaviours strong enough to impact prey demography (Schmitz 2005a; Preisser *et al.* 2007). Recent field studies in the GYE have found conflicting evidence, with some showing that wolves influence elk behaviour strongly enough to reduce foraging (Winnie & Creel 2007), nutrition (Creel *et al.* 2009; Christianson & Creel 2010) and reproduction (Creel *et al.* 2007), and others showing the opposite (White *et al.* 2009, 2011). Reconciling these findings has been challenging because our picture of the cascading effects of wolf predation risk is highly fragmentary. Studies tend to focus on one or two response variables at a time, such as prey behaviour (Winnie & Creel 2007), nutrition (White *et al.* 2009; Christianson & Creel 2010), or reproduction (Creel *et al.*

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2007; White *et al.* 2011), and often use short-term proxies of the prey response, such as faecal hormones and metabolites (Creel *et al.* 2007; Christianson & Creel 2010). However, 'connecting the dots' between predation risk, anti-predator behaviour and prey demography requires more integrative studies capable of tracking whether repeated prey behavioural responses scale up to incur nutritional costs and demographic losses, within the context of the annual life cycle of individual prey.

We employed such an approach to evaluate the hypothesised mechanism for a NCE of wolves: that frequent encounters with wolves reduce the foraging success of wintering elk sufficiently to accelerate fat losses, increasing foetal mortality and reducing calf recruitment (Creel *et al.* 2009; Christianson & Creel 2010). Our approach is unique in that we tracked wolves while also sampling the movements, foraging behaviour, body fat and pregnancy of the elk they hunted over three winters in the northeastern GYE (Fig. 1). We considered four questions: (1) What is the spatiotemporal scale of elk behavioural responses to the presence of wolves? (2) At that scale, do wolves influence elk feeding rates and habitat use? (3) How frequently do elk experience these encounters? (4) Do cumulative encounters with wolves influence elk body fat and pregnancy? This integrative approach provides new, mechanistic insights into the factors that mediate NCEs on the vast, seasonal landscapes where large carnivores hunt their prey.

## MATERIALS AND METHODS

### Wolf and elk collaring

We captured wolves by helicopter darting ($n = 15$) or leg-hold trapping ($n = 1$) during January to March, 2007–2010 and fitted them
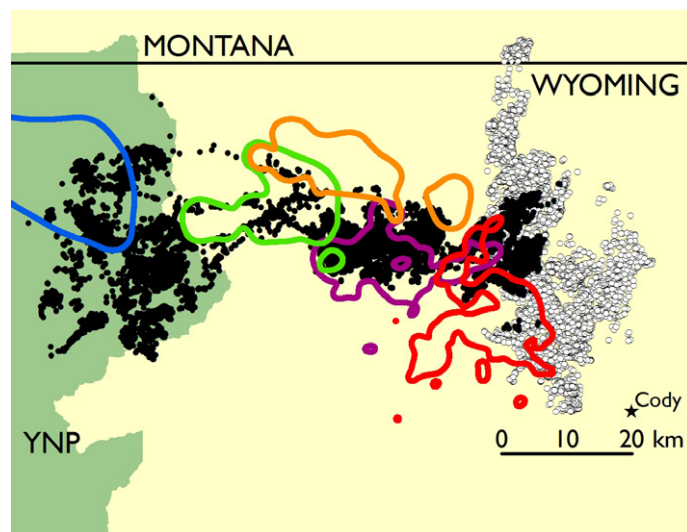


**Figure 1** Representative GPS locations of migratory (black, $n = 10$) and resident (grey, $n = 13$) elk. The migratory subpopulation experienced predation risk from three wolf packs during winter (centre), whereas only a portion of the resident subpopulation experienced predation risk from a single pack. Pack boundaries, represented by an 80% kernel home range, are for the Druid (blue), Hoodoo (green), Beartooth (orange), Sunlight (purple) and Absaroka (red) packs. The Druid pack hunted migratory elk during summer, but not winter, and was not monitored for this study. Figure reproduced with permission from Middleton *et al.* (2013a).

with GPS collars (Model TGW-3580/4580, Telonics, Mesa, AZ, USA) programmed to acquire one location every 3 h for 12–16 months. We collared ten wolves in three packs that hunted wintering migratory elk and six wolves in a pack that hunted resident elk (Fig. 1); four individuals were collared for two successive years. We captured adult female elk via helicopter netgunning in January 2007 ($n = 60$) and 2008 ($n = 30$) and fitted them with GPS collars ($n = 70$; Model TGW-3600, Telonics, Mesa, Arizona, USA) programmed to acquire a location every 3 h from January 1 through March 31.

