Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A.

John W. Laundré, Lucina Hernández, and Kelly B. Altendorf

Abstract: The elk or wapiti (*Cervus elaphus*) and bison (*Bison bison*) of Yellowstone National Park have lived in an environment free of wolves (*Canis lupus*) for the last 50 years. In the winter of 1994–1995, wolves were reintroduced into parts of Yellowstone National Park. Foraging theory predicts that elk and bison would respond to this threat by increasing their vigilance levels. We tested this prediction by comparing vigilance levels of elk and bison in areas with wolves with those of elk still in "wolf-free" zones of the Park. Male elk and bison showed no response to the reintroduction of wolves, maintaining the lowest levels of vigilance throughout the study (≈12 and 7% of the time was spent vigilant, respectively). Female elk and bison showed significantly higher vigilance levels in areas with wolves than in areas without wolves. The highest vigilance level (47.5 ± 4.1%; mean ± SE) was seen by the second year for female elk with calves in the areas with wolves and was maintained during the subsequent 3 years of the study. As wolves expanded into non-wolf areas, female elk with and without calves in these areas gradually increased their vigilance levels from initially 20.1 ± 3.5 and 11.5 ± 0.9% to 43.0 ± 5.9 and 30.5 ± 2.8% by the fifth year of the study, respectively. We discuss the possible reasons for the differences seen among the social groups. We suggest that these behavioural responses to the presence of wolves may have more far-reaching consequences for elk and bison ecology than the actual killing of individuals by wolves.

Resumé : Durant ces 50 dernières années, le Wapiti (*Cervus elaphus*) et le Bison (*Bison bison*) du parc national de Yellowstone ont vécu dans un environnement d'où le Loup (*Canis lupus*) était absent. Les loups furent réintroduits dans certaines parties du parc pendant l'hiver 1994–1995. La théorie admise prédit que le Wapiti et le bison devraient répondre à cette menace en augmentant leurs niveaux de vigilance. Nous avons testé cette prédiction en comparant les niveaux de vigilance des Wapitis et des bisons vivant en zones avec loups avec ceux des Wapitis vivant en zones « sans loups ». Les Wapitis et bisons mâles n'ont montré aucune réponse à la réintroduction du loup, maintenant leur vigilance au niveau le plus bas rencontré pendant l'étude (≈12 et 7 % du temps de vigilance). Les Wapitis et bisons femelles ont montré une vigilance significativement plus importante dans les zones avec loups que dans les zones sans loups. Nous avons rencontré le niveau de vigilance le plus haut (47,5 ± 4,1 %; moyenne ± erreur type) dès la 2^{e} année dans la zone avec loups chez les Wapitis femelles avec des petits. Celles-ci ont maintenu ce niveau durant les 3 années suivantes de l'étude. À mesure que les loup sont gagné les zones qu'ils n'occupaient pas au début de l'étude, les niveaux de vigilance des Wapitis femelles vivant dans ces zones, avec ou sans petit, peu à peu, de leurs valeurs initiales respectives de 20,1 ± 3,5 et 11,5 ± 0,9 % à des valeurs de 43,0 ± 5,9 et 30,5 ± 2,8 % atteintes au cours de la 5^{e} année de l'étude. Nous discutons ici des raisons qui peuvent expliquer les différences observées entre les groupes sociaux. Nous croyons que ces réactions comportementales liées à la présence des loups affectent beaucoup plus l'écologie de le Wapiti et du bison que la perte directe des individus chassés par les loups.

Introduction

For the past 50 years, elk or wapiti (*Cervus elaphus*) and bison (*Bison bison*) of Yellowstone National Park, Wyoming, U.S.A., have lived in an environment free of wolves (*Canis lupus*) (Meagher 1973; Weaver 1978; J.W. Laundré, unpublished data). Principal predation risks were from grizzly bears (*Ursus horribilus*), which prey primarily on elk in spring and mostly on young of the year. Coyotes (*Canis latrans*) threaten only the very young calves of elk, and mountain lion (*Puma concolor*) predation occurs primarily in more mountainous areas. However, in winter 1994–1995, 20 wolves were reintroduced into the Park, where they formed several packs (J.C. Halfpenny and D. Thompson, unpublished data). The

Received January 8, 2001. Accepted May 16, 2001. Published on the NRC Research Press Web site at http://cjz.nrc.ca on July 20, 2001.

J.W. Laundré.[1,2] Instituto de Ecología, A.C., Chihuahua Regional Center, Km 33.3 Carretera Chihuahua-Ojinaga, 32900, Aldama, Chihuahua, Mexico, and Department of Biological Sciences, Idaho State University, ID 83209, U.S.A.
L. Hernández. Instituto de Ecología, A.C., Chihuahua Regional Center, Km 33.3 Carretera Chihuahua-Ojinaga, 32900, Aldama, Chihuahua, Mexico.
K.B. Altendorf. 4242 N 32nd Street, No. 5, Phoenix, AZ 85018, U.S.A.

[1] Corresponding author (e-mail: launjohn@isu.edu).

[2] Address for correspondence: Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, U.S.A.

DOI: 10.1139/cjz-79-8-1401

structure of wolf packs makes wolves effective predators on adult elk, and current studies indicate that they can pose a predation threat to bison, especially to females with calves (Carbyn and Trottier 1987). This reintroduction, then, represented a significant increase in predation risk to elk and bison. Consequently, it is of interest to determine the impacts of this reintroduction on these two species.

Aside from the obvious impact of wolves directly killing individuals (lethal effects), there is growing evidence that predators can have significant nonlethal impacts on their prey (Kotler and Holt 1989; Brown and Alkon 1990; Brown 1992). Predators scare their prey (Brown et al. 1999), and not just when they are about to attack. Even in the absence of imminent attack, prey should maintain a baseline level of apprehension because of the constant possibility or risk of predation (Brown et al. 1999). Additionally, this baseline risk can vary over space and time, e.g., risky versus safe habitats or times of day (Brown and Alkon 1990; Brown 1992; Kotler et al. 1994; Brown et al. 1999). How, then, do animals respond to these changing levels of risk?

