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Reduced mortality selects for family cohesion in a social species

Michael Griesser*, Magdalena Nystrand and Jan Ekman

Population Biology, Department of Ecology and Evolution, Evolutionary Biology Centre,
Uppsala University, Norbyvägen 18 D, 75236 Uppsala, Sweden

Delayed dispersal is the key to family formation in most kin-societies. Previous explanations for the evolution of families have focused on dispersal constraints. Recently, an alternative explanation was proposed, emphasizing the benefits gained through philopatry. Empirical data have confirmed that parents provide their philopatric offspring with preferential treatment through enhanced access to food and predator protection. Yet it remains unclear to what extent such benefits translate into fitness benefits such as reduced mortality, which ultimately can select for the evolution of families. Here, we demonstrate that philopatric Siberian jay (*Perisoreus infaustus*) offspring have an odds ratio of being killed by predators 62% lower than offspring that dispersed promptly after independence to join groups of unrelated individuals (20.6% versus 33.3% winter mortality). Predation was the sole cause of mortality, killing 20 out of 73 juveniles fitted with radio tags. The higher survival rate among philopatric offspring was associated with parents providing nepotistic predator protection that was withheld from unrelated group members. Natal philopatry usually involves the suppression of personal reproduction. However, a lower mortality of philopatric offspring can overcome this cost and may thus select for the formation of families and set the scene for cooperative kin-societies.

Keywords: evolution; families; kin-societies; predation; nepotism; delayed dispersal

1. INTRODUCTION

Group living is a widespread phenomenon throughout the animal kingdom and represents for many species a fundamental aspect of their lives. Groups can form in a variety of manners, ranging from transient aggregation of unrelated individuals to the formation of stable kin clusters. While the benefits and costs of grouping are well documented (Krause & Ruxton 2002), the reasons why groups vary in their genetic structure are less-well understood. In particular, our understanding of factors that select for the formation of families is still limited. Knowledge of such factors, however, is critical to understanding the evolution of cooperative breeding (Emlen 1994) as well as the evolution and dissolution of families in our own species.

The vast majority of families arise when offspring remain with their parent(s) beyond independence (Brown 1987; Emlen 1994). Because prompt dispersal and independent breeding are viewed as the optimal tactic for young animals, family formation has typically been viewed as a consequence of ecological or demographic constraints on dispersal and independent breeding, and experimental studies largely uphold this conjecture (Stacey & Koenig 1990; Emlen 1991). For example, philopatric offspring in splendid fairy-wren (*Mahurus cyaneus*) dispersed immediately after the experimental creation of a suitable territory

opening near by (Pruett-Jones & Lewis 1990). In the absence of high-quality openings, offspring of Seychelles warbler (*Acrocephalus sechellensis*) preferred to stay within the parental territory and engage in alloparental care (Komdeur 1992). Furthermore, in the cavity roosting woodhoopoe (*Phoeniculus purpureus*) physiological constraints have been found to limit offspring dispersal due to the thermoregulatory cost of roosting alone (Williams *et al.* 1991). However, while constraints can explain why individuals postpone independent reproduction, it does not provide a satisfying explanation of family formation *per se* since most animal populations face some constraints.

An alternative explanation for the formation of families focuses on the benefits offspring gain through philopatry (Brown 1987; Stacey & Ligon 1991; Ekman *et al.* 2004). It has been suggested that by remaining in the parental territory, philopatric offspring can receive a variety of benefits such as enhanced survival, indirect fitness benefits through alloparental care, access to high quality nearby breeding openings or increased access to resources within the parental territory (Stacey & Ligon 1991; Emlen 1994). Because indirect fitness benefits of alloparental care are a consequence rather than a cause of family living, they cannot select for the formation of families. In contrast, direct benefits have the potential to select for offspring philopatry, in particular those benefits that are unique to the parental territory. Empirical studies have demonstrated that philopatric offspring gain enhanced resource access (Verbeek & Butler 1981; Ekman *et al.* 1994), enhanced predator protection (Griesser & Ekman 2004, 2005) and access to high-quality breeding sites (Ekman *et al.* 1999, 2001). Experimental evidence further supports a role for benefits gained from philopatry in

* Author and address for correspondence: Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK (m.griesser@sheffield.ac.uk).

