



Associating with kin affects the trade-off between energy intake and exposure to predators in a social bird species

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Individuals have to trade-off energy intake against the risk of predation when foraging. However, in group-living species, social interference will limit the range of choices for subordinate individuals. The trade-off between foraging and predation risk may be even more complex in species that associate in family groups because relatives can provide benefits to each other that are withheld from nonrelatives. As a consequence, nonrelatives may be forced to take greater risks to gain similar amounts of energy as relatives. Here, I investigate how the energy–risk trade-off varies among individuals in a social, group-living species, the Siberian jay, *Perisoreus infaustus*. Groups in this species consist of a breeding pair, together with retained offspring and/or nonrelated immigrants. I manipulated food quality at feeding sites that differed in their visibility to predators and observed the differences in foraging patterns between different group members. Adults and their offspring fed more often at the protected feeding site when it contained high-quality food, but switched to the more exposed site when this site offered higher quality food than the protected site. In contrast, immigrants spent a similar amount of time at each feeding site, independent of food quality. Birds generally spent more time waiting for access to the high-quality food source and protected feeding site, and family members generally harassed immigrants that tried to access these sites. None the less, all birds had a similar overall food intake, suggesting that immigrants pay substantially higher costs than other members to attain the equivalent level of energy intake.

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Foraging theory has expanded from focusing simply on how to maximize feeding efficiency (MacArthur & Pianka 1966), to incorporate a number of additional factors that can have large effects on individual foraging decisions (e.g. Millinski & Heller 1978; Caraco 1979; Barnard 1980; Sih 1980; Hilton et al. 1999; Dolby & Grubb 2000). Of all the factors affecting an individual's decision-making, few will have as large an impact as the risk of predation (Lima & Dill 1990). There are a number of ways that individuals can regulate the trade-off between energy intake and predation risk, for instance, through increasing vigilance in more exposed sites (Barnard 1980), choosing the most rewarding

patch (Lima et al. 1985; Ekman 1987; Brown 1988; Hogstad 1988; Kotler & Blaustein 1995; Kotler 1997; Walther & Gosler 2001; Brown & Kotler 2004), or through simple diet selection (Lima 1987). Perhaps the most efficient way, however, is by associating in groups (Caraco 1979; Elgar 1986; Ekman 1987; Krause & Ruxton 2002).

Much research has focused on the advantages of group-living to explain why individuals aggregate in numbers (see Krause & Ruxton 2002). A widely acknowledged benefit is the 'dilution effect', in which the per capita risk of predation declines with an increase in group size (Foster & Treherne 1981; Krause & Ruxton 2002). Similar ideas are the 'selfish herd theory', which in addition to numbers also takes into account the spatial context of the individual within a group (Hamilton 1971), the 'confusion by number theory' that suggests that predators will struggle to single-out individual prey from a group (Neill & Cullen 1974), and the 'many eyes effect', which predicts that larger

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groups are better at detecting predators, hence allowing the individual to invest less in vigilance (Pulliam 1973).

In many species, individuals do not only associate in groups, but in kin groups or family units. These family groups form when offspring delay dispersal and continue to reside with their parents into adulthood (Emlen 1994). In the majority of cases, being philopatric means foregoing personal reproduction, thus inducing a substantial cost to the individual. Hence, living in kin groups must offer advantages beyond the general benefits of group-living to explain why offspring choose to stay in their natal territory rather than disperse to other groups where they may have a better chance of finding a mate and reproducing (Ekman et al. 2004; Ekman 2006). Much of the early research investigating the phenomenon of kin groups focused on cooperatively breeding species. In these systems, one of the primary explanations for the maintenance of delayed dispersal, and thus family living, has been attributed the acquisition of indirect (inclusive) fitness benefits received through remaining in the natal territory and helping kin to rear offspring (alloparenting; Brown 1987; Emlen 1995; Richardson et al. 2002; Ekman et al. 2004). However, several species that delay dispersal and associate in family groups do not practise alloparenting (Ekman 2006). This diversity of kin systems suggests that the general importance of inclusive fitness in the evolution of kin groups may be overestimated. Instead, direct fitness benefits, such as an increased access to resources (e.g. Scott 1980; Ekman et al. 1994) or the acquisition of high-quality breeding sites (Brown & Brown 1984), may be important in explaining the evolution and maintenance of family groups in many species.

There are also a number of potential costs associated with group-living in general, many of which are associated with foraging activities (Krause & Ruxton 2002). An increased demand for a limited resource is likely to increase competition between group members and, thus, optimal energy intake for individuals associating in groups may vary according to social interference (Goss-Custard & Durell 1987a, b, c; Slotow & Paxinos 1997). For example, dominant individuals may exclude subdominants from safer feeding sites, thereby forcing them to take higher risks (e.g. Schneider 1984; DeLaet 1985; Hegner 1985; Ekman 1987; Desrochers 1989). Thus, even though all the individuals within a group should aim to optimize their foraging strategy, not all individuals will have equal freedom to do so. Moreover, in species that associate in groups containing both related and nonrelated members, individual trade-offs between foraging and predator avoidance become even more complex since relatives may provide benefits to one another that are withheld from nonrelatives (Hamilton 1964; Scott 1980; Black & Owen 1989; Ekman et al. 1994; Griesser 2003). In such cases, dominance hierarchies within the group may not only be related to factors such as age and sex, but also to kinship (relatedness). Even so, the advantages of joining a group of conspecifics or heterospecifics (e.g. Ekman 1987; Dolby & Grubb 2000; Wu & Giraldeau 2005) may outweigh the costs associated with these social interactions.

