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Influence of age, kinship, and large-scale habitat quality on local foraging choices of Siberian jays

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Animals face a constant conflict between gaining benefits and the risks associated with achieving them. In particular, the trade-off between gaining food and avoiding predation has been the subject of much attention. Here, I investigate the preferences for foraging sites in the group-living Siberian jay (*Perisoreus infaustus*), focusing on how energy intake is traded against proximity to cover. The main predator of this species relies primarily on visual cues to locate its prey, and thus, foraging in open habitat should be associated with higher exposure to a predator. Jays generally chose to feed in cover, a pattern that became stronger toward late winter. In particular, the strength of this preference varied with age, relatedness to other group members, and large-scale habitat quality. Adult territory holders and their retained offspring demonstrated similar preference for cover over seasons, a pattern not observed in nonrelated immigrants that showed no response to either forest structure or season. These results suggest that the benefits of parental nepotism enables retained offspring to take less risk, in regards to predators while foraging compared to similar-aged immigrants whose foraging options are constrained by social interference. Also, this study indicates that large-scale forest structure influences small-scale individual behavioral decisions. *Key words:* feeding site, predation, relatedness, Siberian jay, social groups. *[Behav Ecol 17:503–509 (2006)]*

Predation is a strong selective force that may play a major role in the evolution of several traits ranging from morphological adaptations to reproductive strategies and behavioral traits such as sociality (Lima and Dill, 1990). The challenge facing foraging individuals that must jointly avoid both starvation and predation, has received much attention from a descriptive as well as an experimental and theoretical perspective (e.g., Brown and Kotler, 2004; Caraco et al., 1980; Kotler, 1997; Lima and Bednekoff, 1999; Lima and Dill, 1990; McNamara and Houston, 1992). One frequently used approach in the study of energy intake/predation risk trade-offs has been to look at an individual's choice of feeding site (e.g., Ekman, 1987; Hogstad, 1988; Walther and Gosler, 2001). This choice can be expressed at several geographical scales. At a large scale, such as at the landscape level, individuals may be restricted in their choice of feeding site if large areas contain unsuitable feeding habitat and if individuals possess limited dispersal abilities (e.g., Emlen, 1982), or if there are limited dispersal opportunities due to local resource competition (e.g., Emlen and Vehrencamp, 1985). In contrast, at a smaller scale, choice of feeding site may be expressed as patch choice within a home range or territory or even more fine-scaled, microhabitat choice within a patch. To date, the majority of studies investigating choice of feeding site have focused on an individual's habitat choice at a relatively fine-tuned scale (e.g., reviewed in Lima and Dill, 1990). Many of these studies found that individuals prefer feeding in or close to vegetation cover, which is interpreted as a response to a predation risk (e.g., Brown, 1988; Brown et al., 1992; Grubb and Greenwald, 1982; Kotler et al., 1991; Lima, 1987). Although there are studies that have looked at responses in energy intake/predation risk behavior in relation to relatively large-scale levels of habitat quality (e.g., Barnard, 1980; Repasky, 1996), the majority have not related actual small-scale habitat choice to the large-scale habitat. In fact, few studies have incorporated both scales into a single study, and of those studies that have, habitat choice has been explored at the species/population or multispecies level (see Gill et al., 2001; Hilton et al., 1999; Nour et al., 1997; Robinson and Sutherland, 1999; Sharpe and Van Horne, 1998; Tellería et al., 2001; Turcotte and Desrochers, 2003). To my knowledge, few studies have investigated this multiscale habitat choice on the level of the individual, incorporating factors such as age, sex, or rank into the analysis (but see Goss-Custard and Durell, 1987b).

