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Dispersal, Migration, and Offspring Retention in Saturated Habitats

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abstract: We examine the evolutionary stability of year-round residency in territorial populations, where breeding sites are a limiting resource. The model links individual life histories to the population-wide competition for territories and includes spatial variation in habitat quality as well as a potential parent-offspring conflict over territory ownership. The general form of the model makes it applicable to the evolution of dispersal, migration, partial migration, and delayed dispersal (offspring retention). We show that migration can be evolutionarily stable only if year-round residency in a given area would produce a sink population, where mortality exceeds reproduction. If this applies to a fraction of the breeding habitat only, partial migration is expected to evolve. In the context of delayed dispersal, habitat saturation has been argued to form an ecological constraint on independent breeding, which favors offspring retention and cooperative breeding. We show that habitat saturation must be considered as a dynamic outcome of birth, death, and dispersal rates in the population, rather than an externally determined constraint. Although delayed dispersal often associates with intense competition for territories, life-history traits have direct effects on stable dispersal strategies, which can often override the effect of habitat saturation. As an example, high survival of floaters selects against delayed dispersal, even though it increases the number of competitors for each breeding vacancy (the "habitat saturation factor"). High survival of territory owners, by contrast, generally favors natal philopatry. We also conclude that spatial variation in habitat quality only rarely selects for delayed dispersal. Within a population, however, offspring retention is more likely in high-quality territories.

Keywords: cooperative breeding, delayed dispersal, floating, parent-offspring conflict, partial migration, philopatry, territoriality.

In territorial species, dominating a suitable habitat patch is a major prerequisite for successful breeding. If habitats vary in quality, individuals should have an incentive to leave occupied sites and to search for a better breeding site. However, if suitable habitats are mostly already occupied, individuals that leave their current territory to search for better sites are not necessarily guaranteed ever to obtain another territory. Competition for limited breeding sites could thus favor year-round residency. Residency—which we define as a year-round occupation of a single territory—may occur in very different contexts. One example is partial migration (Lundberg 1987, 1988), where some individuals in a population remain resident, whereas others migrate. Alternatively, breeding individuals may stay resident after the breeding season and their offspring disperse to become floaters (Greenwood and Harvey 1982; Newton 1992). Finally, residency may take the form of offspring retention, where not only parents but also their offspring remain resident in the natal patch (Koenig et al. 1992).

The purpose of this article is to investigate how residency strategies depend on life-history traits and spatial variation in habitat qualities. We focus on species that live in saturated habitats (Brown 1969), where there is competition for a limited supply of breeding site vacancies. Analyzing residency decisions requires a game-theoretic treatment because the success of strategies is density and frequency dependent. The number of other individuals, and the residency strategies that they use, will determine the rate at which territories become available and the number of competitors that are searching for new vacancies. These in turn influence the relative fitness gains of staying on a territory versus searching for other sites.

We contrast year-round residency with a broadly defined "nonresident" alternative. Our model pertains both to species that migrate seasonally and to those in which "nonresidency" means dispersal to reach other breeding sites. In both cases, the payoff from residency is priority access

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to a territory. Nonresident behavior requires an individual to compete for vacant habitats elsewhere. There are two potential benefits of nonresidency: first, the nonresident may find a better breeding site than it was inhabiting before, and second, it may survive better than a resident, particularly if nonresidency permits migration to an overwintering area. The "dispersing" and "migratory" interpretations of nonresidency differ in the importance of these two benefits. Dispersal is primarily aimed at finding new breeding sites and is often associated with decreased survival, whereas migration is explained as an escape from temporarily unfavorable conditions and thus should improve survival. Our conclusions apply to both interpretations. We use the general term "nonresidency" in the modeling part of this article but address the conclusions for migration separately.

Our model also includes the possibility of a parent-offspring conflict over territory ownership. This enables us to interpret some of our results in the light of cooperative breeding. In cooperatively breeding species, some offspring delay dispersal and stay as helpers (Stacey and Koenig 1990; Solomon and French 1997). Delayed dispersal is generally viewed as a prerequisite to the evolution of helping behavior (e.g., Brown 1987; Emlen 1995, 1997; Cockburn 1998). Our model includes a simple form of delayed dispersal, where offspring can choose to depart at the start of the next breeding season, rather than immediately after their own natal season. This requires parental consent since retained offspring may compete with their parents for local resources. One potential advantage of this strategy is territorial inheritance (Brown and Brown 1984; Zack and Stutchbury 1992; Kokko and Johnstone 1999; Ragsdale 1999) if the parent dies during the nonbreeding season. However, we exclude any future interactions among kin such as helping behavior (see Kokko et al. 2001*a*, for an evaluation of group dynamics in the presence of helping).

Theoretical (Brown 1974; Emlen 1982; Reeve 1998) and empirical work (Pruett-Jones and Lewis 1990; Komdeur 1992; Walters et al. 1992; Komdeur et al. 1995) suggests that intense competition for breeding sites—generally viewed as a "constraint on independent breeding" (Emlen 1982)—may make dispersal less favorable and thus facilitate the evolution of cooperative breeding. Cooperative breeding should thus predominantly occur in species that inhabit saturated habitats (Brown 1969). However, this view has been recently challenged (Arnold and Owens 1998) with the suggestion that life histories (mainly, low adult mortality) of species explains cooperation better than does any specific habitat property (Arnold and Owens 1999; see also Hatchwell and Komdeur 2000).

Yet a "constraint on independent breeding" in general, and habitat saturation in particular, is not an external property of the environment but arises from birth, death, and dispersal in a population occupying a specific area. Competition for limited breeding sites influence optimal dispersal decisions, but these decisions in turn affect the intensity of competition. Dispersal decisions necessarily influence both the rate at which territories become vacant and the number of competing individuals (see also Koenig et al. 1992). A model of dispersal in saturated habitats must therefore link individual decisions (residency strategies) with population-level consequences (degree of competition for each vacancy). Also, one should distinguish the mere existence of saturation from the intensity of competition in saturated habitats. We define a habitat saturation factor, H, as the average number of competitors for each breeding vacancy. Habitats are saturated for $H \geq 1$, but competition is more intense when the value of H is high.

The Residency Game

Consider a population limited by the area available for breeding. The potential habitat includes territories of either high (denoted by 1) or low (denoted by 2) quality, giving n_1 and n_2 possible breeding sites, respectively (we present results assuming $n_1 = n_2$). The expected number of (same sex) offspring produced, r, is higher in high-quality territories: $r_1 > r_2$. These may also yield higher overwintering survival: $s_1 \geq s_2$. With sufficient offspring production and survival, the number of competitors will exceed the number of available territories. After territories are filled, surplus individuals become nonbreeding floaters, with no fitness gain in the current breeding season. If floaters survive to the next breeding season, they may acquire a territory through scramble competition and become breeders (fig. 1). Each season consists of one breeding attempt, followed by a nonbreeding period. At the end of each breeding attempt, territorial individuals can decide whether to remain resident.

