

Delayed Dispersal as a Route to Breeding: Territorial Inheritance, Safe Havens, and Ecological Constraints

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Submitted May 2, 2001; Accepted February 25, 2002

ABSTRACT: The relative roles of ecological constraints, the benefits of philopatry, and the role of life history continue to be debated in the evolution of natal philopatry and cooperative breeding. We compare three routes to breeding: departing to search for territories as a floater, staying and queuing to inherit the natal territory, or queuing and eventually shifting to a neighboring vacancy. Our model assumed a dominance-structured population. It quantifies the benefits of philopatry for varying-rank subordinates and contrasts it against the benefit of dispersal. We apply the model to data on Siberian jay *Perisoreus infaustus*, a species in which retained offspring do not help at the nest. The results indicate that territorial inheritance plays a small role in this species (presumably due to inbreeding avoidance), and territory acquisition is less constrained for dispersing than philopatric offspring. Nevertheless, small family groups—one or, at the most, two same-sex queuers—are predicted to form because philopatric offspring gain nepotistic benefits that improve their survival. This fits with data on group sizes and supports the idea of the natal territory as a safe haven for waiting for breeding opportunities. We also discuss our predictions in the light of ecological constraints and clarify recent confusingly different predictions on the role of habitat saturation as an explanation for delayed dispersal and cooperative breeding. We argue that “ecological constraint” is too wide a term to yield useful predictive power and that it is more appropriate to examine the consequences of specific life-history traits on the success of dispersers.

Keywords: dispersal, benefits of philopatry, ecological constraints, cooperative breeding, competition for breeding, queuing.

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Cooperative breeding has provoked questions about how the maintenance of such a behavior can be reconciled with natural selection. One key issue is to explain postponing dispersal to breed on one's own, since staying in a group often entails that subordinates forego personal reproduction (Wiley and Rabenold 1984; Koenig et al. 1992). This cost on direct fitness has to be overcome by some advantage of staying at home (benefit of philopatry) if delayed dispersal is to be explained. Some authors emphasize that the cost on direct fitness is small if personal reproduction after dispersing would have been unlikely, which happens if habitats are saturated and gaining a breeding position elsewhere is, therefore, difficult (the “ecological constraint” hypothesis; Selander 1964; Brown 1969; Emlen 1982*a*, 1995). Others put more emphasis on the benefits that natal philopatry can bring about (Stacey and Ligon 1987, 1991; Zack and Stutchbury 1992) or on life-history traits, such as longevity, that predispose species to become cooperative (Arnold and Owens 1998; Hatchwell and Komdeur 2000). Often, nonreproductive subordinates gain indirect fitness through helping (Emlen and Wrege 1989; Mumme et al. 1989; Koenig et al. 1992; Mumme 1992; Cockburn 1998), but in some species, delayed dispersal occurs without offspring helping their parents (Gayou 1986; Veltman 1989; Ekman et al. 1994; Green and Cockburn 2001). This suggests that direct benefits can suffice to explain delayed dispersal and serves as a useful reminder that the decision to help does not automatically follow from the decision to stay (Emlen 1982*a*, 1982*b*; Brown 1987; Kokko et al. 2001).

A variety of direct benefits can favor philopatry: subordinates may breed (females) or gain paternity (males) despite the presence of a dominant (Arnold 1990; Brown and Brown 1990; Rabenold et al. 1990; Jennions and Macdonald 1994; Sherman et al. 1995; Laranzo-Perea et al. 2000), they may eventually inherit the dominant position within the group (territorial inheritance; Woolfenden and

Fitzpatrick 1978; Zack and Stutchbury 1992; Russell and Rowley 1993; Ragsdale 1999; Queller et al. 2000), or they may gain a breeding position elsewhere after having spent time in the group (Walters et al. 1988; Zack 1990; Zack and Stutchbury 1992; Russell and Rowley 1993; Green and Cockburn 2001). These advantages may co-occur with a "safe haven" mechanism, by which we mean improved survival of offspring in the natal territory (Ekman et al. 2000). If individuals have to wait for breeding positions, survival during the waiting period becomes an important predictor of fitness (Faaborg and Bednarz 1990; Ekman et al. 2000; Green and Cockburn 2001).

Naturally, to explain delayed dispersal, both costs and benefits of delaying have to be considered (Koenig et al. 1992). Despite the general agreement that philopatric advantages must be weighed against the profitability of dispersal, formal comparisons of fitness benefits have been lacking for a long time (Wiley and Rabenold [1984] provide an exception). A probable reason is that benefits of philopatry are often delayed, and a potentially complicated dynamic approach is needed to calculate fitness (Lucas et al. 1997), although, in a conceptual approach, the benefits can also be summarized as a single benefit variable (Ragsdale 1999). Recent models have made progress in this respect: they derive fitness benefits of being n th in a queue for breeding positions (Field et al. 1999) or compare the advantages of staying in a queue with either a fixed payoff from dispersing (Kokko and Johnstone 1999) or, more properly, a payoff that depends on how the population as a whole occupies territories (Kokko and Sutherland 1998; Pen and Weissing 2000; Kokko and Lundberg 2001). However, these models assume either that there is only one queuer to inherit the territory or that queuing is strict, and so the only way in which a low-ranking individual can gain fitness is through waiting until all predecessors in the hierarchy have died (see Monnin and Ratnieks 1999 for an exception in a slightly different context where the alternative to queuing is helping). Another simplifying assumption of the earlier models is that territory inheritance is guaranteed to be successful: floaters or neighbors never compete with queuers over a vacancy.

In reality, in many species a vacancy created by the death of a dominant breeder can be filled by individuals from nearby territories (e.g., Mumme and de Queiroz 1985; Zack and Rabenold 1989; Zahavi 1990). The individual who wins the vacancy is not always the one who has been queuing for the longest (Russell and Rowley 1993; Laranzo-Perea et al. 2000), although queuing often appears relatively strict (Wiley and Rabenold 1984; Creel and Waser 1994; Field et al. 1999; East and Hofer 2001). Also, breeding positions may be occupied by floaters, that is, dispersers who have left their natal territories (Zack and Stutchbury 1992). These alternative routes to breeding can

be more important than territorial inheritance, especially if incest avoidance frequently prevents territory inheritance (Koenig et al. 1998).

Here we build a general model of different routes to breeding and show under which conditions queuing at home (philopatry) is favored. Our aim is threefold. First, we define the fitness benefit of dispersing in a way that allows direct comparisons to the benefit of philopatry at a specific rank position. The model is used to obtain interspecific predictions on characteristics that promote delayed dispersal. Second, we apply the model to data on Siberian jays *Perisoreus infaustus*, a species in which delayed dispersal occurs without helping (Ekman et al. 1994), to judge if the model can predict group sizes in a specific case. Finally, we use our model to make conceptual arguments about the ecological constraint hypothesis; here we also compare and clarify predictions from recent models that make use of constraints.

In our model, we consider the following routes to becoming a breeder. An individual may leave the natal territory and become a floater who competes for territories elsewhere. We assume that a floater is not able to observe an arbitrarily large area but is restricted to a specific part of the population (Zack and Stutchbury 1992). The individual may also stay as a philopatric subordinate in its natal territory, from where it may eventually inherit the territory, or it may seize a breeding opportunity in nearby territories. We call this latter process "shifting." While the philopatric individual probably observes a smaller number of potential vacancies than a floater, it may survive substantially better. Higher survival in the natal territory may be a result of parental nepotism (Ligon 1981; Brown and Brown 1984; Ekman and Rosander 1992; Ekman et al. 1994), but it can also occur simply because it is advantageous to live in a familiar environment and have access to resources within the territory. The benefits of philopatry therefore include using the natal territory as a safe haven from which to vie for local breeding opportunities.

The Model

When should an individual disperse? A disperser potentially gains both direct and indirect fitness. Dispersal influences direct fitness whenever it influences the chances to obtain a breeding position. Indirect fitness may also increase, since the absence of the dispersing individual may improve the fitness of relatives who remain in the group, for example, through reduced competition for local resources (Hamilton and May 1977). Here we concentrate on the direct fitness of the disperser for two reasons: it is conceptually useful to examine how dispersal would evolve if one process operated in isolation from the others (Perrin and Mazalov 2000), and relatedness has two opposing ef-

fects on dispersal. While other group members may benefit from the absence of a relative because of reduced local competition for resources (Hamilton and May 1977), they may also experience negative fitness consequences if a group member leaves (Courchamp et al. 1999). This is because the member could have given alloparental care or aided group performance passively, for example, through a dilution of predation risk (Emlen 1997; Kokko et al. 2001). Given that fitness of other group members may either increase or decrease in the absence of the focal individual, we examine the “baseline” benefits of philopatry in the absence of inclusive fitness effects.

