

Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity?

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Abstract: To maximize fitness, mothers must both provision and protect neonates, demands that may be in conflict, particularly in systems that still experience high levels of natural predation. Whether variation in offspring behaviour alters this putative conflict is not known. The objective of this study was to test hypotheses about the extent to which neonatal activity and ecological variables mediate trade-offs between maternal vigilance and foraging. To address these questions we contrasted data from behavioural observations on female moose (*Alces alces*) that differed in parity, calf activity, and habitat use at a site in south-central Alaska where they are subject to high levels of grizzly bear (*Ursus arctos*) and wolf (*Canis lupus*) predation. Our analyses revealed that females with active juveniles were more vigilant (and as a consequence spent less time feeding) than those with inactive young; vigilance of females without attendant young was intermediate. Distance to apparent protective refugia (e.g., vegetative cover) was positively related to vigilance for all calf-status categories, but lactating females spent more time closer to thick vegetation than did nonlactating females. These results suggest that (i) mothers adjust vigilance when young are inactive to compensate for the loss of foraging opportunities during periods of neonate activity, thereby reducing juvenile vulnerability and increasing the overall feeding rate, and (ii) females with young reduce foraging compromises and, presumably, predation risk by spending more time close to protective cover than do nonlactating females. We conclude that maternal trade-offs can be highly labile and that mothers are able to adjust rapidly to environment-specific situations.

Résumé : Pour maximiser le fitness, les mères doivent à la fois approvisionner et protéger leurs nouveau-nés, deux exigences qui peuvent être en conflit, particulièrement dans les systèmes où il se fait beaucoup de prédation naturelle. Le comportement de la progéniture peut-il modifier cet éventuel conflit? Nous avons éprouvé les hypothèses selon lesquelles l'activité des nouveau-nés et certaines variables écologiques forcent les mères à faire des compromis entre la vigilance et la recherche de nourriture. Pour résoudre ces problèmes, nous avons comparé les données de comportement obtenues chez des femelles de l'Orignal (*Alces alces*) distinctes par le nombre de leurs mise-bas, l'activité de leurs petits et leur utilisation de l'habitat à un site du centre-sud de l'Alaska où il se fait une importante prédation par les Grizzlis (*Ursus arctos*) et les Loups (*Canis lupus*). Nos analyses ont démontré que les femelles dont les jeunes sont actifs sont plus vigilantes (et, conséquemment, vouent moins de temps à l'alimentation) que les femelles dont les jeunes sont inactifs; les femelles sans petit occupent une position intermédiaire. La distance jusqu'à un refuge apparent (e.g., la couverture végétale) est en corrélation positive avec la vigilance, quel que soit le statut des nouveau-nés, mais les femelles nourricières passent plus de temps dans le voisinage d'une végétation épaisse que les femelles non nourricières. Ces résultats indiquent (i) que les mères ajustent leur vigilance quand les petits sont inactifs de façon à compenser la perte des occasions de recherche de nourriture durant les périodes d'activité des nouveau-nés, réduisant de cette façon la vulnérabilité des jeunes, tout en augmentant la fréquence des périodes d'alimentation et (ii) que les femelles avec des petits réduisent les compromis et, présumément, les risques de prédation en passant plus de temps dans le voisinage de couvertures protectrices que les femelles non nourricières. Les compromis envisagés par les mères sont donc très labiles et les mères sont en mesure de s'ajuster rapidement à des situations environnementales spécifiques.

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Introduction

Predictions of "optimal foraging" indicate that individuals develop foraging strategies that maximize energetic and nu-

trient gain while minimizing costs associated with acquiring energetic resources (Krebs 1973; Charnov 1976). However, a more complete assessment of fitness correlates results when such factors as predation, disease, and abiotic variability are

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considered (Stephens and Krebs 1986). In this context, mammalian systems can offer unique insights. In ungulates, for example, mothers face challenges because they must balance increased foraging demands associated with the high energetic costs of lactation (Bunnell and Gillingham 1985; Oftedal 1985; Carl and Robbins 1988) with the protection of vulnerable neonates from predators, a trade-off that may be especially important in populations which still experience intense natural predation.