Foraging efficiency and habitat choice may be largely affected by interference among consumers (Sutherland and Dolman, 1994). Dominance hierarchies will affect an individual's access to resources and, thus, in a foraging situation, the different members of a group may not have equal freedom to select the most optimal foraging sites (e.g., DeLaet, 1985; Desrochers, 1989; Ekman, 1987; Ekman and Askenmo, 1984; Goss-Custard and Durell, 1987b; Hegner, 1985; Hogstad, 1988; Schneider, 1984; Slotow and Paxinos, 1997). In particular, intrinsic factors such as age, relatedness, and sex can cause differences in competitive ability among individuals (e.g., Brotons et al., 2000; Goss-Custard and Durell, 1987a; Goss-Custard et al., 1982; Sutherland and Dolman, 1994). For instance, a lack of experience among younger individuals may impede their ability to adequately assess predation risk. Moreover, in social groups where young birds differ in relatedness to the dominant individuals, nonrelatives may in addition to being inexperienced also pay a cost of subordination (Ekman, 1987). However, in addition to intrinsic factors, abiotic factors such as seasonal variation in weather conditions and ambient temperatures that cause variation in food availability (Brown, 1989; Goss-Custard and Durell, 1987a; Turcotte and Desrochers, 2003), physiological demands (Yasué et al., 2003 and references therein), and predation

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pressure (e.g., Brotons et al., 2000) may further affect habitat choice. Moreover, variation in environmental conditions over an even shorter timescale, such as time of day or levels of illumination may also influence behavioral decisions (Kotler et al., 1991, 1993, 2002; Price et al., 1984; Ziv et al., 1993).

In this study, I investigate the classic trade-off between energy intake and exposure to predators, incorporating the effect of both intrinsic and environmental characteristics. In doing so, I relate fine-tuned behavioral decisions to the larger scale habitat structure. To achieve this, I examined the trade-off between proximity to cover and access to food in foraging Siberian jay (*Perisoreus infaustus*) groups, an ideal model species in many respects. Siberian jays live in social groups that, in addition to the breeding pair, often contain retained offspring and/or unrelated immigrants (Ekman et al., 1994). Also, adult breeders are nepotistic toward their retained offspring by giving them benefits (e.g., relaxed feeding conditions and predator protection) that are withheld from nonrelated group members (Ekman et al., 1994, 2000; Griesser, 2003; Griesser and Ekman, 2004). Thus, this system allows me to study the effects of both dominance as well as relatedness on the choice of foraging sites. Furthermore, Siberian jays inhabit an extreme climate in which they maintain territories year-round. Throughout winter, there are few hours of daylight (down to 3–4 h/day), and daytime temperatures regularly drop to around −20°C. Thus, during this time, both the jays and their predators face a physiologically demanding climate. Yet, in Siberian jays, predation is the main factor of mortality and their main predator is the goshawk (*Accipiter gentilis*). During 1996 and 2001, individuals from the study population were frequently fitted with radio transmitters that enabled the recovery of dead individuals. All the retrieved jays had been killed by raptors and then almost exclusively by hawks (Griesser, 2003). Moreover, an extensive study of juvenile mortality demonstrated that all jays that died in their first winter had been killed by predators and then in particular by the goshawk (accounting for 70% of mortality; Griesser M, Nystrand M, Ekman J, in preparation). This study also showed a strong effect of habitat, where mortality among juveniles was significantly higher in open forests. Siberian jays have previously been described as a species requiring old-growth forest (Brotons et al., 2003; Lindgren, 1975), probably because older forest consists of several different successional stages, thus providing more cover from predators. Because the jay's main predator the goshawk is a hunter that relies on surprise attacks and uses visual cues to detect the prey (Kenward, 1978), feeding close to cover should enhance the prospects of a jay to both avoid being sighted by a predator and, due to the proximity of protective cover, escape an attack once sighted. Hence, an open forest structure is likely to facilitate a visually hunting predator, as well as reducing the access to cover for the prey. The choice of foraging site by jays should thus reflect the trade-off between energy intake and the risk of exposure to a predator.

METHODS

I conducted the experiments on a color-banded population of Siberian jays near Arvidsjaur, northern Sweden (65° 40′ N, 19° 0′ E). The habitat within the study site is composed of a range of different forest structures, ranging from forest plantations (age < 50 years) and heavily managed forest (monocultures), consisting mainly of young pine (*Pinus sylvestris*), to pristine old-growth forest stands (age > 100 years), consisting primarily of spruce (*Picea abies*) and pine, but with occasional patches of birch (*Betula pubescence*) and aspen (*Populus tremula*). To characterize forest openness, I used the proportion of forest within the territory that had not been actively managed (i.e., thinned or logged) for the last 50 years as an index of large-scale habitat quality. The proportions were calculated from forest field inventories of all territories where areas of unmanaged forest stands were mapped using Global Positioning System (Garmin 12 XL receiver) to gain coordinates. Each of these areas was then transformed to proportions by plotting them on jay territory maps (plotted as 95% polygons). This same index was used in a study of first-year winter mortality in the Siberian jay (Griesser M, Nystrand M, Ekman J, in preparation). It is based on the assumption that forests that have not been managed for the last 50 years constitute a higher quality habitat because they are more species diverse and multilayered in structure and, thus, should provide more protection from predation.

