Male Seychelles warblers use territory budding to maximize lifetime fitness in a saturated environment

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In cooperatively breeding species, helping at the nest and budding off part of the natal territory have been advanced as strategies to increase fitness in an environment that is saturated with territories. The importance of helping or territory budding as a determinant of lifetime reproductive success (LRS) has been debated because the potential benefits of both strategies could not be separated. Here we test the causes and the immediate and future fitness consequences of single dispersal decisions taken by male Seychelles warblers (*Acrocephalus sechellensis*). Males breeding in high-quality territories (high food abundance) have significantly higher LRS than similar-aged males budding off part of the parental territory. Initially, budders have a low reproductive success (because of limited food resources or absence of a breeding partner). However, they have a long life span and inherit high-quality territories through site dominance, by which they gain higher LRS than breeders on low-quality territories, helpers, or floaters. Experimental creation of male breeding territory vacancies showed that most young males became budders because of intense competition for high-quality territories. The translocation of warblers to the previously unoccupied Aride Island shows that males behave according to the expected fitness benefits of each dispersal strategy. In the absence of competition for territories on Aride, all young males bred in high-quality territories. However, after saturation of high-quality habitat with territories, most males became budders rather than breeders on low-quality habitat, helpers, or floaters. *Key words: Acrocephalus sechellensis,* budding, dispersal, helping, lifetime reproductive success, Seychelles warbler, territory inheritance. *[Behav Ecol 12:706–715 (2001)]*

In many taxa there is variability among individuals in age at first breeding, and frequently the delay in reproduction extends past the time of sexual maturity (Bourke, 1997; Brown, 1987; Emlen, 1995; Lawton and Lawton, 1986; Riedman, 1982; Stacey and Koenig, 1990; Taborsky, 1994; Zack and Stutchbury, 1992). The main reason for delayed reproduction is the forfeiture of fitness costs associated with missed or suppressed reproductive opportunities or with gaining reproductive status in inferior territories (Cockburn, 1998; Emlen, 1994, 1997; Sibley and Calow, 1986; Studd and Robertson, 1985; Wittenberger, 1979). In only 3% of bird species with delayed reproduction do individuals remain with their parents on their natal territory (Cockburn, 1998; Emlen, 1995). Remaining offspring providing alloparental care to close relatives can indirectly increase the number of their genes in future generations, whereas budders can increase their direct fitness by "budding off" a portion of the natal area as their own breeding territory. For more than twenty years researchers have debated how remaining nonterritorial individuals improve their fitness through helping others to breed (reviewed by Cockburn, 1998; Emlen, 1991, 1994; Heinsohn et al., 1990). This research has been hampered by the fact that the potential fitness effects of delayed dispersal, helping, and budding behavior could not be separated due to individuals using mixed strategies. In addition, few studies have been long

enough to investigate the fitness benefits accrued to helpers and budders (Arcese, 1989; Chepko-Sade and Halpin, 1987; Emlen, 1995), and experimental studies under natural conditions have yet to be performed (Balshine-Earn et al., 1998; Emlen, 1991, 1995). In this study, we tested the causes and the immediate and future fitness payoffs (e.g., territory inheritance) of remaining and dispersing tactics used by male Seychelles warblers (*Acrocephalus sechellensis*).

Until 1988, the entire world population of Seychelles warblers was confined to Cousin Island (29 ha), where it had reached carrying capacity since 1973. Given this and the vulnerability of one small island in the Indian Ocean, an additional breeding population was successfully established on Aride Island (68 ha) in September 1988 (Komdeur, 1992). The warblers are insectivorous, usually have clutches of a single egg (91.0%, $n = 223$), are single brooded, and have high annual adult survival (81.1%, 334 bird-years). Once paired, the breeding pair remains in the same territory until the death of one member of the pair. Territories differ in quality, measured in terms of insect prey availability (Komdeur, 1992). Young birds are excluded from breeding due to habitat saturation and are more likely to stay on high-quality natal territories because of higher foraging success leading to increased survival (Komdeur, 1992). In addition, remaining female offspring increase their lifetime fitness by helping, through which they gain indirect benefits and parental experience (Komdeur, 1996a). Because helpers are mainly females (88%, $n = 271$), we assume that males must have developed other strategies to increase their fitness.

In this study we had two principal aims. First, we wanted to describe reproductive tactics and the fitness consequences of young males born in a saturated, high-quality environment on

Cousin Island. We analyzed the fates and fitness consequences of all tactics used: breeding, floating, and remaining as helper or nonhelper. We used 14 years of data from an individually marked population of which the behavioral parents (breeders) for all the produced young are known. For an entire cohort of males, the dispersal tactics, every nesting attempt, and its outcome are known throughout their lives. Second, we sought to establish whether the lifetime payoffs of the tactics predicted the observed dispersal behavior after experimental manipulation of the habitat. We tested this by creating male breeding vacancies that differed in reproductive prospects and then monitoring whether males using lower fitness-related tactics took over the available vacancies. In addition, the transfers of same-aged male warblers, with different previous background, to the unoccupied island of Aride allowed us to test the extent to which the fitness payoffs associated with the dispersal tactics on Cousin island also hold true in the new situation on Aride. We also expected that the dispersal tactics of males born on Aride gradually change over time when competition over territories becomes more intense.

METHODS

Study area and data collection

The entire population of Seychelles warblers on Cousin Island (115–123 groups, 310–400 birds) was under study from December 1982 till October 1996. Between 23 and 29 September 1988, 29 color-ringed adult warblers (16 males and 13 females; all between 3 and 5 years old) were transferred from Cousin Island to Aride Island by motorboat. On the high-quality habitat on Aride (see below), all breeding groups and their male offspring were studied from September 1988 to March 1997. Data were based on individually color-ringed males, ringed as nestlings, of which the dispersal, settlement patterns, and reproductive success were monitored monthly after hatching. All territories were checked regularly for 1 h (every 2 weeks, 1985–1991; every 4 weeks, 1982–1984, 1992–1997) for nests with a clutch or young and for presence of color-ringed birds to assess dispersal and survival of birds. As warblers rarely colonize other islands by themselves [out of 2156 ringed adults, only one bird (0.05%) is known to have flown from Cousin Island to Cousine Island], we assumed that missing birds had died if they were not found on other territories on the same island. We recorded the status of each male each month during the male's entire adult life using the following definitions. A helper was a male present on the natal territory engaged in helping at the nest. A nonhelper was a male present on the natal territory that did not help at the nest if a nest was present. A budder was a male that defended part of the parental territory against his parents and other warblers to acquire a territory (budded territory) for himself, in the absence of a vacancy. A floater was a male that was rarely present on the natal or a particular breeding territory; in contrast, helpers, nonhelpers on the natal territory, and budders could be engaged in exploratory forays searching for reproductive vacancies and could be absent from their natal territories for 1–5 days (Komdeur, 1991), but they had not severed the ties with their natal group. A breeder was a male that obtained a vacant breeding territory with a female partner when he had not been a helper, a nonhelper, a budder, or a floater after reaching maturity. When a helping, nonhelping, budding, or floating male eventually acquired a breeding territory with a female partner, these males were still referred to as helpers, nonhelpers, budders, or floaters, respectively, because we wanted to quantify the fitness of males initially performing each of these strategies upon reaching the age of maturity.

