

Experimental evaluation of sex differences in territory acquisition in a cooperatively breeding bird

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In many species, territory ownership is a prerequisite for reproduction; consequently, factors that affect success in territory acquisition can have a large impact on fitness. When competing for territories, some individuals may have an advantage if, for example, they are phenotypically superior or more familiar with the site than others. The relative importance of the many factors involved in territory acquisition is, at present, unclear. We studied patterns of natural territory acquisition in a closed and saturated population of Seychelles warblers. Furthermore, by removing breeders, we experimentally investigated the relative importance, to territory acquisition, of a range of factors and assessed whether this differed between the sexes. In both sexes, the main route to natural territory acquisition was to disperse from the natal territory to immediately claim a vacant dominant position. Males were older than females when acquiring a territory for the first time. In the removal experiment, for both sexes, the proximity of an individual's natal territory to a vacant dominant position was positively related to the individual's chance of claiming the vacancy. Older males were more likely to gain an experimental vacant dominant position than were young males, whereas age did not affect territory acquisition in females. In the Seychelles warbler, the degree of intrasexual competition for territory ownership may be stronger for males than for females because territory ownership is a prerequisite for male reproduction, whereas females can reproduce on their natal territory. In such competition, young males subsequently lose out to older ones. *Key words:* *Acrocephalus sechellensis*, age-related dominance, cooperative breeding, female choice, intrasexual competition, natal dispersal. [*Behav Ecol* 20:207–214 (2009)]

As territory ownership is a prerequisite for reproduction in many species (Clutton-Brock et al. 1982; Beletsky and Orians 1993), factors that affect success in territory acquisition can have a large impact on fitness. Territory ownership may be achieved either through passive acquisition, such as claiming a vacancy left after the death or desertion of a previous resident (e.g., Piper et al. 2000), or through active acquisition, by displacing a breeder of the same sex (e.g., Heg et al. 2000) or by creating a completely new territory (e.g., Arcese 1989).

When competing over territories, some individuals may have an advantage over others; for instance, they may be phenotypically superior (Parker 1974; Piper et al. 2000) or more familiar with a site and its surroundings (Stamps 1987; Jakobsson 1988; Yáber and Rabenold 2002). Phenotypic superiority may be especially important in active territory acquisition because active acquisition involves competition with territory owners that have more to lose than the nonbreeders (Maynard Smith and Parker 1976). Familiarity with a site may depend not only on the proximity to the site of the nonbreeders but also on the number of exploratory forays made by nonbreeders to the site (Bruinzeel and Van de Pol 2004). Furthermore, when the quality of an individual's phenotype, or its knowledge about a site, increases with age, then older nonbreeders may out compete younger nonbreeders (Zack and Rabenold 1989). Success in territory acquisition may also increase when non-

breeders are allowed to wait within the relative safety of the natal territory until they locate a vacant dominant position (Mulder 1995; Eikenaar et al. 2007).

Many studies have dealt with specific factors that affect territory acquisition (e.g., familiarity, Jakobsson 1988; resource-holding potential, Shutler and Weatherhead 1991; body size, Piper et al. 2000; intrusion behavior, Bruinzeel and Van de Pol 2004); however, studies that investigate the relative importance of multiple factors in territory acquisition remain scarce (but see Zack and Rabenold 1989; Martin 1991; Hatchwell and Davies 1992; Beletsky and Orians 1993). Moreover, no study has specifically addressed whether the relative importance of such factors differs between the sexes, despite the fact that many behaviors related to territory acquisition, such as patterns of natal dispersal, are often sex biased (Greenwood 1980; Clarke et al. 1997). To investigate the relative importance to territory acquisition of multiple factors and how this differs between sexes, we use a combination of an in-depth analysis of 12 years of observational data on the Cousin population of Seychelles warblers, *Acrocephalus sechellensis*, and a breeder removal experiment undertaken in the same population. This population has almost no migration on or off the island (0.1%, $n = 1924$, Komdeur et al. 2004), and during our study nearly all warblers on Cousin were individually marked (>91%). Furthermore, for many ($n = 191$) individuals, we have their natal dispersal histories. Consequently, our data on territory acquisition are virtually complete and unbiased.

