

**Behaviour and life-history responses
to chick provisioning
under risk of nest predation**



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ABSTRACT

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This thesis examines risk management in breeding Siberian jays (*Perisoreus infaustus*), which is indigenous to the northern taiga. Parent behaviour and the nest are cryptic. A new nest is built each year. It is placed on spruce or pine branches close to the trunk and well insulated with lichens, feathers and reindeer hair.

Nest failure rate was the main factor driving annual variations in jay numbers. The probability for nesting attempts to be successful ranged annually between 0.08 and 0.70. Nest predation was rampant and a main cause of nest failure. Nest predators were mainly other corvids (primarily the Eurasian jay *Garrulus glandarius*). Habitat quality was the main factor determining the risk of predation. The risk for nest failure due to predation was higher in thinned forests with an open structure and with a high abundance of man-associated corvid species (jays, crows, raven).

Siberian jay parents show several strategic adjustments in life-history and behaviour to the risk of nest predation. Parents traded reduced feeding rates for a lower predation risk and allocated feeding to low risk situations. Chick provisioning imposes a cost by drawing the attention of visually hunting predators to the location of nests, and parents adjusted their daily routines and avoided exposure by allocating provisioning to times of low activity among nest predators. These strategic adjustments of feeding efforts were estimated to reduce the exposure to nest predators by 26 percent. Also, parents adjusted their reproductive efforts to the perceived presence of predators in a playback experiment. Siberian jays reduced their reproductive investment by laying a smaller clutch size when high risk of nest predation reduced the value of current reproduction, as predicted from life-history theory.

Key words: Chick provisioning, clutch size, delayed dispersal, nest concealment, nest predation, parental care, population decline, *Perisoreus infaustus*, Siberian jay.

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To Simon, Tim and Jeanette

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

- I** Ekman, J., Eggers, S., Griesser, M. & Tegelström, H. 2001 Queuing for preferred territories: delayed dispersal of Siberian jays. *Journal of Animal Ecology*, **70**, 317-324.
 - II** Eggers, S., Griesser, M., Andersson, T. & Ekman, J. Predation-related costs of chick provisioning affect annual fluctuations in Siberian jay numbers. Submitted manuscript.
 - III** Eggers, S., Griesser, M. & Ekman, J. Testing Skutch's hypothesis of activity-related exposure to nest predation: an experimental study. Submitted manuscript.
 - IV** Eggers, S. Predation-related nestling growth and fattening in the Siberian jay. Manuscript.
 - V** Eggers, S., Griesser, M., Nystrand, M. & Ekman, J. Nest predation risk reduces clutch size: an experimental study. Manuscript.
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The order of the authors reflects their involvement in the papers. I have personally written, and performed most of the statistical analyses in papers **II**, **III**, **IV** and **V**. Field data were collected by all authors. The co-authors discussed ideas and commented on the text.

Cover: © Reine Jonsson, 'Stubbe', Arvidsjaur, May 2001

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INTRODUCTION

In many animal species, parents increase the fitness of their offspring by providing food and protection. Such parental care behaviour is a major component of the life histories of animals (Edmunds 1974; Clutton-Brock 1991). However, decisions about how much reproductive effort to devote to offspring will depend upon trade-offs between life history traits (Roff 1992; Stearns 1992). In general, investment in one trait can be increased only at the expense of another. Two major categories of trade-offs have been described: the first one has been termed *the cost of reproduction*, where current reproductive efforts impose a cost in terms of reduced chances of future reproduction. The second major category focuses on the division of resources between offspring, and is referred to as the trade-off between *the number and fitness of offspring* (Lack 1947; Lessells 1991; Roff 1992).

In the latter case a critical trade-off situation may arise when current reproductive efforts impose a cost through increased predation risk. Altricial bird parents need to provide their growing nestlings with food to prevent starvation, ensure a proper development and minimise the possible negative effects of a poor start in life (Richner 1989; Daan *et al.* 1990; Nilsson 1990; Metcalf & Monaghan 2001). Malnutrition is, however, not the only threat to the offspring. For example, provisioning may impose a cost if parental activity draws the attention of predators to the location of the nest. This predation cost is expected to limit the rate at which parents can provide food to their nestlings. Skutch (1949) originally proposed this idea, which predicts the evolution of smaller clutch sizes and lower parental activity under increased predation risk (Martin & Ghalambor 1999, Conway & Martin 2000; Martin *et al.* 2000a). However, these adjustments in reproductive investment should derive from an increase in nest predation as a function of parental activity. Evidence for this link has been found only quite recently (Martin *et al.* 2000b). Hence, the importance of nest predation for the evolution of parental care behaviour might have been underestimated so far (Lima & Dill 1990; Ruxton & Humphris 2001).

Environmental hazards such as nest predation may reduce the suitability of habitat for breeding substantially. Hence, individuals should

fill the better territories first (Brown 1969; Pulliam 1988; Sutherland 1996). The quality of remaining breeding vacancies will then eventually be so low that postponement of dispersal entails better prospects in a lifetime perspective (Ekman *et al.* 1999; Kokko & Johnstone 1999). However, offspring in many birds do not postpone dispersal, although they are constrained from independent breeding (Patterson 1980). If delayed dispersal is to maximise lifetime reproduction, then remaining in the natal territory has to offer benefits that the offspring cannot gain elsewhere (Ekman *et al.* 1994, 2000).

Paper **I** explores the role of delayed dispersal in the Siberian jay *Perisoreus infaustus* as a queuing strategy to obtain high quality breeding openings in response to a poor quality of current dispersal options. Paper **II** attempts to identify the mechanisms linking habitat quality to population dynamics, highlighting the importance of nesting cover and predation-related costs of chick provisioning for reproductive success. Papers **III** and **IV** focus on strategic adjustments of chick provisioning efforts to avoid nest predation and their possible consequences for fledgling size and the potential for juveniles to become a breeder. Paper **V** examines if parents exposed to increased risk of nest predation adjust their reproductive investment by laying a smaller clutch size.

METHODS

The study species

The Siberian jay (family: Corvidae) is a highly sedentary resident across higher latitudes of the western Palaearctic. It predominantly inhabits northern boreal and sub-alpine coniferous forest between 50° and 70°N from Norway in the west to the Pacific and upper Omolon River in the east. Occupation of permanent all-purpose territories in this harsh environment is made possible by the bird's food storage behaviour. The species is omnivorous, eating a variety of animal and plant foods (Andreev 1982). Territorial pairs are monogamous maintaining long lasting pair-bonds (unpublished data). Both sexes build comparatively small nests characterised by camouflage of the exterior of the nest cup to

resemble the immediate environment, which makes them highly cryptic (Blomgren 1964; Lindgren 1975; Kokhanov 1982). Ambient temperatures may occasionally drop below -25°C during the incubation and nestling stages and nests are well insulated with lichens, feathers and reindeer hair. In northern Sweden the egg laying period normally starts in the first half of April while the terrain is still snowbound. Parents produce a single brood per season with a highly variable but relatively small clutch size (*range*: 1-5, *mean* \pm *s.e.*: 4.04 ± 0.7 , $n = 50$, Blomgren 1964; Lindgren 1975; this study). Incubation feeding by males allows females to incubate their eggs and newly hatched chicks almost continuously. Older nestlings (> 7 d) are provided with food by both parents. Fledging takes place in mid May through early June 18-24 d after the first chick has hatched. Offspring is provided with food for about 3 weeks after fledging. The timing of dispersal varies substantially, but most first-year birds disperse within 8 weeks after fledging. Postponed dispersal is the preferred option. Sibling rivalry precedes dispersal, and the larger and socially dominant siblings within broods normally stay in the natal territory for up to three years (Ekman *et al.* 1994, 2002). Offspring retention may require little effort by parents but increases juvenile survival substantially (Ekman *et al.* 1994, 2000).