We assume a temporally stable population where reproduction produces a surplus of potential breeders compared with the number of breeding sites. The population is dominance structured. Individuals can exist in one of three states: as breeders (the dominant individual on a territory), as floaters who have left the natal territory, and as subordinates of varying rank who form a linear queue. Floating and queuing correspond to the “depart-and-search” and “stay-and-foray” tactics of Brown (1987). Breeding vacancies occur when the dominant breeder dies or is evicted in a takeover. The first-ranking subordinate has rank 1, and lower ranks are marked with an increasing index of $n = 2, 3, \dots$. The mortality of breeders and floaters is μ_b and μ_f , respectively; μ_b also includes the rate of takeovers if these lead to the eviction of the previous dominant. The first-ranking subordinate’s mortality is μ_s . The mortality of subordinates may depend on rank: mortality of the n th-ranking subordinate is $\delta_n \mu_s$, that is, by a factor $\delta_n \geq 1$ higher than the first-ranking subordinate’s mortality μ_s . We define $\delta_1 = 1$ and assume that the δ_n forms a nondecreasing function of n (survival does not improve as rank gets lower). If $\delta_n = 1$ for all n , mortality does not depend on rank.

We use a continuous-time model, which is suitable for many cooperative breeders in which breeding vacancies can be occupied at any time of the year. Also, we assume no senescence, which is an appropriate approximation especially for birds (Ricklefs 2000) and eusocial insects (Field et al. 1999) but also serves as a first step of analysis in other cooperative breeders. This assumption greatly simplifies fitness calculations: with no senescence, the expected life span as a breeder does not depend on the age at which this position was achieved. Also, we do not explicitly consider the effects of helping behavior in groups, as we wish to determine under which conditions territory acquisition can favor natal philopatry on its own. Therefore, an individual’s direct fitness only depends on the probability that it ever obtains a breeding position. This means that we use lifetime reproductive success as our fitness measure. This is a valid fitness measure in a temporally stable population regulated by offspring recruitment probabilities

(Mylius and Diekmann 1995). In our model, recruitment will be regulated through a measure of habitat saturation, H (sensu Kokko and Lundberg 2001).

We denote by $p_{F \rightarrow B}$ the probability that a floater ever obtains a territory in its lifetime. Likewise, $p_{S1 \rightarrow B}$ is the probability that a first-ranking subordinate ever obtains a territory. Lower-ranking subordinates acquire territories with probabilities $p_{Sn \rightarrow B} = q_n p_{S1 \rightarrow B}$, where the queuing factor q_n defines the success of a subordinate of rank n in the queue, compared with a first-ranking one. Under our direct fitness approach, an individual should disperse rather than accept a position as an n th-ranking subordinate if

$$p_{F \rightarrow B} > p_{S1 \rightarrow B} q_n. \quad (1)$$

Below, we derive expressions for $p_{F \rightarrow B}$, $p_{S1 \rightarrow B}$, and q_n in order to study the conditions under which delayed dispersal is expected to evolve.

Routes to Breeding

A vacancy can be occupied by a philopatric subordinate from within the same territory, by a queuing subordinate from a different nearby territory, or by a floater. Individuals are not equally good competitors for all vacancies, and we therefore introduce state-dependent “propensities” that define the relative ability of an individual to gain access to a vacancy. To set a scale, we give the arbitrary value 1 to the propensity of a first-ranking subordinate to shift to a vacancy in a neighboring territory.

The state of an individual affects its propensity to acquire a territory in three ways. First, incest avoidance may prevent philopatric individuals from occupying the natal territory (Koenig et al. 1998). Therefore, we define their propensity as α when they are competing for a vacancy in the natal territory. If incest avoidance frequently prevents breeding in the natal territory, we have $\alpha < 1$ (i.e., it is easier to gain a breeding position in a nearby territory than the natal one). The case $\alpha > 1$ describes species in which incest avoidance is not a problem and individuals instead have preferential access to the natal territory, compared with outsiders.

Second, individuals may differ in their competitive abilities. Floaters may be less competitive than queuing subordinates since they might know a given area less well (Zack and Stutchbury 1992). The relative propensity of floaters equals β , and we may typically expect that $\beta < 1$. However, $\beta > 1$ is possible if floaters can spend more time inspecting territories than philopatric subordinates who are constrained by group activities such as helping, or if subordinates are constrained by incest avoidance not only in their natal territory but also in nearby territories.

Finally, low-ranking subordinates may be disadvantaged in the queuing hierarchy, so that their propensity to acquire any breeding position is lower than that of higher-ranking individuals. The queuing factor q_n depends on the mortality of low-ranking subordinates (q_n increases if they survive well) but also on their competitive ability while alive (q_n increases if subordinates can “jump the queue”). We model the latter using a parameter γ : the propensity of the n th subordinate is a fraction γ of the propensity of its predecessor in the hierarchy. This means that a subordinate of rank n has the propensity $\alpha\gamma^{n-1}$ to inherit the territory if a vacancy arises. If $\gamma = 0$, the queue is strictly hierarchical, and territory acquisition can only follow if all predecessors in the queue have died (as in many previous queuing models, e.g., Kokko and Sutherland 1998; Field et al. 1999). If $\gamma = 1$, territory acquisition is random with respect to a subordinate’s rank. Values between 0 and 1 describe incomplete queue discipline, when low-ranking subordinates can sometimes acquire territories ahead of their predecessors.

While floaters may be disadvantaged in their propensity β , they may enjoy the advantage of being able to sample a larger number of territories. The number of territories in the “neighborhood observation range” (or “assessment sphere” sensu Zack 1990) is denoted by T_F . The observation range of subordinates is T_S territories; that is, subordinates are aware of breeding vacancies on T_S neighboring territories, in addition to their own.

Dispersal versus Philopatry

The probability that a floater obtains a territory before dying is calculated as follows. The floater can observe T_F territories and, hence, finds vacancies at a rate $\mu_B T_F$. The probability of acquiring a breeding position at an open vacancy is β/H , where H describes the strength of competition for each vacancy in the population (the habitat saturation factor sensu Kokko and Lundberg 2001). The value of H is the effective number of competitors per vacancy, that is, the sum of propensities of each individual that competes for a single vacancy. The floater therefore acquires a territory and starts to breed at a rate $\mu_B T_F \beta/H$. The rate at which it dies is μ_F .

When two possible transitions “compete” for the individual with rates A and B, the probability that A occurs before B equals $A/(A + B)$. For floaters, the probability that the transition to breeding status occurs before death therefore equals

$$P_{F \rightarrow B} = \frac{\mu_B T_F \beta/H}{\mu_B T_F \beta/H + \mu_F}. \quad (2)$$

The probability that a first-ranking subordinate obtains a

breeding position before dying is calculated likewise. The rate of acquiring the natal territory is $\mu_B \alpha/H$, and the rate of shifting to nearby territories is $\mu_B T_S/H$. Thus, territory acquisition occurs before death with probability

$$P_{S1 \rightarrow B} = \frac{\mu_B(\alpha + T_S)/H}{\mu_B(\alpha + T_S)/H + \mu_S}. \quad (3)$$

For lower-ranking subordinates, the probability of obtaining a breeding position is more complicated. The probability that a rank 2 subordinate accedes to rank 1 is determined by four competing rates. The previous first-ranking subordinate may obtain a breeding position (rate $\mu_B(\alpha + T_S)/H$) or may die (rate μ_S), and two other transitions do not lead to rank 1: the focal second-ranking subordinate may obtain a breeding position directly (rate $\mu_B[\alpha + T_S]\gamma/H$) or may die (rate $\delta_2 \mu_S$):

$$P_{S2 \rightarrow S1} = \frac{\mu_B(\alpha + T_S)/H + \mu_S}{\mu_B(\alpha + T_S)/H + \mu_S + \mu_B(\alpha + T_S)\gamma/H + \delta_2 \mu_S}. \quad (4)$$

The probability of becoming a breeder directly from a second-ranking queuing position is

$$P_{S2 \rightarrow B} = \frac{\mu_B(\alpha + T_S)\gamma/H}{\mu_B(\alpha + T_S)/H + \mu_S + \mu_B(\alpha + T_S)\gamma/H + \delta_2 \mu_S}. \quad (5)$$

The expressions are derived similarly for further transitions $P_{S3 \rightarrow S2}$, $P_{S3 \rightarrow B}$, and so on. For example, the transition $P_{S3 \rightarrow S2}$ can occur either if the first-ranking or second-ranking subordinate becomes a breeder or if either of these dies. These compete with the rates of the third-ranking subordinate becoming a breeder directly or dying.

