



## Vigilance by female Dall's sheep: interactions between predation risk factors

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**Abstract.** Data on adult female Dall's sheep, *Ovis dalli dalli*, were used to assess how predation risk factors combine to affect vigilance. An interactive factors hypothesis was proposed, and whether predation risk factors have interactive (or multiplicative) effects on vigilance was tested. Because most studies have implicitly assumed additivity, for illustrative purposes the alternative but less plausible independent factors hypothesis, in which predation risk factors have independent (or additive) effects on vigilance, was also tested. It was predicted that natural selection would favour interactive relationships because, rather than making redundant investments in anti-predator behaviour, animals that are already 'safe enough' can make greater investments in foraging (i.e. an animal in a very large group need not have a strong vigilance response to increasing distance to refuge). Results supported the interactive model and did not support the independent model. Sheep became less vigilant as group size increased, but this relationship became weaker as they got closer to cliffs. Sheep also became more vigilant as distance to cliffs increased, but this relationship became weaker as group size increased. Finally, a posteriori analysis suggested that when sheep were within 20 m from obstructive cover, the interaction between group size and distance to cliffs affected vigilance more strongly than when sheep were further from obstructive cover. Rather than implicitly assuming that predation risk factors have additive effects, as most previous studies have done, generating predictions with the interactive factors hypothesis may be a more realistic approach for understanding vigilance and other anti-predator behaviours.

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Vigilance is not mutually exclusive with processing food, but it generally is with food searching and handling. Thus, unless plant density and biomass are high and food intake is limited only by processing rates, herbivores tend to experience a trade-off between vigilance and feeding (Illius & FitzGibbon 1994; reviewed in Lima & Dill 1990).

Although food density, intra-group competition and other factors not directly related to predation may also affect vigilance, it is largely concerned with looking for predators (reviewed in Elgar 1989). A more vigilant individual may be safer, but excessive vigilance may also bring an unnecessary loss of feeding opportunities. Thus, the optimal level of vigilance during feeding should be sensitive to predation risk factors (reviewed in Elgar 1989; Lima & Dill 1990). This hypothesis is supported by empirical studies in which vigilance decreased as group size increased (reviewed in

Elgar 1989; Lima & Dill 1990), as distance to obstructive cover increased (reviewed in Elgar 1989; Lazarus & Symonds 1992) and as distances to a refuge decreased (Risenhoover & Bailey 1985; reviewed in Elgar 1989).

Responses of vigilance to the independent effects of the above and other factors are relatively well known, and some studies have assessed how different species (e.g. Underwood 1982; Berger & Cunningham 1988; Cords 1990; FitzGibbon 1990; Scheel 1993) or sex-reproductive classes (e.g. Berger 1991) differ in their vigilance response to the same risk factors. Most studies that have considered multiple risk factors, however, have not discussed how such factors interact to affect vigilance within a species or sex-reproductive class (e.g. Underwood 1982; Cords 1990; Berger 1991; Lazarus & Symonds 1992; Pöysä 1994). An exception is Risenhoover & Bailey's (1985) study of bighorn sheep, *O. canadensis*, which implicitly assessed interactions and concluded that foraging efficiency (as affected by vigilance costs) was more

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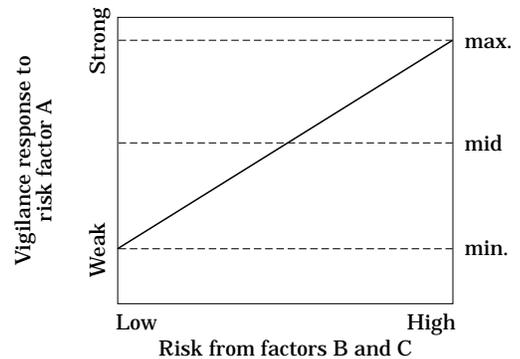
sensitive to the effects of distance to refuge (cliffs) and density of obstructive cover in groups of 1–5 than in groups of 6–10 and 11–36 sheep.

In this study I used data on adult female Dall's sheep to assess how predation risk factors combine to affect vigilance. I proposed an interactive factors hypothesis ('interactive model') and tested whether predation risk factors have interactive (or multiplicative) effects on vigilance. Also, given that most studies have implicitly assumed additivity, for illustrative purposes I tested the alternative but less plausible independent factors hypothesis ('independent model'), in which predation risk factors have independent (or additive) effects on vigilance.