Study area and data collection (I-V)

Here I present an analysis of data collected between 1989 and 2001 in a population of Siberian jays northwest of Arvidsjaur, northern Sweden ($65^{\circ} 40' \text{N}$, $19^{\circ} 0' \text{E}$). The study area encompasses about 60 km^2 being located in the northern boreal vegetation zone. Large areas of mature forest stands in the region have been subjected to modern forestry through clearing of Norway spruce *Picea picea* before the final cutting. This practice leaves a forest of old Scots pine *Pinus sylvestris* with trunks bare of branches, which leaves Siberian jay territories with little cover and the reproductive success is poor in such habitats (Lindgren 1975; Ekman *et al.* 2001).

All birds in the population have been individually colour-ringed since 1990. Nestlings were given a metal ring in the nest. In March the jays were caught and fitted with radio transmitters (1.85 g, Holohil, Canada), and nest sites could be located by radio tracking. Between 1998

and 2001 nests were controlled regularly in order to determine clutch size and to measure body mass and size (tarsus length) of nestlings. The residuals from a regression of body mass on tarsus length were used as an index of body reserves (Johnson *et al.* 1985). We collected 100 µl of blood from the alar vein of both nestlings and adults to confirm parenthood by minisatellite fingerprinting and determined their sex using molecular markers (Ekman *et al.* 1994; Griffiths *et al.* 1998). Successful reproduction was confirmed by observation of fledglings outside the nest in company with their parents.

Reproductive success and territory quality

To express the relative reproductive success within territories we designed a nest success index (NSI, **I-V**). It consists of the sum of differences over years between the actual reproductive success within a given territory and year (0 = failure, 1 = success) to the probability of nest success in the population as a whole the same year:

$$\text{NSI} = \sum_{\text{year} = 1}^n (\text{brood success}_{\text{year}} - \text{proportion broods fledged}_{\text{year}}) / n$$

To estimate the risk of nest predation in territories we ranked the quality of 35 territories (16 territories before 1998; paper **I**) by the reproductive success of birds breeding there (**III, IV**). This way we identified 17 territories with lower and 18 territories with higher than average risk of nest failure (low and high-risk habitat). To study the average number of young reared to fledging in each territory we designed a brood size index (BSI) which expresses the relative brood size the same way as the NSI (**V**). This index, however, does not consider effects of brood reduction and thus may not reflect clutch size.

Nest sites and predator density

To test for the effect of habitat structure on the risk of nest predation we assessed the quantity of nesting cover on a larger scale around the nest. The density of low spruce < 15 m / 100 m² was chosen to distinguish nest sites characterised by a dense forest structure from those with open structure (**I, II, IV and V**). To examine if forest openness can have mediated the effect of visually hunting corvids on nest predation risk we

further censused number of corvids in sight of Siberian jay nests between 1998 and 2000 (**II**, **III**).

Nest predation and nest activity (II, III, IV)

To study nest activity and to identify nest predators we videotaped nests (n = 32) almost continuously during the incubation and nestling periods between 1998 and 2001. Videotapes were viewed critically every day to determine the status of the nest. Predation rates were calculated by using the Mayfield (1975) index. To study parental activity in relation to nest fate we sampled the number of trips to and from the nest by both parents.

Supplemental food provisioning (II, IV)

To evade any effects of variation in food supplies between territories we provided parents with extra food in both territories with high (n = 7) and low risk of nest predation (n = 7) between 1999 and 2001. We provided 20 g ground beef (10 % fat contents) per nestling and day except in 14 control territories. This amount of extra food corresponds approximately to the daily amount of food required by 10 – 17 days old nestlings (Kokhanov 1982).

Temperature

We studied the effect of severe weather conditions for the risk of nest failure by analysing annual variation in reproductive success in relation to mean temperatures at hatching from the end of April until mid May in 1989-2001 (**II**). To study if safer nest sites require increased reproductive investment through higher thermoregulation in denser vegetation we studied the microclimate (temperature) at nest sites in relation to variation in nesting cover (**V**).

Manipulation of nest predation risk

To test for if parents assess nest predation risk and whether variation in reproductive effort (clutch size, chick provisioning) is in fact a response to differences in the risk of nest predation we simulated presence of corvids by playback of a mixture of calls (Eurasian jay *Garrulus glandarius*, hooded crow *Corvus corone* and raven *Corvus corax*; **III**, **V**). In paper **IV** we manipulated the perceived risk of nest predation risk by

presenting a mounted Eurasian jay at nest sites differing in the density of understory to test for the effect of nesting cover on provisioning rates.

Parent phenotypic quality and habitat quality

To disentangle the roles of parental phenotype from that of habitat characteristics for reproductive performance we designed an artificial nest experiment so that we could test for both the effect of habitat structure and activity of corvids on nest survival (**II**). In paper **III** and **V** we designed playback experiments so that these confounding effects on reproductive efforts were controlled for. Finally, we controlled for non-random association between parent phenotype and habitat quality by testing for consistent associations between tarsus length of parents and offspring under different nesting conditions (**IV**; Falconer 1981).

RESULTS AND DISCUSSION

Queuing for preferred territories (I)

There are two alternative routes for Siberian jays to become breeders. Some offspring dispersed in their first summer of life, but one third of birds ringed as nestlings (39 of 117; 40 broods) postponed dispersal beyond their first winter and up to 3 years of age (Fig. 1).

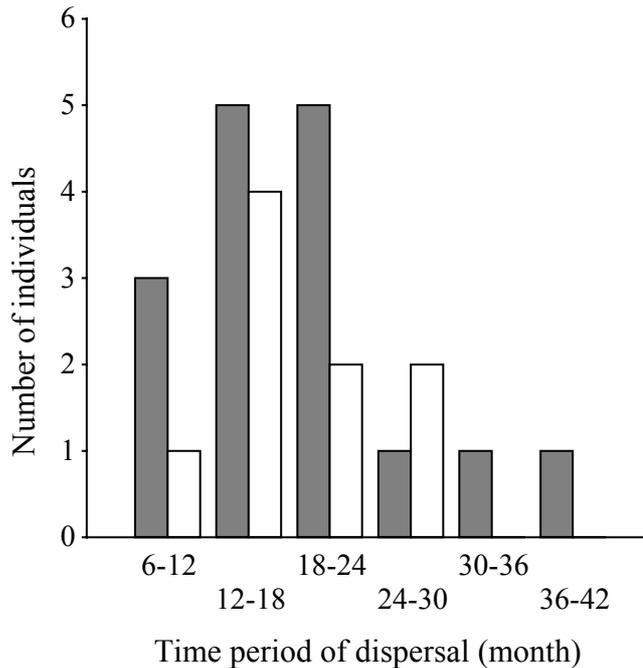


Figure 1. Dispersal time for retained offspring (shaded bars, males; open bars, females). The bimodality in timing of dispersal is illustrated by the fact that the eventual dispersal among the offspring, which postponed dispersal, peaked first in the second year of life.

