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Vigilance and predation of a forest-living bird species depend on large-scale habitat structure

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Prey often use visual cues to detect predators, and consequently, many studies have assessed the effect of small-scale habitat structure on prey antipredator vigilance. This scale may be inappropriate to assess the link between habitat structure and vigilance, however, because visually hunting predators often detect prey from several hundred meters away. As a result, large-scale habitat structure could affect both the hunting decisions of predators and antipredator behaviors of prey. Here we investigated the effect of small- and large-scale habitat structure, as well as group composition (kinship) on vigilance allocation of breeders in the Siberian jay *Perisoreus infaustus*. Vigilance had an antipredator function and was increased after exposure to a predator model. Small-scale habitat structure did not affect vigilance rates, however, habitat structure of the whole territory, measured as the proportion of visual cover, affected vigilance depending on group composition. Breeders with retained offspring (kin) in their group were more vigilant in managed open territories than on pristine dense territories, whereas breeders without kin in their groups did not adjust vigilance rates in relation to large-scaled habitat structure. Earlier studies have revealed that hawks, the main predators of jays, primarily kill non-kin group members living in groups inhabiting open territories. Therefore, we suggest that breeders adjusted their vigilance depending on the habitat-specific predation risk to protect their retained offspring. This demonstrates that large-scale habitat structure affects predator–prey interactions and is crucial to understanding spatial variation in antipredator allocation and mortality. *Key words:* delayed dispersal, family group, goshawk *Accipiter gentilis*, population dynamics, predation, risk taking, sparrow hawk *Accipiter nisus*. *[Behav Ecol 20:709–715 (2009)]*

The risk of being killed by a predator affects the majority of prey decisions. Numerous studies have demonstrated that prey respond quickly to changes in predation pressure (Lima and Bednekoff 1999) and that animals manage their predation risk by changing feeding areas, activity levels, or dispersal patterns (Lima and Dill 1990; Brown 1999; Caro 2005). Perhaps, one of the most intensely studied antipredator responses is the trade-off individuals make between energy intake and vigilance (Lima and Dill 1990; Lima and Bednekoff 1999). Most prey regularly scan their surroundings to detect threats, but such antipredator vigilance comes at the cost of reduced foraging efficiency (Elgar 1989). In a long-term perspective, increased vigilance allocation has a negative impact on fitness through a higher risk of starvation (McNamara and Houston 1987; Watson et al. 2007).

To minimize the costs of antipredator vigilance, many animals forage in groups. Being in a larger group results in a higher overall vigilance, allowing individual group members to lower their time allocated into vigilance (Pulliam 1973). As a result, an individual can maximize the energy intake while reducing its current predation risk. Individuals that live together with relatives have been demonstrated to cooperate in their antipredator allocation, to create safer feeding conditions for kin (Clutton-Brock et al. 1999; Griesser 2003).

In addition to vigilance benefits that arise from grouping together, prey can manage their predation risk through selection of their foraging habitat. The effect of habitat structure on vigilance, however, is not straightforward because it depends on the way prey escape from their predators (Hannon et al. 2006). Animals that lack antipredator refuges and escape attacks by sheer speed generally increase their vigilance when foraging in dense patches. This increased vigilance is due to dense vegetation impeding predator detection (Underwood 1982; Metcalfe 1984; Devereux et al. 2006). In contrast, animals that escape from their predators by seeking cover in dense patches adapt higher vigilance levels when foraging further away from cover (Arenz and Leger 1997; Brown and Kotler 2004; Carrascal and Alonso 2006).

Most studies have assessed antipredator allocation only from the prey perspective and neglected the behavior of the predators (Lima 2002). As a result, these studies have assessed the interplay between habitat structure and antipredator vigilance on a small scale in the direct vicinity of an individual (but see Tellería et al. 2001). However, the habitat scale that should determine antipredator effort is likely to depend on the hunting behavior of predators (Lima 2002; Roth et al. 2006). Visually hunting predators often detect prey from several hundred meters away and only measuring habitat effects on a small scale may give misrepresentative results. For visually hunting predators, which take their prey by surprise, the key to a successful hunt is to approach potential prey close enough before the prey becomes aware of the ongoing attack. For example, accipiter hawks (*Accipiter* spp.) initiate attacks when 50–100 m away from prey (Kenward 1982: Roth et al. 2006), and the average stalking distance of lions (*Panthera leo*) is 320 m (Stander 1991). Consequently, the distance from which predators initially detect potential prey could be much larger than the distance from which an attack is initiated.