In this study, I investigate the trade-off between energy intake and exposure to predators, at the level of the

individual, in the Siberian jay, *Perisoreus infaustus*. This is, in many respects, a suitable system in which to address this issue. The Siberian jay is a year-round, territorial and group-living species that forms social units consisting of a breeding pair together with additional birds that are either retained offspring of the breeding pair or unrelated immigrants (Ekman et al. 2002). Neither the retained offspring, nor the immigrants, help raise young at the nest and, thus, the Siberian jay is not a cooperatively breeding species (Stacey & Koenig 1990). However, a hierarchy is formed among subordinates within the groups, because parents are nepotistic towards their retained offspring, providing them with direct benefits, such as increased access to food (Ekman et al. 1994, 2000; Nystrand 2006a) and predator protection (Griesser 2003; Griesser & Ekman 2004, 2005). This results in retained offspring having a higher probability of survival than same-aged immigrants (Griesser et al. 2006). Moreover, survival is strongly dependent on habitat structure. Previous studies have shown that predator-related mortality is higher in open forests, a pattern that is attributed to open forests having higher visibility, which facilitates the hunting success of predators of Siberian jays (Griesser et al. 2006; Nystrand 2006a, b). Predation is indeed the main cause of mortality in this study population of Siberian jays (Griesser 2003; Griesser et al. 2006). The main predator, the goshawk *Accipiter gentilis* (Griesser 2003), is a visually oriented hunter that relies on surprise attacks (Kenward 1978), and hunts primarily along woodland edges bordering open areas (Kenward 1982). When attacked by a hawk, Siberian jays seek protection in the closest tree (Griesser & Ekman 2004). Together, this information suggests that jays should generally prefer feeding close to cover over feeding in the open terrain assuming that both sites offer equal energy return, a suggestion that is consistent with previously established foraging patterns in this species (Nystrand 2006a). The choice of feeding site, however, should also be affected by the quality of the food available at a given site. Furthermore, foraging patterns should differ between individuals of different social rank.

Hence, to test the above trade-off, I manipulated two feeding stations per territory so that they differed in distance to cover, and thus visibility to predators, and food quality. This experimental design enabled me to examine individual foraging behaviour at two levels (cf. Lima 1988): (1) the individual choice of feeding station and the time spent on it represented a 'higher level' decision, whereas (2) the actual behaviour once a bird had chosen a feeder represented a 'lower level' decision (i.e. pecking and vigilance rates). Both levels should be coordinated to maximize net energy intake relative to the costs of predation and interference. Thus, at the 'higher level', I tested whether increasing the food quality in the more exposed site relative to the one in cover (protected site) would result in a general switch in feeding preferences towards feeding more in the exposed site associated with a higher risk. In addition, I investigated differences in aggression levels and waiting times at different feeding sites to further elucidate the value of each site, given that a feeding site in high demand should be worth both waiting and fighting for. An animal foraging in

a riskier environment may compensate for the increase in risk by decreasing pecking rates and increasing vigilance (Barnard 1980). Thus, at the 'lower level' of decision-making, I tested whether birds feeding further from cover or on high-quality food had higher vigilance and lower pecking rates. Of primary interest to all analyses was whether the foraging patterns varied with rank (age and kinship). At the higher level, I predicted that adult breeders and their retained offspring will have a greater freedom of choice than socially constrained immigrants, allowing them to choose safer feeding sites (Nystrand 2006a, b) and feeding sites offering higher energy return. It is also likely that birds will adjust their lower-level decision-making according to rank. However, because traditional hierarchical patterns are complicated by the influence of kinship in this species, it is difficult to predict the general directions of these lower-level decision-making patterns a priori.

METHODS

Study Area

I conducted the experiments on a colour-banded population of Siberian jays located near Arvidsjaur, northern Sweden (65°40'N, 19°0'E). The experiments were carried out in March 2004 (late winter) in 10 different groups of jays. Territories were randomly selected among groups that contained a breeding pair and additional birds. Specifically, each group comprised two adult breeders, together with yearling (i.e. birds in first year of life) offspring ($N = 3$ groups; range = 1–2 per group, $N_{\text{total}} = 4$), yearling immigrants ($N = 5$ groups; range = 1–2 per group, $N_{\text{total}} = 10$) or a mixture of both ($N = 2$ groups; 1 offspring and 1 immigrant per group). The area is covered in snow (snow cover lasts from October to May) during this time and average temperatures range from +6°C to –14°C (information from climatic maps produced by Swedish Meteorological and Hydrological Institute, SMHI), but regularly drops to around –20°C. This climate is physiologically demanding to both jays and their predators (Nystrand 2006a). The study site consists of a range of different forest structures, ranging from heavily managed forest (monocultures) consisting mainly of pine, *Pinus sylvestris*, to pristine forest consisting primarily of old-growth forest (age ≥ 100 years) with a mixed composition of spruce, *Picea abies*, and pine, *P. sylvestris*.