For simplicity, we assume that a successful breeding attempt fledges just one (same sex) offspring. The productivity r_i of a habitat is thus the probability of breeding successfully. A low number of offspring ($0 \leq r_i \leq 1$) requires relatively high survival to avoid population extinction. This assumption allows us to ignore complications arising from sibling competition because at most two individuals (the parent and a single offspring) inhabit a territory at the end of a breeding attempt ("summer"). We assume that offspring leave the natal territory no later than at the end of the nonbreeding period ("winter") if the parent survives. If the parent dies during winter, the offspring inherits the natal territory.

Movement decisions taken at the end of the summer depend on individual state, of which there are six: first,

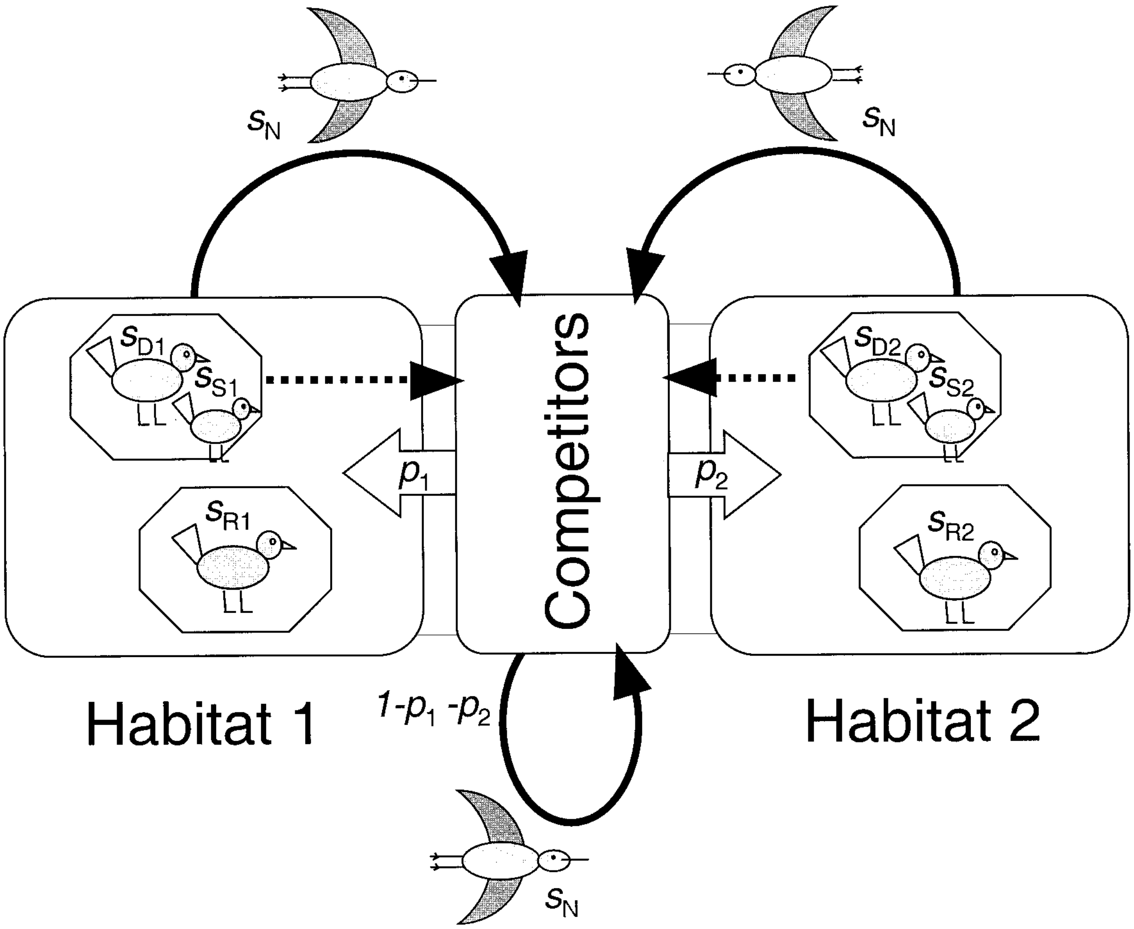

Figure 1: Structure of the residency model. Habitats 1 and 2 are divided into territories (here, two are shown for each habitat). Individuals may stay resident in them either in groups of a parent and an offspring, or solitarily. Their survival s depends on this decision as well as on the habitat type, as indicated. Alternatively, they may leave to become nonresidents (shown as flying birds). Nonresident survival equals s_N. Nonresident individuals compete for breeding vacancies (*wide arrows*) and obtain a territory with probabilities p_1 and p_2 for good and poor habitat, respectively. They fail to obtain a territory with probability $1 - p_1 - p_2$ and have to survive as a nonresident to the next breeding season in that case (*loop arrow*). Finally, spring competitors also include retained offspring that are evicted at the start of the new breeding season, if their parent has survived (*dotted arrows*).

individuals may be alone or dominant (parent with an offspring) or subordinate (offspring), and second, they may inhabit a good or poor territory. Floaters are not included in the list of states since, lacking a territory, they have no option but to use the nonresident strategy. Thus, there are $2^6 = 64$ different strategies, according to whether an individual disperses in each of the six states. For example, one of the strategies could be "become nonresident if you are an offspring on a poor territory, otherwise, stay resident."

We define s_N as the overwintering survival probability of a nonresident and s_{Ri}, s_{Di}, and s_{Si} as the survival probabilities of a lone resident, a dominant (the parent), and a retained subordinate (the offspring), respectively, in territories of quality i ($i = 1$ or 2; fig. 1). Since survival may differ between residents and nonresidents, the population-wide strategies affect both the number of competitors for the vacant territories and the number of vacancies available. For instance, for the example strategy stated above, the number of vacancies v_i in the spring will be

$$v_1 = n_1[r_1(1 - s_{D1})(1 - s_{S1}) + (1 - r_1)(1 - s_{R1})], \tag{1a}$$

$$v_2 = n_2(1-s_{R2}). \tag{1b}$$

The equilibrium number of competitors in spring, c, depends on the number of floaters from the previous year (surviving with probability s_N), as well as the number of new competitors, c_n. New competitors can be either retained offspring that are now evicted if their parents have survived, territorial birds of the previous year that have become nonresident, or nonresident offspring. In our example, new competitors number

$$c_n = n_1 r_1 s_{D1} s_{S1} + n_2 r_2 s_N. \tag{2}$$

Noting that $c - v_1 - v_2$ competitors remain as floaters each year, the equilibrium number of spring competitors is $(c - v_1 - v_2)s_N + c_n = c$, or

$$c = \frac{c_n - s_N(v_1 + v_2)}{1 - s_N}. \tag{3}$$

The ratio of competitors to vacancies is the habitat saturation factor, $H = c/(v_1 + v_2)$.

Similar expressions for population-level consequences can be derived for each of the 64 possible strategies. We do not present them here for the sake of brevity but will provide a complete list by request.