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Thus, large-scale habitat structure should affect both the hunting behavior of predators and the vigilance of prey.

In this study, we investigated how small-scale and large-scale vegetation structure and group composition affected vigilance allocation of breeders in a forest-living bird species, the Siberian jay (*Perisoreus infaustus*). This group-living bird is a typical species of boreal forests of northern Eurasia. Jay groups occupy year-round territories and consist of a breeding pair and up to 4 nonbreeding group members (Ekman et al. 2001). The nonbreeders are either retained offspring that have delayed dispersal after independence or unrelated individuals that have immigrated into the group (Ekman and Griesser 2002; Griesser et al. 2008). The breeding pair provides their retained offspring with access to food and predator protection, benefits that are not available for immigrant group members (Griesser 2003, 2008; Griesser and Ekman 2004, 2005). As a consequence of this nepotism, retained offspring have much higher survival rates than immigrants (Griesser et al. 2006, 2008).

The main predators of jays, accipiter hawks (goshawk *Accipiter gentiles* and sparrow hawk *Accipiter nisus*; Griesser et al. 2006), are visual hunters that hunt primarily using ambush techniques (Kenward 1982; Roth et al. 2006). Jays escape from attacking hawks by seeking cover in dense vegetation patches (Griesser 2008). Earlier studies on Siberian jays have demonstrated that habitat structure of the whole territory (territory size about 0.5–1 km^2) affects both predation risk and foraging decisions. Jays living in more open territories had higher mortality rates than jays living in more visually obstructed territories (Griesser et al. 2006; Nystrand 2006a). As a consequence, jays that lived in open, high-risk territories preferred to forage closer to cover, whereas jays living on dense, low-risk territories had no such preference (Nystrand 2006b). The difference in predation risk between these 2 habitats, and thus also the antipredator behavior of jays, has been suggested to be an effect of increased prey detection rates in open territories. This is not due to a difference in predator abundance because predators are often equally observed in these 2 habitat types (Griesser et al. 2006).

Based on this background, we investigated 4 questions regarding vigilance allocation in Siberian jay breeders. 1) We examined if vigilance in jays is an antipredator behavior reflecting the current predation risk by comparing vigilance rates (i.e., the frequency of head turning during foraging; see below) of breeders before and after exposure to a predator model. 2) We assessed the effect of large-scale habitat structure on predator attack rates. An earlier study showed that predators occur equally often in open and dense habitats. However, it did not investigate if attack rates depended on habitat structure, although attack rates are a more reliable measure for the risk posed by predators. 3) We investigated whether vigilance rates depended on the large-scale habitat structure of the whole territory and/or on the small-scale habitat structure in the direct vicinity of an individual. Given that jays have higher predation rates in open territories and that jays escape an attacking predator by seeking cover in dense vegetation, breeders should be more vigilant on these high-risk territories. The effect of small-scale habitat structure is less clear. Breeders could lower their vigilance in dense patches because these patches offer shelter from attacking predators. Alternatively, dense vegetation aggravates predator detection and jays could have higher vigilance rates when foraging in dense patches. 4) We investigated the effect of the social environment on vigilance allocation. Breeders in kin groups containing retained offspring were expected to have higher vigilance levels than breeders in non-kin groups that only contained immigrants because of the nepotistic antipredator behaviors of breeders in Siberian jays.

MATERIALS AND METHODS

Study population and study site

We collected data for this study between 1999 and 2007 in a natural population of Siberian jays outside Arvidsjaur, northern Sweden (65°40′N, 19°0′E). The number of studied territories increased during the study period from 26 to 54 territories. All individuals in the study population were color banded for individual recognition. Because Siberian jays are monomorphic, we took a blood sample from all individuals for molecular determination of sex using the method described in Griffiths et al. (1998).

