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Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics?

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Many animals benefit from the presence of conspecifics by reducing their rate of scanning for predators while increasing their time spent foraging. This group size effect could arise from a decreased perception of individual risk (dilution hypothesis) and/or an increased ability to detect predators (detection hypothesis). We compared individual and group vigilance of Rocky Mountain elk, *Cervus elaphus*, in three regions of Yellowstone National Park, Wyoming, U.S.A. that varied in their encounter frequency with coyote, *Canis latrans*, grizzly bear, *Ursus arctos*, and grey wolf, *Canis lupus*, predators. Adult females without calves increased scanning and decreased foraging with high encounter risk and small herd size. Adult females with calves increased scanning and decreased foraging with high encounter risk, but showed no decrease in scanning with large herd size. Yearlings increased scanning and decreased feeding with small herd size, but not with high encounter risk. Adult males were least vigilant, fed most and were not influenced by encounter risk or herd size. These age–sex class differences led to significant differences in group vigilance depending on the composition of the herd. Herds with a majority of mothers were significantly more vigilant than herds with a majority of adult males. However, these differences in group vigilance had no influence on the individual scanning of females without calves. Thus, the decrease in individual scanning with herd size may depend more on changes in individual risk than on cooperative detection of predators.

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Predation is an important agent of natural selection and can have a strong influence on the evolution of certain behaviours (Lima & Dill 1990). One proposed behavioural mechanism used by individuals to reduce predation risk is to aggregate with conspecifics (Hamilton 1971; Treisman 1975). Individuals in a group of conspecifics can potentially benefit by coordinated group defence, increased predator detection, increased probability of escape or decreased probability of death per encounter (Bertram 1978; Turner & Pitcher 1986). For many species, especially birds and mammals, vigilance behaviours may serve to increase predator detection, but often they reduce the time available for other activities such as foraging or mating (Pulliam & Caraco 1984). Therefore, groups of vigilant individuals potentially benefit by a collective ability to detect predators sooner than solitary

individuals, allowing for reduced levels of individual scanning and increased foraging effort (Pulliam 1973; Powell 1974; Kenward 1978; Elcavage & Caraco 1983).

It is extremely difficult to determine the degree to which detection and dilution benefits have influenced the evolution of vigilance, because both benefits predict that individual scanning should decrease with increasing group size (Elgar 1989; Roberts 1996; Bednekoff & Lima 1998). Coordinated group vigilance is unlikely to be evolutionarily stable, because selfish individuals that reduce their own scanning would still potentially benefit from the predator detection of others (Pulliam et al. 1982; Lima 1987; McNamara & Houston 1992). However, if individuals in a group benefit primarily by dilution benefits rather than detection benefits, then changes in the vigilance of conspecifics should have little effect on an individual's optimal level of scanning. Few empirical studies of the group size effect have specifically examined this prediction (Lima 1995).

Ungulates have long been a model system for the study of the interaction between predation risk and the group size effect. Studies have shown that individual vigilance

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decreases as a function of herd size (Berger 1978; Lagory 1986; Dehn 1990; Bednekoff & Ritter 1994), body size (Underwood 1982; Laundré et al. 2001), sex (Lipetz & Bekoff 1982; Frid 1997; Laundré et al. 2001), predation pressure (Hunter & Skinner 1998; Laundré et al. 2001), distance to obstructive cover (Underwood 1982; Lagory 1986; Bednekoff & Ritter 1994; Frid 1997), distance to refuge (Berger 1978; Frid 1997), nearest-neighbour distance (Underwood 1982) and position in the herd (Underwood 1982; Bednekoff & Ritter 1994). All of these factors potentially interact to determine an individual's perception of predation risk.

Rocky Mountain elk, *Cervus elaphus*, in Yellowstone National Park (YNP) are an ideal study system in which to examine the influence of predation risk on individual and group vigilance. Since 1968, the YNP elk population has increased under a management policy of 'natural regulation' (Huff & Varley 1999; Shafer 2000). Elk mortality has been influenced primarily by the availability of forage, drought and winter severity rather than predation (Coughenour & Singer 1996; Boyce 1998; Singer et al. 1998). In 1995 and 1996, 31 grey wolves, *Canis lupus*, were reintroduced in the Lamar Valley and Firehole Basin of YNP. The wolves had an immediate impact on the behaviour and survivorship of elk, moose, *Alces alces*, and bison, *Bison bison* (Smith et al. 2000a; Berger et al. 2001; Laundré et al. 2001; Mech et al. 2001). As the wolves established and expanded territories, a gradient of encounter risk across the park from high risk 'wolf-use areas' to low risk 'non-wolf-use' areas was established (Laundré et al. 2001; Ripple et al. 2001). Differences in the vigilance of elk across different regions of the park are assumed to be the result of differences in their risk of encountering wolves.

An elk's risk of predation is determined by both intrinsic and extrinsic risk factors (Dehn 1990; Laundré et al. 2001). Intrinsic risk factors include age, sex, nutritional status and reproductive status. Extrinsic risk factors include predator encounter frequency, herd size and group vigilance. We refer to differences in the encounter frequency of predators across study locations as 'encounter risk', the increased vulnerability of an individual in a small group as 'herd size risk', and the differences in the vulnerability of an individual to different predators as 'age–sex class risk'. Collectively, these three factors are assumed to influence an individual's overall 'predation risk'.