Using simultaneous wolf and elk locations for the winter period, we calculated the distance to the nearest collared wolf for all elk GPS locations that fell within the 95% minimum convex polygon of a GPS-collared pack. Wolf mortalities caused several gaps in our GPS coverage, resulting in known wolf pack movement for 58% of migratory elk locations ($n = 68\ 364$) and 73% of resident elk locations ($n = 52\ 724$). We assumed little or no GPS relocation bias due to a fix success rate of $91.6\% \pm 1.2\%$ for wolves and $97.9\% \pm 0.4\%$ for elk.

### Elk movement and displacement rates

The proposed mechanism of wolf-induced NCEs is that of cumulative nutritional costs of fine-scale responses by elk to wolves (Creel *et al.* 2009; Christianson & Creel 2010). Previous studies suggest that although elk respond to wolves at a variety of spatiotemporal scales (e.g. Fortin *et al.* 2005; Mao *et al.* 2005; Kittle *et al.* 2008), their most pronounced responses occur when the threat of predation is relatively imminent (Creel *et al.* 2005; Liley & Creel 2007; Winnie & Creel 2007). Such anti-predator behaviours are consistent with the prediction of Schmitz (2005a) pertaining to wide-ranging prey of active hunters. Thus, we focused our analysis on the encounters of individual elk with wolves, first identifying the distance at which elk increased their movement and displacement rates, then evaluating the duration of the increase in movement rate following an encounter (see Supporting Information). This approach also allowed us to compare elk foraging behaviour and habitat use before and after wolf encounters.

In our analyses, we treated changes in movement rates and displacement before and after an encounter as the dependent variables, and the 'encounter bout' as the sampling unit. We used generalised linear mixed models (GLMM) to evaluate the influence of wolf encounters on the change in movement rates and displacement while accounting for the repeated observation of individuals with random effects. We used a likelihood ratio test (LRT) to compare models of elk movement response as a function of encounter distance. Because we assumed that elk movement responses would be stronger at the closest (1-km) distance, we evaluated models that described the response by incrementally adding 1-, 2-, 3- and 4-km categories for comparison with all other distances up to 10 km. To evaluate the duration of the elk movement response, we used a repeated-measures analysis of variance (ANOVA) with comparisons between paired time periods to evaluate how long movement rates remained elevated.

### Elk foraging behaviour and habitat use

From January 1 to March 31, 2008–2010, we sampled the time budgets of individual, GPS-collared elk (see Supporting Information).

With the observation as the sampling unit, we used GLMM with a random effect of individual to evaluate the influence of wolves on elk vigilance and foraging rates (arcsin square root transformed) with a LRT to compare nested models.

In evaluating elk habitat use following wolf encounters, we considered factors previously shown to influence elk movement. These included distance-to-timber (i.e. conifer forest; Creel et al. 2005; Mao et al. 2005), openness (Mao et al. 2005), distance-to-roads, elevation and slope (Creel et al. 2005). We compared habitat attributes of elk locations during paired 24-h periods before and after 1-km encounters with wolves (n = 338 pairs) using a principal components analysis (PCA) with the varimax rotation. We used Hotelling's $T^2$ test to compare multivariate pre- and post-encounter means for the principal components (PCs). We also evaluated diel pattern of habitat use, since the time of day is well known to influence elk activity.

### Individual variation in wolf encounter frequency

To facilitate comparison of predation risk across studies, we calculated the annual ratio of wolves per 100 elk, from 2000–2012 when elk counts (Middleton et al. 2013a) were conducted (n = 9 years). For each individual elk, we estimated the mean annual proportion of winter days with a 1-km wolf encounter (see Supporting Information), which we considered an index of how frequently elk responded to wolves at the salient spatial scale identified in our prior analyses.

### Elk body fat and pregnancy

We recaptured a subset of GPS-collared elk via helicopter darting to determine body fat and pregnancy rates in late February 2009 and early March 2008 and 2010 (hereafter 'late winter'), and body fat and lactation status in early September 2008 and 2009 (hereafter 'autumn'). Two experienced investigators (RCC, JGC) used ultrasonography and manual palpation to estimate per cent body fat (Cook et al. 2004, 2010) (see Supporting Information). We determined age via cementum annuli (Matson's Laboratory, Milltown, MT, USA) using a vestigial canine.