An individually numbered metal ring was applied to the right tarsus of each nestling between April and May in each year of the study (2002 and 2003). Later in the year (September–October), these same individuals (and any incoming immigrant birds) were recaptured and fitted with a unique combination of color bands for individual recognition. Age of immigrants of unknown origin was determined by examining the shape of the outermost retrices, which are more squared in adults than yearlings. The sex of each bird was determined using the molecular technique described in Griffiths et al. (1998). Banding of nestlings provided data on the relatedness between adults and yearlings. In the few cases where the origin of a yearling was unknown ($n = 2$), I determined the relatedness by assessing aggressive interactions (Griesser, 2003), a method that has proved reliable when tested against DNA fingerprinting (Ekman et al., 1994). There are no observational records or any genetic evidence for extrapair paternity in this species (Ekman et al., 1994; Griesser, 2003; Lillandt et al., 2001). Furthermore, based on prior observations, I assumed that yearling birds were subordinate to adults. This assumption was later confirmed by observing interactions on feeders during the experimental treatments.

Data collection

The study was carried out between the autumn (September and October) 2002 ($n_{\text{ind}} = 42$, $n_{\text{flocks}} = 11$) and late winter (March) 2003 ($n_{\text{ind}} = 37$, $n_{\text{flocks}} = 11$). With the exception of two birds, all immigrants were yearlings. The two adult immigrants were excluded from analyses due to the low sample size of this class. I conducted experiments in a total of 14 different flocks representing different social structures (adult alpha pair and retained yearling offspring, alpha pair and immigrant yearlings, or alpha pair together with both yearling offspring and immigrants). Henceforth, alpha birds will simply be referred to as "adults." All trials were conducted between 0930 and 1830 h under similar weather conditions. Furthermore, trials were randomized in time to avoid any confounding effects caused by differences in hunting behavior among different predators. Territories were chosen randomly from a larger sample and varied in large-scale forest structure.

In each trial, jays of a given territory were simultaneously presented with three feeders, each placed within the territory in a standardized manner in one of three different forest structures. The first feeder (feeder 1) was placed within dense forest cover (i.e., in or near a spruce surrounded by several other trees), "feeder 2" was placed at the edge of the forest, no more than 2 m from the closest tree, and "feeder 3" was placed within a forest opening at least 10 m from the closest tree. Each feeder represented a different small-scale habitat with respect to distance to cover where an increased distance to cover was assumed to be associated with a higher exposure to predators. The feeders were positioned approximately 16-m apart (±2 m) in a triangular fashion so that all three feeders were equidistant to each other. This enabled the birds to see the other two feeders from any given feeder and also allowed the observer to watch all three feeders simultaneously from the same distance, thus avoiding an observer bias or any influence of the observer on the choices made by the birds.

Each feeder was baited with pig lard of equal quality and size, in amounts large enough to avoid any depletion effect. Feeders were designed to allow two birds to eat simultaneously, but occasionally there were more birds on them. I repeated the trials on average three times per flock in autumn and once per flock in late winter. For various practical reasons, trials differed in time, ranging from 30 min to about 1 h in the autumn, whereas in late winter, each trial lasted for 1 h. I only recorded the number of visits made by an individual to each feeder (but not the time an individual remained on the feeder). By allowing all individuals within a group to simultaneously choose among several feeders rather than introducing them to one feeder at a time, the effect of intraspecific competition was represented in every decision made by an individual given several choices.