We examined how these three predation risk factors interacted to influence individual and group vigilance in elk and compared the predictions of the detection and dilution hypotheses to determine how both factors influenced the group size effect. We measured group vigilance using a scan sampling rule and individual vigilance using a focal sampling rule. Our three study locations within YNP differed in their probability of encounter with grey wolf, grizzly bear, *Ursus arctos*, and coyote, *Canis latrans*, predators. We observed the behaviour of elk in three regions of the park to examine how changes in encounter risk, age–sex class risk and herd size risk interacted to influence both individual and group vigilance.

METHODS

Study Area and Elk Life History

Our study area was in Yellowstone National Park, Wyoming, U.S.A., where Rocky Mountain elk are the most numerous ungulate numbering approximately 18 000–22 000 individuals (Mech et al. 2001). Elk in YNP occur in several distinct migratory herds that have different seasonal migratory routes (Houston 1982; Shafer 2000). Elk in the Madison migratory herd tend to summer along the Gibbon, Madison and Firehole Rivers and winter along the Madison River. Elk in the Northern migratory herd summer in the Lamar Valley and Mirror Plateau and winter along the Lamar, Yellowstone and Gardner Rivers. Elk in the Jackson migratory herd summer in the Hayden Valley and winter along the Snake River. Elk in the northern Rockies mate during late September and give birth during late May to early June. Elk herd composition changes dramatically with the seasons. During the autumn rut, dominant males defend harems of 10–50 females and aggressively exclude other males into bachelor herds. During the winter, males and females come together to form massive wintering herds numbering in the thousands. By spring, males form small herds (1–10 individuals) with other males, and females, yearlings and newborn calves herd together (1–50 individuals). Often these male and female herds merge while individuals are actively foraging (Houston 1982).

The elk in YNP are preyed upon by coyotes, grizzly bears, pumas, *Felis concolor*, and grey wolves. Pumas occasionally kill elk, but because of their low population number and preference for mule deer, *Odocoileus hemionus*, prey, they are a relatively minor encounter risk (Murphy 1998). Coyotes and grizzly bears primarily target newborn elk calves as prey and represent a substantial encounter risk during the spring and summer season (Houston 1978; Gunther & Renkin 1990; Gese & Grothe 1995; Mattson 1997). Grey wolves prey on calves, yearlings, adult females and even adult males. Elk are preyed upon year-round (∼285 elk per year per pack), and the Park Service Wolf Recovery Program estimates that more than 85% of the wolves' diet consists of elk (Smith 1998; Smith et al. 1999, 2000b, 2001; Mech et al. 2001). Therefore, wolves probably represent the most significant predator encounter risk to elk in YNP.

Grey wolves were reintroduced into YNP in the springs of 1995 and 1996 (Phillips & Smith 1997). During our study, the number of wolves in YNP increased from 85 in spring 1998 to 165 in spring 2001 (Smith 1998; Smith et al. 1999, 2000b, 2001). The location of each of the wolf packs has been carefully monitored and mapped by the Wolf Recovery Program. This has allowed us to compare the behaviour of elk in different regions of the park where encounter rates with wolves have ranged from daily to less than once a year.

We observed elk in three regions of YNP, Norris Basin, Hayden Valley and Lamar Valley. All three regions have extensive, open grassland meadows surrounded by conifer forests. The Hayden Valley has the highest elevation (2350 m) and is occupied by elk only during the spring

and summer months. The Norris Basin (elevation 2275 m) and the Lamar Valley (elevation 2000 m) are occupied by elk year-round. Elk in these regions are primarily from distinct migratory herds that have different winter ranges. The frequency of encounter with different predator types in each region was inferred from previous studies (Laundré et al. 2001; Ripple et al. 2001) and our own 4 years of direct observation. In the Norris Basin, we saw coyotes on 8 of 19 observation days and grizzlies on 2 days, but no wolves. In the Hayden Valley, we saw coyotes on 10 of 17 observation days and grizzlies on 5 days, but no wolves. In the Lamar Valley, coyotes were seen on 30 of 36 observation days, grizzlies on 12 days and wolves on 22 days. We used these natural differences in predator encounter frequency to compare the behaviour of elk under three expected levels of predator encounter risk (Norris: low; Hayden: intermediate; Lamar: high). Because the degree of encounter risk in each location is likely to change with hour, week and year, we tested for these temporal variables in our analysis of elk vigilance.

General Methods

We made 495 direct observations on 275 'herds' of elk between 16 May and 26 June over 4 years 1998–2001. We defined a herd as a group of elk with a nearest-neighbour distance of not more than 100 m regardless of their behavioural state. Individuals more than 100 m from another elk were not considered part of that herd. This distance corresponds to the maximum distance that we have observed elk to respond to the bark of another elk. Solitary individuals more than 100 m away from another elk were considered herds of one.

Elk were observed whenever they were visible and active between 0530 and 2130 hours. We tested for and found no effect of time of day on our dependent variables. All observations were made from along side the park roads using binoculars (7×35) and spotting scopes (32×82). For each herd observed, we recorded the date, time, location, total herd size, distance to forest cover, distance to the road and the number of individuals in each sex and age category. Total herd size included all calves, yearlings and adults. Distance to road and distance to forest cover were estimated by eye and then classified into seven categories: <5 m, 5–10 m, >10–50 m, >50–100 m, >100–500 m, >500–1000 m, >1000 m.