Habitat quality is closely linked to these differences in timing of dispersal. Males dispersing in their first year acquired territories close to human settlements, and with few low spruces (< 15 m). Reproductive success was low in those territories. Conversely, high-productive territories of retained offspring are located further away from human settlements and such birds therefore avoided potential nest predators, such as other corvid species associated with man (Table 1).

Table 1. Territory characteristics and their relation to reproductive success; SAS Proc GLM, Type III SS.

Territory characteristic	Breeding success (probability of successful nesting)	
	Estimate (SE)	<i>P</i> -value
Distance to house (0, 1 or 2) *	0.25 (0.076)	0.01
Density low spruces (< 15 m) †	0.059 (0.016)	0.01
Density tall pines (> 15 m) †	-0.058 (0.018)	0.01

*0 = House within territory; 1 = house in neighbouring territory; 2 = nearest house further away. † Density equals number of trees per 100 m² estimated as mean of two 2 × 50 m sampling areas.

Furthermore, males dispersing later in life acquired territories with a denser forest due to a higher abundance of low spruces. A dense habitat structure makes the search for nests more difficult for predators guided by visual cues, a factor which could contribute to the higher probability of breeding success in such territories (Table 1).

A preference of all birds for high-productive territories, regardless of their timing of dispersal, suggests a causal relationship to habitat characteristics. A non-breeding surplus of retained offspring had priority to vacancies at high densities and these birds claimed territories where reproductive success was high (Table 2). At low densities and without a non-breeding surplus it was possible for birds dispersing as yearlings to shift territory, and acquire vacant sites of high quality. Birds settled in the territories with lowest reproductive success shifted, and at low population density their territories remained vacant (Table 2). There would be no incentive for a preference for territories with better prospects of successful reproduction unless reproductive success is linked to properties of the territory, rather than being an individual property reflecting phenotypic quality.

The behaviour of retained Siberian jay offspring to forego dispersal options of low quality implies that the timing of dispersal is a trade-off between current and future opportunities (Kokko & Sutherland 1998).

Table 2. Territories ranked by the breeding success of birds breeding there (NSI = nest success index), together with the origin (retained / immigrant) for breeders with known dispersal history and preferences as reflected in territories vacated in 1998. The probability for breeding to be successful was higher in the territories where retained males had settled ($P < 0.01$, $U = 3.5$, $n_1 = 9$, $n_2 = 8$, Mann-Whitney U -test).

Territory NSI	Origin of breeders				Territories vacated 1998
	Males		Females		
	Retained	Immigrant	Retained	Immigrant	
0.72					
0.32				1	
0.32			1	2	
0.23					
0.10	1		1	2	
0.07	1		1	3	
0.02				1	
0.02	1			2	
-0.02	1			2	
-0.08	2		1	4	
-0.15	1	2	1		
-0.16					Vacated
-0.21	1	1			
-0.31	1			2	Vacated
-0.36		2		1	Vacated
-0.38		3		2	Vacated

Retained offspring, which postpone dispersal and remain in the natal territory, queue for a high-quality vacancy. A similar role of habitat quality for dispersal has been suggested by several other studies of species with delayed dispersal (Zack & Ligon 1985; Komdeur 1992). However, a nepotistic parental behaviour towards retained offspring implies that a fitness gain of delayed dispersal is not only a question of habitat quality (Ekman *et al.* 2000).

Nest predation and annual fluctuations in jay numbers (II)

Nest failure was strongly correlated to the change in Siberian jay numbers to the next breeding season (Fig. 2). Hence, any density-dependent factors operating on survival during the non-breeding season were not sufficient to eliminate variations in reproductive output. This point to that factors limiting reproductive output contribute substantially to drive fluctuations in Siberian jay numbers.

Nest predation is an important cause of nest failure in the Siberian jay (proportion 0.67). All nest predators that could be identified were hunting by using visual cues. The nest predators identified were squirrel

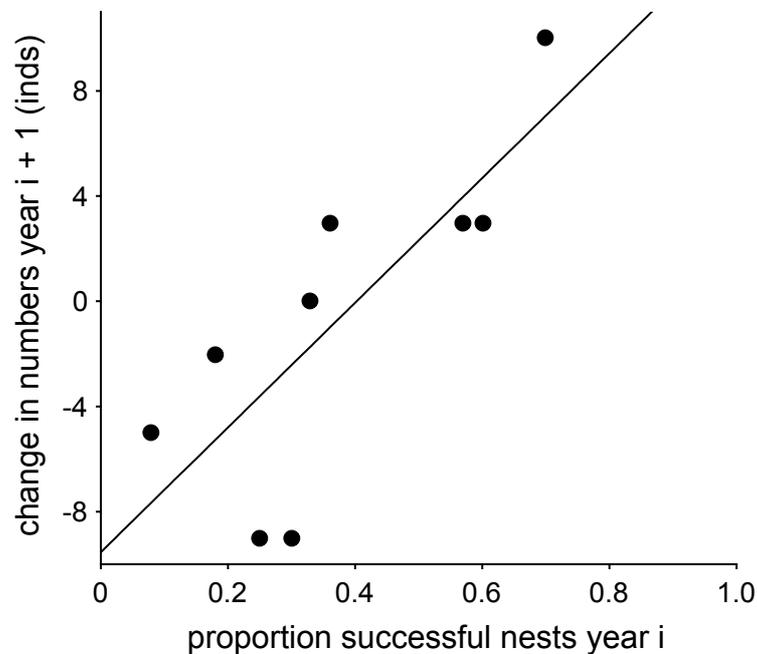


Figure 2. Annual variation in the proportion of Siberian jay nests ($n = 126$) that were successful in relation to the change in jay numbers to the next breeding season (16 territories studied during 1991-1999). This change was positively correlated to the proportion of nests that produced young ($F = 11.1$, $P = 0.01$, $df = 1$, SAS, Proc GLM) indicating that any density-dependent factors operating between breeding seasons were weak and not sufficient to cancel variations in reproductive output.

Sciurus vulgaris, sparrowhawk *Accipiter nisus* and most importantly other corvid species (Table 3). Correlative evidence further suggests that

mortality early in life due to corvid nest predators is a primary factor in mediating the effect of human-induced reductions in nesting cover (Table 4).

Variation in reproductive success could be the result of parent phenotype rather than habitat characteristics itself (Norris 1993; Cresswell 1997; Przybylo *et al.* 2001). However, an experiment with artificial nests uncoupled the role of habitat structure from parent phenotype and confirms the idea that reductions in nesting cover increase the risk of nest predation by other corvid species (see paper II).

Table 3. Nest predation events (n = 41) and predators identified (n = 27) at natural Siberian jay nests (n = 28) and nests used in an artificial set-up (n = 13) using video cameras, photo-cameras and plasticine-eggs between 1998 and 2001. Indirect evidence for predators was used when physical damages of nests and chicks could be linked to nest predation or predator identity as revealed by video recordings from other nests.