Territory and habitat quality

Territory quality, which was not determined by the presence of nest sites and nest predators (Komdeur, 1991, 1994a,b), was measured in terms of insect prey available. Because the warblers are insectivorous, taking 98% of their insect food from leaves (Komdeur, 1991), the quality of a territory depends on insect prey available and amount of foliage. Territory quality was therefore expressed as mean number of prey invertebrates available within a territory. The quality of territories was assessed every 3 months (Cousin: June 1982–June 1996; Aride: September 1988–June 1996). Before translocation of birds, the area of low- and high-quality breeding habitat present on Aride Island was estimated as follows. The total vegetated area of Aride Island (62.7 ha) was subdivided into 36 plots of 132 × 132 m. Within each plot a subplot of 50 × 50 m (the same size as an average warbler territory on Cousin) was mapped, and the insect quality of this plot was measured monthly from September 1987 to September 1998. The method used to measure territory quality on Cousin and Aride and area quality on Aride is presented elsewhere (Komdeur, 1992, 1994a). Because the quality of breeding territories remained constant between years (Komdeur, 1996b), territory and area quality was expressed as the average quality over the whole research period and divided into low quality (lqt: 0–3000 insects present) and high quality (hqt: >3000 insects present). On Aride Island the total area of high-quality and low-quality breeding habitat was calculated as the total area of high- and low-quality plots, respectively (see Methods, Experimental removals and translocations). We defined saturation of high-quality habitat as the complete occupation of high-quality habitats with territories. We calculated annual saturation index of high-quality habitat on Aride Island as the quotient of the number of territories in this habitat in a given year and the number of territories at first saturation of high-quality habitat (i.e., 24 territories; see Results).

Fitness accounting

Lifetime reproductive success (LRS) is expressed as the total number of yearling offspring produced over a male's lifetime. The analyses on Cousin were restricted to males born on high-quality territories in the years 1982–1986 who reached at least 8 months of age (the minimum age of reproduction), died before the end of the study period, and did not fill experimentally created breeding vacancies (see below; $n = 46$). Ages were based on known hatching date. On Cousin, we excluded the younger cohorts because their LRS was not yet known, as some males are still alive. On Aride, however, because some of the cohort males are also still alive at present, we calculated the reproductive performance over their first 5 years of life to gain adequate cohort sizes for analyses. Because cohorts were equally spread over the years (Cousin: 8, 9, 9, 10, and 10 males; Aride: 15, 11, and 13 males), we did not examine for cohort variation. In all years between 1982 and 1996 on Cousin, the density of warblers (300–326 adults), and territories of different qualities (hqt: 15–18; lqt: 100–105 territories) remained the same (Komdeur, 1996b).

LRS was calculated as $V_h + V_b$, where V_h = indirect helping benefits, and V_b = direct breeding benefits. The indirect helping benefit, which is the production of additional related yearlings as a result of the activities of the male helper, beyond the expected reproduction of the focal breeding without the male helper, is estimated as

$$V_h = 2 \sum_{i=1}^{a-1} R_{m,o} V_{hi}$$

where a is the age of the male of first independent reproduc-

tion as a breeder, $R_{m,o}$ is the putative coefficient of relatedness between the male helper m and the offspring o he helps to raise (calculated using data from an individually marked population of which the behavioral parents [breeders] for all the produced young are known), and V_{hi} is the additional number of yearlings produced by the breeding pair through help of a helper of age i, estimated as

$$V_{hi} = (V_{ni} - V_p)$$

where V_{ni} is the number of yearlings produced by the focal breeding pair with helper(s) in year i, and V_p is the mean number of yearlings produced by the breeding pair with one helper less in other years. In some case the value of V_{hi} is negative due to a decrease in production through resource competition (Komdeur, 1992). To express V_h in offspring equivalents accrued to the helper, we multiplied $R_{m,o}$ in the expression of V_h by a factor of 2 because the coefficient of relatedness to both classes of young (additional sibs "produced" by the helper and offspring produced by the breeder) is 0.5.

The fitness obtained through direct reproduction of the male is given by:

$$V_b = \sum_{j=a}^{w} V_{bj}$$

where V_{bj} is the number of yearlings produced by the male at age j (including the offspring due to help received). We did not control for double counting of the direct fitness value, V_b (see also Queller, 1996) given the conditional expression of the breeder–helper distinction and the asymmetry in choosing the breeder or helper role (male reproducers never become helpers, and male helpers never become reproductives in their natal territories; Richardson et al., 2001).

Experimental removals and translocations

The extent to which males discriminate among breeding opportunities according to likely reproductive potential, and the extent to which competition for territories that vary in reproductive potential contributes to changes in male dispersal tactics were analyzed by a removal experiment and a translocation experiment. Experimental removals accelerate the natural process of breeder replacement and make the behavioral mechanisms of competition for reproductive status more accessible to study. Within a season, territories chosen for removals were separated from each other by at least four territories to avoid mutual interactions.

First, we selected five high-quality and five low-quality breeding territories with highest and lowest reproductive potential, respectively (see Results), on Cousin Island. Each territory contained an unaided breeding pair and was situated next to one high-quality budded territory with second-highest reproductive potential (see Results) containing a male without a breeding partner. The male of the breeding pair was removed and translocated to Aride, and the budding male was observed on successive days after removal. This experiment was conducted 23–29 September 1988.

Second, the translocation of warblers to Aride Island allowed us to test the influence of male status and habitat quality on dispersal tactics used by these males. We transferred 16 male warblers that were of similar age (3–5 years) but had a different status (five breeders on high-quality territory, five breeders on low-quality territories, three budders, two helpers, and one floater) from Cousin Island to the unoccupied island of Aride, with high- and low-quality breeding habitat available (5.6 ha and 62.4 ha, respectively). The males were released in the low-quality habitat and subsequently followed weekly to monitor the habitat in which they eventually established territories. In addition, with increasing competition over territories, we expected males born on Aride to discriminate among the various dispersal tactics according to likely reproductive potential. On Aride Island, there was no competition over high-quality vacancies until October 1990, but thereafter the high-quality habitat had become completely saturated with territories (Komdeur, 1992). On Aride we distinguished two male cohorts born on high-quality territories: Cohort A_{before} consisted of 15 males born between October 1988 and January 1990 that had reached the reproductive age of 8 months before 1 October 1990 (the time of first saturation of the high-quality habitat); cohort A_{after} consisted of 24 males born between February 1990 and January 1992 that had reached 8 months of age after 1 October 1990. The internal controls in this study are the dispersal and settlement pattern of two male cohorts born on the saturated, high-quality habitat on Cousin Island. Cohort C_{before} consisted of 14 males born between October 1988 and January 1990, and cohort C_{after} consisted of 19 males born between February 1990 and January 1992.

Statistical analysis

Means are expressed with standard deviations, the presented probability values are two-tailed, and the null hypothesis was rejected at $p < .05$. We analyzed normally distributed continuous data of different categories using ANOVA with post-hoc Tukey testing to establish group identities; the relationship between similar data and a continuous variable was analyzed by means of linear regression. The relationship between proportions and a continuous variable was analyzed by means of logistic regression; proportions in a contingency table were analyzed using a log-linear modeling approach, where all frequencies were increased by 0.005 to avoid high numbers of cells with zero scores. We tested repeated measures of normally distributed, continuous data of different categories with multivariate analysis of variance (MANOVA). Differences between repeated measures within categories and differences between categories within repeated measures were tested by constructing the appropriate A- and C-matrices for hypothesis testing. We used SYSTAT 7.0 (1997) for analyses.

RESULTS

Variance in LRS on Cousin

The total number of yearlings produced by 46 adult male warblers was 153 (Figure 1), of which 64 were males. The highest observed LRS of a male was 10 yearlings ($n = 2$), but the average LRS was 3.3 ± 3.0 yearling per male. Of the observed males, 26.1% died without having produced offspring of their own. Only a few males were successful: of the 153 yearlings, 82 (53.6%) were produced by only 11 (23.9%) adult males. The production of male yearlings was 39.1% $[(64–46)/46 \times 100]$ more than the total sample of adult males. Recruitment on high-quality territories was therefore significantly higher than adult mortality, and hence competition for high-quality vacancies was intense.