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family maintenance: in the Siberian jay, families broke up and offspring dispersed after fathers had been removed and were replaced by stepfathers who no longer provided benefits to philopatric offspring (Ekman & Griesser 2002); similarly, the reduction of available food resources from the parental territory resulted in family break-up in western bluebirds (*Sialia mexicana*; Dickinson & McGowan 2005); and provisioning of food enhanced family cohesion in the carrion crow (*Corvus corone corone*; Baglione *et al.* 2006). While such proximate benefits could be responsible for family cohesion, it remains unclear how these factors interact and whether benefits gained through philopatry have an effect on fitness correlates (i.e. reduced mortality) and thus can ultimately select for the evolution of families.

Here, we test whether nepotistic benefits translate into a fitness benefit and, as a result, select for family living in the Siberian jay. This year-round territorial species is well suited for the investigation of these questions since philopatric offspring do not engage in allo-feeding and thus gain no indirect fitness benefits (Ekman *et al.* 1994). Groups consist of a socially dominant breeding pair and up to four additional individuals (Ekman *et al.* 1994). Jay parents provide their offspring with a wide range of anti-predator behaviours, such as nepotistic increase in vigilance (Griesser 2003), nepotistic predator mobbing (Griesser & Ekman 2005) and nepotistic alarm calls during predator attacks (Griesser & Ekman 2004). Philopatry seems to be the preferred option among juvenile Siberian jays. As a consequence of conflicts among fledglings, socially dominant siblings within broods were more likely to stay in the parental territory than subordinate brood mates that dispersed to immigrate into other groups (Ekman *et al.* 2002).

Group members are recruited through retention of grown offspring, which can remain for up to 3 years in the parental territory, through immigration of unrelated individuals or through both pathways (Ekman *et al.* 2002). Extra pair mating is absent in this species and the dichotomy in relatedness among group members (family members versus immigrants) has been genetically confirmed (Ekman *et al.* 1994; H. Tegelström 2000, unpublished work), allowing for a critical test of kinship effects. A previous correlative study suggested that a prolonged association with the parents reduced mortality of philopatric offspring (Ekman *et al.* 2000). In this study, we explicitly test if first-winter mortality in the Siberian jay is influenced by territory quality, individual quality and social environment (parental nepotism or group augmentation). The natural variation in territory quality and individual quality allow us to test for their effect on first-winter mortality, whereas the natural variation in group relatedness and group size allows critical testing of the role of nepotism and group augmentation on mortality.

2. MATERIAL AND METHODS

Siberian jays were studied in a natural population outside Arvidsjaur (65°40' N, 19°0' E), northern Sweden from 1990 onwards. At the onset of each breeding season we caught female breeders and fitted them with radio tags to locate the nests. All nestlings were banded, allowing us to identify philopatric offspring. Unbanded juveniles in such territories were considered to be immigrants. In the territories where we

lacked information on reproductive success, relatedness of juveniles was determined by assessing aggressive interaction between breeders and juveniles foraging on feeders (in this study $n=4$ philopatric offspring, $n=6$ immigrants). Previous studies have confirmed that this method is a reliable indicator of relatedness (Ekman *et al.* 1994; Griesser 2003). Blood samples (100 µl of blood from the alar vein) were taken from all individuals for sex determination according to the methods described in Griffiths *et al.* (1998).

(a) Assessment of mortality

In September 2001 and 2002 we visited all groups and colour banded juvenile group members (2001, $n=15$ philopatric offspring, $n=7$ immigrants; 2002, $n=19$ philopatric offspring, $n=32$ immigrants). In late October, all these juveniles were re-captured to mount a radio tag on the tail feathers (Holohil BD-2G; weighing 1.80 g, corresponding to 2.0% of a bird's body mass). This allowed us to monitor juvenile mortality until the onset of the breeding season in March of the following year. To follow seasonal patterns in mortality, we visited the study site each winter in October/November, December/January, February and March to locate and identify all live birds and retrieve the dead juveniles. Moreover, we recorded the time observers spent in each territory and recorded all observations of potential predators of Siberian jays between September and March of both study years (goshawk, *Accipiter gentilis*; sparrowhawk, *Accipiter nisus*; hawk owl, *Surnia ulula*; Tengmalm's owl, *Aegolius funereus*; and Ural owl, *Strix uralensis*).

