Why offspring delay dispersal: experimental evidence for a role of parental tolerance

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Approximately 3% of all bird species live in families based on a prolonged parent–offspring association. Formation of family groups often appears to be associated with various constraints on the possibilities of independent reproduction for the offspring. However, delayed dispersal is not the only alternative for offspring that defer reproduction. To account for the formation of a family group it is also necessary to explain why non-dispersing offspring forego the alternative options to join other groups as ‘extra birds’ or to become ‘floaters’ and roam between territories. We removed fathers from Siberian jay *Perisoreus infaustus* family groups to test the proposal that nepotistic parental tolerance gives the natal territory a special value for the offspring, which they cannot find elsewhere and that makes them stay. In this species, parents are more tolerant of their retained offspring than towards immigrant extra birds. In response to the removal of fathers, retained offspring dispersed, whereas there was no similar response among the unrelated extra birds. Retained offspring, however, left only after despotic immigrant α -males replaced removed fathers, indicating that the presence of fathers is an essential motive for offspring to delay their dispersal. By blocking immigrant 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.

Keywords: kinship; dispersal; families; parental care; nepotism

1. INTRODUCTION

Kin relations have not played a prominent part in attempts to explain why birds associate in family groups. This may seem surprising with respect to the attention given to the potential for inclusive fitness gains from acting as a helper in cooperatively breeding family units. However, cooperative breeding is generally considered as beneficial while dispersal is delayed, rather than being the reason why the offspring stay with their parents (Brown 1987; Stacey & Ligon 1991; Koenig *et al.* 1992; Emlen 1994). Help at the nest may not enhance reproductive output under all conditions (Skutch 1961; Koenig *et al.* 1992) and inclusive fitness gains that derive from cooperative breeding may thus not be the primary reason for the postponement of dispersal. A growing number of species, where offspring are known to delay dispersal without engaging in cooperative breeding, support this conclusion (Verbeek & Butler 1981; Gayou 1986; Veltman 1989; Birkhead 1991; Ekman *et al.* 1994; Newton *et al.* 1994; Walls & Kenward 1998; Robinson 2000; Green & Cockburn 2001).

As an alternative to focusing on kin relations, attention turned to ecological conditions. It is a widely held belief that delayed dispersal may be a response to the low quality of vacant habitat discouraging dispersal, such that offspring would rather forego personal reproduction than attempt independent breeding in a poor-quality habitat (Selander 1964; Brown 1969; Emlen 1982, 1997). However, a weakness in this approach is that the decision to forego personal reproduction does not necessarily require that offspring must stay in the natal territory and maintain an association with the parents (Ekman *et al.* 2001). Non-

reproductive offspring have the option either to join other groups or just to roam as ‘floaters’ (Brown 1969). In order to account for delayed dispersal among non-breeding offspring ‘home’ must have a special value, making it the best place to wait for a breeding opportunity.

Even if inclusive fitness gained through cooperative breeding is a means for retained offspring to benefit from staying rather than being the cause of delayed dispersal, relatedness may still play a part in the decision to postpone dispersal. Parents could themselves make direct fitness gains from an extended parental investment that enhances offspring survival simultaneously, such extended parental care gives ‘home’ a special value to the offspring, which could provide an incentive to postpone dispersal (Ligon 1981; Brown & Brown 1984; Fitzpatrick & Woolfenden 1986; Ekman *et al.* 2001; Kokko & Ekman 2002). In several bird species, including the Siberian jay, parents are nepotistic and give preferential treatment to their offspring (Scott 1980; Black & Owen 1989; Barkan *et al.* 1986; Ekman *et al.* 1994; Pravosudova 1999; Griesser 2002). Unlike high habitat quality, parents can only be found in the natal territory. Therefore, such ‘extended parental care’ of parents could give the offspring an incentive to postpone dispersal and stay with their parents.

There are several options for parents to boost the survival prospects of their offspring. Vigilance, alarm calls and communal defence are among the countermeasures available to reduce the risk of predation. Nepotistic alarm calling is known from social mammals (Sherman 1977, 1985; Hoogland 1983; Cheney & Seyfarth 1990), while evidence for nepotistic vigilance has recently been found for birds (Griesser 2002). Social dominance is a main factor limiting access to resources for individuals in groups (Ficken *et al.* 1990; Ekman & Lilliendahl 1993; Ekman *et al.* 1994). If survival is food-limited, then parents could

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enhance the survival prospects of their offspring by ensuring their access to food. A nepotistic parental tolerance (Barkan *et al.* 1986; Ekman *et al.* 1994; Pravosudova 1999) may thus relax competition for resources for offspring with delayed dispersal. Parental nepotism could then create a 'safe haven' out of the natal territory for the retained offspring (Kokko & Ekman 2002).