General Data Collection in the Study Population

The population used in this study has been studied routinely since 1989, and nestlings are banded each year between April and May. They are later recaptured and fitted with colour bands between September and October, as are any new immigrants to the study area. The approximate age of these immigrants can be established by examining the shape of the outermost retrices (Ekman et al. 1999). Kinship (relatedness) can be determined from a database containing the identity of all nestlings born within the study area or inferred from the level of

aggressive interactions between adult breeders and first-year individuals (Ekman et al. 1994; Griesser 2003). I only use the term 'related' or 'kin' in reference to first-order relatives (parent–offspring, sibling–sibling). The assignment of kinship based on assessing aggressive interactions is reliable when compared with kinship data obtained using DNA fingerprinting (Ekman et al. 1994) and with data on individuals of known origin (Griesser 2003). There are no genetic or anecdotal evidence of extrapair paternity in this species (Ekman et al. 1994; Lillandt et al. 2001; Griesser 2003). Blood samples were taken from the alar vein (100 μ l) and the sex of each individual was determined using the molecular technique described in Griffith et al. (1998). The capture of birds for banding and bleeding were carried out under the licence of Umeå djurföröksetiska nämnd.

Experimental Design

The groups selected for experiments contained adult breeders together with yearling individuals that differed in their relatedness to the breeders. This group composition enabled me to disentangle the effects of age (i.e. adults versus yearlings) and kinship (i.e. family members versus immigrant yearlings).

Two feeding stations were placed within each territory. One of these was located in cover (2 m into the forest measured from the forest edge) and the other 12 m outside of the forest in a natural opening (i.e. exposed). The feeders were baited with equally sized and weighed pieces of pig lard, secured to the feeders by steel wire. I manipulated a difference in food quality by slicing the top layer of the lard into 7-mm cubes on one of the feeding stations, while leaving the lard on the other station unsliced. Slicing the lard into cubes enables the birds to tear away larger chunks, thereby significantly decreasing the handling time and imposing a difference in energy return per time unit (but not in actual energy content). This effectively creates a difference in the quality of the food source. Two video cameras were set up to film each feeder throughout each trial. Video recordings were used to capture the details of the trial, such as time on feeder, pecking rates and vigilance for each individual. Additionally, I actively observed every trial to confirm that there were no unexpected disturbances, such as predators appearing or intrusions from neighbouring groups that may have confounded the results. I also monitored the identity of each individual visiting the feeders, reading the colour-band combinations out loud to the camera. This was necessary since colour bands could not be distinguished in the video footage. Observations and filming of feeding behaviour were made at an equal distance from both feeders (approximately 19 m) to avoid any observer bias or influence of the observer on the birds.

I carried out a cross-over experiment that comprised two randomly assigned trials (30 min/trial) per group. In one trial, the high-value food was attached to the feeder in cover and the low-value food to the exposed feeder. The other trial had the reverse set-up. All groups had fed on the feeders at least once before the experiment and were

thus familiar with them. No experiments were started before I was certain that all individuals had investigated both feeders and noticed the differences in food quality between them, after which I started recording. Trial order was randomized and all trials were carried out under similar weather conditions, with the time of day randomized.

From the videotapes, I sampled data on individual pecking rates, choice of feeder, time spent on feeder, social interactions and vigilance rate. Vigilance rates were measured using 'time point measurements' (Altman 1974), recording head-turns every 2 s. A head-turn was defined as a movement of the head to the side when the head was held on or above an imaginary horizontal line. A frequently used method for measuring vigilance in birds is simply counting the number of 'head ups'. However, when consuming lard, the jays need to raise their head to swallow. Therefore, I used turns of the head in a sideways motion as a measurement of vigilance because this is the only movement that is not mandatory for feeding (Griesser 2003). Thus, vigilance was measured as an activity incompatible with food intake. Vigilance was only measured from feeding bouts ≥ 15 s, and only in cases where a bird was alone on the feeder. The vigilance of interest in this study was that reflecting differences in food quality and choice of feeding site when the influence of other individuals had been accounted for, hence this sampling procedure. The experimental design allowed me to account for the effects of food density, type of food and habitat effects on vigilance rates.

Pecking rate was defined as the number of times a jay pecked on the lard divided by the time of the feeding bout, regardless of whether the peck successfully detached food. Thus, pecking rate symbolizes feeding *effort* rather than feeding *success*. Additionally, I weighed the lard before and after the experiment, which allowed me to calculate the amount of food eaten by a given group divided by the total number of pecks in the group (i.e. grams extracted per peck). From this value, I estimated the average amount of food an individual obtained per peck, assuming no difference in feeding skills between individuals. There was no significant difference in general food intake/peck between groups (repeated ANOVA: $N = 10$, $F_{9,27} = 0.23$, $P = 0.99$), suggesting that this was indeed a reasonable approximation.

In a social system, interference between individuals may decrease the ability to choose the most productive or safest feeding site. To estimate these direct costs of interference, I recorded the number of times an individual was observed waiting for access to food (≤ 3 m away). During these 'waiting bouts', birds typically sat in a nearby tree or on the ground, watching the food source. The waiting bird would immediately approach the feeding site when it became vacant, and if successful (not chased away by an arriving dominant), start feeding. These waiting bouts should be a reliable indicator of the perceived value of a particular feeding site. I also recorded the number of times an individual was displaced by another group member while foraging during a given trial. Displacements were recorded as either aggressive or passive, where aggressive displacements involved physical contact such as pushing or bill snapping whereas passive displacement

was defined as events where a bird left as a consequence of another bird arriving at the feeder (≤ 1 s between one bird leaving and the other one landing on the feeder).