We consider only cases where $c > v_1 + v_2$, which guarantees a viable, temporally stable population with all territories occupied. Given this, the probability p_i of a spring competitor obtaining a territory of quality i is

$$p_i = v_i/c. \tag{4}$$

The probabilities p_i define the average fitness (reproductive value) w_c of a spring competitor in a population at equilibrium. It may become a territorial on a good (fitness w_1) or bad (fitness w_2) site or float and survive (s_N) to become a competitor next year; hence,

$$w_c = p_1 w_1 + p_2 w_2 + (1 - p_1 - p_2)s_N w_c. \tag{5}$$

We still need expressions for the fitness of territorial birds, w_1 and w_2. These depend on the strategies they and their offspring use. For our example, where parents and offspring remain resident in good territories, and only parents in poor ones, we have

$$w_1 = r_1\{s_{D1}w_1 + s_{S1}[s_{D1}w_c + (1 - s_{D1})w_1]\} + (1 - r_1)s_{R1}w_1, \tag{6a}$$

$$w_2 = s_{R2}w_2 + r_2 s_N w_c. \tag{6b}$$

Equation (6a) specifies that, if an individual reproduces this year (probability r_1), it will retain one offspring and hence reenter this state the next year with the survival probability of a dominant (s_{D1}). Additionally, it gains fitness from a surviving offspring (probability s_{S1}). The magnitude of this gain depends on whether the parent itself survived: if so (s_{D1}), the offspring will compete for vacancies next spring (and gain fitness w_c), and if not ($1 - s_{D1}$), the offspring will become a new breeder at the current site (fitness w_1). The fitness equation in low-quality habitats (6b) is simpler because parents always survive with the probability of a lone resident (s_{R2}) and their offspring with that of a nonresident (s_N).

Note that the fitness equations (6a) and (6b) exclude the relatedness coefficient one-half between parent and offspring. The reason is that productivity r is measured as the expected number of same-sex offspring; counting offspring of both sexes doubles the fitness (see Kokko and Ruxton 2000). The equations define the relationship between w_c, w_1, and w_2 but render their scaling arbitrary (as in reproductive value problems in general; Houston and McNamara 1999). In our example, if we set $w_c = 1$, equations (6a) and (6b) give

$$w_1 = \frac{r_1 s_{D1} s_{S1}}{1 + r_1(s_{R1} - s_{D1} - s_{S1} + s_{D1}s_{S1}) - s_{R1}}, \tag{7a}$$

$$w_2 = \frac{r_2 s_N}{1 - s_{R2}}. \tag{7b}$$

This also satisfies equation (5) with the appropriate values of p_i.

When deriving the evolutionarily stable strategy (ESS), we assume that a parent can force offspring to leave. If evicting an offspring is optimal for the parent, we then also check whether the offspring's fitness would have been higher if it were allowed to stay. If so, there is parent-offspring conflict over residency. We do not assume that the parent can force an offspring to stay, as this is biologically unlikely.

For a strategy to be evolutionarily stable, the following conditions must be met: First, if the parent fails to reproduce either in good or poor habitat, it benefits more from its current strategy (resident or nonresident) than the corresponding alternative. In our example,

$$s_{R1}w_1 > s_N w_c, \tag{8a}$$

$$s_{R2}w_2 > s_N w_c. \tag{8b}$$

Second, if the parent reproduces successfully, it benefits most from its current strategy compared to alternatives where it, its offspring, or both change their behavior. However, if the offspring is nonresident, a parent cannot force it to stay. In our example, these criteria translate to

$$s_{D1}\left(w_1 + \frac{1}{2}s_{S1}w_c\right) + (1 - s_{D1})\frac{1}{2}s_{S1}w_1 > \max\left\{s_{R1}w_1 + \frac{1}{2}s_N w_c,\ s_N w_c + \frac{1}{2}s_{R1}w_1,\ \left(1 + \frac{1}{2}\right)s_N w_c\right\} \tag{9a}$$

for the parent in the high-quality habitat, and

$$s_{R2}w_2 + \frac{1}{2}s_N w_c > \left(1 + \frac{1}{2}\right)s_N w_c \tag{9b}$$

for the parent in the low-quality habitat.

Third, if the offspring stays resident, it should benefit more from doing so than by becoming nonresident. In our example, this applies to good quality habitat:

$$\frac{1}{2}s_{D1}w_1 + s_{S1}[s_{D1}w_c + (1 - s_{D1})w_1] > \frac{1}{2}s_{R1}w_1 + s_N w_c. \tag{10}$$

Fourth, if the offspring is nonresident, either of the following two should be satisfied: the offspring benefits more from residency than from nonresidency (criterion [11a]), or it has no choice since the parent benefits more from evicting offspring than from accepting its presence (criterion [11b]). In our example, this applies to poor habitat, and one or both of these two criteria,

$$\frac{1}{2}s_{R2}w_2 + s_N w_C > \frac{1}{2}s_{D1}w_1 + s_{S1}[s_{D1}w_c + (1 - s_{D1})w_1], \tag{11a}$$

$$s_{R2}w_2 + \frac{1}{2}s_N w_c > s_{D2}w_2 + \frac{1}{2}s_{S2}[s_{D2}w_c + (1 - s_{D2})w_2], \tag{11b}$$

must be satisfied for the strategy to be an ESS. If the offspring would benefit from staying (criterion [11a] not fulfilled) but the parent wants it to leave (criterion [11b] fulfilled), there is a parent-offspring conflict in this particular habitat.

Again, we do not present a complete list of the criteria here for all 64 possible strategies. These are available by request from the authors.

Results

Migration and Partial Migration

Under what conditions should all individuals leave their territories at the end of the breeding season? The residency game provides particularly simple conditions for the evolutionary stability of complete nonresidency, which can be interpreted as migration. The criteria (derived in the appendix) for nonresidency in habitat i are

$$s_N(1 + \bar{r}) \geq 1, \tag{12a}$$

$$s_{Ri}(1 + r_i) < 1. \tag{12b}$$

In the first equation (12a), $\bar{r}$ is the average breeding output in the population (appendix). This equation specifies that migrants have to survive well enough to produce a stable persistent population. The second equation specifies that, in a temporally stable population, migration is stable against invasion by a resident alternative only if residents do not reproduce well enough in habitat i to balance their mortality in that habitat. Condition (12b) means that migrating is never optimal in a temporally stable habitat that is a source (Dias 1996) for year-round residents. Equation (12b) does not depend on migratory survival s_N at all, and competition for prime breeding sites can therefore lead to residency, even if survival of residents falls clearly below that of migrants (Lundberg 1987). Migration should only occur if mortality of year-round residents is too high for their subsequent reproduction to balance it.

Results (12a) and (12b) can also describe partial migration, when resident survival and breeding success (eq. [12b]) differ between habitats. A habitat may be poor because of high overwintering mortality, poor productivity during the breeding season, or both. Reproduction may therefore exceed mortality in good habitat only. In this case, priority for a good breeding site outweighs low resident survival for inhabitants of good habitat, who should stay resident. Inhabitants of poor habitat should migrate after the breeding season. It is nteresting that this does not necessarily require any difference in overwintering mortality in the two habitats, $1 - s_{Ri}$. Differences in overwintering survival are therefore not necessarily the key to understanding differential migration—a difference in breeding success can be sufficient (cf. Lundberg 1987; Kaitala et al. 1993).

