

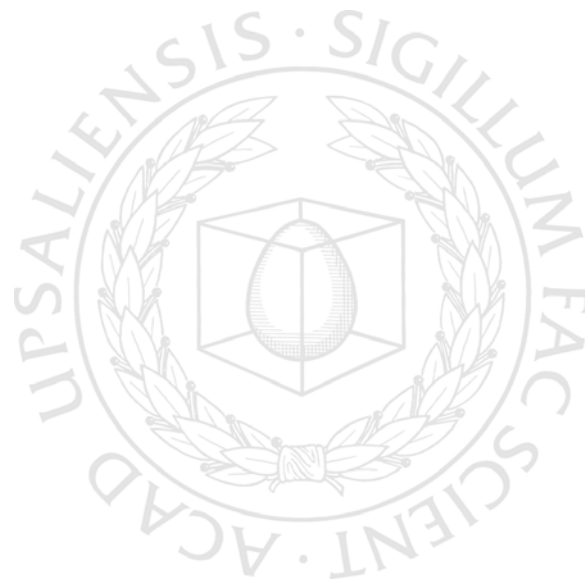


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Effects of Habitat Quality on Behavioural Decisions and Population Dynamics in the Siberian Jay

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Abstract

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The dynamics of natural populations may be influenced by a variety of factors, ranging from feeding interference and territoriality to the risk of predation and climatic effects. The relative influence of these factors may be contingent upon the quality of the habitat in which individuals reside. A factor that can largely affect population dynamics and that often covaries with habitat structure is predation risk. However, the combined effect of habitat and predation risk can vary according to the social context and intrinsic characteristics that affect individual behavioural responses. This thesis investigates the effects of habitat quality at the level of the population and the individual, and examines how it relates to the above factors in Siberian jays (*Perisoreus infaustus*), a territorial, group-living species in which the main cause of mortality is predation. The results demonstrate a strong effect of habitat on survival, reproduction and behaviour. Mortality was generally higher in open areas and managed forests and reproductive success decreased after forest management. Breeding females were more sensitive to environmental factors than males, possibly because of higher reproductive costs. Estimates of spatial demography suggested that there were more sinks than sources, and that they were located in open, managed forests. Behavioural decisions confirmed that open forests were associated with higher predation risks. However, decisions depended on social context; immigrants took highest risks and were the recipients of most aggression, largely an effect of social subordination. Also, parents provide their offspring with benefits that are withheld from immigrants. As a result, first-year survival was higher in retained offspring. Investigating the effects of multi-scale habitat quality on individual behaviour and population dynamics has generated an increased understanding of the effects of forest management on the dynamics of this population. This approach should facilitate development of an effective conservation management policy for this species.

Keywords: Perisoreus infaustus, relatedness, delayed dispersal, predation risk, foraging, trade-off, demography, source-sink dynamics, forest structure

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To my family

List of papers

This thesis is based on the following five papers, which will be referred to in the text by their Roman numerals.

- I** Nystrand M, Griesser M, Eggers S, and Ekman J. Habitat-specific demography in a social, territorial bird species. Manuscript.
 - II** Griesser M, Nystrand M, Ekman, J. 2006. Reduced mortality selects for family cohesion in a social species. *Proceedings of the Royal Society B*, in press.
 - III** Griesser M, Nystrand M, Eggers S, Ekman J. Impact of forestry practices on fitness correlates in an open-nesting bird species. Manuscript.
 - IV** Nystrand M. Influence of age, kinship, and large-scale habitat quality on local foraging choices of Siberian jays. *Behavioral Ecology* 17:503-509.
 - V** Nystrand M. Associating with kin affects the trade-off between energy intake and exposure to predators in a social bird species. Submitted manuscript.
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The order of the authors reflects their involvement in the papers. In paper (I), I personally extracted data, performed all the statistical analyses and did all the writing. All authors collected field data and commented on the text. In paper (II), I helped collecting field data, discussed ideas and made significant comments on several versions of the manuscript. In paper (III), I helped collecting field data, discussed ideas, and performed parts of the writing, statistical analysis and figures.

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Introduction

The dynamics of natural populations may be influenced by a variety of factors, ranging from feeding interference and territoriality to predation, parasitic load, disease and weather conditions (Sutherland 1996). Most of these factors will be largely influenced by the habitat in which an individual lives. In fact, habitat destruction is the most important cause of the decline of populations and ultimately, the loss of species (Primack 1993; Pullin 2002; Wilcox and Murphy 1985). Habitat loss can be caused by natural processes (e.g. Picket and Thompson 1978; Wright 1974) or be the result of anthropogenic alterations to the environment (Sutherland 1996, 1998). Although the process of habitat destruction may vary both according to intervention and scale, it will always increase the fragmentation of the landscape to some extent, thus, resulting in increased habitat heterogeneity (Pullin 2002). This can lead to indirect changes in both physical (e.g. wind, radiation) and biogeographic attributes (e.g. connectivity, surrounding matrix) (Saunders et al. 1991). The new conditions may have a large impact on species diversity (Ambuel and Tempel 1983; Brotons et al. 2003; Whitcomb et al. 1981), individual fitness parameters and population growth (Matthysen and Adriaenssen 1998).

Habitat effects may be expressed at several geographical scales. For example, 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). Large areas of unsuitable habitat can also make it difficult to find a mate (Allee 1931; Begon et al. 1996). At an intermediate or a small scale, individual dispersal can be affected by local resource competition (e.g. Perrin and Mazalov 2000). Moreover, processes such as foraging behaviour or mate competition may vary on a small scale, where for example, choice of feeding site or position within a lek (Höglund and Alatalo 1995) may be expressed as patch choice within an area or a territory, or as microhabitat choice within a patch.

A factor that often co-varies with habitat structure is predation risk. Predation is a strong selective force that plays a major role in the evolution of several traits. Also, changes in predation pressure may have a direct effect on population dynamics (e.g. Andrén 1992; Chalfoun et al. 2002; Gates and

Gysell 1978). A range of studies has suggested indirect or direct effects of predation risk on demographic parameters such as reproductive success (Andr n 1990; Martin and Ghalambor 1999; Eggers et al. 2005b), survival (Cohen and Lindell 2004; Kotler and Blaustein 1995; Pettorelli et al. 2003; Sullivan 1989), dispersal (B lichon et al. 1996; Matthysen and Currie 1996; Yoder et al. 2004), but also on characteristics such as morphological adaptations (Lima and Dill 1990) and behaviour (Brown and Kotler 2004; Desrochers 1989; Elgar 1989; Godin and Briggs 1996; Lawler 1989; Lima and Dill 1990).

An increased individual activity may increase the risk of being detected by a predator. Most animals face a constant challenge of gaining sufficient energy, a process often associated with higher levels of activity, while at the same time avoiding being detected by a predator. This trade-off 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). There are a number of ways that individuals can regulate the trade-off between energy intake and predation risk, some of which includes increasing their vigilance in more exposed sites (Barnard 1980), choosing the most rewarding patch (Brown 1988; Brown and Kotler 2004; Ekman 1987; Hogstad 1988; Kotler 1997; Kotler and Blaustein 1995; Lima et al. 1985; Walther and Gosler 2001), associating in groups (Caraco et al. 1979; Elgar 1986; Ekman 1987) or by simple diet selection (Lima 1987). However, although all individuals should aim to optimize their foraging strategy, not all individuals have equal freedom to do so. For group-living individuals, energy intake may vary according to social interference (Goss-Custard and Durell 1987a; 1987b, 1987c; Slotow and Paxinos 1997). Dominant individuals can exclude subdominants from safer feeding sites, thereby forcing them to take higher risks (e.g. Schneider 1984; Hegner 1985; DeLaet 1985; Ekman 1987; Desrochers 1989). Even so, the advantages of joining a group of conspecifics or heterospecifics (e.g. Dolby and Grubb 2000; Ekman 1987; Wu and Giraldeau 2004) may outweigh the costs associated with social interferences. Furthermore, in groups that contain both related and non-related members, energy intake and predator avoidance may become even more complex since relatives can provide benefits to one another that are withheld from non-relatives (Black and Owen 1989; Ekman et al. 1994; Griesser 2003a; Hamilton 1964; Scott 1980). In such cases, dominance hierarchies may not only be related to factors such as age and sex, but also to relatedness *per se*.

