The Nepotistic Parent;
Predator Protection, Kinship and Philopatry

BY

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ABSTRACT

Griesser, M. 2003. The nepotistic parent; predator protection, kinship and philopatry. Acta Universitatis Upsalensis. *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 824. 38 pp. Uppsala. ISBN 91-554-5575-1.

Evolution is fuelled by independent reproduction events. Yet, the offspring of at least three percent of all bird species postpone dispersal and forego independent reproduction. The Siberian jay, *Perisoreus infaustus,* is such a species where some offspring are philopatric and remain in their natal territory for up to three years, forming family groups. The main finding of this thesis is that nepotistic anti-predator behaviour displayed by parents provided philopatric offspring benefits, which could be an incentive to stay and forego independent reproduction. Predation, (hawks - 80 % and owls - 15% of deaths observed) is the main cause of mortality. Parents increased their vigilance nepotistically; they were more vigilant against surprise predator attacks, and gave alarm calls when attacked when feeding together with offspring. However, the two parents differed in their behaviour. Mothers gave calls only when together with their offspring, while males also warned unrelated immigrants. Sitting predators were approached and mobbed more intensely by parents in the presence of philopatric offspring. The vocalisation of Siberian jays provides information about predation risk. Specific calls are given for hawks and owls, and calls also varied with hawk behaviour. The nepotistic anti-predator behaviour of parents is a benefit, which the offspring can gain only "at home", and such behaviour appears to promote offspring to forego dispersal and independent reproduction. This was confirmed in an experimental manipulation; philopatric offspring dispersed when fathers were removed and replaced by a despotic, immigrant stepfather. From a life-history perspective, parents have an incentive to protect their reproductive investment. Nepotistic anti-predator behaviour create a safe haven in the natal territory for philopatric offspring and provides direct fitness benefits. Without such direct fitness benefits offspring may disperse and wait for a breeding opening elsewhere.

Key words: referential alarm calls, delayed dispersal, nepotism, vigilance, alarm calling, mobbing, extended parental care, families, *Perisoreus infaustus*, Siberian jay

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

I   **Griesser, M.** Referential antipredator calls in the Siberian jay (*Perisoreus infaustus*) depend on predator behaviour. Submitted manuscript.

II   **Griesser, M.** 2003. Nepotistic vigilance behavior in Siberian jay parents. *Behavioral Ecology*, **14**: 246-250.

III   **Griesser, M. & Ekman, J.** Nepotistic alarm calling in the Siberian jay (*Perisoreus infaustus*). Submitted manuscript.

IV   **Griesser, M. & Ekman, J.** Nepotistic mobbing behaviour in the Siberian jay (*Perisoreus infaustus*). Manuscript.

V   **Ekman, J. & Griesser, M.** 2002. Why offspring delay dispersal: experimental evidence for a role of parental tolerance. *Proceedings of the Royal Society of London, Series B*, **269**: 1709-1713.

Paper **II** and **V** are reproduced with the permission from the publisher. First authorship reflects the main contributor to the papers. I have personally developed the ideas, designed experiments, collected and analysed data, performed statistical analysis and written the papers **I-IV**. In paper **V** I was involved in all those steps.

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INTRODUCTION

Protection from predation is a major force for the evolution of sociality in many species (Alexander 1974; Bertram 1978; Krause & Ruxton 2002). Individuals in groups can reduce their predation risk due to the increased numbers of individuals diluting the predation risk, increasing the confusion of predators, or due to a "many eyes effect" increasing the level of vigilance (Hamilton 1971; Curio 1978; Pulliam 1973). However, while many studies on group living mammals have reported enhanced predator protection of relatives, especially for inexperienced offspring (Sherman 1977; Hoogland 1983; Cheney & Seyfarth 1985), such antipredator behaviours have not played a prominent role in explaining why birds associate in kin groups. Anti-predator behaviour can promote survival of relatives and thus have an indirect fitness benefit. For kin group living birds, some authors have instead suggested that the costs of postponing personal reproduction are low since available breeding openings are of low quality (Selander 1964; Brown 1969; Emlen 1982). Other studies emphasised more the benefits that offspring can gain from remaining on their parents territories (Staecy & Ligon 1987, 1991). This "benefit of philopatry" model requires that habitat quality varies and relies on individuals waiting for a high-quality breeding opening rather than taking a lower quality breeding opening. However, a recent model demonstrates that variation in habitat quality is not necessary for delayed dispersal since variation in quality among territories simply promotes more variable dispersing behaviour within a population, but has little impact on queuing for territories (Kokko & Lundberg 2001).

Clearly, a key issue in the evolution of philopatry is an understanding of why offspring postpone dispersal considering the relative costs and benefits of philopatry (Koenig et al. 1992). Most studies of delayed dispersal have focused on cooperative breeders (Brown 1987), giving the impression that helping at the nest and delayed dispersal are inextricably linked. However, any inclusive fitness benefit of helping would certainly augment the indirect benefits of delaying dispersal, but such benefits are neither necessary, nor in most of the cases sufficient to explain the observed delays in dispersal (Cockburn 1998, Ekman et al. 2003). Offspring that remain in their natal group often forego personal reproduction (Koenig et al. 1992). Such postponement may reflect the lack of high quality available breeding openings (Ekman et al. 2001a), yet, lack of dispersal opportunity is inadequate to explain why non-breeding young birds

should forego alternative options, such as associating with other groups or roaming as a floater between groups (Brown 1987; Ekman et al. 2001b). In many species, offspring do not delay dispersal despite a lack in breeding openings of sufficient quality (see Ekman et al. 2001b for examples). Thus, while a lack of breeding openings is important for maintaining philopatry, this can be overridden by other life-history variables (Kokko & Ekman 2002). The degree on dispersal constraints (number of available breeding openings) depends on many life-history traits, which can have opposing effects and constraints as such have therefore little explanatory power (Kokko & Lundberg 2001).

Delaying dispersal, is however, determined by both the actions of the offspring and their parents (Ekman & Rosander 1992; Cockburn 1996; Ekman et al. 2003). Parents trade-off between the number and energy invested in each offspring and between the investment in current and future reproduction (Lessells 1991; Roff 2002). Recent models have focused on differences across species with respect to life-history strategies. Avian life-histories seem to have diverged into two strategies: species that have low survival, but have high levels of fecundity, fast growth and early breeding, or species that have high survival, low levels of fecundity, slow growth and deferred maturation (Bennett & Owens 2002). Cockburn (1996) found that philopatry is not randomly distributed between taxa and proposed a link between long lifespan and retention of offspring. A recent phylogenetic analysis confirmed such a link between delayed dispersal and life-history (Arnold & Owens 1998). This study found that philopatry is more prevalent in species with low adult mortality, low reproductive rates and deferred maturation (Arnold & Owens 1998). Increased longevity is suggested to lower the territory turnover in stable environments leading to a saturation of the habitat, thereby further facilitating the evolution the philopatry (Arnold & Owens 1998; Hatchwell & Komdeur 2000). However, this argument is not consistent with the observation that some short-lived species also live in saturated habitats and must queue for breeding openings (Ekman et. al 2001b). A link between "slow" life-histories and philopatry may instead be due to the fact that parental survival in long-lived species is less impaired by the presence of offspring compared to short-lived species. Long-lived species can therefore afford to invest in their offspring for more prolonged periods (Ekman & Rosander 1992). While the life-history hypothesis provides some interesting patterns in terms of parental longevity and reproductive rates it does not explain why offspring should wait at home for a breeding opening,

instead of floating or associating with another group (Ekman et al. 2001b). Furthermore, it is important to keep in mind that any correlation between longevity and philopatry may be a consequence, rather than a cause, of delayed dispersal (Ekman et al. 2003).