The first-ranking subordinate should disperse rather than stay in the queue if it is more likely to gain a breeding position by doing so:

$$P_{F \rightarrow B} > P_{S1 \rightarrow B}. \quad (6)$$

If we substitute values from equations (2) and (3) and simplify, we obtain the condition for dispersal of the first-ranking subordinate, which is independent of the habitat saturation factor H :

$$\frac{\beta T_F}{\mu_F} > \frac{\alpha + T_S}{\mu_S}. \quad (7)$$

We call the left-hand side of equation (6) the benefit of dispersal (denoted D); it is proportional to the lifetime probability of acquiring a territory when dispersing. The right-hand side is the benefit of philopatry for a subordinate of rank 1 (denoted P), which is proportional to the lifetime territory acquisition probability when staying phil-

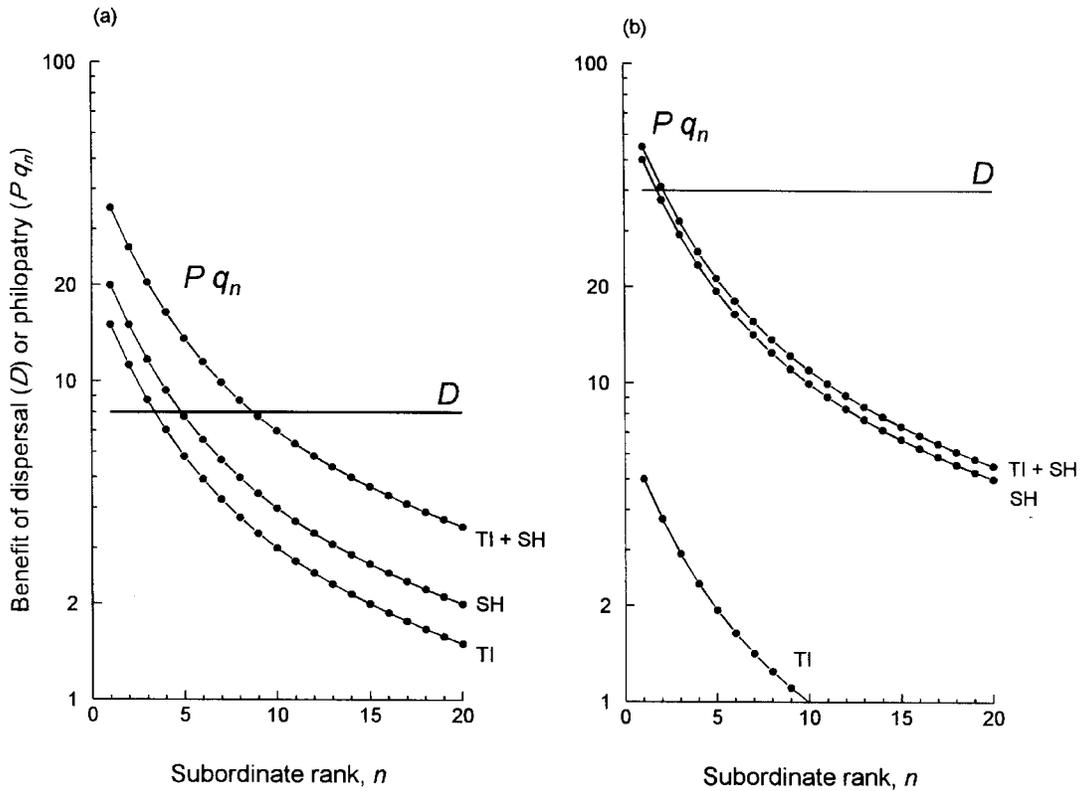


Figure 1: Examples of the benefits of dispersal and philopatry. The benefit of philopatry, Pq_n (lines with dots), can be derived assuming that philopatry pays only as a result of territorial inheritance (TI; obtained by setting $T_s = 0$) or only as a result of shifting (SH; obtained by setting $\alpha = 0$), or that philopatry yields both kinds of benefits (TI + SH). Maximum group size is the last n for which philopatric benefits Pq_n exceed the benefit of dispersal (horizontal line), $Pq_n \geq D$. In *a*, territorial inheritance can explain philopatry for up to three queuing subordinates even if it acts alone; shifting alone would produce groups with four subordinates, and they together reduce the relative benefit of dispersal to a level that makes groups of eight subordinates benefit from philopatry. This example assumes that floaters cannot prospect many more territories than can philopatric subordinates, and they suffer mortality three times as high as do philopatric individuals ($T_F = 3$, $T_S = 2$, $\mu_F = 0.3$, $\mu_S = 0.1$, $\alpha = 1.5$, $\beta = 0.8$, $\gamma = 0.5$, and $\delta_n = 1$ for all n). In *b*, the survival advantage of philopatry is smaller ($\mu_F = 0.2$, $\mu_S = 0.1$), territorial inheritance is more difficult ($\alpha = 0.5$), and floaters can observe many more territories than philopatric individuals ($T_F = 10$, $T_S = 5$); other parameters as in *a*. Now territorial inheritance alone cannot explain philopatry, but shifting enables group formation either alone (for up to one queuing subordinate) or together with territorial inheritance (for up to two subordinates).

opatric. We also call D/P the relative benefit of dispersal; when $D/P < 1$, the first-ranking subordinate benefits from staying in the group.

We next derive the condition for dispersal for lower-ranking subordinates. Assuming that the first-ranking subordinate does not disperse, the second-ranking individual should disperse rather than stay in the queue if floating gives a higher probability of territory acquisition than direct acquisition from position 2 or queuing through position 1 taken together:

$$P_{F \rightarrow B} > P_{S2 \rightarrow B} + P_{S2 \rightarrow S1} P_{S1 \rightarrow B}. \tag{8}$$

This simplifies to $D > Pq_2$, where the queuing factor $q_2 = (1 + \gamma)/(\delta_1 + \delta_2)$ and the definitions of D and P co-

incide with those in equation (7). For the third-ranking subordinate, the condition becomes $D > Pq_3$, where $q_3 = (1 + \gamma + \gamma^2)/(\delta_1 + \delta_2 + \delta_3)$. Generally, for the n th rank, equation (1) becomes equivalent to $D > Pq_n$, where $D = \beta T_F / \mu_F$, $P = (\alpha + T_S) / \mu_S$, and

$$q_n = \frac{\sum_{i=0}^{n-1} \gamma^i}{\sum_{i=1}^n \delta_i}. \tag{9}$$

Equation (9) gives the general condition under which dispersal is favored over philopatry. If the benefit of dispersal exceeds that of philopatry ($D/P > 1$), groups do not form at all, since philopatry does not pay for subordinates

