

Social constraints limit dispersal and settlement decisions in a group-living bird species

Michael Griesser,^{a,c} Magdalena Nystrand,^a Sönke Eggers,^a and Jan Ekman^a

^aPopulation Biology, Department of Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, SE-75236 Uppsala, Sweden, ^bDepartment of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK, and ^cSection of Ecology, Department of Biology, Turku University, FI-20014 Turku, Finland

Dispersal is a fundamental process affecting the genetic structure of populations, speciation, and extinction. Nevertheless, our understanding of the evolution of dispersal is limited by our paucity of knowledge on dispersal decisions at the individual level. We investigated the effect of interactions between residents and juvenile dispersers on individual dispersal and settlement decisions in Siberian jays (*Perisoreus infaustus*). In this group-living bird species, some offspring remain on the parental territory for up to 3 years (retained juveniles) whereas other offspring disperse within 2 months of fledging (dispersers). We found that retained juveniles constrained settlement decisions of dispersers by aggressively chasing dispersers off their territory, resulting in dispersers continuing to disperse and settling in groups without retained juveniles. Experimental removal of male breeders during the dispersal period also demonstrated that dispersers were unable to settle in high-quality breeding openings, which were instead filled by older nonbreeding residents. Rather, dispersers immigrated into groups without retained offspring where they became subordinate group members, queuing for a breeding opening. Also, they preferably settled in groups with short queues where no same-sex juveniles were present. Dispersal did not inflict a cost to dispersers through increased mortality. However, the presence of immigrants was costly for breeders because it increased the rate of conflicts during the breeding season which negatively affected nestling condition. These results demonstrate that resident individuals constrain both dispersal and settlement decisions of dispersers. Social interactions between residents and dispersers can thus be a key factor to understand the evolution of dispersal. *Key words*: dispersal cost, movement, natal dispersal, queuing strategies. [*Behav Ecol* 19:317–324 (2008)]

The simple act of an individual moving from one place to another—dispersal—has important evolutionary and ecological consequences for population dynamics, speciation, and extinction (Clobert et al. 2001; Bullock et al. 2002). The ultimate causes of dispersal are well investigated, and many of the key mechanisms driving dispersal have been identified, for example, reduction of the negative effects through crowding (Olivieri et al. 1995), gene spreading (Gandon and Michalakis 2001), or avoiding inbreeding and kin competition (Hamilton and May 1977; Bengtsson 1978). However, the proximate, behavioral mechanisms of dispersal are still not well understood (Stamps 2001; Doerr and Doerr 2005) which significantly hamper our comprehension of the evolution of dispersal strategies. Thus, we still lack a comprehensive framework that can link dispersal theory to empirical data (Kokko and López-Sepulcre 2006).

In territorial species, dispersal and settlement decisions have been suggested to be the results of interactions between residents and dispersers (Krebs 1978; Rosenberry et al. 2001). Studies in group-living fish and mammals have shown that dominant group members can control group membership of subordinates, and failure to be accepted into a group or being evicted from a group can be costly for subordinates (Clutton-Brock et al. 1998; Buston 2003a). Hence, dominants

can control dispersal decisions of subordinates. As a result, subordinate group members in some fish species have developed strategies to be accepted into the group. For example, immigrants in the clown anemonefish (*Amphiprion percula*) and the daffodil cichlid (*Neolamprologus pulcher*) can regulate their growth in order to maintain stable size hierarchies within the group and thereby avoid being evicted (Buston 2003b; Heg et al. 2004). Although our understanding of the role of residents on the control of group membership is increasing, the influence of residents on dispersers during the dispersal phase and on settlement decisions remains unknown.