Not only can predation be an important source of mortality in terrestrial and aquatic systems (Frame 1974; Gasaway et al. 1992; Sih et al. 1992), but variation in the intensity of predation can modify antipredator responses (Berger 1998; Hunter and Skinner 1998). Since behaviour can be linked to predation in numerous organisms (Lima and Dill 1990), study of trade-offs between foraging and antipredator behaviour can be enhanced with knowledge of actual predation risk. Few studies, however, have relied on direct measures of predation pressure (White 1999), and the resulting lack of direct knowledge has precluded more precise assessments of how predation shapes behaviour. Acquiring an understanding of such relationships in the case of some types of organisms, such as large mammals in human-dominated landscapes, may be impossible. For example, grizzly bears (*Ursus arctos*) and wolves have been extirpated from about 98% of North America from the Canadian border south, which means that predation on some herbivores as a selective force has been lost (e.g., on bison (*Bison bison*) and moose (*Alces alces*); Berger 1998, 1999).

Investigation of maternal antipredator behaviour in mammals has focused on habitat shifts (Festa-Bianchet 1988; Berger 1991; Kohlmann et al. 1996; Rachlow and Bowyer 1998), presence or absence of young (Lipetz and Bekoff 1982; Burger and Gochfield 1994; Molvar and Bowyer 1994), effects of predator–scavenger associations (Berger 1999), offspring age (Caro 1994), mother–young spatial relationships (Byers and Byers 1983; FitzGibbon 1993; Byers 1997), or active defense of young (Smith 1987). However, little is known about the extent to which offspring activity affects maternal investment in antipredator behaviour. Offspring activity may have important consequences for maternal fitness. For example, prey activity enhances the detection efficiency of visually orientated predators (Daly et al. 1990; FitzGibbon 1990) and can result in increased predation, particularly on naïve and vulnerable neonates, whether native (Harcourt 1991) or domestic (Tigher and Larson 1977; Gluesing et al. 1980). Nevertheless, increased or rigorous activity such as locomotor “play” or dyadic interactions of neonates is critical for the subsequent development of survival and reproductive skills (Byers and Bekoff 1981; Fagen 1981; Caro 1994; Byers 1998). Thus, selection may favour mothers that tolerate active and conspicuous behaviour in young even if it requires enhanced use of antipredator behaviours that necessitate a decrease in foraging efficiency.

To maximize fitness, mothers must both protect and provision young. Females might respond to proximate changes in neonate activity by adjusting antipredator strategies. For example, if offspring engage in play-fighting, locomotor play, and other behaviours that putatively increase their conspicuousness to predators, then mothers may opt to redirect foraging behaviour to vigilance. Other antipredator behaviours

may also be used in concert with vigilance to achieve an optimal offspring protection/provisioning strategy. Use of protective cover is one behavioural means by which predation risk is reduced (Mech 1966; Caraco et al. 1980; Lazarus and Symonds 1992; Molvar and Bowyer 1994; Kunkel and Pletscher 2000). Protective cover (after Lazarus and Symonds 1992) inhibits prey detection, facilitates escape, and reduces the capture efficiency of visually oriented predators (Daly et al. 1990; Longland and Price 1991). If prey with vulnerable young confine their foraging activity to areas in or near vegetative refugia, foraging compromises might be minimized (Molvar and Bowyer 1994; Weixelman et al. 1998).