Data analysis

All statistical analyses were performed in the statistical package SAS 9.1, using a general linear mixed model (GLMM) type III (Proc Mixed) that allows both random and fixed effects to be fitted to the model and that accounts for unbalanced data (Litell et al., 1996). The response variable was the number of times an individual chose each feeder, which was transformed to a "mean" value to attain a continuous response variable that conformed to normality. This value was calculated for every individual per trial by giving each feeder (F) a number that reflected its distance from cover ($F_{cover} = 1$, $F_{edge} = 2$, and $F_{open} = 3$) and then multiplying this number with the number of times it was chosen (n), adding the individual values for each feeder together, and finally dividing them by the total number of choices made by that individual $[(1n + 2n + 3n)/n_{total}]$. Consequently, the received response variable represents an index of the preferred feeding "distance" to cover where a value of 1 represents always feeding in cover and a higher value represents an increasing distance to cover. This transformation causes some loss of "within-individual" information which may cause a problem with interpretation if, for example, an individual was to equally choose feeder 1 and 3 and avoid feeder 2 (which after transformation would indicate a primary choice of feeder 2). However, when examining the raw data of rank classes, this proved to be highly unusual (as illustrated in Figure 1a). Thus, this transformation provides an ideal, normally distributed index of the mean preferred feeding distance to cover for each individual.

Initially, I conducted an overall analysis over both seasons because this enabled me to investigate interactions of interest, in particular between an individual's social rank and season. However, there was a significant heterogeneity between ranks (Levene's test, $F_2 = 5.10$, $p = .0072$) that could not be correctly accounted for in the complex full model. Therefore, it was more appropriate to do separate analyses for each rank (see Morrow et al., 2003). Additionally, I conducted a one-factor ANOVA (Proc Mixed) for each season with rank as the fixed effect, controlling for flock size, to establish any overall difference in the choice of feeding site depending on social rank. In contrast to the multifactor model mentioned above, this simple model allowed me to model split variances for rank where adults and yearling retained offspring were grouped in one class and immigrant yearlings in another (immigrant yearlings was the group that significantly deviated in its variance), hence producing the best fitting model according to Akaike's information criteria. In each analysis, individual nested within territory was included as a random factor to model variation between territories and to account for correlated covariances due to some individuals being measured repeatedly. Also, this modeled the structure of the data where a certain individual only occurred in one territory. Fixed factors were sex, season, and flock size, whereas forest structure (proportion managed forest) was fitted as a covariate. All possible two-way interactions were included in the full models. Models were reduced by sequentially removing nonsignificant terms from the model, only leaving in terms involved in significant interactions (p-values $< .05$).

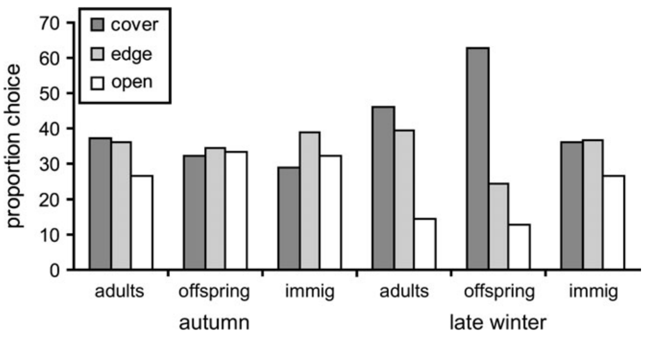

Figure 1
Feeder choice based on untransformed proportions.

All data were tested for normality, and residual plots were investigated for deviations to validate the final model. Homogeneity of variances was examined using Levene's variance test. Any appearing outliers were always moderate except for one that was extreme (GLMM of immigrants). This outlier was removed from the model because of its potential influence on the F-statistics. All moderate outliers were kept in the models because there was never any apparent biological reason for removing them. However, the models containing outliers were reanalyzed without them to determine whether they had a significant impact on the results. The moderate outliers never influenced the results. All post hoc tests of pairwise means of significant interactions were corrected for type I error by applying Tukey-Kramer adjustments.

RESULTS

The overall analysis showed a strong interaction between social rank and season ($F_{2,135} = 4.72$, $p = .0105$), social rank and forest structure ($F_{2,47.9} = 7.69$, $p = .0013$), and forest structure and season ($F_{1,131} = 11.10$, $p = .0011$) on choice of feeding site. However, due to the heterogeneous variances of rank, I split the data into three separate tests to further explore these patterns and in order to obtain reliable F-values. When exploring the raw data of feeder choice, it is evident that there is a seasonal pattern; in late winter, the feeder furthest away from cover is the least chosen feeder (Figure 1). This is supported by the statistical model where the feeding preference of family members (i.e., adults and yearling retained offspring) indicate that feeding sites closer to cover are selected at this time of year (Table 1, Figure 2). Adults and retained offspring significantly changed their preference from feeding further away from cover in autumn to foraging closer to cover in late winter (Table 1, Figure 2). In contrast, immigrants did not change their preference.