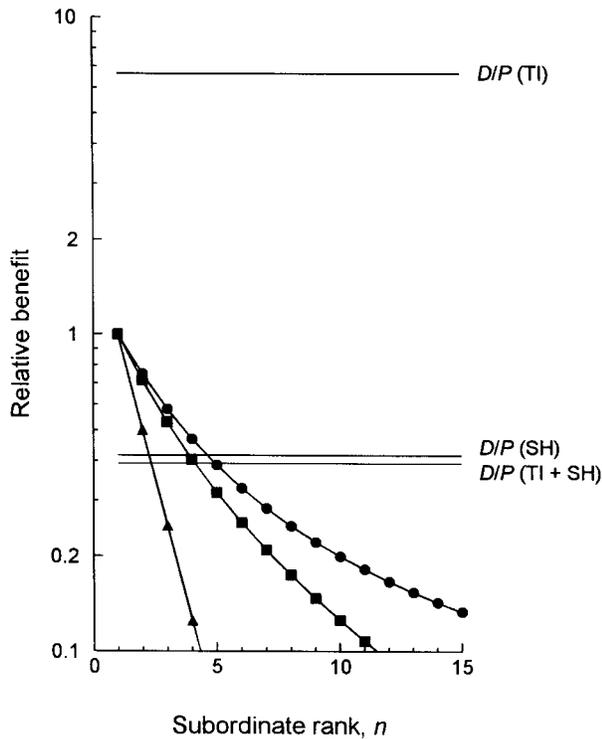


Figure 2: Groups remain smaller if low-ranking individuals have higher mortality. To enable comparison of several combinations of P and q_n , horizontal lines indicate the relative benefit of dispersal D/P (where TI, SH, and TI + SH indicate various alternatives of P as in fig. 1), and curves indicate the queuing factor (q_n) for three alternatives: no relationship between rank and mortality ($\delta_n = 1$ for all n ; dots); slow increase in mortality with lowering rank ($\delta_n = 1.1^{n-1}$; squares); and a rapid increase in mortality with lowering rank ($\delta_n = 2^{n-1}$; triangles). Philopatry pays when $D/P < q_n$. The first two alternatives for q_n predict groups with four subordinates when philopatric individuals have prospects of both territorial inheritance and shifting. The first alternative predicts four subordinates even if territorial inheritance is prevented, while a rapid increase in mortality reduces group size to only two subordinates even if territorial inheritance is possible. Other parameters: $\alpha = 0.5$, $\beta = 1$, $\gamma = 0.5$, $\mu_F = 0.3$, $\mu_S = 0.1$, $T_F = 10$, $T_S = 8$.

of any rank. The benefit of philopatry for a subordinate of rank n is Pq_n , and it decreases with rank n since we assume that $\gamma \leq 1$, and δ_n is nondecreasing. This benefit therefore determines how large groups will form, assuming that the condition $D/P < 1$ is met, which allows the evolution of philopatry in the first place. Low-ranking individuals disperse once their philopatric benefit Pq_n falls below the dispersal benefit D .

Model Results

From the equation for D (eq. [9]), we immediately see that both territorial inheritance and shifting can explain philo-

patric behavior, as parts of the safe haven mechanism. Philopatry can be favored even if philopatric individuals observe far fewer territories (T_S) than floaters (T_F). According to equation (9), any of the following factors, or their combination, can bring about this low benefit of dispersal: low competitive ability of floaters ($\beta < 1$), lower mortality of philopatric than dispersing individuals ($\mu_S > \mu_F$), or a high propensity of inheriting the territory ($\alpha > 1$). A safe haven from which to observe the T_S nearby territories, alone or together with inheritance prospects of the natal territory, can therefore favor queuing over dispersal, and the effect is stronger (D is reduced more) if both act together (fig. 1). However, if philopatric queuers do not survive better than floaters ($\mu_S = \mu_F$) and floaters are equally good competitors as queuers ($\beta = 1$), dispersers need only observe, on average, slightly more territories than philopatric subordinates for dispersal to be beneficial; under these conditions, all subordinates disperse if $T_F > \alpha + T_S$.

The number of nearby territories, T_S , can be substantially larger than the propensity to acquire the natal territory, α , especially if inbreeding avoidance makes α small. The safe haven mechanism, together with shifting, therefore has potential to explain philopatry in cases where territorial inheritance alone is too weak. In the example of figure 1b, floaters can observe many more territories than philopatric subordinates, and their mortality is not much higher. This destroys group formation ($D > P$) if territorial inheritance is the only mechanism for acquiring territories near home. However, small groups (breeder and one subordinate) can still form based on the safe haven mechanism that allows shifting to nearby vacancies, and groups with two subordinates are stable if territorial inheritance and shifting act together (fig. 1b).

Low-ranking subordinates have to wait longer and therefore risk higher mortality if they stay in the queue (encapsulated by the denominator of q_n ; eq. [9]). This reduces their benefit of philopatry compared with the first-ranking subordinate (q_n diminishes). The decrease is especially pronounced if low-ranking individuals suffer from increased mortality; stable group size decreases in this case (fig. 2). If low-ranking subordinates have a chance to gain breeding positions while queuing ($\gamma > 0$), the decrease in q_n with group size is slower. Groups will then become larger (fig. 3).

The model predicts that dispersal decisions will be affected by rank: low-ranking subordinates mainly disperse to become floaters (since their q_n is small), while individuals who disperse as a response to a nearby breeding vacancy are mainly those of high rank (since their propensity to achieve this is higher). The only exception to this occurs if $D/P < 1$, and rank influences neither mortality ($\delta_n = 1$ for all n) nor the propensity to acquire territories ($\gamma = 1$). In this case, the sums in the definition of q_n cancel

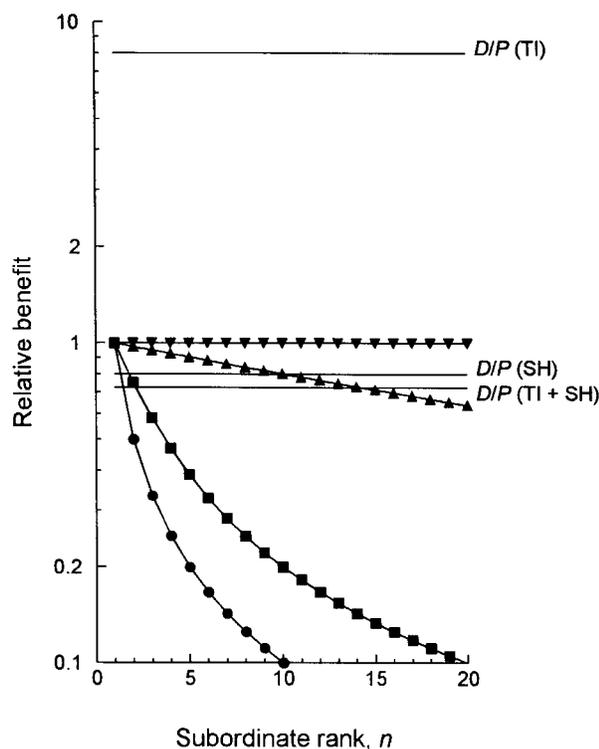


Figure 3: Stable group sizes are larger if low-ranking individuals can seize breeding vacancies directly. Horizontal lines indicate the relative benefit of dispersal D/P , as in figure 2, and curves indicate the queuing factor (q_n) for four values of $\gamma = 0$ (dots), $\gamma = 0.5$ (squares), $\gamma = 0.95$ (upward-pointing triangles), and $\gamma = 1$ (downward-pointing triangles). The higher the propensity of low-ranking individuals to obtain vacancies while queuing (high γ), the larger the groups that can form. If $\gamma = 1$ and territory shifting is possible, group size becomes limited by reproduction and mortality rather than dispersal of low-ranking individuals (as $D/P < q_n$ for all n). Other parameters: $\alpha = 0.5$, $\beta = 0.8$, $\delta_n = 1$ for all n ; $\mu_F = 0.2$, $\mu_S = 0.1$, $T_F = 10$, $T_S = 5$ (note that, apart from δ_n , these influence the position of the D/P lines only, not the shape of the q_n curves).

out, and all individuals benefit from philopatry equally (fig. 3). Group sizes will in this case become limited by a balance of reproductive output and mortality in the population, rather than dispersal of lowest-ranking individuals.

Territory Acquisition in the Siberian Jay

The Siberian jay has no helpers but shows the pattern of delayed dispersal typical for cooperative breeders. The timing of dispersal is bimodal, with one peak in the number of offspring leaving in their first summer of life, while about one-third or more of the offspring postpone dispersal beyond their first year of life. The Siberian jay does

not have floaters in a literal sense. Dispersers settle in flocks so that, in addition to parents and their retained offspring, Siberian jay groups contain immigrants hatched in other groups. Usually these immigrants have dispersed in their first summer of life (Ekman et al. 2001b). Retained offspring normally do not breed, but they can stay with their parents till the age of 3 yr and, in rare cases, even longer. They rarely inherit their parents' territory except if both parents die in quick succession, suggesting inbreeding avoidance. While retained offspring do not help to rear younger siblings, they are treated preferentially by their parents. These benefits include access to food as well as nepotistic predator warnings (Ekman et al. 1994; M. Grieser and J. Ekman, unpublished manuscript). Benefits of this preferential treatment are available to natively philopatric offspring only, and only while they remain in association with their parents.