Here we assess behavioural patterns of maternal investment, specifically the trade-off between offspring protection and subsequent provisioning, by using moose in a system where offspring are subjected to high mortality due to predation. This issue is of interest for two principal reasons. First, most studies investigating the trade-off between predation risk and foraging were carried out at sites where rates of prey mortality are unknown and therefore the risk of predation has not been directly assessed (White 1999). Second, although lactating females may be more vigilant than non-mothers (Lipetz and Bekoff 1982; FitzGibbon 1993; Molvar and Bowyer 1994; Burger and Gochfield 1994), the extent to which offspring activity affects maternal antipredator behaviour is unclear and to our knowledge has never been investigated. It may be possible to gauge whether risk perception by mothers changes when offspring vulnerability to predation is exacerbated by activity of the offspring, and, further, to determine whether variation in offspring behaviour modulates the trade-off between food-acquisition and predator-avoidance behaviour.

To examine these issues we tested two principal hypotheses: (1) lactating females adjust vigilance and foraging in relation to putative neonate vulnerability to predation, and (2) females with young spend more time in close proximity to protective cover than individuals without them.

Methods

Study area and predation

Data were collected in the Oshetna River valley in the eastern Talkeetna Mountains, Alaska (62°N, 147°W). The 100-km² study area was bounded by the Black River to the north and the Little Oshetna River to the south. Moose densities were high (0.8/km²) and reproductive success was low (Testa and Adams 1998) for northern populations (Boer 1992; Gasaway et al. 1992). Moose typically occurred at elevations of 850–1060 m in a broad sub-alpine valley bounded to the east and west by steep foothills of the Talkeetna Mountains. Both lactating and nonlactating females used similar habitats, and distributional overlap between reproductive classes was ubiquitous throughout the study area. Vegetation in the Oshetna River valley is typical of treeline habitats of central Alaska and composed primarily of a mosaic of dense spruce forest (*Picea glauca* and *P. mariana*) and open, brushy tundra dominated by dwarf birch (*Betula glandulosa*) and willow (*Salix planifolia pulchra*, *S. richardsonii*, *S. alexensis*) (Johnson et al. 1995). Moose in this region are primarily browsers; *Salix* spp. constitute 80–85% of their summer diet in central Alaska (Van Ballenberghe et al. 1989). Summer foraging patterns of moose in this environment are characterized by elevated intake rates of abundant high-quality browse and are limited primarily by physiological constraints associated with energy and nutrient assimilation (Renecker and

Schwartz 1997), as well as a lack of opportunities for uninterrupted foraging.

The Oshetna River valley supports a full complement of natural predators of moose. Densities of grizzly bears (21.3–23.5/1000 km²; Miller et al. 1997; Testa et al. 1999) and wolves (6.2–9.9/1000 km²; Testa 1997) are relatively high but typical of moose ranges throughout south-central Alaska (Testa 1997). Between 1994 and 1997, mortality rates of moose calves averaged 76% annually; 85% of calf mortality occurred during the first 6 weeks of life, and grizzly bear and wolf predation is considered the principal cause (Testa 1999). By contrast, during the same period, survival rates of adult females were high, though lactating females suffered considerably higher mortality than nonlactating individuals (9 and 3%, respectively; Testa 1999).

Sampling and data collection

Data were collected during May–July 1997 and May–June 1998, thereby encompassing the birth period, which typically begins in mid-May (Testa and Adams 1998). Focal-animal sampling (Altmann 1974) was used to gather data on 18 radio-collared and 49 non-radio-collared adult female moose using both binoculars and spotting scopes. We deemed non-collared individuals to be independent sampling units if they (i) were observed simultaneously in different locations; (ii) possessed unique physical characteristics; (iii) were spatially separated by distances ≥ 5 km within seasons; and (iv) had calves and were observed in different years (because the likelihood of observing females with calves in consecutive years during our annual sampling periods was low; based on calculations taken from Testa 1998; Testa et al. 2000). Sampling units were defined as focal-animal observation periods lasting ≥ 360 s (determining a minimum observation length is necessary to maintain equal variance between samples; see White 1999), during which time we quantified distance to protective cover (m), calf activity (only for females with single calves), and duration of adult behaviour. The former two measures were quantified at 180-s intervals. Data in which an individual's proximity to cover varied by more than 5 m or its calf-activity status changed during a 180-s observation period were rare and were not used in the analysis because measures under these conditions were considered either unreliable (for distance measures) or incompatible with the sampling protocol (for activity measures).