Dispersal strategies and LRS on Cousin

Table 1 summarizes the demographic benefits and duration of dispersal strategies and reproductive life span of males using different strategies. The average age at which males became breeders, budders, helpers, or floaters was 1.0–1.2 years, which was similar for all strategies. The dispersal strategies affected both annual reproductive success and longevity, and consequently LRS. The best option for male yearlings to gain
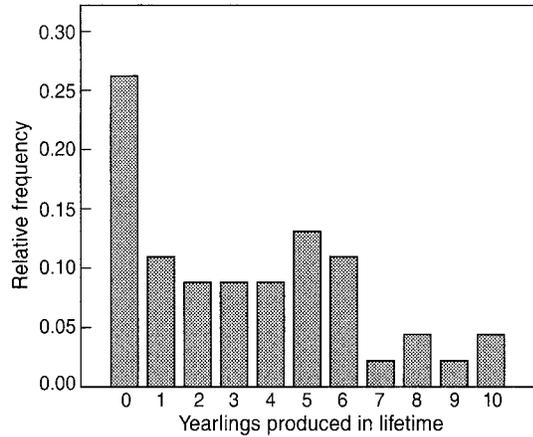
Figure 1
Lifetime reproductive success for 46 adult male Seychelles warblers hatched on high-quality territories on Cousin Island between 1982 and 1986.

highest LRS is breeding immediately on high-quality territories, whereas the second best option is budding on high-quality territories. Males starting as budders had the same high longevity as those breeding immediately on high-quality territories. Budding males started the budding process in their natal territories at an average age of 1.1 years old, expanded their budded territory at the expense of adjacent territories, and lived in the budded area for, on average, 2.6 years (two examples of this process are illustrated in Figure 2). The shortest and longest period a male lived in a budded territory was 0.9 and 6.2 years, respectively. Even though nearly all budders (90.5%; $n = 21$) acquired a mate at a later stage during the budding process, annual reproductive success in the budded territory was low and similar to annual indirect reproductive success of helpers on high-quality territories, to annual direct reproductive success of floaters, and to breeders on low-quality territories (Table 1). However, reproductive potential was not sacrificed by budding. By the average age of 3.7 years, budders had left their budded territory and filled high-quality breeding vacancies, either on their natal territories or on adjacent territories (33.3% and 66.7%, respectively; $n = 21$). The annual reproductive success on these newly ac-

quired territories was comparable to that of males breeding on high-quality territories at 1 year of age (Table 1). Considering each dispersal strategy separately, males starting as budders had significantly lower LRS than males breeding immediately in high-quality territories but significantly higher LRS than males starting either as a helper, a floater, or a breeding bird on low-quality territories at 1.0–1.2 years of age (Table 1). Males using one of the last three strategies had a two to five times lower longevity, with virtually no successful reproduction (Table 1). All floaters ($n = 5$) and 50% of the helpers ($n = 6$) died without having acquired a breeding territory.

Even though males born in high-quality territories can expect to gain highest lifetime reproductive success by breeding immediately in high-quality territories, only a few did so (15.2%, Table 1) because of the shortage of high-quality breeding vacancies. In all years from 1982 to 1996, in the high-quality habitat production of adult males was significantly higher than could be accommodated in the male breeding vacancies (annual mean: 7.1 ± 2.4 and 1.7 ± 1.3, respectively; paired t test: $t = 11.11$, df = 14, $p < .001$), whereas in the low-quality habitat the number of adult males produced was equal to the number of male breeding vacancies (annual mean: 22.7 ± 5.0 and 19.3 ± 2.9, respectively; $t = 1.84$, df = 14, ns). Of 316 breeding vacancies for males, 91.8% were on low-quality and only 8.2% were on high-quality territories. Even though competition for low-quality breeding vacancies was less, most male offspring that were not breeding immediately in high-quality territories ($n = 46$–$7 = 39$) budded off a portion of their natal territory (53.8%), whereas a small fraction filled breeding vacancies on low-quality territories (17.9%), became floaters (12.8%), or remained with their parents as helpers (15.4%) (Table 1). Although some of the budders and helpers did eventually fill a breeding vacancy, budders, helpers, and floaters were never observed switching between the strategies of budding, helping, and floating. These findings suggest that competition for high-quality territories and LRS payoffs have caused the males to become budders on Cousin. This led us to test two concomitant predictions. First, budders on high-quality territories should fill high-quality breeding vacancies only. Second, in the absence of habitat saturation on Aride, young males born on high-quality habitat should establish breeding territories in the unsaturated high-quality habitat immediately after reaching independence. However, after saturation of the high-quality

Table 1

Demographical benefits, duration of dispersal strategies, and reproductive life span of males using different strategies

Strategy	Age	Before filling breeding vacancy		After filling breeding vacancy			Life span (years)	n
		Annual RS	Years	Annual RS	Years	LRS		
Breeder hqt: vacancies	1.0 (0.2)	—	—	1.0 (0.3)[A]	7.2 (1.9)	7.0 (1.3)[A]	8.2 (1.8)[A]	7
Budder hqt	1.1 (0.3)	0.2 (0.4)[A]	2.6 (1.7)	1.1 (0.5)[A]	4.6 (2.5)	4.6 (2.2)[B]	8.4 (2.1)[A]	21
Helper hqt	1.1 (0.1)	−0.2 (0.9)[B]	0.9 (0.4)	0.2 (0.8)[B]	0.6 (0.9)	0.3 (0.5)[C]	2.6 (0.8)[B]	6
Floater	1.0 (0.1)	0.0 (0.0)[AB]	0.7 (0.1)	—	—	0.0 (0.0)[C]	1.7 (0.1)[B]	5
Breeder lqt: vacancies	1.2 (0.1)	—	—	0.3 (0.3)[B]	2.8 (1.3)	0.9 (0.8)[C]	3.9 (1.4)[B]	7
F (ANOVA)	0.78	4.01		8.90		23.6	26.9	
χ^2								19.2
df	4	2		3		4	4	4
p	ns	.029		<.001		<.001	<.001	<.001