Offspring Retention: The Role of Habitat Saturation

The previous section showed that residency may be favored even if survival of residents falls below that of nonresidents. A nonresident floater may fail to find a breeding site, and an attempt to survive and to defend the current territory may therefore be less risky. If residency additionally provides superior survival prospects, the advantages of residency increase further, leading to much stronger forms of residency than partial migration. These include year-round residency in all habitats and delayed dispersal (offspring retention). Do residency strategies evolve because of superior survival of residents or because of low chances that a dispersing individual can breed? These two are necessarily linked: low resident mortality reduces territorial turnover, and it will consequently be more difficult for a disperser to find a breeding site (Arnold and Owens 1998; Hatchwell and Komdeur 2000). According to the "habitat saturation" hypothesis (Brown 1969; Koenig et al. 1992; Emlen 1995), such difficulties underlie the evolution of delayed dispersal.

Figure 2 shows stable strategies and the habitat saturation factor H (defined as the number of competitors for each vacancy) for various values of resident survival, when the survival of nonresidents equals 0.6. At low values of resident survival, nonresidency in all habitats is the ESS, and the habitat saturation factor is relatively low ($H = 1.05$). Increasing resident survival first leads to residency of parents in good habitats ($s_R = 0.575$), then to a parent-offspring conflict over residency in good habitats ($s_R = 0.6$), to conflict-free offspring retention in good habitats ($s_R = 0.6 \ldots 0.625$), and to a strategy where offspring are retained in good habitats but poor territories exhibit a conflict between resident parents and their offspring ($s_R = 0.625$). Some of these alternatives may occur at overlapping values of resident survival, indicating multiple ESSs determined by initial conditions. Highest values of resident survival predict the most completely resident strategy, offspring retention in both habitats ($s_R \geq 0.65$; fig. 2).

What is the role of habitat saturation in offspring retention? All solutions, nonresidency included, describe habitats where some individuals are unable to breed because of the lack of suitable breeding sites: the habitat saturation factor H always exceeds one competitor for each breeding vacancy (fig. 2*B*). Thus, our first conclusion is that the mere existence of habitat saturation does not explain the variation in strategies in figure 2.

Even if habitat saturation per se (i.e., $H \geq 1$) does not explain residency decisions, intense competition for few vacancies (indicated by a high value of H) decreases the fitness of dispersing individuals (eqq. [4], [5]). We therefore next examine whether increasing competition for vacancies, as measured by H, always enhances residency in the population.

Figure 2 provides a counterexample. Resident survival $s_R = 0.55$ predicts $H = 1.05$ and complete nonresidency, whereas $s_R = 0.575$ generates a marginally lower saturation factor $H = 1.03$, yet produces a partially resident strategy (resident parents in good habitat). In both cases, residents survive less well than nonresidents. Although a switch to residency reduces the number of vacancies (and therefore increases competition), residents also remain absent from the pool of competitors. Regarding the strength of competition in the floater population, these effects would cancel each other out if the survival of residents and nonresidents were equal. However, since survival of residents is lower than of nonresidents (0.575 vs. 0.6), the net effect is a marginally lower habitat saturation factor in the resident population.

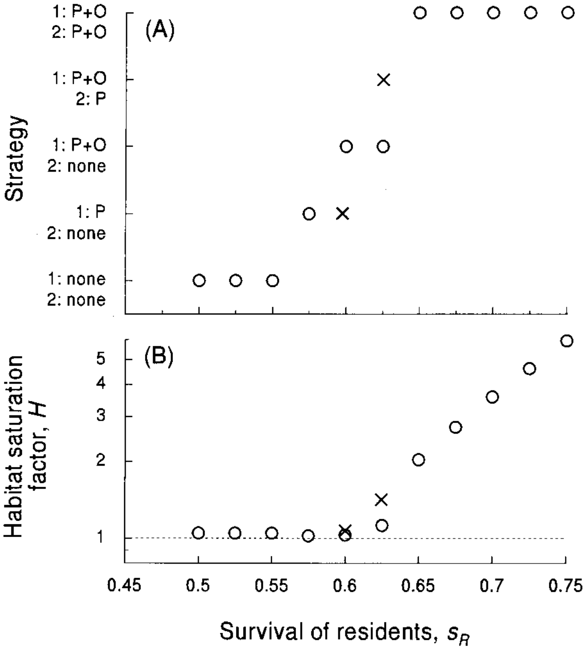

Figure 2: *A*, Examples of evolutionarily stable strategies (ESSs) in the residency game. Solutions are indicated as parents (*P*) or offspring (*O*) being resident in good (*1*) or poor (*2*) habitats. These are derived for different values of resident survival s_R, when nonresident survival is $s_N = 0.6$ (marked by arrow) and the presence of two individuals in a territory decreases the survival of both by 2.5%: $s_D = s_S = 0.975 s_R$. The two habitats differ in their offspring production: probability of successful breeding $r_1 = 0.8$ in good habitat, and $r_2 = 0.6$ in poor habitat. Circles indicate conflict-free ESSs, whereas a strategy with parent-offspring conflict is marked with a cross. *B*, Habitat saturation factor H (number of competitors for each vacancy) as a result of the residency game.

Overall, figure 2 predicts most intense competition for territories when not only parents stay resident but their offspring also delay dispersal. This begs the question whether the above counterexample is general or merely a minor deviation from an overall robust pattern of habitat saturation driving residency.

Figure 3 examines this question by varying resident and nonresident survival over a wide range of values. Apart from the region where neither survival is high enough to sustain a population, solutions include "no residency" and "partial residency" (marked with *P*). These require low survival of year-round residents and can be interpreted as a seasonal escape from seasonally harsh conditions (migration or partial migration). There are also cases with no pure ESS, and ESSs with offspring retention in good territories only (O_1 and O_2). Finally, high values of resident survival produce offspring retention in both good and poor habitats.

Either of the two most extreme strategies—complete nonresidency and offspring retention—can have either low or

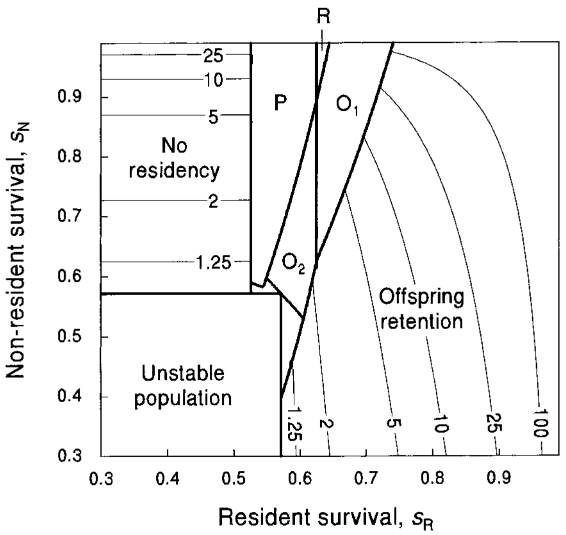

Figure 3: Solutions of the residency game at different values of resident survival s_R and nonresident survival s_N, assuming $s_{Di} = s_{Si} = s_{Ri} = s_R$ for both habitat types $i = 1$ and 2. Good and poor habitats have productivities $r_1 = 0.9$ and $r_2 = 0.6$, respectively. In the lower left corner, survival is too low to produce a viable population saturating both habitats. Solutions are classified as "*no residency*" in any habitat (interpretable as complete migration), "*offspring retention*" where parents and offspring stay resident in both habitats, *P* denoting partial residency (only parents stay resident in good habitats; interpretable as partial migration), *R* denoting residency of parents in both habitats, O_1 denoting offspring retention in good habitat only (parents stay and offspring disperse in poor habitats), and O_2 where offspring are retained in good habitat and no residency occurs in poor habitats. In unmarked regions, no pure evolutionarily stable strategy exists. Thick solid lines indicate a change in strategies, and thin contour lines indicate values of the habitat saturation factor *H* in the areas of "*no residency*" or "*offspring retention.*"