Known females were observed multiple times under different conditions, including when their calves were both active and inactive. To ensure independence between samples we used only a single, randomly selected data point for each individual in our analyses, except for intra-individual comparisons. In these cases we contrasted behaviour of given lactating females at fixed distances from cover when only calf activity varied. Female reproductive status was assessed by means of ultrasound and daily follow-up observations of known individuals during the calving season (Testa 1999; J.W. Testa, Alaska Department of Fish and Game, personal communication).

Definitions

To obtain a representative sample of foraging behaviour, observation periods commenced only when a focal adult female was feeding. Foraging was defined as the biting or chewing of food. Vigilance was behaviour in which an animal's head was raised and in the alert posture with ears forward and (or) actively scanning the local environment (Molvar and Bowyer 1994). Behaviours associated with locomotion, such as walking and running, were also recorded but comprised $<10\%$ of an individual's time budget and were not directly incorporated into the analysis. Periods during which a focal animal's foraging behaviour was interrupted by social interactions, elimination behaviour, grooming, or resting for <10 s were omitted (Berger et al. 1983). Measures of foraging and

vigilance were expressed as the proportion of time an animal spent engaged in each behaviour during a focal observation period. Neonates were designated as active when they played, fed, walked, ran, or stood; inactive calves were recumbent. Protective cover was operationally defined as vegetation that was tall and dense enough to hide a moose from view (Molvar and Bowyer 1994). Distance of the focal animal (adult females only) to cover was visually estimated to the nearest 5 m, using the body length of a moose (~ 2 – 2.5 m) as a gauge. Distance measures were quantified at 180-s intervals and averages were calculated across each focal animal observation period. "Nonlactating" females were individuals known to be not pregnant or individuals that were pregnant but gave birth to calves that died prior to sampling and, and "lactating" females were those who were known to be pregnant and subsequently gave birth to calves that lived. Lactating females were further distinguished on the basis of whether attendant calves were "active" or "inactive".

Analyses

Proportional data were arcsine square root transformed to meet equal variance and normality assumptions of analysis of covariance (ANCOVA) (Neter et al. 1996; Wilkinson et al. 1996). Multifactor ANCOVA was used to compare the effect of calf status (active, inactive, or no calf), distance to protective cover, and date since initiation of the parturition season (a gauge of calf age) on vigilance and foraging (Zar 1999). (Date since initiation of parturition was subsequently removed from the full model because it did not significantly explain variation in vigilance ($F_{[1,61]} = 0.028$, $P = 0.867$) or foraging ($F_{[1,61]} = 0.172$, $P = 0.680$)). ANCOVA was used to test for differences in vigilance and foraging between calf-status levels while accounting for the effect of distance to cover. A posteriori mean comparison procedures (Tukey's HSD test) were used to check for differences among calf-status categories (Zar 1999). We used a paired t test to examine the intra-individual effect of calf activity on maternal vigilance and foraging by contrasting observations of a known female during periods when its calf was active and inactive (Zar 1999). This comparison was based on data collected from individuals at all distances to protective cover. We also compared mean distances to protective cover among females of each calf-status category using non-parametric Kruskal–Wallis and Mann–Whitney analyses (Zar 1999). We used t tests to evaluate overall differences in vigilance and foraging between lactating and nonlactating females, as well as differences in calf-activity budgets, during maternal observation periods.

Results

Neonate status

Both calf status ($F_{[2,61]} = 15.189$, $P < 0.0001$) and distance to protective cover ($F_{[1,61]} = 19.544$, $P < 0.0001$) exerted a significant effect on adult female vigilance (Fig. 1); vigilance was not significantly affected by an interaction between distance to protective cover and neonate status ($F_{[2,61]} = 0.169$, $P = 0.845$). When we accounted for the effect of distance to protective cover, we found that vigilance differed between females in each calf-status category: females with active calves were significantly more vigilant than females without calves (Table 1) and females with inactive calves were significantly less vigilant than nonlactating females (Table 1). Females with active calves spent 79.5% more time vigilant than those with inactive calves.