The forest structure at the study site is typical of the boreal zone of Fennoscandia, covering a gradient from intensely managed patches to pristine forests (Ahti et al. 1968). Territories located in forests that have been affected by forestry consist of a mixture of clear-cuts, pine plantations of varying age, and a few pristine patches (Griesser et al. 2007). Managed forests at the study site are thinned every 30–40 years (i.e., all small spruces and deciduous trees are removed), and as a result, these forests become more open providing less visual cover. Managed patches are dominated by Scots pine (*Pinus sylvestris*), whereas unmanaged patches are dominated by Norway spruce (*Picea abies*) with a varying proportion of pine depending on soil characteristics (Ahti et al. 1968). The change of the dominant tree species from spruce to pine in managed patches generally increases the transparency because pine forests are more open than spruce forests (Griesser et al. 2007). Deciduous trees such as birch (*Betula pubescens*), aspen (*Populus tremula*), and willow (*Salix* spp.) are less abundant than conifers in the study site. The northern part of our study site is a forest reserve that has not been affected by logging or thinning for at least 200 years. As a result, forests in this area are structurally diverse and consist of a mixture of various age classes, thus creating a habitat which is visually more obstructed than in the forest in managed areas.

Determination of group composition and relatedness of group members

We visited all studied territories at least 4–6 times per year: during the breeding season (March to May), during summer (June to July, only years 2000 and 2003), and in late autumn (September to October), to assess group composition and ring new group members. The breeding success in most territories was assessed by directly monitoring reproduction. We caught female breeders in March before the onset of the breeding period and fitted a radio tag on the 2 central tail feathers (Holohil BD-2G; weighing 1.8 g, corresponding ca., 2.0% of a bird's body mass). After finding the nest by locating radio-tagged females, we banded all nestlings approximately 1–2 weeks before fledging ($n = 200$ broods) or directly after fledging ($n = 24$ broods). All unbanded individuals appearing in these groups were considered to be unrelated immigrants. In groups where we were unable to find the nest or where we did not radio tag female breeders, we determined kinship of nonbreeders each autumn by assessing the aggressive interactions between breeders and nonbreeders on feeders ($n = 15$ groups). Breeders tolerate their grown offspring but aggressively chase unrelated individuals off a feeder. Previous studies have confirmed that this method is a reliable assessment of kinship (Griesser 2003).

Measuring large-scale habitat structure and small-scale habitat structure

To be able to assess the effect of large-scale and small-scale habitat structure on vigilance rates, we measured habitat structure

Table 1

Number of male and female breeders in kin and non-kin groups in managed (open) and pristine (dense) habitat used in this study

Territory habitat structure		Vigilance data	Predator exposure experiment	*N* groups
Pristine habitat	Kin breeders:	4 ♀, 3 ♂	—	5
	Non-kin breeders:	5 ♀, 10 ♂	—	10
Managed habitat	Kin breeders:	7 ♀, 8 ♂	5 ♀, 7 ♂	8
	Non-kin breeders:	14 ♀, 15 ♂	13 ♀, 11 ♂	15

at these 2 scales. We measured the large-scale habitat structure as the proportion of forests that had not been managed for the last 50 years in each territory. The size of unmanaged patches was either directly sampled in the field using a GPS receiver (accuracy ± 10 m) or calculated from satellite images. To define approximate territory borders, we created 95% polygons based on monitoring data of groups collected with a GPS receiver during the study period. We classified territories either as managed (<50% unmanaged) or as pristine (>50% unmanaged) because the forests of the managed territories were all heavily affected by forestry (proportion of unmanaged forest = 0.17 ± 0.02 mean ± standard error [SE]) while all pristine territories were largely unaffected by forestry (proportion of unmanaged forest = 0.92 ± 0.03).