In the interactive factors hypothesis, the magnitude of the vigilance response to a given factor depends on the level of predation risk created by other factors. For example, if overall risk is high because animals are far from a refuge and near obstructive cover, then vigilance should increase strongly as group size becomes smaller. In contrast, if overall risk is low because animals are near a refuge and far from obstructive cover, then vigilance should increase little or not at all if group size becomes smaller, thus allowing the animal to take greater advantage of feeding opportunities (Fig. 1). We would expect natural selection to favour such interactive relationships.

In the independent factors hypothesis, the vigilance response to a given factor always has a constant magnitude, regardless of the level of predation risk created by other factors. For example, vigilance will have the same response to group size, regardless of distances to refuge and obstructive cover. Thus, in this model, the vigilance response to a given factor overemphasizes safety at the expense of foraging when risk from other factors is low, and overemphasizes foraging at the expense of safety when risk from other factors is high (Fig. 1). We would not expect natural selection to favour such independent relationships.

Dall's sheep are well suited for testing these hypotheses. Like other mountain Caprinae (Geist 1987), they can find almost complete security from terrestrial predators on cliffs (Murie 1944; Sumanik 1987) where food is usually scarce, but can also feed in food-rich areas away from cliffs. They have a wide range of group sizes, and live where large carnivores still abound. Furthermore, in other taxa it may not be obvious whether



**Figure 1.** Interactive versus independent models. In the independent model (broken lines), the vigilance response to risk factor A is constant, regardless of risk from factors B and C. In the interactive model (solid line), the vigilance response to factor A is sensitive to risk from factors B and C. Thus, a response to factor A predicted by an independent model overemphasizes safety at the expense of foraging when above the diagonal line of the interactive model, and overemphasizes foraging at the expense of safety when below the same line. In contrast, the diagonal line of the interactive model predicts a weak vigilance response to factor A when risk is low due to factors B and C, and a strong vigilance response to factor A when risk is high due to factors B and C.

vegetation cover is obstructive or protective, leading to confounding interpretations of the utility of vigilance (Lima 1987; Lazarus & Symonds 1992). In mountain sheep (*Ovis* spp.), however, tall/dense vegetation cover appears to be only obstructive (Geist 1971), and its effect on vigilance should be straightforward to interpret.

For adult female sheep engaged in a foraging bout, I tested the interactive factors hypothesis with the following predictions.

- (1) Vigilance increases with decreasing group size, but the magnitude of this response becomes smaller as distance to cliffs decreases and/or distance to obstructive cover increases.
- (2) Vigilance increases with increasing distance to cliffs, but the magnitude of this response becomes smaller as group size increases and/or distance to obstructive cover increases.
- (3) Vigilance increases with decreasing distance to obstructive cover, but the magnitude of this response becomes smaller as group size increases and/or distance to cliffs decreases.

Predictions of the independent factors hypothesis were that group size, distances to cliffs and obstructive cover would affect vigilance in the

directions described above, but that these effects would be additive rather than multiplicative.

## METHODS

### Study Site Characteristics

#### *Study site, season and animals*

Field work took place on the Sheep Mountain winter range (61°00'–61°10'N, 138°30'–138°150'W), Kluane National Park Reserve, Yukon Territory, Canada, between 13 March and 24 May 1993. The study site has a semi-arid, continental climate, and its phytogeography has been described by Hoefs et al. (1975). Except for the occasional harvest by native people, which was legalized in the 1970s, this population has not been legally hunted since 1942.

The southerly slopes of Sheep Mountain, along with adjacent Williscroft Creek, are the traditional winter and lambing range of a population that was estimated at about 300 sheep in early June 1993. This estimate included 100 males (3 years and older), 108 adult females (>2.75 years old, sensu Hoefs & Cowan 1979), 30 2-year-olds of both sexes (pooled), 12 yearlings, and 40–50 young of the year (M. Hoefs, personal communication).

Only data on non-lactating adult females within 6 weeks prior to the 1993 lambing season are presented here. The proportion of pregnant females was unknown.