high habitat saturation factors (fig. 3). Competition for territories can be very intense in nonresident populations (e.g., $s_R = 0.5$, $s_N = 0.95$ predicts 14.3 competitors/vacancy), if nonresidents survive well, since this generates a population of long-lived floaters. Despite the intense competition for breeding sites, residency is not favored simply because residents survive poorly (as is the case in migratory species). Conversely, if nonresidents survive poorly, offspring retention may evolve even if dispersing offspring do not encounter very intense competition for breeding sites (e.g., solution with $s_R = 0.6$, $s_N = 0.3$ has 1.32 competitors/vacancy; fig. 3). The habitat saturation factor *H* remains low because floaters die off quickly. Offspring delay dispersal because dispersal is risky, not because strong competition would constrain independent breeding. Figure 3 therefore shows that the above counterexample is not a special case; habitat saturation is not a good predictor of residency.

Generally, competition for breeding sites is intensive not only if survival of residents is high (vacancies occur less often) but also if nonresidents survive well (floaters remain alive competing for territories for a longer time). The former favors residency and delayed dispersal of offspring. The latter, however, may destroy the stability of offspring retention (fig. 3).

High survival of dispersing offspring can destroy offspring retention especially if sharing a territory with an offspring is costly for the parent. Figure 4 derives solutions of the residency game, when retaining an offspring harms parental survival. Offspring retention is now constrained to moderately high values of resident survival and low values of nonresident survival. Because parents do not necessarily tolerate offspring that harm their survival, there are regions of conflict where an offspring would benefit from delaying dispersal but the parent is better off evicting it. Parents refrain from evicting offspring only if these would survive poorly as nonresidents (fig. 4).

Competition for territories is most intense when both nonresident survival, s_N, and resident survival, s_R, are highest. This region exhibits parent-offspring conflict in both habitats, rather than offspring retention (fig. 4), even

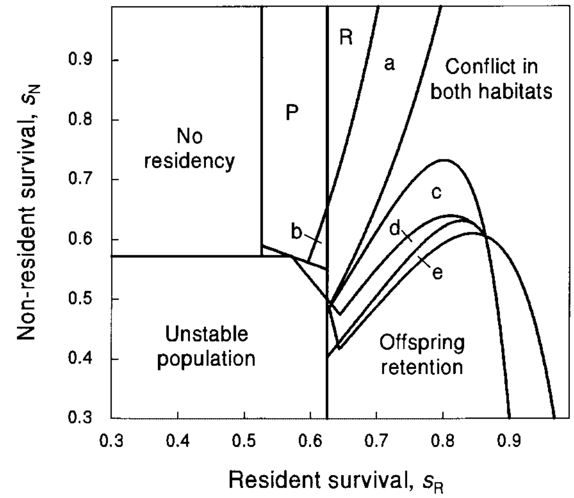

Figure 4: Solutions of the residency game at different values of resident survival s_R and nonresident survival s_N. Parameter values are as in figure 3, but survival decreases by 10% if two individuals share a territory: $s_{Di} = s_{Si} = 0.9s_{Ri}$. Solutions include, in addition to those found in figure 2, five types of conflicts, marked with *a* to *e*. In *a* and *b*, the conflict occurs in good habitat only. In *a*, poor habitats have resident parents, whereas in *b*, there is no residency in poor habitat. In *c*, there are two alternative evolutionarily stable strategies (ESSs): conflict in both habitats, or conflict-free retention in good habitat and conflict in poor habitat. In *d*, conflict-free retention in good habitat and conflict in poor habitat is the only ESS. *e*, There are again two alternative ESSs: conflict-free offspring retention in both habitats, and retention in good habitat and a conflict over residency in poor habitat. Unmarked regions have no pure ESS but may have mixed ESSs; for example, a fraction of occupants of a habitat retain their offspring.

Table 1: Solutions of the residency game

Alternative	Productivity of good habitat	Productivity of poor habitat	Residency in good habitat	Residency in poor habitat	Habitat saturation factor, H
A	.75	.75	Parent only	Parent only	2.04
B	.90	.60	Parent + offspring	None	1.73
C	.75	.60	Parent only	None	1.58
D	.90	.90	Parent + offspring	Parent + offspring	3.54

Note: With nonresident survival $s_N = 0.7$ and resident survival $s_{Ri} = s_{Di} = s_{Si} = 0.6$ regardless of habitat type, for different productivities r_i of good ($i = 1$) and poor ($i = 2$) habitat.

though a dispersing offspring will face extremely intense competition (e.g., $s_N = s_R = 0.9$ would produce 58.5 competitors for each vacancy). Why does a parent evict the offspring if high survival of both nonresidents and residents combines to produce the most extreme competition? First, if a nonresident floater survives well, the probability that it eventually finds a territory is improved. This compensates for the intense competition in any one year. Second, life-history theory predicts that reductions in survival have the strongest impact on fitness in long-lived species (Roff 1992). The cost of retaining a harmful offspring is therefore highest when parental survival is high.

Figures 2–4 together demonstrate that habitat saturation is not the main causal factor that promotes residency and delayed dispersal. However, competition for breeding sites is obviously one component that determines the fitness of a dispersing individual. All other factors being equal, more intense competition yields more residency. This effect is clearest in comparisons where survival of residents and nonresidents is varied without changing their relative survival. In figure 3, $s_N = s_R = 0.6$ produces offspring retention in high-quality habitat only (O_2). Improving the survival of both types, $s_N = s_R = 0.8$, leads to retention in both habitats. This change is solely due to competition for territories, which has intensified from 1.21 to 13.5 competitors per vacancy.

Offspring Retention: The Role of Habitat Variability

An alternative to the habitat saturation hypothesis emphasizes the role of habitat variability (Stacey and Ligon 1991). According to this idea, offspring should remain in the natal, high-quality territory to avoid ending up in a low-quality patch, if local habitat varies greatly in quality. Our model describes habitat quality variation by breeding success r_i and survival s_{Ri}, s_{Di}, and s_{Si} in the two habitat types $i = 1$ and 2. As any change in survival or production of offspring in either habitat type is likely to change the overall degree of habitat saturation, one must disentangle changing overall habitat quality and introducing variation per se.