Predator identity	Natural nests		Artificial nests		Σ
	Video-cameras (n = 5)	Indirect evidence (n = 23)	Photo-camera (n = 1)	Plasticine-eggs (n = 12)	
Eurasian jay Magpie	2	6	0	3	11
Hooded crow Raven	1	3	1	9	14
Sparrow hawk	1	0	0	0	1
Squirrel	1	0	0	0	1
unknown	0	14	0	0	14

Yet, evidence from other studies show that the relationship between nesting cover and nest success is equivocal (Martin & Roper 1988;

Martin 1992a; Götmark *et al.* 1995; Howlett & Stutchbury 1996; Burhans & Thompson 1998). This has been attributed mainly to interactive effects of nest concealment, parental and predator behaviour (Cresswell 1997; Martin *et al.* 2000a; Weidinger 2002). However, most studies have focused on concealment in the immediate vicinity of nests. We suggest that habitat structure on a larger scale surrounding the nest may often be more important when visually hunting predators use nest visits by parents as a cue to the location of the nest. Considerations of nest-site selection on this larger scale may thus improve our understanding of how exposure to nest predation influence fecundity and habitat preferences in birds (Martin & Roper 1988, Ekman *et al.* 2001).

Table 4. Activity of corvid nest predators (ravens, hooded crows and Eurasian jays) and openness of forest structure around Siberian jay nests in relation to reproductive success. SAS Proc GLM, Type III SS.

	df	Breeding success (probability of successful nesting)		
		Type III SS	F-ratio	<i>P</i> - value
Eurasian jay (0 or 1)*	1	0.55	18.5	0.0002
Raven, hooded crow §	1	0.53	18.0	0.0003
Density low spruces (< 15 m) †	1	0.32	11.0	0.005

* 0 = no observations, 1 = one or more observations per territory

§ Number of corvids heard or seen at nest sites per hour (see Methods)

† Density equals number of trees per 100 m². Estimated as mean of four 2 x 50 m sampling areas centred on nesting trees (see Methods).

The importance of nest predation for the evolution of nest defences has been considered mainly in attempts at explaining aggressive behaviours towards predators, nest site selection and timing of breeding (Montgomerie & Weatherhead 1988, Martin 1992b). Provisioning strategies to reduce the exposure of nests to visual oriented predators have

received little attention (but see Skutch 1949, Ghalambor & Martin 2000, 2002). Such a strategy should aim to forestall an increase in nest predation as a function of parental activity. In Siberian jays nest predation increased during the nestling period when parental activity was greater than during the incubation period (see paper II). Other evidence for a link between provisioning behaviour and nest predation is scarce and has been found only quite recently (Martin *et al.* 2000a; Weidinger 2002).

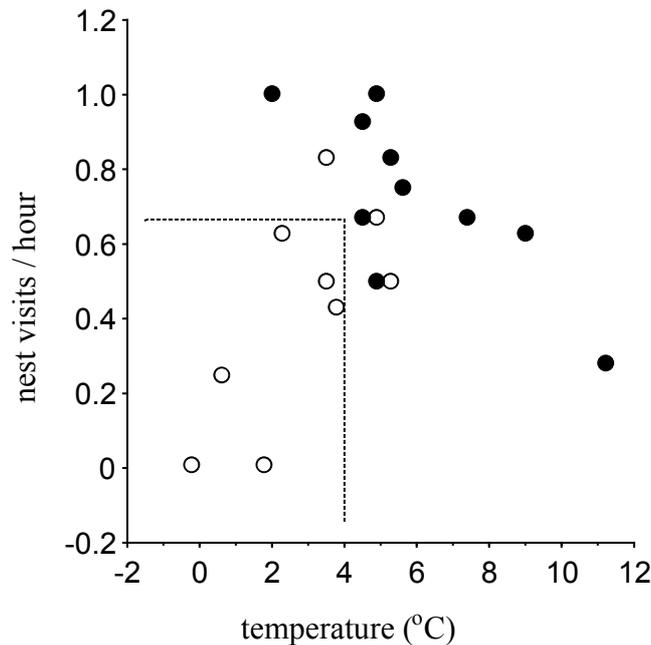


Figure 3. Mean number of nest visits per hour by Siberian jay parents in relation to the mean temperature at hatching ($n = 19$). Newly hatched chicks were provisioned at a lower rate in open forest (open dots; < 5 low spruces < 15 m / 100 m²) than chicks in dense forest (filled dots) when temperature and brood size were controlled for. Temperature affected visit rates unequally in dense and open forest. Only parents in dense forest increased their provisioning efforts as temperature declined (spruce, $df = 1$, $F = 21.9$, $P < 0.0005$; temperature * spruce, $df = 1$, $F = 14.7$, $P < 0.005$; temperature, $df = 1$, $F = 0.87$, ns; brood size, $df = 3$, $F = 0.27$, ns; SAS Proc GLM Type III). Low visit rates (< 0.65 / hour) at temperatures below 4 °C were associated with chick death, probably due to starvation.

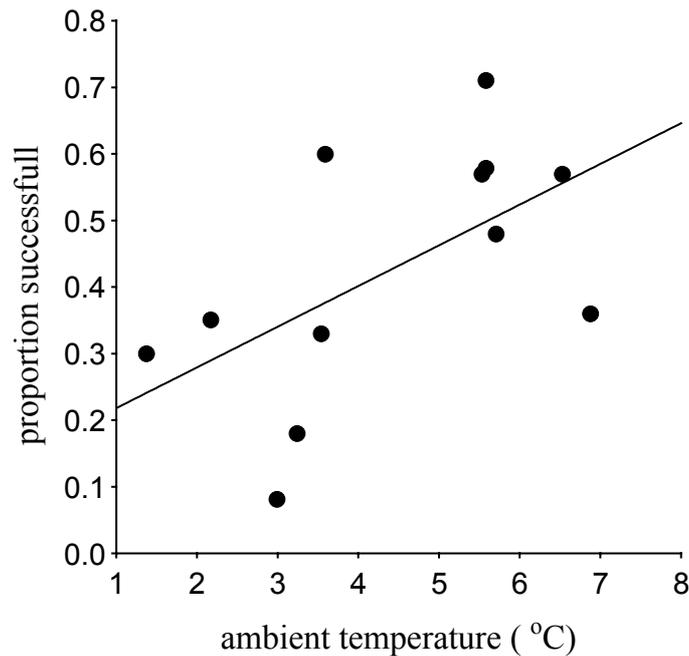


Figure 4. Annual variation in mean temperatures ($^{\circ}\text{C}$) at hatching in the Siberian jay (hatching period: 24th April to 14th May, $n = 19$), in relation to the proportion of jay nests that were successful (period 1989-2001; $n = 185$). The proportion of successful nests decreased significantly with mean temperatures at hatching ($F = 6.2$, $P < 0.05$, $df = 1$, SAS Proc GLM).

