Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal

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In a crowded environment the natal territory could serve as a haven for young and inexperienced offspring until a breeding vacancy emerges. Delayed dispersal and association with kin could then offer adaptive benefits through an individual fitness gain. Here we report that delayed dispersal is associated with a higher lifetime individual fitness in Siberian jay (*Perisoreus infaustus*) males. Sons bred more successfully and had more reproductive events in life when they delayed dispersal. The higher lifetime reproductive success when sons disperse later in life is sufficient to promote postponement of natal dispersal, suggesting that dispersal is delayed due to ecological constraints on access to high-quality habitats. We argue that the maintenance of this variation in the timing of dispersal and reproductive success can be reconciled with non-genetic mechanisms driving dispersal. Social dominance within broods reflecting environmental conditions during growth is such a mechanism.

Keywords: reproductive success; *Perisoreus infaustus*; dispersal; kin; retained offspring

1. INTRODUCTION

In birds, retained offspring typically, although not always, use a stay-and-foray strategy to search for a breeding vacancy (Brown 1987). The natal territory could serve as a haven for young and inexperienced offspring until a vacancy emerges. Access to resources in the natal territory is a direct consequence of delayed dispersal and could offer an individual fitness benefit in a crowded environment when ecological constraints limit the availability of suitable habitat elsewhere (Selander 1964; Brown 1969; Emlen 1982). Such an individual fitness benefit from remaining in the natal territory will be enhanced further when parental tolerance facilitates access to resources (Scott 1980; Brown & Brown 1984; Barkan *et al.* 1986; Ekman *et al.* 1994).

The role of ecological constraints on access to habitat and individual fitness gains as an incentive to delay dispersal has been evaluated with different techniques. The timing of natal dispersal has been related to variations in population density on the assumption that such variations reflect constraints on the availability of habitats (Stacey 1979). A more direct approach has been to remove experimentally any constraint on access to habitat through removals (Pruett-Jones & Lewis 1990; Komdeur 1992). These approaches have confirmed that birds respond to density variations and opening of vacancies as predicted when dispersal is delayed due to ecological constraints on access to habitat. The approach of the present study is different in that the objective is to

evaluate the timing of natal dispersal in survival and reproduction and how intrabrood variation in the timing of dispersal (e.g. Strickland 1991) can be maintained.

We capitalized on an intrabrood variation in the timing of natal dispersal of the Siberian jay (*Perisoreus infaustus*) to evaluate its consequences for lifetime reproductive success. This variation in the timing of dispersal spans from the first summer of life up to several years of age (Ekman *et al.* 1994). The Siberian jay is suited for testing whether delayed dispersal can be driven by individual fitness advantages as the offspring of broods from previous years do not provide care for younger siblings in the nest (Ekman *et al.* 1994). Therefore, comparisons of individual fitness accruing from the timing of dispersal evade confounding inclusive fitness gains from care lavished on non-descendent offspring as nestlings.

2. METHODS

Our results are based on observations of reproduction and natal dispersal between 1989 and 1997 in a population of individually colour-banded Siberian jays north-west of Arvidsjaur, North Sweden (65°40' N, 19°0' E). In addition to observations within our study area, there was a ringing scheme run by amateurs in extensive surrounding areas. Bandings, recaptures and reobservations within this scheme allowed us to detect immigration to and emigration from our study area.

The Siberian jay is a territorial, singular breeder, living in small winter flocks of around four to five members. The core of this group is the breeding pair, which is resident in its year-round territory. Extra birds are a mixture of retained offspring and immigrants hatched outside the territory. The Siberian jay is

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unusual in that retained offspring from previous years do not provide care for younger siblings while in the nest (Ekman *et al.* 1994), although we cannot exclude cooperation between fledged siblings in parallel to that found in the congeneric grey jay (*Perisoreus canadensis*; Waite & Strickland 1997).

The reproductive outcome was monitored by locating nests and newly fledged broods. The Siberian jay is an open nester, building highly cryptic nests and breeding at low densities (about two pairs per km²) in a typical taiga habitat. We therefore relied largely on radio tagging of breeding birds to locate nests. Successful reproduction was confirmed by observations of fledglings outside the nest in the company of their parents. We climbed and inspected nests which had failed to produce offspring to identify the causes. The signs interpreted as predation were when pieces of material had been torn out of the nestcup lining, probably as the nestlings tried to hang on while being lifted out of the nest. Sometimes entire nests had been displaced. Video surveillance of nests has confirmed nest predation which leaves such traces.