We measured the small-scale habitat structure with the help of digital images taken with a camera fitted with a wide-angle lens (resulting in a horizontal angle of view on the pictures of 68°). Pictures were taken in all 4 compass directions (north, south, east, and west). Each shot was set up with the lowest point of the horizon positioned on the pictures' midline. We measured the percentage of unobstructed sky in each image with the help of the software ImageJ 1.34s (National Institutes of Health). This measure should be a good proxy for the openness of each place and thus reflects the ability of prey to detect predators. In groups where vigilance rates were sampled on multiple occasions, we chose a different patch with varying density for each sampling session. Given that small-scale habitat structure was not dependent on large-scale habitat structure on each territory (Spearman rank correlation: Roh = 0.188; $P = 0.11$), we were able to separate the effects of small-scale and large-scale habitat structure on vigilance.

Measuring vigilance rates

To measure vigilance rates of breeders, we attracted jay groups to standardized feeders baited with a piece of pig fat in autumn during the years 1999, 2000, and 2006. The feeders were placed in the middle of a small forest opening about 5 m from the nearest cover. This sampling protocol allowed us to control for the influence of distance to cover on vigilance rates. We sampled vigilance rates of breeders only when they were alone on the feeder and when no other group member was closer than 10 m to the feeder. This setup was used to control for effects on vigilance caused by direct interactions with other group members (Griesser 2003; Nystrand 2007). Sampling sessions during which we observed a real predator were excluded from the analyses ($N = 2$). We recorded feeding jays with a video camera for about 20–30 min from 10- to 15-m distance. This distance was chosen because it allowed us to read the color bands without interfering with the feeding behavior of the birds. From the videotapes, we sampled the position of the head in 2-s intervals, using time-point measurements (Altman 1974). Feeding jays have to lower their head to peck at the food and have to raise their head in a vertical position to store the collected food in their throat. Thus, the only head movement that is not mandatory for feeding is turning the head horizontally, and we therefore only recorded horizontal head turns as vigilance (Griesser 2003; Nystrand 2006b). We calculated the vigilance rate of individuals as the proportion of scans where an individual turned its head. We used only those individuals where we had more than 40 time-point observations per sampling event to reduce random noise (mean ± SE time-point observations per individual: 78.7 ± 2.6), resulting in 124 vigilance measurements of 31 females (mean ± SE sampling events per individual: 1.8 ± 0.17) and 35 males (2.0 ± 0.18; Table 1) in 38 groups.

Assessing the function of vigilance

To test if vigilance in Siberian jays had an antipredator function, we measured the vigilance rate of undisturbed breeders, breeders that were exposed to a predator model and a control treatment in autumn in years 1999 and 2000. We exposed 36 breeders in 20 groups to 1 of the 3 treatments ($N = 12$ breeders for each treatment; see Table 1). We measured vigilance rates of undisturbed breeders using the method described above. To measure vigilance rates after exposure to a predator model, we exposed the foraging breeders to a model of 1 of the 2 main predator categories (sparrow hawk female and Ural owl male *Strix uralensis*). The models were fitted with a remote control, allowing us to turn their heads to imitate a live predator. We placed the model covered with a plastic bag 5 m away from the feeder on a 1-m pole in the middle of a small natural forest opening. When jays had fed undisturbed for about 15 min, we removed the plastic bag and exposed the feeding jays to the model. Jays immediately started to mob the exposed models up to 10 min before taking off (mobbing behavior described in Griesser and Ekman 2005). When all group members were at least 50 m away from the feeder, we covered the model with the plastic bag. When the birds returned to the feeder, we measured the vigilance rate of the breeders during the first 10 min. In the control treatment, we simply moved the plastic bag without actually removing it (to control for any potential adverse effect of the noise or movement of the bag or the observer). All experiments were done in managed territories to control for effects of large-scale habitat structure on vigilance.

Effect of large-scaled habitat structure on predator attack rates

We collected data on attack rates throughout the study period (1999–2007) in all different habitat types. These data were collected during all observations of jays foraging on feeders. Because all these observations were done during experiments where group members were closely followed, it is unlikely that an attack would have been overlooked even in natural, dense forests.