Foraging theory predicts that animals will sacrifice feeding effort to reduce this predation risk (Sih 1980; Kotler et al. 1994; Lima and Dill 1990). They do so by either reducing their time spent foraging and (or) increasing their level of vigilance while foraging in riskier areas (Brown 1999). Large ungulate species and their predators are behaviorally sophisticated animals and should rely heavily on behavioral responses, i.e., vigilance, to nonlethal predation risk (Brown et al. 1999). Indeed, various authors (Underwood 1982; Lagory 1986; Scheel 1993; Bednekoff and Ritter 1994; Molvar and Bowyer 1994) have shown this to be the case for a variety of ungulate species. As predicted, when animals are in riskier habitat or even in riskier areas (edges) within a group, they respond with increased vigilance. Thus, data suggest that as animals move about the physical landscape they are constantly adjusting their behavior in response to changing levels of predation risk. We can envision, then, that prey individuals live in a second landscape, one with differing levels of risk or fear of predation: a “landscape of fear.” The topographic “hills” and “valleys” of this landscape represent the differing base levels of predation risk, e.g., edges versus open areas. Further, the baseline topography of this landscape for a specific prey species will depend on its particular predator or predators and factors such as encounter rate with a predator (e.g., group edges), predator lethality (e.g., dense habitat), and the effectiveness of vigilance (e.g., group vigilance) (Brown 1999; Brown et al. 1999).

What happens to this landscape, however, when a new predator is introduced, or in this case reintroduced? Based on foraging theory, a reasonable prediction is that base vigilance levels of elk and bison would increase initially in response to the added predation risk posed by wolves. However, because an animal cannot devote all its time to vigilance, we further predict that over time, vigilance would eventually stabilize at some higher level. This level would represent the new equilibrium between increased predation risk and an animal’s foraging needs. It can be asked what that new level will be, or, basically, how much will elk and bison trade foraging effort for safety in the face of an increase in predation risk?

With regard to how prey may respond initially to a new predator, Hunter and Skinner (1998) did find significant increases in vigilance by impala (*Aepyceros melampus*) and wildebeest (*Connochaetes taurinus*) within 9–10 months after reintroductions of lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*) into their study area. Their study, however, was not long enough to test if vigilance eventually stabilized and at what level (Hunter and Skinner 1998). Thus, the question of exactly how much foraging effort a prey will sacrifice in the face of an increase in predation risk remains unanswered.

The release of wolves into Yellowstone National Park provided a similar design to that of Hunter and Skinner (1998) for testing the two predictions. Park personnel released 20 wolves, mainly in the Lamar Valley region (Fig. 1), where wolves quickly established territories in different areas of the valley (Fig. 1). Consequently, during the first few years, some of the Park’s elk and bison were exposed to wolf predation, while others in different areas still lived in a wolf-free environment and could act as a control. In subsequent years, wolf numbers increased (estimated to be >100 by 2000; J.C. Halfpenny and D. Thompson, unpublished data) and they expanded into the wolf-free areas. This expansion allowed us to make comparisons between areas before and after the wolves arrived and these initial wolf-free areas. We tested the first prediction, that vigilance would increase in response to the presence of wolves, by comparing the percentage of time that focal animals in wolf and non-wolf areas were vigilant (head up surveying area; Berger and Cunningham 1994; Hunter and Skinner 1998) during 30-min (elk) and 20-min (bison) sample blocks. To test the second prediction that vigilance would eventually stabilize, we collected data annually for the first 5 years after the reintroduction.

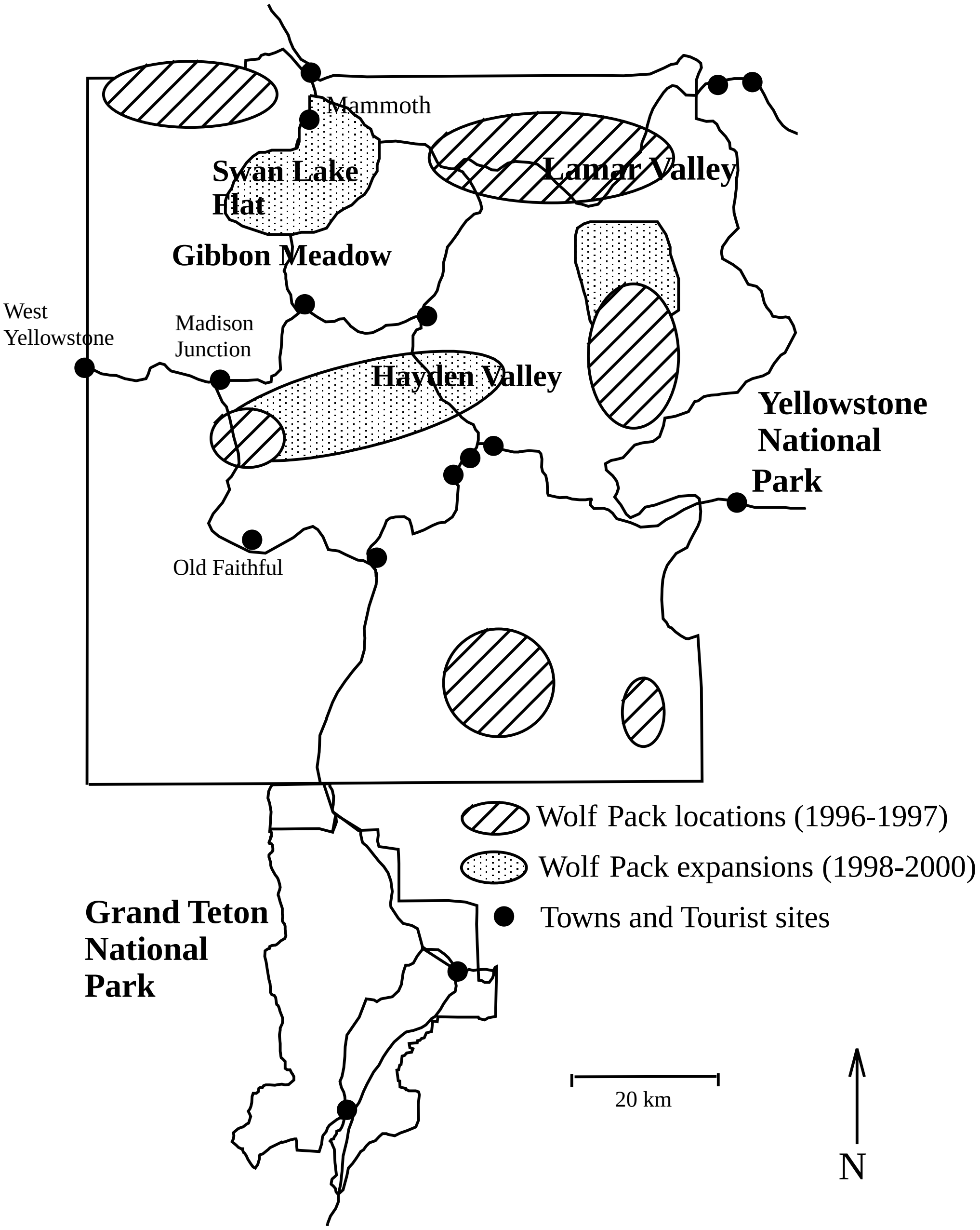
The results of testing these two predictions could help determine the short- and long-term nonlethal impacts of wolves on elk and bison. Additionally, they could further our understanding of the role played by predation risk in the foraging strategies of large ungulate prey species.