In this study, we address the effect of social factors on dispersal and settlement decisions in a group-living bird species, the Siberian jay (*Perisoreus infaustus*). This species lives in cohesive groups on year-round territories in boreal forests throughout the northern Palearctic (Griesser et al. 2006). In addition to the dominant breeding pair, groups can consist of up to 4 retained offspring and/or immigrants from up to 3 different cohorts (Ekman et al. 2001). The breeding pair produces a single brood per year (1–5 eggs) and 3.2 ± 0.14 (mean \pm standard error [SE]) offspring fledge in successful broods (Eggers et al. 2006). Although the socially dominant offspring postpone dispersal and remain on their natal territory for up to 3 years (hereafter referred to as “retained juveniles”), they expel their subordinate brood mates from the natal territory about 3–6 weeks after fledging. Dominance among brood mates, and therefore also their dispersal strategy, is determined by hatching order, which is independent of sex (Ekman et al. 2002). Thus, similar numbers of juvenile males (0.63 ± 0.06) and juvenile females (0.68 ± 0.06) postpone dispersal in groups with successful reproduction. As a consequence of sibling rivalry, subordinate siblings disperse up to 20 km before resettling. We refer to these individuals as

Address correspondence to M. Griesser. E-mail: michael.griesser@ebc.uu.se. M. Nystrand is now at the Centre for Evolutionary Biology, School of Animal Biology, University of Western Australia, Crawley 6009, Australia. S. Eggers is now at the Department of Conservation Biology, Swedish University of Agricultural Sciences, Box 7002, SE-75007 Uppsala, Sweden.

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“dispersers” until they settle in a new group, from which point they are referred to as “immigrants.” Irrespective of dispersal status, almost all juveniles have to queue up to 3 years before acquiring a breeding position (Ekman et al. 2001; Kokko and Ekman 2002).

Despite living in family groups, retained offspring in the Siberian jay do not engage in helping at the nest and thus gain no indirect fitness benefits from a prolonged association with their parents (Ekman et al. 1994). However, retained offspring do gain direct fitness benefits from their parents that protect them through nepotistic antipredator behaviors (Griesser 2003; Griesser and Ekman 2004, 2005; Nystrand 2006, 2007), and as a result, retained juveniles have a substantially higher first winter survival than unrelated immigrants (Griesser et al. 2006). Moreover, retained offspring become breeders in better territories than immigrants and thus retained offspring have a higher lifetime reproductive output (Ekman et al. 1999; Ekman et al. 2001). Neither retained offspring nor immigrants gain access to reproduction because extrapair paternity and covebreeding are absent in our study population (Ekman et al. 1994; Tegelström H, unpublished data, 2000).

Here, we specifically address 4 questions pertaining to dispersal and settlement decisions in Siberian jays. First, we investigate interactions between residents and dispersers during dispersal. If the presence of immigrants in a group inflicts costs to breeders through competition over the breeding position, we expect breeders to prevent dispersers from settling. Alternatively, if immigrants compete with retained offspring over queuing positions for future breeding openings, retained offspring are predicted to prevent dispersers from settling on their territory. If immigrants cause a cost to all group members through increased competition over resources (i.e., food), all resident group members are expected to prevent

dispersers from settling. Second, we examine the role of resident individuals on actual settlement decisions. We expect immigrants to settle preferably in a breeding vacancy and, if not available, on territories with short queues where there are no same-sex juveniles present. We test the ability of dispersers to directly acquire a breeding opening by experimentally removing breeders during the dispersal period. Third, dispersers are predicted to preferably settle in high-quality patches because queuing jays only disperse locally to occupy a breeding opening and thus the initial settlement decisions affect the quality of a potential future breeding territory (Kokko and Ekman 2002). Finally, we address the consequences of dispersal and settlement decisions for both dispersers and residents. We examine the mortality rate of radio-tagged dispersers compared with the mortality rate of radio-tagged resident juveniles during the same period. The cost to breeders of having immigrants in their groups was tested by examining the effect of immigrants on breeding success and nestling condition.

METHODS

Study site

We collected data for this study in a color-banded population of Siberian jays close to Arvidsjaur, Northern Sweden (65°40'N, 19°0'E). Our study population has been monitored since 1989 with the number of studied territories having increased over the study period from 3 to 51. For this study, we analyzed data collected between 1990 and 2004 (Table 1). The vegetation at the study site is characteristic of Scandinavian boreal forests, consisting of a mosaic of clear-cuts, plantations, managed forests, and pristine patches (Griesser et al. 2007).