The hypothesis of wolf-induced NCEs (Creel et al. 2009; Christianson & Creel 2010) predicts that (1) elk in populations with wolf predation will be less fat in late winter than elk in populations without wolf predation and (2) individual elk experiencing the highest wolf predation risk will be the least fat in late winter. Thus, we first broadly compared the late-winter body fat of elk in our study population with that of elk in other populations (n = 19) without wolf predation (Cook et al. 2013). Because migratory elk in our study area occupy habitats with much higher wolf densities than resident elk (Middleton et al. 2013a) (Fig. 1), we next compared the overwinter fat loss of the migratory subpopulation with that of the resident subpopulation. Here, we used GLMM with a LRT to evaluate the influence of migratory status (i.e. subpopulation) on winter body fat while accounting for autumn body fat.

At the individual level, we evaluated the influence of predation risk on late-winter body fat, while accounting for several other factors known to influence fat dynamics in temperate ungulates. To characterise wolf predation risk, we used the proportion of winter days that each elk encountered a collared wolf within 1 km (hereafter, 'predation risk'). This approach should be more powerful than using indices of specific anti-predator behaviors in the event that

encounters incur any additional elk responses beyond those we documented. When the annual proportion of encounter-days was unknown for an individual elk due to a gap in wolf GPS coverage, we used the mean proportion of encounter-days observed during other winters for that individual [29% of elk-winters (n = 38) in models including autumn fat; 24% of elk-winters (n = 79) in models excluding autumn fat]. A linear regression indicated that the mean encounter rate of an individual elk across the study period was a good predictor of its annual encounter rate (F = 399.8, d.f. = 124, P < 0.001, $r^2$ = 0.76), supporting this approximation.

Recent studies of elk and mule deer in the western United States have identified autumn body fat as a key predictor of late-winter fat levels (Cook et al. 2013; Monteith et al. 2013). Because we had a smaller sample size of paired, autumn-to-winter recaptures (n = 38) than of late-winter recaptures (n = 79), we separately evaluated influences on late-winter body fat for data sets with and without autumn body fat. In addition to autumn body fat, we considered the influence of predation risk, subpopulation, age (both linear and quadratic terms) and a year effect on late-winter body fat. We used GLMM with random effects to account for individual re-sampling and Akaike's Information Criterion adjusted for small sample size (AIC$_c$) to select the best model, and average among models, of body fat. To assess fit of the best models, we calculated the pseudo-$R^2$ statistic as the square of the Pearson correlation between predicted and observed values (Moreau et al. 2012). We included only known-age individuals in these analyses.

Because migratory elk had lower pregnancy rates than resident elk (Middleton et al. 2013a), we sought to evaluate whether predation risk was linked to low pregnancy among migratory individuals. This also allowed us to avoid the confounding effects of summer habitat quality and predation risk when comparing migrant and resident elk in this population (Middleton et al. 2013a). We included the same independent variables and used the same information theoretic approach as in our models of body fat. We used Program R for analyses (packages 'lme4,' 'glmulti,' and 'gmodels').

## RESULTS

### Elk movement and displacement rates

Our analyses revealed an influence of wolves on elk behaviour following encounters within 1 km, but not greater distances. The 24-h movement rates of elk increased after wolves approached within 1 km (LRT $\chi^2$ = 15.8, P < 0.001; Fig. 2a), but not after 2-km ($\chi^2$ = 1.12, P = 0.29), 3-km ($\chi^2$ = 1.12, P = 0.57) or 4-km ($\chi^2$ = 2.16, P = 0.54) encounters (Fig. 2a). Similarly, the 24-h displacement of elk increased after wolves approached within 1 km ($\chi^2$ = 15.8, P < 0.001; Fig. 2b), but not after 2-km ($\chi^2$ = 0.17, P = 0.68), 3-km ($\chi^2$ = 0.75, P = 0.69) or 4-km ($\chi^2$ = 2.32, P = 0.51) encounters (Fig. 2b).