Methods

Yellowstone National Park is an extensive area of forested and open grassland habitat. Because of the long history of the park, elk and bison can be observed readily in most areas of the Park along the several roads that connect the various tourist attractions. Observations were made of elk and bison exposed to predation by wolves in the Lamar Valley (Fig. 1). Wolf-free areas were selected on the basis of data provided by the Park Service on the occurrence of the wolf packs within the Park. Primary wolf-free areas were near Hayden Valley, Swan Lake Flat, and Gibbon Meadows (Fig. 1).

We made our observations from existing paved roads within each of these areas. We drove along the roads until we located elk or bison actively feeding. We then stopped along the road to make our observations. Distances of animals from the road varied from <20 m to ≈2.0 km. For animals close to the road, we parked no less than 50 m distant to insure that we were not affecting their behavior. If there was any indication that our presence or the presence of others was having an effect, we discarded these data. For animals farther from the roads, we made our observations with the aid of variable-power spotting scopes. A given observation bout consisted of first selecting an individual animal that was actively feeding. For small groups of animals (<10), we stayed long enough to observe all of the animals. For larger groups, we attempted to balance our observation of animals in all locations (center or periphery) of the group. We monitored the chosen animal until it stopped feeding

Fig. 1. Locations of study sites within Yellowstone National Park. Areas where wolves (*Canis lupus*) occurred during the first 2 years of the study period (1996–1997) and their expansion into other areas by 2000 are indicated.



and lay down, or for a maximum of 30 min for elk and 20 min for bison. We discarded the data when an animal lay down for <20 min for elk or <15 min for bison after initiation of observations. Analysis of preliminary field data indicated that 20–30 min was sufficient time to obtain a stable running mean of the percentage of time spent vigilant for elk and 15–20 min was adequate for bison. During the period of observation, we maintained visual contact with the animal continuously and recorded the starting and ending times when an animal raised its head to survey. When an animal raised its head, we distinguished between whether it was standing and looking around (vigilant) (Hunter and Skinner 1998), moving to another feeding spot, or engaged in some maintenance behavior (grooming, nursing a calf, etc.). From such observations, we calculated the time (in minutes) spent vigilant, feeding, and in other behaviors by summing all blocks spent performing each behavior. To test the two predictions, we only used the time spent vigilant; however, we also analyzed the time spent feeding to determine if changes in vigilance level were made at the expense of feeding.

Predation risk is potentially affected by a variety of factors, such as the types of predator present, time of year/day, group size, or distance of individuals from forests. We considered the type of alternative predators (grizzly bears, coyotes) to be standardized simply because they were regularly seen in all of our observation areas. Although preliminary data indicated few changes in behavior over spring–summer (unpublished data), we minimized possible variation due to seasonal effects by concentrating our sampling in late May – early June. This time was chosen because it is when the elk and bison are concentrated in the Lamar Valley, and if animals are going to show a behavioral response to the presence of wolves, it should be highest during this period. Possible effects of time of day, herd size, and location (distance from roads/forests) were reduced by stratifying the samples a priori to include balanced samples from each of these categories for both wolf and non-wolf areas. Because of all these considerations, it was felt that our design should adequately test the main treatment: absence and presence of wolves. However, as others have reported that herd size can have a significant influence on vigilance levels (Elgar 1989; Bednekoff and Ritter 1994), we did test for this effect to determine if it might be biasing our estimates.

Data collection was limited to adult animals, and target sample sizes per year were 20 males, 20 females with young, and 20 females without young in each of the areas with and without wolves. Because predator lethality and encounter rates may vary among different social classes, division into social classes allowed us to test the separate responses of each group. Analyses of running means of the percentage of time spent vigilant for all social groups indicated that the means stabilized around 15 samples, so 20 samples were considered adequate to test for differences. Observations on elk were made in 1996–2000. Bison were observed in 1998–2000. Within a given sample year and area, an effort was made not to resample any given animal. Normally, we were able to distinguish among individuals in small groups according to their location within the group. For larger groups, we were confident we did not resample given animals during the same day. It is possible that we resampled the same animals on subsequent days, but because of the group size we felt that the probability was low.

Although the exact amount of time (in minutes) animals spent vigilant was recorded, the percentage of time spent vigilant during the observation block was analyzed. Percentage was used to allow comparisons of unequal time blocks. Statistical comparisons were of the arcsine-transformed percentages of time animals spent vigilant in areas with and without wolves. The statistical null hypothesis was that no difference existed in percentages of time spent vigilant between areas (wolves vs. no wolves), among social categories (males vs. females with calves vs. females without calves), and among years. We used SigmaStat® version 2.0 (Quinton et al. 1995) software for all our statistical calculations.