First, using the observational data, we describe patterns of territory acquisition. Specifically, we determine 1) the age of

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birds at dispersal and when they first acquire a territory, 2) the route by which individuals normally acquire a territory, and 3) if patterns of territory acquisition differ between the sexes. Furthermore, we test for phenotypic differences (size and age) between 1) individuals that create a new territory and those that acquire a territory through other routes and 2) individuals that claim a vacant dominant position in a given territory and the subordinates, of the same sex as the claimant, that were living in those territories at that time. Second, we use the simultaneous experimental creation of multiple vacant dominant positions (as a result of dominant territory owners being permanently removed as part of a translocation program undertaken by Nature Seychelles) to further investigate patterns of territory acquisition. This allowed us to study the effects that the sex of the removed dominant, the quality of the vacant territory, the density of competitors around the vacancy, and the presence or absence of nonbreeders on the vacant territory had on the speed at which vacant dominant positions are claimed. It also allowed us to assess the effect that factors, such as the removal of dominants, the level of local competition, and the age, size, sex, and proximity to vacancies of a competitor, have on its chances of acquiring a territory.

We made the following predictions regarding the time taken for experimental vacant dominant positions to be claimed in the Seychelles warbler. We expected vacancies for males to be claimed faster than vacancies for females. This is because competition for territories is expected to be stronger for males than for females because territory ownership is a prerequisite for male, but not female, reproduction (Richardson et al. 2001, 2002). We predicted that the time taken for a vacancy to be claimed would be negatively correlated with both the quality of the vacancy and the local density of competitors outside the vacancy. We also predicted that the time taken for a vacancy to be filled would be delayed by the presence of potential heirs within the territory as these individuals may attempt to exclude competitors from outside the territory (Hannon et al. 1985). Furthermore, we had a series of specific predictions regarding a competitor's chances of claiming an experimental vacant dominant position. In other bird species, competitive ability may increase with age and size (e.g., Brown 1975; Shutler and Weatherhead 1991; Piper et al. 2000; Bose and Sarrazin 2007); therefore, we expected size and age to be predictors of an individual's ability to claim a vacancy. Because Seychelles warbler females settle further from their natal territories than do males (Eikenaar et al. 2008), we also expected proximity to the experimental vacancy to be less important in territory acquisition for females than for males. Finally, we predicted that a competitor's chances of claiming a vacant dominant position would be negatively correlated with an increasing level of local competition.

METHODS

Study species and population

Seychelles warblers have a facultative cooperative breeding system. They live either in pairs or in groups consisting of a dominant pair and, normally, one or more offspring that have delayed dispersal and remained in the natal territory as subordinates (Komdeur 1992). The dominant male and female were defined as the individuals in the dominant pair bond on the territory. Dominance and pair bonding were inferred from behavioral observations during both the prebreeding and breeding phase. Each pair or group occupies an all-purpose territory year-round, and both sexes engage in territory defense (Komdeur 1992). Although subordinates are resident within a territory, only the dominant breeders were defined to be territory owners. Many (ca. 40%) of the female

subordinates successfully reproduce each year by directly laying and incubating the eggs in the same nest as the dominant female, whereas male subordinates only reproduce after they have acquired a dominant breeder position (Richardson et al. 2001, 2002). The likelihood of dispersal in the first year of life is equal for the sexes (Eikenaar et al. 2007), but female natal dispersal distance is twice as large as that of males (median and range in territory widths: females: 4 and 0–13; males: 2 and 0–11, Eikenaar et al. 2008). Breeder dispersal is rare (1.3% of breeders dispersed on average each year, Eikenaar et al. 2008). Annual survival of adults is high (84%) and equal for the sexes (Brouwer et al. 2006).

The current study was carried out on Cousin Island (29 ha, 04°20'S, 55°40'E) in the Seychelles. Except for a barren rocky outcrop in the center of the island, all the habitat is occupied by warblers. All the data presented are based on color-ringed individuals and were gathered from 1995 to 2006. During this period, the total number of territories on the island was stable (yearly average \pm standard error [SE]: 111.6 \pm 1.7) and most birds in the population were individually color ringed (yearly average \pm SE: 91.3 \pm 1.4%).

Birds were caught using mist nets, and each unringed bird received a unique combination of 3 color rings and a British Trust for Ornithology metal ring. For all birds, the length of the right tarsus and total head-bill length were measured to the nearest 0.1 mm using a vernier caliper. However, because some birds were ringed as chicks and not caught and measured again after fledging, tarsus and head-bill size were not available for all birds in this study. Blood samples (ca. 25 μ l) were collected by brachial venipuncture and stored in 100% ethanol at room temperature. Molecular sexing using the polymerase chain reaction method devised by Griffiths et al. (1998) was used to confirm the sex of each ringed individual.

Territories were mapped in detail in all years of the study using observations of individual warblers and territory boundary disputes between groups. During the breeding seasons, all territories were checked for the presence of warblers at least every 2 weeks. For all individuals, the status (dominant or subordinate) and territory of residence were determined in each year during the peak breeding season (June–August) and from 1997 to 1999 and 2003 to 2006 also during the minor breeding peak (December–February). As interisland dispersal is extremely rare (Komdeur et al. 2004), warblers that were missing from their territory and never seen afterward were presumed to have died.