To test whether calf status also affected foraging, we replaced vigilance in the model and found that calf status ($F_{[2,58]} = 10.881$, $P < 0.001$) and distance to protective cover

Fig. 1. Effect of calf status and distance to protective cover on the proportion of time spent vigilant for adult female moose (*Alces alces*) ($r^2 = 0.567$, $F_{[5,61]} = 35.333$, $P < 0.0001$).

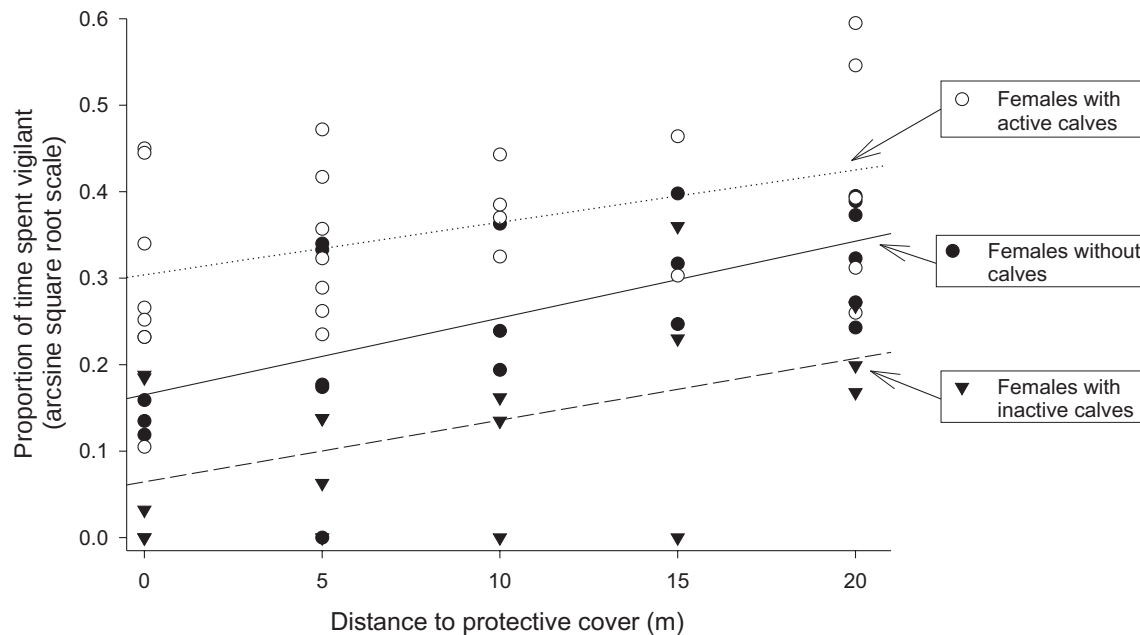


Table 1. Comparison of percent time spent vigilant and foraging for adult female moose (*Alces alces*) of different calf status ($n = 66$ and $n = 66$, respectively).

Calf status	Percent time spent vigilant				Percent time spent foraging			
	Mean	SE	<i>n</i>	Grouping*	Mean	SE	<i>n</i>	Grouping*
Active calf	12.7	1.1	25	a	80.5	2.6	25	a
No calf	7.1	1.2	23	b	88.6	2.7	23	b
Inactive calf	2.6	1.3	18	c	92.8	3.1	18	b

*Different letters denote significant differences among calf-status categories (Tukey's HSD test, $P < 0.05$).

Table 2. Comparison of time that calves were either active or inactive during observation periods of focal lactating females (≥ 30 min) ($t = 1.96$, $n = 27$, $P = 0.03$).