The seasonal shift in adults depended on forest structure, where adults in territories containing a low proportion of managed forest did not change their preference of foraging site with season while those in territories with more open forest (due to a higher proportion of managed forest) fed significantly closer to cover in late winter (Table 1, Figure 3a).

Table 1

Separate analyses of choice of feeding site for each rank

	Numerator Degrees of Freedom	Denominator Degrees of Freedom	F	p
Adult alpha birds				
Flock size	**2**	**53.7**	**7.63**	**.0012**
Forest structure	**1**	**31.9**	**0.15**	**.7000**
Season	**1**	**70.3**	**10.18**	**.0021**
Season × forest structure	**1**	**64.8**	**9.10**	**.0036**
Retained offspring				
Flock size	2	16.4	2.97	.0793
Forest structure	**1**	**12.4**	**12.61**	**.0038**
Season	**1**	**28.1**	**17.62**	**.0002**
Season × forest structure	1	26.1	1.10	.3042
Immigrants				
Flock size	**2**	**26.7**	**14.26**	**<.0001**
Forest structure	1	5.72	3.49	.1134
Season	1	32.7	0.02	.8962
Season × forest structure	1	32.3	0.00	.9785

GLMM describing final model after stepwise removal of nonsignificant terms not involved in any interactions (α a priori = 0.05). Values given in bold writing denote the final model.

Retained offspring did not show a similar interaction between season and forest structure but did demonstrate a general response to forest structure (Table 1, Figure 3b). I found no corresponding seasonal shift or response to forest structure among immigrant individuals (Table 1, Figure 3c). To examine whether the response in habitat choice could be explained by a simple difference in predator density between different forest structures, I compared the number of predators observed in more open forest compared to closed forest during autumn and winter (based on observations done between 2000 and 2003; due to lack of sufficient data on the territorial level, I grouped the forest structure into the groups "dense" versus "open" forest according to the trends shown in the graphs). Predator density was similar between the two types of forests in both seasons ($Z_{\text{autumn}} = 0.1160$, $p = .9076$ [$\bar{x} = 0.115$ versus 0.119] and $Z_{\text{winter}} = 0.4587$, $p = .6465$ [$n = 0.023$ versus 0.014]), indicating that the observed mortality differences are best explained by the jay's ability to escape or avoid an attack rather than by predation pressure per se.

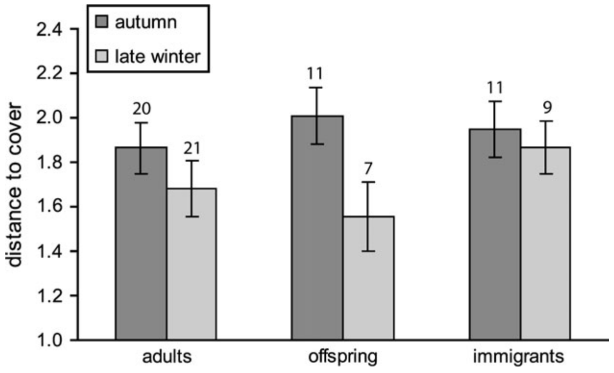

Figure 2

Choice of feeding site during different seasons. The response variable is an index of the preferred feeding distance to cover per individual (based on the choice of feeding sites; see Methods). Columns represent least square means ± SE. Numbers above bars show sample size (number of individuals). Pairwise differences of least square means indicate a significant difference between adult alpha birds and retained offspring versus immigrants in late winter.

