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Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*

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In 1995, wolves *Canis lupus* were reintroduced into Yellowstone National Park, USA, where they began to prey on ungulate species. In response to this new predation risk by wolves, we predicted that the two main ungulate species, elk *Cervus elaphus* and bison *Bison bison*, should compensate by reducing their use of riskier open meadows and increasing their use of safer forest. Additionally we predicted that this shift in habitat use would result in reduced diet quality. We tested the first prediction by regressing the number of faecal groups in 10-m^2 sampling plots against distance from forest edges. To test the second prediction, we compared percent faecal nitrogen in elk and bison faeces between areas with and without wolves. We found a significant negative relationship between number of elk faecal groups and distance from forest edge in areas with wolves ($r^2 = 0.65$, $P = 0.001$), but we did not find a relationship between these two factors in areas without wolves. Mean percent faecal nitrogen in elk was significantly lower ($F_{(1,116)} = 13.9$, $P < 0.001$) in areas with wolves (1.7%, SE = 0.09, N = 40) than in wolf-free areas (2.1%, SE = 0.08, N = 80). For bison, we did not find any significant relationship between numbers of faeces and distance from forest edge nor in dietary nitrogen between wolf and wolf-free areas. We concluded that predation pressure from the reintroduced wolves was consistent with our prediction that elk shifted habitat use, thus lowering the quality of their diet. However, a similar change in use pattern and dietary quality of bison in response to wolf presence was not found.

Key words: bison, diet quality, elk, habitat use, predation risk, wolves

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Predation risk can influence habitat use patterns of a wide spectrum of prey species (e.g. Fraser & Cerri 1982, Edwards 1983, Kotler 1984, Cassini 1991, Kotler et al. 1991, Sweitzer 1996, Hilton et al. 1999). Predators establish a 'landscape of fear' (Laundré et al. 2001) whose topography is determined by the level of predation risk that prey face in different habitat types. When foraging in this landscape, prey will often shift their use from riskier to safer areas to reduce their predation risk (Mech 1977, Edwards 1983, Stephens & Peterson 1984, Altendorf et al. 2001). Because there is often a trade-off between selection of areas for security and areas of high-quality forage, it has been suggested that these habitat shifts result in a poorer diet quality (Edwards 1983, Sweitzer 1996). Based on optimal foraging theory, in the absence of predation risk prey should select the highest quality habitats when making their foraging decisions (Edwards 1983, Phelan & Baker 1992). Any shift in habitat use in response to predators would, by default, be a change to poorer quality habitat, resulting in decreased diet quality (Edwards 1983).

Some authors have previously reported a shift in habitat use when ungulates are faced with predation pressures from large predators such as wolves *Canis lupus* and pumas *Puma concolor* (Mech 1977, Edwards 1983, Stephens & Peterson 1984, Altendorf et al. 2001), and evidence of reduced diet quality has also been presented (Edwards 1983). However, most of these studies were of long-extant predator-prey systems. Although in these cases, it seems reasonable to assume a cause-and-effect relationship among predation risk, habitat use and diet quality in ungulates, it does not in itself constitute a critical test of this hypothesis.

The reintroduction of wolves into Yellowstone National Park, USA, in 1995 (Bangs & Fritts 1996) presented a unique opportunity to test the hypothesis that predation risk can alter habitat use patterns and consequently lead to poorer quality diets in ungulates. Prior to the release of wolves, the two most abundant ungulate species in the Park, adult elk *Cervus elaphus* and bison *Bison bison*, lived in a relatively predator-free environment. Predation by the only two other large carnivores, puma and grizzly bear *Ursus arctos* was either localized or limited to younger elk (Murphy 1997). Under these conditions, elk and bison could forage freely and grazed extensively in the open sagebrush *Artemisia* spp. communities (Collins & Urness 1983, Frank & McNaughton 1992, Singer & Renkin 1995). Once released, wolves quickly reestablished a landscape of fear in which female elk and bison rapidly responded with higher vigilance levels (Laundré et al. 2001). Additionally, wolves hunt primarily by chasing their prey so that they can attack vulnerable hind quarters, and their prey commonly flee into heavy cover for protection (Mech 1966, Smith et al. 2000, Mech et al. 2001). Consequently, open sagebrush meadows where wolves can readily outrun their prey should present the highest risk areas for elk and bison. Based on the hypothesis above, we would predict that the return of wolves to Yellowstone National Park should cause elk and bison to shift their habitat use closer to the safer forest areas (Mech 1966, Carbyn 1983, Stephens & Peterson 1984). Concurrent with this shift should be a reduction of diet quality as animals move to safer, but poorer quality habitats. If we find such changes, the most likely explanation for them is the increased predation risk from wolves, whereas the lack of these changes would refute the hypothesis.