Average (± SD) for age of first dispersal, annual reproductive success (annual RS; number of yearling offspring produced per year), and duration of dispersal strategy before filling a breeding vacancy, annual RS and duration of breeding after filling breeding vacancy, lifetime reproductive success (LRS; total number of yearling offspring produced over a male's lifetime), and life span of Seychelles warbler males using different dispersal strategies on Cousin Island. All males were born on high-quality territories (hqt) between 1982 and 1986, had reached at least one year of age ($n = 46$) and have died before the end of the study. Statistical differences in annual RS, LRS, and life span between dispersal strategies and statistical differences between the frequency of dispersal strategies (n values) were tested by ANOVA, with a post-hoc Tukey-test to identify groups. Group identities are indicated by superscript A, B and C; n, sample size; lqt, low-quality territory.
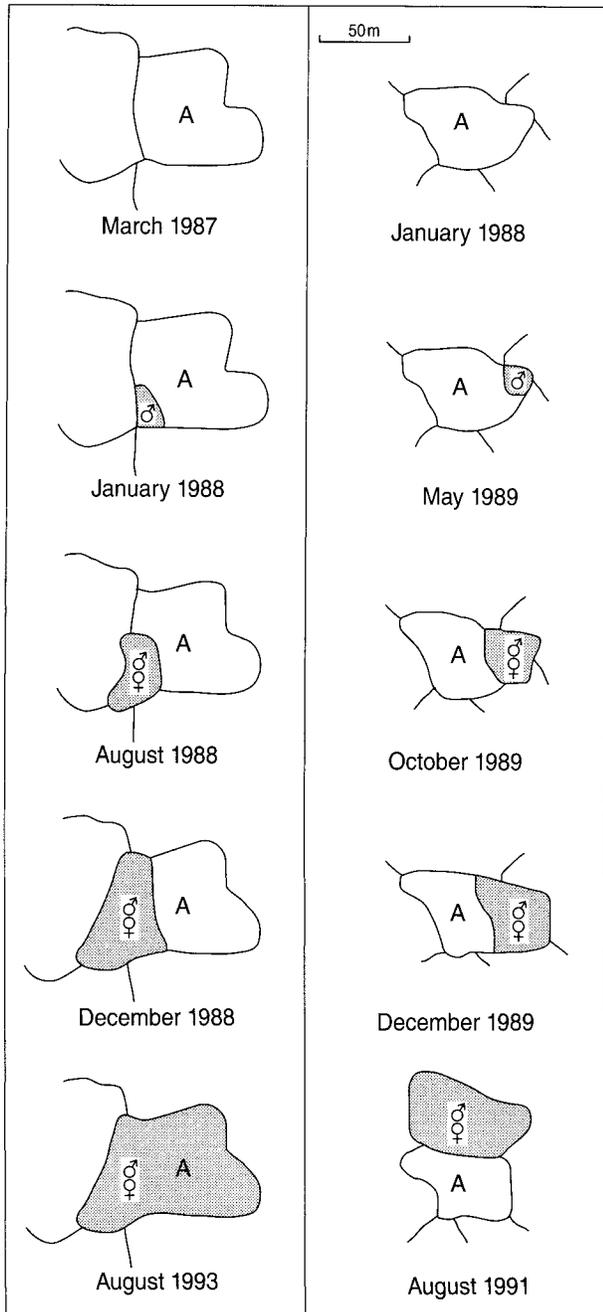
Figure 2
The process of territory fission and territory inheritance as illustrated by two Seychelles warbler males, hatched in March 1987 and January 1988, respectively. The shaded areas represent land inherited by the son of the original pair which occupied territory A. The territory boundaries of the original pair of breeders (since hatching of their son) and of their son are shown across a span of several years. After about 1 year the son defended and budded off part of the natal territory. Subsequently, a female was acquired and a new territory was formed. The territory boundaries of the son expanded at the expense of the natal territory first and neighboring territories later. The budding males inherited their natal territories through the death of their fathers, 5 years and 8 months, and 2 years and 4 months after the start of budding, respectively.

habitat, young, mature males born in high-quality territories should remain on their natal territories as budders; they should not become breeders on low-quality territories, helpers, or floaters.

Facultative dispersal on Cousin and Aride

Removals on Cousin Island
The relative quality of the breeding vacancy significantly influenced the budder's dispersal behavior. On Cousin Island, all five experimental high-quality breeding vacancies were filled by budders from adjacent high-quality territories within 2 h after the removal of the senior breeding male. However, none of the five low-quality vacancies were filled by budders from adjacent high-quality territories. These were all filled by males born on low-quality territories (two-tailed Fisher's Exact test, $p = .008$).

Translocation to Aride Island
The 16 males with different dispersal status translocated to Aride Island all established territories in the high-quality habitat during the month after translocation. Before saturation of the high-quality habitat, all males belonging to cohort A_{before} left their natal territories at 0.7 ± 0.2 years of age ($n = 15$). Most of these males established new territories in the high-quality habitat, some filled breeding vacancies on high-quality territories, but none became budders, helpers, floaters, or breeders on low-quality habitat (Figure 3). After the high-quality habitat became saturated, none of the cohort A_{after} males established territories on the high-quality habitat directly. The fraction of these males filling high-quality breeding vacancies was the same as before saturation (Figure 3). Most cohort A_{after} males became budders on their natal territories, few became helpers, breeders on low-quality territories, or floaters. The first males seen helping, breeding in lower-quality territories, and floating were observed in 1991, 1991, and 1996, respectively. On Cousin Island, however, most males of cohorts C_{before} and C_{after} became budders; none established new territories in the high-quality habitat, and few became helpers, floaters, or breeders on low-quality habitat (Figure 3). The change in the frequency of budding before (cohort A_{before}) and after saturation of high-quality habitat on Aride Island (cohort A_{after}) compared with the control groups on Cousin Island (C_{before} and C_{after}) was significant (Figure 3).

The number of territories on high-quality habitat increased linearly from 13 in September 1988 to 24 in September 1990 to 39 in September 1993. From 1993 onward, the number of territories on the high-quality habitat has remained stable between 39 and 41 territories (Figure 4). Mean annual territory size remained the same from 1988 to 1990, but declined from 1991 to 1996 (Figure 4).

Between 1990 and 1992, all budders converted their budded territory into permanent, high-quality breeding territories by enlarging their territory at the expense of the natal territory and surrounding territories ($n = 15$; see also next section). These territories were still present at the end of the study period (March 1997). As a consequence, more territories became established in the already saturated, high-quality habitat (Figure 4). The annual increase in number of territories on high-quality habitat until 1993 was the same as before saturation (mean annual increase: 1990–1993: 5.0 territories [$n = 3$ years]; 1988–1990: 5.5 territories [$n = 2$ years]). From 1993 onward, however, only a few of the then-budded territories became permanent, high-quality breeding territories (10.5%, $n = 19$; Figure 5). Most disappeared (89.5%) because the budder ascended to high-quality territories by taking over breeding vacancies either on his natal territory or on adjacent territory, after which the budded area merged with
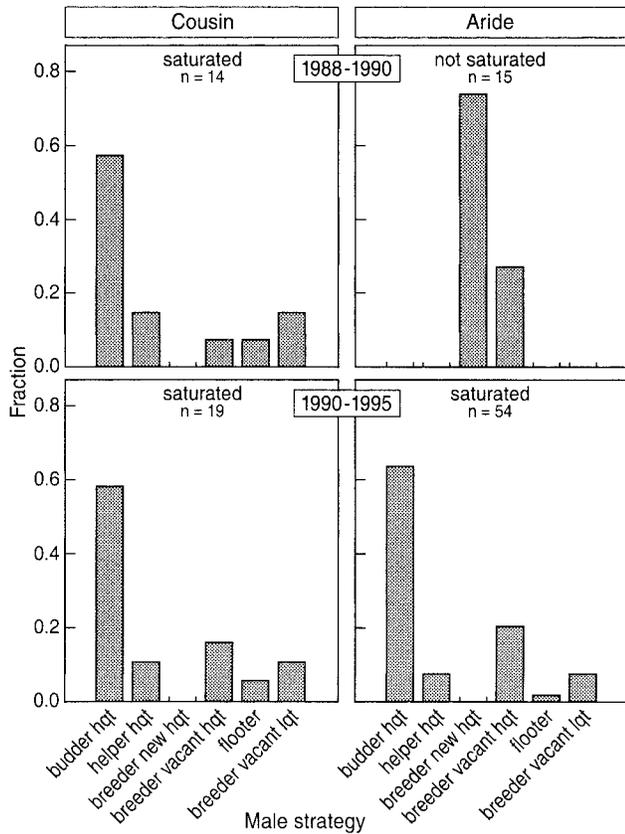
Figure 3
Percentage of young male Seychelles warblers using one of the six dispersal strategies in nonsaturated (September 1988–September 1990) and saturated high-quality habitat (October 1990–October 1995) on Aride Island and in saturated, high-quality habitat on Cousin Island during corresponding periods. After fitting the most parsimonious log-linear model (all factors and two-way interactions significant, χ^2 of final fit = 8.99, p = .110), the strategy most contributing to the interaction strategy × time period is the number of budders. After fitting the model, the most outlying cell (Freeman-Tukey deviate) remains the low number of budders on Aride before saturation (χ^2 = 4.57, p = .033); n, sample size.

adjacent territories. The higher the competition over high-quality territories (measured as the saturation index) in a given year, the smaller the size of the budded territory in the next year, and the lower the fraction of budders still present on their budded territories (Figure 5). The average age at which budders filled breeding vacancies was 2.7 ± 1.0 years (n = 17).