In this thesis, I investigate the effects of habitat quality at multiple levels on various components of population dynamics (I, II, III), and also examine how the habitat influences behavioural decisions involved in foraging under

different risks of predator exposure (IV, V). In addition, I relate these processes to intrinsic characteristics and the social context. I chose to address these questions in a population of Siberian jays (*Perisoreus infaustus*), which in many respects provides an excellent model system. The population has been studied for more than 15 years which has generated substantial knowledge on both the ecology and behaviour in this species. The study site contains territories of varying quality, thus allowing detailed studies of how the environment affects individual fitness and different aspects of population dynamics. Moreover, Siberian jays form social groups that in addition to a breeding pair may contain retained offspring and/or unrelated immigrants from neighbouring groups (Ekman et al. 1994). Previous studies on this population have demonstrated that parents are nepotistic towards their offspring by giving them benefits such as increased access to food and protection against predators (Ekman et al. 1994, 2000; Griesser 2003a). Thus, in addition to the effects of factors such as sex or group size on behavioural decisions and demography, this system also allows one to study how these processes are affected by relatedness *per se*.

Methods

Study species and study area

The Siberian jay is a sedentary, territorial bird with a distribution ranging from Norway in the west, throughout the boreal Palaearctic to North-east China in the east (Jonsson 1992; MacKinnon and Phillips 2000). The breeding pair is monogamous and pairs stay together for life and there are no recorded cases of extra-pair paternity (Ekman et al. 1994; Griesser 2003; Lil-landt et al. 2001). Siberian jays produce one brood per season with clutch sizes ranging from 1–5 eggs (average 3.9 ± 0.1 ; Eggers et al. 2005a). Only females incubate the eggs, during which time the male provides her with food. Nestlings of seven days of age or more receive food from both parents (Eggers 2002). Approximately one-third of all fledglings produced within the population delay dispersal and remains in their natal territories for up to three years (Ekman et al., 2001; Ekman and Griesser 2002). Breeders are nepotistic towards these retained kin, providing them with benefits (e.g. relaxed feeding conditions and predator protection) that are withheld from non-related group members (Ekman et al. 1994; Ekman et al. 2000; Griesser 2003b; Griesser and Ekman 2004, 2005; Nystrand 2006). However, neither retained offspring, nor immigrant birds engage in allo-feeding (Ekman et al. 1994), help at the nest (Ekman et al. 1994) or participate in anti-predator activities (e.g. mobbing, alarm calling, vigilance; Griesser 2003a). Moreover, retained offspring rarely inherit the natal territory at the death of a parent (Ekman et al. 2001; Ekman and Griesser 2002; Kokko and Ekman 2002) and there are no records of a breeder being evicted from a territory by a kin or immigrant bird (unpublished data).

We studied a population of Siberian jays near Arvidsjaur, northern Sweden ($65^{\circ} 40' N 19^{\circ} 0' E$) between 1989 and 2004. 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 (both 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*). Large parts of the study site have been severely affected by forestry, resulting in either a complete loss of jay territories due to

clear-cutting, or a significant reduction in habitat quality due to heavy alterations of the habitat. The general practice before clear-cutting an area is to thin the forest by removing bushes and trees of poorer quality from the stand. This procedure increases the growth of the remaining crop, hence increasing its economic value. As a result, the forest becomes more open and provides less visual cover from predators. Despite the natural vegetation in the study site being dominated by spruce, forest companies almost exclusively re-plant pine seedlings since pine trees are economically more valuable (Loman 2005). This contributes to changing the visual properties of the forest since pine trees do not have live branches in the lower two thirds of the trunk, thus further increasing the openness of the forest. In contrast, spruce trees often have live branches that extend almost down to the base of the trunk.

Reproductive success (I, II)

All birds in the study population have been individually colour-ringed since 1989. Since Siberian jays are open-nesters with highly cryptic nests (Eggers et al. 2005b), we located most nests with the help of radio-telemetry ($N = 277$). Female breeders were caught and fitted with a radio-transmitter before each breeding season (March). We applied an individually numbered metal ring to the right tarsus of each nestling one to two weeks before fledgling. In the cases where we were unable to catch the female breeder or the female breeder was preyed upon between radio-tagging and the onset of incubation, breeding success was determined with two alternative methods. We visited groups shortly before juvenile dispersal in June (Ekman et al. 2002) and caught juveniles with mist nets ($N = 27$ broods). Alternatively, we determined breeding success in autumn by checking the presence of retained offspring ($N = 66$ broods). In the majority of groups that have successful reproduction, at least one offspring delays dispersal and remains in the parental territory where they stay until the next breeding season or longer (Ekman and Griesser 2002). By assessing aggressive interactions between breeders and juveniles on feeding sites in autumn, it is possible to determine relatedness between individuals in a group (see Griesser 2003b for detailed description). The sex of each bird was determined using the molecular technique described in Griffiths et al. (1998).

Mortality and group composition (I, II)

We collected data on group composition at least twice a year; in the breeding season (March, May, June) and in late autumn/early winter after juvenile dispersal (September, October). This observational scheme allowed us to assess territory occupancy and to capture breeding dispersal events.

Siberian jay breeders rarely divorce their partners and disperse ($n = 5$ out of 220 pairs; Griesser et al. in prep). Hence, adult mortality could be estimated by simply monitoring the group composition in each territory each year. We only used data from territories that had not been subject to prior experiments (e.g. extensive feeding, removal of breeder males) to assess breeder mortality. Juvenile mortality was studied by active monitoring of juveniles that had been fitted with radio-transmitters (October). We followed the juveniles during October/November, December/January, February and March. During monitoring, we managed to identify all live birds and retrieve the dead individuals.

Habitat quality (I, II, III, IV, V)

We applied slightly different methods to estimate habitat quality. In study (I), we extracted environmental parameters for each territory from digital maps and aerial photographs by applying a 30 ha circular buffer zone to the breeding area. The parameters used for analysis were average volume spruce and pine, distance to human settlement and area of natural openings within the territory. These parameters were selected based on their expected influence on mortality risk and reproductive success of the jays, mainly because of their potential to increase fragmentation and enhance the openness of the forest. These factors are likely to facilitate search for prey and hunting success of predators using visual cues. In study (II) and (IV), we measured the proportion of forest that had not been managed for the last 50 years (i.e. not thinned, partially cut or clear cut and re-planted) in each territory. Unmanaged forests had a denser understorey, thus providing more visual protection from predators. Habitat data were sampled in the field and borders between vegetation types were recorded with a GPS receiver. To define approximate territory borders, we created 95 % minimum convex polygons based on all locations taken of groups (using GPS receivers) during the study period. Finally, in study (IV) and (V), habitat quality was also estimated on a smaller scale. Here, the patches selected for experiments were located in dense forest (close to dense spruces), at an edge zone (only IV), and in an open area.

Assessment of territory quality (I, II)

In study (I), we assessed the general quality of each territory by comparing total breeder mortality to both the likelihood of successful reproduction (i.e. the production of at least one fledgling) and to the magnitude of reproduction success (i.e. number of recruits produced). The values were standardized to control for the effects of year and bringing them to a common scale. Hence, the average quality for each territory was based on the average of these standardized values. Territories where mortality exceeded basic repro-

duction (i.e. likelihood of one successful fledgling) or actual recruitment (i.e. total number of fledglings surviving until reproductive age) were considered low quality or sinks respectively, whereas territories exhibiting the opposite pattern were considered high quality or sources. These ‘quality classes’ were also tested against the environmental parameters extracted from maps and aerial photographs.