In the Siberian jay, the offspring either delay dispersal to stay with their parents until a breeding opportunity becomes available, or they disperse in their first year in search of one. Unlike the siblings that have dispersed to associate with groups of unrelated birds, retained offspring have access to resources without, or only mildly limited by, a social dominance, as parents treat them with tolerance (Ekman *et al.* 1994). Hence, parents provide benefits that the offspring can gain only in their company in the natal territory. We studied whether the presence of such non-despotic, nepotistic parents was essential to the decision to delay dispersal in young Siberian jays.

2. MATERIAL AND METHODS

We performed removal experiments in a colour-banded Siberian jay population, which has been studied since 1990, near the village of Arvidsjaur in northern Sweden. In March each year, we caught females and attached radio transmitters (Holohil) and, by radio tracking, we located their nests. In this study, the nestlings in all successful nests were banded with a metal band and a unique combination of colour bands. The sex of all birds was determined using the P2/P8 technique (Griffiths *et al.* 1998).

We tested whether the presence of parents is essential to delayed dispersal by removing fathers. The removals were carried out in 1999 (September) and 2000 (July–August). The family groups produced from successful broods were randomly allocated to become either removal or control groups. The offspring in groups selected for removals were recaptured in 2000, about three weeks after fledging, when their tail feathers were fully grown and large enough to allow radio transmitters to be attached. The seven groups selected for removal were then each visited, on average, 19 times on different days (number of observations, henceforth $n = 137$ total visits) in the period preceding removals (15 June–15 July; visit rate was 0.64 day^{-1}) to record interactions and whether dispersal had occurred. Some Siberian jay offspring disperse in their first summer of life (Ekman *et al.* 2002). We took precautions to exclude such spontaneous dispersal of first-year birds, which would confound a response by retained offspring to removals. Therefore, during the removals we also monitored the seasonal changes in the composition of nine groups, which were left non-manipulated.

Fathers were caught in walk-in traps baited with sausage. After capture, they were put into cloth bags and removed to a distance of more than 20 km (under Swedish Ethical Board licence). We released them in prime habitat, and afterwards they were re-sighted in this area. We chose to remove only the fathers for several reasons. Paternal removal reduces the risk that group-size effects would confound our results, which could potentially be a problem with the removal approach. Vacancies in the Siberian jay population are often filled by immigrants (Kokko & Ekman 2002) and we expected that a removed father would probably be replaced by an individual from outside the group. A female immigrant extra bird from inside the group would only have to be accepted by the father to replace a removed breeder

female, while breeder males are top dominants in groups and to replace him a juvenile male in the group would have to hold his ground against would-be dominant males from outside. Regardless of the mechanism involved, all replacement males were recruited from outside the removal groups as expected, with one exception. A second reason to remove fathers was that sons are normally dominant to their mothers (Sklepkovych 1997). Therefore, nepotism in the form of paternal tolerance is important, while maternal tolerance is not an issue for sons.

After the removal of males, we monitored the behaviour of the offspring by radio tracking and by visiting groups approximately every second day up to mid-October 1999 and the end of September 2000. Furthermore, there was a final check in December (1999) and on 1 November (2000) when the composition of experimental and control groups was surveyed, after which we discontinued the experiment for the year. Only offspring that left before that time were considered to have responded. This design is likely to be conservative, as we have not recorded spontaneous dispersal in the winter. On our visits to groups, we recorded the interactions between non-dispersing offspring and fathers before removals, and how replacement α -males behaved towards offspring and group immigrants. We classified aggressiveness with the following scores: 0, feeding together without aggression; 1, subordinate displaced from food, but allowed to remain on bait site; 2, subordinate displaced from bait site; 3, subordinate chased outside bait site.

We used Fisher's exact test to assess the outcome of removals. This test makes no assumptions about the distribution. It is also suitable when the outcome is binomial, as it is here (disperse–stay), and it is not sensitive to the low frequencies in some of our outcomes, which makes χ^2 -based statistics, such as logistic regressions, unsuitable. Probabilities were calculated using Proc FREQ with the Fisher option enabled in the SAS software package (SAS 1996). All probabilities are two-tailed. To avoid pseudoreplication, in the form of correlated responses due to individuals being members of the same group, treatment effects were tested with groups as the sample unit. Immigrant extra birds, hatched outside territories, control for effects of group size, which they shared with the retained offspring in removal groups. In both years, fathers were removed from experimental groups only after we considered the spontaneous dispersal of first-year birds to be over. This was confirmed by monitoring seasonal changes in the composition of nine groups where no removals were made.