For the analysis of individual activity patterns and estimates of vigilance, we divided elk into four age–sex classes. Mothers were adult females with a nursing calf present. Females were adult females with no nursing calf present. Yearlings were markedly smaller females and those males with only one antler point per side. Males were adults with two to six antler points per side. These designations can sometimes be difficult to estimate in the field. For example, it is difficult to determine whether an adult female is a mother if the calf is resting out of view. It is also difficult to distinguish yearlings at great distance. In both of these cases, the age–sex class 'female' is likely to include a few individuals from these other categories.

We observed 83 mothers, 179 adult females without calves, 86 yearlings and 147 males.

Herd composition was measured as the relative abundance of these different age–sex classes within a herd. Because adult males and mothers with calves were rarely ever found in the same herd, we used the ratio of adult females to the other adult age–sex class present as our classification of herd composition. The five levels of herd composition were >50% mothers, <50% mothers, 100% adult females without calves, <50% males and >50% males. For example, if a herd contained 10 adult females without calves and three males, we considered it a <50% male herd, and if a herd contained 10 adult females without calves and three mothers, we considered it a <50% mother herd. The presence of yearlings influenced herd size but not herd composition. We observed 23 herds with >50% mothers, 34 herds with <50% mothers, 103 herds with 100% females without calves, 35 herds with <50% males and 80 herds with >50% males. Herd composition was used as an independent variable to determine whether individual or group vigilance was influenced by the ratio of age–sex classes present in a herd.

Observational Methods

We divided elk activity into six mutually exclusive behavioural states: feeding, scanning, travelling, grooming, aggression and resting as follows.

Feeding: standing or walking slowly with the head below the level of the shoulder.

Scanning: standing with the head at or above the shoulder level.

Travelling: walking, trotting or running with the head at or above the shoulder level.

Grooming: licking or scratching oneself or another.

Aggression: kicking, biting or charging another with head fully raised.

Resting: any behaviour while lying on the ground.

We used scanning behaviour as our estimate of vigilance. Although we recognize that elk engaged in these other behavioural states may also be able to detect predators, we decided that scanning was the best estimate of vigilance because (1) the head-up posture brings all the sensory organs to a position that should increase the detection range, (2) it entails a cost of lost time that could be used in other activities, and (3) it is the observed state of alertness when a predator is detected. Scanning and feeding were the two most common behavioural states of active animals, accounting for 75–95% of the average activity budget. Therefore, we analysed only these two behavioural states as dependent variables.

Individual vigilance was estimated by a focal animal sampling rule and a continuous recording rule (Martin & Bateson 1993). Focal individuals were haphazardly selected from the herd based on their age–sex class and position in the herd. To reduce the probability that the same individual elk was observed more than once, only one to three individuals were observed in each herd, and herds at a particular location were revisited on a future date only if they contained more than 10 individuals.

Each focal individual was observed for 15 min, until they were no longer visible, or they began to rest, whichever came first. Observations for less than 3 min were excluded from the analysis. The length and frequency of each scan was recorded and used to calculate average scan duration (s), scan frequency (number of scans/min) and the percentage of time scanning (time scanning/time active). We considered time active as the total time engaged in all behavioural states except resting.

Group vigilance and group scan level was estimated using a group scan sampling rule and a fixed-interval, time-point recording rule (Martin & Bateson 1993). The observer noted the behaviour of each member of the herd from left to right at the instant of the scan sample signal. The fixed-point interval was 15 s for herds of fewer than 15 individuals and was extended 1 s for each additional herd member beyond 15. We took 30 samples (usually 7.5 min total duration) for each herd scanned. Group scan level was estimated as the average percentage of individuals in the herd engaged in scanning at the instant of the scan sample. Group vigilance was estimated as the percentage of 15-s intervals where at least one elk was scanning. For very large herds (>50), scan samples included as many individuals as possible, but rarely were we able to record every individual. For these three observations, we adjusted the estimate of group vigilance to the number of individuals actually sampled.

For each herd observed, we conducted one to three focal observations and one group scan observation. Observations were recorded by a pair of researchers, one observing and the other recording the information on a data sheet. The recorder kept time (± 1 s) on a stopwatch, and focal sample intervals were signalled with a count-down timer. Because multiple observers collected data, we tested for observer bias in the data and found no significant effect of observer. Five additional variables were recorded: disturbance, dominant/subordinate status, nearest-neighbour distance, nearest-neighbour status and position in the herd. Disturbance was defined as any observation where the focal animal underwent a sudden change in behaviour due to an immediate and identifiable nonpredator cause. The most common causes of disturbance were cars, airplanes and tourists. The methodology described above was reviewed and approved by the Idaho State University Animal Welfare Committee (Protocol No. AWC 11-00381).