In study (II), we used a nest success index (NSI) to express relative territory quality. This index has been used in previous studies on this population (Ekman et al. 2001; Eggers 2002), and enables a straightforward comparison between sites. The NSI consists of the sum of differences over years between the actual reproductive success within a given territory and year (0 = failure, 1 = success) and the average success probability in the whole population the same year. By using the NSI, we had access to more data since it allowed for the inclusion of territories where nests had not been found but where successful reproduction could be confirmed by observations before juvenile dispersal or through the presence of retained offspring. We calculated a separate NSI before and after the habitat change in those territories that were affected by forestry (thinning, partial cutting). Because our aim was to measure the direct effects of forestry on breeding success, we only included years during which a territory was occupied in the calculations. However, we also assessed the number of retained offspring in each territory. Previous studies have demonstrated that retained offspring are the individuals that end up occupying high quality sites and they therefore contribute most to the productivity of the study population (Ekman et al. 1999, 2001).

Assessment of individual quality (II)

We measured all juveniles (weight and wing length to calculate wing load = weight/wing length) and counted the number of faulty growth bars on the right or left wing feather depending on which one that had the maximum number of faulty growth bars. Wing load is likely to be the physical measure that is of most relevance to the escape ability during a predator attack. Faulty growth bars in the wing feathers of juveniles reflect suboptimal growth condition as a nestling (Grubb 1989). To be able to assess current condition we removed the outermost left tail feather (in September 2002) and collected the re-grown feather when attaching the radio-tag 47 to 52 days later (N = 43 individuals). Thus, the growth rate of the re-grown feather indicated individual resource access.

Predator activity (II, IV)

We assessed predator activity by recording all observations of predators made by an observer during a certain unit of time. We only recorded preda-

tors that are known to be a potential threat to Siberian jays (i.e. goshawk, *Accipiter gentilis*; sparrowhawk, *A. nisus*; hawk owl, *Surnia ulula*; Tengmalm's owl, *Aegolius funereus*; and Ural owl, *Strix uralensis*). This data was collected between spring 1996 and 2003, and it represents more than 10 000 hours of field data.

Behavioural observations under natural conditions (II)

We observed each juvenile once or twice for 30 min in October/November and February to assess the effect of kinship on their behaviour. During these observational bouts, we recorded the position of juveniles relative to other group members (distance to the closest group member: < 50 m = together, > 50 m = alone) as well as foraging activity (foraging or not) at 5-minute intervals using time-point measurements. We also counted all aggressive interactions between group members during these observation bouts.

Local foraging choices (IV)

To test if Siberian jays preferred feeding in some patches over others (small-scale habitat level), and if so, how this pattern varied with respect to social context and large-scale habitat structure, I presented 14 groups of jays to three different feeders, representing different levels of predator exposure (i.e. forest structure). The experiment was performed in two seasons associated with different levels of predation risk. The first feeder ('feeder 1') was positioned within dense forest cover (i.e. in or near a spruce surrounded by several other trees), 'feeder 2' was positioned at the edge of the forest, no more than 2 m from the closest tree and 'feeder 3' was positioned within a forest opening at least 10 m from the closest tree. An increased distance from cover was assumed to be associated with a higher exposure to predators. Each feeder was baited with pig lard of equal quality and size, in amounts large enough to avoid any depletion effect. I repeated the trials on average three times per flock in autumn and once per flock in late winter. I only recorded the number of visits made by an individual to each feeder (but not the time an individual remained on the feeder).

Trade-off between energy intake and safety (V)

The experimental design consisted of two feeding stations placed in two different small-scale habitats within a given territory: one in cover (2 m into the forest measured from the forest edge) and one 12 m outside of forest in a natural opening (i.e. exposed). The two feeders were baited with food that differed in 'quality'; one feeder contained high quality food (i.e. short handling time) whereas the other contained low quality food (i.e. long handling time). I performed a cross-over experiment that consisted of two randomly-

assigned trials (30 minutes/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, whereas the other trial had the reverse set-up. I observed the feeding behaviour at an equal distance from both feeders. In addition, there were two video cameras triggered to film each feeder respectively. From the videotapes and by weighing the food before and after trials, I collected data on individual pecking rates, food intake, choice of feeder, time spent on feeder, social interactions and vigilance rate. Finally, to estimate additional costs associated with foraging, I recorded the number of times an individual was observed waiting for access to food (≤ 3 m away) and how many times an individual was displaced by another group member while foraging (passive displacement did not involve direct physical contact whereas aggressive displacement included pushing or bill snapping).

Results and Discussion

Habitat-specific demography in a social, territorial bird species (I)

The average number of birds per territory showed no consistent trend over the years of study (linear regression, $n = 14$, $r^2 = 0.02$, $F_{1,12} = 0.20$, $p = 0.66$). Average fledgling production was similar over years (linear regression, $r^2 = 0.32$, $F_{2,11} = 2.53$, $p = 0.12$) and did not depend on overall population size (linear regression, $r^2 = 0.0020$, $F_{2,11} = 0.02$, $p = 0.88$) or group size (GLMM, Poisson error, log link, $n = 117$, $F_{1,66} = 0.40$, $p = 0.88$), indicating that there was no density-dependent suppression of productivity in the population. In addition, overall mortality did not differ between sexes or years (Table 1), nor did it depend on group size.

Table 1. Generalised linear mixed model (GLMM) testing the effects of sex, year and group size on mortality. Full model is displayed (removal of non-significant terms does not generate significant effects).

	Num DF	Den DF	F	p
year	1	114	0.50	0.4799
sex	1	94	0.67	0.4137
group size	1	114	0.00	0.9444
year*sex	1	114	0.69	0.4095
sex*group size	1	114	1.26	0.2637
year*group size	1	114	0.01	0.9418

Females and males showed different responses to the environment (Table 2). Females had a higher mortality in territories consisting of higher volumes of spruce and pine, whereas male mortality was not related to either of those factors. This discrepancy in habitat-dependent mortality between sexes is probably best explained as sex-differential reproductive costs. Females increase in weight at the onset of breeding which probably cause them to be more sensitive to predation than males. In addition, females may invest more in offspring care than males. However, both sexes suffered an increased

mortality when there were more open areas in the territories, indicating a negative effect induced by edge effects (Fig 1).

Table 2. GLMM testing the effects of environmental parameters on mortality in females (n = 19) and males (n = 19). Emboldened text denotes the best fitting model according to AIC (Akaike Information Criteria).

	<i>female</i>				<i>male</i>			
	Num	Den	F	P	Num	Den	F	P
	DF	DF			DF	DF		
year	1	55	0.75	0.3916	1	57	0.57	0.4528
\bar{X} volume pine	1	55	9.69	0.0029	1	55	0.08	0.7837
\bar{X} volume spruce	1	55	9.63	0.0030	1	55	0.20	0.6561
natural openings	1	45	7.56	0.0086	1	45	4.50	0.0394
dist. settlement	1	44	0.88	0.3533	1	44	0.22	0.6389

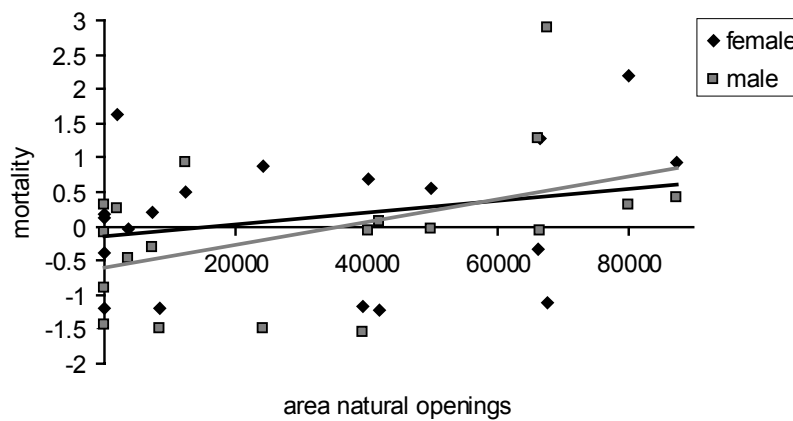


Figure 1. Female and male mortality in relation to the area of the territory consisting of natural openings ($n_{\text{female}} = 19$, $n_{\text{male}} = 19$).