We took several precautions to prevent our activities revealing the positions of nests to predators. The radio transmitters allowed us to discover nests at a distance of 30–40 m, which did not cause any disturbance to the breeding birds. We visited the nests regularly, but, to minimize the possible disturbance from our activities, we avoided approaching nests closer than 30–40 m while the parents were present. Ongoing breeding attempts are easily confirmed from a distance. The female can be seen in the nest while incubating and, later on, the parents can be seen feeding the chicks. To reduce the risk of attracting nest predators further, we climbed the nest trees only when banding the nestlings or when inspecting abandoned nests.

To minimize the disturbance at banding, we held the nestlings in cloth bags and removed them a considerable distance from the nest (200–300 m) before handling them so that calling by the nestlings would not attract predators to the nest. Further, the parents did not appear to be able to identify a chick as their own this far from the nest. At least they did not give alarm calls if they detected us banding a chick. To avoid giving parents the impression that the nest had been predated, we never removed all nestlings simultaneously for banding, unless there was only one chick. As parents normally feed nestlings at long intervals (up to 1 h) these procedures normally allowed us to band nestlings in a majority of nests without being detected by the parents and without them giving out alarm calls. We could not detect any increase in nest losses after banding.

All retained offspring were banded either as nestlings or shortly after fledging. Offspring which had not been banded as nestlings could easily be distinguished from immigrants by the behaviour of their parents. The non-aggressive parental tolerance of offspring is distinctive (Ekman *et al.* 1994, fig. 2). DNA fingerprinting using multilocus minisatellite analyses (for methods see Ekman *et al.* (1994)) corroborated identifications of first-order kinship based on behaviour. Seven out of 38 retained offspring identified in this study were banded after fledging. Their classification as retained offspring from behaviour was corroborated by their DNA-fingerprint band sharing with putative parents which was in the range of 0.565–0.683, identifying them as offspring. The degree of band sharing within breeding pairs was 0.186 ± 0.091 ($n=17$). The band sharing between parents (both sexes) and offspring (=nestlings) was 0.625 ± 0.088 ($n=91$, 17 broods), while it was only 0.173 ± 0.032 ($n=7$) between parents and immigrants. We could identify first-year immigrants from their appearance in a territory during the

year following a failed breeding attempt there or by excluding the possibility that they were not retained offspring for pairs with successful breeding. For calculations of lifetime reproductive success we used only birds banded in their first year. Non-offspring extra birds are not necessarily birds dispersing in their first year as they could be retained offspring from outside our study area. We therefore caught all such unbanded birds and aged them in combination with banding. Siberian jays are easily aged from the shape of their rectrices, which are more rounded for first-year birds. Sexual dimorphism is small in the Siberian jay and we therefore determined their sex from behaviour during courtship, incubation and, sometimes, copulation.

We could follow and record offspring production over the entire reproductive career for birds that settled and became breeders in our study area. These data, however, cannot be used directly for a comparison of lifetime reproductive success of sons with delayed dispersal and males dispersing in their first year (e.g. Grafen 1988). Sons that initially delay dispersal, eventually to disperse successfully and then have a long reproductive career, will be underrepresented in our samples as some of them emigrated from our study area upon reaching reproductive status. However, this bias towards short-lived sons that delay dispersal can be corrected by taking the data on lifetime reproduction we have for males that did reach reproductive status and devalue it by an independent estimate of the probability of surviving until reaching reproductive status. This procedure generates an estimate corrected for the fact that we cannot record lifetime reproduction for sons which, after having been retained, eventually dispersed successfully and bred outside our study area.