(b) Influence of habitat structure on mortality

Within each territory we measured the proportion of forest that had not been managed for the last 50 years (i.e. not thinned, partially cut or clear-cut and re-planted). Unmanaged forests had a denser understory, thus providing more visual protection from predators. Habitat data were sampled in the field with a GPS receiver. We used the locations of all groups taken during the study period (using hand-held GPS receivers) to define approximate territory borders (95% minimum convex polygons; Kenward 1987).

(c) Assessment of individual quality and condition

We measured the weight and wing length of all juveniles to calculate wing load (weight/wing length), and counted the number of faulty growth bars on the wing feather that had the most faulty growth bars. Wing load is likely to be the physical measure of most relevance for escape during a predator attack. Faulty growth bars in the wing feathers of juveniles reflect suboptimal growth condition as a nestling (Grubb 1989). To be able to assess current condition, in September 2002 we removed the outermost left tail feather and collected the re-grown feather 47–52 days later when attaching the radio tag ($n=43$ individuals). The growth of the re-grown feathers were measured with callipers to the nearest 0.1 mm as the total width of 20 growth bars (i.e. the growth during 20 days). We started to measure 10 mm from the top, measuring downwards.

(d) Kinship and group size effects on mortality

We followed each juvenile for behavioural observations once or twice for 30 min in October/November and February to assess the effect of kinship on their behaviour. During these observational bouts, we recorded the position of juveniles relative to other group members (<50 m to the closest group

Table 1. The number of surviving juveniles during their first winter (September to March). (Birds that disappeared in winter were retrieved dead and had all been killed by predators.)

	September	November	December/January	February	March	survived (%)
philopatric offspring	34	33	32	27	27	79.4
immigrants	39	32	27	26	26	66.7

Table 2. Linear mixed model showing the effect of independent model terms on first winter mortality of Siberian jays (34 kin birds, 37 non-kin birds). (The model was reduced by sequentially removing non-significant terms from the model, leaving only significant terms (p -values < 0.05). The effect of non-significant terms was estimated by adding them individually to the model. Sample size for feather re-growth data, $n = 43$ individuals; for all other terms, $n = 73$. Effects indicate direction of relationship and are presented after setting the mean of the covariate to zero.)

model term	Wald χ^2	d.f.	p -value	effect	s.e.	
proportion of unmanaged forests	8.44	1	0.004	-5.60	1.93	
faulty growth bars per wing feather	7.53	1	0.006	0.93	0.34	
kinship	4.83	1	0.028	1.74	0.79	(immigrants > philopatric offspring)
time associated with group	2.10	1	0.15	-1.77	1.22	
wing load	1.72	1	0.19	6.12	4.67	
sex	0.32	1	0.57	0.37	0.68	(females > males)
group size	0.19	1	0.65	-0.24	0.54	
feather re-growth	0.01	1	0.97	0.01	0.10	
constant				-1.39	0.59	

member=together, > 50 m to the closest group member=alone) as well as foraging activity (foraging or not) at 5 min intervals using time-point measurements. We also counted all aggressive interactions between group members during these observations. During all visits to groups, we recorded which groups breeders had disappeared from in order to be able to assess the effect of group composition on juvenile and breeder mortality. Earlier studies confirmed that predation was the sole cause behind the disappearance of breeders (M. Griesser, M. Nystrand & J. Ekman 2005, unpublished work); thus, breeders that disappeared during this study were assumed to be dead.