#### *Risk-related habitat attributes*

Sheep Mountain is a mosaic of open areas with unobstructed visibility and areas with obstructive cover made up of *Salix* spp., *Picea glauca* and *Populus* spp. Cliffs of different sizes are present throughout the study area, but some of the lower slopes used by sheep may be over 500 m from them (see map in Hoefs et al. 1975). Given that predators such as wolves, *Canis lupus*, can manoeuvre on extremely rugged terrain (Hoefs et al. 1986; Sumanik 1987), small isolated outcrops are unlikely to provide sufficient safety for sheep. Thus, I defined cliffs as continuous areas of exposed bedrock with a minimum incline of 45°, reaching a minimum height of 20 m and minimum width of 100 m. I intuitively judged these to be the minimum topographic features that would give

sheep a substantial advantage for escaping predators. Most cliffs in the study area were much larger and steeper.

#### *Predators*

At Sheep Mountain, coyotes, *C. latrans*, are the main predators of adult sheep. Other potential predators include wolves, wolverines, *Gulo gulo*, grizzly bears, *Ursus arctos* and lynx, *Felis lynx*. In addition to being at risk from these predators, very young lambs can also be taken by golden and bald eagles (*Aquila chrysaetos* and *Haliaeetus leucocephalus*, respectively), and red foxes, *Vulpes vulpes* (Hoefs & Cowan 1979; Burles & Hoefs 1984; Nette et al. 1984; Hoefs et al. 1986).

During the study, predation pressure was particularly low. I recorded my data during a low in the 10-year population cycle of snowshoe hares, *Lepus americanus* (e.g. Krebs et al. 1986), which are the winter staple of coyotes and lynx (Keith et al. 1977). In a study area with its western boundary only 5 km away from Sheep Mountain, the populations of these predators plunged in response to hare declines. At the onset of the 1992–1993 winter, lynx and coyote populations were estimated to be, respectively, a quarter and one-fifth of what they had been during the previous peak of the hare cycle (Kluane Boreal Forest Ecosystem Project; S. Boutin et al., personal communication). By the time I began the study in late winter, lynx and coyotes were probably even scarcer. The extreme coyote decline coincided with a sheep population that was slightly larger than the average recorded since 1969 (M. Hoefs, personal communication), suggesting a particularly low ratio of this main predator to sheep.

Coyotes were known to be present on 22 days of the study (31.9% of field days, including 14 days in which they were heard but not seen). Bears or wolves were also recorded on 3 days. I am aware of only two chases of sheep by terrestrial predators (one by a coyote, the second by a grizzly bear), and neither resulted in predation. Only four sheep mortalities were recorded for the winter and spring of 1992–1993. Of these mortalities, three were of unknown cause (M. Hoefs, personal communication) and one involved one wolf and six coyotes (both species were present at the carcass, but the actual killing was not observed: Kluane National Park Staff, personal communication).

When predators interacted with sheep, or when coyotes vocalized either during the focal animal sample or within 2 h prior to it, I considered predator presence to be a factor potentially affecting vigilance. Sample sizes were inadequate for analysis of direct predator effects on vigilance. Thus, I excluded all samples with predator presence from analyses.

### **Defining a Group**

Deciding which individuals do or do not belong to a group is one of the most overlooked issues in the methodology of behavioural studies. Ambiguities arise when animals are not tightly clumped, particularly if individuals enter and leave clusters of conspecifics during short periods of time (Martin & Bateson 1993). Some ungulate studies have offered either no definition (e.g. Berger 1978, 1991; Risenhoover & Bailey 1985; Prins & Iason 1989) or an ambiguous one (e.g. Berger & Cunningham 1988). Others have defined groups on the basis of some arbitrary inter-individual distance (e.g. Alados 1985; FitzGibbon 1990; Scheel 1993; Frid 1994). Although, the latter may be convenient, it is also tautological. Small shifts of inter-individual distances are not necessarily biologically meaningful, and a definition of group should be robust to these differences.

I defined a group as a set of individuals which, in terms of the structural attributes of the environment, were under similar predation risk. In other words, I considered sheep to be in the same group if they shared an open space contained by the same obstructive cover and/or cliffs, or if they were on the same aspect of the same cliff. This rationale is based on the fact that obstructive cover may hide predators (e.g. Prins & Iason 1988) and that cliffs may be refuges for sheep (Murie 1944; Sumanik 1987). Perhaps most importantly, these three-dimensional structures may visually separate sheep from each other, affecting their ability to stay together in large groups (Jarman 1974), which ultimately affects predation risk (reviewed in Elgar 1989).