Calf behaviour	Time (%)		<i>n</i>
	Mean	SE	
Active	61.3	0.6	27
Inactive	39.7	0.6	27

($F_{[1,58]} = 13.929$, $P < 0.001$) exerted significant effects on the amount of time females spent foraging (Fig. 2); foraging was not affected by an interaction between these factors ($F_{[2,61]} = 0.705$, $P = 0.498$). When the effect of distance to cover was held constant, significant differences in foraging existed among all calf-status categories. Specifically, females with active calves spent significantly less time foraging than nonlactating females and females with inactive calves, respectively (Table 1). Nevertheless, while females with inactive calves foraged substantially less than nonlactating females, these differences were not significant (Table 1). Overall, our results show that females with young increase foraging rates, on average, by more than 13% when calves are inactive compared with periods when calves are active.

To evaluate whether these results might be a consequence of our use of different females in each group, including unknown ones, rather than indicating differences within individuals that adjusted their vigilance and foraging in response to calf activity per se, we restricted our analyses to known females when calves were either active or inactive at the same fixed distance to cover. These contrasts revealed that maternal behaviour during calf activity was characterized by significant increases in intra-individual vigilance ($t = 3.778$, $n = 18$, $P = 0.002$) and decreases in foraging ($t = -3.982$, $n = 18$, $P = 0.001$). Hence, these two types of results demonstrate that calf activity and maternal behaviour are associated both within and among individuals.

By comparing pooled data from females with and without young, irrespective of activity, it is possible to evaluate directly the degree to which foraging rates are compromised by the presence of young. Because calves did not spend equivalent periods of time active and inactive during female-observation periods (based on continuous focal observations ≥ 30 m, $n = 27$) (Table 2), calculations of overall foraging rates for lactating females combined the predicted foraging rates for females during periods of calf activity and inactivity (see Table 1) as well as the amount of time, on average, during which calves were engaged in each behavioural modality (see Table 2). Our results indicate that neonate pres-

Fig. 2. Effect of calf status and distance to protective cover on proportion of time spent foraging for adult female moose ($r^2 = 0.509$, $F_{[5,58]} = 25.833$, $P < 0.0001$).

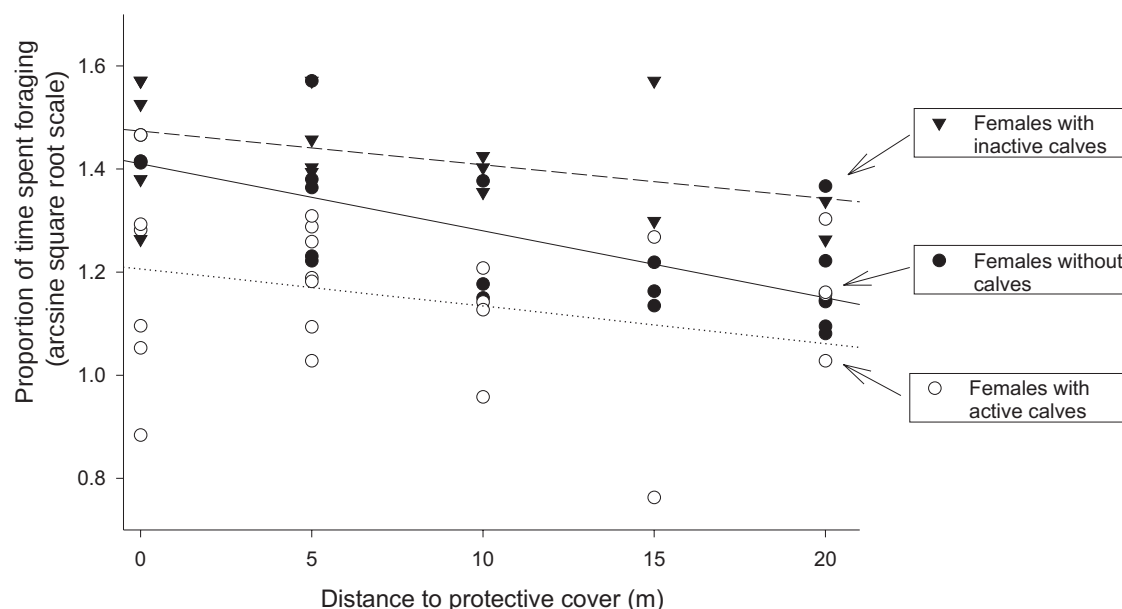


Table 3. Comparison of overall time lactating and nonlactating females spent foraging during focal animal observation periods.