Finally, nest success was lower close to human settlements, an effect that reflects negative interactions with human-associated corvids, which are common nest predators of Siberian jays (Ekman et al. 2001). In addition, predation pressure probably interacts with the habitat structure close to human settlements since the forest tends to be more fragmented and open in these areas.

Comparison of breeder mortality to basic reproductive success or recruitment demonstrated that 54 % of the territories studies were of high quality, but only 37.5 % of these were actual sources. Furthermore, source territories consisted of a lower volume of pine, indicating that sources were located in denser and more diverse forest areas.

There may be large individual variation in response to habitat loss depending on the mode of territory acquisition and territory choice, and simply estimating population dynamics by numbers can give misleading results (Kokko et al. 2001; Pulliam 1988, 1996). Detailed data on the various factors governing population dynamics provides information that can reduce the risk of implementing management decisions that are based on unrepresentative data. Thus, the identification of sources and sinks can be of vital importance for successful management of heterogeneous landscapes (Dias 1996).

Reduced mortality selects for family cohesion in a social species (II)

We were able to determine the fate of all 73 juveniles that fitted with radio-tags. Predation was the sole reason of first-winter mortality, and 20 juveniles were retrieved killed in their territories (Table 3). The majority had been killed by goshawks (*Accipiter gentilis*).

Table 3. The number of surviving juveniles observed between September and March of the following year. Birds that disappeared in winter were retrieved dead and had all been killed by predators.

	Sept	Nov	Dec/Jan	Feb	March	% survived
Philopatric offspring	34	33	32	27	27	79.4
Immigrants	39	32	27	26	26	66.7

Three factors affected first-winter predation rate: habitat structure, individual quality and kinship (Table 4).

Individuals with more faulty growth bars in their wing feathers, reflecting suboptimal growth conditions as nestlings, had a higher probability of being preyed upon during their first winter. However, condition at the onset of winter (as measured by the capacity to regenerate feathers) did not differ between philopatric offspring and immigrants.

The odds of being killed by a predator during the first winter of life were higher for immigrants than for philopatric juveniles (Table 4). However, this was not an effect of habitat structure since there was no difference in the proportion of unmanaged forest on territories containing philopatric off-

spring (0.44) compared to territories with immigrants (0.44; $\chi^2 = 0.01$; $df = 1$, $p = 0.98$).

Table 4. Linear mixed model showing the effect of independent model terms on first winter-mortality of Siberian jays (34 kin birds, 37 non-kin birds). The model was reduced by sequentially removing non-significant terms from the model, leaving only significant terms (p -values < 0.05). The effect of non-significant terms was estimated by adding them individually to the model. Sample size for feather re-growth data $N = 43$ individuals, for all other terms $N = 73$. Effects indicate direction of relationship and are presented after setting the mean of the covariate to zero.

Model term	Wald χ^2	df	P-value	Effect	SE
Prop. unmanaged forests	8.44	1	0.004	-5.60	1.93
Faulty growth bars wing	7.53	1	0.006	0.93	0.34
Kinship	4.83	1	0.028	1.74	0.79 (nk > kin)
Time associated with group	2.10	1	0.15	-1.77	1.22
Wing load	1.72	1	0.19	6.12	4.67
Sex	0.32	1	0.57	0.37	0.68 (f > m)
Group size	0.19	1	0.65	-0.24	0.54
Feather re-growth	0.01	1	0.97	0.01	0.10
Constant				-1.39	0.59

As a consequence of frequent displacements, immigrants spent significantly less time foraging than did philopatric offspring. They also spent more time away from the group (18.9 % of time point observations; $N = 39$ individuals) than philopatric offspring (10.6 %; $N = 34$ individuals; $\chi^2 = 13.99$; $df = 1$, $p = 0.0002$). Therefore, immigrants not only allocated a lower proportion of total time to foraging, but they were also unable to fully benefit from the anti-predator protection resulting from a close association with the group.

The beneficial treatment of breeders towards their offspring could be fuelled by group augmentation benefits. However, we were unable to detect any influence of the number of philopatric offspring ($\chi^2 = 0.83$, $df = 1$, $p = 0.36$) or immigrants ($\chi^2 = 0.62$, $df = 1$, $p = 0.40$) in a group on breeder mortality, thus making group augmentation an unlikely explanation behind the beneficial offspring treatment.

Delayed dispersal is the key to family formation in most kin-societies. Previous explanations for the evolution of families have focused on dispersal constraints (Emlen 1991; Stacey & Koenig 1990). Recently however, an

alternative line of explanation was suggested that emphasises the benefits gained through philopatry (Brown 1987; Stacey & Ligon 1991; Ekman et al. 2004). Empirical data in this species have confirmed that parents provide their philopatric offspring with preferential treatment through enhanced access to food and predator protection (Ekman et al. 1994; Griesser 2003b; Griesser & Ekman 2004, 2005). Yet it remains unclear from these studies to what extent such benefits translate into fitness benefits such as reduced mortality, which ultimately can select for the evolution of families. The results of this study demonstrate that the higher survival rate among philopatric offspring was associated with parents providing nepotistic predator protection that was withheld from unrelated group members. Natal philopatry usually involves the suppression of personal reproduction. However, a lower mortality of philopatric offspring can overcome this cost and may thus select for the formation of families and set the scene for cooperative kin-societies.

Impact of forestry practices on fitness correlates in an open-nesting bird species (III)

Forest management strongly affected NSI (nest success index) (Table 5). Pairs living in territories that were partially thinned or partially cut had a significantly lower breeding success after management. However, this reduction in nesting success was independent of the management method, resulting in a NSI that was reduced equally in thinned and partially cut territories (Least Square means difference: estimate = -0.13, SE = 0.14, $t = -0.86$, $p = 0.38$). The reduction in breeding success was unlikely to be a result of breeder quality since most of the affected territories were occupied by the same breeding pair ($N = 8$) or by one of the members of the breeding pair ($N = 4$) before and after the habitat alterations.

Table 5. Analyses of repeated measures data of effect of forest management practices on the NSI (nesting success index) of territories.

fixed effects	n.d.f.	d.d.f.	<i>F</i>	<i>p</i>
area	1	40	3.25	0.078
before vs. after	1	41	14.96	0.0004
management	2	40	5.26	0.0094
before vs. after * management	2	41	8.19	0.001

The reduction in breeding success due to forest management resulted in a lower productivity of high quality offspring (Fig. 2). Both partially cut and thinned territories had a significantly lower production of retained offspring after the habitat had changed due to forestry, independent of management

method (LS means difference: estimate = -0.03, SE = 0.22, t = -0.15, p = 0.88).

In addition, territories with a generally lower NSI remained unoccupied more often than territories with a generally higher NSI (GLMM, binomial distribution, logit link: $\chi^2_1 = 8.88$, p = 0.003). Hence, empty territories with a high NSI were significantly more often re-occupied than empty territories with a low NSI (GLM: effect of NSI: t = 2.24, p = 0.025). Furthermore, territories that were thinned or partially clear-cut remained unoccupied significantly more often than unaffected territories (GLMM, binomial distribution, logit link: $\chi^2_2 = 11.06$, p = 0.004).

Forestry affected both breeding success and territory occupancy, factors that both contribute to the total population productivity. Thus, as expected, there was a significant decrease in productivity of the whole population (including both unaffected and managed territories) in the managed area of the study site, where the average annual number of retained offspring (N = 34 territories) decreased from 21.80 to 9.18 offspring ($\chi^2 = 7.31$, p < 0.01). In contrast, the average productivity in the area of the study site consisting of pristine habitat (N = 17 territories) did not significantly change during the same time period (slight, but non-significant, increase from 8.17 to 10.00, $\chi^2 = 0.41$; NS).