Traditionally, studies have focused on the value of the natal site for young birds that delay dispersal (Brown 1969; Emlen 1982; Stacey & Ligon 1987), but changes in the social environment as a consequence of natal philopatry have been largely neglected (Ekman et al. 2001b, 2003). Philopatric offspring prolong their association with their parents and in a non-migratory species parents are only found on the natal territory. It has been suggested that offspring delay dispersal due to the benefits that accrue from a prolonged association with the parents (the "safe haven hypothesis": Ekman et al. 1994, 2001b, 2003; Kokko & Ekman 2002; but see Ligon 1981; Brown & Brown 1984; Fitzpatrick & Woolfenden 1986).

Individual dispersal decisions can affect personal fitness in different ways. If an individual's presence in a group harms the fitness of other group members (for example through resource depletion or competition among kin for breeding openings), individuals should disperse to avoid competition with kin (Hamilton & May 1977; Ridley & Sutherland 2002). Following this argument, group formation through philopatry is more likely if mortality is caused by predation or if individuals have a superabundance of resources (Houston & McNamara 1999). Competition among individuals over resources is suggested to be a product of dominance, co-operation and kinship. Kinship can mitigate the costs of competitive interactions through nepotism (Hamilton 1964). Nepotism involves preferential treatment of relatives and is the proximate behavioural mechanism by which individuals can enhance survivorship of kin (Sherman 1977, 1985). Parental nepotism increases access to food (Verbeek & Butler 1981; Ekman et al. 1994; Griesser 2003) and enhances the protection from competitors (Scott 1980; Black & Owen 1987, 1989) or predators (Sherman 1977, 1985; Cheney & Seyfarth 1985; Griesser 2003). However, such benefits are of evolutionary importance only if they affect offspring survival. Such a pattern of increased survivorship of philopatric offspring compared to dispersing offspring has been shown in several species (Moses & Millar 1994; Blumstein & Arnold 1998; Ekman et al. 2000; Kraaijeveld & Dickinson 2001).

In this thesis, I explore the role of nepotistic interactions between parents and their offspring for the evolution of philopatry in the Siberian Jay (*Perisoreus infaustus)*. It has been suggested that offspring may delay dispersal due to nepotistic benefits that accrue from living in groups through enhanced foraging efficiency and reduced susceptibility to predation (Ekman et al. 2001b, 2003). However, to date there is no empirical support for this theory. To test this hypothesis, I first investigate the main cause of mortality in the Siberian jay and describe the behaviours and vocalisations of this species during encounters with predators (**I**). I then demonstrate how parents protect their offspring from their main predators through increased vigilance behaviour (**II**), nepotistic alarm calls (**III**) and a nepotistic mobbing of their main predators (**IV**). Finally, I explore with a removal experiment whether the presence of nepotistic parents influences dispersal decisions by young Siberian jays (**V**).

METHODS

Study site and species

We studied Siberian jays in continuous taiga habitat outside Arvidsjaur, northern Sweden (65º 40' N, 19º 0' E) from 1998 to 2003. The study population ranged in size from 80-140 birds (30-45 breeding pairs). Throughout the study period, blood samples (100 μl of blood collected from the alar vein) were taken from all individuals for sex determination with the P2/P8 method (Griffith et al. 1998). The age of first-year birds that had not been ringed as nestlings could be reliably determined from the shape of the outermost rectrices. The Siberian jay is an open nester and the study population breeds under natural conditions. Siberian jays live in small groups (ranging from two to seven individuals) in year-round territories with the breeding pair as a core. They show delayed dispersal typical of cooperative breeders but extra-birds (non-dispersing offspring/immigrants) do not help at the nest (Ekman et al. 1994). We caught α-females in March to attach a transmitter on their tail feathers (Holohil BD-2G transmitter). By radio-tracking we located all nests and gave all nestlings a metal band. We later caught and colour-banded those remaining in our study population beyond their first summer of life. Only 40% of all nests fledge successfully offspring, while most of the nests fail because of predation (Eggers 2002). About 4-6 weeks after fledging, broodmates start fighting among themselves and the larger, socially

dominant siblings within broods expel subordinates. These broodmates are forced to disperse and settle in new groups (Ekman et al. 2002). As a consequence, group composition varies; some groups are composed of only family members, some families are associated with non-related immigrants while others contain only non-related individuals that are a result of breeding failure and subsequent immigration of unrelated individuals. We used this natural variation in group relatedness to test whether kinship had an influence in antipredator behaviours.

Assessment of kinship (II, III, IV)

As parents almost never displace or even chase their offspring whereas breeders frequently displace and chase immigrants, in groups where we did not follow breeding attempts, kinship was determined by assessing the aggressive interactions between α-birds and extra-birds. This method has previously proven to be a reliable indicator of relatedness, either when compared with birds of know origin (banded as nestlings: N=62; immigrants in territories with known breeding success: N=47) or when controlled against DNA mini-satellite printing (N=13; Ekman et al. 1994).

Predator identity and reaction of jays to predator encounter (I, II, III, IV)

We collected data on predator identity and the reactions of Siberian jays to predator encounters from the spring 1996 to the spring 2003 for over 10'000 field hours. Predator identity was obtained by retrieving radio tagged individuals that had been preyed upon. For all observed encounters between predators and Siberian jays, we recorded the reaction of the jays during and after an encounter (including the distance to the predator, behaviours and vocalisations of the detecting individual in addition to other group members) in a notebook or with a video camera.

Antipredator vocalisation of Siberian jays (I, III, IV)

We recorded the vocal response towards predators during experiments (see below) or from natural predator encounters using a Sony CCD1100 Hi8 video cam with Sony HME/HMP video-cassettes (used for attack calls and alert calls) or with a Sony Mini-disc MZ-37 (for all other calls) connected to a directional microphone. The recording level of the Mini-disc recorder was set manually to avoid differences in the signal strength within a recorded sequence. Calls were

extracted from the sound track of the videotapes or the minidiscs and spectrograms plotted with Syrinx sound analysis program (John Burt, www.syrinxpc.com).

Vigilance rates (II)

Vigilance rates were sampled with time point measurement from individuals foraging on a standardised feeder from video recordings. For individuals on the feeder I recorded the position of the head with two-second intervals. The only head movement that is not mandatory for feeding is turning the head horizontally. I therefore only recorded turning the head horizontally as vigilance. To test for the effect of kinship on vigilance rates I focused on the response of breeders/parents when feeding together with an offspring/immigrant controlling for group size (number of individuals on the feeder).

Predator exposure experiments (I, III, IV)

We performed experiments to record calls and behaviours in response to exposure of Jays to 3 models; sitting owls, sitting hawks and attacking hawks. A chosen experimental group was attracted to a feeder and was allowed to feed undisturbed for 15 minutes prior to the start of the experiment. We then exposed the group to one experimental treatment (sitting owl, sitting hawk, attacking hawk; see below for details). When a group abandoned the feeder in response to the predator model (both α-birds > 50 m away from the feeder), we measured the time until the first group member returned on the feeder to forage. We performed only one experiment per predator model, per year, per group (for sitting predators) or dyad (for attacking hawk) to avoid habituation. Finally, all experiments were performed in random order and not all groups were exposed to all experimental treatments.