Following 1-km encounters, wolves remained within that distance for an average of 5.5 h (± 1.7 h). The movement rates of elk returned to pre-encounter levels within 24 h of the initial encounter (Fig. 2c). A repeated-measures ANOVA indicated that time-since-encounter was significantly associated with the movement rate (F = 17.89, d.f. = 198, P < 0.001). Pairwise comparisons revealed an elevated movement rate 0–12 h (P = 0.002) and 12–24 h (P = 0.003) post-encounter, but not at 24–36 h (P = 0.83) or 36–48 h (P = 0.8).
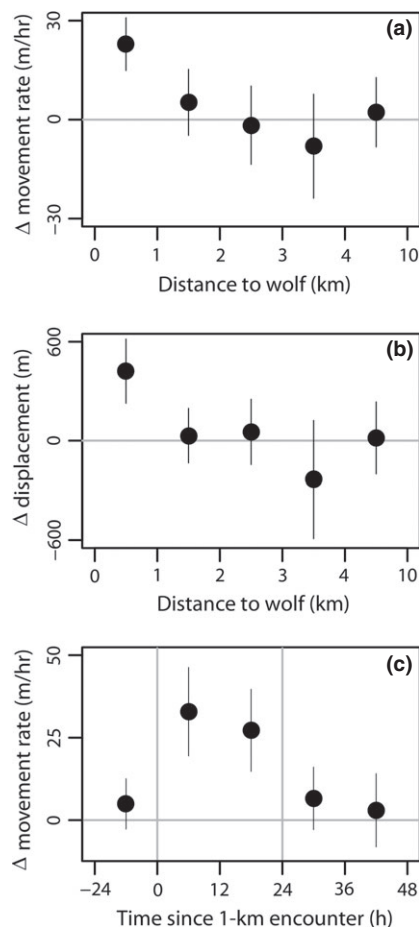
**Figure 2** Elk movement rates (a) and daily displacement (b) increased during the 24 h after wolf encounters within 1 km, but not longer distances. (c) Elk movement rates were elevated during the 24-h period following a wolf encounter. All values are mean ± 95% CI.



**Figure 3** (a) Elk were more vigilant following encounters within 1 km, but not longer distances. (b) Elk did not feed at a lower rate following wolf encounters. Right-hand axes provide back-transformed rates. (c) The use of conifer habitat (correlated with the first principal component in our PCA, see main text) did not differ between days with (black) and without (grey) 1-km wolf encounters. Conifer use varied by time of day.

### Elk foraging behaviour and habitat use

The vigilance rates of elk were also elevated when wolves had recently approached within 1 km ($\chi^2 = 9.34$, $P = 0.002$; Fig. 3a), but not after 2-km ($\chi^2 = 0.02$, $P = 0.89$), 3-km ($\chi^2 = 3.31$, $P = 0.19$) or 4-km ($\chi^2 = 4.33$, $P = 0.23$) encounters. Feeding rates, however, were not reduced in the 24 h after wolves approached within 1 km ($\chi^2 = 0.003$, $P = 0.95$), 2 km ($\chi^2 = 0.07$, $P = 0.8$), 3 km ($\chi^2 = 0.33$, $P = 0.85$) or 4 km ($\chi^2 = 0.67$, $P = 0.88$) (Fig. 3b), suggesting that the small increases in vigilance that we observed did not incur a reduction in feeding.

In our PCA of elk habitat use in the 24 h before and after 1-km wolf encounters, we retained the first two PCs based on Kaiser's criterion (eigenvector > 1). The first PC explained 91% of the variation in openness and 86% of the variation in distance-to-timber, reflecting open habitats far from the forest edge (positive loadings). The second PC explained 91% of the variation in elevation and 92% of the variation in distance-to-roads, reflecting habitats above the valley bottom and further from roads (positive loadings). We found no differences in the habitat attributes of elk locations before and after 1-km wolf encounters ($T^2 = 0.51$, d.f. = 653, $P = 0.6$). Habitat use differed between day and night ($T^2 = 83.02$, d.f. = 657,
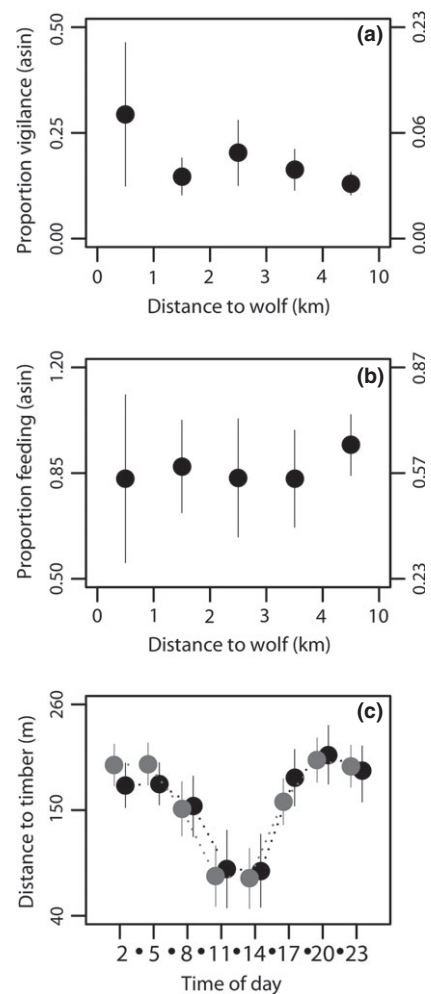
$P < 0.001$), with elk moving closer to timber during daylight hours (Fig. 3c).