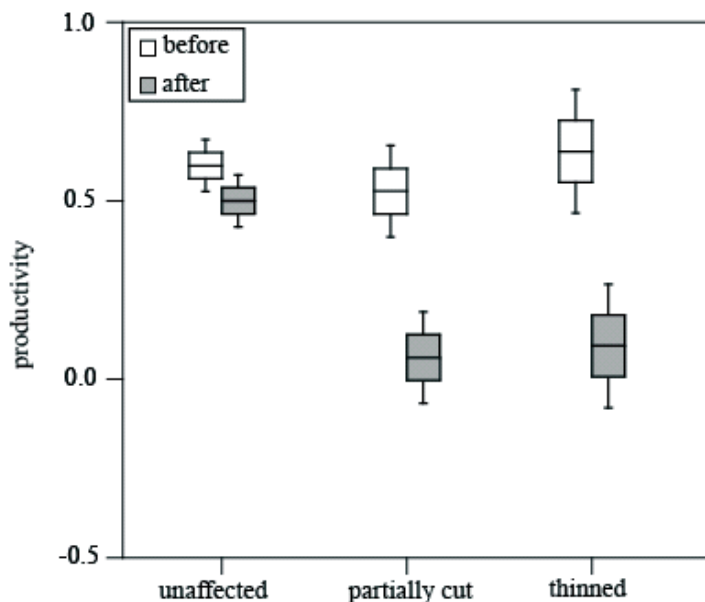


Figure 2. Annual number of retained offspring produced per territory (\pm SE) on unaffected, thinned and partially cut territories before and after management. Unaffected territories were split in equal halves (see methods of paper III). Repeated measures GLM: F 2.48 = 3.82, p = 0.029).

This study demonstrates a strong effect of habitat alteration caused by forest management practices on Siberian jay breeding success *per se*, and on the total productivity of offspring in the population. The experimental design of this study enables a straightforward assessment of the consequences of forest management. In contrast, most previous studies that have investigated the effects of habitat change on species abundance or species diversity have used a correlative approach (Trzcinski et al. 1999; Villard et al. 1999) and also, have reported ambivalent results (McGarigal and McComb 1995; Drapeau & Leduc 2000; Sallabanks et al. 2000; Marzluff et al. 2000).

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

Adults and yearling retained offspring significantly changed their preference from feeding further away from cover in autumn to foraging closer to cover in late winter (Table 5, Fig. 3). In contrast, yearling immigrants did not change their preference. Moreover, jays showed no significant difference in choice of foraging sites among ranks during autumn (GLMM, $F_{2,38.1} = 1.64$, $p = 0.2083$), whereas in late winter, there was an overall difference in choice of foraging site among ranks (GLMM, $F_{2,28.6} = 7.12$, $p = 0.0031$). The observed difference was between adults and immigrants (post-hoc pairwise differences between least square means from the GLMM; $t_{28.7} = -2.38$, $p = 0.0224$) and retained offspring and immigrants ($t_{29} = -2.81$, $p = 0.0234$), whereas there was no difference between adults and retained offspring ($t_{24.5} = 1.02$, $p = 0.5728$).

Table 5. Separate analyses of choice of feeding site for each rank.

	Num DF	Den DF	F	p
<i>adult alpha birds</i>				
flock size	2	53.7	7.63	0.0012
forest structure	1	31.9	0.15	0.7000
season	1	70.3	10.18	0.0021
season*forest structure	1	64.8	9.10	0.0036
<i>retained offspring</i>				
flock size	2	16.4	2.97	0.0793
forest structure	1	12.4	12.61	0.0038
season	1	28.1	17.62	0.0002
season*forest structure	1	26.1	1.10	0.3042
<i>immigrants</i>				
flock size	2	26.7	14.26	<.0001
forest structure	1	5.72	3.49	0.1134
season	1	32.7	0.02	0.8962
season*forest structure	1	32.3	0.00	0.9785

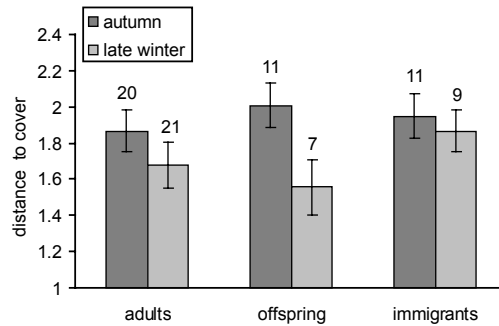
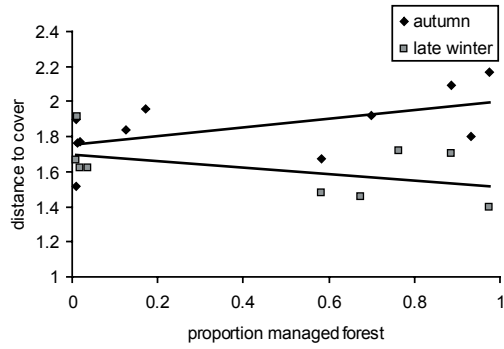


Figure 3. Choice of feeding site during different seasons. The response variable is an index of the preferred feeding distance to cover per individual (based on the choice of feeding sites; see methods paper IV). Columns represent least square means \pm SE. Numbers above bars show sample size (number of individuals).

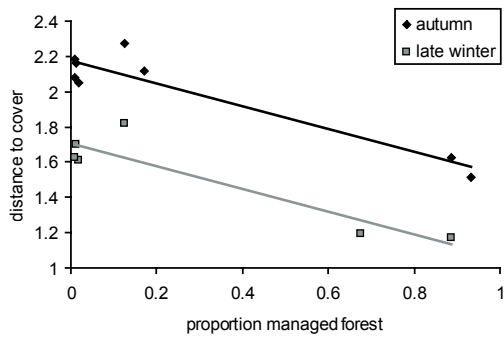
The seasonal shift in adult behaviour depended on forest structure, where adults in territories containing a low proportion of managed forest did not change their preference of foraging site with season while those in territories with more open forest (due to a higher proportion of managed forest) fed significantly closer to cover in late winter (Table 5, Fig. 4a). Retained offspring did not show a similar interaction between season and forest structure, but did demonstrate a general response to forest structure (Table 5, Fig. 4b). There was no corresponding seasonal shift or response to forest structure among immigrant individuals (Table 5, Fig. 4c).

There was a also 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 5).

a)



b)



c)

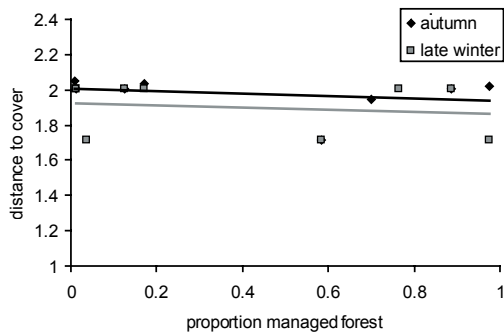


Figure 4. Choice of feeding site in different forest structures during different seasons. The response variable is an index of the preferred feeding distance to cover (based on the choice of feeding sites; see methods). a) adults ($n_{\text{autumn}} = 21$, $n_{\text{late winter}} = 21$), b) retained offspring ($n_{\text{autumn}} = 11$, $n_{\text{late winter}} = 7$) and c) immigrants ($n_{\text{autumn}} = 11$, $n_{\text{late winter}} = 9$).

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 (De-Laet 1985; Hogstad 1988; Schneider 1984; Slotow 1996). Furthermore, the seasonal difference among family members, and 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. 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 predation 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.

The behaviour of non-related immigrants was generally less plastic to variations in predation risk, as reflected by the lack of change in choice of feeding site between seasons. This is probably a result of social constraints. Previous studies of this species have also shown that non-related subordinate flock members take more risks with regards to predation than do family members (Griesser 2003b; Griesser and Ekman 2005).

The results of this study suggest how behaviour may be affected by both intrinsic and multi-scale extrinsic factors and thus, highlight the underlying constraints on behaviour that might be crucial to an individual's fate. To my knowledge, few studies have investigated this multi-scale 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).