Sitting predator experiments (I, IV)

We collected responses to sitting predators by performing experiments with a mounted Ural Owl (*Strix uralensis*) and a female Sparrowhawk (*Accipiter nisus*) both in the sitting posture. To ensure natural responses to the predator models, the models were partially mobile such that their heads could be rotated with an inbuilt remote control. We positioned the predator model 5 m away from a feeder on the top of a 1 m high pole. The predator model was hidden with a green plastic cover before and after the experiment. To expose the model we

lowered the cover with a rope from 15 m distance when a randomly chosen α-bird was together with an extra bird on the feeder. To assess the impact of movement of the cover, we first lowered the cover after 15 minutes of undisturbed feeding but kept the predator model covered with a plastic bag. Jays never abandoned the feeder or started mobbing the covered model. Following this control trial we lifted the plastic cover again, removed the plastic bag from the model and waited a further 15 minutes before exposing the group to the predator model. As some groups abandoned the predator model after four minutes of exposure, we analysed the calling behaviour of the jays only during the first four minutes of the experimental trials.

Hawk attack experiments (I, III)

For the hawk attack experiments, we mounted a 15 m long static rope over a feeder. One end of the rope was attached about five meters above ground in a tree 10 m away from the feeder, while the other end was attached to the ground around five meter away on the other side of the feeder. A wooden and painted Goshawk model (*Accipiter gentiles*; a female in attack posture) could glide down the rope on small carbon wheels. The model was hidden for the jays before and after an attack and was released with a trigger from a distance. It accelerated to a natural attack speed of around 40 k.p.h. over the feeder. We exposed dyads composed of one α-bird and one extra bird to simulated hawk attacks. All calls, reaction times and times to resumption of feeding on the feeder were recorded on videotape for later detailed analysis.

Playback experiment of the different calls for hawks (I, III)

To examine if antipredator calls given by the Siberian jay are functionally referential, we performed a playback experiment with the different calls that jays give for hawks (the attack call, mobbing calls, the alert call, and a control) across 19 different groups in September 2001. Groups were exposed to between one and three of the call treatments in random order on different days. We used calls recorded during attack and mobbing experiments for the playbacks. The mobbing sequence, which contained the most common mobbing calls for hawks was recorded during an experiment with the sitting hawk model and had a length of 1 minute 50 seconds. The alert call was recorded during a natural encounter. To control for potential effects of the experimental set-up, we also played the song from the robin (*Erithacus rubecula*). This sequence had the same length as

the mobbing sequence. Robins are abundant in the study area and sing until the end of September. It was not possible to use different playback stimuli from the same class stimuli during the study as we could only record one alert call of sufficiently high quality. Therefore, as we used the same call for each of the four treatments (alert call, attack call, mobbing sequence, control) the playback experiment tests if a single exemplar of a stimuli rather than the stimuli class itself is referential (McGregor et al. 1992; Kroodsma et al. 2001). Calls were copied to TDK audiotapes and broadcast using a Panasonic tape player connected to two Cobalt SP-101 external speakers with a 15 m standard speaker cable. The speakers were attached to each other and positioned such that they were concealed in a tree five meters away from the feeder, one meter above ground level. All calls were played at about the same sound level they were originally given. For an experiment, we attracted the experimental group onto a feeder. We permitted the group to forage undisturbed for ten minutes before and after the treatment. All behaviours within the group were recorded with a video camera from a distance of 10 m. Videotapes were later analysed for the behaviours occurring during the playback (mobbing call, or control call) or for 2 minutes after the playback (alert call, attack call).

Removal experiment (V)

We removed fathers in September (N = 3; 1999) and July-August (N = 7; 2000) to test whether the presence of both parents is essential to delayed dispersal. Family groups from successful broods were randomly allocated to either a removal (N = 10) or control group (N = 9). Offspring in removal groups were captured about 3 weeks after fledging and a transmitter attached to their tail feathers. Following the spontaneous dispersal of subdominant brood mates (see Ekman et al. 2002), we caught all fathers from the removal groups and released them in prime habitat more than 40 km from their territory away. After removal of the fathers, we monitored the behaviour of retained offspring using radio tracking and we visited groups about every second day. Offspring that dispersed prior to the final check in December (1999) and on 1 November (2000), were considered to have responded to the paternal removal.

Ethical note (I, II, III, IV, V)

Jays were caught for banding or to attach a radio transmitter using either mist nests or wire cages with a swing door. We used Holohil type BD-2G

transmitters with a weight of 1.8 g and a lifetime of 16 weeks. The weight of the transmitters corresponds to approximately 2% of a bird's body mass (ca. 90 g). Radio transmitters were tied with dental floss and glued with superglue on the two central rectricies. This method permits attachment of a tag close to the bird's centre of gravity within less than 15 minutes. Transmitters that where mounted in late summer or autumn were removed by re-catching the tagged individuals in spring. Those individuals that were tagged in spring shed the transmitters in the annual moult of the tail feathers in early summer. We have never observed any effect of radio tagging on the bird's behaviour or survival in any of the 12 years of studying tagged jays. The Ural owl and the Sparrowhawk mounts used in the predator exposure experiments were made from animals that were found dead and which we obtained from the Swedish Museum of Natural History. All predator exposure experiments (sitting predator experiments, hawk attack experiment, playback), removing males and attaching radio tags were carried out under a licence from Umeå djurförsöksetiska nämd.

RESULTS AND DISCUSSION

Predator identity (I, II, III, IV)

In total, 42 Siberian jays were found killed between spring 1996 and spring 2003. Hawks (in particular the Goshawk and to a lesser extent the Sparrowhawk) were the main predators of Siberian jays. Of the 41 radio-tagged individuals that were found killed, 32 were most probably killed by hawks judging from the remains, footprints in the snow and faeces. Owls were assumed to have killed seven individuals (as remains were found hanging in dense trees, and pellets found) and martens (*Martes martes*) killed two further individuals (as indicated from bite marks on the colour bands or feathers). Finally, a domestic cat (*Felis silvestris f.*) killed an untagged individual. The two main predator categories of Siberian jays, hawks and owls, are both aerial predators but have different hunting strategies. Hawks are ambush hunters and rely on surprise attacks (Kenward 1978). A hunting sequence of a hawk has three distinctive phases: sitting to rest between attacks, searching a target and attacking the target by surprise (Kenward 1982). Hawk owls and Ural Owls are the most abundant large owl species in the study area. These owls are perch

hunters that use a sit-and-wait hunting strategy with frequent changes of the perches (Mikkola 1970, 1971).