We can now illustrate the model predictions by applying the model to territory acquisition data for male Siberian jays in Arvidsjaur, northern Sweden ($65^{\circ}40'N$, $19^{\circ}0'E$) from the years 1991 to 2000 (data from 1995 are lacking). Different routes to becoming a breeder coexist in the same population in this species, and groups usually have one, and rarely two, queuing males (table 1). The ratio of mortality in retained offspring versus dispersers is approximately 1 : 2 in their first year (Ekman et al. 2000), which suggests that $\mu_S/\mu_F \approx 0.5$.

The number of territories that a subordinate can observe, T_S , can be estimated as follows. Since jays routinely obtain vacancies in neighboring territories (table 1), we assumed that they always become aware of vacancies in immediately neighboring territories. We first calculated the mean number of such territories, $T_1 = 4.2$, from territorial maps. Additionally, two out of 17 natively philopatric males and one out of 10 immigrant males were able to shift to a vacancy two territories away (table 2). We therefore also estimated the mean number of territories that lie within

Table 1: Frequency of presence in groups and territory acquisition for Siberian jay males

	Male years, subordinate rank 1	Male years, subordinate rank 2	Inherited	Shifted
Philopatric males	35	8	1	19
Immigrant males	21	6	13	10

Note: Data are pooled for 1991–1994 and 1996–2000. Ranks are calculated implicitly: groups usually had only one queuing male whose rank naturally equals 1, and bigger groups had two queuing males, of which one was given rank 1 and the other, rank 2. For the purposes of this table it does not matter which male was which, except in the rare case ($n = 1$) where a philopatric and an immigrant male queued together. In this case, we assumed that the philopatric male was of rank 1, but changing this assumption does not qualitatively alter our results.

Table 2: Distances (by territories) associated with shifting

	1	2	3	4	5
Philopatric males	17	2	0	0	0
Immigrant males	9	1	0	0	0

Note: Distances moved by male group members that did not inherit the territory but eventually shifted to a nearby vacancy.

this range but do not directly share a border with the natal territory. Based on the territorial maps, this number is $T_2 = 4.0$. Both numbers of nearby territories, but especially T_2 , are underestimates, since unmapped territories beyond the borders of our study area could not be included. This will make our estimate of T_s conservative.

Assuming that vacancies occur, on average, equally often in each territory, we can estimate T_s as $T_1 + dT_2$, where d specifies how often individuals were able to shift to a vacancy two territories away compared with an immediately neighboring vacancy. Data (table 2) from philopatric individuals predict that $T_1 : dT_2 = 17 : 2$, which gives an estimate of $d = 0.1235$. Immigrant group members (table 2) show a similar pattern, $T_1 : dT_2 = 9 : 1$, which yields $d = 0.1167$. Using $d = 0.12$ gives an overall estimate of $T_s = 4.68$.

The number of territories a floater can observe, T_p , and the relative territory acquisition propensity of a floater, β , are not usually easy to measure. However, in the Siberian jay, the true floating stage is short, typically less than 24 h, and is followed by life as an immigrant group member (Ekman et al. 1999, 2000). Since the estimated value of d is similar for immigrants as well as for retained offspring, immigrants do not appear to observe more neighboring vacancies than do philopatric individuals. It appears, therefore, reasonable to assume that $T_p = T_s$. Also, dispersers generally appear able to find groups that they can join without being associated with another male subordinate; breeding failures caused an average of 42% of flocks to lack any male subordinates in any given year, and only three of 117 group years comprised a philopatric son and an immigrant male. Routine joining of groups is also supported by radiotracking data (M. Griesser and J. Ekman, unpublished manuscript). This means that β can be estimated by calculating the success of immigrants who have joined groups.

Immigrants also are often able to inherit the nonnatal territory in which they reside (table 1). This is an additional route to breeding that was not explicit in our more general derivation above (eq. [9]). For the special case of Siberian jays, the expression βT_p in the definition of D must therefore be replaced by $\alpha' + \beta T_p$, where α' indicates the inheritance propensity of an immigrant male. We can

now estimate α , β , and α' by comparing the number of first-ranking immigrant males and first-ranking philopatric males to the frequency with which males have obtained territories (table 1). For example, table 1 specifies that 19 philopatric and 10 immigrant males became breeders by territory shifting. When the number of males who potentially were able to shift was 35 in the former and 21 in the latter group (assuming $\gamma = 0$, i.e., only first-ranking males shift), and the numbers of territories they were able to observe average T_s and T_s , respectively, the relative propensity of immigrants can be calculated as

$$35T_s : 19 = 21\beta T_p : 10 \Rightarrow \beta = 0.877. \quad (10a)$$

The propensities for territory inheritance are likewise obtained as

$$35T_s : 19 = 35\alpha : 1 \Rightarrow \alpha = 0.246, \quad (10b)$$

$$35T_s : 19 = 21\alpha' : 13 \Rightarrow \alpha' = 5.337. \quad (10c)$$

These values give us an estimate of $D/P = 0.958$ (assuming that $\mu_s/\mu_p = 0.5$). The above estimates are based on $\gamma = 0$. Assuming that $\gamma = 1$ does not change the estimate much; in this case, we include second-ranking subordinates in the numbers of potentially shifting males, which leads to $D/P = 0.916$. Since the relative benefit of dispersal D/P falls below 1, the model predicts that groups should form in the Siberian jay (fig. 4). Note that while we have probably underestimated T_s and T_p , this does not bias our estimates of propensities: if we had observed a larger number of territories, both the numerator and the denominator would have changed by the same factor f ; for example, in (10a), observing $T_s f$ target territories is expected to yield 19 f observed shifts.

To predict group sizes, we also need estimates for γ and δ_n . Data for these are largely lacking because Siberian jay groups only rarely contain more than one same-sex subordinate. We have only three cases where two brothers were retained for a long time on the same natal territory, and there are indications that one of them obtained a territory. The age difference between brothers was 1 yr in each instance. In two out of three cases, the older brother took over a neighboring vacancy. In the remaining case, the older brother disappeared and was not found again; this territory was near the edge of the study area, and we cannot exclude the possibility that he shifted to a nearby vacancy. These anecdotal observations support a small value of γ . If we assume that $\gamma < 0.8$ and $\delta_n = 1$ (no effect of rank on mortality), the queuing factor equals 1 (by definition) for the first-ranking subordinate but falls below 0.9 for the second-ranking subordinate. This means that

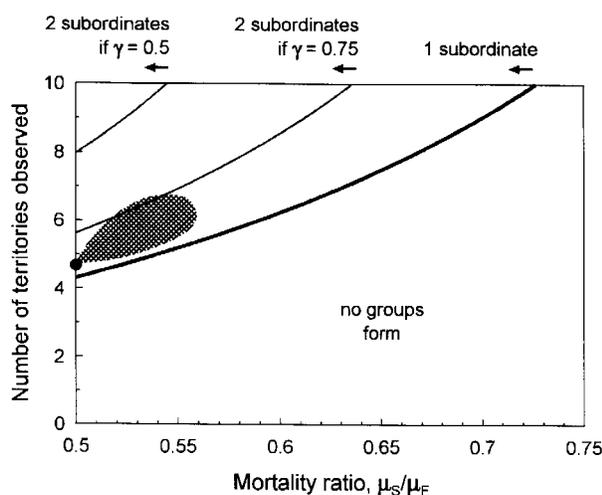


Figure 4: Model predictions for Siberian jay data, assuming $\delta_n = 1$ for all n . Philopatry pays for at least one subordinate, if the number of territories observed ($T_s = T_r = T$) exceeds the solid line, solved from $(\alpha + T)/\mu_s > (\alpha' + \beta T)/\mu_F$. Our minimum estimates for T and μ_s/μ_F are shown as a dot. Since the true values are probably larger, the shaded area indicates a likely region for these parameter values. Our estimates of γ are uncertain, but they indicate relatively low values of γ . Whether philopatry pays for two or more subordinates depends on the value of γ , as shown for $\gamma = 0.5$ and $\gamma = 0.75$ (additionally, the curve for $\gamma = 0$ lies outside the figure; i.e., retaining two offspring requires unrealistically high values of T if γ is low). The figure implies that γ must be large to predict retention of two offspring in the Siberian jay. Hence, the predicted group size falls between one and two same-sex retained offspring, with reasonable robustness.

