



Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves

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Many studies have examined grouping as a form of antipredator behaviour, but relatively few studies have examined how group size responds to natural variation in predation risk across space and through time. We studied the responses of elk, *Cervus elaphus*, herd size and composition to natural variation in the risk of predation by wolves, *Canis lupus*, in the Gallatin Canyon of Montana. We found that elk herd size increased as distance to protective cover increased. A positive association between group size and distance to cover is often interpreted as evidence that grouping is an antipredator response. However, we found that herd size increased only on days that wolves were absent. When wolves were present, herd sizes remained small at all distances from cover. This suggests that aggregation far from cover on days that wolves were absent was a foraging response, rather than an antipredator response. These data highlight interaction between temporal and spatial variation in predation risk, and suggest caution in conclusions about the antipredator benefits of grouping in the absence of direct data on risk or predator presence.

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When faced with the risk of predation, an animal can conceptually adopt one of two 'pure' strategies, or a mixture of the two. The first pure strategy is to continue to behave in a manner that would be optimal in the absence of predation, but does nothing to reduce the risk of predation. The second pure strategy is to do everything possible to avoid predation, and accept the costs that these antipredator responses incur. It is generally accepted that selection will favour individuals who optimally balance the benefits of risk reduction against its costs (Illius & Fitzgibbon 1994). Behavioural responses to predation risk include increased vigilance (Elgar 1989), reduced foraging time (Hughes & Ward 1993; Abramsky et al. 2002), reduced movement (Sih & McCarthy 2002), habitat shifts (e.g. retreat to low-risk areas or refuges; Bergerud et al. 1983; Formanowicz & Bobka 1988; Blumstein & Daniel 2002), reduced use of conspicuous behavioural displays (Sih et al. 1990), and changes in group size.

The effect of group size on predation risk is one of the most-studied aspects of interactions between predators and prey (Kenward 1978; Lazarus 1979; Bertram 1980; Dill & Fraser 1984, 1997; Formanowicz & Bobka 1988; Elgar 1989; Lima & Dill 1990; Sih et al. 1990; Uetz & Hieber 1994; Roberts 1996; Sih 1997; Brick 1998; Lange & Leimar 2001; Martin & Lopez 2001; Boland 2003; Caro et al.

2004). In general, an individual's risk of predation decreases as group size increases (once a group of prey has been encountered by a predator) due to collective vigilance, collective defence, or dilution of risk. This pattern has been confirmed by many observational and experimental studies of birds, fish and invertebrates (Kenward 1978; Pulliam & Caraco 1984; Lima 1995a, b; Krause & Ruxton 2002; Uetz et al. 2002), although less is known about group size and predation risk for mammalian predators and prey (Messier & Barrette 1985; Fitzgibbon 1990; Creel & Creel 2002; Goldspink et al. 2002; Hebblewhite & Pletscher 2002).

There are fairly serious limitations to our understanding of group size effects on predation, even in well-studied taxa such as songbirds, because most studies of predation risk have good data on prey behaviour, but little information about predators (Creel & Creel 2002; Lima 2002; Boland 2003). Consequently, we know a great deal about the effect of prey group size on the probability that an attack will lead to a kill, but we know less about the effect of group size on the probability that a predator will encounter prey, or the probability that a predator will attack once it has detected prey. For wolves, *Canis lupus*, hunting bison, *Bison bison*, in Alberta, only 26% of 281 encounters provoked an attack (Carbyn & Trotter 1987). For African wild dogs, *Lycaon pictus*, hunting wildebeest, *Connocheates taurinus*, and impala, *Aepyceros melampus*, only 45% of 903 encounters provoked an attack: large herds are more likely to be detected, and more likely to be

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attacked upon detection (Creel & Creel 2002). Studies of stalking predators also confirm that prey group size can affect encounter rates, attack probabilities, or both (cheetahs, *Acinonyx jubatus*, preying on gazelles, *Gazella thompsoni*: Fitzgibbon 1990; wasps preying on orb-weaving spiders, *Metapeira incrassata*: Uetz & Hieber 1994; lions, *Panthera leo*, preying on mixed ungulate herds: Scheel 1993; cichlids, *Aequidens pulcher*, preying on guppies, *Poecilia reticulata*: Krause & Godin 1995; sparrowhawks, *Accipiter niscus*, preying on redshanks, *Tringa tetanus*: Cresswell & Quinn 2004). These results suggest that selection will favour prey behaviour that reduces the likelihood of encounter or attack, in addition to better studied mechanisms such as collective vigilance, cooperative defence, and dilution of risk.