Referential alarm calls (I)

Siberian jays produced both predator and situation-specific calls for both owls and hawks (Fig. 1, Table 1). In addition, they showed specific behavioural patterns associated with each type of predatory attack. Jays approached sittings owls and hawks producing calls. They also hopped from branch to branch moving closer to the predator and swooped over it both during natural encounters and experiments with predator models (see **IV**). Upon detection of a searching hawk, one group member produced alert calls (see below). During hawk attacks, jays gave attack calls in both natural and model attacks. Furthermore, a playback experiment confirmed that calls given towards hawks depended on the hunting stage of the hawk and these signals were referential. In response to playback of alert calls, all individuals on the feeder flew to cover, stayed cryptic and thereby reduced the chance of being detected by a searching hawk. Similarly, playbacks of attack calls resulted in all jays immediately seeking cover, where they hid and searched both passively and actively for a predator. Upon hearing mobbing calls, jays always searched actively for a predator. Combined, this data indicates that the perception of a specific anti-predator call provides jays with sufficient information to react with a situation specific behavioural response. Functional reference of alarm calls has been demonstrated for several mammalian species (Seyfarth et al. 1980; Macedonia 1990; Zuberbühler 2000, 2001; Manser 2001; Fichtel & Kappeler 2002). To my knowledge, this is the first study to demonstrate that birds have functional referential anti-predator calls that vary with predator category. Moreover it suggests that animals can evolve different referential anti-predator calls that signal predator behaviour.
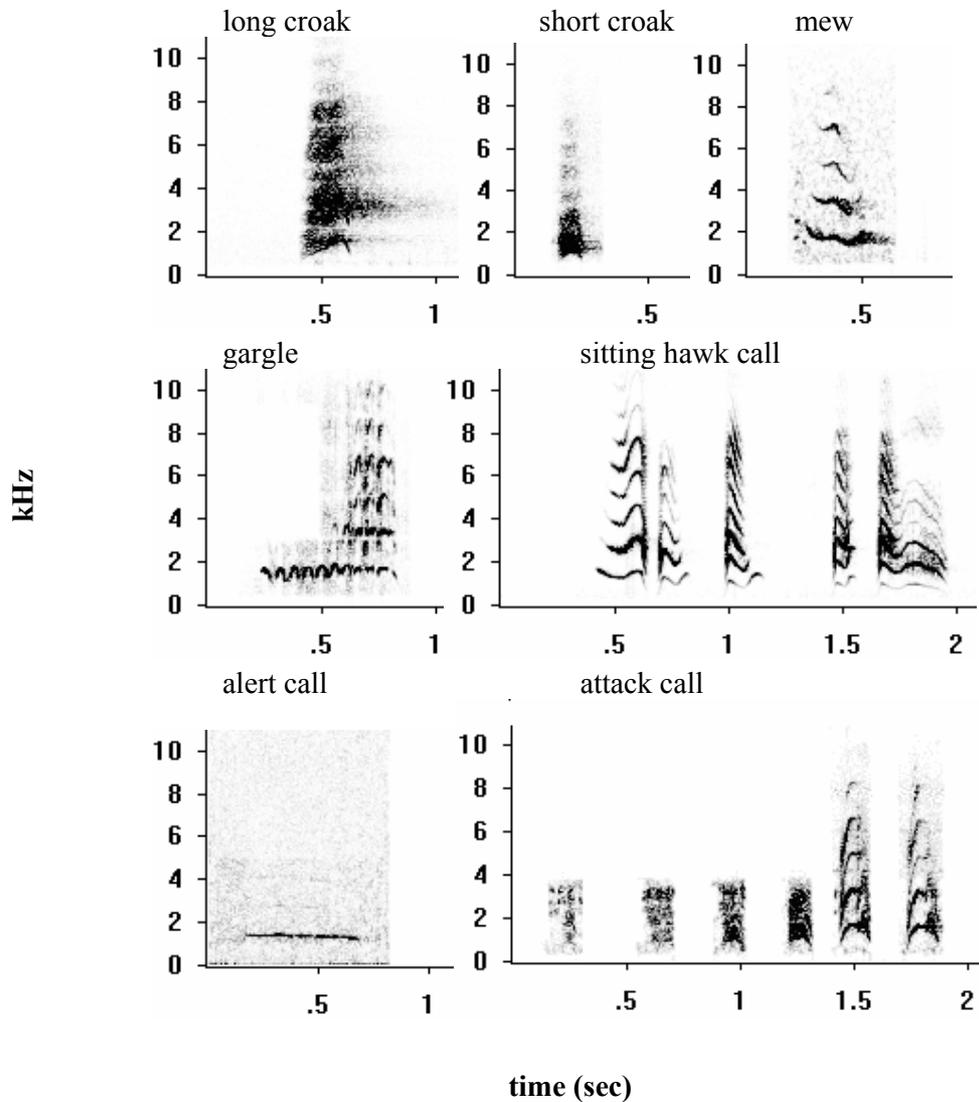
Figure 1. Spectrograms of predator and situation specific Siberian jay vocalisations. Calls were recorded with 22 kHz (16 bits accuracy) and plotted using a 256 point Fourier transformation (Blackman window function). Croaks, mew and gargle are uttered towards sitting owls and sitting hawk call towards sitting hawks. Alert call was uttered after detection of a target searching hawk and attack calls during a hawk attack.

Table 1. Mean number of calls (± SE) given in response to sitting hawks, searching hawks, attacking hawks, sitting owls, nest predators and calls given without presence of a predator (control). Specificity for the different antipredator calls was tested with a Fisher exact test. I tested the observed number of calls in each specific situation against the probability that calls would be equally likely uttered in any predator encounter situation. Expected call frequency for attack call was adjusted to 40 minutes.

call type	number of calls given in observation period mean±SE			calls given / not given in observation period			total number of specific calls	p
	sitting owls	sitting hawks	control	searching hawks	attacking hawks	nest predators		
short / long croak	8.95 ± 2.02	0	0	0	0	0	180	<0.00001
mew call	0.8 ± 0.41	0	0	0	0	0	16	<0.00001
gargle	0.45 ± 0.21	0	0	0	0	0	9	<0.001
sitting hawk call	0	5.15 ± 2.12	0	0	0	0	106	<0.00001
kew call	0	0.15 ± 0.11	0	0	0	0	3	ns
alert call	0	0	0	17	0	0	17	<0.00001
attack call	0	0	0	0	34	0	34	<0.00001
crowing	0	0	0	0	0	37	37	<0.00001
pickering	0	0	6.3 ± 0.72	0	0	0	-	-
mew-a	0.25 ± 0.12	0.45 ± 0.27	0	0	0	0	-	-
ki call	1.85 ± 0.85	4.1 ± 1.54	0	0	0	0	-	-
submissive call	0.55 0.31	0.2 ± 0.16	3.1 ± 0.82	0	0	0	-	-
babbling	3.75 ± 0.65	1.9 ± 0.43	0.15 ± 0.08	0	0	0	-	-
y call	10.65 ± 2.21	1.7 ± 0.38	0.15 ± 0.08	0	0	0	-	-
dyy call	5.1 ± 1.32	10.1 ± 1.86	0.05 ± 0.05	0	0	0	-	-
observation time	80 min	80 min	80 min	80 min	40 min	80 min	440 min	
N experiments	20	20	20		40	40	140	
N encounters				17			17	17

Nepotistic vigilance (II)

Parental vigilance was nepotistic and parents increased their vigilance while feeding together with retained offspring (Tab. 2, Figure 2). Parental vigilance rates were significantly higher than for breeders in groups of a corresponding size that did not contain any retained offspring. While parents feeding together with a retained offspring may have also responded to group size, kinship had an overriding effect in their vigilance rates.

Table 2. Factors influencing vigilance rate in parents/breeders (GLM Type III SS).