This point is best illustrated by an example. Assume resident survival $s_{Ri} = s_{Di} = s_{Si} = 0.6$ regardless of habitat type, nonresident survival $s_N = 0.7$, and no difference in habitat qualities $r_1 = r_2 = 0.75$. At the ESS, parents stay resident, offspring disperse, and habitat saturation equals $H = 2.04$ competitors/vacancy (table 1, alternative A). If habitat quality variation is introduced by setting $r_1 = 0.9$ and $r_2 = 0.6$, the new ESS has offspring retention in good habitats, no residency in poor habitats, and 1.73 competitors per vacancy (table 1, alternative B). Habitat quality variation encourages residency in the good habitat, although it decreases habitat saturation.

This appears to support the importance of spatial habitat variation in offspring retention. However, while variability enhances residency in good habitat, residency ceases in poor habitat (table 1, alternatives A, B); it is less profitable to stay in a poor patch as it becomes worse. Residency in the good habitat may likewise be a direct response to increased quality (from $r_1 = 0.75$ to 0.9), rather than to increased variation across habitats. Indeed, reducing the quality of the poor habitat, without changing the quality of the good habitat, introduces variability in habitat qualities but does not bring about offspring retention in the good habitat (table 1, alternative C). Increasing the quality of both habitats causes offspring to be retained in both habitats, even if variability remains absent (table 1, alternative D). Table 1 suggests that residency in a given habitat mainly reflects the quality of that habitat, not the quality of the alternative habitat, and is therefore independent of habitat variability.

To investigate whether this applies generally, we solved the model for 10,000 randomly chosen parameter values and scored the effects of increasing quality of good habitat and/or decreasing that of poor habitat (table 2). In each case, we first assumed constant resident survival across habitats, $s_{R1} = s_{R2}$, having a random value between 0.5 and 0.96. Survival of resident parent–offspring pairs was either higher or lower than survival of lone residents, with $s_{D1} = s_{S1} = s_{R1} + \delta$ and $s_{D2} = s_{S2} = s_{R2} + \delta$, δ randomly

Table 2: Effects of introducing variation in habitat quality by increasing quality of good habitat, decreasing quality of poor habitat, or both

Change	(+, +)	(+, 0)	(+, −)	(0, 0)	(0, −)	(0, +)	(−, −)	Other[a]
Increase quality of good habitat:								
Breeding success	122	2,130	0	6,686	63	1	0	998
Survival	266	2,405	0	5,681	64	0	98	3,410
Both	434	2,237	0	5,506	62	0	99	3,690
Decrease quality of poor habitat:								
Breeding success	0	41	0	6,155	2,180	1	134	2,451
Survival	0	0	1	1,629	7,033	0	91	1,249
Both	0	0	0	1,481	6,511	0	79	1,934
Increase good and decrease poor quality:								
Breeding success	25	1,682	270	4,521	2,188	0	30	2,759
Survival	20	1,556	360	5	6,380	0	427	1,225
Both	0	1,566	331	0	6,246	0	511	1,296

Note: Each row is based on 10,000 randomly chosen parameterizations of the model. The table indicates the number of outcomes that fall into specified categories; for example, increase of residency in good, no change in poor habitat is marked as (+, 0). For example, increasing breeding success in good habitat leads to a switch to more residency in both habitats (+, +) in 122 cases.

[a] "Other" includes cases where no pure evolutionarily stable strategy was found or the chosen parameters did not lead to a viable population.

chosen between –0.1 and 0.1 (yet constraining maximum survival to 0.96). Nonresident survival s_N was chosen randomly between 0.5 and 0.96, and productivity $r_1 = r_2$ between 0.4 and 0.9. We then examined the effect of introducing habitat quality variation in the following nine alternative ways: first, increase productivity of habitat 1 (to $r_1 = 0.95$); second, increase resident survival in habitat 1 ($s_{R1} = 0.96$, $s_{D1} = s_{S1} = \min\,[0.96, s_{R1} + \delta]$); third, combine the first and second alternative; fourth, decrease productivity of habitat 2 ($r_2 = 0.4$); fifth, decrease resident survival in habitat 2 ($s_{R2} = 0.5$, $s_{D2} = s_{S2} = s_{R2} + \delta$); sixth, combine the fourth and fifth alternatives; seventh, increase productivity difference across habitats by combining the first and fourth alternatives; eighth, increase survival difference across habitats by combining the second and fifth alternatives; and, finally, increase productivity and survival differences across habitats by combining the third and sixth alternatives. For each of these nine cases, we scored the changes in residency strategies.

Introducing habitat variability often causes no change in strategies (table 2). Where it does, increasing the quality of habitat *i* mainly enhances residency in that habitat. Optimal behavior in the alternative habitat changes less often, and a change can either increase or decrease residency. Unsurprisingly, introducing habitat quality variation tends to lead to more residency in good habitats and less residency in poor habitats. However, increasing variation may either increase or decrease the intensity of competition for breeding sites, depending on how average breeding quality changes. Therefore, it is even possible—though rare—to observe a decrease in residency in both habitats, if good habitats improve and poor habitats deteriorate (table 2).

Discussion

Our model demonstrates how competition for limited breeding sites can favor strategies with various degrees of site-tenacious residency. The choice between residency and nonresidency is relevant to the evolution of dispersal, migration, and offspring retention (delayed dispersal), and we discuss the implications for each of these in turn.

Evolution of Dispersal in Territorial Populations

Factors such as kin selection (e.g., Hamilton and May 1977; Frank 1986; Taylor 1988; Ozaki 1995), inbreeding avoidance (Motro 1991; Gandon 1999; Perrin and Mazalov 2000), or temporal variability in population size or habitat quality and availability (e.g., Boulinier and Lemel 1996; Holt and McPeek 1996; Doebeli and Ruxton 1997; Paradis 1998; Parvinen 1999; Travis and Dytham 1999) have been shown to promote dispersal, even if dispersers suffer from increased mortality. By contrast, our results show that residency may be favored even if survival of residents falls below that of nonresidents, and if resident kin compete for the same local resources. How can this difference be explained?

Our focus is on territorial species where habitat availability constrains breeding success. Several assumptions made by general dispersal models are not necessarily valid in this context. These models usually assume that the currently occupied patch does not differ from other regions of the environment, possibly apart from increased relatedness to other individuals (e.g., Taylor 1988). In territorial species, however, "home" has a special status because ownership there is already established. Also, in social animals, harmful competition with relatives may be attenuated by mutualistic interactions among kin in the natal patch (Brown and Brown 1984; Ekman et al. 1994, 1999; Kokko et al. 2001*a*). Our model allows a simple form of mutualism, where parents accept the presence of retained offspring. Territoriality therefore favors residency, especially in locally good habitat (Boyce and Boyce 1988; Korpimäki 1993; Boulinier and Lemel 1996). The dispersal rate is not determined by an ESS that equalizes fitness of dispersers and nondispersers. Instead, dispersal may simply occur because dispersers have no option to stay resident, as they have been forcefully evicted by parents or other group members (e.g., Clutton-Brock et al. 1998). Indeed, our model consistently predicts lower fitness for floaters than for territory owners (see also Smith and Arcese 1989).