### Individual variation in wolf encounter frequency

Elk varied widely in their exposure to wolves at the subpopulation and individual levels. During the past decade, the annual ratio of wolves per 100 elk was higher for the migratory subpopulation ($\bar{x} = 1.09$) than the resident subpopulation ($\bar{x} = 0.32$; $t = 8.77$, d.f. = 8, $P < 0.001$; Fig. 4a). At the individual level, migratory elk experienced a higher proportion of days with 1-km wolf encounters ($\bar{x} = 0.11$) than did resident elk ($\bar{x} = 0.02$) ($t = 9.5$, d.f. = 68, $P < 0.001$; Fig. 4b). The wolf encounter frequency of migratory elk equates to one encounter every 9 days (max 4 days) compared with every 50 days (max 14 days) for residents, indicating that wolf-induced increases in elk movement rates, displacement and vigilance occurred relatively infrequently.
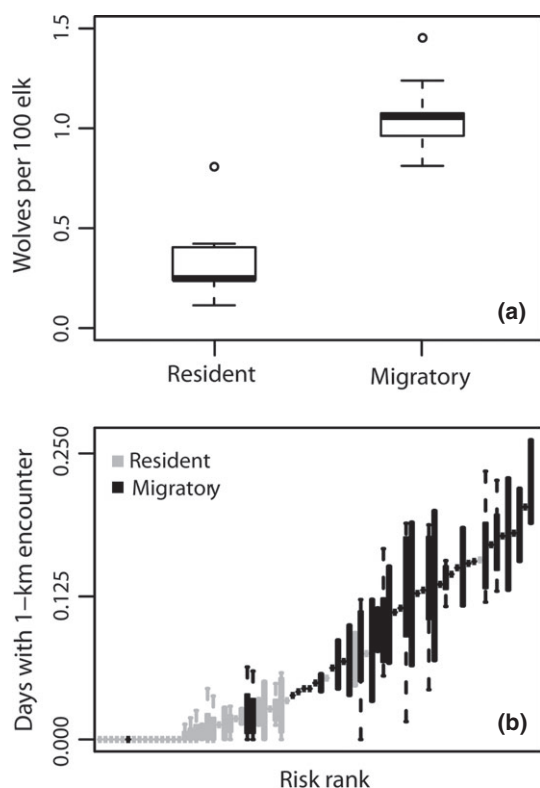
**Figure 4** (a) Locations of pack territories (see Fig. 1) translate into a higher number of wolves per 100 elk for migratory than resident elk subpopulations. (b) Individual elk ($n = 78$) varied 20-fold in the proportion of winter days that they experienced a 1-km wolf encounter. Where 3–4 winters of encounter data were available, a box-and-whisker is shown; two winters, a box only; and one winter, a closed circle only. Migrants experienced more frequent encounters ($\bar{x} = 0.11$ encounters/day) than residents ($\bar{x} = 0.02$ encounters/day).

### Elk body fat and pregnancy

We found no association between wolf encounter frequency and the body fat or pregnancy of elk. The late-winter body fat of migratory and resident elk was within the range of 19 other populations sampled in the northwestern US (Fig. 5a), and migratory elk were fatter than resident elk (Middleton *et al.* 2013b). When accounting

for individual effects and autumn body fat using GLMM, we found that subpopulations had similar rates of winter fat loss ($\chi^2 = 0.47$, $P = 0.49$) despite highly divergent levels of predation risk. Migratory elk lost on average 8.4% body fat ($\pm$ 0.97%, $n = 20$) over winter, and resident elk 7.2% ($\pm$ 1.14%, $n = 18$).

Among models of late-winter body fat where we could account for autumn body fat, the best model included autumn body fat as a single predictor (pseudo-$R^2 = 0.86$; Fig. 5b). Models that included autumn body fat had more summed weight (0.99) than models with subpopulation (0.24), age (linear, 0.22; quadratic, 0.05), predation risk (0.22) and year (0.21). Among models from the larger data set where we could not account for autumn body fat, the best model included predation risk and age (quadratic) (pseudo-$R^2 = 0.2$). Models that included predation risk had more summed weight (0.95) than models with age (linear, 0.14, quadratic, 0.65) and year (0.21). However, the association between predation risk and late-winter body fat was positive, indicating no support for an NCE of wolves on elk nutrition.