Reproductive performance in relation to age and habitat saturation

Using longitudinal data, we investigated age-related changes in territory size and reproductive success of the two male cohorts on Aride Island (Figure 6). Annual territory size of cohort A_{before} males (which established new territories or filled breeding vacancies at 1 year of age) remained stable over their first 5 years of life (MANOVA: $F_{4,52}$ = 0.83, ns) and did not differ between dispersal strategies (MANOVA: $F_{1,13}$ = 0.77, ns; strategy × age: $F_{4,52}$ = 2.27, ns; Figure 6). Reproductive success of these males was low in their first year of life but increased in their second year of life (univariate test for difference contrast: $F_{2,13}$ = 17.7, p < .001). From 2 to 5 years of age, no further improvement in reproductive success was ev-
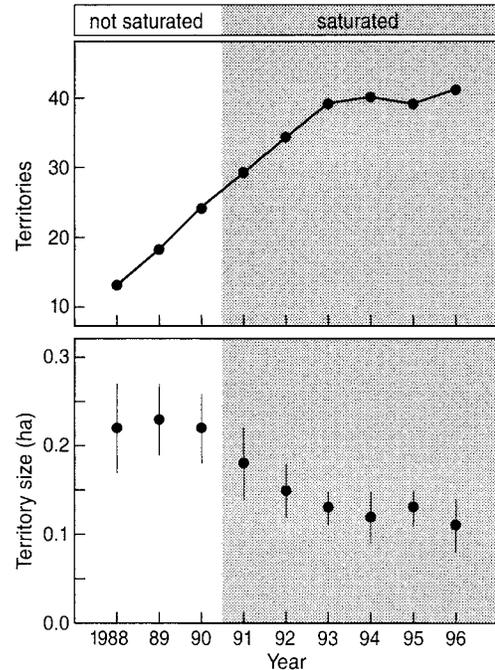
ident (all univariate tests for difference contrasts: $F_{2,13}$ < 0.80, ns). Total reproductive success after 5 years was similar for both strategies ($F_{1,13}$ = 0.44, ns).

After saturation of the high-quality habitat, annual territory size of cohort A_{after} males differed between dispersal strategies (MANOVA: $F_{2,19}$ = 939, p < .001). There was also an effect of age on territory size, but this effect was different for males
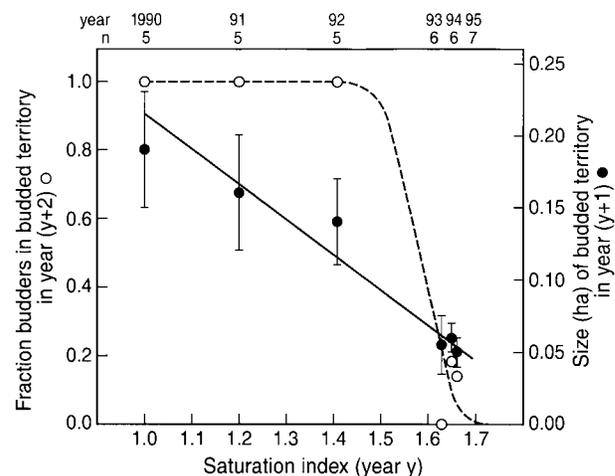

Figure 4
Number and mean size of Seychelles warbler territories in the high-quality habitat on Aride Island (1988–1996).

Figure 5
The effect of saturation intensity of high-quality habitat measured in year y on the size (ha) of budded territories 1 year later and the fraction of budders still present on their budded territories 2 years later. Saturation index (si) was measured in the year when the males started the budding process (year y). Territory size and fraction remaining were measured 1 and 2 years after the start of budding process, respectively. Territory size in year (y + 1) = −0.217 × (si in year y) + 0.418; r^2 = .94, n = 6, p = .002. Fraction budders present on budded territories in year (y ± 2) = 1/ (1+e^{-z}); z = 48.335–30.695 × (si in year y); G test of independence: D = 34.11, df = 1, p < .001.

Figure 6
Dispersal strategies, age first dispersal (years), number of yearling offspring produced per year, annual territory size (ha), and total number of yearling offspring produced by male warblers in their first 5 years of life (total reproductive success, RS) in relation to habitat saturation on Aride island. Two cohorts were considered: A_{before}, 15 males born between October 1988 and January 1990 that had reached the reproductive age of 8 months before the high-quality habitat became saturated with territories (1 October 1990), and A_{after}, 24 males born between February 1990 and January 1992 that had reached the reproductive age after first saturation of the high-quality habitat (1 October 1990). Statistical differences between dispersal strategies in total RS were tested by ANOVA with a post-hoc Tukey-test to identify groups. Group identities are indicated by superscript A, B, and C, for each of the two cohorts separately. Values are presented ± SE; *n* denotes sample size.
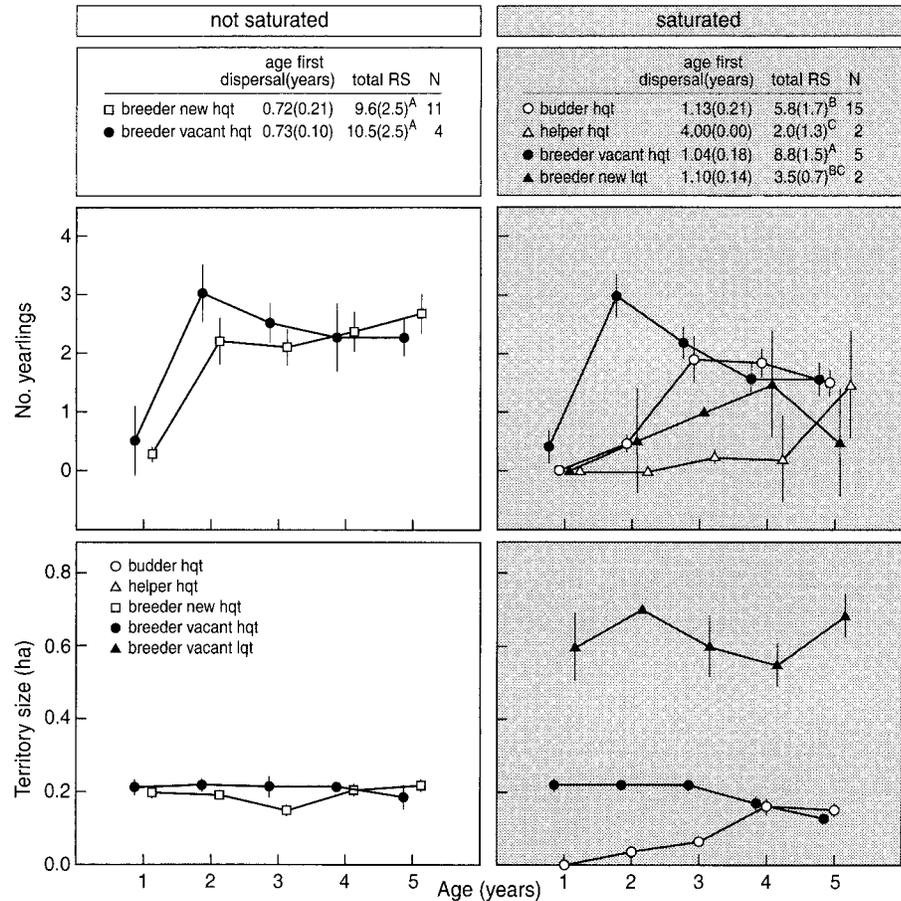
following different dispersal strategies (MANOVA: age: $F_{4,76} = 6.38$, $p = .002$; strategy × age: $F_{8,76} = 39.6$, $p < .001$). Territory size of males that had filled high-quality breeding vacancies at 1 year of age tended to decline when they were 4 and 5 years old because the budded territories increased in size at the expense of these territories (MANOVA difference contrast: 1>2 [change in territory size from age 1 to 2]: $F_{1,19} = 0.00$, ns; 2>3: $F_{1,19} = 0.00$, ns; 3>4: $F_{1,19} = 3.78$, $p = .067$; 4>5: $F_{1,19} = 3.47$, $p = 0078$; Figure 6). In comparison with males breeding immediately on high-quality territories, annual territory size of same-aged budders was significantly lower during their second and third year of life, but had become similar in their fourth and fifth year of life (MANOVA hypothesis testing: age 2: $F_{1,19} = 535$, $p < .001$; age 3: $F_{1,19} = 149$, $p < .001$; age 4: $F_{1,19} = 0.09$, ns; age 5: $F_{1,19} = 2.38$, ns; Figure 6).