Observational data on territory acquisition

Seychelles warblers may acquire a territory through a number of different routes. They may remain on the natal territory and 1) leave only to claim an external breeding vacancy or to create a new territory in a space among existing territories, 2) inherit a breeding position on the natal territory, and 3) successfully bud off part of the natal territory (a male-only strategy, Komdeur and Edelaar 2001). Alternatively, they may leave the natal territory and, before settling in a vacant dominant position or creating a new territory, join another group (defined as staging) or otherwise become a floater—a bird that roams over the island without having a resident territory (Komdeur and Edelaar 2001).

A bird was defined to have first dispersed either when it left its natal territory to join another group or become a floater or when it acquired its first territory (i.e., held a dominant breeder position for the first time). Not all individuals were ringed in the nest; therefore, the exact age of some birds was unknown. However, the breeding season in which each individual was born was always known. With breeding seasons 6 months apart, individuals could be assigned to the following

age classes: 0.5 year old, 1 year old, 1.5 years old, etc. In the analyses of age at dispersal and first territory acquisition, the age was set to 0.5 year for individuals that were known to have dispersed/first claimed a dominant breeder position in the season after they fledged, to 1 year when this occurred 2 seasons after they fledged, etc.

The length of the right tarsus was used as a metric of size. Age and tarsus length were not correlated (Spearman's rho, males: $Z = -0.08$, $P = 0.44$, $n = 93$ and females: $Z = -0.01$, $P = 0.95$, $n = 76$).

Experimental data

Breeder removal experiment

Just prior to the breeding season of 2004 (the first nesting attempt occurred on 24th of June), 17 dominant female and 20 dominant male breeders were translocated from Cousin Island to Denis Island (131 ha). This translocation was carried out by Nature Seychelles as part of their ongoing conservation program for this species (Richardson et al. 2006). Our participation in the translocation provided us with the opportunity to undertake a breeder removal experiment. During the 2 weeks prior to the first removals, all territories were searched to ascertain the status and territory of residence of as many individuals as possible. Birds were caught over 2 separate periods (the mornings of 29 and 30 May and a period covering the evening of 11 June and the subsequent morning) and translocated by helicopter. In 10 territories, the dominant breeding female was removed, in 13 the dominant breeding male was removed, and in 7 territories both dominant breeders were removed (hereafter all termed removal territories). After translocation, removal territories were searched twice a day for 15 min over a period of 3 weeks until the vacancy (or vacancies) was filled. Searches started the afternoon after the removals and were made in silence (no playback song or whistling). The identity of all birds that were sighted, both resident and new to the territory, was noted, as was their territorial behavior (e.g., fighting and singing) at the time of sighting. Daily searches ceased after 3 weeks due to time constraints; however, ad lib observations were made over the next 3 months in those territories in which no new replacement breeders were observed within the 3-week monitoring period.

Time until claiming of vacant dominant positions

The effect that sex of the removed dominant, territory quality, competitor density, and presence of subordinates had on the time until occupancy of experimental vacancies was analyzed using a Generalized Linear Model. The interval between the creation and the claiming of experimental vacancies was expressed in days and log transformed prior to analysis. The quality of the territory supporting the vacant dominant position was measured in terms of insect prey availability, as described by Komdeur (1992), and entered as a continuous variable. Competitor density was measured as the number of subordinates (excluding the ones living in the removal territory) of the same sex as the removed breeder, living within 2 territories of the experimental vacancy (2 widths being the median distance dispersed in the experiment for both males and females). The presence in the removal territories of subordinates that were of the same sex as the removed breeder was entered as a binary variable. Instances of territory inheritance ($n = 7$) were excluded from the analysis because it was unclear how many days after their creation the vacancies were claimed. Model selection was based on the backward stepwise deletion method, in which nonsignificant terms ($P > 0.05$) were removed from the model in order of least significance.