Table 2

Linear mixed model (normal error and identity link) testing the effect of predator exposure on vigilance rates in Siberian jay breeders

Fixed effects	n df	ddf	F value	P value
Intercept	1	28.7	43.2	<0.0001
Predator exposure[a]	2	28.7	10.10	0.002
Group composition[b]	1	18.9	1.95	0.18
Small-scale habitat structure[c]	1	29	2.71	0.12
Sex	1	22.1	0.09	0.77

Differences of least square means of predator exposure

	Estimate	SE	df	t	P value
Undisturbed vs. control	0.05	0.02	29.9	2.07	0.03
Control vs. predator exposure	0.10	0.02	29.4	4.48	0.0001
Undisturbed vs. predator exposure	0.05	0.02	28.3	2.7	0.04

Territory and year were included as random effects. Denominator degrees of freedom (ddf) estimated by the Satterthwaite method.

[a] Predator exposure: undisturbed, after predator exposure, and after control treatment.

[b] Group composition: kin groups (with retained offspring), non-kin groups (with only unrelated group members).

[c] Small-scale habitat structure: proportion of visible sky in feeder location.

Effect of small- and large-scale habitat structure and social environment on vigilance

Data on vigilance rates of breeders were collected in 33 randomly selected groups (20 groups in high-risk habitat and 13 groups in low-risk habitat; Table 1). We tested if vigilance rates depended on the social environment by comparing vigilance patterns in groups that varied in their level of relatedness between group members (Table 1). Henceforth, any groups containing retained offspring are defined as "kin groups," whereas groups consisting only of nonrelated group members are defined as "non-kin groups."

Statistical analyses

We used SAS 9.1 (SAS Institute, Cary, NC) to analyze the data. To analyze the effect of predator exposure on vigilance rates, we used a linear mixed model (normal error distribution and identity link; Table 2). All vigilance data were arcsin square-root transformed to achieve a normal distribution (Zar 1998). We included predator exposure, group composition, sex, and small-scale habitat structure as fixed effects into the model. Year and territory identity were included as random effects in this model to control for their effect on the fixed effects. Because we could not find any effect of predator category (sparrow hawk or Ural owl model) on vigilance rates (generalized linear model [GLM]: $F = 0.20$, $P = 0.67$), we pooled these data into one category. The effect of the different treatments on vigilance rates was clarified with the help of least squares means (also called adjusted means), which are the "predicted population margins" (Littell et al. 1996). We analyzed the effect of large-scale habitat structure on hawk attack rates using a GLM. Given that we only observed 1 attack on each territory, we used a binomial error distribution (attack observed on territory vs. no attack observed on territory). The number of attacks we observed and large-scale habitat structure were entered as main effects into the model, whereas the number of years a territory was studied was entered as a random variable to control for differences in sampling effort. The vigilance rates in relation to small-scale and large-scale habitat structure, group composition (kin groups or non-kin groups), and group size were analyzed using a linear mixed model (normal error distribution and identity link) where individual identity, territory identity, and year were fitted as random variables to control for their effects (Table 3).

RESULTS

Assessing the function of vigilance

Vigilance rates of breeders depended on the current risk. Breeders that had been exposed to a predator model exhibited

Table 3

Linear mixed model (normal error and identity link) of the factors affecting vigilance rates of breeders

Fixed effects	n df	ddf	F value	P value
Intercept	1	48.7	3.65	0.06
Group composition[a]	1	55.9	0.13	0.71
Large-scale habitat structure[b]	1	12.3	0.89	0.36
Small-scale habitat structure[c]	1	45	0.63	0.43
Group size	1	66.3	1.05	0.31
Sex	1	51.8	0.06	0.81
Group composition × large-scale habitat structure	1	47.4	14.69	0.0004

Differences of least square means of the interaction (group composition × large-scale habitat structure)

	Estimate	SE	df	t value	P value
Kin managed vs. non-kin managed	4.36	1.26	52.2	3.47	0.001
Kin managed vs. kin pristine	6.38	2.02	43.3	3.16	0.003
Kin pristine vs. non-kin pristine	−5.28	2.18	37.5	−2.42	0.02
Non-kin managed vs. non-kin pristine	−3.27	2.12	10.5	−1.54	0.15

Territory and year were included as random effects. Denominator degrees of freedom (ddf) estimated by the Satterthwaite method.

[a] Group composition: kin groups with retained offspring and non-kin group with only unrelated group members.

[b] Large-scale habitat structure: proportion of unmanaged forests on territory.