Statistical Analyses

I used SAS version 9.1 (SAS institute Inc., Cary, NC, U.S.A.) and SYSTAT version 11 (SYSTAT, SPSS Inc., Chicago, IL, U.S.A., 2004) for the statistical analyses. I conducted a number of preplanned generalized linear mixed models (GLMMs). The territories chosen were a subset of a larger sample and therefore territory identity was treated as a random effect (Littell et al. 1996). Furthermore, individuals were nested within territories to accurately model the structure of the data and to control for repeated sampling of the same unit (covariance structure was determined to be compound symmetry, i.e. the random statement produces the same result as the repeated statement; Littell et al. 1998). The full models contained all possible second-order interactions, and when there was a large enough sample, third-order interactions. All models were reduced with backward elimination of nonsignificant terms. I checked the model's assumptions of normality and homogeneity of variances by using Shapiro–Wilk's test of normality and Levene's test of homogeneity of variances, respectively, in combination with visual inspection of residual plots and normality plots. All models were checked for residual outliers. In only one case (i.e. pecking rate) did the removal of one outlier (representing 1.4% of the data in that analysis) change the results of the model, and then from a nonsignificant result to a significant one. This outlier proved to be a data point of a bird that made only one short visit to that feeder before taking off together with the rest of the group, suggesting this was an unrepresentative data point. Furthermore, the exclusion of this group from the model altogether gave the same result as when removing the outlier. Hence, I chose to exclude the data point from the model. Nonlinear effects of group size are not interpreted in this study because the low sample sizes within this class preclude robust interpretation. I present the output means from all the mixed models as least square means (i.e. adjusted means).

Specifically, I analysed how many times a bird chose the feeding site in cover using a GLMM (SAS Proc Glimmix) with binomial error distribution and logit link function. The response variable was the number of choices of the feeder located in cover and the binomial denominator was the total number of choices of both feeders. Fixed effects were food quality (i.e. handling time), social rank (i.e. kinship; adult, yearling offspring and yearling immigrant), sex and group size, controlling for trial order. Additionally, I used a GLMM (SAS Proc Mixed, normal error distribution, identity link) to investigate whether there was a trade-off in time spent on respective feeders, using the same model parameters as above. Here, the response variable was time spent on the feeder in cover (as a proportion of time spent on both feeders).

GLMMs were also used to test for differences in vigilance rates, pecking rates and food intake (the latter was fourth-root transformed to fulfil model assumptions)

according to food quality, location of feeder, rank, sex and group size, controlling for trial order. In the model investigating pecking rates, food quality showed strong heterogeneity in the residual variances ($P = 0.004$). GLMM tolerates mild departures from homogeneity of variance (Palmqvist 1997), but since the departure in this study was substantial, I split this analysis into two tests. Convergence criteria were fulfilled in all GLMMs. Finally, I analysed data on the number of displacements and the number of times a bird was observed waiting for a feeder depending on location, food quality or rank, using χ^2 tests.

RESULTS

Higher Level Decisions: Choice of Feeder, Time on Feeder and Direct Costs

As predicted, adults and yearling offspring chose to feed at the feeding site located in cover more often when that site offered high-quality food than when offered low-quality food (Table 1, Fig. 1a). Alternatively, when the high-quality food was offered on the exposed feeder, this site appeared to be chosen equally much by retained offspring and more by adults than the feeding site in cover (Table 1, Fig. 1a and b). Yearling immigrant birds chose the site in cover equally much as the exposed site, independent of food quality (Fig. 1a and b). Group size and sex had no effect on feeder choice (Table 1).

The proportion of time spent at each feeding site followed the same pattern as the choice of feeding site (Table 1). However, there was a significant nonlinear difference between group sizes. Furthermore, there was a significant interaction between sex and rank showing that immigrant females spent less time foraging, independent of feeder location and food quality, than birds of other ages and classes (Table 1, Fig. 2).

Table 1. Effects of social factors, sex and food quality on the proportion choice (GLMM with binomial error and logit link) and on the time spent on the feeder in cover (GLMM with normal error and identity link)

| Effect | <i>df</i> | <i>F</i> | <i>P</i> |
|--------------------------|---------------|--------------|-------------------|
| Proportion choice | | | |
| Rank | 2,33 | 2.08 | 0.1407 |
| Sex | 1,31 | 0.03 | 0.8628 |
| Group size | 3,31.1 | 1.49 | 0.2379 |
| Food quality | 1,33 | 17.07 | 0.0002 |
| Trial | 1,33 | 5.38 | 0.0267 |
| Rank*food quality | 2,33 | 4.58 | 0.0176 |
| Proportion time | | | |
| Rank | 2,28.4 | 0.77 | 0.4718 |
| Sex | 1,28.9 | 1.48 | 0.2337 |
| Group size | 3,36.8 | 6.33 | 0.0014 |
| Food quality | 1,33.3 | 20.47 | <0.0001 |
| Trial | 1,36 | 3.09 | 0.0875 |
| Rank*food quality | 2,32.3 | 6.77 | 0.0035 |
| Rank*sex | 2,28.5 | 5.51 | 0.0095 |

The emboldened factors denote the final models.