The following observation of a coyote chase supports this rationale. Fifteen sheep (adult females and juveniles) were about 350 m from the nearest cliff when a single coyote ran towards them. The sheep reacted with a short run, stopped, clustered tightly and turned staring at the coyote. Shortly after, the coyote left without

attempting any further attack. Only 75–100 m from the attacked group, but visually separated by a strip of forest, 11 sheep not only showed no reaction to the coyote, but continued to feed during the attack.

It could be argued that my definition of a group is invalid if individuals are widely spaced. This problem did not exist in my study. In the 94 focal animal samples in which I recorded it, the mean  $\pm$  SD distance between individuals was  $11.47 \pm 10.93$  m. (Inter-individual distances were calculated dividing mean spread of the group recorded with scan samples during a recording session (see below) divided by group size). These distances are well within the range of the arbitrary inter-individual distances of 30–50 m used by other ungulate studies to define the boundaries of groups (e.g. Alados 1985; FitzGibbon 1990; Scheel 1993; Frid 1994).

A shortcoming of my definition of a group is that it does not address social bonds. Although social bonds might not affect how group size dilutes the probability of an individual being preyed on (Hamilton 1971), they might affect vigilance by determining whether a group has sentinels (reviewed in Lima & Dill 1990). Given the short-term nature of my study and that animals were unmarked, it was impossible to consider social bonds in the definition. On the other hand, my definition of a group has biological validity because it addresses factors that affect both group cohesion and the boundaries of safe and dangerous zones. Furthermore, as long as animals are in discrete three-dimensional habitats, with cliffs and/or obstructive cover bounding open spaces, the definition is applicable to other ungulate studies.

### **Recording Behaviour**

#### *Behaviour definitions*

I considered sheep to be handling food if they stood clipping vegetation with their mouths, and/or if they, without walking, quickly moved their mouths from the vegetation patch they had just clipped to the next patch where they continued clipping. I considered sheep to be searching for food if they took one or more steps away from either the vegetation patch where they had been handling food or from where they had stood in vigilant posture. I considered sheep to be vigilant

if they interrupted food searching or handling to stand with the head raised above shoulder height. Vigilance was not mutually exclusive with processing food (chewing and swallowing).

Mountain sheep are primarily grazers (Geist 1971); thus their heads were down to the ground during most of the time that they were food searching or handling. The only times when food handling and vigilance may have not been entirely mutually exclusive was when sheep kept their head above shoulder height while browsing on tall shrubs. Vigilance under this condition is probably much less intense than when sheep are not handling food and was not recorded. These criteria are unlikely to have substantially affected results; the mean  $\pm$  SD proportion of observation time for which sheep browsed on shrubs above their shoulder height was less than  $0.94 \pm 3.31\%$  ( $N=105$  focal animal samples).

#### *Focal animal sampling*

Collection of data used for analyses began after 12 days of preliminary behavioural observations. This practice period allowed observers to fine-tune recording skills. To minimize disturbance to the focal animal and potential predators, observers used spotting scopes and were over 200 m from focal animals.

I used continuous recording of focal individuals (reviewed in Martin & Bateson 1993) to measure the time that sheep spent vigilant, food searching and food handling during feeding bouts. From these records, which were timed to the nearest second, I calculated the proportions of observation time that sheep spent vigilant. A notebook computer (TRS-80 Model 100) programmed as an event recorder was the recording medium.

Simultaneously with the continuous recording, a second observer recorded the focal animal's group size, distances to the nearest cliffs and nearest obstructive cover, the spread of the group (or maximum distance between two group members), and other variables with an instantaneous scan (reviewed in Martin & Bateson 1993) at the start of the sample and every subsequent 3 min. These measurements were averaged to describe the mean conditions that may have affected focal animals' vigilance (group size rarely changed during a recording session). To estimate the distances recorded during scans, observers used the 1:6200 phytogeographic map of Hoefs et al. (1975), as

well as known reference points on the landscape (e.g. sheep torso lengths, flagging, the length of cliff bands). One oversight is that observers measured distance to the nearest obstructive cover only, and I did not account for the potential effect of having obstructive cover in more than one direction (as in a clearing surrounded by forest). During scans, observers also recorded whether an animal's position in the group was central or peripheral. I considered position in the group to be undefined if group geometry was linear or if there were less than five animals in the group.