After saturation of the high-quality habitat, reproductive success differed between dispersal strategies and between ages (MANOVA: strategy: $F_{3,20} = 11.4$, $p = .001$; age: $F_{4,80} = 5.22$, $p < .001$; strategy × age: $F_{12,80} = 3.08$, $p < .005$). Reproductive success of budders increased from 2 to 3 years of age, but remained the same from 3 to 5 years of age (MANOVA difference contrast: 2>3: $F_{1,19} = 14.9$, $p = .001$; 3>4: $F_{1,19} = 0.025$, ns; 4>5: $F_{1,19} = 1.83$, ns; Figure 6). Compared with same-aged males breeding immediately on high-quality territories, budders produced fewer yearlings during their second year of age, but the same number of yearlings from 3 to 5 years of age (MANOVA hypothesis testing: age 2: $F_{1,19} = 73.4$, $p < .001$; age 3 to 5: all $F_{1,19} < 0.4$, ns; Figure 6). Overall, total reproductive success (RS) over the first 5 years of life of budders was significantly lower than total RS of males breeding immediately on high-quality territories but was significantly

higher than total RS of helpers on high-quality territories and higher than breeders on lower quality territories (Figure 6).

The average size of territories and reproductive success of six unassisted breeding pairs (the same breeding birds which remained on the same territories during the period October 1988–October 1993) had decreased considerably after October 1990 when all the space in the high-quality habitat was occupied. During the 2 years before saturation, these breeding pairs occupied larger territories and had higher annual reproductive success than during the 3-year period after saturation (mean territory size: 0.25 ± 0.03 ha vs. 0.15 ± 0.01 ha, paired-sample *t* test: $t = 7.22$, df = 4, $p < .001$; mean annual reproductive success: 2.75 ± 0.69 vs. 1.03 ± 0.34, $t = 6.24$, df = 4, $p = .004$).

DISCUSSION

Dispersal strategy and perception of reproductive potential

Variation in reproductive success among territories is a common feature of most noncooperative (e.g., Bensch and Hasselquist, 1991; Bollmann et al., 1997; Both and Visser, 2000; Lundberg and Alatalo, 1992; Stutchbury and Robertson, 1988; Tye, 1992) and most cooperative breeding systems (e.g., Nias and Ford, 1992; Stacey and Koenig, 1990; Stacey and Ligon, 1991; Walters et al., 1992). It is clear that many species can assess territory quality and that the selection pressure to do so is high (sensu Ens et al., 1995; Lucas et al., 1997). Many studies have shown that individuals of noncooperatively breeding taxa increase their reproductive success after moving (e.g., Baeyens, 1981; Beletsky and Orians, 1987; Petersen and Best,

1987; but see Newton and Marquiss, 1982) and that poorer territories are less likely to be occupied (Krebs, 1971; Wauters and Dhondt, 1990). However, for cooperatively breeding species, not only must sufficient resources exist within a given territory to support additional animals (Blackwell and Bacon, 1993), but also some form of fitness benefit for both the dominant pair and the subordinate is necessary (Lindström, 1986; Macdonald and Carr, 1989). Without such relative benefits, alternative behavioral strategies, principally dispersal, will be favored. In other words, apart from assessing territory quality, mature offspring should be able to perceive which dispersal strategy would maximize their future inclusive fitness (sensu Lucas et al., 1997).

In this study we assessed the relative costs and fitness benefits of different dispersal strategies used by male Seychelles warblers born in high-quality territories on the islands of Cousin and Aride. Dispersing and breeding in high-quality territory or staying on their natal territories as budders yield the longest life span (Cousin: dispersing and breeding: 8.4 years; budding: 8.2 years), as compared to helping, floating, or breeding on a low-quality territory. Furthermore, breeding in a high-quality territory upon reaching reproductive maturity yields the highest LRS because of high annual reproductive success. The second-best reproductive option for a male's whole life is budding. Although most budders acquired a breeding partner, annual reproductive success during the budding process was low and comparable to helping, floating, or breeding in low-quality territory. However, the future beneficial component of budding is the guarantee that the male will survive to become the primary breeding male on a high-quality territory. Male helpers caused a significant reduction in the reproductive success of their parents. An experimental study showed that this was due to greater depletion of food resources (Komdeur, 1994b).

Young male Seychelles warblers do sample different territories all over the island before making a choice where to settle, as shown by observational (Komdeur, 1991) and by radiotelemetry studies (Komdeur J, Daan S, Madsen V, and Tinbergen JM, unpublished observations). Our observations and experiments clearly demonstrate that young males also assess the relative costs and benefits of different dispersal strategies. Despite the high fitness returns of breeding on high-quality territory, only a few males on Cousin became breeding males in high-quality territories. We think this was due to high competition for these territories for three reasons. First, in the high-quality habitat on Cousin, the number of adult males produced exceeded the number of male breeding vacancies. Second, experimentally created high-quality male breeding vacancies were filled immediately by nonbreeding budders from adjacent territories. Third, on Aride, with no shortage of high-quality habitat and breeding partners, all translocated Cousin males that were using different dispersal strategies at the time of translocation established high-quality breeding territories. In addition, all males born on Aride either established high-quality territories or filled breeding vacancies in high-quality territories before reaching 1 year of age. After saturation of the high-quality habitat on Aride, with no shortage of breeding partners and unoccupied, lower-quality habitat, few males obtained high-quality breeding territories. If males were unable to breed in a high-quality breeding territory, most males took the second best reproductive strategy of remaining in their natal territories to become budders (Cousin: 63%); few used strategies yielding lower fitness benefits. None of the experimentally created low-quality male breeding vacancies were filled by budders from adjacent high-quality territories, but all by males from low-quality territories. However, it is unclear why some males became helpers. First, they do not need to help in return for being permitted to stay in their natal territory (pay-to-stay hypothesis; Gaston, 1978; Taborsky, 1984, 1985). We have never observed breeders responding aggressively toward related nonhelping male offspring (which include future budders that remain in their natal territory) or to nonhelping floaters (which occasionally return to their natal territory for a total period of up to 2 weeks during a year floating; Komdeur, 1991). Second, unlike female helpers, male helpers caused a significant reduction in the reproductive success of their parents (Komdeur, 1996a). Compared to female helpers, male helpers do not contribute to nest building and incubating the clutch, providing less offspring care and competing for food resources (Komdeur, 1996a). Third, helping never results in inheritance of a breeding spot. All breeding spots were inherited by budders that, compared with helpers, were more abundantly present and had site-dominance over territory inheritance (Komdeur and Edelaar, in press). Fourth, helping never results in siring offspring with the helper's mother (Richardson et al., 2001). Potentially, helping males gain breeding experience, for which there is observational and experimental evidence in the Seychelles warbler (Komdeur, 1996a).

In addition, it is unclear why some males became floaters. The floaters of the cohort studied between 1982 and 1986 (this study) are short-lived and do not produce any offspring. However, of all the floaters studied up till 1999 ($n = 16$), 18.8% ($n = 3$) did eventually fill a breeding vacancy, which happened in 1997 after the death of many breeding males due to torrential rains (Blaakmeer K, unpublished observations). The three floaters that acquired a breeding territory produced offspring and have reached ages older than the 1–2 years of floaters of this study; one was 4 years old, and two (still alive at present) were at least 3 and 4 years old.