Among models of migratory elk pregnancy where we were able to account for autumn body fat, the best model indicated that pregnancy was a function of age (quadratic). Models that included age (quadratic) had more summed weight (0.60) than models including autumn body fat (0.49), predation risk (0.16) or age (linear, 0.13). Among models of pregnancy where we could not account for autumn body fat, the best model indicated pregnancy was a function of winter fat (Fig. 6) and age (quadratic). Models that included late-winter body fat had more summed weight (0.84) than models including age (quadratic, 0.77), predation risk (0.26) or age as a linear predictor (0.09).

### DISCUSSION

Our findings provide novel evidence from a large mammal system that a wide-ranging, active predator does not influence prey behaviour strongly enough to induce NCEs on prey demography (Schmitz 2005a, 2008; Preisser *et al.* 2007). Our approach was uniquely integrative. By connecting the predator encounter rate of individual prey to their nutrition and reproduction, we found that large mammalian prey can invoke anti-predator behaviours whose foraging costs are inconsequential in the context of the annual cycle of fat losses and gains.
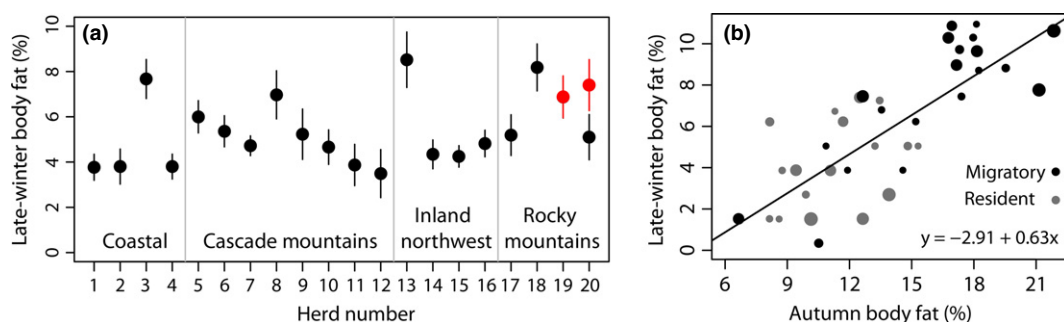


**Figure 5** (a) Counter to the hypothesised NCE of wolves on elk in the GYE, migratory elk (herd 20, red) were fatter in late winter than their resident counterparts (herd 20, black), as well as elk in a number of areas where wolves do not occur (data modified from Cook *et al.* 2013). Elk on Yellowstone's Northern Range (herd 19, red), which experiences a relatively high risk of predation, were also relatively fat in late winter. (b) The risk of wolf predation was not an important predictor of late-winter body fat. Instead, in models where we could account for autumn body fat, late-winter fat was largely a function of autumn fat (pseudo-$R^2 = 0.86$), indicating a strong carryover effect of growing-season conditions. Symbol size is proportional to the ranked predation risk of individual elk.
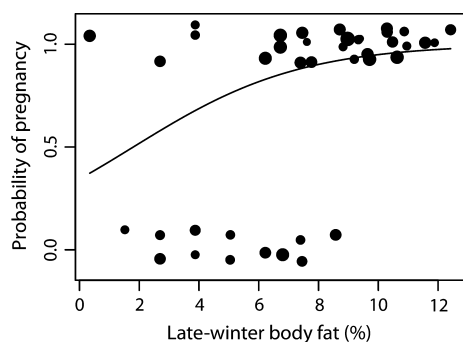
**Figure 6** The late-winter pregnancy status of migratory elk was a function of late-winter fat and age (quadratic). The carryover of autumn body fat into late winter (Fig. 5b) suggests that pregnancy is determined by growing-season conditions influencing conception, rather than winter conditions influencing foetal survival. Data values are offset (around 0 and 1) for display.

We observed clear behavioural responses of elk to wolves – increases in elk movement, displacement and vigilance rates – which were mostly consistent with previous studies (e.g. Liley & Creel 2007; Proffitt *et al.* 2009). However, these responses were not associated with potentially costly reductions in feeding or shifts in habitat use (Christianson & Creel 2010), and were apparent only when wolves approached within 1 km (Figs 2 and 3). Such encounters occurred only about once every 9 days for migratory elk, even though they interacted with a similar number of wolves relative to other sites in the GYE (cf. Creel *et al.* 2007; Vucetich *et al.* 2011) (Fig. 4a). Ultimately, although individual elk experienced 20-fold variation in the frequency of encounters with wolves (Fig. 4b), the accumulation of these interactions over the winter was not associated with reduced body fat or pregnancy (Figs 5 and 6). These findings suggest that the absence of a significant link from predation risk to prey reproduction in this system is attributable to weak and infrequent prey responses to the diffuse risk cues produced by an active hunter (Luttbeg & Schmitz 2000; Schmitz 2008). Predator hunting mode may be an important natural history attribute whose mediating effect scales up from mesocosms (Preisser *et al.* 2007; Schmitz 2008) to large vertebrates interacting over vast landscapes.