$D/P < 1$ but $D/P > q_2$; that is, the second-ranking subordinate should disperse. Indeed, group sizes in the Siberian jay are small. Retained offspring usually comprise only one retained male and/or one retained female (table 1; see also Ekman et al. 2001b), and the dispersal probability of juveniles is strongly negatively related to the number of same-sex subordinates (M. Griesser and J. Ekman, unpublished manuscript).

Our estimate of D/P should be seen as an illustrative best guess rather than as a statistically solid argument. Several uncertainties in its estimation mean that the robustness of our results must be examined in detail. Most important, the survival benefit of philopatric offspring may be smaller than is predicted by data on their first year. Immigrant survival may improve later, as they become familiar with their new home range, although in most cases they acquire territories with their first year (table 1; acquisition events do not greatly outnumber immigrant male years). Also, parents eventually may be replaced by step-parents, which reduces the nepotistic advantage of retained offspring. The ratio μ_s/μ_F may thus exceed 0.5. Also, as a result of logistic limitations, our estimate of the number

of observable territories T_s is bound to be conservative. Even though this does not bias our estimates of individual propensities, it will affect our conclusions on the relative success of dispersers (Koenig et al. 2000). Finally, if second-ranking subordinates are often able to obtain breeding positions directly (large γ), the benefits of philopatry increase for the second-ranking subordinate.

Figure 4 summarizes the sensitivity analysis of model predictions for the Siberian jay. In the region where μ_s/μ_F somewhat exceeds 0.5, T_s somewhat exceeds 4.68, and γ is not very high, the model predicts that one same-sex offspring should stay. Consider a case where the true value of T_s equals eight territories. Second-ranking subordinates are half as likely to obtain territories as are first-ranking ones ($\gamma = 0.5$). Rank does not predict survival of philopatric individuals, but the survival difference between immigrants and retained offspring remains strong throughout their queuing period ($\mu_s/\mu_F = 0.5$). Under these assumptions, the relative benefit of dispersal is $D/P = 0.749$, while the sequence of queuing factors becomes $q_1 = 1$, $q_2 = 0.75$, and $q_3 = 0.58$. These values probably approach the upper limit for the benefits of queuing in the Siberian jay, and they predict retention of two offspring ($D/P < q_2$) with a very narrow margin (fig. 4).

Overall, we can therefore conclude that Siberian jay groups are predicted to retain between one and two philopatric offspring of the same sex. Although our estimates are rough, we find the correspondence between model predictions and the social behavior of the Siberian jay encouraging. Nevertheless, the main value of the model lies not in providing a point estimate for group sizes but in quantifying the various benefits and costs to dispersal in the Siberian jay. Since inbreeding avoidance typically prevents philopatric jays from inheriting their parents' territories, α is small (below 0.25). Territorial inheritance presents a very viable route to breeding for immigrants, however, and their propensity to inherit the nonnatal territory is more than five times the propensity of a neighbor seizing it ($\alpha' = 5.34$). Consequently, dispersing jays observe breeding opportunities at a much higher rate ($\alpha' + \beta T_F = 9.4$) than do philopatric offspring ($\alpha + T_s = 4.9$). Dispersers are thus less constrained in their search for a breeding position than are philopatric individuals. In order to explain philopatry in the Siberian jay, such a large difference in favor of dispersers must be counteracted by some other parameter. Favorable kin interactions that enhance the survival of offspring who stay in the safe haven appear, therefore, necessary to explain why all offspring do not follow the route of dispersers in the Siberian jay. Our calculations show that the survival benefit not only is necessary but also is sufficient to retain one or, at the most, two same-sex offspring. These findings echo those of Perrin and Lehmann (2001), who showed

that ecological constraints can become irrelevant for the evolution of delayed dispersal, when residents can discriminate kin from non-kin and can adjust their behavior accordingly.

Discussion

An Interpretation of Model Predictions

Our model develops a formal way to compare the benefits of dispersal with the benefits of philopatric queuing. The relative benefit of dispersal, D/P , summarizes the cost-benefit balance for dispersal versus philopatry for the first-ranking subordinate. When $D/P > 1$, groups do not form at all; philopatry then does not pay even for the first-ranking subordinate. The relative benefit of dispersal D/P increases if floaters do not suffer much higher mortality than philopatric subordinates (large μ_s/μ_f), if floaters compete well for territories (high β), if floaters can monitor vacancies at many more territories than philopatric subordinates ($T_f > T_s$), and if inbreeding avoidance often prevents territorial inheritance (small α). All these predictions are very intuitive, yet our model is the first one that combines these factors into a single number that indicates the relationship and relative importance of these factors.

In addition to the benefits of dispersal D and philopatry P for the first-ranking subordinate, we also derive the benefits of philopatry at queuing position n , Pq_n . This sequence of values specifies how quickly the philopatric benefits diminish for lower-ranking subordinates. The decline is steep if low-ranking subordinates rarely obtain territories (small γ) and if they suffer from high mortality (large δ_n). The maximum group size increases with q_n but decreases with D/P ; all the factors listed above that increase the relative benefit of dispersal D/P will limit the maximum group size.

A central prediction of our model is that dispersers should exhibit a variety of tactics: some individuals delay dispersal and leave only when an obvious vacancy is available, but as group size increases, the lowest-ranking individuals do better by dispersing to search for other sites. Our Siberian jay data clearly support this pattern, and many other species show similar coexistence of dispersing and nondispersing tactics (Rood 1990; Strickland 1991; Walters et al. 1992; Russell and Rowley 1993; Komdeur et al. 1995; Green and Cockburn 2001). In Siberian jays as well as in Gray jays *Perisoreus canadensis*, subordinate brood members appear to be the ones who leave, and dominant ones stay (Strickland 1991; Ekman et al. 1999). By contrast, strict territorial inheritance would predict that high-ranking subordinates do not shift to occupy other vacancies, and consequently, only lowest-ranking subor-

dinates disperse (Kokko and Sutherland 1998). This situation may apply to hover wasps *Liostenogaster flavolineata*, which form a strict age-dependent queuing hierarchy and in which newly emerged females are most prone to disappear from their natal nests (Field et al. 1999).

Although we have considered a wider variety of routes to breeding than previous modeling, a single model never encompasses all the variety that can abound in nature. For example, we predict that low-ranking individuals should be more prone to disperse because they gain smaller benefits from philopatry than do individuals higher up in the hierarchy. This result relies on the assumption that all floaters are equally good competitors. When the success of dispersers depends on age, size, or experience (Hunter 1987; Creel and Waser 1994; Lucas et al. 1997), the benefit of dispersal may increase for high-ranking, relatively old individuals. If so, safe havens could still function if they improve survival up to the optimal age of dispersal (Hunter 1987).

Overall, predictions from models become more varied as they incorporate more factors and interactions. Often, it is possible to make predictions of the type "all other things being equal, X will favor Y," but it must be remembered that all other things are rarely equal among species (Komdeur et al. 1995; Kokko and Lundberg 2001). A single explanation for dispersal and group formation is, therefore, unlikely to fit all species. For example, to accommodate data on the Siberian jay, it was necessary to modify the model to incorporate the "inheritance" of a nonnatal territory by an immigrant. Further alterations on immigrant dynamics will be needed, for example, to predict under which conditions floaters should join queues and the preferred length of such queues (Lucas et al. 1997; Heg et al. 2000). Likewise, the rules of dispersal will be different in species in which dispersers form coalitions (Koenig and Pitelka 1981; Ligon and Ligon 1990; Packer et al. 1991; Heinsohn et al. 2000). We therefore recommend that empiricists generally should not try to squeeze their data to fit one particular model but should strive toward direct measurement of the various consequences of alternative life-history tactics. Fine examples of such an approach are the studies by Walters et al. (1992) on dispersal in red-cockaded woodpeckers *Picoides borealis* and by Russell and Rowley (1993) on splendid fairy-wrens *Malurus splendens*. In these species, dispersers achieve equal or almost equal fitness compared with nondispersers. In the Siberian jay, lifetime fitness is higher for retained offspring than for dispersers (Ekman et al. 1999). Our model predicts that disperser fitness should fall below or, as a limit, be equal to that of nondispersers (see also Kokko and Lundberg 2001). More important than merely deriving values for fitness, Walters et al. (1992) show that there is a fitness cost associated with the delay in breeding for

philopatric individuals, but the relative benefits of dispersal are kept in bounds because nondispersers survive well and because the probability is low that a disperser attains breeding status.