Statistical Methods

The distribution of herd sizes between the three study locations was compared using a log-linear G test. Scan duration and scan frequency were log transformed and analysed using a three-way analysis of variance, ANOVA (herd size, encounter risk, age–sex class). Percentage of time spent scanning and feeding were arcsine square-root transformed and analysed using a three-way ANOVA (herd size, encounter risk, age–sex class). Time spent scanning for each age–sex class was arcsine square-root transformed and analysed using a two-way ANOVA (herd size, encounter risk) and a three-way ANOVA (herd size, encounter risk, herd composition). Group scan level,
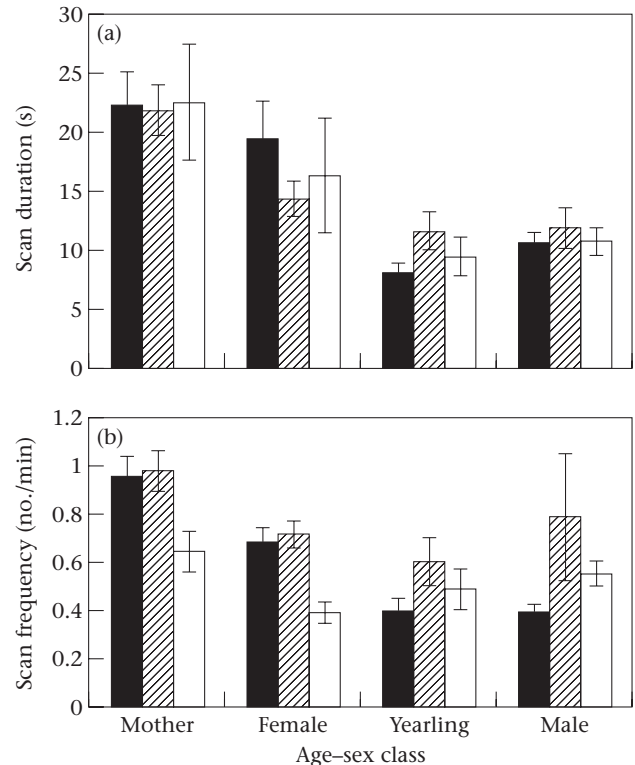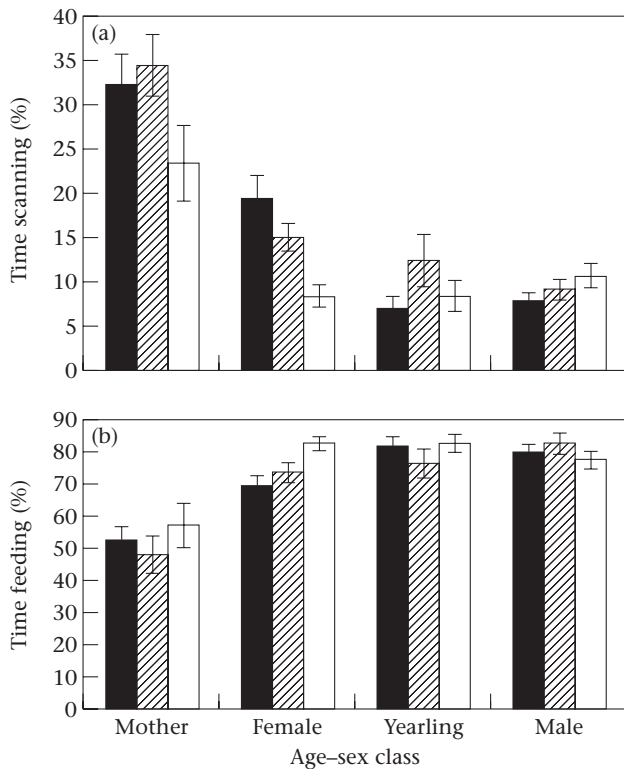

Figure 1. The influence of social status (mother, adult female without calf, yearling, male) and encounter risk (high: ■; intermediate: ▨; low: □) on (a) mean±SE scan duration (s) and (b) mean±SE scan frequency (number of scans/min) of focal individuals.

defined as the percentage of individuals scanning during an instantaneous scan sample, was arcsine square-root transformed and analysed using a three-way ANOVA (herd size, encounter risk, herd composition). Group vigilance, defined as the percentge of 15-s intervals with a least one individual scanning, was arcsine square-root transformed and analysed using a three-way ANOVA (herd size, encounter risk, herd composition). All significant main effects with three or more categories were compared with a Fisher's least significant difference (LSD) post hoc comparison. Uncontrolled variables were evaluated by a stepwise (backward) multiple regression from the residuals of the time spent scanning ANOVA. All statistical tests were performed using SYSTAT 10 for Windows.

RESULTS

We observed 275 elk herds over the 4 years of the study (Lamar Valley, $N=115$; Hayden Valley, $N=76$; Norris Basin, $N=84$). Herd size ranged from 1 to 68 individuals, with a median size of 8 in Lamar, 6 in Hayden and 6 in Norris. The distribution of herd sizes did not differ between the three study locations ($G_8=8.672$, $P=0.363$).

We observed 495 individuals over the 4 years of the study (Lamar Valley, $N=200$; Hayden Valley, $N=136$; Norris Basin, $N=159$). Mothers were more vigilant than the other three age–sex classes as measured by longer scans (Fig. 1a), greater scan frequency (Fig. 1b) and overall

Figure 2. Influence of social status (mother, adult female without calf, yearling, male) and encounter risk (high: ■; intermediate: ▨; low; □) on (a) mean±SE time spent scanning (%) and (b) mean±SE time spent feeding (%) of focal individuals.

vigilance (Fig. 2a). Adult females without calves were more vigilant than yearlings or males as measured by longer scans (Fig. 1a) and overall vigilance (Fig. 2a). Both mothers and adult females without calves spent significantly less time feeding than did yearlings or males (Fig. 2b).