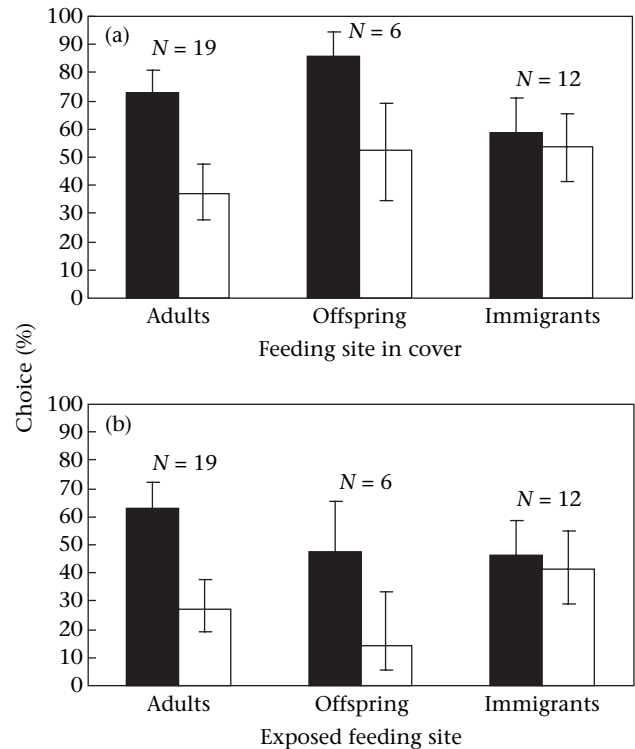


Figure 1. Choice of feeder ($\pm 95\%$ CI) by birds of different rank depending on food quality. (a) Results for the feeding site in cover and (b) results for the exposed feeding site. When the feeder in cover contained high-quality (■) food, the exposed feeder simultaneously contained low-quality (□) food. Values are back-transformed to the original scale. Sample sizes (number of individuals in each rank class) presented above bars.

Direct costs: waiting for access and displacements according to feeding site, food quality and rank

Birds were more likely to wait for access to food if the food source was of high quality across both feeding sites (site in cover, high- versus low-quality site: $N_1 = 64$, $N_2 = 25$, $\chi^2 = 95.06$, $P < 0.0001$; exposed site: $N_1 = 9$, $N_2 = 1$, statistical test not carried out because of low

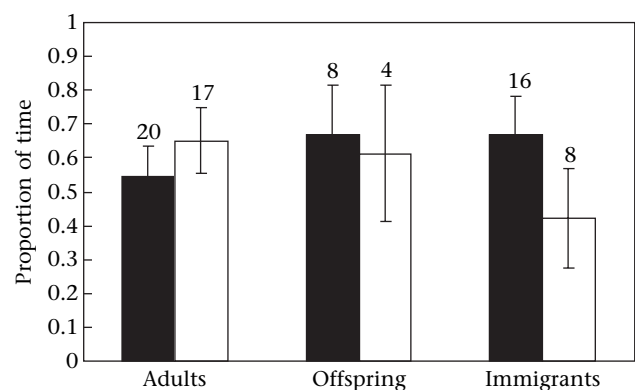


Figure 2. Proportion of time spent on feeders ($\pm 95\%$ CI) by birds of different rank and sex, independent of feeder location or food quality. ■: male; □: female. Sample sizes (number of individuals in each rank class) presented above bars.

frequencies). Also, birds were more likely to wait for access to the feeder in cover, independent of food quality (high-quality food, cover versus open: $N_1 = 64$, $N_2 = 9$, $\chi^2 = 41.44$, $P < 0.0001$; low-quality food: $N_1 = 25$ versus $N_2 = 1$).

The number of passive displacements did not depend on food quality in the safer feeding site (cover: $N_1 = 62$, $N_2 = 56$, $\chi^2 = 0.31$, $P = 0.58$, Fig. 3). However, aggressive interactions occurred significantly more often when high-quality food was presented at this site ($N_1 = 29$, $N_2 = 9$, $\chi^2 = 10.53$, $P = 0.001$, Fig. 3). The exposed feeding site invoked more passive and aggressive displacements when the food quality was high compared to when it was low (passive: $N_1 = 61$, $N_2 = 36$, $\chi^2 = 6.4$, $P = 0.01$ and aggressive: $N_1 = 14$, $N_2 = 0$; Fig. 3). A comparison of the feeder in cover to that in the exposed site, independent of food quality, revealed a difference between the number of aggressive displacements where the feeding site in cover had more displacements than the exposed feeding site ($N_1 = 37$, $N_2 = 14$, $\chi^2 = 10.37$, $P = 0.001$) but no difference in the number of passive displacements ($N_1 = 116$, $N_2 = 97$, $\chi^2 = 1.70$, $P = 0.19$).

There were differences in both the number of aggressive and passive displacements according to rank (passive: $N = 213$, $\chi^2 = 207.1$, $P < 0.001$ and aggressive: $N = 51$, $\chi^2 = 60.12$, $P < 0.001$; Fig. 4). The observed differences were between family members (adults and retained offspring) and yearling immigrants, with immigrants being displaced significantly more often than family members ($N = 265$: adults versus offspring, $\chi^2 = 0.961$, $P = 0.33$; offspring versus immigrants, $\chi^2 = 139.90$, $P < 0.001$; and adults versus immigrants, $\chi^2 = 152.97$, $P < 0.001$, Fig. 4).