3. RESULTS

(a) *Timing of dispersal*

We identified 38 successful broods over the nine years of the present study. From these broods we identified a total of 38 retained offspring (number of retained offspring per brood: two offspring $n=2$, one offspring $n=34$ and no offspring $n=2$), which had delayed dispersal and remained in the company of their parents until September of their first year. Natal dispersal was delayed for three years at the most among these retained offspring. It was possible to follow the eventual dispersal for 24 out of the 38 retained offspring (18 sons and six daughters). All such dispersal, events occurred in the period April–September (23 in April–May and one in May–September) but we could not record any territory shifts during the period September–March. Thirteen retained offspring (11 sons and two daughters) settled in our study area after dispersal, while the remaining 11 (seven sons and four daughters) became established in territories outside the study area. Lifetime reproductive data, however, are only available for birds breeding in our study area.

Resightings outside the natal territory of first-year birds banded as nestlings and an influx during the summer (June–September) of yearling birds born elsewhere confirm that there is a summer dispersal phase of Siberian jays during their first year. Territory shifts were recorded less frequently for immigrants than among retained offspring. There was a total of 45 immigrant first-year birds (both sexes) during the study period. Of these 45 first-year immigrants, only eight moved to a new territory

later on ($\chi^2=16.0$, d.f. = 1 and $p < 0.001$). Territory shifts among immigrants, as among retained offspring, occurred during the period April–May, except for one which took place in the period between May and September.

(b) Nest success

Due primarily to nest predation, on average Siberian jay pairs had a probability of only 0.38 (95% confidence limits 0.29–0.48) of raising any offspring from a clutch ($n=106$ clutches). The low probability for nests being successful and producing at least one fledged offspring was a main factor linking the timing of dispersal to lifetime reproductive success. The influence of dispersal timing (delayed dispersal versus dispersal as first-year bird) on the probability of nests being successful (minimum one fledged offspring) was tested with a logistic regression model as nest success is a binary response variable (entered in models as failed = 0 and success = 1). Apart from dispersal timing, the model included year, male age and habitat structure (density of spruces lower than 15 m) as explanatory variables. Year was entered as the proportion of successful nests, which varies strongly between seasons (0.08–0.67). Dispersal timing (delayed dispersal versus dispersal as first-year bird) and year (1989–1997) are discrete nominal variables which function as identifiers without any numeric significance. Therefore we analysed the logistic regression using SAS Proc Catmod, which is specifically designed to handle such data.

The remaining explanatory variables (male age and habitat structure) are continuous covariates. Our analysis is confined to males of known year of birth and, thus, male age can be entered as a continuous numeric variable (1–7 years). For territory structure we chose the density of spruce trees lower than 15 m (mean of two random samples of 100 m² per territory). In a comparison between territories over the entire study period, when pooling the data for all located nests, this habitat structure correlated strongest to overall reproductive success among a set of variables describing tree composition ($p < 0.01$; ANOVA).

The logistic regression revealed a significant association between the timing of male dispersal (retained/yearling disperser) and the probability of their nesting attempts being successful ($p < 0.01$, logistic regression, SAS Proc Catmod). A stepwise backwards elimination procedure could not detect a significant contribution by any other factor. Age came closest with a p value of 0.19. Hence, pairs with a male who had delayed dispersal bred more successfully than pairs with males which had dispersed to settle as first-year birds (probability of raising at least one young: retained offspring $p = 0.42$, $n = 36$ nests and 11 males, and males dispersing in their first year $p = 0.17$, $n = 41$ nests and 15 males). The logistic regression did not identify habitat characteristics as an independent explanatory factor. Still, the habitat structure of a male's territory is not independent of the timing of dispersal. Males with delayed dispersal settled in territories containing significantly more low and dense spruce forest (density of spruce < 15 m, $r^2 = 0.45$ and $p < 0.01$, logistic regression).

(c) Number of breeding events

The number of breeding events is another factor linking the timing of dispersal to differences in lifetime

Figure 1. Distribution of the number of breeding events (in years) in life for retained sons (black bars, $n = 11$ individuals) and males settling as immigrants in their first year (white bars, $n = 15$ individuals). Retained sons breed for significantly more years ($Z = 2.01$ and $p < 0.05$; Mann–Whitney U -test).