To test the hypothesis, we first tested the prediction that elk and bison should decrease their use of open meadow areas and increase their use of areas closer to and along forest edges. Based on the optimal foraging model (MacArthur & Pianka 1966, Charnov 1976, Pyke et al. 1977), our assumption was that before the wolf reintroduction the two species were selecting the highest quality habitats for foraging. Consequently, any shift in area use, by default, should be to poorer quality forage and thus, the second prediction we tested was that diet quality of elk and bison should decline in response to the wolf reintroduction. We tested these two predictions by comparing habitat use patterns and diet quality of elk and bison exposed to wolf predation and animals still living in wolf-free areas within Yellowstone National Park.

Methods

Our study was conducted in Yellowstone National Park which consists of extensive areas of varied forested and open grassland habitat. We collected data on habitat use and diet quality in the same areas where we made our behavioural observations (Laundré et al. 2001). The area exposed to predation by wolves was the Lamar Valley (Fig. 1). Wolf-free areas were selected based on data

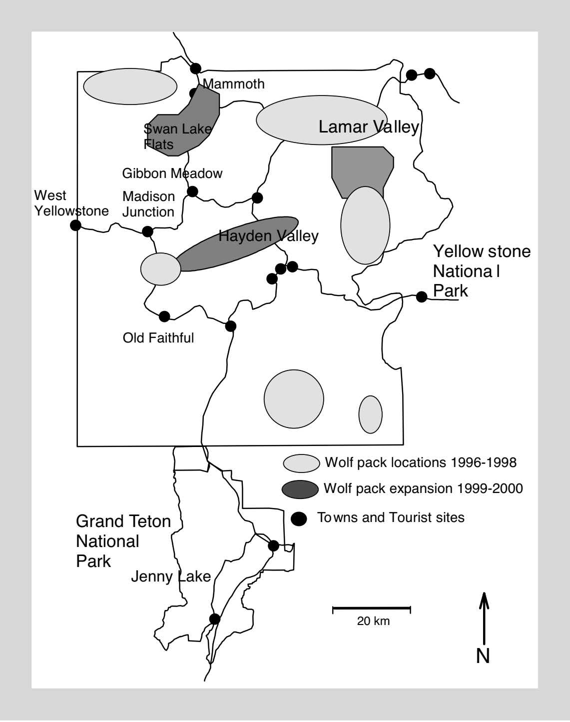

Figure 1. Location of study sites within Yellowstone and Grand Teton National Parks. Areas where wolves occurred during the first three years of the study period (1996-1998; ●) and their expansion into other areas by 2000 (●) are indicated.

available on the occurrence of the wolf packs within the Park (J.C. Halfpenny & D. Thompson, unpubl. data). Primary wolf-free areas within Yellowstone National Park were Hayden Valley and Swan Lake Flat (see Fig. 1). During the first year of data collection (1998) we also included data from the Jenny Lake area in Grand Teton National Park, > 100 km south of the Yellowstone study areas. These data provided an external wolf-free control to compare with the Yellowstone data. All the observation areas were similar in that they consisted of large (> 1,000 ha) open meadows boarded by dense coniferous forests. Additionally, wolves began to move into some of the wolf-free areas, and by the end of the study in 2000 they had established themselves in the Hayden Valley area. This enabled us to compare the distribution of elk pellet groups and bison flops in the Hayden Valley before and after wolves arrived.