The mean ± SE duration of scans was 14.6 ± 0.8 s. Scan duration for mothers (22.3 ± 1.9 s) was significantly longer than for females without calves (16.7 ± 1.9 s), and both classes of females scanned significantly longer than did yearlings (9.4 ± 0.8 s) or males (10.9 ± 0.7 s) ($F_{3,468}=23.8$, $P<0.001$). Neither herd size ($F_{1,468}=1.47$, $P=0.225$) nor encounter risk ($F_{2,468}=0.855$, $P=0.426$) influenced scan duration.

An elk scanned, on average, 0.60 ± 0.02 times/min. Scan frequency for mothers (0.88 ± 0.05 scans/min) was significantly higher than for females without calves (0.60 ± 0.03 scans/min), yearlings (0.48 ± 0.04 scans/min) and males (0.52 ± 0.06 scans/min) ($F_{3,468}=20.1$, $P<0.001$). Scan frequency decreased with decreasing encounter risk ($F_{2,468}=6.09$, $P=0.002$) and with increasing herd size ($F_{1,468}=27.2$, $P<0.001$).

Overall vigilance or the percentage of time that an elk spent scanning was influenced by both scan duration and scan frequency. An elk spent, on average, $14.4 \pm 0.7\%$ of its time scanning. The time that mothers spent scanning ($30.3 \pm 2.2\%$) was significantly higher than that of females without calves ($14.3 \pm 1.1\%$), and both classes of females spent significantly more time scanning than did

yearlings ($8.7 \pm 1.1\%$) or males ($8.9 \pm 0.7\%$) ($F_{3,488}=56.6$, $P<0.001$). As encounter risk decreased, there was a significant decrease in the time spent scanning ($F_{2,488}=7.45$, $P=0.001$). Time spent scanning also decreased with increasing herd size ($F_{1,488}=26.1$, $P<0.001$).

The percentage of time feeding was significantly affected by encounter risk ($F_{2,488}=3.45$, $P=0.033$). Elk fed more in the low-risk Norris Basin ($77.1 \pm 1.7\%$) than in the Hayden ($71.5 \pm 1.8\%$) or Lamar Valleys ($71.5 \pm 2.1\%$). The percentage of time feeding also differed significantly between age–sex classes ($F_{3,488}=34.7$, $P<0.001$). Mothers fed less ($52.4 \pm 3.2\%$) than did other adult females (74.7 ± 1.7), yearlings ($80.4 \pm 1.9\%$) and males ($79.2 \pm 1.5\%$). The percentage of time feeding also increased with increasing herd size ($F_{1,488}=11.1$, $P=0.001$).

The relation between time spent scanning and herd size depended upon both the age–sex class risk of the individual and the encounter risk (Fig. 3). Herd size and encounter risk had no influence on the time spent scanning for males. Yearlings reduced their time spent scanning only with increasing herd size ($F_{1,82}=10.5$, $P=0.002$). Adult females without calves reduced their time spent scanning with increasing herd size ($F_{1,175}=11.51$, $P=0.001$) and decreasing encounter risk ($F_{2,175}=9.54$, $P<0.001$). Mothers marginally reduced their time spent scanning only with decreasing encounter risk ($F_{2,79}=3.05$, $P=0.053$).

Group scan level, defined as the average percentage of individuals scanning during a scan sample, decreased with increasing herd size ($F_{1,191}=21.7$, $P<0.001$; Fig. 4a). This result reflects the change in individual scan frequency observed in our focal animal observations. However, group vigilance, defined as the percentage of scan intervals with at least one individual scanning, increased with increasing herd size ($F_{1,195}=16.6$, $P<0.001$; Fig. 4b). This result reflects overall vigilance of the group as defined by Pulliam's (1973) model of detection.

Group vigilance increased with increasing encounter risk ($F_{1,195}=6.10$, $P=0.003$). The differences in encounter risk for mothers and adult females without calves strongly influenced group vigilance in these mixed age–sex class herds (Fig. 5a). This result is demonstrated by the significant influence of herd composition ($F_{1,195}=13.1$, $P<0.001$).

Herd composition did not influence individual female vigilance ($F_{1,78}=1.41$, $P=0.237$). Although not significant, females without calves tended to be less vigilant in herds with males and more vigilant in herds with mothers (Fig. 5b).