Figure 2. The distribution of lifetime production of offspring for retained sons (black bars, $n = 11$ individuals) and males settling as immigrants after dispersing in their first year (white bars, $n = 15$ individuals). Sons with delayed dispersal produce significantly more offspring ($D = 0.55$ and $p < 0.05$; Kolmogorov–Smirnov test).

reproductive success. Males with delayed dispersal had a significantly longer breeding career than males dispersing in their first year (3.27 versus 2.73 years; figure 1). Breeders were highly sedentary and disappearances are unlikely to be due to dispersal. We recorded a shift of breeding territory between years only twice among 151 breeders (actually breeder years; multiple years for many individuals) despite extensive search efforts in areas surrounding the study area. Further, both shifts were made by the same individual in two consecutive years. Breeders in all the remaining 149 cases used the same territory in consecutive years. In contrast, there is positive evidence of local mortality. Three of the 11 retained males and two of the 15 males dispersing in their first year were retrieved dead having been killed by goshawks.

(d) Lifetime reproductive success

We recorded offspring production after reaching breeding status for 11 sons with delayed dispersal and for 15 immigrant males dispersing as first-year birds. These males normally bred only after they had dispersed and

acquired a territory. There are rare events where retained sons having mates have been allowed to breed within their natal territory. Two sons bred unsuccessfully, one attempt each, within the natal territory. One was killed doing so by a goshawk, while the other male dispersed after the breeding attempt. Males with delayed dispersal produced significantly more offspring over their lifetime (mean = 4.72) than males which had dispersed in their first year (mean = 1.4; figure 2). The number of offspring recorded for males after reaching breeding status is treated as the total production during their reproductive career considering the low mobility of breeders and the evidence for local mortality (see above). Too few retained daughters remained in the study area after dispersal to allow a similar comparison for females.

Pre-breeding survival indicated no link to the timing of dispersal, which should cancel out the higher reproduction in favour of retained offspring relative to first-year dispersers. Out of 26 retained sons, 18 were resighted after dispersal (proportion 0.69; 95% confidence limits 0.47–0.85), which includes the seven emigrant males from our study area (see above). Out of 21 immigrant males settled in our study area as first-year birds, 14 reached breeding status (proportion 0.68; 95% confidence limits 0.46–0.86). With a mean production of 2.36 offspring over the breeding career of retained sons (allowing for two parents; see above) their lifetime reproductive success is 1.63 (0.69×0.36) offspring. The corresponding value for males dispersing in their first year is 0.48 (0.68×0.7) offspring. This difference is conservative. The survival of retained sons is underestimated if sons settling outside our study area escape detection. In contrast, the survival estimate of males dispersing in their first year includes only mortality after settlement and disregards potential losses during dispersal. Further, even if the true survival of retained sons was at the lower end and that of yearling dispersers at the upper end of the confidence intervals (0.47 and 0.86; see above), the lifetime reproductive success of males with delayed dispersal would still be approximately twice as high (1.10 versus 0.60).

4. DISCUSSION

While there is no evidence that Siberian jays gain inclusive fitness from contributing care to younger siblings of subsequent broods (Ekman *et al.* 1994), there is a higher individual fitness of retained offspring which is sufficient to account for the maintenance of delayed dispersal. The higher reproduction of sons with delayed dispersal, once they have eventually dispersed, obtained a territory and achieved reproductive status, suggests that dispersal is delayed for an ecological constraint on the access to breeding vacancies. Such a link between a saturated habitat and delayed dispersal was suggested by Selander (1964) and, in a graphical model, Brown (1969) showed how delayed dispersal could offer an adaptive advantage when there is a shortage of high-quality habitat. Dispersal by retained offspring when high-quality breeding vacancies were made available experimentally (Pruett-Jones & Lewis 1990; Komdeur 1992) demonstrated a behaviour in line with the predictions from Brown's (1969) model. However, the model does not only predict such a

behaviour but it also predicts an individual fitness gain from delayed dispersal. Here we provide data on survival and reproduction which establish a link between delayed dispersal and high individual fitness, confirming that a behaviour with delayed dispersal is linked to fitness benefits.