Results

Group sizes for elk and bison ranged from one individual to several hundred individuals. When we tested for group-size effects on vigilance rates, we found no correlation for any of the three social classes of elk or bison. Based on these results, we did not adjust for group size in our further analyzes.

For elk, results of three-way analysis of variance tests indicated significant differences in the three levels: social status ($F_{[2,639]}$ = 104.2, $P < 0.001$), exposure to wolves ($F_{[1,369]}$ = 20.6, $P < 0.001$), and year ($F_{[4,639]}$ F = 8.5, $P < 0.001$). There were also significant interactions: year × exposure (P = 0.002), year × status ($P < 0.001$), status × exposure (P = 0.002), and year × status × exposure ($P < 0.001$). Based on the results of the multiple comparisons, we determined the following patterns of annual changes in vigilance levels of each social class and interpreted them relative to our two predictions of increasing (No. 1) but eventually stabilizing (No. 2) vigilance levels in response to increased predation risk.

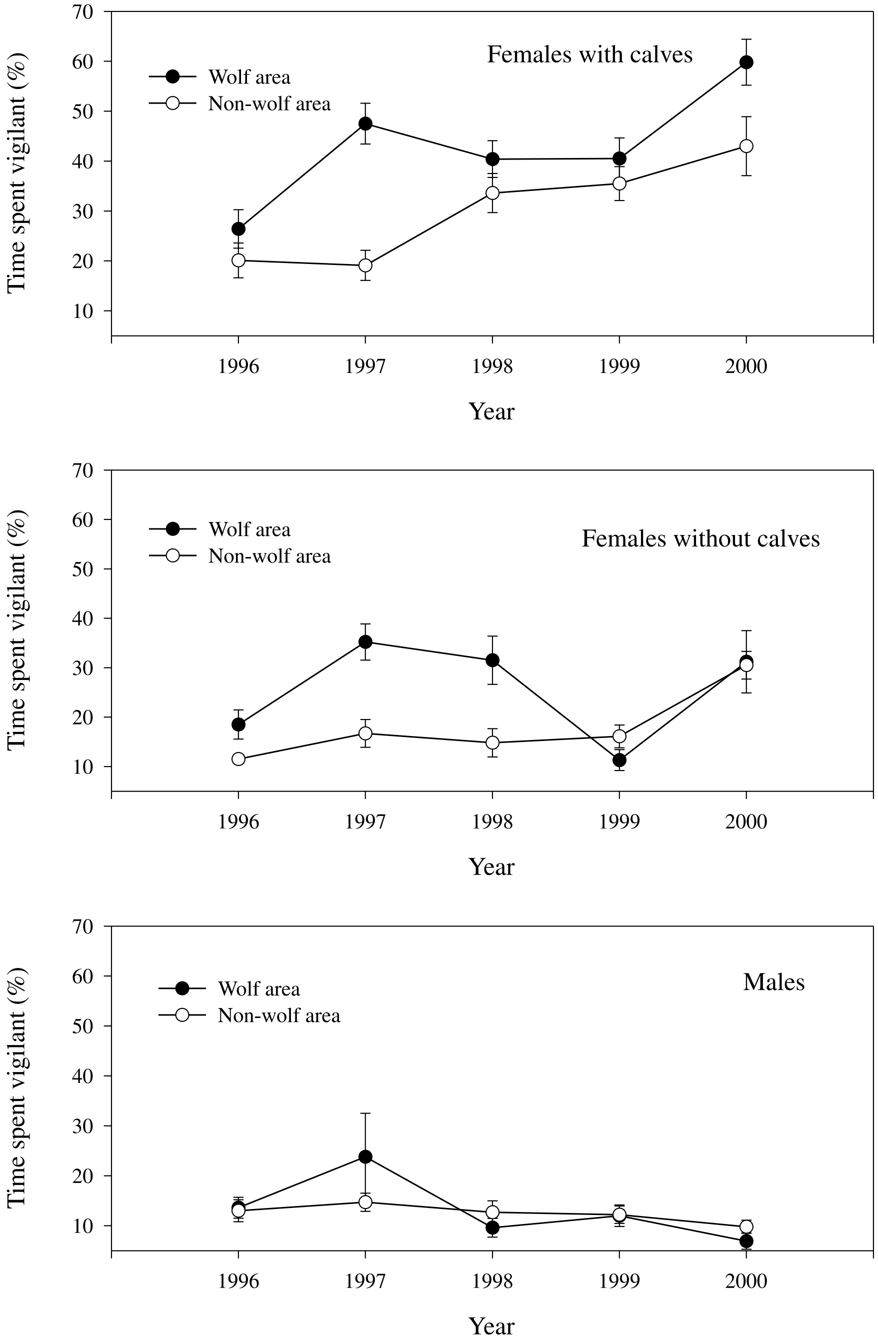
The clearest pattern seen was for males (Fig. 2). Male vigilance levels averaged 12.8% (SE = 1.3; n = 10) and did not differ between wolf and non-wolf areas or over years. The higher vigilance levels seen in males in the wolf areas in 1997 may be attributed to the extremely small sample (6) for that year. Thus, the data for males did not support our initial predictions. Females without calves in the areas without wolves also maintained vigilance levels similar to those of males over the first 4 years (11.5–16.7%) but significantly increased their vigilance by the fifth year (30.5 ± 2.8%; Fig. 2). Their counterparts in the areas with wolves, however, had a higher vigilance level (18.5 ± 2.9%) the first year after the reintroduction (Fig. 2) and it increased to 35.2 ± 3.6% by the second year, then stabilized for 2 of the subsequent 3 years (Fig. 2). Thus, the data from females without calves supported the two predictions. The most responsive social group overall was the females with calves (Fig. 2). This group had a significantly higher vigilance level than the other two groups in the first year, even in areas without wolves (20.1 ± 3.5%). In these areas they maintained that vigilance level through the second year (19.1 ± 3.0%). By the third year, wolves had moved into most of the areas previously without wolves (J.C. Halfpenny and D. Thompson, unpublished data) and, as predicted, vigilance increased to 33.6 ± 3.4% and eventually to 43.0 ± 5.9% by the fifth year. In the areas with wolves, females with calves had higher vigilance levels by the first year after the reintroduction (26.4 ± 3.8%), as predicted. Levels increased significantly by the second year (47.5 ± 4.1%) but then, as predicted, stabilized. In all cases where there was an increase in vigilance, we found a corresponding decline in the percentage of time spent foraging (Fig. 3).