In addition to the wolf's active hunting mode, several other factors might help explain our findings. Recent syntheses suggest that predation risk effects can be weakened by resource limitation (Preisser *et al.* 2009) and social behaviour (Creel 2012) – and indeed, elk can experience both strong bottom-up limitations (Parker *et al.* 2009) that might require them to maintain feeding in spite of predation risk (sensu McNamara & Houston 1986), and gather in large groups to potentially lessen the need for other anti-predator behaviours (Mao *et al.* 2005). These two factors could act to weaken anti-predator responses. A third factor, the vast spatial scale of large mammal interactions, could act to diminish the predator–prey encounter rate independently of predator hunting mode. Classic experimental studies in ecology demonstrated weaker predator–prey interactions at larger spatial scales (Huffaker 1958), presumably because predators encountered prey at a lower rate. Several lines of evidence point to limitations on the encounter rates of large carnivores and their prey. Predator–prey density and biomass ratios tend to decrease with increasing body size, particularly among Carnivora (Carbone & Gittleman 2002). Wolves, for example, occur at low densities relative to their prey (Fuller *et al.* 2003) and make infre-

quent contact with prey groups – perhaps due to a combination of large travel distances, long prey handling times, and the need for territorial maintenance (Mech & Boitani 2003). Although low encounter rates are predicted to limit risk effects (Brown 1999), this notion has received surprisingly little study. Exploring the influence of spatial scale and predator–prey ratios on encounter rates – and whether these vary independently of predator hunting mode – is an important area for research because these factors could complicate the scaling of predictions across study venues and ecosystems (cf. Skelly 2002; Schmitz 2005b).

Instead of an influence of wolf predation risk, we found strong evidence that the body fat gained by female elk during the summer growing season was the primary predictor of late-winter body fat (Fig. 5b). The strength of this carryover effect suggests that an influence of autumn body fat on conception was the true driver of the relationship we observed between late-winter body fat and pregnancy (Fig. 6), rather than an influence of winter body fat on foetal mortality. In wild elk populations, including many experiencing nutritional limitation, intrauterine mortality accounted for only 1% of pregnancy losses in late winter, and no foetal losses were documented between late winter and parturition in 220 animals carrying vaginal implant transmitters (Cook *et al.* 2013). These findings support a growing recognition that summer–autumn conditions can strongly influence the nutrition and reproduction of temperate ungulates (Cook *et al.* 2004; Parker *et al.* 2009; Cook *et al.* 2013) including both captive (Cook *et al.* 2004) and wild (Cook *et al.* 2013) elk populations.

Several recent ecological changes in the GYE may have increased the importance of summer carry-over effects. The region has experienced warmer temperatures (Shuman 2012) and severe droughts which have affected hydrology (Barnett *et al.* 2008) and snowpack (Pederson *et al.* 2011). These climatic trends also appear to have reduced the length of the spring growing season on the high-elevation summer ranges of the migratory elk we studied (Middleton *et al.* 2013a). Additionally, the recovery of large carnivores, particularly grizzly bears (*Ursus arctos*), has brought major increases in direct predation on newborn elk during early summer (Barber-Meyer *et al.* 2008). These effects of drought and predation could largely explain both low pregnancy and declining calf recruitment among GYE elk (Middleton *et al.* 2013a). Meanwhile, high rates of neonate predation have the additional effect of relieving most migratory females of the nutritional costs of lactation (Middleton *et al.* 2013a), the likely reason that non-lactating migrants are on average 35% fatter than non-lactating residents by the end of summer (Fig. 5b). In mammals that nurse rapidly growing offspring for much of the year, we would expect such heavy predation on neonates to enhance maternal condition (Parker *et al.* 2009) – an effect of direct predation that could, counter-intuitively, buffer some prey against NCEs.