In the views of Selander (1964) and Brown (1969), postponed dispersal is a strategy where individuals forego current opportunities to wait for better breeding vacancies to become available. Variation in the quality of breeding opportunities is then critical, allowing for delayed dispersal to offer adaptive benefits. Brown (1969) incorporated this assumption in his model by confining the ecological constraint to access to 'suitable habitat'. Later analyses confirmed the critical role of this assumption (Koenig & Pitelka 1981; Stacey & Ligon 1991). The logic of this quality-variation argument is that delayed dispersal could offer an advantage provided that it will only be possible to gain a better breeding opportunity than currently available in the future. The poor performance of those Siberian jay sons that disperse promptly in their first summer is consistent with such an ecological constraint where the best breeding opportunities are not immediately available. Conceivably, retained sons do better because the more dense forest with lower visibility in their territories provides better breeding habitat than the more open and transparent forest in the territories that males dispersing in their first year acquire. Given a major role of nest predation for lifetime reproductive success and that nest predators such as ravens, crows and common jays are visual hunters, there may well be a causal link between low visibility in the territory and the high reproductive success of retained sons.

Males do not only end up in territories which differ in habitat structure depending on their timing of dispersal. It is likely to be the competitively superior offspring having the first choice which postpones dispersal. The within-brood difference in performance would then reflect dominance, as in the grey jay (Strickland 1991). Despite high fitness costs of prompt dispersal, the intra-brood variation in the timing of dispersal would be maintained if it is the result of a variation in dominance among brood mates without a genetic basis, such as when it reflects hatching asynchrony or growth conditions. The higher reproductive success of males with delayed dispersal would then represent what Endler (1986) called 'phenotypic selection' as it will not result in an evolutionary response. Hence, there are arguments suggesting a role for both phenotypic and habitat quality determining the timing of dispersal, but the correlational nature of our data does not allow us to disentangle the two factors. Experiments will be necessary to that end. However, the two mechanisms cannot be mutually exclusive. There is the possibility that phenotypic and habitat quality are causally dependent so that they cannot be functionally separated. Dominance has to be mediated through some tangible factor and Siberian jays of high phenotypic quality could conceivably do better, because they, by virtue of their dominance, can acquire high-quality territories.

Lack of habitat alone does not appear to be sufficient to account for delayed dispersal, even when ecological constraints on habitat are a necessary condition. The

offspring disperse promptly in several tit species (*Parus* spp.), although access to space is as limited as in cooperative species, which constrains yearling tits to a second-rate option of settling as subordinates in non-kin flocks (Ekman 1989; Matthysen 1990). Brown (1969) also pointed out that ecological constraints *per se* are not sufficient for dispersal to be delayed. He emphasized that many species whose offspring do not delay dispersal live in habitats which are as saturated as those for species where the offspring postpone dispersal.

The value of delayed dispersal will not only depend on what can be gained elsewhere. Such benefits have to be balanced against conditions in the natal territory, and parental tolerance towards retained offspring has been found in several species, including the Siberian jay (Scott 1980; Brown & Brown 1984; Barkan *et al.* 1986; Ekman *et al.* 1994). A consequence of such tolerance (parental facilitation *sensu* Brown & Brown 1984) is to promote delayed dispersal as retained offspring then require an alternative habitat of higher quality before it becomes a 'suitable' alternative to the natal territory and dispersal is favoured. The role of parental facilitation has received little attention despite its potential to account for dispersal timing. Parents which gain in individual fitness from being despotic under harsh conditions and drive offspring to disperse will gain direct fitness through their descendent kin if they become tolerant and concede resources to retained offspring when competition is relaxed (Ekman & Rosander 1992).

Here we tested whether delayed dispersal may be maintained by offering adaptive benefits. As an alternative explanation delayed dispersal could be a historic legacy with little or no current adaptive value. Delayed dispersal and cooperatively reproducing family units is an ancestral state of several bird taxa (Peterson & Burt 1992; Edwards & Naeem 1993) like the *Corvini* branch of oscine passerines, which includes jays (Cockburn 1996). However, it is clear from our data that delayed natal dispersal is not maintained merely as a historic legacy in the Siberian jay. The higher reproductive success of sons with delayed dispersal will maintain postponed dispersal regardless of the actual mechanism (genetic or phenotypic) behind this variation in the timing of natal dispersal. A genotype for prompt dispersal would not be established and fixed as it would be selected against. Further, a correlation between social behaviour and phylogeny does not necessarily imply phylogenetic inertia. It could merely be a phylogenetic effect (Miles & Dunham 1993), which in our case would predispose corvids to selection for offspring retention and a cooperative social behaviour.