Factors influencing territory acquisition

The effect on territory acquisition of the age, size, and proximity of a competitor to a vacancy, competitor sex, dominant removal, and the level of local competition was analyzed using a multilevel mixed-modeling procedure in MLwiN (Rasbash et al. 2004). The binary response variable was whether or not a competitor claimed an experimental vacancy. Because breeder dispersal is rare, dominant breeders were excluded as competitors in the analysis of factors affecting territory acquisition. Therefore, in this analysis, the competitors were all the subordinates in the population. Age was expressed using the age classes described earlier. Because young have never been observed to disperse within 6 months of fledging on Cousin (Komdeur 1996), individuals that fledged in the last breeding season before the translocation (and hence were only about 4 months old) were excluded from the analyses. In the Seychelles warbler, the sexes differ in size; therefore, tarsus values were centered on the population mean for the individual's own sex by subtracting the sex-specific mean trait value from the individual's trait value. For each competitor, proximity was expressed as the average distance (in territory widths) between its territory and all the same-sex vacancies within 7 territory widths. This radius was chosen because it was the maximum dispersal distance that was observed in the experiment (for both sexes). Because the experimental vacancies were created in 2 rounds 10 days apart, individuals claiming a vacancy created in the first round did not compete for vacancies created in the second round. For these individuals, proximity measures were based on vacancies in the first round only. Dominant removal was defined as when one or both dominant breeders were removed from the competitor's territory. The level of local competition over vacant dominant positions for each competitor was estimated as the number of same-sex subordinates present in the focal competitor's own and adjacent territories.

Because, on 5 occasions, more than 1 same-sex competitors lived in the same territory at the time of the experiment, competitor identity was nested within territory as a random effect. Model selection was based on the backward stepwise deletion method (as above). Only competitors for which the resident territory immediately prior to the experiment was known were included in the analyses.

RESULTS

Observational data on territory acquisition

After having survived the first 6 months after fledging, (6 months being the minimum age required for dispersal, Komdeur 1996), 20.2% of females ($n = 109$), and 22.4% of males ($n = 134$) died without acquiring a territory. In total, 191 (87 female and 104 male) natural acquisitions of a dominant breeder position by a subordinate with known dispersal history were recorded (Table 1). For both sexes, the predominant route was to remain on the natal territory and leave only to claim either a vacant dominant position in a foreign territory or create a new territory. During our study period, 20 new territories were formed, of which 6 were created by males budding off part of their natal territory (Table 1). The formation of the other 14 territories also appeared to be initiated by males as only male subordinates foraged from their natal territory to the exact locations where they later created new territories ($n = 4$).

Males that created a new territory were not larger than males that acquired a territory through the other routes; tarsus length was similar between the 2 groups (mean \pm SE: new territory = 25.9 ± 0.09 mm [$n = 18$], other routes = 25.7 ± 0.17 mm [$n = 74$]; t -tests: $t = -0.95$, $P = 0.35$). Age of first territory

Table 1

The percentages of male and female subordinate Seychelles warblers that followed different routes to gaining a dominant breeding position between 1995 and 2006

	From natal territory	From staging territory	Floating	Territory budding	Territory inheritance
Males	64.4	7.7	18.3	5.8	3.8
Females	74.7	6.9	16.1	—	2.3

Birds may remain on the natal territory and leave only to claim an external vacant dominant position or to create a new territory ("From natal territory"), inherit a dominant breeding position on the natal territory ("Territory inheritance"), or successfully bud off and defend part of the natal territory ("Territory budding"). Alternatively, they may leave the natal territory and join another group as a subordinate ("From staging territory") or become a floater ("Floating"), before subsequently acquiring an existing territory or creating a new territory. Total natal dispersal events males, $n = 104$ and females, $n = 87$.

acquisition was also not different between these 2 groups (median age in years: active acquisition = 2 [$n = 20$], passive acquisition = 2 [$n = 84$]; Mann-Whitney U : $Z = 0.43$, $P = 0.99$). Therefore, all males were pooled when we compared age at dispersal or at first territory acquisition between the sexes. The age at which birds dispersed was not different between the sexes (median age in years = 1.5 for both males and females, Mann-Whitney U : $Z = -0.85$, $P = 0.40$, $n = 191$), and the majority of males and females dispersed within 2 years of fledging (Figure 1). Females acquired territories for the first time at a significantly younger age than males (median age in years: females = 1.5, males = 2, Mann-Whitney U : $Z = -2.25$, $P = 0.03$, $n = 191$; Figure 2). Individuals acquiring a territory by dispersing directly from the natal territory into a vacant dominant position did so at a younger age than birds acquiring a territory through an alternative route (staging territory, floating, budding, or inheritance, Mann-Whitney U : males: median ages in years: from natal territory = 1.75, alternative routes = 2, $Z = -3.55$, $P < 0.01$, $n = 104$; females: from natal territory = 1.5, alternative routes = 2, $Z = -3.67$, $P < 0.01$, $n = 87$). The age at which birds acquired a territory for the first time did not depend on tarsus length ($F_{1,167} = 0.50$, $P = 0.48$).