Additional uncontrolled factors, such as year, week, hour, observer, disturbance, distance to cover, distance to road, nearest-neighbour distance, nearest-neighbour status and position in the herd were evaluated along with the main effects of herd size, encounter risk and age–sex class risk using a stepwise multiple regression analysis. The only significant uncontrolled factors were year, week and disturbance. They accounted for approximately 11% of the remaining residual variance and were less influential than the main effects of herd size, encounter risk and
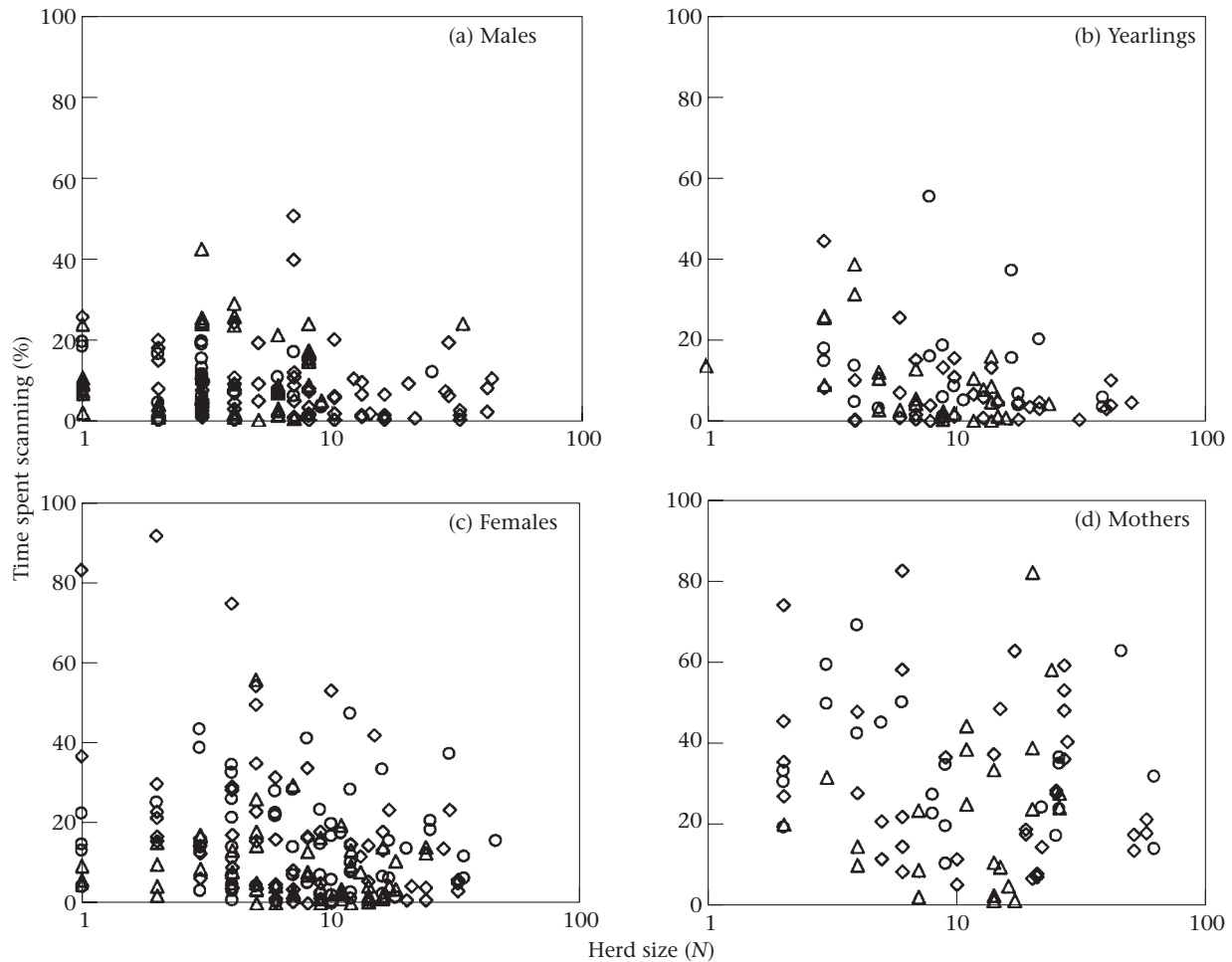
Figure 3. The influence of herd size and encounter risk (high: ◇; intermediate: ○; low: △) on the time spent scanning (%) for (a) males, (b) yearlings, (c) adult females without calves, (d) mothers.

age–sex class risk, which explained more than 34% of the variance.

DISCUSSION

Encounter Risk

Based on our assumption of differences between locations in their levels of encounter risk, we expected to find higher levels of vigilance for elk in the Lamar Valley and lower levels in the Hayden Valley and Norris Basin. These expected differences between locations in the levels of encounter risk were supported by our observation of wolves in the Lamar Valley on 22 days in the field while wolves were never observed in the Hayden Valley or Norris Basin.

Scan frequency and overall vigilance (percentage of time scanning) were indeed significantly influenced by encounter risk, but post hoc tests indicated that elk in the Lamar and Hayden valleys had higher levels of vigilance than in the Norris Basin. The finding of increased vigilance by elk in the Lamar Valley was similar to findings by Laundré et al. (2001) that elk in 'wolf-use areas' of YNP spent more time scanning and less time feeding.

However, a more unexpected result was that elk in the Lamar and Hayden Valley elk showed similar levels of vigilance. One possible explanation is that both the Lamar and Hayden Valleys have an abundance of grizzly bears. We observed grizzlies on 29% of our observation days in the Hayden Valley and 33% of our observation days in the Lamar Valley. Grizzly bears are effective predators of elk calves during the spring (Gunther & Renkin 1990). Alternatively, it is possible that we missed seeing wolves in the Hayden Valley. One of the YNP wolf packs (Nez Perce) did hunt in the Hayden Valley during some of our spring observation periods (Smith et al. 1999, 2000b, 2001; Laundré et al. 2001). Another possible explanation is that Hayden Valley elk may be responding to a recent exposure to wolves during their seasonal migration. Exposure to a novel predator may cause a very rapid and pronounced change in behaviour that might persist for some time after the encounter (Lima & Bednekoff 1999; Berger et al. 2001; Laundré et al. 2001).