Table 1
Number of occupied and empty territories and settlement decisions of dispersers in relation to group size before settlement between 1990 and 2004

Year	Number of occupied territories studied	Number of empty territories ^a	Number of dispersers settling on empty territory	Maximum number of breeding openings during dispersal period ^b	Number of dispersers settling directly becoming breeder	Number of dispersers joining groups to queue for breeding position			
						Group size before immigration			
						2	3	4	5
1990	9	0	0	0	0	2	1	0	—
1991	14	0	0	0	0	2	2	—	—
1992	13	0	0	2	0	2	1	0	—
1993	12	0	0	1	0	3	2	1	1
1994	12	0	0	1	0	1	3	2	1
1995	14	0	0	2	0	1	3	—	0
1996	13	1	0	1	0	2	1	—	—
1997	14	1	0	2	0	0	0	—	0
1998	18	0	0	0	0	4	2	1	0
1999	26	1	0	4	0	4	9	0	0
2000	39	3	0	15 ^c	1	13	9	5	0
2001	46	3	0	3	2	6	0	0	0
2002	44	7	0	11	3	22	10	6	—
2003	41	5	0	4	1	9	6	8	1
2004	42	4	0	9	0	11	6	2	1
Total	357	21	0	55	7	82	55	25	4

^a Excluding all territories that were abandoned as a result of forest logging.

^b The number of breeding openings during the dispersal period is a maximum estimate because this number is based on all breeding openings counted between the end of May and the beginning of September.

^c Seven of these openings were created experimentally.

Assessment of breeding success and group composition

We collected data on breeding success and group composition in all territories ($N = 357$ group years; Table 1). We used 2 different methods to assess breeding success. In most territories, we caught female breeders at the onset of each breeding period (March) and fitted them with a radio-tag that was glued to the 2 central tail feathers (Holohil BD-2G; 1.78–1.85 g). We never observed adverse effects of this tagging method. After locating the nest with help of the radio-tags, we banded all nestlings in successful nests approximately 1–2 weeks before fledging ($n = 264$ broods) or directly after fledging ($n = 27$ broods). In groups where we were unable to locate the nest, we determined breeding success in autumn by checking the presence of retained juveniles ($N = 66$ broods). The reliability of this latter method is substantiated because successful reproduction leads in the majority of cases to the presence of retained offspring in autumn (279 out of 291 successful broods where breeding success was confirmed before dispersal, excluding all cases where one breeder disappeared during summer and all offspring thus dispersed, see Ekman and Griesser [2002]). The relatedness of juvenile members ($N = 44$ individuals) in these groups was determined by assessing aggressive interaction between breeders and group members on feeders. This method is a reliable cue to assess relatedness of juvenile group members when compared among individuals of known origin (Ekman et al. 1994; Griesser 2003).

To assess group composition, we visited all territories regularly throughout the breeding season (March–May) and at least 3 times during autumn (September–October). All new group members were color banded and could be aged from the shape of the outermost rectrices, which are more rounded in juveniles than in adults. Because Siberian jays are sexually monomorphic, we took blood samples (50–100 μL of blood collected from the alar vein) from all individuals for molecular sex determination using the method described in Griffiths et al. (1998). The capture of birds for banding, bleeding, and radio-tagging as well as the breeder removal experiment were performed under the license of the responsible ethics board (Umeå djurförsöksetiska nämnd).

Behavioral interactions between resident individuals and dispersers

We studied the behavioral interactions between resident individuals and dispersers in 21 groups during the juvenile dispersal period (mid June to end of July) in 2000 and 2003. We attached a radio-tag to at least one juvenile group member to be able to track the group. We followed groups for 30 min (11.0 ± 0.95 observation bouts per group). The bouts were randomly distributed among and within days. We judged the level of antagonism of interactions between residents and dispersers using the following definitions.

Level 1 (=no aggression): other individual was allowed to be close.

Level 2 (=displacement): other individual was approached and forced to move from its perch.