The individuals that claimed a vacant dominant position in a given territory were not larger than the same-sex subordinates already living in that territory at the moment of claiming (mean tarsus length \pm SE: males: claimants = 25.15 ± 0.22 mm, subordinates = 25.59 ± 0.21 mm; females: claimants = 24.3 ± 0.15 mm, subordinates = 24.33 ± 0.14 mm; paired

samples t -test: males: $t = -0.85$, $P = 0.41$, $n = 12$; females: $t = -0.12$, $P = 0.91$, $n = 11$). Males that claimed a vacant dominant position in a given territory were older than the male subordinates already living in that territory (median age in years: claimants = 2, subordinates = 1; Wilcoxon signed-ranks: $Z = -2.3$, $P = 0.02$, $n = 15$). For females, there was a nonsignificant trend in the same direction (median age: claimants = 2, subordinates = 1; Wilcoxon signed-ranks: $Z = -1.9$, $P = 0.06$, $n = 14$).

Breeder removal experiment

Time until claiming of vacant dominant positions

Of the 37 experimental vacant dominant positions, 6 (3 territories where both dominant breeders were removed) were lost to the experiment because the dominant breeders in an adjacent territory expanded their own territories and took over the entire vacant territory. These takeovers were observed 2, 5, and 6 days after breeder removals. Of the remaining 31 experimental positions, 2 remained vacant for more than 3 months and were not considered here. The territory of residence just prior to the experiment was unknown for 2 of the 29 individuals that claimed the experimental vacancies (hereafter termed claimants). Of the remaining 27 claimants, 26 were subordinates and 1 was a dominant breeder that abandoned its previous territory to claim an experimental vacancy. Of the 26 subordinates, 19 claimed an experimental vacancy outside their resident territory and 7 "inherited" a vacancy on their resident territory.

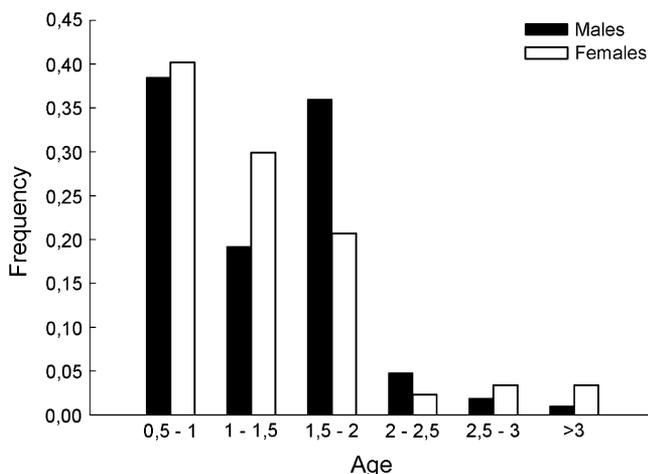


Figure 1

The frequency distributions of the age (in years) at which male and female Seychelles warblers dispersed from their natal territory in the years 1995–2006. Males, $n = 104$, females, $n = 87$.

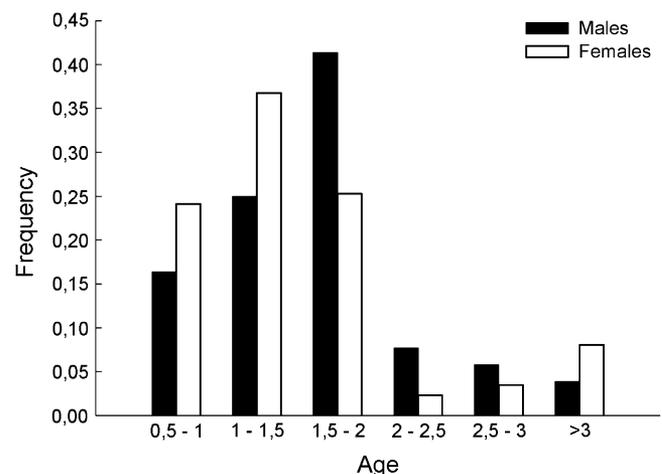


Figure 2

The frequency distributions of the age (in years) at first territory acquisition of male and female Seychelles warblers in the years 1995–2006. Males $n = 104$, females $n = 87$.

Occupancy of vacant dominant positions seemed to be on a first-come-first-served basis. First, in none of the 15-min searches ($n = 159$) of the removal territories were fights or disputes observed. Second, in all except 1 of the 20 (10 male and 10 female) instances of nonresidents claiming vacancies, the first nonresident bird observed in the removal territory became the new breeder. The median time to claiming of these 20 vacant dominant positions was 3.5 days (range 1–20 days). Male vacancies were claimed faster than female vacancies (Table 2, median: male = 2 days vs. female = 4 days). The presence of a subordinate of the same sex as the removed breeder in a territory increased the time it took for a vacancy to be claimed. Claiming time did not depend on competitor density or on the quality of the territory supporting the vacancy (Table 2).