Lower Level Decisions: Vigilance and Pecking Rates

There were no differences in vigilance rates between the different feeding sites or food qualities, or between individuals of different rank (Table 2). There was, however, an interaction between group size and food quality (Table 2).

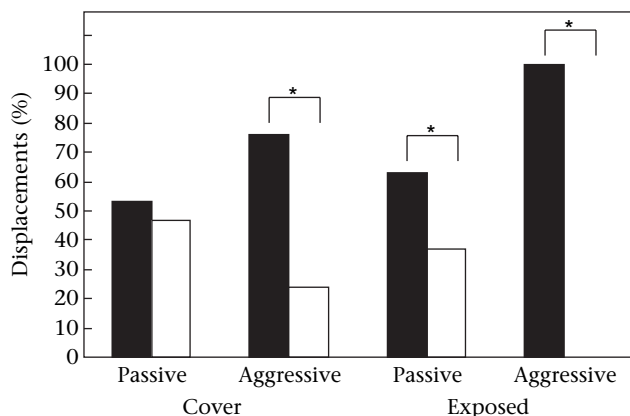


Figure 3. Number of passive and aggressive displacements in the two different feeding sites. ■: high quality; □: low quality. Comparisons with asterisks above them indicate significant differences (see text for more information).

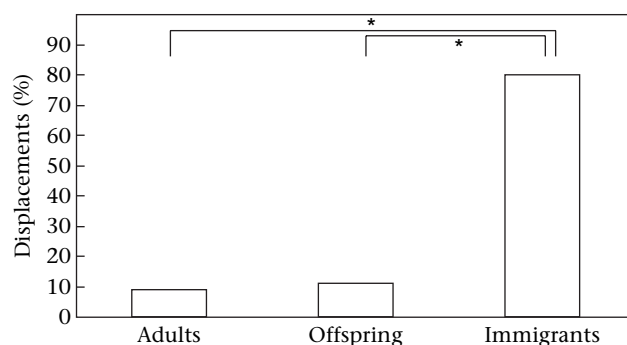


Figure 4. Displacement for birds of different rank (pooled for both passive and aggressive displacements since the results were similar for both categories). Comparisons with asterisks indicate significant differences.

Here, groups of three individuals ($\bar{X} \pm \text{CI}$: 0.51 ± 0.06) had higher vigilance rates than groups of four ($\bar{X} \pm \text{CI}$: 0.42 ± 0.04), five ($\bar{X} \pm \text{CI}$: 0.42 ± 0.06) or six ($\bar{X} \pm \text{CI}$: 0.46 ± 0.08) when they foraged on high-quality food. Groups of three also showed within-group differences, where vigilance rates were higher when feeding at the high-quality than the low-quality food source ($\bar{X} \pm \text{CI}$: 0.51 ± 0.04 versus 0.42 ± 0.06).

Pecking rates did not differ according to feeding site for high-quality food, rank or group size when birds were feeding at the high-quality food source (Table 3). However, when feeding at the low-quality source, there was a main effect of feeding site, with a lower pecking rate at the exposed feeder ($\bar{X} \pm \text{CI}$: 0.43 ± 0.08) than at the feeder in cover ($\bar{X} \pm \text{CI}$: 0.38 ± 0.04).

Net Result of Foraging Decisions: Intake

There was a higher relative intake of high-quality compared to low-quality food across all birds, confirming a difference in food return according to food quality (Table 4, Fig. 5). Additionally, there was an interaction between rank and food quality on intake. Specifically, immigrants had a slightly lower intake than both adults and retained offspring at the high-quality food source (Table 4, Fig. 5). Notably, the main effect of rank was not significant (Table 4; remains nonsignificant after removing interactions), suggesting that all birds, independent of

Table 2. Effects of social factors, sex, feeding site and food quality on vigilance rates

| Effect | df | F | P |
|-------------------------|---------------|-------------|---------------|
| Rank | 2,29.5 | 0.80 | 0.4598 |
| Sex | 1,29.4 | 0.00 | 0.9983 |
| Group size | 3,50.6 | 0.69 | 0.5604 |
| Feeding site | 1,82.6 | 0.11 | 0.7417 |
| Food quality | 1,82.2 | 0.21 | 0.6477 |
| Trial | 1,84.2 | 0.79 | 0.3768 |
| Group size*food quality | 3,83.6 | 5.24 | 0.0023 |

The results are obtained from a GLMM with normal error and identity link. The emboldened factors denote the final model.