[c] Small-scale habitat structure: proportion of visible sky in feeder location.

higher vigilance rates (vigilance rate = 0.39) than undisturbed breeders (0.26) or breeders that had been exposed to a control treatment (0.22; $P = 0.002$; Table 2). Thus, vigilance investment was a direct response to the presence of a predator and has therefore an antipredator function in Siberian jays.

Effect of large-scaled habitat structure on predator attack rates

During the study period, we observed 5 attacks by hawks on Siberian jays. All these attacks took place in open, managed territories (GLM: territory habitat structure: $\chi^2 = 3.90$, $P = 0.05$; controlling for time spent on each territory). Hence, hawks seem to specifically choose open habitat for hunting jays, despite the fact that hawks occur equally often in both habitat types (Griesser et al. 2006).

Effect of small- and large-scale habitat structure and social environment on vigilance

Small-scale habitat structure had no influence on vigilance rates (Figure 1; Table 3). However, habitat structure of the whole territory affected the vigilance rates, but this effect depended on the social structure of the group ($P = 0.0004$; Figure 2; Table 3). Breeders in kin groups living on open, high-risk territories (i.e., managed forests) had higher vigilance rates than breeders in such groups occupying pristine, low-risk territories with a high proportion of visual cover. In contrast, breeders living with unrelated immigrants did not demonstrate this difference in vigilance depending on the territory habitat structure (Figure 2; Table 3).

DISCUSSION

The experiment where we exposed foraging jays to a predator model showed that the vigilance behavior of Siberian jay breeders indeed has an antipredator function. Moreover, vigilance depended on both the large-scale variation in habitat structure and the social structure of groups (Figure 2). Breeders with retained offspring in their group (kin groups) were more vigilant when living in managed, high-risk territories than when living in pristine, low-risk territories offering a higher proportion of visual cover. Breeders associating with unrelated individuals (non-kin groups) did not adjust their vigilance levels according to territory habitat structure. The assumption that living on open territories is more risky is supported by the fact that all attacks by hawks on jays were observed in open habitats, despite the presence of hawks being largely similar between habitat types.

Variation in small-scale habitat structure did not influence vigilance allocation, suggesting that jays did not perceive any difference in risk on a local scale. Alternatively, the benefits that jays receive by foraging in open patches (early predator detection) and the cost of foraging in such patches (reduced availability of protective cover) may cancel each other out, making it impossible to find a relationship between vigilance rates and small-scale habitat structure.

Effect of small-scale and large-scale habitat structure on vigilance rates

Across species, the effect of small-scale habitat structure on antipredator behaviors appears to depend on how prey escape from their predators. Animals that use swift escape maneuvers to outdistance attacking predators increase their antipredator vigilance when foraging close to cover (Kenward 1982; Underwood 1982; Metcalfe 1984; Cresswell 1994; Whittingham et al. 2004; Devereux et al. 2006). Because cover both aggravates predator detection by the prey and provides hiding places for hunting predators (Quinn and Cresswell 2004; Grant et al. 2005), these prey avoid foraging close to cover and are therefore mainly found in open habitats. In contrast, animals that escape from their predators by seeking shelter in burrows or dense vegetation increase their vigilance when foraging further away from a shelter. This has been demonstrated in mammals, in particular small rodents (see Brown and Kotler 2004) and in forest-living small passerine birds (Krams 1996; Carrascal and Alonso 2006). Our results strengthen the generality of this link between escape strategy and small-scale habitat structure. An earlier study in Siberian jays demonstrated a preference for food patches close to cover (Nystrand 2006b). Thus, distance to cover seems in species that escape from predators by seeking shelter to be more important than the actual openness of a foraging patch.