Factors influencing territory acquisition

The number of same-sex competitors present in the removal territory and adjacent territories did not influence neither a competitor's chance of territory acquisition nor a competitor size or any of the other interactions (Table 3).

The age of the competitor did affect territory acquisition, and the significant interaction between sex and age indicated that the effect of age differed between the sexes (Table 3). Therefore, we analyzed the effect of age on territory acquisition separately for the sexes. For males, there was a positive relationship between age and the likelihood of territory acquisition ($\beta \pm SE = 1.86 \pm 0.62$, Wald = 9.1, degree of freedom [df] = 1, $P = 0.003$, Figure 3). For females, age did not affect the chance of territory acquisition ($\beta \pm SE = 0.15 \pm 0.55$, Wald = 0.76, df = 1, $P = 0.78$, Figure 3). The experimental removal of one or both dominants tended to increase the chance that the competitor within that territory would gain a breeding position (Table 3). This was probably the result of territorial inheritance; when competitors that inherited an experimental breeder position were excluded from the analysis, removal of a dominant did not explain variation in territory acquisition ($\beta \pm SE = -0.66 \pm 0.75$, Wald = 0.79, df = 1, $P = 0.39$, $n = 53$). The proximity of a competitor's territory to same-sex vacancies positively influenced its chances of acquiring an experimental vacant dominant position (Table 3). However, of the 20 experimental vacancies claimed by individuals from other territories, 11 (5 female and 6 male vacancies) were not by the competitor that lived closest to the vacancy. In fact, in 10 of these 11 instances, on average 5 same-sex competitors lived closer to the vacancy than the eventual claimant. In males, the age of the eventual claimants was higher than the median age of the closer nonclaimants (Wilcoxon signed-ranks: $Z = -2.03$, $P = 0.04$, $n = 6$). This suggests that for males being older than your competitors is more important in gaining a vacant dominant position than is living close to a vacancy. For females, the median age of the closer nonclaimants was not different from the age of the claimants

(Wilcoxon signed-ranks: $Z = 0.00$, $P = 1.00$, $n = 5$). This indicates that for females, chance or other unidentified factors may also play a part in territory acquisition.

DISCUSSION

The results of the nonexperimental part of this study show that the main route to territory acquisition for both male and female Seychelles warblers was the passive claiming of a vacant dominant position outside the natal territory. Territory acquisition through the creation of a new territory seemed to be a secondary strategy followed only by males. The phenotype (size and age) of males that created a new territory was not different from that of males that acquired a territory through another route. Although individuals that claimed a vacant dominant position in a given territory were not larger than the same-sex subordinates living in the territory at the moment of claiming, they were older, especially in males. Males and females were found to disperse at the same age, but males were older than females when acquiring a dominant breeding position within a territory for the first time.

The experiment part of the study revealed that vacant dominant positions were not filled as rapidly as in other cooperatively breeding bird species (e.g., the superb fairy wren, *Malurus cyaneus*, Pruett-Jones and Lewis 1990) and that male vacancies were claimed faster than female vacancies. Furthermore, the presence, in the removal territory, of a subordinate of the same sex as the removed breeder delayed the uptake of the vacancy. In agreement with the nonexperimental part of the study, size did not affect a competitor's chances of acquiring a territory. For both sexes, the proximity of a competitor's resident territory to an experimental vacancy positively affected its chance of claiming the vacancy. Interestingly, the competitors' age affected the chance of acquiring a territory differently for males and females. Older males were more likely to claim a vacancy than were young males, whereas age did not affect females' chances of claiming a vacancy. This result matches the observation that males were older than females when acquiring a territory for the first time. Our findings thus demonstrate that even when the majority of individuals of both sexes follow the same route to territory ownership, there may be sex-specific differences in which factors are important in territory acquisition.

Slow claiming of experimental vacancies

The relatively slow claiming of experimental vacant dominant positions seems strange given the surplus of independent

Table 2

The effect of the sex of the removed dominant, the quality of the territory supporting the vacancy, the presence of subordinates on the territory supporting the vacancy, and the density of competitors around the vacancy on the interval between removal and claiming of experimental vacant dominant positions ($n = 20$)

Explanatory variables	$\beta \pm SE$	<i>F</i>	df	<i>P</i>
Sex	-0.34 ± 0.16	4.6	1	0.05
Territory quality	0.11 ± 0.11	1.0	1	0.34
Subordinate presence	-0.49 ± 0.19	6.6	1	0.02
Competitor density	-0.06 ± 0.04	2.7	1	0.12

Factors included in the final model are in bold.