With regard to bison, we did not collect data for the first 2 years after the wolf reintroduction; however, for the third, fourth, and fifth years after reintroduction, we did find significant differences in vigilance levels among social classes ($F_{[2,313]}$ = 13.3, $P < 0.001$), between wolf and non-wolf areas ($F_{[1,313]}$ = 7.1, P = 0.008), and among years ($F_{[2,313]}$ = 4.7, P = 0.009) (Fig. 4). We also found significant interactions for year × exposure (P = 0.048), year × status (P = 0.03), status × exposure (P = 0.001), and year × status × exposure (P = 0.002). When we examined the data for bison, we saw a pattern similar to that of the elk. Over the 3 years, contrary to the prediction, male bison maintained equal and low vigilance rates in the areas with and without wolves (5.0 ± 0.8 vs. 8.0 ± 0.9%). Females without calves in the areas without wolves had similar vigilance levels (9.6 ± 2.0%) to males. Data from females without calves in areas with wolves initially supported the predictions, their vigilance level the first year being 15.6 ± 2.6%, but their vigilance levels declined to 5.7–6.8% during the next 2 years (Fig. 4). Females with calves in areas without wolves had vigilance levels similar to those of males and females without calves (9.1 ± 1.4% over 3 years) (Fig. 4). As predicted, females with calves in areas with wolves had the highest vigilance level all 3 years: 18.9 ± 2.5% (Fig. 4). As with the elk, increases in vigilance levels were accompanied by corresponding decreases in foraging (Fig. 4).

Discussion

Although various authors have reported a negative correlation between vigilance levels and group size (group-size effect) in ungulates (Lagory 1986; Elgar 1989; Bednekoff and Ritter 1994; Hunter and Skinner 1998), this effect was not found in our study. The idea of the group-size effect is an appealing one: individuals in a group cooperating to gain the

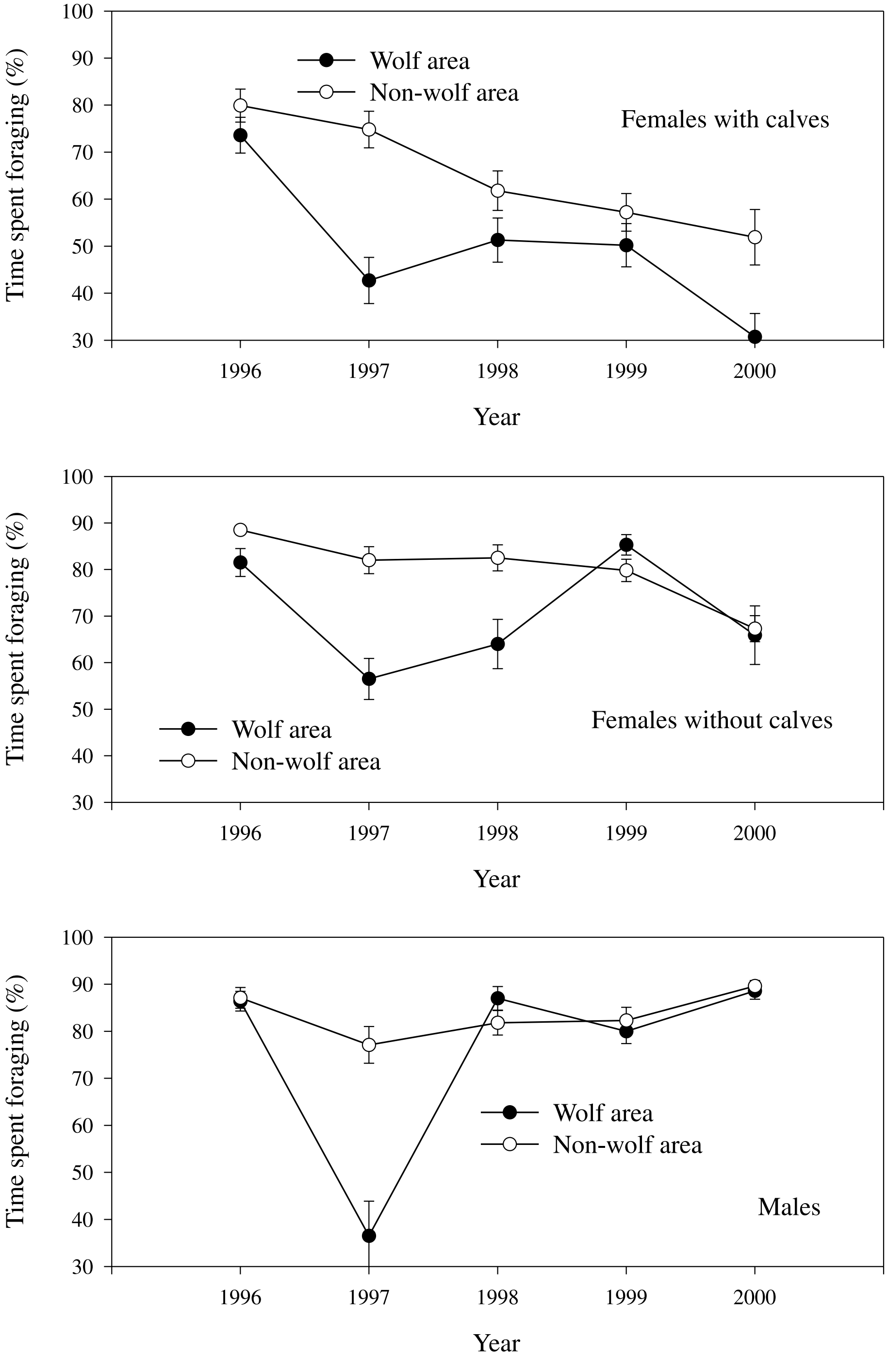
Fig. 2. Changes in the percentage of time spent vigilant by elk (*Cervus elaphus*) in the different social classes during the 5 sampling years in the areas with and without wolves. Vertical bars show the standard error.



common benefit of a reduced need for vigilance. In reality, however, the empirical evidence for such cooperation is not convincing. Elgar (1989, p. 28), in his review of field evidence obtained from birds and mammals, concluded that most correlations were weak, with high amounts of unexplained variation, and thus "failed to provide convincing evidence that individuals …alter their scanning rates as a direct result of changes in group size." Additionally, Lima (1995) found no support for the two essential elements of the group-size effect: collective detection and behavioral monitoring. In our study, the lack of a negative correlation in either species and in the three social groups seems to support the suggestion that a reevaluation of the group-size effect is in order (Lima 1995).