On the other hand, our model also shows that residency ceases to be evolutionarily stable when the survival of residents is too low to sustain a viable population. Contrary to the assumptions of dispersal models, leaving a site does not always increase mortality. Nonresidency may allow individuals to follow favorable conditions, even to migrate to other continents and to return when local environmental conditions have improved. Therefore, residents do not always enjoy higher survival (Lemel et al. 1997). Seasonal changes in resources, competition for these resources, and differences in survival and reproduction in different habitats then leads to the variety of dispersal and migration strategies of our model.

Residency versus Migration: The Role of Habitat Quality

Our model shows that migration is never an ESS if reproduction in a particular habitat exceeds the mortality of year-round residents. In other words, no matter how much better migrants survive, migration will be an inferior strategy if migrants lose to residents in competition for breeding sites and if resident survival is high enough so that the habitat is a source, rather than a sink, for year-round residents. Competition for prime breeding sites therefore strongly favors residency.

Where habitats differ in qualities, reproduction may exceed resident mortality in some areas but not in others. We then predict the evolution of partial migration, where poor sites are abandoned after the breeding season but occupants of good territories stay resident. Kaitala et al. (1993) concluded that density-dependent winter survival in residents and density-independent survival in migrants could account for the evolution of partial migration in birds. Our results show that partial migration can also occur when habitat quality does not affect the survival of residents but only their expected success during the following breeding season.

In common with earlier models of partial migration (Lundberg 1987; Kaitala et al. 1993; Kokko 1999), we find that residents should occupy better sites than migrants. This relationship to habitat quality is an example of state dependency of migration decisions (Smith and Nilsson 1987; Weber et al. 1998; Houston and McNamara 1999; Kokko 1999). Empirical studies indeed support the idea that residency provides priority to high-quality habitats (Smith and Nilsson 1987; Adriaensen and Dhondt 1990; Sandell and Smith 1991). However, we also show that given sufficient degree of habitat saturation, it may pay to remain resident even in the poorest habitat, to avoid the risk of not obtaining a territory at all. Partial migration may thus give way to complete residency, even if survival of all residents falls below that of migrants. This is an extreme form of a cascading competition for early arrival in the race to obtain breeding positions, as discussed in Kokko (1999).

Cooperative Breeding: A Life-History Strategy or a Response to Habitat Saturation?

We have modeled offspring retention in a "precooperative" setting, where parents may allow offspring to stay in their territory up to the start of the next breeding attempt. We focus on the evolution of delayed dispersal per se, without confounding fitness calculations by any effects that retained offspring might later have on the productivity of their parents. Despite the absence of helping behavior in this first step of cooperation, offspring retention can yield kin-selected benefits for the parent if it dies and the offspring inherits the territory. Alternatively, if dispersal is risky, staying in the natal territory may increase the offspring's survival through the nonbreeding season. This improves its chances of acquiring a breeding site elsewhere, even if it does not inherit the natal territory (Ekman et al. 2000). Either way, offspring retention can evolve to ensure that offspring survive to obtain a (preferably high-quality) territory (parental facilitation; Brown and Brown 1984), even at a cost of reducing the parent's own survival (Ekman and Rosander 1992; Kokko and Johnstone 1999).

Delayed dispersal is generally considered the first step in the evolution of cooperative breeding (Brown 1987). The prevailing consensus is that increasing habitat saturation decreases the benefits of dispersal and thus makes natal philopatry the better option (e.g., Emlen 1997). The effects of habitat saturation are well documented in several species of cooperative breeders. Experimental removal of saturation has been shown to bring about independent breeding in superb fairy wrens *Malurus cyaneus* (Pruett-Jones and Lewis 1990), Seychelles warblers *Acrocephalus sechellensis* (Komdeur 1992), and red-cockaded woodpeckers *Picoides borealis* (Walters et al. 1992). Nevertheless, the core of the argument remains to some extent unclear, as habitats often appear saturated in numerous uncooperatively breeding species as well (Brown 1969; Hatchwell and Komdeur 2000). Removal experiments of territorial temperate-zone birds typically lead to rapid replacements by "floaters" (reviewed in Newton 1992). Radiotracking has similarly revealed floaters in noncooperative species such as great horned owls *Bubo virginianus* (Rohner 1997). Indeed, recent modeling suggests that populations limited by habitat availability may generally evolve toward a maximum number of competitors for territories (Kokko and Sutherland 1998; see also Pen and Weissing 2000; Kokko et al. 2001*b*). The fact that saturation per se does not explain delayed dispersal has first been pointed out more than 3 decades ago (Brown 1969; see also Koenig et al. 1992), but it is still presented as the primary reason behind offspring retention and consequent evolution of cooperative breeding (e.g., Emlen 1997; but see Hatchwell and Komdeur 2000).

In studies on cooperative breeding, "habitat saturation" has been viewed as an "ecological constraint," which limits the opportunities for independent breeding of offspring. Research has thus focused on a direct link from saturation to delayed dispersal and cooperative breeding (fig. 5). Our model shows that increasing intensity (as opposed to mere existence) of habitat saturation, that is, a high ratio of competitors to vacancies, may indeed favor delayed dispersal. However, saturation is not determined externally by the environment: it is a dynamic outcome of the dispersal decisions of individuals. A few recent papers have considered other links in figure 5. Arnold and Owens (1998) and Hatchwell and Komdeur (2000) discuss the indirect link from high resident survival to cooperative breeding via increased habitat saturation (lowered turnover rate of territories), while Kokko and Johnstone (1999) consider the direct link from resident survival to cooperative breeding, as a result of enhanced importance of future rather than current fitness payoffs in long-lived species. Our results show that high resident survival favors delayed dispersal both directly (residents survive better than floaters) and indirectly (vacancies become scarce), even though parent-offspring conflict may cause exceptions to this rule.

The model in Kokko and Johnstone (1999) is a variant of reproductive skew theory (see Reeve 1998; Johnstone 2000 for reviews), where "ecological constraint" is defined as the probability of a disperser obtaining a breeding position. Tightest constraints should combine poor survival of dispersers and a high degree of habitat saturation. However, our results reveal that poor survival of dispersers has two opposing effects (fig. 5). It makes offspring retention more favorable (to avoid entering the dangerous dispersal stage; Spinks et al. 2000), but it also directly decreases habitat saturation as fewer floaters survive to compete for vacancies. Hence, we must treat with caution the suggestion that a single measure, such as the rate of territorial turnover (which roughly corresponds to the inverse of the habitat saturation factor, $1/H$), can sufficiently summarize the effect of life-history traits on cooperative breeding (Hatchwell and Komdeur 2000).