Table 3

Claiming of experimentally created dominant breeder positions by subordinate Seychelles warblers ($n = 60$) in relation to sex, age, and size of the subordinate, its proximity to the vacancy, removal of one or both dominants from the subordinate's territory and the degree of competition

Explanatory variables	$\beta \pm SE$	χ^2	df	<i>P</i>
Sex (female)	4.67 ± 1.86	6.3	1	0.01
Age	2.34 ± 0.73	10.2	1	0.01
Proximity	-1.12 ± 0.51	4.9	1	0.03
Sex (female) × age	-2.16 ± 0.96	5.1	1	0.02
Size	-1.18 ± 0.89	1.0	1	0.32
Competition	-0.06 ± 0.54	0.4	1	0.54
Dominant removal	-1.12 ± 0.68	3.1	1	0.08

Summaries derived from the binomial response mixed-modeling procedure in MLwiN. Factors included in the final model are in bold. Nonsignificant interactions are not presented.

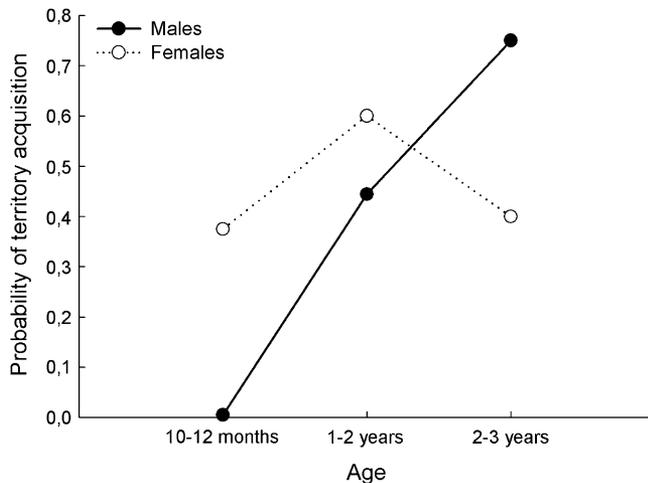


Figure 3
The probability that 10–12 month, 1–2 and 2–3 year old subordinate male and female Seychelles warblers claimed a vacant dominant position in the breeder removal experiment. Males $n = 34$, females $n = 26$.

nonbreeders in the population at the time of the experiment. It is possible that potential claimants were slow to discover vacant dominant positions as a result of a low foray rate; in a total of 116 h of radio telemetry observations on 11 different individuals, only 6 forays were observed (Eikenaar C, unpublished data). However, in our experiment, the interval between the opening and filling of a vacant dominant position did not depend on competitor density as would be expected if the rate of vacancy claiming depended on the foray rate. In a similar removal experiment in acorn woodpeckers, Hannon et al. (1985) showed that breeder replacement was delayed substantially in groups containing helpers of the same sex as the removed bird. They argued that this was caused by these subordinates attacking potential replacements. Although our findings are comparable, in our experiment, this cannot be the whole explanation because such subordinates were present in only 5 of the 20 removal territories. An alternative explanation could rest on the idea that when parental investment is extensive, breeders are expected to exhibit choosiness in finding their mates, especially when pairing for life (Trivers 1972; Parker 1983; Shellman-Reeve 1999). Because in Seychelles warblers, parental investment is high in both sexes and pair bonds usually are for life (Komdeur 1991, 2003; Eikenaar et al. 2008), “widowed” breeders may be choosy about replacement mates. This may have contributed to the slow claiming of vacant dominant positions. However, in clear contradiction to this concept of resident dominant individuals being choosy about their replacement mates is the finding that occupancy of vacant dominant positions seemed to be on a first-come-first-served basis.

Age and territory acquisition

We observed that females were younger than males when acquiring a territory for the first time. This may appear to be at odds with the observation that the age at dispersal did not differ between the sexes but can, at least in part, be explained by the diversity of routes which individuals may take to becoming a breeder. Some individuals did not disperse off the territory but instead acquire a territory by inheriting or budding off part of the natal territory. Furthermore, some individuals that did disperse did not immediately acquire territory, but first became a floater or a subordinate in a staging territory.

Individuals of both sexes that followed these alternative routes acquired a territory at an older age than birds dispersing directly from the natal territory into a vacant dominant position. As more males followed an alternative route than females (36% and 25%, respectively), this contributed to the difference in the age of the sexes when first acquiring a territory. A second explanation for this difference may lie in the observation that there appears to be a sex bias in the turnover rate of dominants; the chance that a dominant becomes a subordinate in the same territory is higher for females than for males (Richardson et al. 2007). Consequently, female subordinates have to wait for a shorter period of time than males before they can claim a dominant position.