Factor	df	Sum of squares	F-ratio	p
Kinship	1	0.192	30.11	0.00001
Group size * Kinship	1	0.042	6.625	0.01
Group size	1	0.0002	0.03	0.85
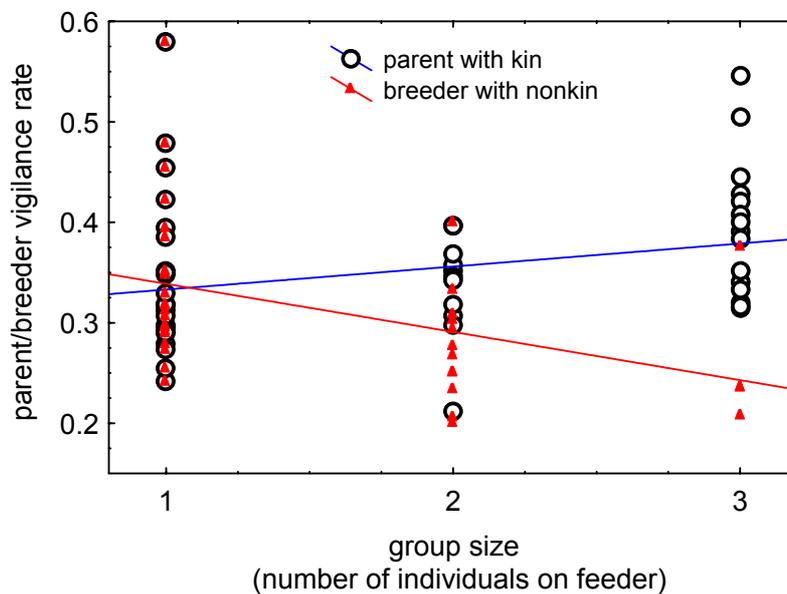
Figure 2. Nepotistic vigilance behaviour of breeders/parents. Vigilance rates of parents/breeders for different group sizes when feeding together with retained offspring (open circle) or with unrelated immigrants (filled triangle). Data for parent/breeder alone is shared for both regressions. Parent / breeder alone: N=24; parent with offspring: N=12, breeder with unrelated immigrant: N=12, parent with offspring and other individual: N=15, breeder with 2 unrelated individuals: N=3.

Breeders aborted aggressively feeding bouts of non-related immigrants only, but not their offspring (logistic regression testing the way a feeding bout of a retained offspring/immigrant was terminated; kinship: $\chi^2 = 202.99$, p< 0.0001, N= 568 departures, 33 individuals). This aggressive abortion of feeding bout is reflected in the distribution of feeding bout lengths (Fig. 3). The feeding bout length in immigrants followed a negative exponential distribution ($r^2=0.66$). Such a distribution features a constant probability that the feeding time ends at any moment, suggesting that the access to food was outside the control of immigrants (Feller 1966). In contrast, the feeding bout length of family members followed a polynomial distribution ($r^2=0.77$), suggesting that bout length of family members was more likely under their own control. A relaxed time constraint of retained offspring is also reflected in their initial behaviour on landing on the feeding site. In the majority of instances, retained offspring and parents/adults started feeding bouts with a scanning behaviour (N=601 arrivals with scanning, N=2 arrivals with feeding) whereas in 38% of feeding bouts, non-related immigrants (particularly females) started feeding immediately without scanning to ensure that their was no risk of an imminent attack (N=82 arrivals with scanning, N=50 arrivals with feeding) (logistic regression; kinship: $\chi^2 = 59.05$, p < 0.0001, individual: $\chi^2 = 16.79$, p < 0.0001, rank: $\chi^2 = 12.44$, p < 0.0005 and sex: $\chi^2 = 11.82$, p < 0.001. N = 735 arrivals, 45 individuals).
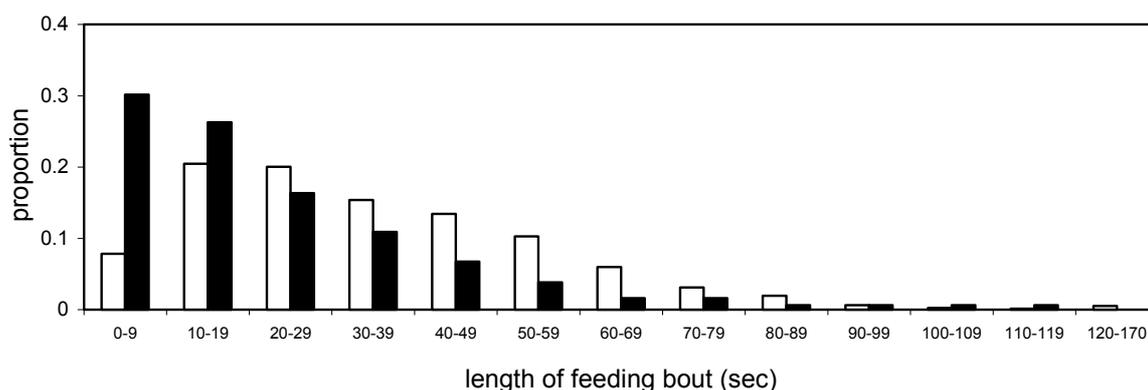
Figure 3. Frequency distribution of feeding bout length by family members (all ranks poled; open bars) and unrelated immigrants (filled bars). The distribution of the visit lengths of family members was best approximated with a polynomial function $r^2 = 0.774$ whereas the distribution of the visits of non-kin individuals followed negative exponential function $r^2 = 0.657$.

These results demonstrate that Siberian jay offspring that delay dispersal potentially benefit in several ways through associating with their parents. Parents are nepotistic in their vigilance behaviour thus protecting their offspring from surprise attacks by hawks. This is a novel approach to vigilance behaviour and may explain why individuals structure themselves in kin societies where mutual aid provides an evolutionary pay-off. Furthermore, parents do not restrict access to food for retained offspring through conspecific aggression. This ensures that offspring are not forced to trade off safer feeding conditions for energy gain. Conversely, unrelated immigrants have a more constrained access to food, and are therefore forced to feed in less safe conditions. My results link parental nepotism with vigilance behaviour and provide behavioural mechanisms that may directly explain the previously observed difference in first winter survival between retained offspring and unrelated immigrants (Ekman et al. 2000).

Nepotistic alarm calling (III)

The escape response of Siberian jays to a simulated hawk attack contained three distinct components. Birds under attack first detected the hawk model (looked at the model with a raised head), they then took off from the bait, and sometimes they gave alarm calls. The α-birds were significantly more likely to detect and leave the feeder first at an attack (proportion 0.81, $p = 0.00031$ H_0: $p = 0.5$, $n = 36$, binomial probability; Table 3). The birds called in 34 out of 40 experiments. In a minority of experiments ($n = 6$) both birds called. Our analysis considers only the first call, however, as subsequent calls may be in response to the first. Consideration of the first calls given in a trial, revealed that α-birds were significantly more likely to give call first (proportion 0.79 in the 34 experiments with calling, $p = 0.0028$, binomial probability, H_0: $p = 0.5$, Table 4). There was an asymmetry not only in that α-birds were more likely to call first but also in that calling was nepotistic. However in this respect there was a sex effect in that only mothers were nepotistic (sex effect $p < 0.05$; Logistic regression, Table 4). Mothers together with retained offspring were more likely to call than α-females together with unrelated immigrants, while fathers/α-males did not vary their calls irrespective of whether they were with retained offspring or unrelated immigrants (Table 4).