Maternal status	Percent time spent foraging		n
	Mean	SE	
Lactating	86.2	2.9	43
Nonlactating	88.6	2.7	23

Note: Foraging budgets for lactating females are adjusted for variation in calf activity ($t = 0.562$, $n = 66$, $P = 0.576$).

ence did not affect the overall time moose spent foraging ($t = 0.562$, $df = 62$, $P = 0.576$), so increased foraging during times of calf inactivity compensated for periods of low foraging when calves were active (Table 3). These findings demonstrate that overall foraging rates for lactating females were equivalent to our baseline, or maximum, values for nonlactating individuals.

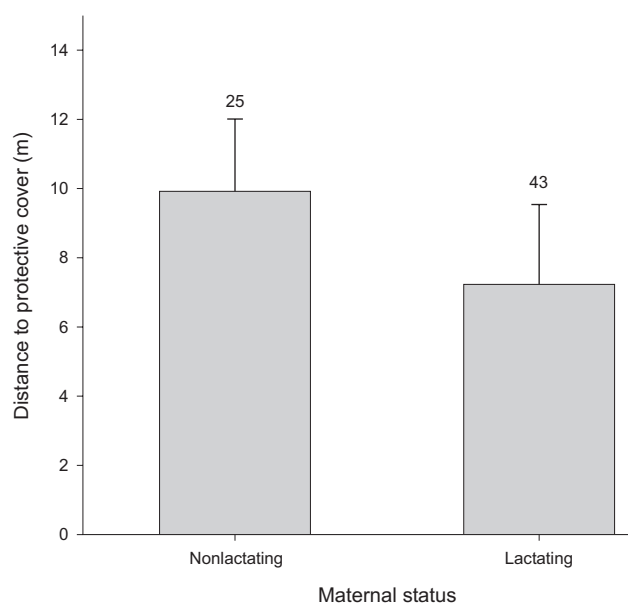
Use of protective cover

When comparing mean distances to protective cover for individuals of differing calf status, we detected a weak association between calf activity and distance to protective cover (Kruskal–Wallis test, $H_2 = 5.496$, $P = 0.064$). However, irrespective of calf activity, females with young spent considerably more time in close proximity to cover than did females without young (Mann–Whitney U test, $U = 361.5$, $n_{\text{calf}} = 43$, $n_{\text{no calf}} = 25$, $P = 0.025$; Fig. 3).

Discussion

The cost of offspring to mothers is high, not only because of energetic and nutrient demands associated with lactation but also because of constraints associated with the anti-predator behaviour that is needed to enhance the protection

Fig. 3. Comparison of distances (mean and SE) to protective cover between lactating and nonlactating female moose ($U = 361.5$, $n = 68$, $P = 0.025$). “Lactating” females included individuals with both active and inactive calves.



of young from predation. Our results indicate that when offspring are under intense predation pressure, female moose adopt an antipredator strategy that is sensitive to variation in calf activity as well as proximity of mothers to protective cover. This behavioural strategy appears to resolve the perceived maternal conflict associated with providing both optimal protection and provisioning of young.

Activity of neonates has potentially important implications with respect to not only their own fitness but also that of their mothers. While neonate activity represents a direct cost to mothers, owing to foraging compromises associated

with increased antipredator behaviour and, perhaps, increased predation per se, benefits may include increased offspring survival and attendant fitness correlates associated with locomotor development (FitzGibbon 1990; Byers 1998). Thus, selection may favour mothers that tolerate potentially risky calf behaviour despite costs associated with increasing vigilance when putative calf vulnerability to predation is increased.