Finally, there are considerable data on the way that group size affects predation risk, but little work has examined how group size responds to natural variation in predation risk. That is, most research has treated group size as an independent variable, and asked how grouping patterns alter dependent variables such as the rate or outcome of attacks. It is less common to use the complementary approach, in which group size is treated as a dependent variable and related to independent measures of risk. In this study, we used behavioural observations of wolves and elk, *Cervus elaphus*, in the Gallatin Canyon portion of the Greater Yellowstone Ecosystem to determine how herd sizes responded to spatial and temporal variation in predation risk.

This study system has generated interest as a potential example of a trophic cascade driven by the behavioural responses of prey to predation risk. Recent studies have proposed that elk change their behaviour in the presence of wolves in ways that affect plant communities, but these studies have included little or no direct data on how predation risk actually varied across space or through time (Ripple & Larsen 2000; Laundre et al. 2001; Childress & Lung 2003; Ripple & Bechsta 2003). In these studies, areas of high or low risk were defined either by habitat features or by large ellipses (Laundre et al. 2001) with a loose relationship to wolf home range polygons (Smith & Guernsey 2002). Our understanding of elk responses to predation risk is likely to benefit from direct data on patterns of risk for several reasons. First, there are large differences between locations (even within a single ecosystem) in variables such as habitat type and herd sizes (e.g. compare our data to elk herds less than 20 km away in the Madison River valley, which are typically one to two orders of magnitude larger: Gude 2004). Second, assumptions about areas likely to be dangerous (e.g. the assumption that open areas are low risk: Ripple & Bechsta 2003) are not supported by direct data on spatial patterns of risk (see below). Third, within the large areas defined as 'high' or 'low' risk by some prior studies (e.g. Laundre et al. 2001; Childress & Lung 2003), there is substantial local variation in risk (see Results). Finally, risk varies temporally, as well as spatially, but temporal variation in risk has received little attention in prior studies of large vertebrates, including work on wolf–elk trophic cascades.

In this study, we mapped the distribution of elk and recorded herd sizes and compositions in four drainages of

the Gallatin Canyon. We simultaneously determined whether wolves were present in each drainage on each day of observation. This approach allows a direct test of the hypothesis that elk herd sizes respond to fine-scale variation in the risk of predation by wolves. In particular, we tested whether herd sizes differed on days with wolves present and absent (temporal variation in risk), and whether herd sizes responded to distance from timber (spatial variation in risk). We used data on the distribution of wolf-killed elk, relative to the distribution of live elk, to confirm that spatial variation in risk increased with distance to timber (see Results). Interestingly, we found a strong interaction between the effects of spatial and temporal variation in risk on herding behaviour. In the absence of fine-scale data on temporal variation in risk, the data on spatial variation in risk would have supported a false conclusion that elk aggregated in open areas to benefit from collective predator detection or defence (e.g. the 'many-eyes' response). With data on temporal variation in risk, we reach a very different conclusion: elk aggregated in the open as a foraging response that occurred only when the short-term risk of predation was low, when wolves were not present in the drainage.

METHODS

Study Area and Populations

Elk

The Gallatin Canyon study site covers 125.8 km² in four drainages (Porcupine: 30.3 km²; Taylor: 56.0 km²; Tepee: 13.1 km²; Daly: 26.4 km²), on a combination of National Forest, National Park, State and private land in the Greater Yellowstone ecosystem. Valley bottoms are primarily sage (*Artemisia*) scrub and grassland (dominated by Idaho fescue and bluebunch wheatgrass: *Festuca idahoensis* and *Agropyron spicatum*) with small riparian zones, coniferous forest and small meadows on the slopes above. Elevation ranges from 1975 m to 2432 m above sea level. Based upon aerial surveys conducted by Montana Fish Wildlife and Parks (Peek & Lovaas 1967; K. Hamlin, personal communication), the Gallatin winter elk herd has held between 1214 and 3028 elk over the past seven decades, holding relatively stable around the long-term average \pm SE of 1725 ± 63 animals (13.7 elk/km²; Fig. 1), with a small but significant decline through time that is driven primarily by low counts in the years since recolonization by wolves (linear regression: $b = -0.46 \pm 0.13$; t test: $t_{46} = 3.56$, $P = 0.0009$, $r^2 = 0.20$). Recruitment in early winter has been at or below 20 calves: 100 cows in five of six winters since colonization by wolves compared with one of 13 winters prior to wolf colonization (Fisher's exact test: $P = 0.12$). Similarly, population size has been below 1500 elk in six of seven winters since wolf colonization, compared with 16 of 41 winters prior to wolves (Fisher's exact test: $P = 0.17$).