Table 3. The order of detecting the hawk model and the order of leaving the bait site first in tests of dyads (dyad composition parent /offspring and α-bird/unrelated immigrant). The order of leaving could not be determined in four experiments.

dyad composition	individual detecting the hawk first	
	parent/ α-bird	offspring/immigrant
parent – offspring	14	5
α-bird – unrelated immigrant	16	1
	individual first leaving feeder	
	parent/ α-bird	offspring/immigrant
parent – offspring	14	5
α-bird – unrelated immigrant	15	2

Table 4. Alarm-calling in response to simulated hawk attacks in kin (parent/offspring) and non-kin (α-bird/immigrant) dyads. One experiment per dyad. Significant kinship (Wald χ^2 = 6.36, p < 0.05) and sex (Wald χ^2 = 9.65, p<0.005) effects (Logistic regression). Tarsus length excluded from the final analysis as p > 0.20.

dyad composition	number of experiments	experiments with call	first call by parent/ α -bird
kin dyads			
father – offspring	10	10	10
mother – offspring	10	10	9
non-kin dyads			
α -male unrelated immigrant	10	9	7
α -female unrelated immigrant	10	5	1

It is important to recognise that alarm-calling by group mates merely complements an individuals' own vigilance as a means for predator protection. In the majority of our experiments the extra bird had already detected the attack themselves and responded prior to the α-birds warning call (proportion 0.89, N= 27 experiments where the α-birds called, Table 3). Yet, calling appears to convey accurate information of danger. Playback of the Siberian jay alarm-call elicited an immediate escape response also in the absence of a simulated hawk model attack, whereas individuals in the control treatment (robin song) continued to feed ($n_1 = 10$, $n_2 = 8$: U = 0.00, p<0.00005, Mann-Whitney U-test). The escape response to a playback was identical to that observed while running the hawk model over the feeding site.

Only a handful of studies have addressed the role of the social context and in particular the presence of relatives for alarm calling. Data for Belding ground squirrels (*Spermophyllus beldingi*; Sherman 1977, 1985), Prairie dogs (*Cynomys ludovicianus*; Hoogland 1983) and Vervet monkeys (*Cercopithecus aethiops*; Cheney & Seyfarth 1985) indicate that adult calling is more likely when relatives are present in the group. The response of Siberian jay mothers to our simulated hawk attacks indicates for the first time that there is also a nepotistic component to alarm calling in birds. Yet, the fact that fathers were relatively indiscriminate in their call giving suggests that alarm-calling may be a more complex behaviour than merely kin protection. To be of evolutionary consequence, offspring survival must ultimately be affected. A conclusive assessment of ultimate fitness consequences would require a comparison of the resulting mortality rates in real hawk attacks without alarm calling compared to when alarm calls are given. Such an experiment would involve live predators and was not considered for ethical reasons. Even in the absence of specific data we feel that a number of conclusions with respect to the significance of alarm calling can be made. Clearly, alarm calling will benefit a group member as long as it is unaware of an ongoing attack. This in itself may reduce the time taken to respond. Our data suggests that it is a rare event where an individual fails to detect an attack before alarm calls are given by group mates. However, the evolutionary consequences of alarm calling are still profound. Unless warned by its parents, an offspring would lose all its future reproduction in case it fails to detect an attack. Thus, it seems likely that even the small number of times where an individual does not detect an attack prior to hearing a warning call may be sufficient to have evolutionary consequences.

Nepotistic mobbing (IV)

When presented with a model predator, all groups approached and inspected the model in a similar manner to that observed during natural predator encounters. Two factors influenced the duration of the inspection. First, the hawk model, which represented the more dangerous of the predatory species, was inspected for a longer period than the owl model. Second, groups with retained offspring inspected both models for a longer period than groups without retained offspring (Fig. 4). Members of kin groups gave more calls than members of non-kin groups towards both the hawk and owl model while predator species had only an effect on total number of specific calls given (Fig. 5). In both kin and non-kin groups α-birds gave most of the calls, but in presence of their retained offspring, α-birds produced almost twice as many calls as α-birds in non-kin groups (Table 5). However, α-birds did not invest equally in calling; it was mainly the α-males rather than the α-females that gave calls during the predator inspection.
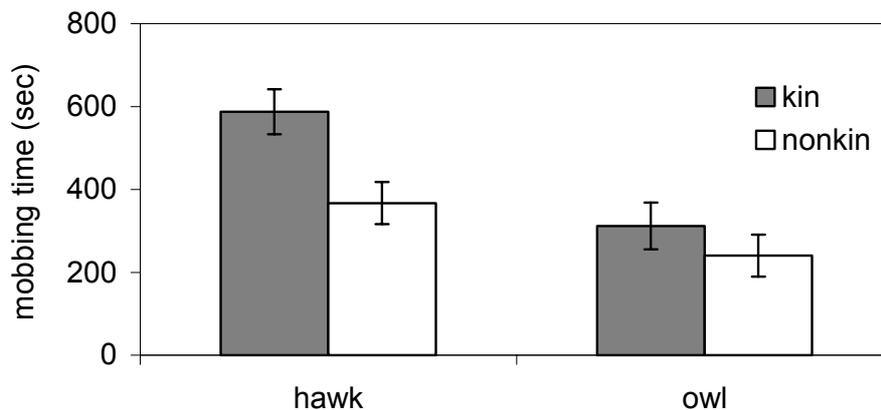
Figure 4. Time of predator inspection (estimate ± SE) in experiments with hawk model and owl model. The duration of the approach was influenced by predator species (hawk model was approached for long time than the owl model; predator, ndf = 1, ddf = 19.8, F = 16.9, p = 0.0006, SAS systems for mixed models, Type III SS) and group composition (kin groups stayed longer close to models than non-kin groups; ndf = 1, ddf = 28.6, F = 6.82, p = 0.014).
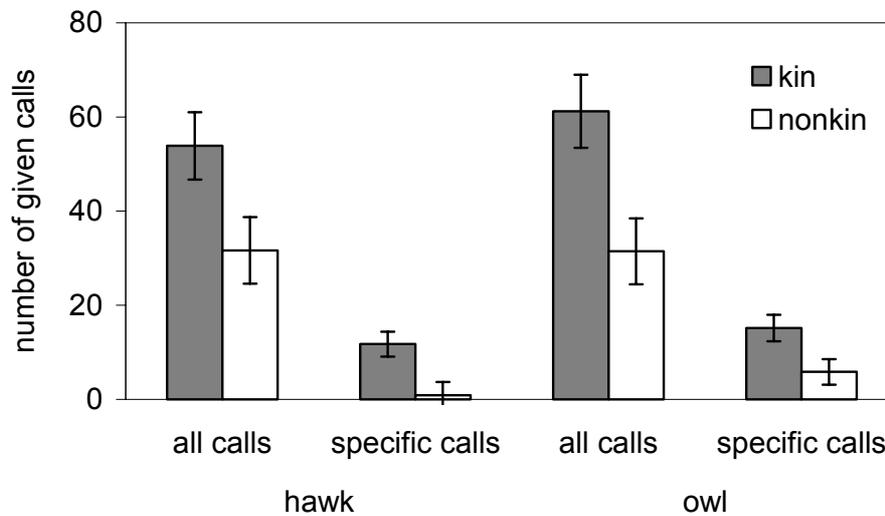
Figure 5. Number of given calls and specific calls (estimate ± SE) per group given during predator mobbing. The number of all calls was only influenced by kinship (ndf = 1, ddf = 36.4, F = 10.76, p = 0.0023, SAS systems for mixed models, Type III SS), whereas the number of specific calls was influenced by both kinship (ndf = 1, ddf = 36.7, F = 10.69, p = 0.0023) and predator species (ndf = 1, ddf = 20.0, F = 4.76, p = 0.041).