Table 3. Effects of social factors, sex, feeding site and food quality on pecking rates (separate models for high and low food quality, see Methods)

| Effect | High quality | | | | Low quality | | | |
|--------------|---------------|---------------|----------|----------|---------------|---------------|-------------|---------------|
| | Num <i>df</i> | Den <i>df</i> | <i>F</i> | <i>P</i> | Num <i>df</i> | Den <i>df</i> | <i>F</i> | <i>P</i> |
| Rank | 2 | 31 | 0.16 | 0.8548 | 2 | 26.0 | 1.10 | 0.3489 |
| Sex | 1 | 31.4 | 0.06 | 0.8105 | 1 | 27.0 | 0.22 | 0.6439 |
| Group size | 3 | 44.5 | 1.77 | 0.1658 | 3 | 38.6 | 0.81 | 0.4970 |
| Feeding site | 1 | 37 | 0.06 | 0.8056 | 1 | 30.3 | 4.95 | 0.0337 |
| Trial | 1 | 37.6 | 0.08 | 0.7850 | 1 | 27.7 | 0.02 | 0.8981 |

The results are obtained from a GLMM with normal error and identity link. The emboldened factors denote the final model.

rank, have about the same absolute food intake over a given period of time. There was also an effect of feeding site on intake that depended on group size, where groups of four had a lower intake in the exposed site ($\bar{X} \pm \text{CI} : 1.05 \pm 0.12$) compared to the one in cover (1.47 ± 0.12 ; Table 4). Such an effect was not observed for any other group size.

DISCUSSION

Here, I examine whether the trade-off between energy intake and predator exposure is affected by a variety of social and intrinsic factors such as kinship, age and sex across different feeding sites and food qualities. I present several lines of evidence that there is indeed an active trade-off that is complicated by social factors that favour access by the dominant breeding pair and their immediate offspring to the highest quality resources. Moreover, birds are willing to queue for access to these better resources, which are also associated with a generally higher level of aggression.

The results I present here are consistent with a previous study on Siberian jays that investigated foraging choices across seasons at feeding sites that differed in their associated level of predator exposure, but had equal food quality across all sites (Nystrand 2006a). In the present study, however, I have included another important variable into the above trade-off by varying the food quality across sites, and thus added further resolution to our understanding of the complex nature of the energy–predation

trade-off in social groups. Increasing the food return in a more exposed foraging patch should increase the value of that patch and thus complicate the foraging decisions of an individual. Nevertheless, the worst mistake an individual can make is failing to avoid a predator. Thus, despite a potentially higher food return in more exposed patches, it may still be worth to sacrifice food for safety. Such complexity in foraging decisions was illustrated in a study of white-throated sparrows, *Zonotrichia albicollis*. Instead of feeding optimally in terms of energy harvested per unit time, these sparrows exploited the protected, safer patches more than expected before moving to the more exposed sites (Schneider 1984).

Foraging decisions in Siberian jays were clearly affected by the quality of the food, but trade-off decisions differed among ranks. Adults fed more than yearlings at the exposed site if the food quality at that site was higher than in the protected, safer site. This is likely to be a result of the adult’s greater experience in assessing risk, in combination with their social dominance that enables them to have an unrestricted choice that is closer to optimal than that of inexperienced and subordinate individuals. Retained offspring showed foraging behaviour that was more similar to adults than to the same-aged immigrants, by also feeding more on the feeder that offered the high-quality food. In contrast, the nonrelated immigrants divided their foraging equally between the

Table 4. Effects of social factors, sex, feeding site and food quality on food intake

| Effect | Num <i>df</i> | Den <i>df</i> | <i>F</i> | <i>P</i> |
|-------------------------|---------------|---------------|----------|-------------------|
| Rank | 2 | 31.1 | 1.69 | 0.2006 |
| Sex | 1 | 31.1 | 0.01 | 0.9346 |
| Group size | 3 | 50 | 0.21 | 0.8860 |
| Feeding site | 1 | 95.7 | 13.60 | 0.0004 |
| Food quality | 1 | 96 | 181.59 | <0.0001 |
| Trial | 1 | 103 | 0.10 | 0.7543 |
| Group size*feeding site | 3 | 96.1 | 4.06 | 0.0091 |
| Rank*food quality | 2 | 96.1 | 3.93 | 0.0228 |

The results are obtained from a GLMM with normal error and identity link. The emboldened factors denote the final model.

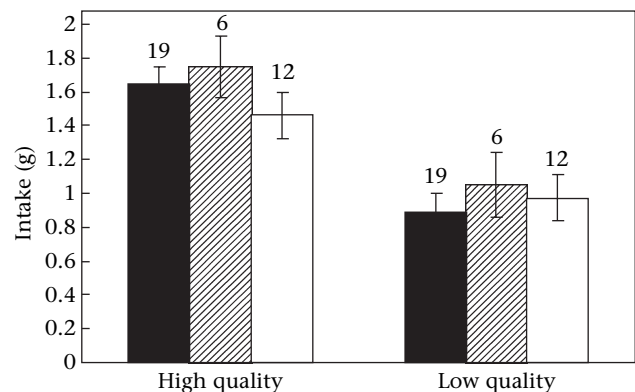


Figure 5. Net food intake (g ± 95% CI) for birds of different rank at the two different food qualities. ■: adults; ▨: offspring; □: immigrants. Sample sizes (number of individuals in each rank class) presented above bars.

two feeders, independent of the associated food quality. As a result, immigrants were forced to feed more often at the site associated with a higher exposure to predators to reach similar levels of total energy intake as the other group members, even when the food return may have been insufficient to compensate for the increased exposure to predators. This result is further supported by the higher overall intake among kin group members relative to immigrants on high-quality food per se, a result that reflects the fact that adults and retained offspring spend more time at this food source.