Regarding our first prediction, results from our study concur with those of Hunter and Skinner (1998), supporting the hypothesis that when faced with the added predation risk, elk and bison would, in general, initially respond with increased vigilance. Also, as seen in Figs. 3 and 4, this increase in vigilance occurs at the expense of foraging effort. This prediction was supported not only by the initial difference in vigilance levels seen in females in the first year but

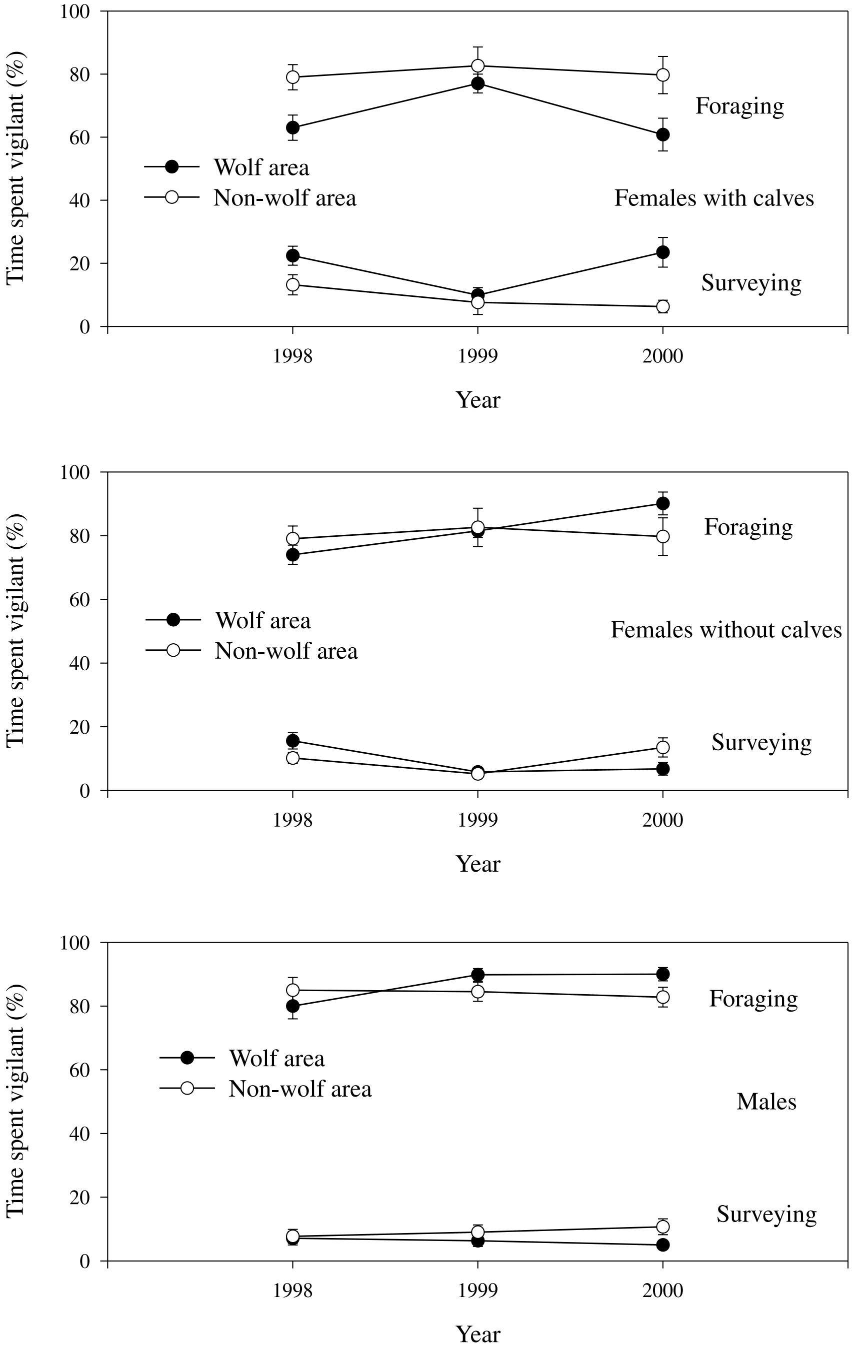
Fig. 3. Changes in the percentage of time spent foraging by elk in the different social classes during the 5 sampling years in the areas with and without wolves. Vertical bars show the standard error.



also by the increase in vigilance seen in female elk in wolf areas in the second year and by the changes in vigilance seen in female elk in areas originally without wolves. By 1998, wolves had begun to expand their movements into the original non-wolf areas, and by 2000 had become well established in several areas (J.C. Halfpenny and D. Thompson, unpublished data). As female elk with calves should be the most sensitive to these movements (for them, predator lethality is highest), it is not surprising that this social group responded the quickest as wolves moved into the new areas. Female elk without calves, however, followed, with higher vigilance levels by the fifth year.