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

There was a higher relative intake of high quality compared to low quality food across all birds (Fig. 5, GLMM, normal error, identity link, $F_{2,96} = 181.59$, $p = < 0.0001$). Additionally, there was an interaction between rank and food quality on intake; immigrants had a lower intake than adults and retained offspring on the high quality food (Fig 5, $F_{2,96.1} = 3.93$, $p = 0.02$).

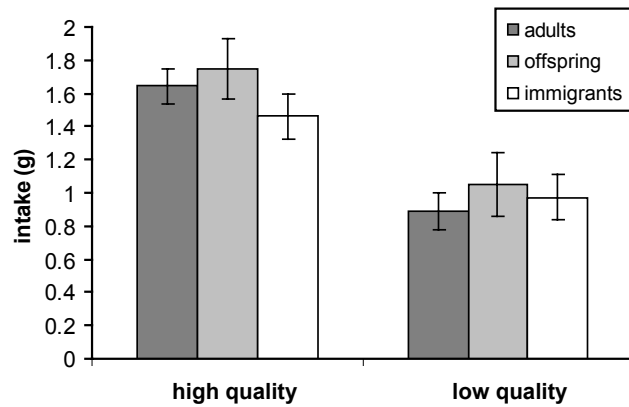


Figure 5. Intake (grams) for birds of different rank. Error bars show 95% confidence limits. Sample sizes are adults $n = 19$, retained offspring $n = 6$ and immigrant $n = 12$.

Adults and yearling offspring chose to feed in cover to a much larger extent when offered high-quality food than when offered low-quality food (Fig 6, GLMM, binomial error with a logit link, rank*quality: $F_{2,33} = 4.58$, $p = 0.018$). In contrast, when the high-quality food was offered on the exposed feeder, this position appeared to be chosen to an equal extent (retained offspring) or more (adults) than the feeding patch in cover (Fig. 6). Yearling immigrant birds chose the patch in cover equally much as the exposed patch, independently of food quality (Fig 6).

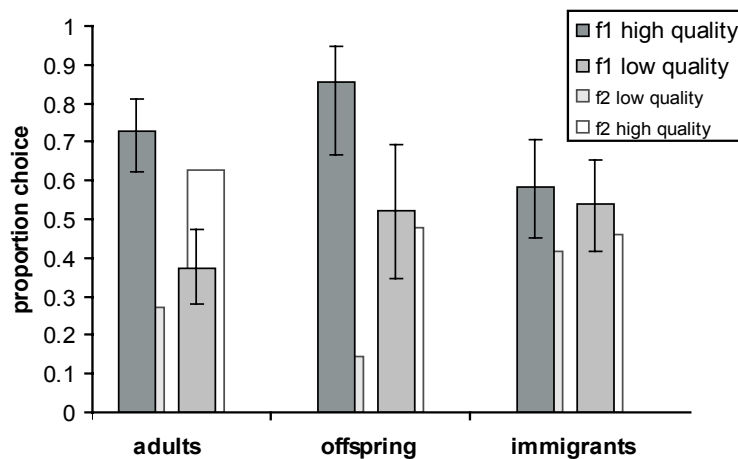


Figure 6. Proportion choice ($\pm 95\%$ CL) made by birds of different rank on different food quality; feeder in cover (f1) is a proportion of total choice on both feeders (f1+f2). GLMM, binomial error with a logit link, For comparison, proportion choice of feeder 2 is presented as lighter coloured bars in the background. Sample sizes are adults $n = 19$, retained offspring $n = 6$, and immigrants $n = 12$.

Pecking rate did not differ between the different feeder positions for high-quality food, or between birds of different rank or groups of different sizes (Table 6). There was however, a significant effect of feeder location in the low-quality food treatment showing a lower pecking rate on the exposed feeder than on the feeder in cover (least square means \pm CL: 0.43 ± 0.04 vs. 0.38 ± 0.02).

Table 6. Pecking rate (separate models for high and low food quality), GLMM, normal error with identity link, bold letters denote final model.

<i>effect</i>	<i>good quality</i>				<i>bad quality</i>			
	df nom	df num	F	P	df nom	df num	F	P
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
feeder pos.	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

There was no difference in vigilance rates between individuals of different rank, feeding positions or food quality. There was however, an effect of group, demonstrating a higher vigilance in smaller groups than in larger groups when feeding on the high quality food (Table 7).

Table 7. Vigilance rate measured as head turns per time unit. GLMM, normal error with identity link, bold letters denote final model.

Effect	df nom	df num	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
feeder position	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* quality	3	83.6	5.24	0.0023

Birds waited more for the high quality food in both foraging sites (cover: n = 64 vs. n = 25, $\chi^2=95.06$, p = < 0.0001; open: n = 9 vs. n= 1). Looking at the effect of feeder location *per se*, birds were observed waiting more often for access to the feeder in cover, independent of food quality (high quality food, cover vs. open: n = 64 vs. n = 9, $\chi^2 = 41.44$, p = < 0.0001; low quality food: n = 25 vs. n = 1).

Displacements depending on food quality and location of food

Aggressive (but not passive) displacements occurred more often on the feeder in cover when it contained high quality food (n = 29 vs. n = 9, $\chi^2 = 10.53$, p = 0.001). The exposed feeding site had more passive and aggressive displacements when the food quality was high compared to when it was low (passive: n_{high} = 61 vs. n_{low} = 36, $\chi^2 = 6.4$, p = 0.011 and aggressive: n_{high} = 14 vs. n_{low} = 0; too low sample size to test statistically) (Fig. 7). Furthermore, both passive and aggressive displacements were more common at high quality food than at low quality food, independent of position (Passive: $\chi^2 = 5.11$, p = 0.024; Aggressive: $\chi^2 = 24.02$, p = <0.0001). Comparing the feeding site in cover to that at 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 ($\chi^2 = 10.37$, p = 0.001) but no difference in the number of passive displacements ($\chi^2 = 1.70$, p = 0.193).

Number of displacements in relation to birds of different rank

Immigrants were exposed to more passive and aggressive displacements than family members (Fig. 8, $\chi^2 = 139.90$, p = <0.001 and $\chi^2 = 152.97$, p = <0.001).

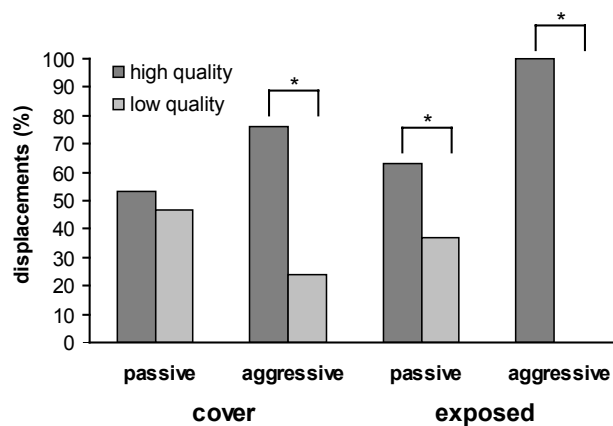


Figure 7. Number of passive and aggressive displacements in the two different feeding sites. Comparisons with asterisks above them indicate significant differences (see text for more information).

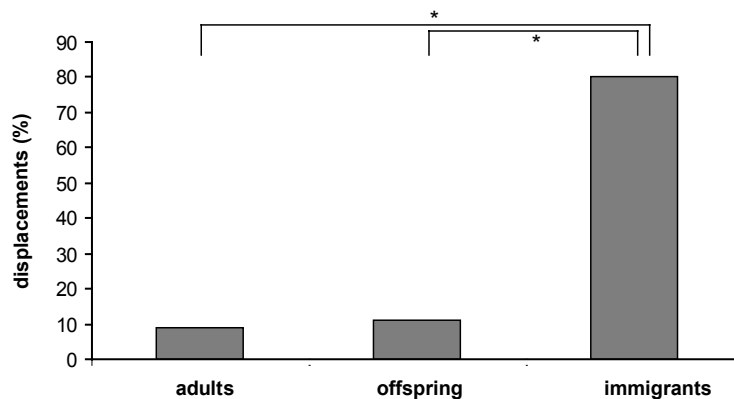


Figure 8. Displacement for birds of different rank (pooled for both passive and aggressive displacements). Comparisons with asterisks indicate significant differences.