We found evidence that parental activity associated with nesting is particularly costly in open habitat where nests were more easily located by visually hunting predators. Typically, it was only in dense forest (> 5 low spruces / 100 m^2) that parents increased provisioning rates in response to higher energy demands of nestlings at low temperatures. Higher risk of chick death in open habitat indicates that parents exposed to elevated risk of nest predation were not able to compensate fully for higher energy requirements without unduly increasing the risk of nest predation (Fig. 3). As a result, cold weather during the early chick stage was associated with high rates of nest failure in open forest habitat leading to annual variation in reproductive output and driving annual variation in jay numbers (Fig. 4).

Predation adjusted provisioning routines (III)

Nest predation is an important cause of nest failure in birds (Lack 1954; Ricklefs 1969). This has resulted in the evolution of a variety of strategies related to nest protection, including distraction behaviour and aggressive nest defence (Collias & Collias 1984; Clutton-Brock 1991). Yet, little attention has been paid to strategic adjustments of timing of chick provisioning aiming to secure survival of nestlings under the risk of nest predation (Lima & Bednekoff 1999; Ruxton & Humphries 2001).

Here we show that Siberian jay parents monitor the risk of predation through the activity of predators around the nest. Their daily routines of provisioning nestlings were adjusted to avoid times of high predator activity (Fig. 5). The argument that variation in provisioning routines reflects an anti-predator strategy is confounded, however, with openness of habitat (e.g.; food supply, microclimate) and parent phenotype (see paper I). Still, parents from low-risk territories experimentally exposed to a higher perceived predation risk adjusted their provisioning routines as predicted from correlations between feeding rates and corvid activity in high-risk territories. Parents increase their antipredator efforts in high-risk situations and allocate most feeding to low-risk situations to compensate for lost provisioning opportunities (Fig. 6). As a result the parents were estimated to gain as much as a 26 percent reduction in the risk of exposing the nest to a predator in a high-risk habitat (Fig. 7). Our results provide strong evidence that non-aggressive behaviours such as altered provisioning decisions under risk of predation form an important component of nest defence in the Siberian jay and presumably in many other birds, with limited capacity to defend their nest by aggression (Collias & Collias 1984).

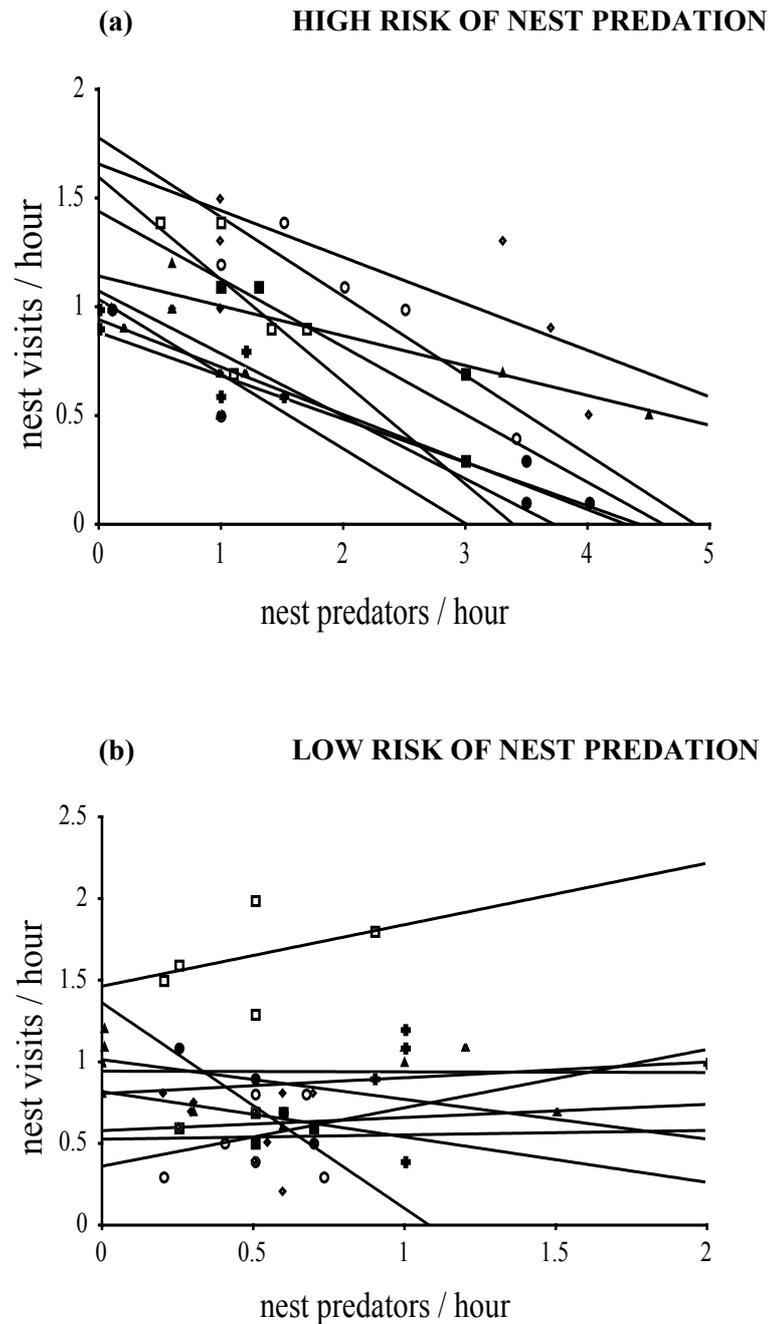


Figure 5. Adjustment to corvid activity in nest provisioning rate by Siberian jay parents in high-risk (a) and low-risk habitat (b). Mean number of nest visits by Siberian jay parents in relation to the mean number of corvids observed per 5-minute intervals and hour. Provisioning rates sampled between 3 a.m. and 6 p.m. for 5 blocks of 3 hours in each of 9 territories in low-risk habitat and 9 territories in high-risk habitat. Nest visit rates decreased significantly with increasing corvid activity in habitat with high risk of nest predation while there was no significant response in nest visit rates in habitat with low risk of nest predation (habitat * corvid activity, $df = 1$, $F = 41.4$, $P < 0.001$, repeated measurement, ANOVA, adjusted for covariate (corvid activity), balanced design).