Recording sessions began when sheep were either handling or searching for food. This recording rule might underestimate vigilance in relation to the other two activities (Altmann 1974), but the bias should be constant and have little bearing on analyses of vigilance responses to risk. Recording sessions ended either after 15 min (69.5% of all samples) or if the animal stopped handling food plants for 1 min. If the latter occurred, I eliminated the last minute from the sample to exclude the transition to non-feeding activities. I assumed that these criteria (Underwood 1982, 1983) limited my sampling to animals that were feeding intensively, and thus that individual differences in short term hunger caused little variability of vigilance (Krebs & Kacelnik 1991) between my samples.

#### *Selecting a focal animal*

When selecting a focal animal for observation, I attempted to evenly distribute sampling throughout the entire range of conditions used by adult females; that is, I tried to avoid skewing the distribution of independent variables towards the sheep's preferred habitats and social situations. Thus, when available for our observation, I chose focal animals in under-sampled combinations of independent variables (e.g. sheep in small groups, far from cliffs and near obstructive cover) over other potential focal animals. If all groups available for observation were under the same potential risk, my choice of group and focal animal was random.

#### *Independence of sheep observations*

Sheep were not marked. To minimize the potential problem of individuals contributing more

**Table I.** Reduced regression model estimating vigilance responses (arcsine square-root of % time vigilant) of adult female Dall's sheep

Variable (log-transformed)	Included in reduced model	Regression coefficient ( $\pm$ 95% CI)	Standardized regression coefficient	Tolerance	<i>P</i>
Constant	Yes	0.12 ( $\pm$ 0.087)			0.008
Distance to cliffs	Yes	0.12 ( $\pm$ 0.052)	0.54	0.59	<0.001
Group size $\times$ distance to cliffs	Yes	-0.056 ( $\pm$ 0.020)	-0.61	0.59	<0.001
Group size	No	0.045		0.055	0.65
Distance to obstructive cover	No	-0.16		0.93	0.10
Distance to cliffs $\times$ distance to obstructive cover	No	-0.16		0.60	0.11
Group size $\times$ distance to obstructive cover	No	-0.081		0.28	0.42
Group size $\times$ distance to cliffs $\times$ distance to obstructive cover	No	-0.087		0.21	0.38

ANOVA summary for reduced model:  $R^2=0.24$ ,  $F_{2,102}=16.21$ ,  $P<0.001$ ,  $SEE=0.11$ . Group sizes ranged from 1 to 100, distances to cliffs from 5 to 850 m and distances to obstructive cover from 3 to 400 m.

than one observation to the data set (Machlis et al. 1985), I considered my observations to be biologically independent only if they (1) involved individuals that I could temporarily distinguish by their position in the landscape or (2) occurred on different days. Furthermore, data were collected from a population of 108 adult females. Given this large population size, I believe that pseudoreplication probably occurred at an acceptably low level.

### Statistical Analyses

Transformations were used to meet the assumptions of normality and homoscedasticity for the dependent variable (Kleinbaum & Kupper 1978; McCullagh & Nelder 1983; Zar 1984). Diagnostic tests were used to confirm the success of transformations and to check other assumptions of regression (Kleinbaum & Kupper 1978; Wilkinson 1990).

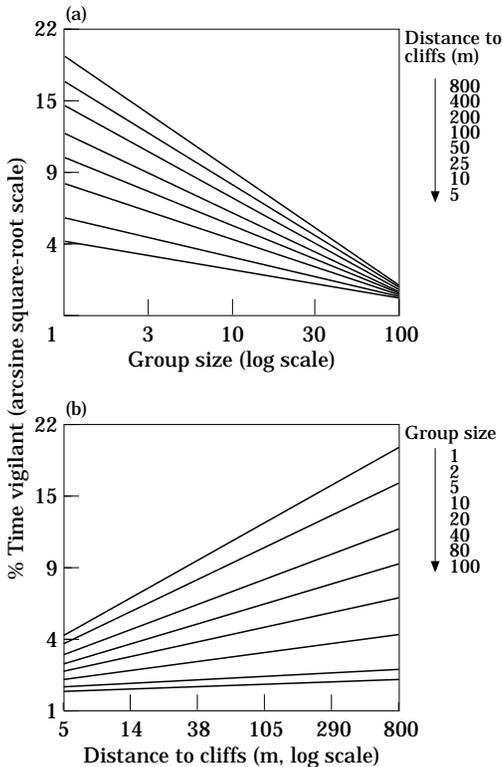
I reduced the model to its most significant form with backward step-wise procedures (Kleinbaum & Kupper 1978; McCullagh & Nelder 1983; Wilkinson 1990). Stepping was non-automated and the criteria for removing or re-entering variables into the model were based both on significance values of 0.05 and on tolerance values. (Tolerance is 1 minus the multiple correlation between a predictor and the remaining predictors in the model. Setting a minimum tolerance value prevents the construction of highly multicollinear models.) Variables could not become part of the

significant model unless their tolerance was greater than 0.1 (Wilkinson 1990).