Level 3 (=aggressive encounter): individual was chased while the persecutor uttered “cha cha” calls that are only uttered during aggressive encounters.

We assessed the maximum level of aggression observed during each observation bout for breeders and retained offspring, pooling the response of all breeders and retained offspring within the same group. All juvenile dispersers were unbanded and could be distinguished from resident individuals that were all color banded. To test whether aggression was specifically directed toward dispersers or if resident

individuals were aggressive toward other juveniles independent of their dispersal status, we also recorded the level of antagonistic behavior in all interactions with resident juveniles of neighboring groups. We used a generalized linear mixed model (GLIMMIX module in SAS 9.1; SAS institute, Cary, NC) to investigate the effect of social rank (resident juveniles, older residents) and disperser status (disperser, neighbor juvenile) on the level of aggression during encounters. Territory identity and year were fitted as random terms to control for the effect of repeated observations in the same groups and years. All statistical models were constructed by entering the variables of interest one by one and subsequently dropping all terms that did not influence the explanatory power of the model (a priori $\alpha = 0.05$). The effect of nonsignificant terms was estimated by adding them individually to the model.

Settlement decisions

We use data collected between 1990 and 2004 to analyze settlement decisions of dispersers. To test if dispersers were able to occupy breeding openings, we reanalyzed data collected from a breeder removal experiment where we investigated the effect of breeder removal on the dispersal decisions of retained offspring (Ekman and Griesser 2002). We experimentally created 7 openings by removing male breeders during the dispersal period from their territory in 2000. We removed only male breeders because they are social dominant group members and to control for sex effects. Male breeders were caught either with walk-in traps or mist nets. After capture, the individuals were transported 20–50 km away from the study site and released in prime habitat.

To test for the effect of social environment and habitat quality on settlement decisions of dispersers, we analyzed data collected between 1998 and 2003 from 48 territories (205 group years, mean \pm SE = 4.1 ± 0.19 years per territory). Breeders were classified according to their dispersal status earlier on in life: breeders that were socially dominant as juveniles and remained on their natal territories or breeders that were subordinate brood members that were evicted from their natal territory and had become immigrant group members in other territories. Breeders that delayed dispersal were expected to be more efficient in keeping immigrants off their territory because they had expelled their subordinate brood members earlier on in life. Habitat quality was assessed using the proportion of area within a territory that consisted of unmanaged forest. The proportion of unmanaged habitat on a territory strongly affects first winter survival of immigrants (Griesser et al. 2006; see Griesser et al. 2006 for sampling protocol). Because dispersal to occupy a breeding opening is only local (Kokko and Ekman 2002), we also calculated a “patch” habitat quality (average proportion of unmanaged forest of the focal territory and all neighboring territories). We used a general linear mixed model (GLMM) (Poisson error distribution, logarithm link) of the Genstat 8.2 statistical package (VSN International Ltd, Herts, UK) to assess the effect of the number of retained juveniles, older retained offspring, older immigrants, breeder phenotype, habitat quality, and patch quality on the number of immigrants that settled on a territory. We included year and territory as the random variable in this model. We analyzed the effect of the sex of resident juveniles on settlement decisions of dispersers with chi-square tests.

Consequences of dispersal and settlement decisions

To investigate the cost of dispersal, we compared the mortality rates of radio-tagged dispersers with radio-tagged resident juveniles (retained juveniles and immigrants) during the same

period (between mid-June and mid-August). Mortality rates between dispersers, retained offspring, and immigrants were compared using a GLMM in Genstat (binary error distribution, logit link) to assess the effect of individual category on mortality. In addition to year, we included individual identity as a random factor in this model because some individuals were observed both as dispersers and as immigrants.