Costs of missed opportunities

In male Seychelles warblers, the cost of helping, floating, or settling on a low-quality territory seems to be a cost of missed opportunities because it never results in obtaining a high-quality territory later and a high reproductive success (fitness). It could be that not all males are capable of using those dispersal tactics yielding the highest fitness. For example, compared with males with a good body condition, males with a relatively worse condition may be less able to compete for high-quality breeding territories or to gain part of the natal territory through fighting and subsequent budding. Instead, such males may gain a higher fitness as helpers or floaters. In addition, it is potentially easier for a helper or a floater to inherit a vacant territory than for a territory holder to do so because territory switching rarely occurs. Most breeding birds (99.1%; $n = 314$) remained in their low-quality breeding territories until their death (Komdeur, 1991). This inflexibility of established breeders, despite the possibility of higher reproductive success elsewhere, is common (Aebischer and Coulson, 1990; Ens et al., 1995; Korpimaki, 1988; Picman, 1987). If territory switching is a possibility—as it is in some species (Beletsky and Orians, 1987; Curry, 1988; Krebs, 1971; Newton and Marquiss, 1982)—the relative advantage of budding decreases (Kokko and Sutherland, 1998). Dominant status over territory inheritance upon the death of the same-sex adult is linked to budding and not to helping and is independent of the male's age (Komdeur and Edelaar, in press). The absence of territory switching and the presence of site dominance over territory inheritance may explain why it pays for Seychelles warbler males to stay and bud in a saturated environment. We favor this explanation because it appears to be the most parsimonious; additional work is required to determine both beneficial and detrimental effects for the parents of tolerating a budding son and for the participants in the

interaction. Experiments in which the male's body condition is changed (through supplementary feeding or handicapping the bird) are needed to show whether the dispersal strategy used is state dependent.

Ideally, the LRS and fitness consequences of each dispersal strategy should be calculated as the precise number of within- and extrapair young produced by each male through DNA paternity studies. However, the LRS values of each dispersal strategy in this study is probably a realistic measure (Richardson et al., 2000), since microsatellite DNA fingerprinting has revealed that only breeding males on low- and on high-quality territories gain extrapair paternity (helpers, floaters, and budders never sire offspring through extrapair fertilizations), and the degree of cuckoldry is equal for breeding males on low- and high-quality territories.

Territorial inheritance: helping and budding as alternative strategies

In cooperatively breeding species in which breeding is constrained, one possible route to becoming a breeder is to remain at home as a helper. It is argued that the act of helping is the route to dominant status over the acquisition of the natal or a nearby territory in future years (Balshine-Earn et al., 1998; Koenig et al., 1992; Lindström, 1986; Reyer, 1984; Stacey and Ligon, 1987; Woolfenden and Fitzpatrick, 1984; Zack, 1990; Zahavi, 1976). By enhancing the reproductive success of the breeders, helpers increase the size of the family unit. Larger groups outcompete smaller ones at territorial boundaries, through which they expand the size of the natal territory. This, in turn, increases the likelihood that the former helper will be able to bud off a portion of the enlarged parental territory for itself. However, it is unknown whether the acquisition of a territory is linked to helping per se or to a passive effect of delayed dispersal alone (Blackwell and Bacon, 1993; Emlen, 1994, 1995). Indeed, in several species helping and budding go together: budders are former helpers (Stacey and Koenig, 1990; Koenig et al., 1992), but not in the Seychelles warbler. None of the warbler helpers became budders ($n = 14$). One reason that keeps helpers from becoming budders could be differences between individual males such that each male adopts the strategy that maximizes his fitness. Young males that ultimately adopted the budding strategy show higher levels of aggressive behavior compared to similar aged males that ultimately adopted the helping strategy (Komdeur and Edelaar, in press). This could be related to (fighting) quality necessary for budding. Alternatively, and perhaps in interaction with the former explanation, males might find themselves in different competitive environments. For example, a helping male might forgo the otherwise high fitness related budding strategy when several budders are already present near the natal territory and local competition over the future vacancy is expected to be high. Recently, Poiani (1994) came up with an alternative model to explain the non-helping behavior as a strategy to increase direct fitness. Non-helpers take advantage of group defense (without paying the cost of helping to raise potential competitors), through which the future probability of becoming a breeder is increased (because of lack of intergenerational competition for breeding status). In the Seychelles warbler, nonhelping males that remained on their natal territories assisted their parents significantly more with territory defense than helping males (Komdeur and Edelaar, in press). It is known for some species that extra individuals (e.g., their own offspring) remain within the breeders' territory but do not help (Caffrey, 1992; Sydeman, 1991; Veltman, 1989; see also Curry, 1988; Poiani, 1994). Also in Seychelles warblers, most young males remaining on their natal territory which had a chance to help because their par-

ents had produced younger offspring, did not help (Cousin and Aride: 83.8%, $n = 68$). In addition, none of the budders had been helpers before ($n = 53$).

The simultaneous presence of helping and nonhelping males in the Seychelles warbler and the absence of switching between the two strategies enabled us to investigate why helpers help. If future fitness effects of helping are taken into account, nonhelping should be selected for in male warblers, even among close relatives, because nonhelping males have higher longevity than helping males, and nonhelping males become budders, through which they gain higher fitness benefits than helping males by inheriting the breeding spot (both a mate and a territory), while helping males never inherit a breeding spot. A budder never obtained a high-quality breeding spot by evicting a breeder from his territory (Komdeur and Edelaar, in press). Instead, this was achieved either through expanding the budded territory into a high-quality territory at the expense of neighboring territories (observed on Aride when the high-quality habitat could still support more territories after saturation) or through inheritance of either the natal or an adjacent territory (observed on Cousin and Aride when no more new territories could be established in the high-quality habitat). However, experimental studies under natural conditions to test the inheritance hypothesis for helping and Poiani's hypothesis for nonhelping have yet to be performed (Balshine-Earn et al., 1998; Emlen, 1991, 1995).

REFERENCES

Aebischer NJ, Coulson JC, 1990. Survival of the kittiwake in relation to sex year, breeding experience and position in the colony. J Anim Ecol 59:1063–1071.

Arcese P, 1989. Intrasexual competition, mating system and natal dispersal in song sparrows. Anim Behav 38:958–979.

Baeyens G, 1981. Functional aspects of serial monogamy: the magpie pair bond in relation to its territorial system. Ardea 69:145–166.

Balshine-Earn S, Neat FC, Reid H, Taborsky M, 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. Behav Ecol 9:432–438.

Beletsky LD, Orians GH, 1987. Territoriality among male red-winged blackbirds. I. Site fidelity and movement patterns. Behav Ecol Sociobiol 20:21–34.

Bensch S, Hasselquist D, 1991. Territory fidelity in the polygynous great reed warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. J Anim Ecol 60:857–871.

Blackwell P, Bacon PJ, 1993. A critique of the territory inheritance hypothesis. Anim Behav 46:821–823.

Bollmann K, Reyer HU, Brodmann PA, 1997. Territory quality and reproductive success: can water pipits *Anthus spinoletta* assess the relationship reliably? Ardea 85:83–98.

Both C, Visser ME, 2000. Breeding territory size affects fitness: an experimental study on competition at the individual level. J Anim Ecol 69:1021–1030.

Bourke AFG, 1997. Sociality and kin selection in insects. In: Behavioural ecology: an evolutionary approach, 4th ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 203–227.

Brown JL, 1987. Helping and communal breeding in birds: ecology and evolution. Princeton, New Jersey: Princeton University Press.

Caffrey C, 1992. Female-biased delayed dispersal and helping in American crows. Auk 109:609–619.