## RESULTS

### Effects of Group Size and Distance to Cliffs

The reduced regression model showed that vigilance decreased with increasing group size. The magnitude of this response, however, became progressively smaller (i.e. the slope of the regression line became progressively shallower) as distance to cliffs decreased (Table I, Fig. 2a). Vigilance increased with distance to cliffs, but the magnitude of this response became progressively smaller as group size increased (Table I, Fig. 2b). Figure 2b suggests that distance to cliffs had almost no effect on vigilance when sheep were in groups of 80 or more members. In fact, standardized regression coefficients (Zar 1984) indicated that, of the significant variables I tested, the interaction between group size and distance to cliffs had the strongest effect on vigilance (Table I). The patterns shown by the reduced regression model can also be seen in descriptive plots of actual data (Fig. 3). These plots show that there is a different relationship between vigilance and group size for sheep that are near and far from cliffs (Fig. 3a), and a different relationship between vigilance and distance to cliffs for small and large groups (Fig. 3b). These results support predictions 1a and 2a of the interactive factors hypothesis (see Introduction) and do not support the independent factors hypothesis.

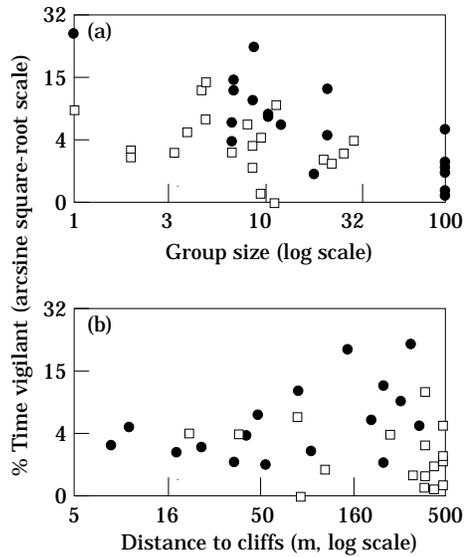


**Figure 2.** Estimated response of vigilance ( $V$ ) to the interaction of group size ( $G$ ) and distance to cliffs ( $C$ ) for adult female Dall’s sheep ( $N=105$  focal animal samples). The families of lines are generated from the model (arcsine square-root  $V=0.12+0.12(\log C) - 0.056(\log C)(\log G)$ ). ( $R^2=0.24$ ;  $P<0.001$ ; Table I). (a) The estimated response to group size for sheep feeding, in decreasing order of  $Y$ -intercept, at 800, 400, 200, 100, 50, 25, 10 and 5 m from cliffs. (b) The estimated response to distance to cliffs for sheep feeding in groups with, in decreasing order of  $Y$ -intercept, 1, 2, 5, 10, 20, 40, 80 and 100 members.

**Effects of Distance to Obstructive Cover**

Distance to obstructive cover had no significant effect on vigilance and was excluded from the reduced model of Table I. Although this result does not support my prediction that vigilance would be affected by distance to obstructive cover, it leads to neither rejection nor support of the interactive or independent models.

The possibility that distance to obstructive cover does affect vigilance as an interactive factor is supported by a posteriori analysis. I tested the significant model estimating the interaction of



**Figure 3.** Examples of the actual response of vigilance to the interaction of group size and distance to cliffs. (a) The effect of group size between sheep within 1–25 m (□) versus sheep within 400–800 m (●) from cliffs. (b) The effect of distance to cliffs between sheep in groups of 30–100 members (□) versus sheep in groups of 2–4 members (●). Because continuous, three-dimensional data had to be categorized to be shown in two dimensions, these examples are only for descriptive purposes; see Fig. 2 for the statistically significant trends.