The costs of immigrants to breeders were assessed by analyzing the effect that immigrants had on the breeding success and nestling growth. Breeders are hostile toward immigrants and regularly displace or chase them, especially when immigrants try to approach the nest during the breeding season (Ekman et al. 1994). An increased investment in aggression could reduce the time available for parental care and hence cause a reduction of nestling growth or breeding success (Eggers 2002). We analyzed the effect of the number of immigrants on a territory on the weight of nestlings using a stepwise forward structured general linear model (normal error distribution, identity link). Tarsus length and time of the day were entered into the model before entering the number of immigrants. We also included habitat quality and the number of retained offspring in the model. Territory and year were included as random factors to control for repeated measurements of the same brood. We used nestlings measurements collected between 1998 and 2003 for this analysis ($N = 942$ measurements from 320 individuals; N territories = 44). With a similar model (GLMM in Genstat; Poisson error distribution, logarithm link), we estimated the effect of the number of immigrants on the number of fledglings produced on a territory.

RESULTS

Behavioral interactions between resident individuals and dispersers

Retained juveniles were hostile toward dispersers and directly approached dispersers passing through their territory ($N = 17$ encounters; Table 2, Figure 1). During 16 of these encounters, retained juveniles chased the disperser for an average of 15.1 ± 2.04 min, whereas during one encounter, the disperser was only displaced. All encounters resulted in the dispersers leaving the territory and continuing dispersal. Older group members (retained offspring, immigrants, breeders) were less aggressive, and their response depended on the presence of retained juveniles (Table 2). In groups without retained juveniles ($N = 2$), older group members approached and displaced dispersers, whereas in the 11 groups with retained juveniles, older group members did not approach the dispersers (Figure 1; Fisher's Exact test: $P = 0.01$). The aggressive behavior of residents was specifically directed toward dispersers and not just a general response toward juveniles. Residents never displaced or chased resident juveniles of neighboring groups (Table 2; Figure 1).

Settlement decisions

Despite that unoccupied territories were frequently available (Table 1), no disperser settled in an empty territory. Instead, all dispersers immigrated into existing groups and remained in the groups where they initially settled. Only 7 dispersers (4.2%) directly occupied a breeding opening, whereas the remaining 159 dispersers settled as a subordinate group member to queue for a breeding opening (Table 1). We tested experimentally whether this low rate of direct occupation of breeding openings was a result of a difference in competitive abilities between dispersers and resident individuals. On re-

Table 2

GLMMIX showing the effect of encounter type (disperser, neighboring juveniles) and rank (retained offspring, older group members) on aggression level (GLMMIX module in SAS 9.1; Poisson error distribution)

Independent variable	Degrees of freedom	Denominator degrees of freedom	χ^2	Estimate	P value
Encounter type	1	31	8.65	0.78	0.006
Rank	1	31	8.54	-0.67	0.006
Constant	1	17		0.24	

Territory identity and year were included as random variable in model to control multiple observations in same group.

moval of male breeders during the dispersal period ($N = 7$), only one out of 14 male dispersers that immigrated during the same time period managed to occupy an experimental breeding opening. The remaining 6 openings were instead occupied by all the 6 older males in the study population that were unpaired during the removal period (older male non-breeders: $N = 4$, widowed male breeders: $N = 2$) (Fisher's Exact test: $P = 0.0002$).

When examining individual settlement decisions, the only factor affecting the number of dispersers settling on a territory was the number of retained juveniles on a territory (Table 3). Dispersers generally settled on territories without retained juveniles (100 out of 115 immigrants; Figure 2). Only 13 immigrants settled on a territory with one retained juvenile, whereas just 2 immigrants settled in a group with 2 retained juveniles. No other factor (habitat quality, breeder phenotype, number of older group members) affected settlement decisions.

Although immigrants avoided settling on a territory where retained juveniles were present, 67 immigrants settled together with other immigrants on a territory. Immigrants settled preferable in groups with short queues avoiding groups where same-sex juveniles were present. In groups containing 2 juveniles, only 5 individuals settled in a group where a same-sex juvenile was present ($\chi^2 = 5.78$, $P = 0.016$). In groups that contained 3 juveniles, groups never contained 3 juveniles of the same sex ($N = 9$; $\chi^2 = 6.5$, $P = 0.01$).