(e) Statistical analyses

We used Generalized linear mixed models (GLMMs) in GENSTAT 8.2 (VSN International Ltd, Hertfordshire, UK) to analyse the data. All mixed models had year and territory identity fitted as random effects. Covariates were fitted with the appropriate error distribution (identity, logarithm or logit link function). We added in all models all explanatory terms of interest and possible interactions, and subsequently dropped all terms that did not influence the explanatory power of the model (*a priori* $\alpha = 0.05$). We tested the effect of habitat structure, the number of faulty growth bars in the wing feathers, kinship, group size, sex, wing load, feather growth rate and proportion of time associated with the group on juvenile mortality with a GLMM (see table 2). A similar model was used to analyse the effect of group size, number of philopatric offspring and immigrants, habitat structure and sex on breeder mortality. The effect of habitat structure on predator abundance (number of predators observed per time unit) in territories was analysed with a GLMM. To test whether habitat structure differed in territories with philopatric offspring and immigrants, we used a GLMM, controlling for year and territory. The effect of independent variables (kinship, group size, sex) on the behavioural correlates (proportion of time foraging; time spent away from group; number of aggressive encounters) were analysed with

GLMMs. Finally, the link between habitat structure and the number of faulty growth bars of nestlings ($n = 69$ individuals; including dispersal timing as random variable in model) was explored with a GLMM. For this test we used data collected between 2000 and 2004.

3. RESULTS

We were able to determine the fate of all 73 juveniles that had been equipped with a radio-tag. Predation was the sole reason of first winter mortality and 20 juveniles were retrieved killed by predators within their territory (table 1). The majority of the dead birds had been killed by goshawks ($n = 14$; judging from faeces, foot or wing prints in the snow; all remains found on ground), while owls (hawk owl or ural owl; $n = 5$; remains found up in dense trees; pellets found) and pine marten (*Martes martes*; $n = 1$; bite marks on the retrieved feathers) also preyed upon jays, but less frequently (see electronic supplementary material, pictures 1 and 2).

Three factors affected first winter predation rate: habitat structure, individual quality and kinship (table 2). Juveniles living in territories that had a higher proportion of managed, and thus more open, forest had higher predation rates. Since goshawks, the main predator, search their prey using visual cues (Kenward 1982), it was expected that juveniles living in territories with more open forests should experience higher predation rates. This difference in predation rate could either be a result of predators preferentially hunting in more open habitat or, alternatively, due to jays being less vulnerable in a denser habitat. Predators were not observed more frequently in more open habitat in the two winters of this study ($\chi^2_1 = 0.32$, $p = 0.54$). Thus, the difference in jay mortality was most likely due to the jays' greater vulnerability in a more open habitat.

Growth condition in early life correlated with first winter mortality. Individuals with more faulty growth bars

in their wing feathers, reflecting suboptimal growth conditions as nestlings, had a higher probability of being preyed upon during their first winter (table 2 and electronic supplementary material, picture 3). However, condition at the onset of winter as measured by the capacity to regenerate feathers did not differ between philopatric offspring and immigrants.

The odds of being killed by a predator during their first winter were 62% higher for immigrants than for philopatric juveniles (20.6% versus 33.3%; tables 1 and 2). However, this was not an effect of habitat structure. There was no difference in the proportion of unmanaged forest in territories containing philopatric offspring (0.443) compared to territories with immigrants (0.440; $\chi^2=0.01$, $p=0.98$). This result is in line with previous studies of the Siberian jay which have demonstrated that parents provide their offspring with nepotistic predator protection and concede food to them at feeders (Ekman *et al.* 1994; Griesser 2003; Griesser & Ekman 2004, 2005). Here, under natural foraging conditions, breeders displayed similar behaviour and never displaced or chased philopatric offspring, whereas they frequently displaced immigrants, especially when the latter were foraging (figure 1 and electronic supplementary material, picture 4). As a consequence of these frequent displacements, immigrants spent significantly less time foraging than philopatric offspring (figure 2) and, in addition, they spent more time away from the group (18.9% of time-point observations; $n=39$ individuals) than philopatric offspring (10.6%; $n=34$ individuals; $\chi^2=13.99$, $p=0.0002$). Therefore, immigrants not only allocated a lower proportion of total time to foraging, but they were also unable to fully benefit from anti-predator protection resulting from a close association with the group.