3. RESULTS

We removed fathers in July ($n = 6$), August ($n = 1$) and September ($n = 3$). In response, seven out of 15 retained offspring in the experimental groups dispersed before 1 November (table 1). Since all of them carried radio transmitters, we were able to locate them after dispersal and confirm that they had survived and settled elsewhere. The response to removals was not immediate. Retained offspring left experimental groups only after a delay of about a month (mean $\pm$ s.e = 31 ± 7.9 days, $n = 7$). Meanwhile, removed fathers had been replaced in six out of ten removals. These replacement males appeared in groups on average three weeks (mean $\pm$ s.e = 21 ± 9.1 days, $n = 6$) after removal of the fathers. No further replacements occurred before the experiments were discontinued for the year. We could record dispersal of retained offspring from all experimental groups where fathers had been replaced

Table 1. Removals and responses of retained offspring and immigrant extra birds: numbers and time.

	time	individual category	number of responses by			
			groups with		individuals	
			dispersal	no dispersals	disperse	stay
removal groups	July	retained offspring	6	0	6	2
		immigrant extra birds	0	6	0	6
	August	retained offspring	1	0	1	1
	September	retained offspring	0	3	0	5
		immigrant extra birds	0	3	0	3
	total	retained offspring	7	3	7	8
		immigrant extra birds	0	9	0	9
non-manipulated	mid-August	retained offspring	0	9	0	15

(before 1 November, $n = 6$ groups, six out of a total of eight retained offspring in these groups dispersed), but in only one group out of four ($n = 4$ groups, one out of seven retained offspring dispersed) without replacement ($p = 0.033$, Fisher's exact test; table 1). Hence, the response occurred, with one exception, only after the group size had been restored, and both dispersal and the probability that an offspring should respond appear to be dependent upon the father being replaced by an immigrant α -male.

Dispersal in removal groups occurred too late in the season to be explained as the regular dispersal among yearlings, which was confirmed by the lack of simultaneous dispersals among retained offspring from non-manipulated groups ($p = 0.003$, Fisher's exact test, based on the number of groups with dispersal; table 1). Sex does not seem to affect the response. There were eight sons and seven daughters with delayed dispersal in the experimental groups. Following the removals, four of the sons (proportion 0.50) and three of the daughters (proportion 0.43) left during the experiment (before 1 November). 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; $p = 0.003$, Fisher's exact test; table 1).

The kinship effect parallels a reduction in the access to resources for retained offspring, but not for immigrants, with the arrival of a new α -male. The replacement α -males treated the retained offspring of the removed father with the same despotism (aggression score 1.87, $n = 58$ interactions, five dyads; for scoring technique see § 2) as any unrelated subordinate immigrant (aggression score 2.11; $n = 103$ interactions, six dyads; $p = 0.27$, n.s., Mann-Whitney U -test, p -value adjusted for multiple tests). This level of aggression towards offspring with delayed dispersal simultaneously implies that replacement α -males were significantly more despotic towards them than their fathers had been (aggression score father-offspring associations 0, $n = 38$ interactions, seven dyads; test for difference in aggression level between replacement males versus offspring and fathers versus offspring, $p < 0.001$, $n = 13$ dyads, Mann-Whitney U -test, p -value adjusted for multiple test).

One potential route to becoming a breeder would be to

inherit the natal territory. However, this option was obviously not open to Siberian jay offspring. Our removals left at least one son in the six groups where immigrant replacement males appeared. In all of these territories, it was the immigrant male that mated with the widowed mother and acquired the territory ($n = 6$, $p = 0.05$, binomial test). Our removal did not offer a corresponding opportunity to daughters, while our removals left a widowed α -female in experimental territories. Ultimately the dispersal decision appears to be a response to the presence of immigrant replacement males.

4. DISCUSSION

Retained offspring may find queuing on the natal territory beneficial, either if they wait to inherit it, or because they improve their probability of survival through the nepotistic acts of their parents. The response of Siberian jay offspring to removals strongly suggests the latter to be more likely. If territorial inheritance were an option, then the value of the natal territory would only improve as one of the breeders disappears. Instead, offspring left the natal territory when one parent was removed, which suggests that the value of the natal territory was enhanced by the benefits that accrued from the presence of parents. In addition, in no removal did the offspring form a pair with the other parent that remained on the territory, which is in accordance with evidence from other species that inbreeding avoidance or reproductive conflict prevents inheritance of the natal territory (Koenig *et al.* 1998). In an earlier study on undisturbed (non-experimental) groups, territorial inheritance occurred too rarely to explain why offspring delay dispersal in this species (Kokko & Ekman 2002). Instead, improved survival of retained offspring, together with the associated opportunity to seize breeding vacancies in neighbouring territories, is sufficient to account for observed group sizes (Kokko & Ekman 2002).