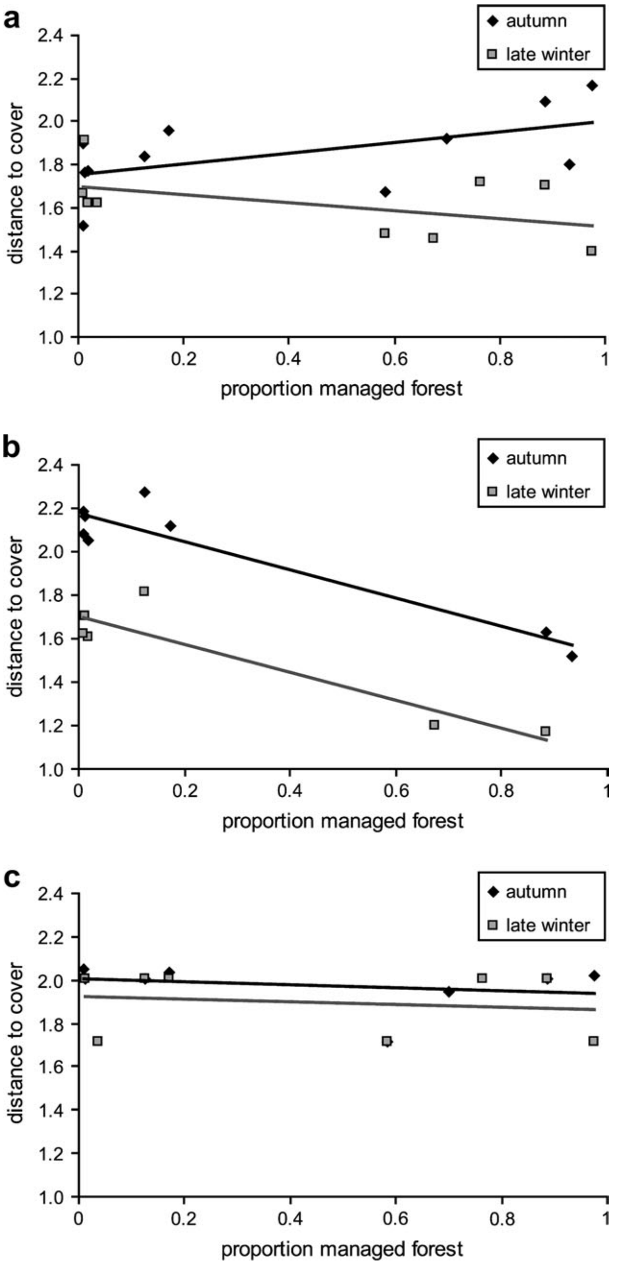

Figure 3

Choice of feeding site in different forest structures during different seasons. The response variable is an index of the preferred feeding distance to cover (based on the choice of feeding sites; see Methods). (a) Adults ($n_{\text{autumn}} = 21$, $n_{\text{late winter}} = 21$), (b) retained offspring ($n_{\text{autumn}} = 11$, $n_{\text{late winter}} = 7$), and (c) immigrants ($n_{\text{autumn}} = 11$, $n_{\text{late winter}} = 9$). Values denote predicted values (including random effects) from the model and represent individuals. Fitted lines are trend lines to visualize scatter patterns. For comparison, the significant seasonal shift for offspring and the absence of a seasonal or a vegetation dependent shift for immigrants are illustrated over the different forest types.

In autumn, jays showed no significant difference in choice of foraging sites among ranks (GLMM, $F_{2,38.1} = 1.64$, $p = .2083$). In contrast, in late winter there was an overall difference in choice of foraging site among ranks (GLMM, $F_{2,28.6} = 7.12$, $p = .0031$). Further exploration of this pattern indicated that the observed difference was between adults and immigrants (post hoc pairwise differences between least square

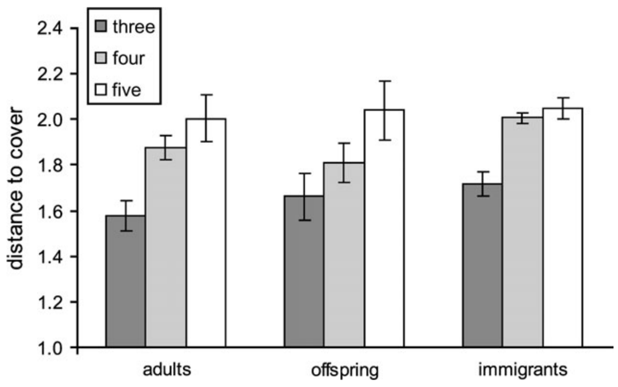

Figure 4
Effect of flock size on choice of feeding site. Number of groups of each flock size is $n_3 = 10$, $n_4 = 9$, and $n_5 = 3$. Columns represent least square means ± SE.

means from the GLMM; $t_{28.7} = -2.38$, $p = .0224$) and retained offspring and immigrants ($t_{29} = -2.81$, $p = .0234$), whereas there was no difference between adults and retained offspring ($t_{24.5} = 1.02$, $p = .5728$).