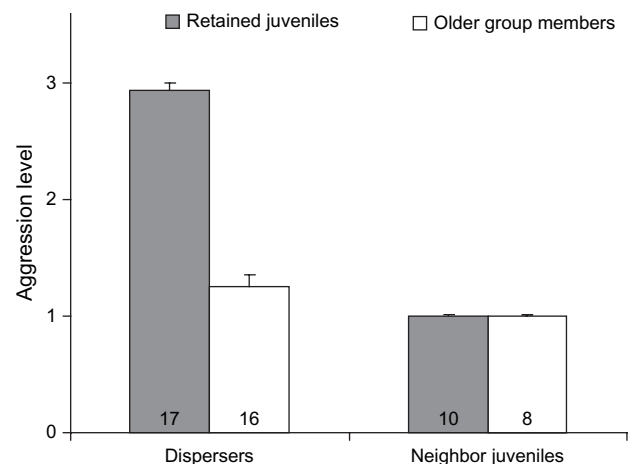


Figure 1

Reaction of retained juveniles and older group members toward dispersers and neighboring juveniles (mean \pm SE). Reaction is ranked according to increasing aggressiveness (1 = individual tolerate to be close, 2 = individual displaced, 3 = individual chased). The number of observations for each group is shown in the bottom of the bars.

Table 3
GLMM of the factors associated with the number of juvenile immigrants on a territory

Model term	Wald χ^2	Degrees of freedom	Effect	SE	<i>P</i> value
Ret	30.03	1	-1.37	0.23	>0.0001
Male origin	4.03	2	-0.85	0.35 (imm > ret)	0.09
Female origin	3.09	2	0.46	0.26 (ret > imm)	0.23
No. of adult immigrant offspring	2.57	1	-0.37	0.23	0.14
No. of adult retained offspring	0.96	1	-0.38	0.39	0.31
Proportion unmanaged forest	0.03	1	-0.04	0.26	0.87
Patch quality	0.02	1	0.13	0.28	0.65
Constant			-0.34	0.26	

Effects indicate direction of relationship and are presented after setting the mean of the covariate to zero. ret, retained juveniles; imm, immigrants.

Consequences of dispersal and settlement decisions

Cost to dispersers

None of the radio-tagged dispersers was killed during dispersal ($N = 13$), and predators only rarely killed radio-tagged retained juveniles ($N = 2$ out of 25) or immigrants ($N = 1$ out of 15) during their first summer of life. Thus, dispersers, immigrants, and retained juveniles did not differ in their mortality (GLMM, binomial error distribution, logit link: dispersal status: Wald = 0.02, $P = 0.99$).

Cost to breeders

The presence of immigrants during the breeding season (March–May) had a negative effect on nestling weight. Nestlings in groups with immigrants had a significantly lower weight than nestlings in groups without immigrants when controlling for tarsus length (Table 4). Neither the number of retained offspring present during reproduction nor habitat quality affected nestling condition. However, the number of immigrants did not affect the number of fledglings produced on a territory (GLMM, Poisson error distribution, logarithm link: number of immigrants: Wald = 0.28, $P = 0.60$; controlling for territory identity and year).

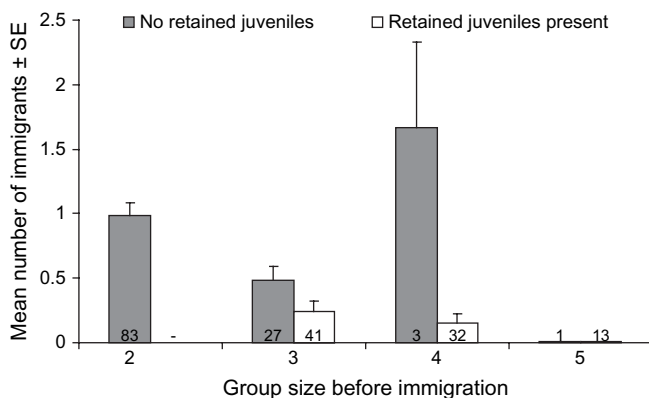


Figure 2
 Number of dispersers (mean \pm SE) that settled in groups with retained juveniles and without retained juveniles. By definition, groups of only 2 group members never contained any retained juveniles. No dispersers settled in groups of 5 individuals. Data from years 1998–2003 ($N = 48$ groups). The number of observations for each group is shown in the bottom of the bars.