We did not consider a potential summer influence of wolf predation risk on elk behaviour and body fat. To date, two pathways for wolf-induced NCEs have been proposed. The first, that declines in elk pregnancy are mediated by elevated glucocorticoid levels during winter, has been rejected (Creel *et al.* 2009). We evaluated the second, that wolves reduce elk pregnancy rates via changes in elk behaviour and nutrition over winter (Creel *et al.* 2009; Christianson & Creel 2010). Although we found no support for this hypothesis, our previous finding that elk body fat and pregnancy are limited by the nutritional demands of summer lactation (Middleton *et al.* 2013a) suggests that wolf-induced NCEs could operate via the anti-

predator behaviours of lactating females in summer. This possibility warrants attention. However, in light of evidence that (1) elk can respond relatively weakly to wolves (Mao *et al.* 2005; Kittle *et al.* 2008; Kauffman *et al.* 2010; this study), (2) declines in elk productivity can be largely explained by direct predation and drought (Middleton *et al.* 2013a) and (3) elk-wolf encounter rates should be lower in summer when elk disperse more widely and wolves tend to pups near the den (Nelson *et al.* 2012); our interpretation is that strong wolf-induced NCEs on elk reproduction are not occurring in the GYE.

Several prior studies have explored correlations between wolf predation risk and elk nutrition and reproduction in the GYE. Our findings are consistent with two of them (White *et al.* 2009, 2011), but contradict two others (Creel *et al.* 2007; Christianson & Creel 2010). The differing results may be due to differences in the ability of studies to account for confounding factors. One study that supported a wolf NCE on elk pregnancy (Creel *et al.* 2007) was based on faecal hormone assays involving elk of unknown age. However, over two decades of predator recovery, some elk populations have experienced steady recruitment declines that can lead to a preponderance of older females with lower pregnancy rates (Middleton *et al.* 2013a). By focusing our sampling on known individuals, we were able to account for the effect of age on elk pregnancy (Cook *et al.* 2004). Another study that supported a wolf NCE on elk nutrition (Christianson & Creel 2010) used relatively indirect, short-term indices of nutrition (i.e. faeces and urine) and did not quantify the frequency of the interactions. By sampling the late-winter body fat of individual elk and the relative frequency of their encounters with wolves, we were able to evaluate the cumulative aspect of behaviour–nutrition interactions. We also explicitly considered confounding factors that might explain declining elk productivity in the GYE, and found that both drought and grizzly bear predation have disproportionately affected elk in core GYE habitats that also have high wolf predation risk (Middleton *et al.* 2013a).

That we did not find frequent elk-wolf encounters, reductions in elk feeding rates, or shifts in elk habitat use also suggests it is unlikely that wolves are inducing a behaviourally mediated trophic cascade in this system. Several studies over the last decade have proposed that elk in the GYE now fear to forage in risky habitats, thus facilitating the recovery of woody plants such as aspen (*Populus tremuloides*) and willow (*Salix* spp.) (e.g. Ripple & Beschta 2006). Our results are more consistent with recent studies that have found little or no evidence for cascading effects of wolf predation risk in YNP (Kauffman *et al.* 2010; Marshall *et al.* 2013) or elsewhere in the GYE (Creel & Christianson 2009; Winnie 2012). Taken together, these studies suggest that wolves' consumption of elk, rather than a 'landscape of fear,' is the more likely pathway for cascading effects. Future studies that evaluate factors governing the scale (Kittle *et al.* 2008) and consistency (Fortin *et al.* 2005) of prey behavioural responses to wolves will be important in resolving questions about the broader ecological implications of risk effects caused by these predators.

Our findings are relevant to the unfolding management of wolves and elk in the GYE. The management plans of Wyoming, Montana and Idaho allow for new wolf harvests in areas where wolves adversely impact ungulates. Large declines in elk calf recruitment, a driver of elk population growth (Raithel *et al.* 2007), have occurred on wolf-occupied winter ranges in outlying areas of the GYE (Middleton *et al.* 2013a). Our work suggests that the consumptive effect of wolves – not 'harassment,' 'stress' or 'fear,' the colloquial terms for NCEs in the region – is the primary means by which wolves influence elk populations. However, for the migratory elk in our study population, high rates of bear predation (Barber-Meyer *et al.* 2008) and reduced habitat quality due to drought (Middleton *et al.* 2013a) – both on summer ranges largely inside YNP – are confounding factors that may combine to limit calf recruitment more strongly than wolves (Middleton *et al.* 2013b). In such a complex predator–prey system as the GYE, predicting the effects of wolf harvest will require monitoring and research that help partition the role of multiple predators and habitat conditions on both seasonal ranges of migratory ungulates.

## AUTHORSHIP

ADM, MJK, DEM and MDJ designed the research; ADM, MJK, DEM, MDJ, RCC, JGC and PJW collected the field data; ADM, MJK, RCC, JGC, SEA and HS analysed the data; ADM wrote the manuscript, incorporating revisions from the co-authors.

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