We also found that as time spent scanning increased, the time spent feeding decreased, but the median herd size and the distribution of herd sizes did not differ with encounter risk. Studies have shown that foraging
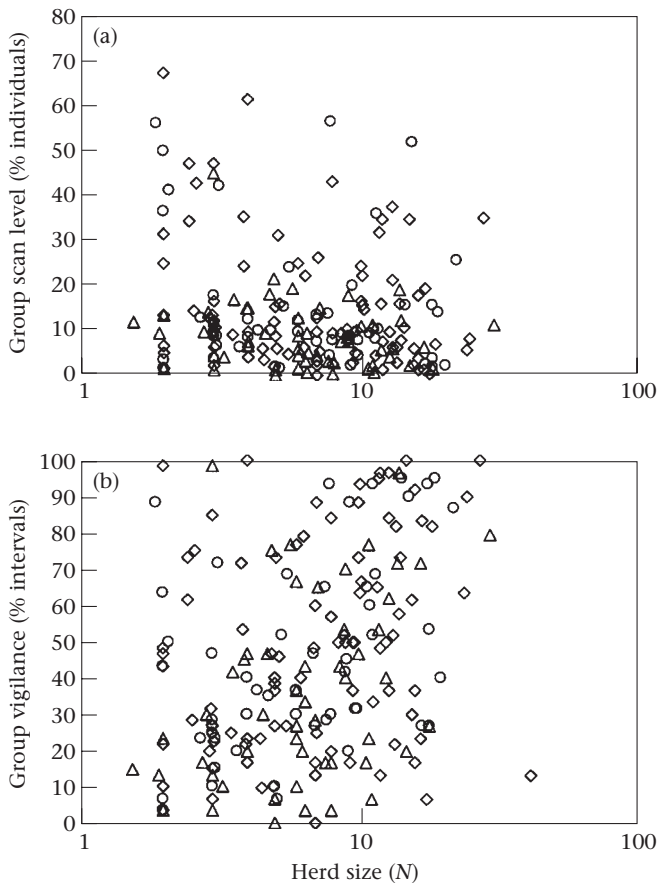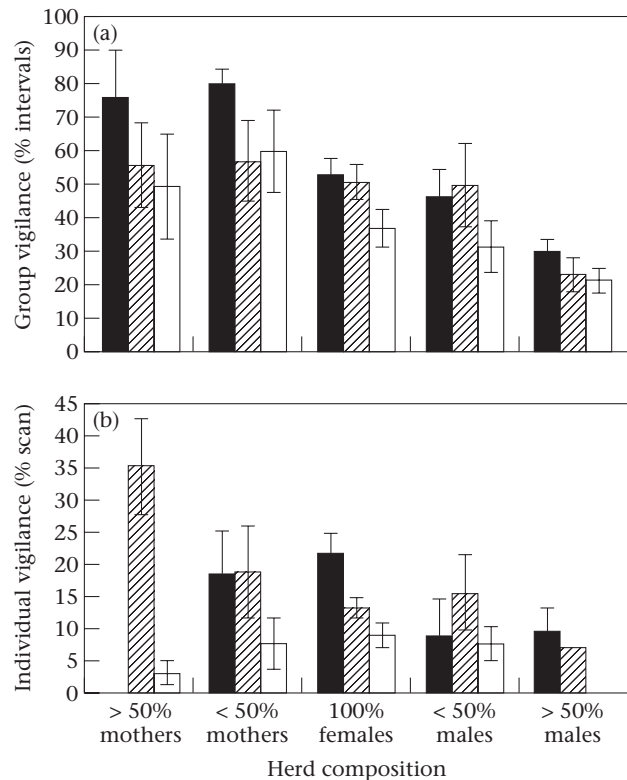
Figure 4. The influence of herd size and encounter risk (high: ◇; intermediate: ○; low: △) on (a) group scan level, defined as the average percentage of individuals scanning during a scan sample and (b) group vigilance, defined as the percentage of scan intervals with at least one individual scanning.

decreases when vigilance increases (Lagory 1986; Laundré et al. 2001), and theoretical models suggest that foraging constraints may at times be more important than minimizing predation risk (Pulliam et al. 1982; Lima 1987; McNamara & Houston 1992; Kie 1999).

Age–Sex Class Risk

Studies of vigilance have shown age–sex class to be an important factor influencing scan behaviour (Frid 1997; Hunter & Skinner 1998; Laundré et al. 2001). We found that mothers with nursing calves had significantly longer scans and a higher scan frequency. These behaviours led to a significantly higher proportion of time spent scanning and a significantly lower proportion of time spent feeding. Mothers remained highly vigilant even when they moved many metres away from their calves. This increased vigilance did not depend on the proximity or even the presence of the calf. We have observed that mothers will even remain vigilant for up to 2 days after the loss of a calf. Despite being the age–sex class that could potentially benefit most from detection, mothers did not decrease their vigilance in response to increasing herd size. One possible explanation is that newborn

Figure 5. The influence of herd composition and encounter risk (high: ■; intermediate: ▨; low: □) on (a) mean±SE group vigilance (% intervals with at least one scan) and (b) mean±SE individual vigilance by females (% time).

calves are the most vulnerable members of the herd and are selectively targeted by predators (Smith et al. 1999, 2000b, 2001). The benefit of detection is an early warning of a predator's approach. This information is of little benefit to a calf that cannot yet outrun the predator. A mother's vigilance in either a large herd or by herself may serve the more important role of keeping track of the distance between her and her calf.