The explanations above cannot clarify why young males were less able to acquire a territory than young females in our experiment. It does not seem likely that this pattern resulted from a sex difference in prospecting behavior because young individuals of both sexes (6–12 months old) have been observed to engage in extraterritory forays (Eikenaar, unpublished data). It seems more likely that this sex difference is the result of sexual selection, that is, males facing more intense intrasexual competition for mates than females, or female choice for certain male characteristics (Trivers 1972), including perhaps male age itself (Richardson and Burke 1999). In the Seychelles warbler, the degree of intrasexual competition for territory ownership may be higher for males than for females. Because for males, territory ownership is a prerequisite for reproduction (Richardson et al. 2001, 2002), every year that a male remains a subordinate is a year without reproduction. Females, however, have the opportunity to reproduce as a subordinate by joint nesting with the dominant female (Richardson et al. 2001, 2002). Competition over vacant dominant positions may therefore be more intense among males than among females. Furthermore, because of the promiscuous nature of this species (40% of young are extrapair, Richardson et al. 2001), there will be greater variance in male reproductive success, thus leading to fiercer competition for mates between males than females (Dobson 1982). If competitive ability increases with age (e.g., Brown 1975; Zack and Rabenold 1989; Bose and Sarrazin 2007), young subordinate males will be outcompeted by older subordinate males. We never observed fights or disputes in territories where there was a vacant breeder position. This suggests that male–male competition was indirect, either because male status within a neighborhood is well established or because older males are more familiar with their surroundings than are young males.

When competition for territories and mates is more direct, for example, in species in which males obtain and defend a territory and females, then choose a male partner, factors related to competitive ability would be expected to be more important in territory acquisition. Although some studies have shown that territory ownership is correlated with body size (e.g., Piper et al. 2000), other studies have failed to find differences in body size between territory owners and their contestants (e.g., Shutler and Weatherhead 1991; Takeuchi 2005). In the willow ptarmigan, *Lagopus lagopus*, paired territorial males were larger than unpaired nonterritorial males (Martin 1991). However, body size did not predict which unpaired males obtained territories and mates when opportunities were experimentally created (Martin 1991). Such inconsistencies between, and even within, studies show that the route by which territories and mates are acquired cannot be reliably used to predict which factors are important in these processes.

Stronger intrasexual competition for territories among males than females could have contributed to our observation that young males were less likely to acquire a territory than young females. The claiming of a vacant dominant position

is, however, not a unilateral decision, and the remaining breeder may be selective about its replacement mate. With females generally being choosier about their sexual partners than males (Bateman 1948; Trivers 1972; Cockburn 2004), female preference for older males could also have contributed to our observation. Female preference for older males has been shown in other species (e.g., Richardson and Burke 1999; Bouwman and Komdeur 2005) and is likely to be present in the Seychelles warbler; reproductive success increases with age (Komdeur 1996) and females should be choosier than males because for females it is more difficult to increase their fecundity through promiscuity than it is for males (40% extrapair paternity, but no egg dumping, Richardson et al. 2001). Seychelles warbler females may distinguish young males from old males by their eye color, which gradually changes from gray, through light brown to red brown during the first 2 years of life (Komdeur 1991; Eikenaar, unpublished data). Support for a preference for old males comes from the observation that in the 3 removal territories where there were no remaining breeder females (both breeders removed), the males that claimed the vacancies were relatively young (1.5, 1.5, and 2 years compared with a median age of 2.5 years when there was a breeder female remaining). On the other hand, male vacancies tended to be claimed slightly faster than female vacancies, contradicting the idea that females are choosier about replacement mates than males. To resolve whether choosiness over mates differs between the sexes, detailed observations on interactions between widowed breeders and potential replacement mates are required. This is challenging because it requires the tracking of widowed breeders for prolonged periods and correct identification of potential replacement mates, which are arduous tasks when individuals are interacting in dense vegetation.

In an experiment on stripe-backed wrens, *Campylorhynchus nuchalis*, where breeder females were removed, older females more often gained the resulting vacancies than young females (Zack and Rabenold 1989). The authors argue that this advantage of age probably promotes the delayed dispersal that is characteristic of this and other cooperatively breeding species. In the Seychelles warbler, the present study shows that both sexes delay dispersal for equally long periods (Figure 1). However, both our observational data, as well as our breeder removal experiment, indicate that the advantage of age when competing for vacant dominant positions is significant only for males. Therefore, an age-related increase in the chance of claiming a vacant dominant position is unlikely to explain why female Seychelles warblers delay natal dispersal. Additional experiments in cooperatively breeding species involving the removal of breeders of both sexes are needed to resolve whether young facultatively delay dispersal to increase their ability to compete for breeder positions.

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