Elk make up more than 90% of the ungulate community, usually in small herds (mean \pm SE = $13.9 \text{ elk} \pm 0.67$, maximum = 253 elk: ground counts of 1143 ungulate herds in winter). Moose, *Alces alces*, mule deer, *Odocoileus*

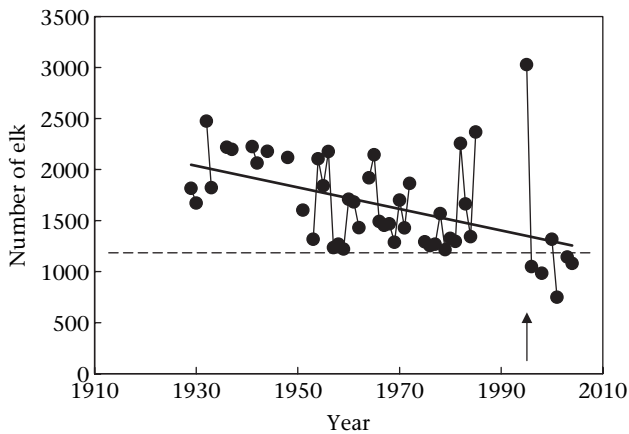


Figure 1. Size of the Gallatin elk herd, 1929–2004, from early winter aerial total counts. Counts for consecutive years are joined by light lines, and the heavy line shows the linear least squares regression. The vertical arrow indicates recolonization by wolves. The dashed horizontal line shows the minimum population size from the 41 counts prior to recolonization by wolves.

hemionus, and white-tailed deer, *O. leucurus*, also used the Gallatin site, at densities much lower than elk (3.3% of 2846 herds, see below). Elk density was low in the steep, rocky terrain between the four focal drainages. Conventional VHF radiotelemetry and geographical positioning system (GPS) telemetry (18 440 fixes from 46 individuals) show that elk move between the four drainages, but rarely during our field season (a pattern originally described by Brazda 1953). Relatively few elk are on the Gallatin Canyon site during the autumn general hunting season, but 80 licenses have typically been issued for a late-season hunt, with a long-term average of 63% success.

Wolves

The Gallatin site has been heavily used by the Chief Joseph wolf pack since 1996–1997. The Chief Joseph pack held 12, 7 and 12 wolves in the winters of 2000–2001, 2001–2002 and 2002–2003, when we conducted this study. The Chief Joseph pack denned in the Daly drainage on the Gallatin site in all three of these years. In 2001–2002, the study site was colonized by a second pair of wolves, which denned in the Taylor drainage and successfully reared pups to become the Sentinel Pack (2 wolves in 2001–2002, 5 wolves in 2002–2003). In 2001–2002, a third pair was present in the Porcupine drainage, but apparently did not rear pups and disbanded. The Chief Joseph pack has one of the largest home ranges in the Yellowstone Ecosystem (Smith & Guernsey 2002), and moves on and off the Gallatin Canyon site regularly. The Sentinel pack remained on the study site for most of 2001–2002, but moved on and off the site regularly in the third winter. Wolf movements, colonization and pack failures caused predation risk to vary spatially and temporally across the site.

Determining Elk Distributions, Herd Sizes and Compositions, and Wolf Presence

For each of the four drainages, we conducted ground transects within each 2-week period throughout the

winter, from early January until the end of the wolf-denning period in June. Transect routes began at the bottom of each drainage and went to the top, following routes that maximized the viewshed and included fixed observation locations on highpoints. We used 7×42 or 10×40 binoculars (Leitz, Canon and Nikon) to scan for elk when we were between observation points, and we used a tripod-mounted $20\text{--}56\times$ Nikon ED spotting scope to scan from observation points. These sampling routes were fixed, and we traversed them in the same way each time, beginning at first light. On each transect, we counted elk, mapped their locations using a GPS and U.S. Geological Survey topographic maps, and recorded herd compositions, for a total of 2752 elk herd observations. We defined a herd as a group with relatively consistent internal spacing, with individuals moving in roughly the same direction at roughly the same rate (or all stationary). Interindividual distance within herds was typically less than five body lengths (73% of 864 herds, 77% of 13 672 individuals) and herds were typically small (mean \pm SE = 13.9 ± 0.67), so that herd membership was usually unambiguous. Of the 2752 herd observations, 1143 cases (including 139 singletons, usually bulls) allowed for an accurate count and classification. We classified individuals as calves (young of the year, either sex), cows (adult females of all ages), spikes (immature bulls with no brow tine) and bulls (adult males with a brow tine). Calves could not be sexed, and yearling females could not be identified reliably. We regularly checked interobserver agreement in the classification of calves.

When herd positions were determined, we recorded the distance to timber in four classes (0–30 m, 31–100 m, 101–300 m and 301+ m), using elk body lengths and familiarity with local geography to assist in estimation. We chose this method rather than using geographical information system (GIS) techniques to estimate distance because ground truthing of the U.S. Forest Service habitat maps of this area showed that edge locations were often not accurate and direct field measurements were preferable.