We tested for habitat shifts by elk and bison by first dividing the length of the forest edges (≈1.5-2.0 km determined from topographic maps) into 50-m intervals and then randomly selecting 10 sample lines in each of the four areas. Sample lines were never closer to each other than 50 m and each extended perpendicular to the forest edge from 50 m within the forest to 500 m into the open meadows. Every 50 m along these lines we established sample points and counted the number of individual animal faecal droppings, pellet groups of elk and flops of bison, within 10-m^2 sample plots placed on these points. If elk and bison shift their habitat use in response to predation risk by wolves, we predicted a negative relationship between densities of elk faecal groups and bison flops and distance from the forest edge in the Lamar Valley and, in the year 2000, the Hayden Valley. We should not, however, see this relationship in Swan Lake Flat, Grand Teton Park, nor, prior to 2000, in the Hayden Valley. To test these predictions, we used a simple linear regression model. The null hypothesis was that the slope of the regression line would not differ from zero.

To test for diet quality changes, we used percent faecal nitrogen (FN) levels. Faecal protein is calculated from FN, and FN is generally considered a reliable indicator of diet quality in grazing ungulates (Leslie & Starkey 1985, Osborn & Jenks 1998, Osborn & Ginnett 2001). We collected elk and bison faecal samples in July of 1998 and 1999 from the 10-m^2 sample plots while we were making the density estimates. From the samples collected, we randomly selected 15-20 samples per year for each species in the three areas of Yellowstone in 1998-2000 and in Grand Teton Park in 1998. The Range Science Nutritional Analysis Laboratory at Colorado State University, Fort Collins analyzed the samples for nitrogen. Laboratory personnel calculated FN in each sample using a LECO CHN - 1000 Carbon Hydrogen Nitrogen Analyzer. To test if diet quality differed between areas with and without wolves, we compared the estimates from the Lamar Valley with the combined estimates from wolf-free areas in Yellowstone (Hayden Valley and Swan Lake Flat combined) and Grand Teton National Park. We used a one-way analysis of variance statistical design with the null hypothesis of no difference in average FN levels among the three areas. As FN was expressed in percents, we arcsine transformed the data before conducting the tests. All statistical tests were run using Sigmastat soft-

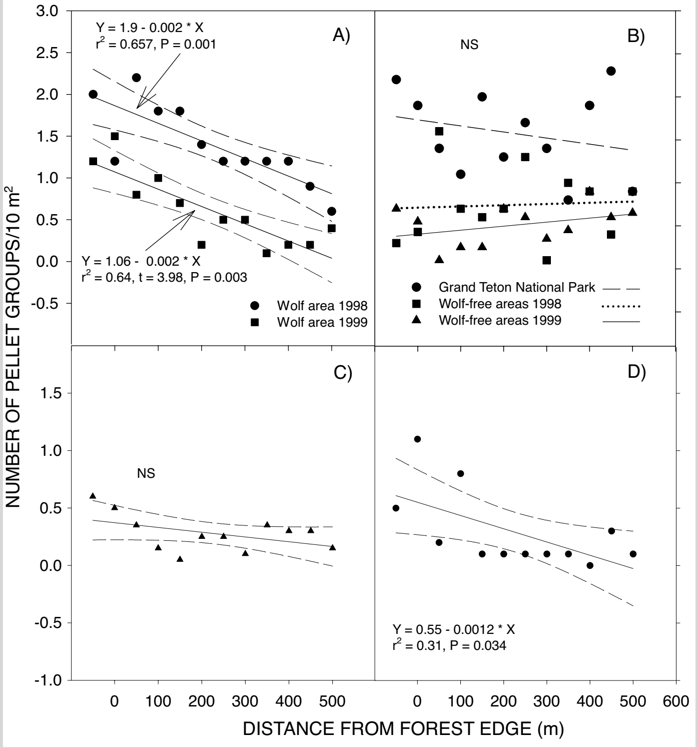

Figure 2. Relationships of mean number of elk pellet groups per 10 m^2 to distance from forest edges for the areas with (A) and without wolves (B), respectively. Data for the Hayden Valley before (C; 1998-1999) and after (D) wolves established themselves in the area are given. Each point is the mean from 10 random transects from the respective areas.

ware (Quinton et al. 1995) with a significance level of $P \leq 0.05$. All means are given ± standard error.