Several facts indicate that retained offspring left as a response to a tolerant father being exchanged for a despotic unrelated α -male. First, for several reasons we can conclude that the response was not confounded by group size. Most important, the response of the offspring occurred only after group size was restored because of the immigration of a new α -male. Hence, groups were of the

original size by the time that retained offspring left. Second, only retained offspring, but not unrelated immigrant extra birds, left; however, we would have expected no difference among offspring and immigrant extra birds if dispersal had been a response to group size. Rather, dispersal seems to be a specific response to the replacement of removed fathers by an unrelated α -male, which is logical if parental nepotism is essential to delayed dispersal. Retained offspring were the only extra birds to suffer, in that they had a tolerant father exchanged for an unrelated and despotic α -male, while immigrant extra birds exchanged one unrelated and despotic α -male for another one. Third, the responses occurred too late in the season to be explained by spontaneous dispersal of yearlings. Although Siberian jays vary greatly in the timing of their natal dispersal, with some offspring leaving in the first summer of life and others staying for up to three years, radio tracking did not show any spontaneous dispersal among yearlings after mid-August (Ekman *et al.* 2002). The lack of simultaneous dispersal by retained offspring in untreated groups, where both parents remained, confirms that the responses to removals occurred too late to be explained as part of this spontaneous yearling dispersal.

Parental nepotism can take several forms. In the Siberian jay, parents provide their offspring with nepotistic protection against predators (Griesser 2002), but they also offer a tolerant social environment where access to resources is only mildly constrained by aggression (Ekman *et al.* 1994). While nepotistic predator protection certainly contributes to the value of postponed dispersal, parental tolerance appears to be the ultimate reason why offspring that cannot obtain a breeding vacancy also remain with their parents. Fathers blocked despotic immigrants from becoming established as α -males in the natal territory. Yet, delayed dispersal appears to more than just a by-product of the territoriality of the parents. Although territoriality plays an essential role in the behaviour associated with kin groups and is consistent with comparative analyses (Bennett & Owens 2002), it cannot, alone, explain why the natal territory should be a better place to wait than elsewhere. Better treatment in the natal territory appears to be the key to delayed dispersal. Kokko & Ekman (2002) used observed survival values and showed that this effect is strong enough to predict that one same-sex offspring should delay dispersal and associate with parents instead. We demonstrate experimental support for the mechanism behind higher survival. In association with a tolerant parent, the offspring evade the aggression that normally befalls subordinate individuals. If the parents had not given their offspring a preferential treatment and been less despotic towards them, it would have made no difference that fathers blocked unrelated immigrants from replacing them. Furthermore, territoriality alone fails to account for the variation in social behaviour between species, as parents can be territorial without the offspring delaying dispersal, as is evident from the large number of all-year territorial *Parus* species without delayed dispersal (Ekman 1989; Matthysen 1990).

Parental care is indeed widespread in birds. Therefore, it may seem like a truism to explain delayed dispersal by parental tolerance, but extended kin interactions are rare. Delayed dispersal has been recorded in *ca.* 3% of bird species worldwide (Emlen 1995). However, time is the

factor defining delayed dispersal and parents may not be tolerant forever. It would be beneficial to give the offspring preferential treatment only for as long as the gain to the offspring, devalued by relatedness, exceeds the cost to the parents. This cost will be reduced when parents are relatively immune to predation or, if mortality is food-driven, when parents have a super-abundance of food. It is only in habitats of high quality and which confer good survival prospects, that the parents would gain from being tolerant and by conceding resources to their offspring (Taylor 1988; Ekman & Rosander 1992; McNamara *et al.* 1994). Such a link to resource abundance provides a mechanism that can reconcile the role of parental tolerance for delayed dispersal with its life-history correlates (Arnold & Owens 1998). The conditions allowing parents a long period of offspring retention may thus be quite restricted. The incentive to delay dispersal may apply only while the offspring are still gaining experience. We suggest that the length of time during which nepotistic tolerance behaviour can enhance offspring fitness, more than it reduces the parent's own fitness, is of crucial importance for the evolution of delayed dispersal and of more complex social interactions among kin. While models to account for associations among kin have focused on access to habitat (Selander 1964; Brown 1969; Emlen 1982; Stacey & Ligon 1987, 1991; but see Brown & Brown 1984), our approach supports models that emphasize the coevolution of altruistic behaviour and dispersal (Ekman & Rosander 1992; Perrin & Lehmann 2001; Kokko & Ekman 2002).

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