While walking elk transect routes, we continuously checked for signs that wolves were present within the drainage on that day. We scored wolves as present within a drainage if we located them via VHF radiotelemetry, or found fresh tracks in the snow, a fresh kill or fresh scat. In the Chief Joseph pack, 0–6 wolves carried radiocollars. In the Sentinel pack, 0–2 carried radiocollars, and no wolves were collared in a third pack that briefly occupied the Porcupine drainage. It was not safe to assume that a drainage had no wolf activity simply because no radio signal was detected, because many wolves were not collared, and wolf packs are not continuously cohesive. Because we did not radiocollar every wolf in the area, it is likely that we failed to detect wolves on some days. Thus, we categorize our data as ‘wolves present’ and ‘wolves not detected’ (which for brevity we call ‘wolves absent’ on figures). This classification is conservative, because failure to detect wolf presence would be expected to mask responses by elk to wolves, but would not be expected to create apparent differences where none exist (see Results).

Determining Spatial Variation in Predation Risk

Locations far from cover are likely to be more dangerous. Many studies have shown that antipredator behaviour is sensitive to distance from cover, although few studies have tested whether distance to cover affects natural variation in predation risk (Elgar 1989; Lazarus & Symonds 1992; Hughes & Ward 1993; Kunkel & Pletscher 2000; Barta et al. 2004). To test this hypothesis directly, we compared the distribution of live elk (see above) to the distribution of 52 wolf-killed elk and nine probable wolf kills of elk. For these 61 kills, we determined the distance to timber (protective cover) using the same methods we used for live elk. To determine the expected number of kills in each of the four categories of distance to timber, we used the distribution of live elk when wolves were known to be present and the total number of detected kills (see above). We then compared the expected pattern to the observed distribution, using a contingency table (following Zar 1999).

A Note on the Distributions of Elk and Wolf Kills

Using ground observations limited our ability to detect live elk and wolf kills in timbered areas. Consequently, our spatial data test the hypothesis that being far from protective cover (timber) is more dangerous than being near protective cover. These data do not directly address the hypothesis that moving into timbered areas might further reduce the risk of predation (although data from GPS radiocollars confirm that elk are more likely to be found in wooded locations when wolves are present (unpublished data)).

Statistical Methods

We used factorial ANOVA to test whether herd size responded to temporal and spatial variation in predation risk, after testing that assumptions were met. Herd size was the dependent variable. The independent variable 'wolf presence' incorporated temporal variation in risk (wolf presence in the drainage on that day = yes or no). The independent variable 'distance to timber' incorporated spatial variation in risk (distance to timber = 0–30 m, 31–100 m, 101–300 m and 301 + m). The factorial design allowed us to test for an interaction between spatial and temporal risk effects. We tested for differences between the four drainages in herd size responses, and pooled the data across drainages because there were no differences. To test for changes in herd composition in response to predation risk, we used a similarly structured set of factorial ANOVAs: in this case, the dependent variable was the proportion of each herd composed of a given age–sex class. These proportions were arcsine transformed to satisfy the assumption of normality (Zar 1999). In the analysis of herd compositions, we detected significant differences between drainages, so the data were not pooled. Degrees of freedom for ANOVAs were based on numbers of herds

counted, which assumes that herd size and composition were free to vary between observations. Elk herd membership changes often on our study site, so we are confident that this assumption was met. Tests of significance were Bonferroni adjusted for multiple comparisons (reported with results).

RESULTS

Predation Risk

Risk and age–sex class

The risk of winter predation by wolves was strongly affected by age and sex (Fig. 2; chi-square test: $\chi^2_1 = 39.2$, $P < 0.001$). The risk of predation differed from random expectation for all age–sex classes. Adult females were killed only one-third as often as expected by chance, whereas bulls and calves were killed 2.2-fold and 2.5-fold more often than expected by chance, respectively. From the perspective of an individual elk, the risk of being killed by wolves was 6.3 times higher for a bull than for a cow.

Spatial variation in risk

For elk of all age–sex classes, the risk of predation was affected by distance to timber. Kills occurred more often than expected in open areas far from timber, and slightly less often than expected near timber (Fig. 3; $\chi^2_3 = 199.97$, $P < 0.0001$). This pattern was clearest for males and calves (Table 1), because they were killed often enough for spatial effects to be well resolved, but the same pattern held for cows (Table 1). Comparing the distribution of kills to the distribution of live elk in periods when wolves were present, areas that were more than 300 m from timber were an order of magnitude more dangerous than areas within 100 m of cover (Table 1). Throughout the study, we saw only 114 live elk further than 300 m from timber when wolves were present, but found 14 wolf-killed elk in this zone (Table 1). For males, we saw only 18 individuals more than 300 m from timber when wolves were present, but found eight wolf-killed bulls in this zone.