The summing up of the results of choice of feeder, time spent on feeder, pecking rate, intake and vigilance levels, illustrates that all birds appear to meet their food requirements, but that non-related immigrants do so at the expense of safety. Individuals managed the trade-off between food requirements and predation risk primarily by making higher-level decisions (at the level of the feeding station) rather than lower level decisions (such as adjusting vigilance and pecking rates). In particular, the most important factors affecting the trade-off between energy intake and predation risk appear to be age and kinship (rank), where immigrants pay a higher cost to attain the same energy intake as family members and where retained offspring take fewer risks than immigrants.

Much of the literature on kinship benefits has focused on the indirect (genetic) fitness benefits (Hamilton 1964) where, for instance, mature offspring can improve their life-time reproductive success by staying in their natal territory to help raise siblings (Ekman et al. 1994). There is, however, a growing body of evidence arguing that the primary benefits of delaying dispersal and forming kin groups may be better explained by direct fitness benefits, such as increased survival (Ekman and Griesser 2000) or an increased chance of acquiring a breeding position (Brown and Brown 1984), thereby increasing life-time reproductive success. The results of this study suggest that parental nepotism may have assisted retained offspring to adopt a more beneficial energy/risk trade-off than same-aged immigrants.

Conclusions

Habitat quality affected both behaviour and demographic traits in the Siberian jay. In the study site, large areas have been subject to forestry regimes where the common practice includes thinning, clear-cutting and re-planting pine (Loman 2005; Hamilton 1982). This creates open, monoculture stands that have a greater visibility than more diverse forest. The Siberian jay's main predator, the goshawk (Griesser 2003b; Griesser et al. 2006) is an ambush hunter that locates its prey using visual cues (Kenward 1982). Thus, an open forest structure should facilitate hunting success for the goshawk. Moreover, this sort of forest structure increases the risk that a nest is detected by nest predators. Prior studies on Siberian jays have demonstrated that nest failure is significantly higher in open forests and close to human settlements (Eggers 2002). In accordance, some of the results presented in this thesis experimentally demonstrate a significant negative effect of thinning and clear-cutting on nesting success and productivity in this population. Moreover, both juvenile and adult mortality was higher in more open forests (i.e. forests that had been subject to management practices).

The classification of territories into sources and sinks showed that close to two thirds (12/21) were sinks, indicating a productivity that was insufficient to compensate for mortality. In contrast, the source territories (9/21) had a recruitment that exceeded mortality. As expected, sink territories had higher average volumes of pine than source territories, which is indicative of a heavily managed forest. Notably, 55.5 % of these source territories are lost today because of habitat destruction.

The effect of habitat quality on demography and behaviour was also related to intrinsic characteristics and to the social context. There was a strong discrepancy in habitat-related mortality between sexes, where breeding females were more susceptible to the surrounding environment than males. This is probably a combination of females having higher reproductive costs than males, causing females to be more exposed to predation. At the onset of breeding, females gain weight (unpublished data) which is likely to have an effect on their escape abilities, thus making them an easier target to predators than males. Thus, in open, managed forests, females are taken by predators more often than males. However, females also had a higher mortality in dense spruce forests, the same habitat that promoted survival in juveniles.

This indicates that females might invest more in offspring protection. The data presented in this thesis does not address this question, which therefore requires further investigation.

Non-related immigrant juveniles suffered higher mortality rates than same-aged retained offspring. Siberian jay parents provide their retained offspring with benefits (e.g. relaxed feeding conditions, predator protection, high quality breeding sites) that are withheld from non-related immigrants (Ekman et al. 1994, 2000, 1999, 2001; Griesser 2003b; Griesser and Ekman 2004, 2005). Thus, non-relatives are forced to pay the cost of subordination (Ekman 1987). Both the experimental as well as the observational data in this thesis demonstrate that immigrants have to take more risks to obtain a similar energy intake as family-members, that immigrants are the recipients of more aggression during feeding, and that they feed more in exposed sites in high-risk habitats and during the season associated with highest predation risk.

Comprehensive knowledge of how habitat quality affects different aspects of demography and how individual responses to the surroundings vary with intrinsic and social context will greatly enhance the chances of accurately assessing key areas and populations in need of conservation measures. For example, there can be large individual variation in response to habitat loss depending on the mode of territory acquisition and territory choice. Thus, a simple estimate of population dynamics by numbers can give misleading results (Kokko et al. 2001; Pulliam 1988, 1996). Moreover, many individuals live and breed in sink habitats. For example, population data based on studies in sink habitats may give misleading results and management decisions based on such studies may be inappropriate (Pulliam 1988). However, empty sites (Hanski 1998) and bad quality sites such as sinks (Howes and Davis 1991; Holt 1997) can be advantageous or even critical for population persistence and as such, have significant conservation value. Sinks can maintain genetic diversity (Gaggiotti 1996) and thus function as a buffer against population extinction. A sink can also function as a buffer in an unstable environment, where the allocation of a fraction of the offspring to sinks can in fact enhance the long-term growth rate of a population by means of spreading the risk (Jansen and Yoshimura 1998).

Summary in Swedish (Sammanfattning)

Effekter av habitatkvalitet på beteende och populationsdynamik hos lavskrikor

De flesta naturliga populationer fluktuerar i antal och sammansättning över både tid och i rymd. Faktorer som kan påverka denna dynamik är t.ex. konkurrens om föda och revir, predationsrisk, parasitangrepp och väder. Hur mycket dessa faktorer påverkar en individ är ofta starkt knutet till habitatkvalitet och individer i bra habitat har generellt en större sannolikhet att överleva och fortplanta sig än individer i dåliga habitat. Därför är det ingen överraskning att det allra största hotet för populationers, och i slutändan arter, överlevnad är habitatförstöring. Idag försvinner naturliga habitat över hela världen med en hastighet som är långt över det normala. Merparten av denna förlust orsakas av mänskliga aktiviteter. Bara i Europa har det kommersiella skogbruket under de senaste 200 åren lett till att endast 1 % av den kvarvarande skogen är av ursprungsskogskaraktär.

En faktor som har stor påverkan på populationsdynamiken hos de flesta arter, och som även är nära knuten till habitatkvalitet, är predationsrisk. En fragmenterad och på andra sätt förändrad miljö kan underlätta för predatorer att hitta byten, och därigenom både attrahera fler predatorer till området samt öka framgången hos de individer som redan finns där. Således kan även små förändringar i predationstryck ha stor påverkan på populationsdynamik. Tidigare forskning har visat starka effekter av predationsrisk på reproduktionsframgång, överlevnad och spridning, vilka alla är faktorer som är involverade i populationsdynamik.

Interaktionen mellan habitatkvalitet och predationsrisk kan också påverka enskilda beteenden. Till exempel kan en ökad aktivitet öka risken att bli upptäckt av en predator, i synnerhet i ett habitat som utsatts för mänsklig påverkan. En situation där denna aktivitets-relaterade risk kan bli väldigt aktuell är när individer söker föda; de flesta individer står inför en konstant utmaning i att avväga hur mycket de ska investera i födosök mot hur stora risker de kan ta under denna aktivitet. Hur individer hanterar denna avvägning har varit föremål för ett stort intresse inom ekologisk forskning, och ett uppbåd av studier har undersökt hur olika strategier anammats. En individ kan reglera hur stora risker den utsätter sig för på flera olika sätt, t.ex. genom

att välja säkrare lokaler för födosök, öka vigilansen om man befinner sig i utsatta lokaler, eller genom att ansluta sig till en grupp.