Although, in general, elk and bison responded to the presence of wolves, we found significant differences among the social classes in their responses to the original predation risks (grizzly bears and coyotes) and to the added risk from wolves. With respect to the differences we saw among social classes in the non-wolf and wolf areas, we propose the following possible explanations. Predation risk is influenced directly by the rate of encounter between a prey and a predator

Fig. 4. Changes in the percentage of time spent vigilant and foraging by bison (*Bison bison*) in the different social classes during the last 3 sampling years (1998–2000) in areas with and without wolves. Vertical bars show the standard error.



and the lethality of the predator in the absence of vigilance by the prey, and indirectly by the effectiveness and rate of vigilance (Brown 1999; Brown et al. 1999). When wolf-free areas are considered a baseline for pre-wolf conditions, the predation risk can be considered low (Grizzly bears) and equal to those incurred by males and females without calves. Encounter rate, predator lethality, and the effectiveness of vigilance would all be similar and, thus, so would the optimal rate of vigilance. Thus, as might be predicted, we saw no differences in vigilance levels between males and females without calves. Females with calves, however, would incur a higher predation risk because of calves' vulnerability to coyotes and bears, i.e., predator lethality and encounter rate would be higher. To counter this higher predation risk and increase the chances of survival of their young, females with calves should sacrifice some of their feeding efficiency for increased surveillance. Because predator lethality would likely be higher for elk, they should respond more than bison females with calves. Thus, the higher surveillance rates we observed for this group are expected, even in the absence of wolves. These results concur with those obtained for impala and wildebeest by Hunter and Skinner (1998), who found that impala, the smaller species, was more vigilant in general and showed the greatest differences between females with young and the other two social classes.

Consider now the changes in the landscape of fear resulting from the wolf reintroduction. First, at the initial release site, the rate of encounter with predators, predator lethality (Brown et al. 1999), and thus predation risk would be expected to increase for all social groups, and an increase in vigilance would be expected. However, we saw no such response from male elk and bison. We propose two possible explanations. Reproductive success in males depends on maintaining a maximum body mass. Thus, males have more to lose from a reduction in feeding than they gain from increased surveillance. It does no good to avoid predation at the expense of reproductive success, so males may be willing to take greater chances. An alternative explanation is that males face a lower risk of predation by wolves because of their larger size, i.e., predator lethality is reduced. This is likely true for male bison. For male elk, recent data on the sex composition of elk killed by wolves in the Park indicate fewer males being taken (29% females vs. 18% males; Smith et al. 2000). However, Houston (1982) estimated adult sex ratios for elk in the Park to be 26–44 males per 100 females. If this is still a reasonable estimate, then proportionally, predator lethality for males is approximately equal to that of females. As wolves are able to successfully kill adult elk of both sexes, the first explanation for the non-responsiveness in males seems more likely.

The increase in surveillance by female elk and bison without calves when they are exposed to wolves can be understood if we consider that females are assured of a chance to mate even when they are in a lowered nutritional state. But they must survive to the next year. Consequently, this group has more to lose than males if they do not counter the increased predation risk with increased vigilance. Females with calves also have investment in possible future reproductive events, but they also require the immediate survival of their current and most vulnerable investment, their offspring. It would seem logical that we should see a greater increase in wolf areas over wolf-free areas in this social group than in other females.

With regard to annual changes in vigilance levels seen in the two female social groups of elk in the wolf area, by the second year females with calves had increased their vigilance rates from 20.1% (based on data from non-wolf areas) to 47.5%. This social group was sacrificing almost half of its foraging effort for safety, assuming that other lost-opportunity costs were minimal. Females without calves exhibited a similar pattern. Unfortunately, we did not collect data on bison during the first 2 years. However, it seems realistic to assume that vigilance rates increased in a similar fashion but at a smaller scale: for instance, females with calves increased their vigilance from 13.3% to at least 22.4% (third-year data). The data indicated, then, that it takes at least 2 years before vigilance levels begin to stabilize. This lag time is likely related to the imperfect information possessed by animals on the lethality of wolves (Brown et al. 1999) and the increasing encounter rates as wolves increased in number (from the original 20 in 1995 to approximately 56 in 1997 and eventually <100 by 2000; J.C. Halfpenny and D. Thompson, unpublished data). Again, as predator lethality would be highest for female elk with calves and lowest for female bison without calves, we would expect to see the following ordering of responses: female elk with calves > female elk without calves > female bison with calves > female bison without calves.

By the third year of the study (1998) we found the vigilance level for female elk to be approximately the same or slightly less than the year before. However, by the fourth year (1999) we found that female elk without calves and both bison social groups had significantly reduced their vigilance levels. We propose two possible but not mutually exclusive reasons for these declines. First, it is possible that after 2 years of experience with wolves, these social groups have learned how to reduce the predation risk, through habitat shifts, changes in group dynamics, formation of “pods” (Carbyn and Trottier 1987), etc., and thus reduce the level of vigilance needed. A second explanation is based in the fact that most of the predation by wolves centers on elk calves (39%; Smith et al. 2000). Rates of encounter with predators for these three social groups (female elk and bison without calves and bison with calves) is likely low, especially during the spring. Thus, after their initial response to wolves as a new, unpredictable predation risk, we propose that these animals adjusted their vigilance levels on the basis of the rates of encounter with wolves that they experienced and a reassessment of predator lethality. The fact that female elk with calves still maintained their high vigilance levels in the fourth year supports this second hypothesis. The increases in vigilance for female elk without calves and female bison with calves in the fifth year argue against this hypothesis. Perhaps, because of higher numbers of wolves (~100 by 2000; J.C. Halfpenny and D. Thompson, unpublished data) and fewer elk calves (personal observation), wolves increased their attacks on these two groups.

Lastly, with regard to the changes in vigilance levels for female elk with and without calves in the previous non-wolf areas, female elk with calves were the first to respond to the movement of wolves to other areas of the Park. This social group responded by the third year, while female elk without calves had only begun to respond in the fourth year (Fig. 2). As predator lethality and encounter rates would be higher for this group, such a reaction would have been predicted. It is interesting to note that by 2000, vigilance levels of these two female groups were similar to those of their counterparts in the original wolf areas. Thus, the answer to the question of just how much foraging effort female elk will sacrifice seems to be approximately 30% for females without calves and 40% for females with calves. This represents a decrease in foraging effort due to the presence of wolves of approximately 20% for both groups.