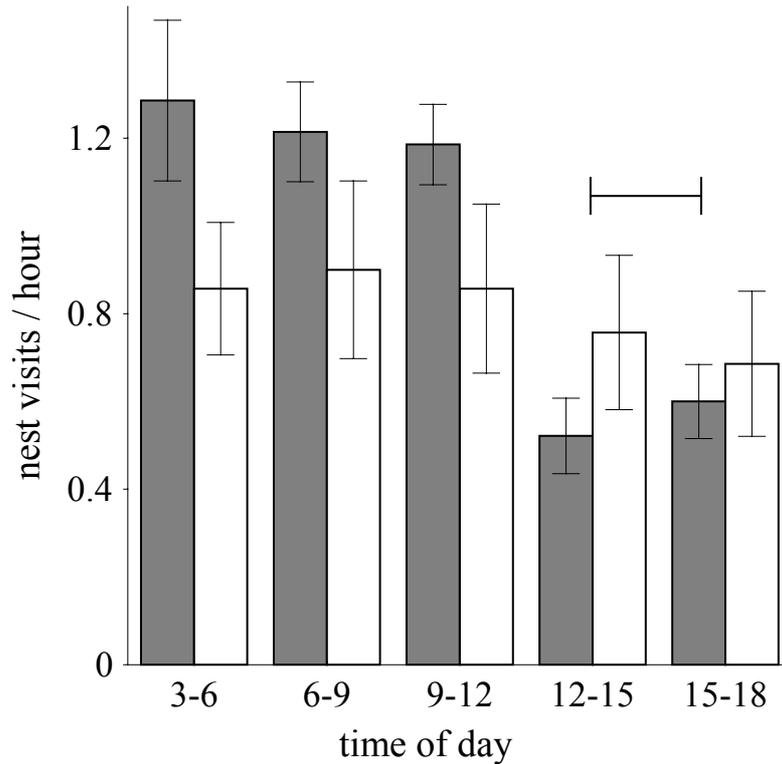


Figure 6. Diurnal provisioning routines by Siberian jay parents in low-risk habitat without a cue to corvid activity (no call playback; open bars) and with a cue (playback of corvid calls; shaded bars). Mean number of nest visits (\pm *s.e.*) by Siberian jay parents per 5-minute intervals and hour sampled for 5 three-hour blocks between 3 a.m. and 6 p.m. in habitat with low risk of nest predation. Nests were their own control and after a control period (3 days) parents were exposed to a mixture of corvid playbacks (Eurasian jay, hooded crow and raven) between 2 p.m. and 4 p.m. (|—|) during three consecutive days ($n = 7$ nests). The daily routines of parents in low-risk habitat responded and converged towards the routines of parents in high-risk habitat with higher activity in the morning (time * treatment (control/exposure), $df = 7$, $F = 10.8$, $P = 0.005$; repeated measurement, ANOVA, balanced design).

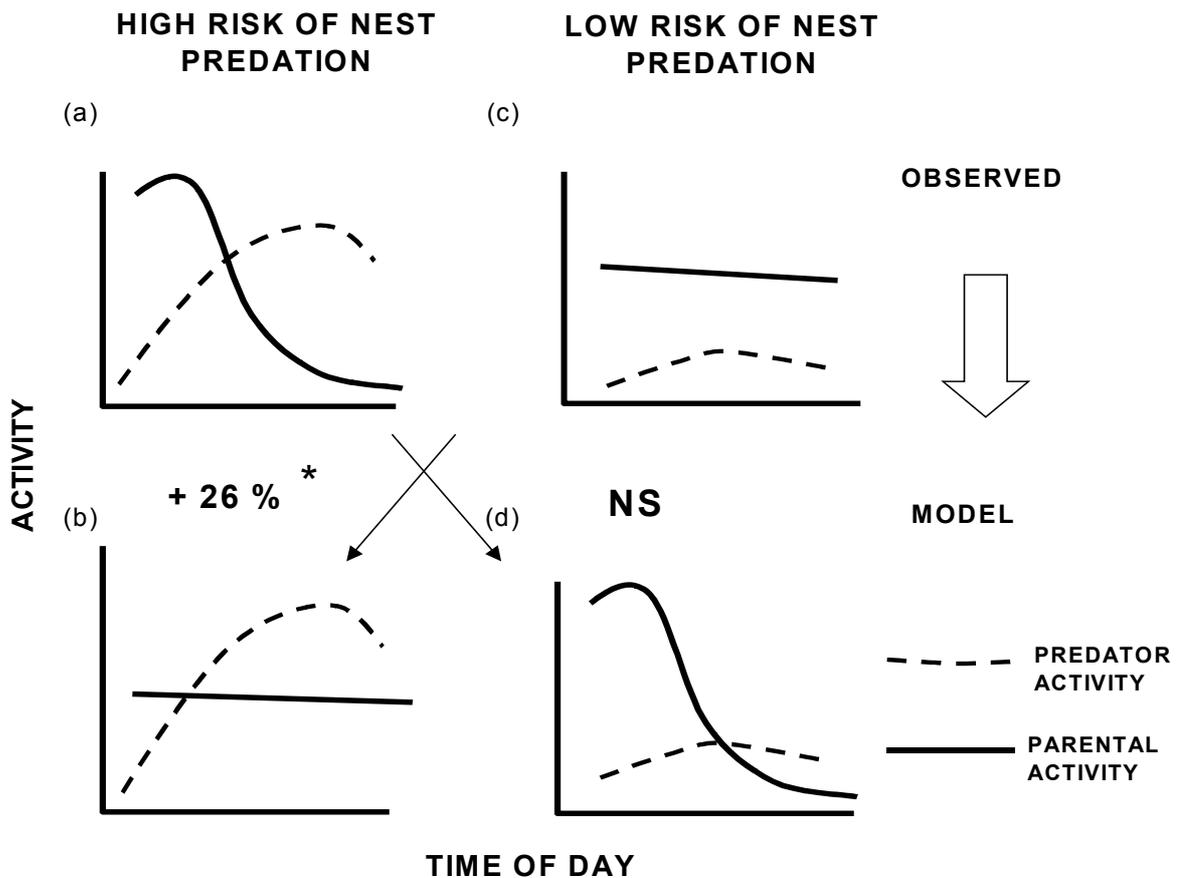


Figure 7. Estimated change of exposure to corvid nest predators for parents in (a) high risk territories ($n = 9$) if their daily routines were not adjusted to the activity of corvids but maintained the mean rate of provisioning (b), and if parents in (c) low risk territories ($n = 9$) did adjust their daily routines as in high-risk territories while they maintained their mean rate of provisioning (d). In high-risk habitat there was a 26 % increase (0.37 ± 0.13 provisioning cues per day; paired t-test, $t = -2.77$ and $P < 0.025$) in the number of cues to other corvids without the daily routine of feeding rates. Parents in low risk habitat would not gain in reduced rate of cues from a daily routine in the nest visit rate with an estimate decrease of only of -0.03 ± 0.03 cues provided per day (paired t-test, $t = 1.09$ and $P = 0.31$, ns).

Predation-related nestling growth and fattening in the Siberian jay (IV)

Poor provisioning conditions at the egg or nestling stages could prevent an individual from developing its optimal phenotype despite its genetic potential (Simons & Martin 1990; Richner 1992; Metcalfe & Monaghan 2001).

High rates of predator encounter in open forest (high risk habitat) may pose a serious constraint on the ability of parents to provide their nestlings with sufficient amounts of food. Thus the provisioning behaviour of bird parents has to balance the risks and benefits of food provisioning to ensure adequate growth and protection against nest predators for their offspring. However, field observations and an experiment demonstrate that cover reduces the exposure to visually hunting predators and allows parents to uphold nest provisioning in the presence of a predator, but less so in open forest where the overall provisioning rate was lower (IV). Nestlings had larger body reserves, showed a trend towards lower body mass and had shorter tarsi in habitats with a high risk of nest predation (Fig. 8). Here the nestlings were provisioned at a less regular interval with high rates during bursts of compensatory provisioning (see paper III). Offspring provisioned at a more even rate in low-risk habitat appear to have been able to channel resources into growth to a higher extent than chicks in high-risk habitat. These habitat-specific differences in growth and fattening are probably due to that the growth rate is physiologically constrained and chicks cannot respond to high provisioning rates and transform all food into growth. (Schmidt-Nielsen 1993). Yet, to maximise the use of digestive capacity chicks should be provisioned at a steady rate, as is the case in the low risk habitat. If chicks are fed at too irregular intervals, they will fledge at a reduced size and quality and suffer reduced fitness (Richner 1989, 1992; Metcalfe & Monaghan 2001).