Results

For elk in the Lamar Valley, where wolves were present, the relationship between pellet group density and distance from the forest edge was significant and negative for 1998 and 1999 (Fig. 2A), and the slope of the regression lines did not differ between years, but the intercept of the regression line was significantly lower in 1999 than in 1998. In the wolf-free areas of Yellowstone in 1998 and 1999 and in Grand Teton Park in 1998, there was no significant relationship between pellet group density and distance from the forest edge (Fig. 2B). In the Hayden Valley there was no relationship between pellet density and distance for the combined data of 1998 and 1999 before the wolves arrived (Fig. 2C). However, in 2000, after wolves had established themselves, we found a significant and negative relationship (Fig. 2D).

For bison, we found no relationship between density of flops and distance from the forest edge in neither the Lamar Valley (wolf area) nor the wolf-free areas in 1998 (Fig. 3A) nor in 1999 (Fig. 3B). For the Hayden Valley, there also was no relationship between flop density and distance from forest edge in any of the three years (1998-2000).

Relative to diets, the FN of elk exposed to wolves in the Lamar valley was significantly lower than in the wolf-free areas of Yellowstone in 1998 and 1999 (Fig. 4A). FN for elk from the Lamar Valley in 1998 was also significantly lower than for elk from Grand Teton National Park (see Fig. 4A). In contrast, there was no difference in FN of elk from the wolf-free areas of Yellowstone Park and Grand Teton Park (see Fig. 4A). Bison FN did not differ between wolf and wolf-free areas of Yellowstone nor from Grand Teton Park (Fig. 4B).

Discussion

Other scientists have attributed shifts in habitat use patterns by ungulates to predation pressure by wolves (Mech 1977, Edwards 1983, Stephens & Peterson 1984), and Edwards (1983) predicted that such shifts could lead to poorer diet quality. However, as mentioned, it can be difficult to confirm such cause-and-effect relationships in long-extant predator-prey systems. The results of our study, however, provide three lines of direct evidence that the reintroduction of wolves caused a shift in habitat use by elk. First, within three years after the release

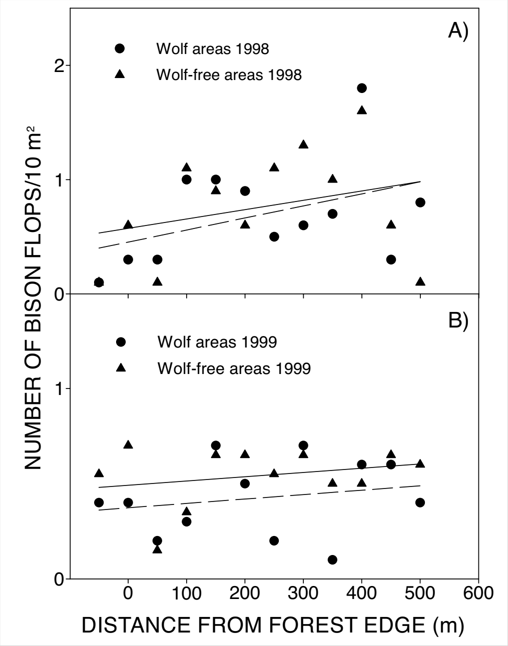

Figure 3. Relationships of mean number of bison flops per 10 m^2 to distance from forest edges for the areas with and without wolves in 1998 (A) and 1999 (B). Each point is the mean from 10 random transects from the respective areas.

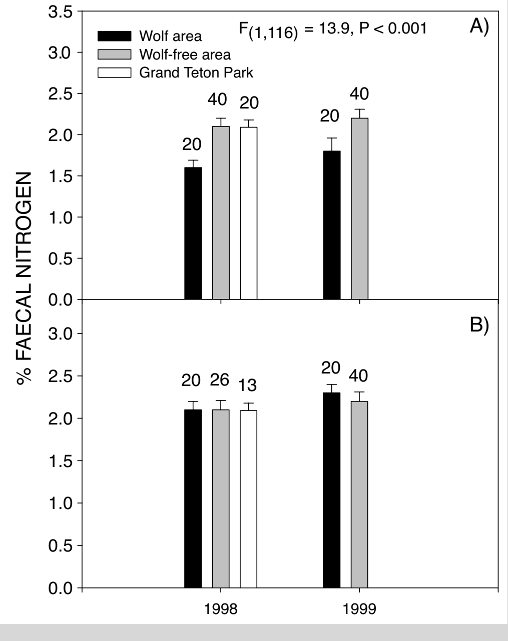

Figure 4. Percent faecal nitrogen for elk (A) and bison (B) from wolf and wolf-free areas for 1998 and 1999. Sample sizes are indicated above the bars.