Elk can detect this spatial variation in risk and respond accordingly. The responses of elk are examined in detail

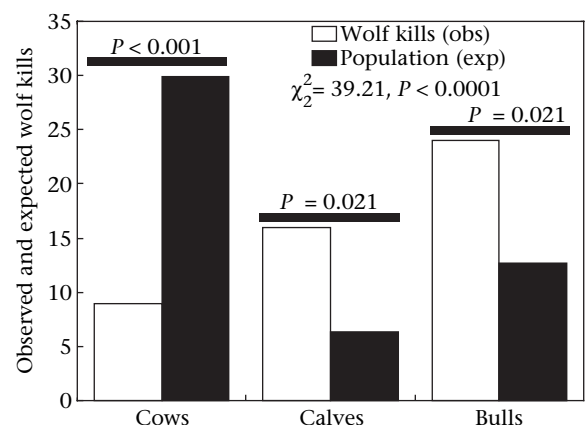


Figure 2. Observed and expected numbers of elk killed by wolves as a function of age and sex.

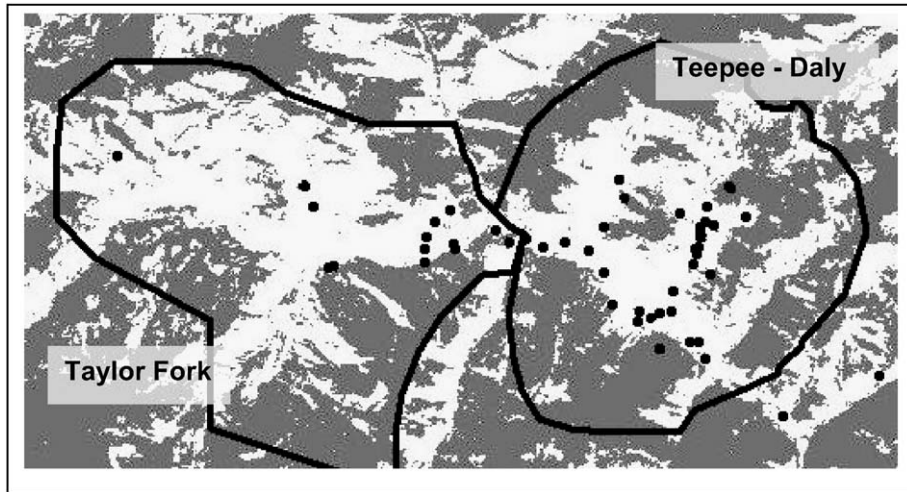


Figure 3. The distribution of 52 wolf-killed elk on the southern portion of the Gallatin study area. Within open areas, kills were nonrandomly likely to occur far from timbered areas (see Table 1). Grey areas are timbered, and white areas are open grassland or sage-steppe. Black dots represent the location of kills. Focal study site boundaries are identified by heavy lines. The Daly and Teepee drainages are in the eastern subsite and the Taylor drainage is in the western subsite (north is to the top of the figure).

below, but a basic response is apparent in their spatial distribution (Table 1). On days that wolves were present within a drainage, elk within 30 m of cover outnumbered elk more than 300 m from cover by a factor of 14.7. This difference was much less pronounced (2.3-fold: Table 1) on days that wolves were not detected in a drainage ($\chi^2_3 = 586.5, P < 0.0001$).

Responses of Herd Size to Spatial and Temporal Variation in Predation Risk

Herd size increased significantly with distance to timber (Fig. 4; $F_{3,982} = 11.06, P < 0.0001$, main effect using least squares means from factorial ANOVA: herd size*distance to timber*wolf presence). Because areas far from timber are more dangerous, this result appears to support the hypothesis that elk aggregate under conditions of high

risk, to take advantage of improved predator detection or defence (e.g. ‘many-eyes’ benefits, see Roberts 1996 for discussion).

However, the response of herd size to wolf presence supports the opposite conclusion, that elk disaggregate under conditions of high risk (Fig. 5). On days that wolves were present, mean herd sizes were less than half of those seen when wolves were absent ($F_{1,982} = 40.1, P < 0.0001$). This response indicates that elk do not assess risk based solely on their location, as is implicitly assumed by many analyses. Rather, they also assess temporal variation in risk, on a scale fine enough to resolve the comings and goings of wolves on (at least) a day-by-day basis.