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

(a) *Link between habitat structure and individual quality*

Immigrants had fewer faulty growth bars (1.18 ± 0.17) than philopatric offspring (1.85 ± 0.22 ; $p=0.029$, $n=73$), indicating a higher phenotypic quality among immigrants. This is the joint effect of juveniles from territories with more cover having fewer faulty bars ($\chi^2=4.02$, $p=0.045$) and reproductive success being higher in a habitat with more cover (Ekman *et al.* 2001; Eggers *et al.* 2005). As a result, more offspring will be produced in this habitat and, thus, contribute with a larger proportion of potential immigrants.

4. DISCUSSION

In our sample of radio-tagged Siberian jays, predation was the sole cause of first winter mortality. We were able to identify three factors influencing mortality patterns in the Siberian jay: habitat structure, individual quality and kinship. While these factors appear to be confounded, precluding a conclusive interpretation, they act at different levels.

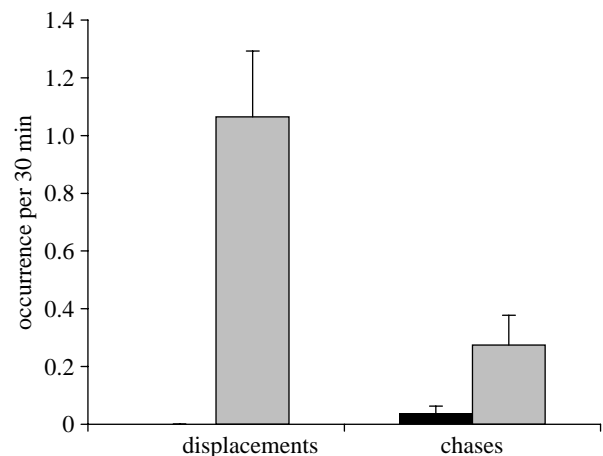


Figure 1. Rate of aggressive encounters of all other group members towards philopatric offspring (black) and immigrants (grey; \pm s.e.). Philopatric offspring were only chased by other juveniles. Kinship: GLMM, $\chi^2=31.46$, $p<0.0001$ (analysing the sum of displacements and chases).

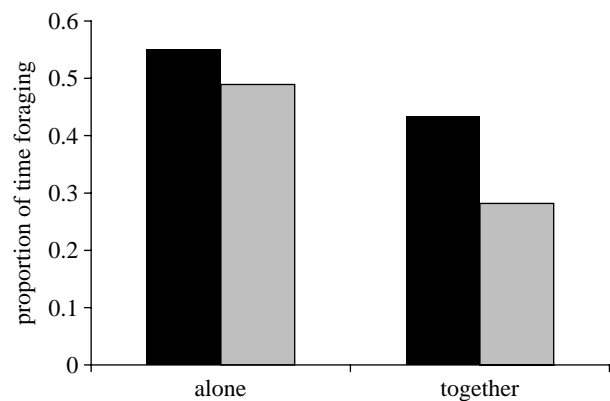


Figure 2. Time spent foraging either alone (more than 50 m from closest group member) or together with other group members (less than 50 m from closest group member) for philopatric offspring (black) and immigrants (grey; kinship, GLMM, $\chi^2=9.02$, $p=0.002$).

(a) *Do philopatric offspring and immigrants differ in phenotypic quality?*

Philopatric offspring are dominant over brood mates that disperse to become immigrants (Ekman *et al.* 2002). Thus, it could be argued that the kinship effect in first winter mortality merely reflects differences in phenotypic quality. Although social dominance determines dispersal timing among siblings, several independent factors suggest that it is not responsible for the mortality difference. Immigrants had, on average, fewer faulty growth bars in their wing feathers than philopatric offspring, indicating that they are born in high-quality territories and have experienced good growth conditions. Thus, immigrants were likely to be of generally better phenotypic quality than philopatric offspring (table 2). While immigrants were subordinate to their siblings that remained in the parental territory, many juvenile immigrant males are dominant over female breeders (Ekman *et al.* 1994) and sometimes even over philopatric offspring (M. Griesser, M. Nystrand & J. Ekman 2004, unpublished work). Yet philopatric offspring have substantially lower winter mortality than immigrants and, thus, social

dominance at the time of juvenile dispersal may be an unreliable predictor of winter mortality. Instead, we suggest that differences in mortality rates are more likely a consequence of habitat effects and social interactions.