distance to cliffs and group size (Table I) in three subsets of distances to obstructive cover: 20 m or less, 21–50 m and over 50 m. For sheep within 20 m of obstructive cover, the interaction between group size and distance to cliffs was much stronger ( $R^2=0.42$ ,  $SEE=0.11$ ,  $P<0.001$ ,  $N=32$ ) than for sheep at distances to obstructive cover of 21–50 m ( $R^2=0.14$ ,  $SEE=0.12$ ,  $P>0.05$ ,  $N=30$ ) and over 50 m ( $R^2=0.16$ ,  $SEE=0.16$ ,  $P=0.04$ ,  $N=43$ ) or for the entire data set (Table I;  $R^2=0.24$ ,  $P<0.001$ ,  $N=105$ ). These results suggest that sheep within 20 m of obstructive cover are more sensitive to the effects of group size and distance to cliffs than sheep further from obstructive cover.

**Position in Group: a Non-effect?**

Whether an animal had a central or peripheral position in the group affected vigilance in studies of various taxa (reviewed in Elgar 1989), including bighorn sheep (Berger & Cunningham 1988).

Thus, although position in group was not a focus of my predictions, it potentially was an important factor to control. Of the 80 samples in which I recorded this variable, the focal animals' position was undefined (group geometry was linear or there were less than five animals in the group) in 29 samples (36.3%), and in 31 samples (38.8%) sheep switched between being central and peripheral. Only once did a sheep remain in a central position throughout the sample. Thus, it is unlikely that position in group significantly affected my results.

## DISCUSSION

The results supported the interactive factors hypothesis, in which predation risk factors have an interactive effect on vigilance. The hypothesis that predation risk factors act independently, which has been implicitly assumed by most previous studies (see Introduction) was not supported.

In accordance with the interactive model, sheep became less vigilant as group size increased, but the magnitude of this relationship decreased as sheep got closer to cliffs. This result suggests that increasing group size decreases predation risk more strongly when animals are far from a refuge than when they are near a refuge. Sheep also became more vigilant as distance to cliffs increased, but the magnitude of this relationship decreased with increasing group size. In their study of bighorn sheep, [Risenhoover & Bailey \(1985\)](#) made a similar observation.

Although distance to obstructive cover had no statistically significant effect on vigilance, a posteriori analyses suggested that this factor is part of a three-way interaction with group size and distance to cliffs. When sheep were 20 m or less from obstructive cover, the interaction between group size and distance to cliffs affected vigilance much more strongly than when further from obstructive cover. I expected distance to obstructive cover to affect vigilance, because coyotes and other predators are likely to hide behind cover while stalking sheep. Perhaps this variable was excluded from the reduced regression model because I measured distance to only the nearest obstructive cover, and having obstructive cover nearby in more than one direction (as in a clearing surrounded by forest) may have affected the results. Future studies

should consider measuring distance to obstructive cover in four standard directions around a 360° radius, and whether these distances should be combined in an additive, multiplicative or some other function.

### Predator and Prey Numbers as Predation Risk Factors

I made observations when the ratio of coyotes (the main sheep predator at my study site) to sheep was particularly low, suggesting a low encounter rate between the two species. The ratio of predator to prey is itself a predation risk factor (see [FitzGibbon & Lazarus 1995](#)). The interactive model predicts that prey respond to temporal shifts of this factor by accordingly relaxing or intensifying their vigilance response to other factors. This prediction may be testable by comparing vigilance responses between periods in which predator and/or prey numbers differ.

### The Interactive Model as a General Hypothesis

With the exception of [Risenhoover & Bailey \(1985\)](#), studies considering multiple predation risk factors have implicitly assumed that such factors affect vigilance independently. This assumption, which I formalized in the independent model, implies that animals should always become more vigilant as risk due to any one factor becomes greater, even though other conditions may have reduced risk to a very low, even negligible level. In the independent model, safety can be over-emphasized at the expense of foraging, and vice versa ([Fig. 1](#)). Selection against these behaviours would be strong.

In contrast, the interactive model allows for the possibility that, when risk is low due to other factors, animals can increase vigilance little or not at all in response to a particular factor that would otherwise strongly affect vigilance. Thus, rather than making redundant investments in anti-predator behaviour (as in the independent model), animals that are already 'safe enough' can make greater investments in foraging ([Fig. 1](#)), which would be favoured by natural selection. Indeed, [Dall's](#) sheep in the present study made decisions based on several simultaneous criteria. Rather than implicitly assuming that predation risk factors have additive effects, generating predictions with the interactive model may be a more realistic

approach for understanding vigilance and other anti-predator behaviours.

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