The number of calls varied with sex, relatedness and rank. Alphamales were more prone to give calls in kin groups (estimate ± SE = kin α-males: 30.31 ± 2.65, α-females: 10.30 ± 2.85; non-kin α-males: 11.24 ± 2.35, α-females: 7.82 ± 2.32). Retained male offspring gave more calls than immigrant males (kin subadults: 10.81 ± 5.03, subordinates: 7.94 ± 3.43; non-kin subadults: 2.63 ± 4.11, subordinates 3.73 ± 4.65). Retained and immigrant female extra birds rarely called. Considering only specific calls, these patterns remained constant with the exception that males, independent of rank, gave more calls towards to the owl model than towards the hawk model.

There were also behaviour differences in the responses to the two models. While inspecting the hawk model, all jays were more careful and almost never swooped over the model, whereas they sometimes swooped over the owl model (estimate ± SE = hawk: 0.00 ± 0.18, owl: 0.98 ± 0.19). Males swooped over the owl more often than females independent of rank or kinship. Jays did not only swoop over the owl model, but they also made short visits on the feeder in

presence of the owl model. In presence of the owl model, juvenile made most of the visits to the feeder. Almost no individual visited the feeder in presence of the hawk model.

Table 5: All and specific calls given per individual during predator approach analysed using a mixed model (SAS proc mixed). All meaningfully interactions were included in the model, but all interactions with $p > 0.2$ were removed form the final analysis.

All calls

Random effect	Estimate	Std error	Z-value	p-value
Territory	8.26	8.26	0.99	0.162
Residual	141.13	16.45	8.85	< 0.0001

Fixed effects	ndf	ddf	F-value	p-value
Rank	2	163	15.77	< 0.0001
Sex	1	167	10.92	0.0012
Kinship	1	116	5.03	0.027
Kinship*sex	1	167	6.29	0.013
Kinship*rank	2	163	2.46	0.088

Specific calls only

Random effect	Estimate	Std error	Z-value	p-value
Territory	2.29	1.55	1.48	0.069
Residual	19.02	2.21	8.57	< 0.0001

Fixed effects	ndf	ddf	F-value	p-value
Sex	1	161	13.03	0.0004
Rank	2	163	10.54	< 0.0001
Kinship*sex	1	160	6.60	0.010
Predator*sex	1	153	5.36	0.022
Kinship*rank	2	164	3.92	0.022

Jays returned back to the feeder more quickly following inspection of the owl model than after inspecting the hawk model. After inspection of the owl model non-kin groups returned faster to the feeder than kin groups. Conversely, following inspection of the hawk model, kinship had no effect on returning time and many groups did not return back.

Our results demonstrate that mobbing behaviour in animals is influenced by nepotism. In the presence of retained offspring, groups mobbed the predator model longer and gave more calls and specific calls than groups without retained offspring and α-birds, especially α -males gave most of the calls and specific calls. Offspring represent an evolutionary asset to their parents who therefore have an incentive to mob a predator more intensely in order to protect their offspring. The idea that mobbing behaviour could have a nepotistic component is not new (Hamilton 1964; Maynard Smith 1965), however, this study demonstrates to our knowledge for the first time in general that this could be the case.

Removal experiment (V)
In response to the removal of the fathers, seven out of 15 retained offspring in the experimental groups dispersed (Table 6). As all offspring carried a radio transmitter we were able to locate them after dispersal and could confirm that they had survived and settled else where. However, the response to removals was not immediate. With one exception, retained offspring left only after removed fathers had been replaced by a stepfather. Thus, the response occurred after group size had been restored. Dispersal in removal groups occurred too late in the season to be explained as regular dispersal among yearlings, which was confirmed by the lack of simultaneous dispersals among retained offspring from non-manipulated, control groups (p = 0.003, Fishers exact test, based on the number of groups with dispersal; Table 6).

Sex does not seem to have affected the dispersal decision (four of eight sons and three of seven daughters dispersed after removal). However, there was a strong kinship effect. Only retained offspring left, whereas no immigrants responded (number of groups with a response of retained offspring versus immigrant extra birds; p = 0.003, Fishers exact test; Table 6). This suggests that that value of the natal territory was enhanced by the presence of parents. If territory inheritance were an option, then the value of the natal territory would only improve as one of the breeders disappeared. Dispersal seems to be a

specific response to the replacement of removed fathers by an unrelated α-male, supporting the hypothesis that parental nepotism is essential to delayed dispersal in the Siberian Jay.

Table 6. Removal and responses of retained offspring and immigrant extra birds: numbers and time.

| | | | number of responses by | | | |
| | | | groups with | | individuals | |
	time	individual category	dispersal	no dispersal	disperse	stay
removal groups	July	retained offspring	6	0	6	2
		immigrants	0	6	0	6
	August	retained offspring	1	0	1	1
	September	retained offspring	0	3	0	5
		Immigrants	0	3	0	3
	total	retained offspring	7	3	7	8
		immigrants	0	9	0	9
control	mid-August	retained offspring	0	9	0	15

CONCLUSIONS

Combined, the results from the experiments presented in this thesis suggest that Siberian jay parents provide their offspring with nepotistic benefits through anti-predator behaviour. Parents increase their vigilance nepotistically when foraging together with offspring and concede resources to them. Resource access for retained offspring is therefore more predicable and in contrast to unrelated immigrants, related offspring do not have to take unnecessary risks while foraging. Under a hawk attack, mothers are nepotistic and only give alarm calls when together with their offspring, but not when together with unrelated

immigrants. Alarm calls benefit offspring that fail to initially detect an attack from a predator. Although this is a rare event, an offspring that fails to detect an attack loses all its future fitness, so the benefits from calling may be considerable. While mobbing predators, parents give more calls and stay longer close to the predator in presence of retained offspring. Mobbing is an important means to displace predators and Siberian jay parents invest more in mobbing in the presence of retained offspring. Upon disappearance of their father, offspring disperse once despotic immigrant α-males replaced their removed parent, indicating that the presence of fathers is an essential motive for offspring to delay dispersal. By blocking immigrants and unrelated males from becoming α-males and by being tolerant themselves, fathers provide a "safe haven" in the natal territory where retained offspring can avail themselves of available resources without any, or only mild, competitive interference.

The effects of group size on anti-predator behaviours has been addressed extensively in birds (Hamilton 1971; Pulliam 1973; Bertram 1978), but the importance of the social environment has received little attention. Both dilution by numbers in a "selfish herd" and a "many eyes effect" benefits individuals irrespective of relatedness. Our results demonstrate that vigilance, alarm calling and mobbing are anti-predator behaviours that in the Siberian jay are nepotistic benefiting kin. Few studies have addressed the possibility of nepotism in anti-predator behaviours (Sherman 1977; Cheney & Seyfarth 1985, 1990; Griesser 2003) or resource concession (Scott 1980; Barkan et al. 1986; Black & Owen 1987; Ekman et al. 1994; Pravodusova 1999). However, the generality of nepotism in these behaviours remains to be demonstrated. Parental concession of resources is a not an obvious behaviour and can easily escape notice. Resource concession does not necessary lead to an increased intake by offspring, as the main benefit may be a more predictable access to resources. This may be important in terms of predation risk as individuals do not need to take unnecessary risks (Griesser 2003). Also, under a more predicable access to resources individuals in many species carry less body fat and reduce thereby their susceptibility to predation (Ekman & Hake 1990; Bednekoff et al. 1994).