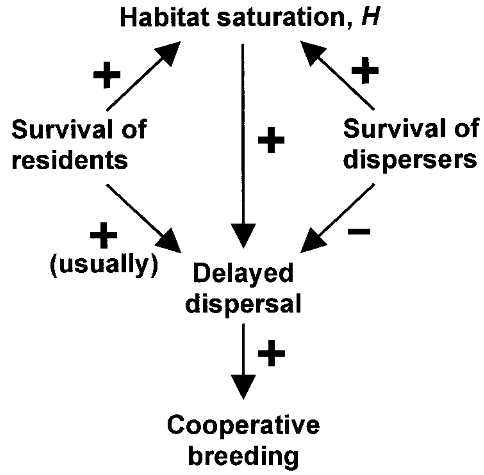

Figure 5: Graphical summary of the model results in the context of delayed dispersal. Intense competition for breeding sites, as measured by the habitat saturation factor, H, will favor delayed dispersal. However, it is not determined externally for each population, but it is a dynamic outcome of survival rates in resident and dispersing individuals. These have independent, direct effects on delayed dispersal, which may override the effect of habitat saturation. Most important, improved survival chances in dispersers increases H but have a negative effect on delayed dispersal. Increased survival of residents usually favors delayed dispersal, but parent-offspring conflicts may sometimes produce the opposite outcome.

Clearly, one must consider both survival and territory acquisition prospects in individuals that choose to stay or leave, instead of summarizing their fate with an externally defined constraint. To put it simply, all other factors being equal, more intense competition for territories (tighter constraints) will encourage delayed dispersal. But since the strength of competition is determined by life-history traits such as survival and productivity across habitats, all other factors will not be equal in natural populations. Even though independent breeding can be expected when breeding vacancies are generated experimentally within a population, interspecific conclusions regarding the relationship between constraints and cooperative breeding are likely to fail because of variations in the underlying opposing effects of life histories of the species concerned.

The importance of the relative survival of residents and nonresidents, as opposed to constraints as such, also supports a possible explanation for the relative rarity of cooperative breeding at temperate latitudes (Brown 1974). In highly seasonal environments, groups may disband simply because low resident survival during the nonbreeding season brings about the migratory ESS. Although previous owners often have priority in conflicts over territories (Krebs 1982; Rohwer 1982; Jakobsson 1988; Bortolotti and Iko 1992; Tobias 1997), maintaining group ownership of a fixed location is likely to be much more difficult in migratory species than in those for which year-round residency is an option (see Pärt 1991). The first prerequisite for cooperation may then be lack of the need to migrate, and the prevalence of cooperative breeding in the Tropics and in Australia could simply reflect a more favorable cost-benefit balance for year-round residency (Russell 1989). A recent phylogenetic analysis indeed finds support for a relationship between mild winter climate, sedentariness, and cooperative breeding in birds (Arnold and Owens 1999). Interesting exceptions to this pattern are provided by species such as the Bewick's swan *Cygnus columbianus*, where families are able to remain united during migration and parents provide protection for their young in their first winter (Scott 1980). It would be interesting to know whether parental facilitation can extend to the acquisition of territories on the breeding grounds in any migratory species.

Our model also considers habitat quality variation. Large local variation in habitat quality might favor cooperation if offspring born in high-quality territories do better by staying than by dispersing to low-quality habitat. Stacey and Ligon (1991) found that two cooperatively breeding species had larger among-territories variation in reproductive success than a similar noncooperative breeder. According to our results, decreasing the quality of poor habitat often induces dispersal from that habitat, but it only rarely selects for increased residency in good habitats. To see why, it is important to consider the production of competitors in the whole population. The success of an individual that disperses to another territory is smallest when neighboring territories are of poor quality, and we might expect residency in territories surrounded by poor habitat. However, the risk of not finding a territory at all is highest if neighboring territories are of high quality, since good territories produce competitors at a high rate. Since failing to breed at all is a greater failure than breeding in poor habitat, the benefit of residency is not necessarily strongest in the most variable environments.

It is therefore not clear that quality variation has the effect proposed by Stacey and Ligon (1991). With particular parameter values, we found that increasing quality variation may indeed select for residency, but this effect is hardly consistent enough to explain the pattern noted by Stacey and Ligon (1991). However, within populations, our model predicts a relationship between habitat quality and offspring retention: given sufficient quality variation, philopatry should be restricted to high-quality habitat. This agrees with empirical observations (Komdeur 1992; Komdeur et al. 1995), as well as with a model of queuing for breeding positions, which predicts longer queues for high-quality sites and the absence of queuing behavior at the worst sites (Kokko and Sutherland 1998).

General Conclusions

We have developed a general theory of habitat use that builds on few simple principles: priority of access to an area by staying resident, a possibility to find a better area by leaving the area, a survival difference between residents and nonresidents, and parent-offspring conflict. Priority-dependent access to resources not only can explain various dispersal and migration strategies but can also favor offspring retention, which may further lead to the evolution of other forms of parental facilitation as well as helping by offspring. These areas of research have traditionally been treated as independent nodes of inquiry, whereas we show that competition for limited breeding sites can underlie and unify this diversity. Most important, we show that an ecological variable such as habitat saturation or ecological constraint is inadequate as an independent driving factor in the evolution of space use strategies. Saturation is not a monopoly of cooperatively breeding species nor can it be treated as an external variable affecting the opportunities available to the individual. Unless habitat saturation is related to the dynamics of a population in which dispersal strategies evolve, it has little explanatory power.

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APPENDIX

Derivation of ESS Conditions for a Migratory Population

The task is to find the criteria under which a migratory population cannot be invaded by any other strategy. First, migrants must survive well enough to produce a stable population. This means that the migratory population breeding at the $n_1 + n_2$ sites produces enough individuals to fill the habitat in the future as well:

$$s_N[n_1(1 + r_1) + n_2(1 + r_2)] \geq n_1 + n_2, \tag{A1a}$$

$$\Leftrightarrow \quad s_N(1 + \bar{r}) \geq 1, \quad \text{where } \bar{r} = \frac{n_1 r_1 + n_2 r_2}{n_1 + n_2}. \tag{A1b}$$

The expression $\bar{r}$ gives the average breeding success in the environment.

Since all individuals migrate and compete for vacant territories in the spring, equations (6a) and (6b) obtain the simple form

$$w_1 = (1 + r_1)s_N w_c, \tag{A2a}$$

$$w_2 = (1 + r_2)s_N w_c. \tag{A2b}$$

We may set $w_c = 1$. The first criterion (eqq. [8a], [8b]) compares the success of a lone individual who migrates or stays resident:

$$s_N w_c > s_{R1} w_1 \Leftrightarrow s_{R1}(1 + r_1) < 1, \tag{A3a}$$

$$s_N w_c > s_{R2} w_2 \Leftrightarrow s_{R2}(1 + r_2) < 1. \tag{A3b}$$

The second criterion (eqq. [9a], [9b]) results in exactly the same equations. This is because, in a migratory population, both failed (eq. [8]) and successful (eq. [9]) parents would become lone residents if they decided to stay. The third criterion does not apply because the offspring are migratory.

The first part of the fourth criterion (eq. [11a]) is again equivalent to (A2a) and (A2b): the offspring has the option either to leave and to obtain fitness $s_N w_c$ or to stay and to obtain fitness $s_{R1} w_1$ versus $s_{R2} w_2$ in good versus poor habitats, respectively. The second part of the fourth criterion (eq. [11b]) again reduces to (A2a) and (A2b), since the migratory parent's own survival is not affected by whether its offspring stays resident or migrates. Hence, equations (A2a) and (A2b) completely describe the criteria for the evolutionary stability of migrating.

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