(b) *Habitat structure and individual quality*

The majority of individuals became prey to goshawks, which is a diurnal bird of prey that relies on visual cues to locate its prey (Kenward 1982). Thus, it is not surprising that habitat structure strongly affected mortality rates. The higher predation rate in open habitats indicates that jays were more vulnerable in these habitats rather than mirroring a habitat preference of the hawks *per se*. The differences in habitat structure at the study site are a result of forest management. Forest thinning is standard practice in modern forestry within the Boreal forest belt to boost productivity by removing dense understorey and smaller trees at regular intervals, thus creating a more open habitat. Hence, current forest management may have consequences for the balance between predators and prey and potentially explain the current loss of species abundance and biodiversity (Hansson 1992).

Moreover, the forest structure acts indirectly on winter mortality by affecting phenotypic quality through growth conditions. Offspring born in territories with a more open structure experience suboptimal growth conditions (Eggers *et al.* 2005), resulting in a higher number of faulty growth bars in feathers. Suboptimal growth conditions have been demonstrated to negatively affect performance later in life in a wide range of species (Metcalf & Monaghan 2001; Lummaa & Clutton-Brock 2002). Here, we provide, to our knowledge, the first evidence that developmental inadequacies may increase an individual's predation rate. Juvenile Siberian jays frequently have broken wing and tail feathers and fractures are more likely to occur at faulty growth bars (M. Griesser, M. Nystrand & J. Ekman 2004, unpublished work). Such handicaps are costly by either increasing energy demands while flying, impairing manoeuvrability or by reducing the escape speed during a predator attack (Williams & Swaddle 2003).

(c) *Role of anti-predator behaviours*

The fact that predation was the sole factor of mortality highlights the important role of anti-predator behaviours. While immigrants and philopatric offspring do not differ in their ability to detect attacking predators (Griesser & Ekman 2004) or react appropriately towards sitting predators when alone (Griesser & Ekman 2005), philopatric offspring benefit from nepotistic protection from their parents. Parents protect philopatric offspring with a range of nepotistic anti-predator behaviours, e.g. by increasing vigilance during foraging (Griesser 2003), by alarm calling during predator attacks (Griesser & Ekman 2004) and by mobbing predators more intensively in company with philopatric offspring (Griesser & Ekman 2005), which all result in efficient protection against surprise predator attacks. Moreover, immigrants are constrained in their access to food, spend more time away from other group members and, therefore, are unable to benefit from the anti-predator behaviours of other group members. In contrast, philopatric offspring have unconstrained access to food, which allows them to take fewer risks than immigrants while foraging. Unlike family members, immigrants start foraging without

scanning for predators, forage in the presence of a predator model and choose more exposed sites to forage (Griesser 2003; Griesser & Ekman 2004, 2005; Nystrand 2006). Thus, it comes as no surprise that breeder disappearance during winter increased the mortality of philopatric offspring but not that of immigrants (Ekman *et al.* 2000). Similarly, experimental removal of a male breeder did not affect immigrants, while philopatric offspring dispersed upon removal of their father (Ekman & Griesser 2002). All these observations indicate that the difference in first winter mortality between philopatric offspring and immigrants is a kinship effect rather than an effect of different phenotypic quality.

(d) *Group size and augmentation effects*

It has been suggested that recruitment of new group members, irrespective of relatedness, may give direct fitness benefits to breeders and thus explain group living (Gaston 1978; Clutton-Brock 2002). A recent model has demonstrated that such benefits of group augmentation could be strong enough for parents to gain even from giving benefits to unrelated individuals (Kokko *et al.* 2001). However, such a mechanism does not appear to be able to account for family cohesion in jays since it would not explain mortality differences among juveniles. More importantly, in our study parents did not treat philopatric offspring and unrelated immigrants equally, contrary to what would be expected if individuals were recruited irrespective of kinship in order to gain group augmentation benefits.