Without an experiment, it would be difficult to fully disentangle the apparently contradictory effects of spatial and temporal variation in risk on herd size, but the interaction term from factorial ANOVA is informative. Elk

Table 1. The distribution of live and wolf-killed elk in relation to distance to timber

Age–Sex class	Distance to timber (m)			
	0–30	31–100	101–300	> 300
All elk				
Wolf kills, observed/expected	16/20.5	11/20.5	10/8.7	14/1.4
Number of elk seen, wolves present	1561	1561	662	106
Number of elk seen, wolves absent	2398	3811	2761	1039
Adult males				
Number wolf kills observed/expected	7/10.0	6/10.3	3/3.3	8/0.38
Number of elk seen, wolves present	479	493	158	18
Cows				
Number wolf kills observed/expected	2/3.36	3/3.83	4/1.42	0/0.39
Number of elk seen, wolves present	454	517	192	53
Calves				
Number wolf kills observed/expected	6/5.7	2/7.1	3/1.6	4/0.60
Number of elk seen, wolves present	86	108	25	9

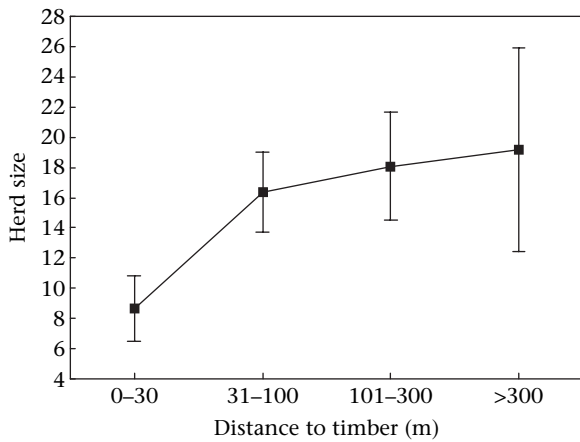


Figure 4. Elk herd size as a function of distance to timber, a measure of spatial variation in predation risk. Points show means. Error bars show 95% confidence limits.

aggregated in risky areas far from timber only when wolves were absent (Fig. 6; $F_{3,982} = 5.98$, $P < 0.001$). When wolves were present, elk did not aggregate into large herds at any distance to timber. These results strongly suggest that the aggregation of elk far from timber is not related to antipredator defence. The fact that aggregation occurred when risk was low suggests that the formation of large herds is a foraging response: when the temporal risk of predation is low, elk take advantage of the opportunity to forage in open grassy habitats (see Fig. 2) from which they are largely excluded by predation risk on days that wolves are present (see Table 1).

Responses of Herd Composition to Variation in Risk

Herd sizes were halved when wolves were present (Figs 2, 3). Consequently, it is of interest to determine whether herd composition also changes. If wolves target large herds more often than expected (Hebblewhite &

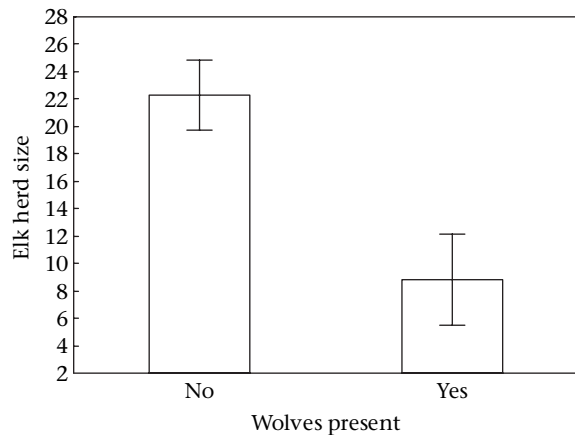


Figure 5. Elk herd size as a function of wolf presence within a drainage on the day of observation, a measure of temporal variation in predation risk. Bars show means. Error bars show 95% confidence limits.

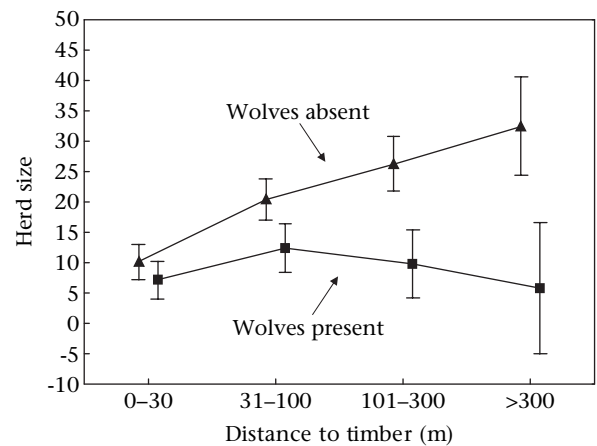


Figure 6. The response of elk herd size to the interaction of spatial and temporal variation in predation risk.

Pletscher 2002), it is logical to expect those individuals at greatest risk to leave large herds when the risk of attack is high (to reduce the likelihood that they will be encountered; Bergerud & Page 1987). In this case, adult males and calves face significantly greater risk than cows (Fig. 2), leading to the expectation that reductions in herd size might be driven by the departure of bulls and calves.