In this study, moose calves exhibited temporal variation in activity that was not always associated with activity of mothers, thereby providing the opportunity to test whether calf activity influenced maternal antipredator strategies. Our results show that when calves were active, mothers adjusted their own behaviour to putative heightened calf vulnerability by increasing antipredator vigilance. By doing so, mothers may enhance visual, auditory, and olfactory sensitivity to environmental stimuli, and thereby maximize their ability to detect and avoid predators. Such behaviour is decreased and may be virtually absent in environments where grizzly bears and wolves have been extirpated (Berger 1999). What remains unclear, however, is whether the loss of predation in other systems may concomitantly alter not only prey behaviour per se but behavioural dynamics involving mothers and neonates and the associated trade-off between foraging and predation risk. Yet in areas with relatively high predation rates, early detection of predators can have a strong effect on the outcome of predator-prey encounters (FitzGibbon 1988). This may be especially true for mothers with relatively non-precocious young, such as moose, whose escape capabilities are compromised by the presence of neonates with limited mobility. Such individuals, being unable to outrun predators, instead adopt a hiding strategy (and in a last resort, active defense) that is critically dependent on early detection of predators in order to be successful (Lent 1974). Therefore, it is not surprising that maternal vigilance, in an area subject to high predation pressure, is highly sensitive to behavioural changes in neonates that influence the consequent likelihood of predator detection.

An important cost of increasing vigilance can be a reduction in forage intake (Illius and FitzGibbon 1994). Our results suggest that moose were able to compensate for foraging losses incurred when calves were active by increasing food intake during periods of calf inactivity. This strategy enables mothers to increase antipredator vigilance during periods when calves are most vulnerable, and increase food intake when calves are, relatively, safe from the risk of predation. Thus, mothers are able to attain an overall rate of forage intake that is similar to baseline values for nonlactating females, thereby minimizing foraging compromises associated with having offspring. Consequently, mothers can mediate two important costs of juvenile survival, protection and energetic provisioning, by adjusting effort allocated to vigilance and foraging depending upon whether calves are active or not.

The use of protective cover, or other physical refugia, can reduce individual vulnerability to predation (Lima and Dill 1990; Lazarus and Symonds 1992). Since individuals with offspring face challenges associated with reducing the risk of predation to vulnerable neonates, such individuals would be expected to increase their use of habitat features that reduce this risk (Edwards 1983; Festa-Bianchet 1988; Berger

1991). Our results suggest that moose with calves adopt a strategy which is consistent with this expectation, so that, irrespective of calf activity, mothers spent significantly more time closer to protective cover than did individuals without young. By concentrating activity in safer areas, mothers may be able to minimize risk of predation to their neonates and concomitantly increase foraging rates, thereby increasing the chances of offspring survival. However, it is possible that inter- and intra-specific variation may exist, so certain predator species or individuals may be more effective at capturing prey in particular habitat types than in others; however, existing empirical data are inadequate to evaluate this possibility in North American moose-predator systems. We contend that the use of protective cover enables prey to limit the effectiveness of key sensory modalities used by all predators to find prey, primarily vision, and that the use of such refugia benefits prey by reducing predator-encounter rates, thus minimizing the overall probability of successful attack.

Although our data stem from a single study in an area with high predation rates, it will be of interest to evaluate whether studies in areas where predation has and has not been relaxed yield similar results with respect to offspring effects on maternal investment. Because some types of behaviour have the capacity to be highly labile (Byers 1997; Berger 1999), it may not be surprising that mothers adjust rapidly to environment-specific situations where predation as a selective force has been relaxed. The future challenge is at least threefold: to assess the extent to which predation operates and (or) has changed rather than merely make simple assumptions about its operation, to determine the temporal pace at which behavioural variability may occur, and to evaluate the causes and consequences at individual and population levels of changing patterns of maternal trade-offs as a consequence of predation intensity.

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