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Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation

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We studied individual and herd level behavioural responses of elk to spatial and temporal variation in the risk of predation by wolves over three winters in the Upper Gallatin drainage, Montana, U.S.A. Within a given drainage, elk of both sexes moved into or closer to protective cover (timber) in response to wolf presence. Cow elk responded to elevated risk by increasing vigilance in exchange for foraging, and large mixed (cow, calf, spike) herds substantially decreased in size. In contrast, when wolves were present, bulls did not increase vigilance levels, or decrease feeding, and small bull-only groups slightly increased in size. As a consequence, small bull-only herds and large mixed-sex herds converged on a similar size when wolves were present. We think this response is a balancing of the benefits of risk dilution with increased detectability or attractiveness of larger herds to wolves. Based on proportions in the population, wolves overselected bulls and underselected cows as prey. Thus, bulls showed weaker antipredator responses than cows, despite facing a greater risk of predation. Using marrow fat content from elk killed by wolves as an indicator of body condition, bulls were in significantly worse body condition than cows throughout the winter, and condition deteriorated for both sexes as winter progressed. Overall, we conclude that antipredator behaviours carry substantial foraging costs, that bulls, because of their poorer body condition, are less able to pay these costs than cows, and that differences in ability to pay foraging costs probably explain sex-specific differences in antipredator behaviours.

Keywords: antipredator behaviour; body condition; *Canis lupus*; *Cervus elaphus*; elk; group size; herd size; predation risk; vigilance; wolf

Antipredator behaviour is well documented across a wide variety of taxa, at many spatial and temporal scales. At relatively broad scales, prey often alter their use of habitats in response to predation risk, trading security for a reduction in forage quality, quantity, or both. Bottlenose dolphins, *Tursiops aduncus*, avoid shallow, productive foraging areas during seasons when tiger sharks, *Galeocurdo cuvier*, are present, but favour these areas when sharks are absent (Heithaus & Dill 2002). Elk, *Cervus elaphus*, move out of open grassy habitats into less nutritionally profitable closed, forested habitats during human hunting seasons (Morgantini & Hudson 1985). When faced with the threat of predation by trained barn owls, *Tyto alba*, desert gerbils (*Gerbillus allenbyi* and *G. pyramidum*) limit their foraging activity and avoid open areas, foraging under cover in brushy habitats (Abramsky et al. 1996). In experimental studies, the presence of predatory large mouth bass, *Micropterus salmoides*, limited small bluegill sunfish, *Lepomis macrochirus*, to vegetated habitats near shore, significantly reducing their growth rate (Werner et al. 1983).

At finer temporal and spatial scales, prey often alter their behaviour in response to changes in predation risk. Among the most studied of these responses are changes in vigilance levels, group formation, and interactions between the two (Elgar 1989; Lima & Dill 1990; Roberts 1996). Individuals may increase vigilance in response to elevated threat, and as with habitat shifts, this response often carries a foraging cost, typically paid with a reduction in foraging time (Jennings & Evans 1980; Underwood 1982; Berger & Cunningham 1988; Lima 1998; Abramsky et al. 2002).

Prey may benefit by grouping through multiple mechanisms, which may interact: collective vigilance (Pulliam

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1973; Powell 1974; Kenward 1978; Roberts 1996); confusion of attacking predators or cooperative defence (Cresswell 1994; Krause & Godin 1995); dilution of individual risk (Lima & Dill 1990; Cresswell 1994); and attack abatement (Turner & Pitcher 1986; Uetz & Hieber 1994). Individual vigilance levels often decline with increasing group size, which implies that prey do indeed perceive themselves as safer in larger groups (Roberts 1996; but see Elgar 1989, for a critical review).

The benefits of grouping are reduced (and potentially reversed) if predators can detect large groups more easily, or prefer to attack them. Several authors have reported that larger groups are more often detected and attacked, but some have shown that despite this, and sometimes despite higher predator success when attacking large groups, individual prey in larger groups are still safer, because of the offsetting benefits of dilution (Creel & Creel 2002; Hebblewhite & Pletscher 2002), collective detection or cooperation in escape (Krause & Godin 1995), or combinations of these effects (Cresswell 1994; Uetz & Hieber 1994).