In general, our results for elk and bison correspond to those of Hunter and Skinner (1998) for impalas and wildebeest. One main difference is that they found males of both species responding to the risk of predation from lions and cheetahs. The reason for this difference is unclear but is likely related to differences in predator lethality, which is determined according to the prey (Brown et al. 1999), between the systems; for instance, Fitzgibbon (1990) found that cheetahs preferred male gazelles (*Gazella thomsoni*) in the Serengeti National Park. Another difference between the results of the two studies is the increase seen in vigilance.

Hunter and Skinner (1998) found vigilance rising to a maximum of only 20% in female impala with young. These results could again be related to differences in predator lethality and encounter rates. However, their study only extended 9–10 months after the release of lions and cheetahs, and this was likely not enough time to evaluate the total impact on vigilance. In contrast to our results, others (Carbyn and Trottier 1987; Berger and Cunningham 1994) report little increase in vigilance by bison except when under immediate attack. In these studies, bison have been exposed to wolves continuously (for decades) and likely have already made the behavioral adjustments that may have led to the reduction in vigilance which we saw by the fourth year in our study.

In conclusion, as foraging theory predicts, the reintroduction of a predator into the system will result in a major increase in vigilance levels. What are the implications of these changes? For females with calves, we predict that unless they compensate (e.g., longer feeding bouts, shifts in feeding times, locations, etc.), reductions of 20% in foraging effort could have a significant impact. Predictions include (*i*) lower body masses or reduced fat content of females; (*ii*) lower survival rates of adults and young of the year during stress periods such as winter; and (*iii*) lower birth masses of calves in the spring. If additional fieldwork supports these predictions, then it can be concluded that fear of predation not only controls the foraging patterns of individuals but can have significant consequences for the population level.

What might be some of the impacts of this on the Park ecosystem? Wolves have reestablished a landscape of fear in which animals, in their effort to reduce their vulnerability to predation by wolves, have increased their levels of vigilance. These animals should also adjust their time allocation, spending more time in areas with lower predation risk, the new-found valleys of the landscape of fear. As elk and bison seek out these valleys, we predict a major change in how they use the Park habitat. Such changes could include temporal and spatial shifts in habitat use, e.g., avoiding higher risk areas. We further predict that if these shifts in use patterns occur, they will lead to significant changes in vegetative composition as plants are "released" from grazing pressure in the high-risk peaks of the landscape. Our work has demonstrated the first step: elk and bison are responding behaviorally to the reintroduction of wolves. As our findings corroborate those of Hunter and Skinner (1998), they demonstrate that this behavioral change is an important first response to alterations in the landscape of fear. Further work needs to center on how that behavioral response may translate into effects at the population, community, and ecosystem levels.

Acknowledgments

We thank Scott Blum, Anna Burke, Tracy King, Brian Holmes, Jenn MacDonald, Anne Mottet, and Gudrun Schwarzer for their help on this study and Joel S. Brown for his helpful comments on the manuscript. The fieldwork was supported by grants from the Rocky Mountain Elk Foundation, The Eppley Foundation for Research, Mazamas, the University of Wyoming – National Park Service Research Center, and the University Research Committee of Idaho State University.

References

Bednekoff, P.A., and Ritter, R. 1994. Vigilance in Nxai Pan springbok *Antidorcas marsupialis*. Behaviour, **129**: 1–11.

Berger, J., and Cunningham, C. 1994. Bison mating and conservation in small populations. Columbia University Press, New York.

Brown, J.S. 1992. Patch use under predation risk: I. Models and predictions. Ann. Zool. Fenn. **29**: 301–309.

Brown, J.S. 1999. Vigilance, patch use, and habitat selection: foraging under predation risk. Evol. Ecol. Res. **1**: 49–71.

Brown, J.S., and Alkon, P.U. 1990. Testing values of crested porcupine habitats by experimental food patches. Oecologia, **83**: 512–518.

Brown, J.S, Laundré, J.W., and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. J. Mammal. **80**: 385–399.

Carbyn, L.N., and Trottier, T. 1987. Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. Can. J. Zool. **65**: 2072–2078.

Elgar, M.A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol. Rev. Camb. Philos. Soc. **64**: 13–33.

Fitzgibbon, C.D. 1990. Why do hunting cheetahs prefer male gazelles? Anim. Behav. **40**: 837–845.

Houston, D.B. 1982. The northern Yellowstone elk. Macmillan Publishing Co., New York.

Hunter, L.T.B., and Skinner, J.D. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour, **135**: 195–211.

Kotler, B.P., and Holt, R.D. 1989. Predation and competition: the interaction of two types of species interactions. Oikos, **54**: 256–260.

Kotler, B.P., Gross, J.E, and Mitchell, W.A. 1994. Applying patch use to assess aspects of foraging behavior in Nubian ibex. J. Wildl. Manag. **58**: 300–308.

Lagory, K.E. 1986. Habitat, group size, and the behaviour of white-tailed deer. Behaviour, **98**: 168–179.

Lima, S.L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Anim. Behav. **49**: 11–20.

Lima, S.L, and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619–640.

Meagher, M.M. 1973. The bison of Yellowstone National Park. Monogr. Ser. No. 1, National Park Service, Washington, D.C.

Molvar, E.M., and Bowyer, R.T. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. J. Mammal. **75**: 621–630.

Quinton, A., Lebedev, G., Youtz, P., Tuerke, T., Sinkler, R., and Kuo, J. 1995. SigmaStat for Windows 95: statistical software, version 2.0. SPSS, Inc., San Rafael, Calif.

Scheel, D. 1993. Watching for lions in the grass: the usefulness of scanning and its effects during hunts. Anim. Behav. **46**: 695–704.

Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? Science (Washington, D.C.), **210**: 1041–1043.

Smith, D.W., Murphy, K.M., Evans, S.B., Wilmers, C.C., and Sheldon, J.W. 2000. Wolf kill rates and biodiversity in Yellowstone National Park. *In* Abstracts from the 14th Annual Meeting of the Society for Conservation Biology, Missoula, Mont. p. 259.

Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. Behaviour, **79**: 81–107.

Weaver, J. 1978. The wolves of Yellowstone. Rep. No. 14, U.S. Department of the Interior, National Park Service, Washington, D.C.