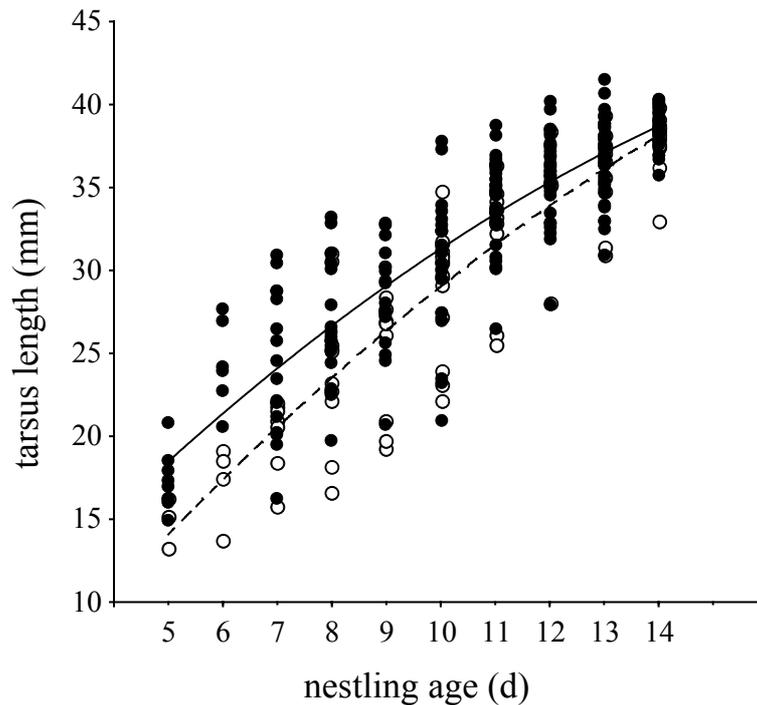


Figure 8. Growth data for tarsus length of Siberian jay nestlings ($n = 68$, 5-14 d) raised in territories with high (dashed line, open dots; $n = 12$) and low (solid line, filled dots; $n = 13$) risk of nest predation. Nestlings in low risk habitat had longer tarsi than nestlings in high risk habitat (habitat, $\text{ndf} = 1$, $\text{ddf} = 69.3$, $F = 10.8$, $P < 0.001$, repeated measurement, SAS System for mixed models, Type III sum of squares). Smaller nestlings in high-risk habitat showed compensatory growth. Their tarsus length increased faster than that of nestlings reared in habitat with low risk of nest predation (nestling age * habitat, $\text{ndf} = 9$, $\text{ddf} = 241$, $F = 4.5$, $P < 0.0001$) indicating that provisioning conditions improved during the nestling stage.

It is important to note that the observed differences in body size may not merely reflect differences in nest provisioning. Maternal effects may have contributed. High risk of predation for parents in open forest could, for example, reduce the nutritional status of females. A variety of bird species show a positive relationship between egg size and body mass and (or) size at hatching (Schifferli 1973; Price & Grant 1985; Magrath 1992; Smith *et al.* 1995) suggesting that maternal effects on egg size (Murphy

1986; Slagsvold & Lifjeld 1989) may contribute to the final body size of juveniles (Amundsen *et al.* 1996).

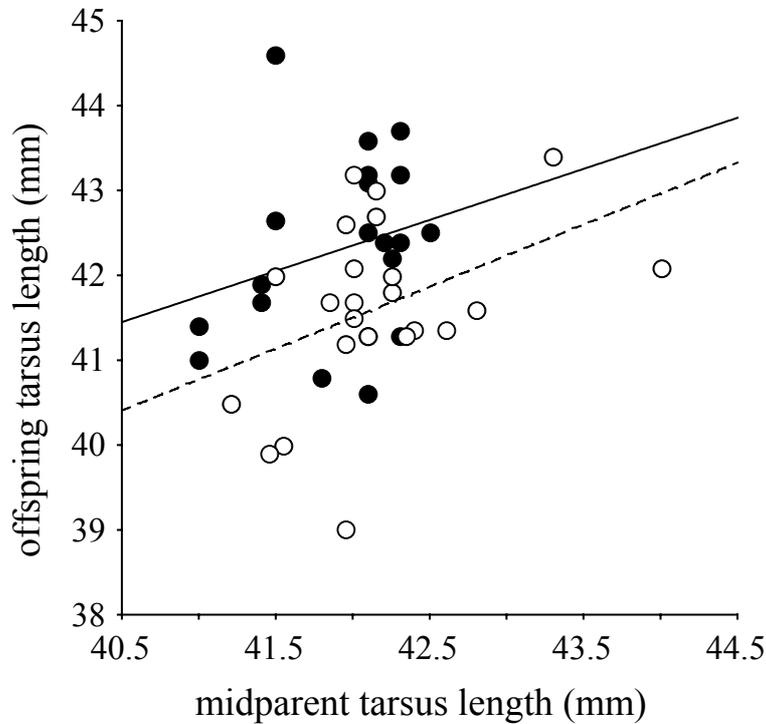


Figure 9. Regressions of Siberian jay mean offspring tarsus length on midparent tarsus length in territories with high (dashed line, open dots; $n = 23$) and low (solid line, filled dots; $n = 19$) risk of nest predation. The slopes of the regression lines are not significantly different, but analysis of covariance showed that offspring retained in high-risk territories had significantly smaller tarsi than those in low risk territories when parent phenotype was controlled for (SAS Proc GLM Type III sum of squares, midparent, $df = 1$, $F = 5.6$, $P < 0.05$; habitat (high- and low risk of nest predation), $df = 1$, $F = 7.2$, $P = 0.01$, midparent x habitat, $df = 1$, $F = 0.04$, $P = 0.84$, ns).

However, differences in final body size of Siberian jays could largely be the result of parent quality rather than environmental factors itself (Norris 1993; Cresswell 1997; Przybylo *et al.* 2001). Still, regression of Siberian jay offspring on midparent for tarsus length in high and low risk habitat provides strong evidence to suggest that habitat quality is a key factor

explaining differences in body size among broods. Retained offspring reared under high risk of nest predation were significantly smaller than predicted from parent phenotype (Fig. 9).

This study provides evidence that habitat-specific provisioning strategies aiming to secure nestling survival can modify the offspring's phenotype and its final body size. Such antipredator efforts may thus affect important life-history parameters as juvenile survival or the potential to become a breeder (Richner 1989; 1992; Metcalfe & Monaghan 2001).