of wolves, elk in the Lamar Valley were using forest edge areas more than open meadows, although elk preferred open meadow areas before the release (Frank & McNaughton 1992, Singer & Renkin 1995). Second, we did not see this pattern in the wolf-free areas of Yellowstone nor in Grand Teton Park, the latter being > 100 km from the Yellowstone study areas. The results from such diverse areas indicate that elk were using the edge areas more in the Lamar Valley in response to predation pressure from wolves rather than it being an intrinsic use pattern for that area. Third, elk increased their use of forest edges in the Hayden Valley a year after wolves established themselves there, a pattern that we did not find in previous years.

In addition to the shift in habitat use, we also found that elk in the Lamar Valley, as predicted, had poorer quality diets than elk in wolf-free areas only 30 km away. The elk in the area without wolves, meanwhile, had FN levels similar to elk from Grand Teton Park, again > 100 km away. Additionally, the FN levels we found in the Lamar Valley (1.7%) reflect extremely poor dietary nitrogen (DN) intakes (Mould & Robbins 1981, Osborn & Ginnett 2001). It is possible that the poorer diets in the Lamar Valley reflected a lower quality forage normally being available than in other parts of the Park. However, we reject this possibility because Frank & McNaughton (1992) reported percent nitrogen levels of ≈ 2.5% for dominant grasses in the Lamar Valley. This level of DN generally correlates to a FN level of 2.0-2.2% for ungulates (Mould & Robbins 1981, Leslie & Starkey 1985, Osborn & Ginnett 2001). In fact, bison in the Lamar Valley, which did not shift habitat use, maintained FN levels of 2.2% which were equal to FN levels of bison in other areas (see Fig. 4B). All this supports our conclusion that the poor diets of elk in the Lamar Valley are a result of their shifting habitat use in response to the wolves.

In contrast to the data for elk, the data for bison did not support any of our predictions. In some areas, bison are the principal prey of wolves (Carbyn & Trottier 1987). However, in Yellowstone National Park, elk are the main prey of wolves and during our study, wolves did not prey extensively on bison (Smith et al. 2000, Mech et al. 2001). Probably the predation risk to bison was insufficient to cause the predicted shifts in habitat use and a corresponding decline in diet quality. We did notice that vigilance in bison females initially increased in response to wolves but in most cases returned to its original levels (Laundré et al. 2001). This also indicates that predation risk from wolves is still relatively low for bison and would not be a sufficient driving force to cause a habitat shift.

In summary, the data for elk support the cause-and-effect relationships inferred in studies of long-extant predator-prey systems and clearly show that predation risk alone can cause a large ungulate to shift its habitat use to safer areas. Additionally, animals make these shifts at the expense of diet quality. Consequently, predation risk can have a cascading effect on nutritional status of prey individuals; not only does it reduce foraging efficiency of individuals, via increased vigilance, but it further restricts foraging efforts to lower quality areas. Others (e.g. Edwards 1983) have predicted that the subsequent decrease in diet quality should result in a poorer nutritional state, lower survival rates, and lower reproductive success. For elk in Yellowstone, this could mean a reduction in numbers to a more sustainable population size. Additionally, as elk can have a major impact on the open sagebrush community (Singer & Renkin 1995), we originally predicted that their reduced use of this habitat could result in significant changes in the vegetal makeup of this community. Recent work in the Lamar Valley of Yellowstone demonstrating an increase in cottonwood *Populus* spp. recovery supports this prediction (Ripple & Beschta 2003). Consequently, foraging in the landscape of fear can have far reaching impacts on the population level of ungulate prey species (Edwards 1983) and on the diversity of the plant communities that support them.

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