(e) *Parental nepotism and family formation*

An understanding of the factors that select for family formation is essential to comprehend the evolution of cooperative societies in animals and our own species. Since natal philopatry usually involves the suppression of personal reproduction (Koenig & Haydock 2004), this cost needs to be reconciled with the maintenance of this behaviour by selection (Dickinson & Hatchwell 2004). Our results highlight that offspring can overcome these costs by gaining a direct fitness benefit from philopatry through enhanced survival prospects. The impact of mortality on individual fitness is particularly pronounced when survival before first reproduction is involved, because the entire lifetime reproductive success is at risk. Yet such benefits have so far gained little attention despite the fact that they may be sufficient to explain the initial step for the evolution of families and cooperative kin-societies.

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REFERENCES

- Baglione, V., Canestrari, D., Marcos, J. M. & Ekman, J. 2006 Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding carrion crows. *Proc. R. Soc. B* **273**, 1529–1536. (doi:10.1098/rspb.2006.3481)

- Brown, J. L. 1987 *Helping and communal breeding in birds: ecology and evolution*. Princeton, NJ: Princeton University Press.
- Clutton-Brock, T. 2002 Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72. (doi:10.1126/science.296.5565.69)
- Dickinson, J. L. & Hatchwell, B. J. 2004 Fitness consequences of helping. In *Ecology and evolution of cooperative breeding in birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 48–66. Cambridge, UK: Cambridge University Press.
- Dickinson, J. L. & McGowan, A. 2005 Winter resource wealth drives delayed dispersal and family-group living in western bluebirds. *Proc. R. Soc. B* **272**, 2423–2428. (doi:10.1098/rspb.2005.3269)
- Eggers, S., Griesser, M., Andersson, T. & Ekman, J. 2005 Nest predation and habitat change interact to influence Siberian jay numbers. *Oikos* **111**, 150–158. (doi:10.1111/j.0030-1299.2005.13802.x)
- Ekman, J. & Griesser, M. 2002 Why offspring delay dispersal: experimental evidence for a role of parental tolerance. *Proc. R. Soc. B* **269**, 1709–1713. (doi:10.1098/rspb.2002.2082)
- Ekman, J., Sklepkovych, B. & Tegelström, H. 1994 Offspring retention in the Siberian jay *Perisoreus infaustus*: the prolonged brood care hypothesis. *Behav. Ecol.* **5**, 245–253.
- Ekman, J., Bylin, A. & Tegelström, H. 1999 Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. *Proc. R. Soc. B* **266**, 911–915. (doi:10.1098/rspb.1999.0723)
- Ekman, J., Bylin, A. & Tegelström, H. 2000 Parental nepotism enhances survival of retained offspring in the Siberian jay. *Behav. Ecol.* **11**, 416–420. (doi:10.1093/beheco/11.4.416)
- Ekman, J., Eggers, S., Griesser, M. & Tegelström, H. 2001 Queuing for preferred territories; delayed dispersal of Siberian Jays. *J. Anim. Ecol.* **70**, 317–324. (doi:10.1046/j.1365-2656.2001.00490.x)
- Ekman, J., Eggers, S. & Griesser, M. 2002 Fighting to stay; the role of sibling rivalry for delayed dispersal. *Anim. Behav.* **64**, 453–459. (doi:10.1006/anbe.2002.3075)
- Ekman, J., Dickinson, J. L., Hatchwell, B. J. & Griesser, M. 2004 Delayed dispersal. In *Ecology and evolution of cooperative breeding in birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 35–47. Cambridge, UK: Cambridge University Press.