The proportion of cows and calves in herds did not change significantly in response to wolf presence (cows: $F_{1,976} = 0.185$, $P = 0.67$; calves: $F_{1,976} = 0.23$, $P = 0.63$). Calves were at greater risk than cows (Fig. 2), but are probably constrained to stay with herds because they are dependent upon their mothers.

The proportion of adult males in herds dropped significantly in response to wolf presence in the Tepee and Daly drainages, which have a substantial population of males (Fig. 7; $F_{1,966} = 7.06$, $P = 0.008$). Relatively few males were present in the other two drainages (Taylor and Porcupine), where male movements did not significantly affect herd sizes (Fig. 7). (Differences between drainages in the relative abundance of bulls and cows are not a response to wolf predation, because these differences have persisted

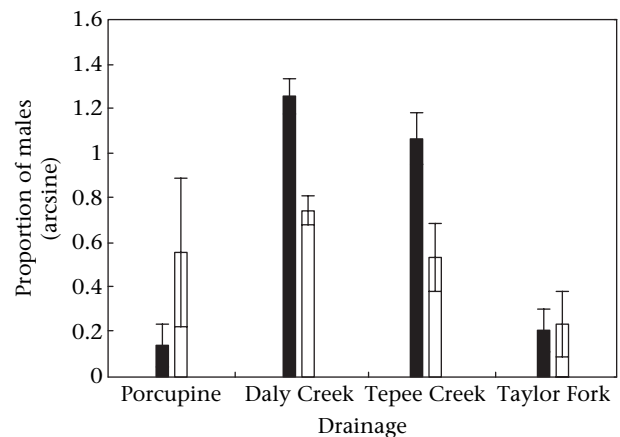


Figure 7. Changes in elk herd composition (proportion of males) in response to wolf presence in each of four drainage systems. □: wolves present; ■: wolves absent.

for decades in the absence of wolves (Brazda 1953; Peek & Lovaas 1967; Lovaas 1970)). The exodus of males from herds corresponds well with data on risk, because males were 6.3 times more likely than females to be killed.

Male movements do not entirely explain the reduction in herd size when wolves were present, because when we restricted our analysis of herd size to the number of cows and calves, herd size still dropped significantly when wolves were present (factorial ANOVA: herd size*distance to timber*wolf presence: $F_{3,982} = 5.43$, $P = 0.001$). When wolves were present, the number of females per herd was more than three times smaller at distances of 101–300 m from cover, and more than five times smaller at distances greater than 300 m.

Thus, changes in herd size are driven by two responses. First, females disaggregate in response to wolf presence. Second, males dissociate themselves from these smaller herds.

DISCUSSION

Our data do not support the generally accepted view that aggregation is an antipredator response. Treating herd size as a dependent variable that responds to variation in risk, aggregation into larger herds occurred in spatially risky areas only when predators were absent. When predators were present, elk dissociated into smaller herds in all locations, both safe and risky. Clearly, the formation of large herds was not a simple response to high levels of risk. We suggest that large herds probably formed as a response to the distribution of resources; that is, when temporal risk was low, elk converged on large open spaces for the grazing opportunities that these areas provided. This view is also supported by a review of elk diets in locations with and without human hunting, which revealed a significant increase in the proportion of woody plants in the diets of hunted populations, again suggesting that elk avoid open grasslands under conditions of high risk (D. Christianson & S. Creel, unpublished data).

The discussion above does not directly identify the benefit of splitting into smaller herds when wolves are present. In general, research on other species suggests that individuals in large groups are less vulnerable to predation (Krause & Ruxton 2002), which would not favour disaggregation under conditions of high risk, as elk showed. Dilution of risk always favours larger groups. Mechanisms such as collective detection or confusion of attackers are more variable, but often favour large prey groups. It is noteworthy that essentially all prior data on these issues come from studies in which the predator relies on stealth or surprise. Combinations that have been studied include fish preying on fish (Pitcher & Parrish 1993), birds preying on birds (Kenward 1978; Lima 1995a, b; Brown & Brown 1996) and mammals preyed on by a stalking mammal (Fitzgibbon 1990) or by a bird (Hoogland 1995). Attack rates are determined jointly by encounter rates and the probability that a predator will choose to hunt upon encountering prey. Prey group size can affect the decision to hunt (Fitzgibbon 1990; Uetz & Hieber 1994), but as Krause & Godin (1995, page 465) noted, 'very few

studies have investigated the choice of predators for prey groups of different sizes'. For cheetahs, *Acinonyx jubatus*, and lions, *Panthera leo*, hunting ungulates, attack probabilities decrease as herd size increases (van Orsdol 1984; Fitzgibbon & Lazarus 1995), but cichlids hunting guppies in tank experiments prefer to attack larger schools (Krause & Godin 1995). Several field studies have shown that large colonies of birds and mammals receive more attacks (Hoogland 1995; Brown & Brown 1996), but it is not clear whether this is due to increased conspicuousness (and thus higher encounter rates) or an increased probability of attack once detected.