Hos en del arter lever individer ensamma medan de hos andra lever i grupp. Några av fördelarna med att leva i en grupp kan vara att det blir svårare för en predator att urskilja enskilda individer, att fler individer hjälper till med födosök, eller att medlemmarna i gruppen på andra sätt samarbetar och skyddar varandra. Nackdelen är en ökad konkurrens eftersom fler individer vill ha tillgång till samma resurser. Denna konkurrens mellan gruppmedlemmar skapar en hierarki där vissa individer är dominanta över andra. En konsekvens av detta blir att de underordnade medlemmarna inte har lika många valmöjligheter och därför kan tvingas ta större risker för att få tillgång till samma eller liknande resurser som de dominanta individerna. Ett exempel på en art där detta förekommer är lavskrika (*Perisoreus infaustus*). Lavskrikan är revirhävdande och lever i grupper på 2 – 7 individer. Dessa grupper består av det häckande paret och ibland även icke-häckande individer bestående av avkommor som stannat i föräldrareviret och/eller obesläktade immigranter. Avkommorna kan stanna i föräldrareviret i upp till tre år. Till skillnad från många andra grupplevande arter hjälper inte dessa avkommor till med att ta hand om syskon. De häckar inte heller själva så länge de bor kvar i föräldrareviret. Anledningen till att lavskrikor stannar hemma istället för att sprida sig och kanske få chansen att omedelbart häcka tycks istället vara att föräldrarna ger dem fördelar. Flera tidigare studier på denna art har visat att föräldrar aktivt skyddar sina ungar från predatorer och ger dem tillgång till föda som inte obesläktade individer har tillgång till. De ungar som inte stannar hemma sprider sig till närliggande revir där de slår sig samman med gruppen som lever där. Trots att dessa individer sprider sig till andra revir där de har större chans att hitta en partner som inte är en släkting (och därmed undvika inavel), är det få av dessa emigranter som får chansen att häcka direkt. Ofta får de vänta upp till några år på att hitta en partner och ett ledigt revir. Trots att de avkommorna som valt att stanna hemma skjuter på möjligheten att fortplanta sig, så har de en högre reproduktionsframgång sett över hela livet. Detta beror på fördelar som givits dem av föräldrarna tidigt i livet, vilket har en positiv påverkan på den framtida framgången.

I denna avhandling undersöks hur habitatkvalitet påverkar överlevnad och reproduktionsframgång och den kombinerade effekten av dess faktorer samt den övergripande populationsdynamiken i en population av lavskrika. Dessutom undersöks skillnader i enskilda beteenden mellan olika habitat samt hur dessa beteenden varierar beroende på karaktärer som kön, släktskap och med det sociala sammanhanget. Lavskrikor finns i nordliga, boreala skogar, och återfinns i Skandinavien i väst, i centrala nordliga Palearktiska områden till Kina i öst. Den populationen som studerats i denna avhandling återfinnes

utanför Arvidsjaur i Norrbotten. Inom stora delar av studieområdet råder ett aktivt skogsbruk där processer som gallring och avverkning är vanligt förekommande. Detta har resulterat i en avsevärd försämring av många revir, och i fallet där avverkning skett, total förlust av revir. Således har studieområdets utformning förändrats avsevärt sedan denna studie startades 1989. Detta har emellertid möjliggjort en detaljerad kartläggning av hur det moderna skogsbruket påverkar lavskrikan. Den förhållandevis massiva kunskapen om lavskrikors ekologi och beteende i kombination med den detaljerade informationen om förändringar i miljön gör detta till ett utmärkt system på vilket frågeställningar rörande habitatets effekter på beteende och dynamik kan appliceras.

Den första artikeln (I) i denna avhandling undersöker hur olika miljövariabler påverkar mortalitet och reproduktion hos vuxna lavskrikor, samt hur den kombinerade effekten av dessa faktorer ser ut. Resultaten visade att skogar med en hög volym tall, vilket är en indikation på en brukad skog, ledde till en högre mortalitet hos lavskrika. Även öppna områden, såsom mossar, hade samma effekt. Honor var emellertid känsligare för skogstruktur än hannar. I många andra studier har man sett att honor ofta har en större reproduktiv kostnad än hannar. Detta skulle också kunna vara förklaring till att honor påverkas starkare av habitatstrukturen i denna studie. Det är dock inget som explicit testats här. Ett sådant antagande baseras emellertid på att tätare granskogar tidigare visat sig ha en positiv effekt på reproduktionsframgång. I andra artikeln (II) undersöktes överlevnaden hos ungfåglar under deras första vinter. Även här hade tätare skogar såsom granskogar en positiv effekt på överlevnad, vilket ytterligare antyder att här finns en reproduktionsrelaterad kostnad hos honor. I utvärderingen av den kombinerade effekten av reproduktion och överlevnad hos både vuxna honor och hannar var det endast volymen tall som gav utslag; ett bra revir hade en lägre volym tall. Detta påvisar återigen den negativa effekten av brukade skogar. Ungfåglares överlevnad visade samma mönster. Överlevnaden var också högre för ungar som stannade hemma än för de som spred sig till andra revir. Detta är ett resultat av föräldrarnas förlängda omvårdnad av ungar.

I tredje artikeln (III) jämförde vi reproduktionsframgången innan och efter att ett revir utsattes för skogsbruk. Som förväntat fann vi att framgången minskade signifikant både efter gallring och efter partiell avverkning. Dessutom stod påverkade revir tomma i större utsträckning än opåverkade. Den totala produktionen i populationen minskade också avsevärt i revir där skogsbruk av någon form skett.

Artikel fyra (IV) och fem (V) undersöker hur lavskrikor avväger födointag mot predationsrisk samt hur detta förhåller sig till släktskap, ålder och gruppstorlek. I fjärde artikeln (IV) relateras detta även till habitatstruktur på

två olika skalor; dels till en lokal skala, dels till skogens sammansättning i hela reviret. I båda dess studier undersökte jag ovanstående avvägning med en försöksuppställning bestående av två (artikel V) eller tre (artikel IV) matplatser vilka placerades i olika skogsstrukturer (tät skog, gränsszon (endast IV), och öppen terräng). Generellt föredrog lavskrikor att äta i eller nära tät skog framför att äta i öppen terräng, vilket indikerar att de upplever den öppna terrängen som mer riskfylld. Valet av matplats skiljde sig emellertid mellan individer, där obesläktade immigranter inte hade lika många valmöjligheter som släktingar och därför tvingades tillbringa mer tid i öppen terräng. Valet av matplats varierade även med skogsstrukturen där en mer öppen (hårdare brukad) skog innebar att släktingar valde den säkra matplatsen mer. Detta berodde dock på vilken årstid det var; under senvintern tog besläktade individer färre risker än under hösten, sannolikt på grund av ett högre predationstryck under denna period. Slutligen så var där en skillnad i hur matplatser valdes när de representerade olika matkvalitet (artikel V). När maten på den exponerade matplatsen (öppen terräng) var av bättre kvalitet så valde besläktade individer denna matplats lika mycket eller mer än matplatsen i tät skog. Detta visar att ett högt energiintag kan kompensera för en ökad exponering för predatorer. Obesläktade immigranter valde däremot båda matplatserna lika mycket, vilket tyder på att de tar högre risker för att erhålla samma mängd energi. Immigranter var också utsatta för mer aggression från andra individer i gruppen än familjemedlemmar var.

Detaljerad information om hur habitatkvalitet påverkar olika aspekter av demografi och hur olika individer svarar på sin omgivning beroende på inboende egenskaper, såsom kön och släktskap, eller sociala faktorer, såsom gruppammansättning, ökar möjligheterna att korrekt bedöma vilka områden och/eller populationer som är har högst bevarandevärde. Att bara bedöma en populations status genom att räkna individer, utan att samla in mer information om systemet, kan ge missvisande resultat. Utan en större kunskap om systemet finns alltid en risk att studien utförts på en population som inte är representativ för studiens syfte. Beslut om åtgärder som baserats på dylika data kan få oväntade konsekvenser och i värsta fall leda till motsatt effekt än den önskade.

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