DISCUSSION

The assumption that behavioral interactions between dispersers and residents largely determine dispersal and settlement decisions is reasonably well established in the literature on dispersal (Krebs 1978; Rosenberry et al. 2001; Stamps 2001). However, this process has remained poorly investigated (Clobert et al. 2001; Bullock et al. 2002; Doerr and Doerr 2005), and hence, our study is one of the first to empirically demonstrate that interactions between dispersers and residents indeed limit both dispersal and settlement options of dispersing juveniles. We found that retained Siberian jay juveniles aggressively approached all dispersers and chased them off their territory, thereby preventing dispersers from settling and forcing them to move on. As a consequence of this aggression toward dispersers, immigrants settled mainly in groups where reproduction had previously failed and hence where no retained juveniles were present. Aggression of residents toward dispersers could be a widespread behavior and has been suggested to prevent dispersers from settlement in other species (Holekamp and Smale 1998; Nunes et al. 1998). Moreover, dispersal and settlement decisions in Siberian jays affect fitness of both dispersers (inability to choose high-quality patches, high winter mortality; Ekman et al. 1999, 2001; Griesser et al. 2006) and breeders (reduced offspring condition; Table 4).

Dispersal decisions

In the Siberian jay and its North American congener species, the gray jay *Perisoreus canadensis* (Strickland 1991), natal juvenile dispersal is a consequence of sibling rivalry within broods reflecting social dominance after fledging (Ekman et al. 2002). The individuals that evict subordinate brood members from the natal territory are the same individuals that evict dispersers from their territory. This is similar to the behavioral mechanism of group eviction in anemonefish and coral-dwelling goby *Paragobiodon xanthosomus* where aggression is primarily directed from a more dominant individual toward its immediate subordinate (Fricke and Fricke 1977; Wong et al. 2007). The lowest ranking group members are thus in these systems in control of settlement decisions (Buston 2003b; Wong et al. 2007). In contrast, in many other group-living species, breeders are in control of subordinate group membership (green jay *Cyanocorax yncas*: Gayou 1986; primates: Pusey and Packer 1987; superb fairy-wren *Malurus cyaneus*: Mulder 1995; daffodil cichlid: Heg et al. 2004). Most models on dispersal consider only the later case where breeders determine group membership of nonbreeding group members (Clobert et al. 2001), hampering the generality of these models.

Table 4
GLMM of the factors associated with nestling weight

Model term	Wald χ^2	Degrees of freedom	Effect	SE	P value
Tarsus	11 365	1	2.59	0.02	>0.0001
Time of day measurement taken	4.24	1	0.08	0.04	0.04
Number of immigrants in group	4.07	1	-1.12	0.59	0.04
Proportion unmanaged forest on territory	0.94	1	0.97	1.00	0.33
Number of retained offspring	0.01	1	0.06	0.86	0.09
Constant			64.24	0.37	

Settlement decisions

All dispersers in Siberian jays settled on existing territories, despite that empty territories were available in most years. Further studies are needed to determine whether this is an effect of dispersers using conspecific attraction as a cue to recognize appropriate habitat (Stamps 1988) or whether benefits of group living outweigh settlement in an empty territory. The settlement patterns of Siberian jays have drastic consequences for the population dynamic of this species. In contrast to the long distances juvenile dispersers move (Ekman et al. 2002), retained offspring and immigrants only move among neighboring territories to occupy a breeding opening (Kokko and Ekman 2002). Reoccupation of isolated unoccupied large areas of suitable habitat will therefore take a long time. This may have a negative effect on future population size because modern forestry often results in serious fragmentation to the landscape (Hansson 1992) and jays abandon intensively managed areas (Griesser et al. 2007).