A cost of subordination was also reflected as a sex-effect, whereby immigrant females spent less time foraging than any of the other classes (rank and sex) of birds. Since male Siberian jays are generally dominant over females (Sklepkovych 1997) and adults are generally dominant over yearlings, but provide kin with benefits (Nystrand 2006a), yearling immigrant females will effectively be lowest in the dominance hierarchy. As a result, immigrant females may suffer the highest absolute costs, forcing them to feed more 'efficiently' than any other group member. This could be accomplished by devoting less time to anti-predator behaviour or social interactions.

Aggressive interactions appear to be the underlying mechanism behind the rank-related higher level foraging patterns observed in this study. Immigrants were essentially the sole recipients of this aggression, a pattern that is consistent with previous findings in this species (Griesser 2003; Griesser et al. 2006). Aggression levels may vary throughout the year, as indirectly suggested by the individual foraging patterns recorded in a study by Nystrand (2006a). Changes in predation pressure and/or natural variations in the access to food could greatly alter these levels. For instance, Siberian jays most likely depend on hoarded resources to survive the long winter (Sklepkovych 1997). By late winter, these hoarded resources may be approaching exhaustion. If so, this will induce a highly competitive situation once birds encounter a new food source. Seasonal variation in aggression levels may also be related to the approaching breeding season per se, which may induce stronger mate competition with, in particular, alpha males becoming more aggressive towards immigrant males in late winter. Additionally, securing food for their future nestlings in the ensuing breeding season may provide another possible incentive for adult breeders to increase the defence of any food source at this time of year.

At a lower decision level, individuals can compensate for an increased predation risk by increasing vigilance, and vigilance rates are typically associated with factors such as social rank (Ekman 1987; Krams 1998) and distance to cover (e.g. Barnard 1980; Lima 1987; Hogstad 1988; Slotow & Rothstein 1995). Siberian jays did not alter their vigilance rates according to such factors, a result that is similar to several other studies that also failed to find such effects (Elgar 1986; Hogstad 1988; Catterall et al. 1992; Slotow & Rothstein 1995). There was, however, an effect of group size on vigilance rates in this study, whereby the smallest groups had higher vigilance rates. This result is consistent with both theoretical predictions (e.g. Pulliam 1973) and other empirical studies (reviewed in Elgar 1989). However, this group size dependent

difference in vigilance was confined only to the high-quality food source. This is best explained as a direct effect of the shorter handling times for high-quality food, enabling individuals to devote more time to vigilance without compromising their total food intake, thus increasing energy gain as well as improving predator avoidance.

Pecking rate is predicted to decrease with increasing distance to cover as a direct result of the increased time devoted to vigilance at more exposed sites (Barnard 1980). In this study, pecking rate was lower in the exposed site compared to the site in cover, but only when it was baited with low-quality food. This suggests that only in the 'worst' situation (i.e. low food return, high predator exposure) was there a measurable adjustment at the lower level of decision-making. However, the lack of a resulting increase in vigilance indicates that this difference in pecking rate may be attributable to more time devoted to behaviours that were not measured in this study (such as short-term scans or head ups). Although vigilance and energy intake have previously been assumed to be mutually exclusive (Lima 1987), this assumption has been questioned (e.g. Lendrem 1984; Lima & Bednekoff 1999; Cresswell et al. 2003). Recent studies have, indeed, showed a more complex and variable scanning pattern than traditionally assumed (Scanell et al. 2001; Bednekoff & Lima 2002). For example, research on ground-foraging birds has shown that the avian vision is versatile and that birds that appear to be 'nonvigilant' may in fact have satisfactory vision over their surroundings (Lima & Bednekoff 1999). In this study, I measured only 'high-cost vigilance', which by definition neglects all vigilance carried out during the actual feeding. Hence, this provides another potential reason for the lack of association between pecking and vigilance rates observed here.

In sum, all birds appear to meet their food requirements, although nonrelated immigrants do so at the expense of safety. Individuals manage the trade-off between food requirements and predation risk primarily by making higher level rather than lower-level decisions. The most important factors affecting the trade-off between energy intake and predation risk appear to be age (experience) and kinship. Costs of subordination through social interference clearly force immigrants to take higher risks while foraging and thus, the realized net benefits to immigrants are less than those to adults and retained offspring. Hence, immigrants pay higher costs to attain energy levels similar to that of other group members. Perhaps the most interesting comparison, however, is between yearling offspring and yearling immigrants because it enables the effects of kinship and age to be disentangled. The differences in foraging patterns between these two classes show the benefits accrued by retained offspring through delaying dispersal and remaining within the natal territory. As the results of this study suggest, the parental nepotism provided by Siberian jay parents may assist retained offspring in adopting a more beneficial energy-risk trade-off than same-aged immigrants. Thus, it is clear that associating with relatives offers advantages beyond those of elementary group benefits. This is in line with a growing number of studies that indicate that the primary benefits of delaying dispersal

and forming kin groups may be best explained by direct fitness benefits in many species (e.g. Scott 1980; Black & Owen 1989; Stacey & Ligon 1991; Ekman et al. 1994, 2000; Griesser et al. 2006). However, adults should only give beneficial treatment to kin as long as it does not impair their own chances of survival (Ekman & Rosander 1992; McNamara et al. 1994), and hence, the extent of the direct benefits offered to kin during foraging is likely to covary closely with the risk of predation and the quality of the available food.

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