Anti-predator signalling in Siberian jays is referential and specific for the behaviour of the Goshawks, their main predator. Anti-predator signalling and behaviours in birds have almost exclusively been investigated in species living in non-kin groups, whereas virtually all studies in mammals have been done with species living in kin groups. Consideration of previous studies would

suggest that antipredator signalling in birds was not as elaborate as in mammals and that nepotism in anti-predator behaviours was restricted to mammals. While, this could simply be the consequence of anti-predator behaviours and vocalisations not being studied in kin-group living birds the experiments presented here offer evidence to suggest that these behaviours do occur.

Nepotistic anti-predator behaviour by Siberian jay parents may be best considered from a life-history perspective in the context of kin group formation due to postponed offspring dispersal (Arnold & Owens 1998; Hatchwell & Komdeur 2000; Kokko & Lundberg 2001). Although the timing of offspring dispersal certainly depends on the quality of available vacancies for potential dispersers (Ekman et al. 2001a), it appears more appropriate to examine the timing of dispersal as a component of a set of life-history traits. In a life-history context, timing of dispersal is an issue for both offspring and parents. From a life-history perspective the consequences of the resolution of the cost-benefit trade-off concerning the timing of dispersal also involves parents and their response to the presence of offspring into adulthood (Ekman & Rosander 1992; Cockburn 1996; Ekman et al. 2001). Nepotistic anti-predator behaviours are one form of extended parental care. It is an investment in offspring that have reached adulthood, and parental care is as an integral component involved in several life history trade-offs (Schaffer 1974; Smith & Fretwell 1974). Conceptually there is no difference between nepotistic anti-predator behaviours and other forms of parental care. Hence, the parent/offspring perspective inherent in the nepotistic behaviour of Siberian jays can be directly incorporated in a life-history approach to philopatry. Recent theory and experimental data suggest that dispersal may not be delayed without such a preferential treatment by parents (Ekman & Rosander 1992; Kokko & Ekman 2002; Ekman & Griesser 2002) and emphasises the role of direct fitness benefits gained from kin associations in maintaining cooperative animal societies (Clutton-Brock 2002). This suggests that nepotism creates a safe haven for offspring and is a pivotal factor promoting delayed dispersal and forming the foundations of sociality in many kin group living animals.

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SWEDISH SUMMARY

Släktskap har visat sig vara en viktig anledning till att djur är sociala och lever i komplexa samhällen. För individen är det avgörande är att dess egenskaper förs vidare till kommande generationer. Släktingar bär på många anlag som är identiska genom att de ärvts från en gemensam förfader. Hjälp som får släktingar att överleva och fortplanta sig bättre har därför en belöning i att individen främjar spridningen av de anlag den delar med sina släktingar.

Lavskrikan lever i familjegrupper utökade med någon eller några obesläktade individer som invandrat. Man har antagit att anledningen till att ungfåglar stannar i föräldrarnas revir på grund av platsbrist. Det skulle inte finnas någon ledig plats där de kan etablera sig. För att vinna något på att stanna måste det dock finnas någon specifik av "hemma". En unge kan finna föräldrar endast i sitt födelserevir, och hjälp från föräldrarna är en fördel som ungen inte skulle kunna finna någon annanstans. I min avhandling testade jag om unga lavskrikor får någon speciell fördel av att stanna med föräldrarna efter det att de skulle kunna klara sig själva. Ett sätt för föräldrarna att skydda den egna avkommen och därmed öka sin egna reproduktiva framgång är att skydda dom från rovdjur. Jag undersökte därför vilka rovdjur som vanligtvis tog lavskrikor och hur föräldrarna skyddade sina ungar ifrån dem. Jag undersökte också vilken roll föräldrarna har för ungarnas beslut att stanna hemma.

Att leva i flock utgör på flera sätt ett skydd mot attackerande rovdjur. En vanlig jaktmetod hos många rovdjur består i att lägga sig i bakhåll för att sedan överraska bytet. Ett sätt för bytet att skydda sig mot detta är att vara vaksamma och spana av omgivningen. Ju större flocken är desto större blir möjligheten att tidigt upptäcka en attack och hinna sätta sig i säkerhet. Dessutom minskar risken för den enskilda individen att fångas genom att den kan gömma sig i massan. Den helt övervägande andelen lavskrikor som dör har fångats och dödats av rovfåglar (mest duvhök, och i mindre utsträckning ugglor; slaguggla, hökuggla). Varningsläten skulle därför vara av potentiellt stort värde. Lavskrikan har också utvecklat ett flertal olika läten som varning för hökar och ugglor (Figur 1). Vad det gäller hökar så varierar varningslätet även beroende på hökens beteende (söker byte, attacker eller sitter endast still). I ett playbackexperiment visade jag att dessa varningsläten är referentiella, d.v.s. varningslätet innehåller information som gör att signalmottagaren reagerar på ett ändamålsenligt sätt (Tabell 1). Sådana beteenden har tidigare bara påvisats hos däggdjur.

Duvhöken jagar genom att attackera ur bakhåll och för att vara framgångsrik är den beroende av överraskningsmomentet. En lavskrika kan skydda sina avkomma genom att varna dem vilket förutsätter att de ägnar tid åt att spana efter attackerande rovfåglar (Figur 2, Tabell 2). Tillsammans med sin avkomma ökar föräldrarna den tid de ägnar åt spaning medan de minskar den tillsammans med obesläktade flockmedlemmar. I ett experiment där vi simulerade en duvhöksattack varnade föräldrarna, men det var bara mödrarna som var bara varnade avkommor (Tabell 4). Så fort lavskrikor upptäcker en sittande uggla eller hök närmar de sig rovdjuret och "mobbar" den, d.v.s. de flyger över den samtidigt som de avger varningsläte. På det sättet försöker de driva bort predatorn. I experiment med uppstoppade slagugglor eller sparvhökar visade sig att flockar bestående av släktingar mobbade längre än flockar som var endast bestod av obesläktade individer (Figur 4). Föräldrarna var de som gav de flesta varningslätena och i flockar bestående av släktingar gavs det mycket mer varningsläten (Figur 5, Tabell 5).

Tidigare studier har oftast ignorerat den sociala miljöns roll för skydd mot rovfåglar. Skydd mot rovdjur har inte ansetts vara en viktig orsak till varför fåglar lever i familjeflockar. Endast ett fåtal studier på däggdjur visar att individer gynnar sina egna släktingar (är nepotistiska) och främst varnar släktingar för attackerande rovdjur som lavskrikorna i den här studien. Här visar vi att även fåglar gynnar sina släktingar genom varningsläten och ett mobbingbeteende.

För att kunna visa att föräldrarnas beslut hade ett direkt inflytande på ungarnas beslut att stanna i familjeflocken flytta vi bort fadern i några flockar. Så fort en ny hanne vandrat in och ersatt fader gav sig ungarna av (Tabell 6) vilket bekräftar föräldrarnas roll för att ungarna skall stanna hemma. Utvecklingen av socialt beteende i form av släktgrupper ger sålunda både bättre förutsättningar för den enstaka individens överlevnad, men ökar också överlevnaden hos släktingar. På så sätt är nepotism en nyckelfaktor för utvecklingen av släktgrupper.