There was a strong effect of flock size on choice of feeding site, where adults and immigrants fed further away from cover in larger flocks than in smaller flocks (Table 1, Figure 4). Post hoc pairwise comparisons of least square means indicated that the observed difference was between flocks of three and four (adults: $t_{55.7} = -3.74$, $p = <.0013$; immigrants: $t_{26.5} = -4.99$; $p = <.0001$), flocks of three and five (adults: $t_{50} = -3.70$, $p = <.0015$; immigrants: $t_{28.4} = -4.78$, $p = .0002$) but not between flocks of four and five (adults: $t_{48.9} = -1.38$, $p = .3572$; immigrants: $t_{26.4} = -0.80$, $p = .7070$). Retained offspring demonstrated the same trend in feeding behavior according to flock size, but the pattern was not statistically significant (Table 1), probably due to low statistical power.

DISCUSSION

Many factors have been found to affect the energy intake/predation risk trade-off. These range from predictability of predation risk to the physical environment (e.g., food availability and quality of hiding places) and individual characteristics (e.g., age, sex, and dominance status) (see van Oers et al., 2003 and references therein). In this study, I combine multiple factors that may influence the response to starvation risk and predation in order to address two main questions; (1) do Siberian jays prefer feeding in some patches over others (small-scale habitat level) and, if so, (2) how does this pattern vary with respect to social context and large-scale habitat structure?

Small-scale habitat preferences

The main predator of the Siberian jay, the goshawk, is a versatile predator that hunts efficiently in both dense and open vegetation (Kenward, 1982; Marcström et al., 1990). Because goshawks rely strongly on visual cues to detect prey, it is likely that jays would seek protection from such a predator by taking advantage of the hiding opportunities associated with cover. The benefits of protection would therefore outweigh the benefits of early discovery of an approaching predator when foraging in more open habitat. The observed feeding preferences among jay family members in late winter suggest that cover was associated with a lower risk of exposure to predators. These results concur with the majority of previous findings on small birds, which have demonstrated that feeding in cover is the preferred option (DeLaet, 1985; Hogstad, 1988; Schneider, 1984; Slotow, 1996). Furthermore, the seasonal difference among family members, and then in particular among experienced adult alpha birds who, being dominant, are not subjected to any social constraints, further indicates that predation risk may pose a more severe constraint on energy access in late winter than in autumn. In this climate, goshawks are under high thermal stress during winter because of the low prey availability (Drennan and Beier, 2003). As a consequence, the predation on Siberian jays, being one of the few prey species available at this time of year, may increase (Marcström et al., 1990), thus explaining a potential shift in predation pressure on jays between seasons. Yet, Siberian jays may also suffer increased thermal stress during winter, suggesting that they might attempt to increase their food intake at the expense of safety. However, in contrast to goshawks, the Siberian jay is a hoarding species (Ekman et al., 1996; Marcström et al., 1990) and thus, their food intake should be more predictable than for a nonhoarder (Brodin, 2000). This suggests that energetic stress may be less severe in jays, resulting in a residual foraging behavior where predator avoidance is given priority. An empirical example in which the exact magnitude of the trade-off between food and safety has been quantified can be found in a study of gerbils (*Gerbillus allenbyi* and *Gerbillus pyramidum*) by Kotler and Blaustein (1995). They demonstrated that the resource patch in the riskier habitat had to be four to eight times richer than the resource patch in the safer habitat for it to be equally valuable.

Nonrelated immigrants were less plastic to variations in predation risk, as reflected by the lack of change in choice of feeding site between seasons. This is, again, probably a result of social constraints. Previous studies of this species have also shown that nonrelated subordinate flock members take more risks in regards to predation than family members (Griesser, 2003; Griesser and Ekman, 2005). Interestingly, those studies were performed in autumn, the season that indicated no difference between social ranks in this study. However, the previously used setup was different in that it only exposed the jays to one feeder in one type of habitat patch, thus enforcing a highly competitive situation. In contrast, this study exposed the jays to three feeders simultaneously, thereby offering a higher resolution to individual decisions in relation to habitat structure.