Nest predation risk reduces clutch size (V)

Life history theory predicts a decrease in reproductive effort when high risk of nest predation reduces the value of current reproduction (Roff 1992). On a functional level, predation-related costs of chick provisioning would limit the amount of food that parents can provide to their nestlings thereby reducing the number of young that parents attempt to rear (nest predation hypothesis; Skutch 1949). This hypothesis provides an explanation for clutch size variation among altricial bird species by resolving the seemingly opposing views of food limitation versus nest predation (Martin 1996). Yet, evidence for reduced clutch size under high risk of nest predation is equivocal (Martin 1988; Cresswell 1997; Martin *et al.* 2000a). This has been attributed to a variety of factors (e.g.; adult mortality, thermoregulatory costs and parental behaviours) that might override the effect of nest predation on the current value of reproduction (Slagsvold 1982; Martin 1988; Lessels 1991; Cresswell 1997). For instance, parents could increase their investment in nest protection to compensate for increased predation risk (Collias & Collias 1984; Andersson *et al.* 1980; Wiklund 1990). Another option is that parents select for safer nest sites (Nilsson 1984; Martin 1988, 1993), where costs are incurred by thermoregulation in denser vegetation (Hafton & Reinertsen 1985; Walsberg 1985).

Here we present experimental evidence that Siberian jays reduce their reproductive effort by laying a smaller clutch size when exposed to increased risk of nest predation (playback territories *mean* \pm *s.e.*: 2.7 ± 0.4 eggs, $n = 15$ nests; control territories 4.1 ± 0.2 eggs, $n = 16$ nests; $P < 0.001$, t-test). Parents also increased reproductive effort by selecting for

safer nest sites where costs are incurred by thermoregulation in denser vegetation. After playback exposure, the parents choose to shift the nest to a nest site where the density of low spruces was about twice as high ($mean \pm s.e.: 9.0 \pm 1.2 / 100 \text{ m}^2$) compared to around the nest site in the previous year with no playback exposure ($4.7 \pm 0.8 / 100 \text{ m}^2$). The lower hatchability of eggs under such conditions reinforced the effect of a lower clutch size and resulted in significantly fewer fledged offspring. We found no signs of brood reduction through competition for food among siblings.

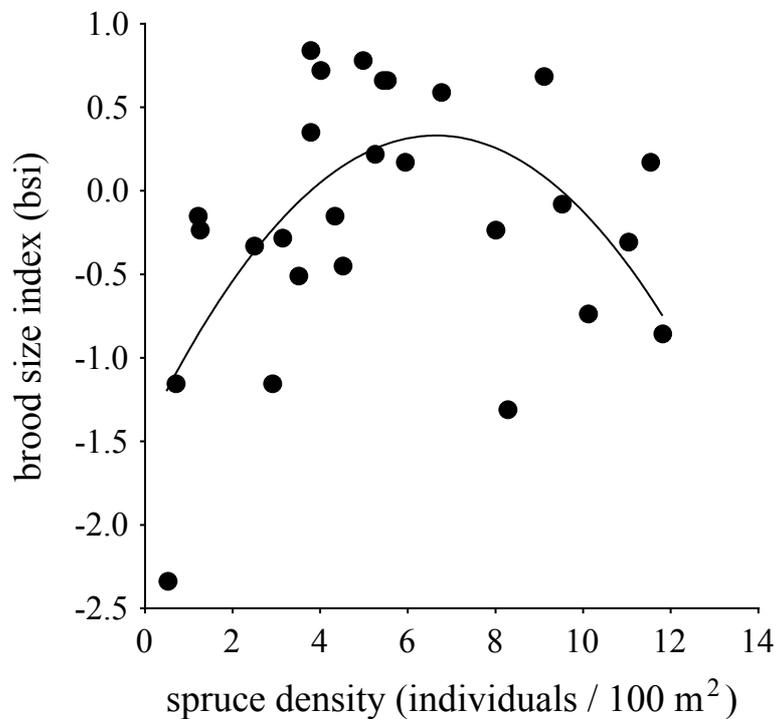


Figure 10. The relationship between forest density around nest sites (spruces < 15 m / 100 m²) and the number of offspring reared there (BSI = brood size index, see Methods). The brood size is calculated from sequences of data for brood sizes in territories that vary between 4 and 11 years.

The amount of nesting cover appears to reflect a trade-off between predator protection gained from a dense forest structure and the thermoregulatory cost of a colder microclimate in a denser forest

(microclimate hypothesis). This is demonstrated by the relationship between brood size and the amount of cover around nest sites. In more open forest the brood size increases as the amount of cover increases. As the forest gets even denser brood size decreases (Fig. 10).

To the best of our knowledge this study demonstrates for the first time experimentally that nest predation limits clutch size. Our results do not argue against the importance of food limitation in driving clutch size variation. Nest predation and food limitation potentially interact to influence clutch size.

CONCLUSIONS

Habitat quality was the main factor determining the risk of nest failure. The risk for nest failure due to predation was higher in thinned forest (< 5 spruces < 15 m / 100 m²) with an open forest structure and with a high abundance of man-associated corvid nest predators. Nest predation by these visual hunters was the main cause of nest failure.

Siberian jays postponed dispersal as a strategic trade-off, where they forego dispersal options of low quality while queuing for high quality habitat. A preference of all birds for territories characterised by high reproductive success, regardless of their timing of dispersal, suggests a causal relationship to habitat characteristics. Postponement of dispersal appears to be the first step in a sequence of decisions aiming to reduce the negative effects of environmental hazards, such as nest predation, on lifetime reproduction.

Siberian jay parents show several strategic adjustments in life-history and behaviour to the risk of nest predation. In line with what is predicted from life-history theory when high risk of nest predation reduces the current value of reproduction, Siberian jays reduced their reproductive investment by laying a smaller clutch size. Chick provisioning imposes a cost by drawing the attention of visually hunting predators to the location of nest and parents traded reduced feeding rates for a lower predation risk and allocated most feeding to low risk situations. This way parents compensated for lost provisioning opportunities during times of high risk of nest predation (see Lima &

Bednekoff 1999). These strategic adjustments of feeding efforts were estimated to reduce the exposure to nest predators by 26 percent.

Still, the risk of giving away the location of the nest on visits may pose a serious constraint on the ability of parents to feed their chicks sufficiently. Cover reduces the exposure to visually hunting predators and allows parents to uphold nest provisioning in the presence of a predator. Conversely, in open forest the overall provisioning rate was lower and chicks were provisioned at less regular intervals with bursts of compensatory provisioning. Offspring provisioned at a more even rate in low-risk habitat appear to be able to channel resources into growth to higher extent than chicks in high-risk habitat. The growth rate of nestlings in high-risk habitat is presumably physiologically constrained and chicks cannot respond to high provisioning rates and transform all food into growth. Hence, habitat-specific provisioning strategies aiming to secure nestling survival can modify the offspring's phenotype and its final body size. Such antipredator efforts may thus affect important life-history parameters as juvenile survival or the potential to become a breeder (Metcalf & Monaghan 2001).

Finally, the results presented in this thesis have important implications for conservation. They demonstrate that modern forestry (forest thinning) and man-associated corvid nest predators (primarily Eurasian jay) increase predation-related cost of chick provisioning. Behaviour and life-history responses to chick provisioning under elevated risk of nest predation were shown to impose a negative impact on reproduction, offspring quality and annual fluctuations in jay numbers. Siberian jays are apparently not able to evolve modified traits fast enough to adapt to current human-caused habitat changes. This may provide an explanation for why the recent decline in Siberian jay numbers is larger than can be explained by habitat loss alone (Helle & Järvinen 1986).

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