- Emlen, S. 1991 The evolution of cooperative breeding in birds and mammals. In *Behavioural ecology: an evolutionary approach* (ed. J. R. Krebs & N. B. Davies) 3rd edn, pp. 301–337. Oxford, UK: Blackwell Science.
- Emlen, S. T. 1994 Benefits, constraints and the evolution of the family. *Trends Ecol. Evol.* **9**, 282–285. (doi:10.1016/0169-5347(94)90030-2)
- Gaston, A. J. 1978 The evolution of group territorial behavior and cooperative breeding. *Am. Nat.* **112**, 1091–1100. (doi:10.1086/283348)
- Griesser, M. & Ekman, J. 2004 Nepotistic alarm calling in the Siberian Jay, *Perisoreus infaustus*. *Anim. Behav.* **67**, 933–939. (doi:10.1016/j.anbehav.2003.09.005)
- Griesser, M. & Ekman, J. 2005 Nepotistic mobbing behaviour in the Siberian jay *Perisoreus infaustus*. *Anim. Behav.* **69**, 345–352. (doi:10.1016/j.anbehav.2004.05.013)
- Griesser, M. 2003 Nepotistic vigilance behaviour of Siberian jay parents. *Behav. Ecol.* **14**, 246–250. (doi:10.1093/beheco/14.2.246)
- Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998 A DNA test to sex most birds. *Mol. Ecol.* **7**, 1071–1075. (doi:10.1046/j.1365-294x.1998.00389.x)
- Grubb, T. C. 1989 Ptilochronology: feather growth bars as indicator of nutritional status. *Auk* **106**, 314–320.
- Hansson, L. 1992 Landscape ecology of boreal forests. *Trends Ecol. Evol.* **7**, 299–302. (doi:10.1016/0169-5347(92)90227-3)
- Kenward, R. E. 1982 Goshawk hunting behaviour, and range size as a function of food and habitat availability. *J. Anim. Ecol.* **51**, 69–80.
- Kenward, R. E. 1987 *Wildlife radio tagging: equipment, field technique and data analysis*. London, UK: Academic Press.
- Koenig, W. D. & Haydock, J. 2004 Incest and incest avoidance. In *Ecology and evolution of cooperative breeding in birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 142–156. Cambridge, UK: Cambridge University Press.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. B* **268**, 187–196. (doi:10.1098/rspb.2000.1349)
- Komdeur, J. 1992 Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358**, 492–495. (doi:10.1038/358493a0)
- Krause, J. & Ruxton, G. D. 2002 *Living in groups*. Oxford, UK: Oxford University Press.
- Lummaa, V. & Clutton-Brock, T. 2002 Early development, survival and reproduction in humans. *Trends Ecol. Evol.* **17**, 141–147. (doi:10.1016/S0169-5347(01)02414-4)
- Metcalf, N. B. & Monaghan, P. 2001 Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* **16**, 254–260. (doi:10.1016/S0169-5347(01)02124-3)
- Nystrand, M. 2006 Influence of age, kinship, and large-scale habitat quality on local foraging choices of Siberian jays. *Behav. Ecol.* **17**, 503–509. (doi:10.1093/beheco/arj055)
- Pruett-Jones, S. G. & Lewis, M. J. 1990 Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature* **348**, 541–542. (doi:10.1038/348541a0)
- Stacey, P. B. & Koenig, W. D. 1990 *Cooperative breeding in birds*. Cambridge, UK: Cambridge University Press.
- Stacey, P. B. & Ligon, J. D. 1991 The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *Am. Nat.* **137**, 831–846. (doi:10.1086/285196)
- Verbeek, N. A. M. & Butler, R. W. 1981 Cooperative breeding in the northwestern crow *Corvus caurinus* in British Columbia. *Ibis* **123**, 183–189.
- Williams, E. V. & Swaddle, J. P. 2003 Molt, flight performance and wingbeat kinematics during take-off in European starlings *Sturnus vulgaris*. *J. Avian Biol.* **34**, 371–378. (doi:10.1111/j.0908-8857.2003.02964.x)
- Williams, J. B., Du Plessis, M. A. & Siegfried, W. R. 1991 Obligate cavity roosting provide a test of the thermo-regulatory insufficiency hypothesis. *Auk* **108**, 285–293.