Chepko-Sade BD, Halpin ZT (eds), 1987. Mammalian dispersal patterns: the effects of social structure on population genetics. Chicago: University of Chicago Press.

Cockburn A, 1998. Evolution of helping behaviour in cooperatively breeding birds. Annu Rev Ecol Syst 29:141–177.

Curry RL, 1988. Group structure, within-group conflict and reproductive tactics in cooperatively breeding Galapagos mockingbirds, *Nesomimus parvulus*. Anim Behav 36:1708–1728.

Emlen ST, 1991. Evolution of cooperative breeding in birds and mammals. In: Behavioural ecology: an evolutionary approach, 3rd ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 301–337.

Emlen ST, 1994. Benefits, constraints, and the evolution of the family. Trends Ecol Evol 9:282–285.

Emlen ST, 1995. An evolutionary theory of the family. Proc Natl Acad Sci USA 92:8092–8099.

Emlen ST, 1997. Predicting family dynamics in social vertebrates. In: Behavioural ecology: an evolutionary approach, 4th ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 228–253.

Ens BJ, Weissing FJ, Drent RH, 1995. The despotic distribution and deferred maturity: two sides of the same coin. Am Nat 146:625–650.

Gaston AJ, 1978. The evolution of group territorial behavior and cooperative breeding. Am Nat 112:1091–1100.

Heinsohn RG, Cockburn A, Mulder RA, 1990. Avian cooperative breeding: old hypotheses and new directions. Trends Ecol Evol 5: 403–407.

Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT, 1992. The evolution of delayed dispersal in cooperative breeders. Q Rev Biol 67:111–150.

Kokko H, Sutherland WJ, 1998. Optimal floating and queuing strategies: consequences for density dependence and habitat loss. Am Nat 152:354–366.

Komdeur J, 1991. Cooperative breeding in the Seychelles warbler (PhD dissertation). Cambridge: Cambridge University.

Komdeur J, 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. Nature 358:493–495.

Komdeur J, 1994a. Conserving the Seychelles warbler *Acrocephalus sechellensis* by translocation from Cousin Island to the islands of Aride and Cousaien. Biol Conserv 67:143–152.

Komdeur J, 1994b. Experimental evidence for helping and hindering by previous offspring in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). Behav Ecol Sociobiol 34:31–42.

Komdeur J, 1996a. Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. Behav Ecol 7:326–333.

Komdeur J, 1996b. Seasonal timing of reproduction in a tropical bird, the Seychelles warbler: a field experiment using translocation. J Biol Rhythms 11:333–346.

Komdeur J, Edelar P, in press. Natural and experimental evidence that helping at the nest does not result in territory inheritance in the Seychelles warbler. Proc R Soc Lond B.

Korpimaki E, 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's owl. J Anim Ecol 57:97–108.

Krebs JR, 1971. Territory and breeding density in the great tit, *Parus major* L. Ecology 52:2–22.

Lawton MF, Lawton RO, 1986. Heterochrony, deferred breeding, and avian sociality. Curr Ornithol 3:187–222.

Lindström ER, 1986. Territory inheritance and the evolution of group living in carnivores. Anim Behav 34:1825–1835.

Lucas JR, Creel SR, Waser PM, 1997. Dynamic optimisation and cooperative breeding: an evolution of future fitness effects. In: Cooperative breeding in mammals (Solomon NG, French JA, eds). Cambridge: Cambridge University Press; 171–198.

Lundberg A, Alatalo RV, 1992. The pied flycatcher. London: Poyser.

Macdonald DW, Carr GM, 1989. Food security and the rewards of tolerance. In: Comparative socioecology (Standen V, Foley RA, eds). Oxford: Blackwell; 75–79.

Newton I, Marquiss M, 1982. Fidelity to breeding area and mate in the sparrowhawk *Accipiter nisus*. J Appl Ecol 51:327–341.

Nias RC, Ford HA, 1992. The influence of group size and habitat on reproductive success in the superb fairy-wren *Malurus cyaneus*. Emu 92:238–43

Petersen KL, Best LB, 1987. Territory dynamics in a sage sparrow population: are shifts in site use adaptive? Behav Ecol Sociobiol 21: 351–358.

Picman J, 1987. Territory establishment, size, and tenacity by male red-winged blackbirds. Auk 104:405–412.

Poiani A, 1994. Inter-generational competition and selection for helping behaviour. J Evol Biol 7:419–434.

Queller DC, 1996. The measurement and meaning of inclusive fitness. Anim Behav 51:229–232.

Reyer HU, 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). Anim Behav 32:1163–1178.

Richardson DS, Jury FL, Blaakmeer K, Komdeur J, Burke T, 2001. Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). Mol Ecol 10:2263–2274.

Richardson DS, Jury FL, Dawson DA, Salgueiro P, Komdeur J, Burke T, 2000. Fifty Seychelles warbler (*Acrocephalus sechellensis*) microsatellite loci polymorphic in Sylviidae species and their cross-specific amplification in other passerine birds. Mol Ecol 9:2226–2231.

Riedman ML, 1982. The evolution of alloparental care and adoption in mammals and birds. Q Rev Biol 57:405–435.

Sibley R, Calow P, 1986. Why breeding earlier is always worthwhile. J Theor Biol 123:311–319.

Stacey PB, Koenig WD, 1990. Cooperative breeding in birds: long term studies of ecology and behavior. Cambridge: Cambridge University Press.

Stacey PB, Ligon JD, 1987. Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. Am Nat 130:654–676.

Stacey PB, Ligon JD, 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. Am Nat 137:831–846.

Studd MV, Robertson RJ, 1985. Life span, competition and delayed plumage maturation in male passerines: the breeding threshold hypothesis. Am Nat 126:101–115.

Stutchbury BJ, Robertson RJ, 1988. Within-season and age related patterns of reproductive performance in female tree swallows (*Tachycineta bicolor*). Can J Zool 66:827–834.

Sydeman WJ, 1991. Facultative helping by pygmy nuthatches. Auk 108: 173–176.

SYSTAT 7.0, 1997. Chicago: SPSS.

Inc., Taborsky M, 1984. Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. Anim Behav 32:1236–1252.

Taborsky M, 1985. Breeder-helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. Behavior 95:45–75.

Taborsky M, 1994. Parasitism and alternative reproductive strategies in fish. Adv Study Behav 23:1–100.

Tye A, 1992. Assessment of territory quality and its effect on breeding success in a migrant passerine, the wheatear *Oenanthe oenanthe*. Ibis 134:273–285.

Veltman CJ, 1989. Flock, pair and group living lifestyles without cooperative breeding by Australian magpies *Gymnorhina tibicen*. Ibis 131:601–608.

Walters JR, Doerr PD, Carter JH, 1992. Delayed dispersal and reproduction as a life-history tactic in cooperative breeders: fitness calculations from red-cockaded woodpeckers. Am Nat 139:623–643.

Wauters L, Dhondt AA, 1990. Red squirrel (*Sciurus vulgaris* Linneaus) population dynamics in different habitats. Z Säugetierkunde 55: 161–175.

Wittenberger JF, 1979. A model for delayed reproduction in iteroparous animals. Am Nat 114:439–446.

Woolfenden GE, Fitzpatrick JW, 1984. The Florida scrub jay: demography of a cooperative-breeding bird. Princeton, New Jersey: Princeton University Press.

Zack S, 1990. Coupling delayed breeding with short distance dispersal in cooperatively breeding birds. Ethology 86:265–258.

Zack S, Stutchbury BJ, 1992. Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. Behaviour 123: 194–219.

Zahavi A, 1976. Cooperative nesting in Eurasian birds. In: Proceedings of the 16th International Ornithological Congress, Canberra, Australia 1975 (Frith HJ, Calaby JH, eds). Canberra: Australian Academy Science; 685–693.