*Ecological Constraints, Life Histories,
and Philopatric Benefits*

The need to consider details of a species' biology is nowhere as clear as in the debated role of ecological constraints. Originally, ecological constraints and the benefits of philopatry have been presented as opposite hypotheses (e.g., Stacey and Ligon 1991), yet both factors obviously influence fitness. Koenig et al. (1992) and Emlen (1994) clearly spoke out that constrained independent breeding and the benefit of philopatry are two sides of the same coin; our model is designed to quantify this comparison. Similar arguments apply to studies of noncooperative queuing for territories (Ens et al. 1995). Nevertheless, it remains valid to ask whether interspecific variation in delayed dispersal and cooperative breeding can best be explained by variation in the strength of ecological constraints or by variation in the magnitude of philopatric benefits. Additionally, it is essential to quantify how constraints depend on the life history of a species (Hatchwell and Komdeur 2000; Kokko and Lundberg 2001).

Although tight ecological constraints clearly reduce the advantages of dispersal, numerous species live under constraints, yet do not delay dispersal (Brown 1969; Stacey and Ligon 1991; Hatchwell and Komdeur 2000; Kokko and Lundberg 2001). In other species, groups form in the absence of constraints (Zack and Ligon 1985; Macedo and Bianchi 1997). Our results add another counterexample in which constraints do not fully explain dispersal behavior. Since inbreeding avoidance hinders territory acquisition by philopatric offspring in the Siberian jay, dispersers are less constrained in territory acquisition than are nondispersers. Nevertheless, some offspring remain philopatric in this species, which can be explained by improved offspring survival in kin groups (a benefit of philopatry).

Recently, many theoretical models have attempted to clarify the role of constraints, but a reader could be excused for becoming perplexed by the results. A plethora of reproductive skew models uniformly predict that group formation is most likely when competition for breeding sites is severe (reviewed in Reeve 1998; Johnstone 2000). By contrast, Pen and Weissing (2000) built a model that similarly compares the alternatives of dispersing to wait for a vacancy and staying at home and helping, but they obtained the result that ecological constraints only explain variation in cooperative breeding if density dependence operates through declining fecundity at higher population

sizes. Kokko and Lundberg (2001) showed that other aspects of a species' life history can override the effect of habitat saturation (a form of ecological constraint). Kokko et al. (2001) and Perrin and Lehmann (2001) both showed that given sufficient mutualistic benefits of group living, groups can be stable even in the complete absence of constraints. Earlier, Zack and Stutchbury (1992) had similarly shown delayed breeding to be advantageous in the absence of ecological constraints—their model implicitly assumed that every disperser can breed—if delaying sufficiently increases the quality of the territory obtained. And finally, our model (this article) derives results where competition for territories is assumed to exist (in the terminology of Kokko and Lundberg 2001, the habitat saturation factor exceeds 1), but dispersal does not directly depend on the strength of this competition.

Mathematically, the reason the strength of competition (expressed as the habitat saturation factor H) cancels out from our dispersal equations is that propensities of territory acquisition are relative. For example, if a floater is 80% as efficient at competing as is a first-ranking subordinate in the competition to seize a particular vacancy, doubling the strength of competition will halve the probabilities that either of them obtains the territory. Yet their relative propensities, and hence the relative merits of either tactic, remain unchanged. Earlier models have usually assumed that territory inheritance is strict, so that queuers routinely surpass floaters regardless of the number of floaters. Under this assumption, the benefit of queuing, and hence the length of queues, tends to increase as vacant habitat becomes scarce. Biologically, this contrast means that intense competition for breeding sites is more likely to co-vary with delayed dispersal in species where territories are strictly inherited than in species where vacancies can be seized by outsiders. Pen and Weissing (2000) obtained a similar contrast in their two scenarios of the evolution of helping.

Nevertheless, an equation that predicts dispersal behavior without a direct reference to the strength of constraint (such as our eq. [9]) does not allow us to predict that prospects for delayed dispersal do not depend on ecological constraints. Even where adding more competitors leaves the relative values of tactics unchanged, such an addition cannot happen without changing some life-history trait values, which then simultaneously influences the criteria for dispersal. For example, decreasing floater mortality increases both the strength of competition for breeding sites and the relative benefit of dispersal. This means that if species vary mainly in the survival prospects of dispersers, delayed dispersal is least likely in the species with strongest competition for each breeding vacancy (see also Kokko and Lundberg 2001). If species vary mainly in

the survival of queuers or breeders, or in fecundity, the opposite (positive) relationship is predicted.

This finding resolves the recent confusion between predictions made by Pen and Weissing (2000) and Kokko and Lundberg (2001). One of Pen and Weissing's (2000) scenarios has territorial inheritance, where density dependence acts via decreasing probability to obtain a territory as population size increases and the habitat becomes saturated. This is probably a common form of density dependence in territorial cooperative breeders (e.g., Komdeur et al. 1995). Pen and Weissing (2000) predict that habitat saturation cannot influence dispersal behavior in this setting, despite territorial inheritance. Kokko and Lundberg (2001) modeled this situation independently and obtained the opposite result: habitat saturation does play a role, albeit one that can easily be overridden by other life-history variables. In these models, delayed dispersal evolves more easily if fecundity is high (eq. [25] in Pen and Weissing 2000). High fecundity will also make the ecological constraint tighter (eq. [14] in Pen and Weissing 2000), since more competitors are produced in a highly fecund species. Similar relationships hold for the survival of breeders or queuers (or helpers in Pen and Weissing's [2000] analysis). Thus, even this scenario of density dependence allows an interspecific relationship between ecological constraints and dispersal, and the predictions of Pen and Weissing's (2000) model are in line with Kokko and Lundberg (2001).

Indeed, conditions for delayed dispersal such as our equations (10) or Pen and Weissing's (2000) equation (25) could easily be reformulated to include the constraint, once density dependence has been specified. But because the degree of constraint depends on many life-history traits, it is, in fact, clearer to think of dispersal directly in terms of its fitness prospects, like the formulation of Pen and Weissing (2000) does, than to resort to "constraints" that can become almost Panglossian. The original definition of "tight constraints" includes everything from high dispersal mortality to high numbers of competitors for each breeding vacancy (Emlen 1982*a*), although the latter implies relatively low dispersal mortality (Kokko and Lundberg 2001). As Hatchwell and Komdeur (2000) pointed out, an overgenerous definition can lead to too easy post hoc identification of constraints.

Thus, the results of recent modeling can be summarized as follows: constraints as such have little explanatory power since they are an outcome of many life-history traits, which can have opposing effects on dispersal behavior (Kokko and Lundberg 2001). If interspecific variation in habitat saturation is due to variation in disperser survival, delayed dispersal should be associated with less intense competition for breeding vacancies. By contrast, a long life span of breeders and subordinates promotes delayed dispersal.

This is partly due to direct effects: immediate breeding success is less important in long-lived species, and a long life span also allows prolonged beneficial interactions between parents and offspring. The other, indirect, effect operates via habitat saturation if territories are inherited: the benefit of dispersal diminishes if low mortality causes intense habitat saturation. The life-history hypothesis (Arnold and Owens 1998; Hatchwell and Komdeur 2000), therefore, includes ecological constraints in a logically consistent way, and it is also supported by comparative data (Arnold and Owens 1998).

High fecundity should similarly promote delayed dispersal. This has not yet been tested comparatively; it may be that interspecific trade-offs between fecundity and survival will mask this relationship (R. Härdling and H. Kokko, unpublished manuscript). Finally, strict territorial inheritance predicts a stronger link between habitat saturation and delayed breeding than does a system where individuals often shift to neighboring territories. We also stress that these predictions are, by their nature, interspecific. Within a species, our model predicts that individual group members will take advantage of suitable vacancies whenever they occur (e.g., Du Plessis 1992; Komdeur 1992), regardless of any interspecific relationship, or lack thereof, between delayed dispersal and the strength of constraints.