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REFERENCES

- Barkan, C. P. L., Craig, J. L., Strahl, S. D., Stewart, A. M. & Brown, J. L. 1986 Social dominance in communal Mexican jays *Aphelocoma ultramarina*. *Anim. Behav.* **34**, 175–187.
- Brown, J. L. 1969 Territorial behaviour and population regulation in birds. *Wilson Bull.* **81**, 293–329.
- Brown, J. L. 1987 *Helping and communal breeding in birds*. Princeton University Press.
- Brown, J. L. & Brown, E. R. 1984 Parental facilitation: parent–offspring relations in communally breeding birds. *Behav. Ecol. Sociobiol.* **14**, 203–209.
- Cockburn, A. 1996 Why do so many Australian birds cooperate: social evolution in the Corvidae. In *Frontiers of population ecology* (ed. R. B. Floyd, A. W. Sheppard & P. J. De Bano), pp. 451–472. Melbourne: CSIRO Publishing.
- Edwards, S. V. & Naeem, S. 1993 The phylogenetic component of cooperative breeding in perching birds. *Am. Nat.* **141**, 754–789.
- Ekman, J. 1989 Ecology of non-breeding social systems of *Parus*. *Wilson Bull.* **101**, 263–288.
- Ekman, J. & Rosander, B. 1992 Survival enhancement through food sharing: a means for parental control of natal dispersal. *Theor. Popul. Biol.* **42**, 117–129.
- Ekman, J., Sklepkevych, B. & Tegelström, H. 1994 Offspring retention in the Siberian jay (*Perisoreus infaustus*): the prolonged brood care hypothesis. *Behav. Ecol.* **5**, 245–253.
- Emlen, S. T. 1982 The evolution of helping. I. An ecological constraints model. *Am. Nat.* **119**, 29–39.
- Endler, J. A. 1986 *Natural selection in the wild*. Princeton University Press.
- Grafen, A. 1988 On the use of lifetime reproductive success. In *Reproductive success* (ed. T. Clutton-Brock), pp. 454–471. University of Chicago Press.
- Koenig, W. D. & Pitelka, F. A. 1981 Ecological factors and kin selection in the evolution of cooperative breeding in birds. In *Natural selection and social behaviour: recent research and new theory* (ed. R. D. Alexander & D. W. Tinkle), pp. 261–280. New York: Chiron Press.
- Komdeur, J. 1992 Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358**, 492–495.
- Matthysen, E. 1990 Non-breeding social organization in *Parus*. *Curr. Ornithol.* **7**, 209–249.
- Miles, D. B. & Dunham, A. E. 1993 Historical perspectives in ecology and evolutionary biology: the use of phylogenetic comparative analyses. *Annu. Rev. Ecol. Syst.* **24**, 587–619.
- Peterson, A. T. & Burt, D. B. 1992 Phylogenetic history of social evolution and habitat use in the *Aphelocoma* jays. *Anim. Behav.* **44**, 859–866.
- Pruett-Jones, S. G. & Lewis, M. J. 1990 Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature* **348**, 541–542.
- Scott, D. K. 1980 Functional aspects of prolonged parental care in Bewick's swans. *Anim. Behav.* **28**, 938–952.
- Selander, R. K. 1964 Speciation in wrens of the genus *Campylorhynchus*. *Univ. Calif. Publ. Zool.* **74**, 1–224.
- Stacey, P. B. 1979 Habitat saturation and communal breeding in the acorn woodpecker. *Anim. Behav.* **27**, 1153–1166.
- Stacey, P. B. & Ligon, J. D. 1991 The benefits of philopatry hypothesis for the evolution of cooperative breeding: variance in territory quality and group size effects. *Am. Nat.* **130**, 654–676.
- Strickland, D. 1991 Juvenile dispersal in grey jays: dominant brood member expels siblings from natal territory. *Can. J. Zool.* **69**, 2935–2945.
- Waite, T. A. & Strickland, D. 1997 Cooperative breeding in grey jays: philopatric offspring provision juvenile siblings. *Condor* **99**, 523–525.