The effect of large-scale habitat structure on antipredator behaviors is less clear and has been addressed only by a few studies, despite the fact that it is well known that predation risk varies across landscapes, affecting the selection of foraging patches (Brown 1999). For example, blue tits (*Parus caeruleus*) that live in fragmented forest patches where predator

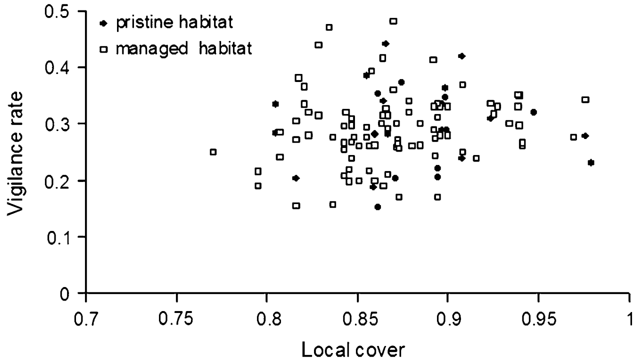

Figure 1
Effect of small-scale habitat structure (measured as percentage of cover around the feeder) on vigilance rates (proportion of head turns per time unit) of breeders foraging alone on the feeder. The proportion of small-scale (local) cover had no significant effect on vigilance rates of breeders. Small-scale cover was measured as the percentage of unobstructed sky as seen from the feeder.

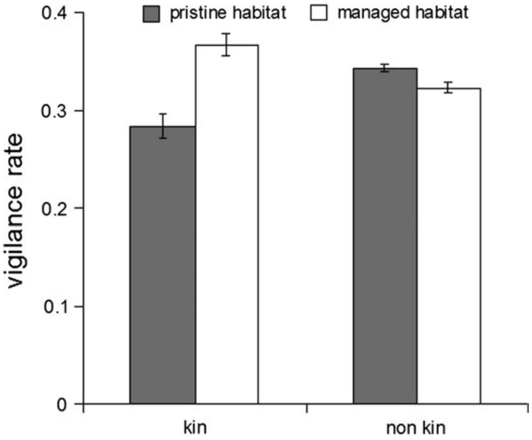

Figure 2
Effect of large-scale habitat structure and group composition on vigilance rates of breeders foraging alone on feeder. Vigilance rates of breeders foraging alone, who belonged to kin groups (parents with retained offspring), were higher in managed, open forest habitats than in pristine, denser forest habitats ($P = 0.003$). Error bars indicate SE.

encounter rates are higher have a higher vigilance rate than individuals living in continuous forests (Tellería et al. 2001). Also, the actual predation risk may affect large-scale foraging habitat choice and vigilance allocation (Brown 1999). Individuals living in habitats where predators are present show higher vigilance rates and display higher "giving up densities" (i.e., the harvest rate at which prey quit foraging in a patch; Brown 1999) than individuals foraging in absence of predators (Krams 1996; Gurung 2003). Large-scale habitat structure affects the habitats that predators choose for hunting (Grant et al. 2005; this study). This in turn affects both the large-scale (Gurung 2003) and small-scale (Nystrand 2006b) habitats that prey prefer for feeding, as well as their antipredator allocation (this study; Figure 2). Thus, the interplay between predator hunting behavior and habitat structure on multiple scales has important ecological consequences for antipredator behaviors and consequently for the spatial distribution of animals.

Vigilance patterns of breeders in relation to the social environment

Many studies have demonstrated that group size affects vigilance rates (Elgar 1989). Our study shows that vigilance rates of social animals can be sensitive to group composition, even when foraging alone. Because we only measured vigilance rates of breeders when foraging alone, the higher vigilance rate of breeders living in family groups is likely to be a general response to the kin structure of the group. Earlier studies on Siberian jays have demonstrated that retained offspring have a substantially lower risk of being killed by a predator than immigrants and that the predation risk in open habitat is generally much higher (Griesser et al. 2006). This suggests, in combination with the results of this study, that the higher vigilance investment of breeders in managed high-risk habitats aims at protecting their retained offspring.

Integrating the landscape perspective into prey–predator interactions

Our results highlight the importance of scale to assess prey–predator interactions. The scale at which predators make their hunting decisions determines both habitat patch selection of prey (Brown 1999) and how prey balance the trade-off between foraging and vigilance (this study). A crucial point will be to develop an easy methodology that allows assessing habitat structure on both the small and the large scale within and across different habitats. This will advance our understanding of the impact of multiscale habitat variation on prey and predators alike, which in turn is crucial to understand spatial variation to antipredator allocation and mortality.

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