Queue length has been demonstrated to be a poor predictor of settlement decisions across species. Whereas dispersing superb fairy-wrens settle preferably on territories with long queues (Cockburn et al. 2003), dispersers in other social species settle rather in groups with short queues (Tasman native hen *Gallinula mortierii*: Goldizen et al. 2002; brown treecreeper *Climacteris picumnus*, white-throated treecreeper *Cormobates leucophaea*: Doerr and Doerr 2006; stripe-backed wren *Campylorhynchus nuchalis*: Zack and Rabenold 1989; Siberian jays: our study). In our study, not only queue length and in particular the presence of retained juveniles but also disperser sex affected settlement decisions. Immigration of same-sex dispersers is costly for retained juveniles because they directly compete over access to future breeding openings. Not surprisingly, we observed few jay groups containing 2 same-sex juveniles. The breeder removal experiment demonstrated that in Siberian jays dispersers and retained juveniles cannot compete with older individuals (retained offspring, immigrants, widowed breeders) over breeding openings. This may explain why the number of older retained offspring and immigrants in a group had no influence on the number of immigrants settling in a territory. Queues in Siberian jay seem thus to be stable, which stands in agreement with many empirical and theoretical studies that report or predict stable queues (Kokko and Johnstone 1999; Buston 2004; but see Kokko and Ekman 2002).

Consequences of dispersal and settlement decisions

Dispersing jays did not have a higher mortality rate compared with same-aged residents during the dispersal period. Despite the importance of dispersal costs for dispersal models (Clobert et al. 2001) and the fact that most models of dispersal are based on the assumption that dispersal increases mortality,

the direct costs of dispersal are rather poorly investigated. The few existing empirical studies assessing mortality of dispersers report either a higher mortality risk for dispersers than non-disperser (Johnson and Gaines 1990; Bélichon et al. 1996; Yoder et al. 2004) or no difference in mortality (Hines 1986; Schieck and Hannon 1989; Beaudette and Keppie 1992; Small et al. 1993). Increased mortality of dispersers may result from moving through unfamiliar space (Greenwood and Harvey 1982, Yoder et al. 2004) or due to increased predator encounter rates because of higher activity rates (Götmark and Post 1996; Lima 1998). In our study, immigrants ended up queuing for breeding openings in low-quality territories where prior reproduction had failed because of the despotic behavior of retained juveniles. This suggests that social constraints confine dispersers to settle on low-quality territories, affecting their future fitness (Ekman et al. 1999, 2001).

Breeders are dominant over immigrant group members, and thus, the initial costs of letting a disperser settle on their territory are low (Ekman and Sklepkovych 1994). Because immigrants are always unrelated to the breeders, opposite-sex immigrants can immediately replace dead partners (Ekman and Griesser 2002), and breeders are only aggressive toward same-sex immigrants but tolerant toward opposite-sex immigrants (Ekman and Sklepkovych 1994). However, immigrants still induce some cost to the breeders through increased levels of aggression during the breeding season (Ekman et al. 1994; Eggers 2002), which reduces nestling condition. Suboptimal growth during the nestling period reduces first winter survival (Griesser et al. 2006) and the possibility of acquiring a breeding opening later on in life (Eggers 2002; Eggers et al. 2005). The presence of immigrants thus poses also a small fitness cost to retained offspring through lowering the fitness of their siblings.

Conclusions

Recent research has identified different proximate mechanisms influencing dispersal distance ranging from morphological traits, physiological traits (Nunes et al. 1998; Clobert et al. 2001), to behavioral traits and personalities (Dingemans et al. 2004). Many of these traits are heritable (Roff and Fairbairn 2001), and single alleles have been linked to dispersal rates of individuals (Haag et al. 2005). However, we still lack knowledge about the behavioral decisions leading to a specific dispersal path of an individual (Macdonald and Johnson 2001; Doerr and Doerr 2005). Our results demonstrate the importance of social interactions between residents and dispersers on both the dispersal process and settlement decisions. Given that group living is widespread in vertebrates, an understanding of social interactions on dispersal decisions will be important to link the proximate, behavioral decisions with the ultimate, evolutionary consequences of dispersal to

bring us a step closer to a comprehensive dispersal framework that links theory with empirical data.

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