The effect of flock size on choice of feeding site may be explained by an increased interference in larger flocks that will force individuals to feed away from cover to a larger frequency. However, this is not necessarily associated with a greater risk of predation when feeding in a "riskier" patch because the cost of associating with a greater number of individuals may be counteracted by a dilution effect (Hamilton, 1971), an increase in predator detection due to an increase in vigilance level (the many eyes effect; Pulliam, 1973) and better prospects of escaping a predator because of the "confusion by number" effect (Neill and Cullen, 1974). The results from this study demonstrate that dominant birds as well as subordinates feed further away from cover in larger flocks than in smaller flocks, suggesting that an increased exposure to predators may indeed be counteracted by group size benefits.

Studies of kin structured groups such as those found in the Siberian jay do not only reveal a cost of subordination but also highlight the benefits to retained offspring of delaying dispersal when it is associated with extended parental care. Yearling retained offspring have an apparent advantage of feeding together with their parents; they experience relaxed access to food (Ekman et al., 1994) and are therefore allowed a wider range of choices and, as a consequence, have a more predictable environment in terms of energy intake. However, yearling immigrants may, despite being forced to take greater risks, also benefit from association with a family group simply because they can take advantage of the protection offered between family members as well as the additional protection of associating in larger numbers.

Effects of large-scale habitat structure

Adults fed closer to cover in territories with more open forest structure (due to a higher proportion of managed forest), suggesting that transparency and lack of cover is associated with a higher risk of exposure to a predator. This effect was confined to late winter, once again suggesting that predation risk was higher at this time of year. Thus, the large-scale habitat data were consistent with the patterns observed on the small-scale habitat. This pattern agrees well with previous studies on Siberian jay's reproductive success that have demonstrated a similar correlation to forest structure (Eggers, 2002; Eggers et al., 2005a,b; Ekman et al., 2001). Hence, the openness of the forest appears to have an impact on both breeding and nonbreeding activities. Furthermore, retained offspring fed closer to cover in forests with a high proportion of managed forest, independently of season, whereas immigrant first-year birds did not show any difference in their seasonal foraging pattern over different forest structures. The foraging patterns observed in yearlings are consistent with previously observed patterns, whereby yearling mortality was significantly higher in forest with a higher proportion of managed forest, and also generally higher among immigrants than among retained offspring in general (Griesser M, Nystrand M, Ekman J, in preparation). The absence of an interaction between season and forest structure among retained offspring may be a result of inexperience in accurately assessing the predation risk associated with different habitats in different seasons. However, they do show a general seasonal response where they converge to a preference for feeding closer to cover in late winter, suggesting that there has been a learning process where they have adopted the same behavior as their parents. It could be argued that this pattern is due to pure selection. However, because all offspring present in autumn were also present in late winter, this can be rejected as the explanation in this case.

Although many studies have investigated the response to predation risk during foraging, surprisingly few studies have attempted to relate more fine-tuned feeding site decisions to large-scale habitat structure (however, see Hobson and Villard, 1998; Nour et al., 1997; Tellería et al., 2001). It is apparent that there is still a large gap in the integration between behavioral ecology and landscape- or conservation-oriented biology (Caro, 1999; Lima and Zollner, 1996; Sutherland, 1998). In this study, I combine the influence of both small-scale and large-scale habitat characteristics on foraging decisions in a social group-living species, thus providing a higher resolution to how intrinsic and abiotic factors may work in concert to shape an individual's behavior. An understanding of individual behavior can be of pivotal importance for conservation management. For instance, distortions in behavior due to forest management may alter extinction probabilities (Caro, 1999). Additionally, detailed knowledge of learning behavior can facilitate species-specific management policies, especially during translocation programs or when attempting to attract animals to new areas. Also, behavioral studies provide valuable information on species-specific habitat requirements (Sutherland, 1998). The Siberian jay studied here is not under an immediate threat of extinction. However, it has suffered a significant decrease in number during the 20th century (Uimaniemi et al., 2000), a decrease that has been attributed to the disappearance and fragmentation of old-growth forest (Helle and Järvinen, 1986). The results of this study suggest how behavior may be affected by both intrinsic and extrinsic factors and thus highlight the underlying constraints on behavior that might be crucial to an individual's fate.

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