For wildebeest and impala being hunted by wild dogs, large herds are significantly more likely to be encountered than small herds, and large herds are also more likely to be attacked once they have been located (Creel & Creel 2002). For elk, we suggest that splitting into smaller herds (together with moving into wooded areas, which limits the line of sight; unpublished data) probably serves to reduce the likelihood of being detected. Because coursing predators like wolves and wild dogs generally succeed in killing on a high proportion of their hunts (Creel & Creel 2002), selection on prey behaviour might favour mechanisms that reduce the likelihood of an attack occurring, in addition to (or instead of) mechanisms that operate once a hunt has begun.

Our conclusions differ from those of Hebblewhite & Pletscher (2002), who argued that elk form large herds in response to predation risk to benefit from risk dilution, even though large herds are encountered by wolves more often than expected by chance. In contrast, our data suggest that aggregation in the Gallatin elk herd is a response to low absolute risk, rather than a mechanism that dilutes high absolute risk. However, Hebblewhite & Pletscher (2002) also concluded that decreasing herd size could reduce the rate of encounter with wolves, and our data support this conclusion. Huggard (1993) also argued that large elk herds, particularly those with predictable locations, may have high rates of encounter with wolves, in part because wolves learn to revisit such herds.

Conceptually, it has long been recognized that encounter rates may be affected by prey group size, but most empirical studies of antipredator behaviour have focused on aspects of predator-prey interaction that occur once an encounter begins (such as collective detection and defence). Our data do not directly demonstrate that small herds were safer, but in combination with the data of Hebblewhite & Pletscher (2002), it is logical to conclude that disaggregation is an adaptation to reduce the probability of being detected by wolves. Like other recent studies, our results highlight the importance of empirical data on all stages of the predation sequence (see Introduction), including avoidance, predator detection, pursuit deterrence, collective defence, confusion effects and dilution of risk.

Why do our conclusions about the function of aggregation differ from those of Huggard (1993) and Hebblewhite & Pletscher (2002)? One possibility is that trade-offs between food and safety take different forms in different ecosystems. If food limitation differs among sites, or the intensity of predation differs, then it is likely that the

optimal trade-off between foraging and antipredator responses will also differ (Messier 1994; Abramsky et al. 2002; Blumstein & Daniel 2002; Heithaus & Dill 2002). In addition, differences in habitat type may alter the ways in which herd size affects detectability. In very open habitats, herds of any size are easily detected, and disaggregation may not be an effective method of avoiding encounters. General observations of elk around the Greater Yellowstone ecosystem suggest that herd sizes are indeed larger in sites that are very open, although we do not have systematic data on this issue. Finally, there are methodological differences between the studies. Huggard (1993) and Hebblewhite & Pletscher (2002) did not directly measure rates of encounter for elk and wolves. Instead, they used intersecting track lines as an index of encounter rates. Tracks will often intersect for animals that are not present simultaneously, so this method will be biased if group size is correlated with the amount of movement. We also did not measure rates of encounter: we used the presence/absence of wolves within a drainage as a measure of risk. The mean area of our four study drainages was 31.3 km², equivalent to a circle with a radius of 3.15 km. The fact that elk showed significant responses to the presence of wolves on this scale raises questions about the ways that prey assess risk, and the definitions of 'encounter' and 'detection'. Most early research on antipredator behaviour focused on ambush predators or experimentally simulated predation (Kenward 1978; Elgar 1989; Lima 1995a, b), and consequently, there is a tradition of viewing predator-prey encounters as events that occur quickly (seconds to minutes), on a small spatial scale (centimetres to metres). In parallel, predator detection is usually measured by an immediate response to the final rush of an ambush predator (or a simulated attack). These are certainly important aspects of the predation sequence, but the responses of elk in this study show that processes working on broader temporal and spatial scales are also important: elk responded quite strongly to the simple presence of wolves. On these broader scales, there are many cues that elk may use to assess their current level of risk. Predators or signs of their recent passage can be detected by sight, smell or hearing. Risk might be assessed by patterns of recent predator presence, or by the distribution of kill sites.

Finally, our results suggest caution in relating group size to indirect measures of risk. Our data relating herd size to distance from cover (Fig. 4) are very similar to many published data sets used to support the hypothesis that aggregation is a response to conditions of high risk. In this case, more detailed data on interactions between spatial and temporal variation in risk (Fig. 6) support the opposite conclusion, that aggregation is a foraging response that occurs only when the risk of predation is low.

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