Our model omits habitat quality variation. The benefit of philopatry argument was originally posited to require variable quality habitats (Stacey and Ligon 1987, 1991; Zack and Stutchbury 1992), based on the benefits of waiting for a high-quality breeding site. However, uniformly high quality habitat allows a high rate of production of competitors; this habitat may therefore cause a more severe constraint on independent breeding and favor philopatry more strongly than highly variable habitat (assuming strict territorial inheritance; Kokko and Lundberg 2001). By excluding quality variation, our model shows that habitat quality variation is not necessary for delayed dispersal. As soon as competition for (any) habitat exists, an increase in the overall chances to live long enough to shift to a neighboring vacancy can be a sufficient benefit of philopatry to generate delayed breeding. If one is to consider habitat quality variation, it is important to calculate the dynamics of the population as a whole, since the benefits of breeding in good or poor habitat must be weighed against a risk of never breeding at all (if waiting in a too competitive environment). Theory then predicts that access to high-quality habitat can become constrained while low-quality habitat remains available (Ens et al. 1995; Kokko and Sutherland 1998; Ekman et al. 2001*b*). Quality variation then simply implies more variable behavior, that is, longer queues toward better sites, absence of queuing at poorer sites, and lack of breeding in very low quality

sites (Emlen 1995; Ens et al. 1995; Kokko and Sutherland 1998; Kokko and Lundberg 2001), but not necessarily more queuing as a whole. Data on Seychelles warblers (Komdeur et al. 1995) and Siberian jays (Ekman et al. 1999, 2001*b*) fit this pattern well.

The Role of Kinship and Parental Nepotism

In our modeling, we have taken the view that delayed dispersal requires an explanation that is independent of the evolution of helping (Brown 1987; Emlen 1995). This is consistent with the growing number of examples of species reported to have delayed dispersal in the absence of cooperative breeding (Gayou 1986; Veltman 1989; Birkhead 1991; Strickland 1991; Ekman et al. 1994; Walls and Kenward 1998; Green and Cockburn 1999, 2001; Robinson 2000; see also Kraaijeveld and Dickinson 2001 for a species in which helping occurs but is rare). Such a secondary role of cooperative breeding for the formation of kin units implies that delayed dispersal requires an independent explanation.

We do not derive group sizes explicitly when queuing subordinates provide help to the breeder. Perrin and Lehmann (2001) consider the coevolution of altruistic behavior and dispersal and show that nepotistic kin interactions can promote philopatry. Combining their results with ours, we suggest three potential mechanisms for how our predictions will be affected by considering inclusive fitness consequences. The first one will decrease group sizes; the latter two will increase it.

First, individuals should disperse “altruistically” if their presence is harmful to other individuals in the group (Hamilton and May 1977). Resource depletion or competition between siblings for territorial inheritance are examples of such harmful effects, and they will decrease the benefit of philopatry. Philopatric groups will therefore be less likely to form and will be smaller than our model predicts if relatedness is high, competition for breeding sites is intense, and mutualistic benefits of group formation are absent. Under these conditions, groups are more likely to form if shifting is possible than if territorial inheritance is the only route to breeding. This is because competition is diluted when it concerns T_s local territories rather than merely the natal territory.

Second, kinship may be needed for the safe haven mechanism that improves survival of retained offspring (Ekman et al. 2000). Reduced mortality ($\mu_s < \mu_F$) of philopatric individuals may occur independently of kin, for example, through familiarity of a given area, but often—as in the Siberian jay—it is based on nepotistic interactions among kin (Ekman and Rosander 1992; Ekman et al. 2001*a*). In this case, the model predicts that higher relatedness will lead to larger groups: the relative benefit of dispersal,

D/P , decreases if the mortality ratio μ_s/μ_F is small, as it will be if offspring survival improves in kin groups. Group formation through nepotism is more likely if resource depletion is of relatively minor importance to the dominant members of the group. This holds if mortality is largely independent of food resources, for example, if it is mainly caused by predation without a strong food–predation risk trade-off (Houston and McNamara 1999). If mortality is food driven, nepotistic resource sharing may still happen if dominant members of the group have sufficient resources so that concession incurs only a small survival cost (Ekman and Rosander 1992; Ekman et al. 2001*a*).

Finally, the benefit of philopatry increases if group-living individuals do not harm each other but instead perform better in larger groups (a within-group Allee effect; Courchamp et al. 1999). In this case, philopatric groups will become larger, especially if relatedness is high. Indirect (Mumme 1992) or delayed (Wiley and Rabenold 1984; Kokko et al. 2001) fitness benefits of helping are one obvious factor that can increase the success of individuals that live in large groups.

Conclusions: How to Reconcile All the Factors

Our model explains group formation based on the direct fitness benefit of improved access to territories through philopatry. Once philopatry has been established, it allows other benefits such as kin-selected helping to evolve. We propose the following general hypothetical scenario for the evolution of cooperative breeding. Consider a species in which breeding opportunities are limited and either strong seasonality does not prevent year-round residency on a territory (Arnold and Owens 1999; Kokko and Lundberg 2001) or the species is otherwise well equipped to cope with seasonality. It also helps if intragroup competition for food does not limit survival. Under these conditions, waiting for vacancies at home may yield survival benefits for the offspring, and the safe haven mechanism together with territorial inheritance and/or shifting can explain delayed dispersal as a route to breeding, without resorting to indirect benefits of helping behavior. This stage may or may not involve habitat quality variation; if habitats vary greatly, delayed dispersal pays off in good but not in poor habitat (and some habitat may remain unused). Species such as the Siberian jay fit this stage.

Given delayed dispersal, there is now scope for the evolution of helping or other mutually beneficial adaptations (Walters et al. 1992). For kin members of the group, the evolution of helping reinforces the benefits of philopatry and therefore increases stable group sizes. This reduces the population-wide number of dispersers and hence decreases competition for breeding vacancies (Kokko and Lundberg 2001). Such a reduction in competition need not threaten

the stability of delayed dispersal, however; if the mutualistic benefits of helping have become sufficiently strong, they can discourage dispersal even in the complete absence of ecological constraints (Kokko et al. 2001; Perrin and Lehmann 2001). Whether or not some degree of constraint remains, at this stage there is potential for group living that combines mutualistic benefits of helping with the benefit of group membership as a route to a breeding position. These benefits can encompass indirect fitness benefits (e.g., Creel and Waser 1994) as well as group-level benefits (e.g., Clutton-Brock et al. 1999), and a population at this equilibrium will show inverse density dependence at the group level (Courchamp et al. 1999).

Finally, if reasons to stay are based on mostly mutualistic interactions (Kokko et al. 2001) and/or if queuing is an efficient route to breeding but nonhelping subordinates will be expelled (Johnstone and Cant 1999; Kokko et al. 2002), it may pay for unrelated immigrants to join the group and help rather than merely compete for vacancies. At such an end point of evolution, the relationship between kinship and helping can be either strong or weak, mainly depending on the relationship between amount of help and its costs (Kokko et al. 2001). Overall, such complexities in the evolution of delayed dispersal mean that ecological constraints need not explain much variation in cooperative breeding between species (Arnold and Owens 1998; Kokko and Lundberg 2001). Our model shows that the initial stages of such a process can nevertheless be based on individual competition for breeding opportunities, without any helping benefits.

When many factors influence dispersal decisions in an "all other things being equal" manner, it is important to assess which things tend to be equal in nature and which ones vary. Phylogenetic analyses (Arnold and Owens 1998, 1999) take this into account automatically and can thus be extremely useful. We also urge modelers and empiricists alike both to compare the fitness of individuals successful in territory acquisition (whether philopatric or dispersing) and to remember to quantify the risk of failure to gain a breeding position when using either tactic. Otherwise, one side of the coin—the constraint on independent breeding or the benefit of philopatry—can become artificially bigger than the other.

Acknowledgments

This work would not have been possible without the enthusiasm of field-workers A. Bylin, S. Eggers, and M. Grieser. We also thank K. Arnold, J. Field, J. Ridley, and F. Weissing, whose comments improved the manuscript. Funding was provided by the Royal Society (H.K.), the Academy of Finland (H.K.), and the Swedish Natural Science Research Council (J.E.).

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Associate Editor: Joan E. Strassmann