Females without nursing calves had significantly longer scans and a higher proportion of time spent scanning than did yearlings and males, but not to the same degree as did mothers. Although these females were more vigilant than males and yearlings, they still had a similar proportion of time spent feeding. Adult females without calves showed higher levels of vigilance in the Lamar and Hayden Valleys than in the Norris Basin and decreased vigilance with increasing herd size. These observations are consistent with both the dilution and detection hypotheses, because females were responsive to both changes in encounter risk and herd size risk. Mech et al. (2001) found that the proportion of female elk killed by wolves in YNP was considerably higher than the proportion of male elk killed. Another possible reason that females were more vigilant as compared with yearlings and males is that they may have had one or more offspring in the same herd. We observed that some females associated with particular yearlings more than others and would even intervene when a yearling was

being chased. Although difficult to do in wild populations, future studies should evaluate whether a female's vigilance is influenced by her relatedness to others in the herd.

Yearlings showed very low levels of vigilance, regardless of encounter risk, but decreased vigilance with increasing herd size. Males showed low levels of vigilance regardless of encounter risk or herd size. These results are not surprising, given that both yearlings and males may need to maximize their fat reserves to survive harsh winter conditions. The energetic demand of the autumn rut often leaves reproductive males in poor condition heading into winter (Mech et al. 2001). When spring arrives, feeding is perhaps more important to their survival than scanning for predators. We observed that male elk in the Lamar Valley were likely to continue feeding even when wolves approached within a few metres, a behaviour predicted by several foraging–predation risk models (Ydenberg & Dill 1986; McNamara & Houston 1992).

Herd Size Risk

Many previous studies of vigilance have shown that individual scanning decreases with increasing group size (see reviews by Elgar 1989; Lima & Dill 1990; Quenette 1990; Roberts 1996). This group size effect may be the result of individuals responding to a decreased perception of predation risk due to the dilution effect (dilution hypothesis) or to the safety of group predator detection (detection hypothesis). We found that elk scan frequency and time spent scanning sometimes decreased with increasing herd size, but only under a certain set of conditions. This group size effect was significant for females and yearlings. Because females and yearlings are more vulnerable to wolves than males, they may benefit more from early detection. However, just demonstrating a group size effect alone cannot distinguish which benefit discussed above is operating.

To compare the relative importance of the dilution and detection hypotheses, we examined the effect of herd size on group vigilance. As group size increased, a smaller proportion of individuals scanned. This decrease in group scan level was statistically significant but not proportional to the change in herd size. In fact, group vigilance, estimated as the percentage of intervals with at least one scanning individual, was positively related to herd size. This means that an individual benefits from a large herd by a decreased proportion of time spent scanning, an increased proportion of time spent feeding and increased overall group vigilance. Therefore, elk in larger herds have a potential benefit of increased predator detection, consistent with the predictions of the detection hypothesis.

Group vigilance significantly increased with increasing herd size. If early predator detection reduces the probability of a successful attack, then detection may still significantly reduce risk for members of the herd. These direct estimates of detection benefits are extremely hard to measure in the field. In our more than 500 h of direct observation, we observed only 20 direct encounters with predators approaching a herd. Only two of these encounters resulted in a successful kill (one adult female and one calf, both killed by wolves). The relation between an individual's level of vigilance and its probability of survival is still unknown, but the fact that elk spend time scanning suggests that early detection is very important.

We also found that the scanning of an individual female without a calf was not influenced by the level of group vigilance. This result suggests that individual elk do not adopt levels of scanning that maximize cooperative predator detection. The cost of this decreased group vigilance to an individual is low, as long as the benefit of predator detection by a conspecific is low, the time remaining for foraging is not limiting and/or other members of the group are more likely to be attacked (FitzGibbon 1989; McNamara & Houston 1992). Lima's (1995) study of dark-eyed juncos, *Junco hyemalis*, also found that the presence of nonvigilant group members did not influence the vigilance of focal individuals.

The Group Size Effect

Both dilution and detection potentially benefit all members of a herd, but some individuals may benefit much more than others. As a result, studies have shown the relationship between individual vigilance and group size to be negative, positive or absent (Elgar 1989; Lima 1995; Roberts 1996). This inconsistency across taxa may be due to the unique set of costs and benefits derived by each individual from their association with conspecifics (Treves 2000; Beauchamp 2001). Ungulates show significant group size effects, but only under conditions of high predation risk. For example, Frid (1997) found that individual vigilance in Dall's sheep, *Ovis dalli dalli*, was best explained by a model that included both distance to cliff and an interaction between distance to cliff and group size. Dehn (1990) found that female elk vigilance in Mist Creek, Alberta, Canada, was best explained by a model that included both benefits of dilution and detection, but males were essentially nonvigilant. Laundré et al. (2001), however, found no group size effect at all for elk or bison in Yellowstone National Park.

Our observation regarding the variability of the group size effect between elk age–sex classes provides insight into the variability across taxa and the debate about the generality of the group size effect. The benefit of the group size effect is likely to depend on the sum of both intrinsic and extrinsic predation risk factors such as size, age, sex, experience, availability of food, encounter risk, escape options, detection risk and any other factors that directly impact the probability of a successful predation event. When the sum of these predation risk factors is high, natural selection should favour those individuals that optimize their vigilance/foraging ratio. When the sum of these predation risk factors is low, natural selection should favour those individuals that maximize foraging. The variability that we see among members of the same herd could be the result of different selective regimes. Future studies should continue to examine whether group vigilance is an emergent property with incidental benefits or a fundamental condition necessary for the evolution of social groups.

Acknowledgments

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