Predation risk varies in space and time. In the absence of constraints, prey would respond to risk and minimize predation rates in all places at all times. However, antipredator behaviours commonly carry foraging costs (Lima & Dill 1990; Lima 1998), and when prey must exchange food for security, constraints on both foraging and antipredator behaviours are inevitable. Constraints vary among individuals depending on nutritional status, and vulnerability to predation should similarly vary (Lima & Dill 1990; Sinclair & Arcese 1995; Lima 1998). Consequently, an individual's physical condition is likely to affect its behavioural response to variation in risk. Nutritionally compromised individuals should be less responsive if they are unable to pay the costs associated with reducing predation risk (Bachman 1993; Lima 1996). Notably, despite the widespread assumption that elevated vigilance confers greater security, few studies have directly shown higher predator attack rates upon, or higher mortality rates for, individuals displaying lower vigilance (but see Fitzgibbon 1988, 1990; and Scheel 1993 for a comparison of species).

Differences in behavioural responses that can be attributed to differences in physiological constraints will give an indication of the costs associated with antipredator behaviours. Because most prey (not just those individuals about to be killed by predators) respond to the threat of predation, the costs of risk reduction are likely to manifest themselves at both the individual and the population level, and may even exceed direct offtake (Ives & Dobson 1987; Bolnick & Preisser 2005). If these costs are sufficiently large in terrestrial vertebrates, then efforts should be made to incorporate them into future models of predator–prey interactions.

We know of no field studies that have attempted to directly assess behavioural responses of prey to interactions between body condition and natural variation in spatial and temporal predation risk. We examined vigilance, grouping and cover-seeking responses of elk, *Cervus elaphus*, to fine-scale variations in both spatial (distance to protective cover, timbered areas; position in herd) and temporal (wolf, *Canis lupus*, presence) risk, and further examined how these behaviours are constrained by prey physical condition.

It was not possible to sample physical condition for the general elk population, so we compared the behaviour of two classes that are under different energetic constraints through winter: bulls (branch antlered males with brow tines) and cows (females > 1 year old). Bull elk enter winter weakened by the autumn rut, having lost as much as 20% of their pre-rut (August) body mass by mid-November, and continue to lose weight more rapidly than cows throughout the winter (Anderson et al. 1972; Mitchell et al. 1976; Geist 2002; Hudson et al. 2002). In contrast, cow elk typically lose less than 10% of their body mass between August and May, ending most winters with proportionally less weight loss than bulls experience prior to winter's onset. In most populations, over 80% of cows are pregnant each winter, and a cow's spring weight includes that of her developing fetus, so most cows' overwinter weight losses are greater than 10%. However, fetus growth is approximately exponential, with the majority of fetal weight gain occurring in the spring, so cow weight loss is typically low for most of winter (Geist 2002; Hudson et al. 2002; Cook et al. 2004). Here we attempt to confirm differences in body condition by comparing the bone marrow of wolf-killed bulls and wolf-killed cows. The chief limitation to this approach is that wolf-killed elk do not represent a random sample of the population at large. Our analysis does not assume that marrow fat is the same in the sample of killed animals as in the general population. It does assume that any differences in condition between live elk and wolf-killed elk are the same for males and females. In other words, the data force an assumption that loss of body condition would increase the risk of predation in the same manner for cows and bulls.

We tested the following hypotheses.

(1) Vigilance levels for elk should increase when wolves are present, for both sexes (i.e. elk are sensitive to short-term temporal variation in risk).

(2) Vigilance should decrease with increasing group size (assuming that elk find greater security in larger groups).

(3) Vigilance should increase with distance to timber (i.e. elk are sensitive to fine-scale spatial variation in risk). Here we assume that elk perceive timber as protective cover, because we have previously used the distribution of kill sites to show that risk increases with distance to timber (Creel & Winnie 2005).

(4) Vigilance should be higher on the periphery of herds since these animals might be the first to encounter attacking wolves (Jennings & Evans 1980; Berger & Cunningham 1988; Fitzgibbon 1990).

(5a) Bulls in our study area should display a greater increase in vigilance than cows when wolves are present. Several studies of wolf–ungulate interactions have found that males are preferentially selected by wolves in winter (Kolenosky 1972; Huggard 1993; Mech et al. 2001). Our evaluation of this hypothesis includes testing whether bulls are preferentially preyed upon in this population. This hypothesis assumes variation in risk is the primary driver of variation in vigilance in elk.