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Eikenaar, Cas

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

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Abstract

Factors that affect success in territory acquisition may have a large impact on individual fitness. Nevertheless, the relative importance of multiple factors in territory acquisition remains unclear and no study has specifically addressed whether the relative importance of such factors differs between the sexes. When competing over territories some individuals may have an advantage if, for example, they are genetically or phenotypically superior or more familiar with the site than others. We studied patterns of territory acquisition in a saturated population of Seychelles warblers, a species in which both sexes defend the territory. We also experimentally investigated the relative importance of multiple factors in territory acquisition and assessed whether this differs between the sexes. Finally, we gathered radio-telemetry data to learn more about prospecting behaviour. For both sexes, the main route to territory acquisition was to disperse from the natal territory to immediately occupy a breeder vacancy. To locate these breeding vacancies, subordinate males and females living within cooperatively breeding groups regularly engaged in prospecting forays. Most experimental breeder vacancies remained unoccupied for several days - probably due to the low foray rate - and overt competition over vacancies was not observed. For both sexes, the proximity of an individual’s natal territory to a breeder vacancy was positively related to its chance of occupying that vacancy. Older males were more likely to gain a breeder vacancy than young males, whereas age did not affect territory acquisition in females. The degree of intra-sexual competition for territory ownership may be stronger for males than for females, because territory ownership is a prerequisite for reproduction for males, whereas females can reproduce on their natal territories while being subordinate. Consequently, young male subordinates may have been out competed by older male subordinates. Alternatively, this sex difference resulted from female breeders being choosier about replacement mates than male breeders.
Introduction

Dispersal from the natal site to the first breeding site (natal dispersal; Greenwood and Harvey 1982) is a crucial step in an individual’s life, as territory ownership is a prerequisite for reproduction in many species (Clutton-Brock et al. 1982; Beletsky and Orions 1993). Factors that affect success in territory acquisition can, therefore, have a large impact on fitness. Territorial ownership may be achieved either through passive acquisition, such as occupying a vacancy left after the death or desertion of a previous resident (e.g. Piper et al. 2000), or by active acquisition, by displacing a breeder of the same sex (e.g. Heg et al. 2000) or creating a completely new territory (e.g. Arcese 1989a).

When competing over territories some individuals may have an advantage over others, for instance they may be genetically or 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, since it involves competition with territory owners that have more to lose during territorial disputes than non-breeders (Maynard Smith and Parker 1976). Familiarity with a site may not only depend on the proximity of the non-breeders resident territory to the site, but also on the amount of exploratory forays made by non-breeders to the site (Bruinzeel and Van de Pol 2004). When the quality of an individual’s phenotype, or its knowledge about a site, increases with age older non-breeders may be better competitors than younger non-breeders (Zack and Rabenold 1989). Furthermore, success in territory acquisition may increase when non-breeders are allowed to wait on the relatively safe natal territory until they locate a breeder vacancy (Mulder 1995; Eikenaar et al. 2007).

Many studies have dealt with specific factors that affect territory acquisition, however, studies which investigate the relative importance of multiple factors in territory acquisition remain scarce (but see Zack and Rabenold 1989; Martin 1991; 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 this seems likely because many behaviours 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 of multiple factors and sex-differences in territory acquisition, we use a combination of a thorough analysis of 12 years of data on territory acquisition in the Cousin population of Seychelles warblers, *Acrocephalus sechellensis*, with a breeder removal experiment in the same population. This population has almost no migration on or off the island (Komdeur et al. 2004a) and during our study period nearly all warblers on Cousin were individually marked (>95%). Furthermore, for many individuals we have their natal dispersal histories. Consequently our data on territory acquisition is virtually complete and unbiased.

Seychelles warblers have a facultative cooperative breeding system. They live either in pairs, or in groups consisting of a primary pair and, normally, one or more off-
spring that have delayed dispersal and remained in the natal territory as subordinates (Komdeur 1992, but see Richardson et al. 2007). Many (ca. 40%) of the female subordinates successfully reproduce each year by directly laying in the same nest as the primary female, whereas male subordinates only reproduce after they have acquired a primary 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), and female natal dispersal distances are twice as large as those of males (Eikenaar et al. 2008).

In the present study we use radio-telemetry data and observations of young warblers foraying outside their resident territories to learn more about this behaviour and to determine how familiar birds are with the territories surrounding their own. We determine i) the age of birds at dispersal and when they first occupy a primary breeder position, ii) the route by which individuals normally acquire a territory (passive acquisition versus active acquisition), iii) whether individuals that engage in active territory acquisition are phenotypically different than those that engage in passive acquisition, and iv) if these aspects differ between the sexes. Finally, we created multiple simultaneous breeder vacancies by removing territory owners in 2004 (as part of a conservation driven translocation program). This allowed us to experimentally study patterns of territory acquisition and gave us a chance to tease apart the effect on territory acquisition of the age, size and proximity of a competitor to a vacancy. It also allowed us to assess the level of competition for breeding vacancies within this population.

Because territory ownership is a prerequisite for reproduction for males but not for females, competition for territories probably is much stronger for males than for females. We therefore expect male vacancies to be occupied faster than female vacancies. Furthermore, as in other bird species competitive ability has been shown to increase with age (e.g. Brown 1975; Zack and Rabenold 1989; Bose and Sarrazin 2007), we expect young subordinate males to be out competed by old subordinate males. Because females disperse further than males, we expect the proximity of a subordinate to experimental vacancies to be less important in territory acquisition for females than for males.

Methods

Study species and population
The primary male and female were defined as the dominant, pair-bonded male and female in the territory. All other birds, resident in the territory and old enough to disperse (on Cousin > six months old; Komdeur 1996), were defined as subordinate. Although most subordinates are previous offspring that have delayed dispersal, some subordinates are former primary breeders that have been demoted and remained on the territory (Richardson et al. 2007). Groups may also hold immigrants unrelated to the primary pair, because a small proportion of subordinates joins a non-natal group (7.9 %, Richardson et al. 2002; 7.3 %, this study). Each pair or group occupies an all-
purpose territory year-round and both sexes engage in territory defence (Komdeur 1992). Previous work has shown that some of the subordinates become helpers and assist their parents in raising non-descendent kin (Komdeur 1992; Richardson et al. 2003b). 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 centre of the island, all the habitat is occupied by warblers. All the data presented is based on colour-ringed individuals and was gathered from 1995 to 2006. During this period the total number of territories on the island was stable (average ± SE: 111.6 ± 1.7) and most individuals in the population were individually colour-ringed (90 – 97 %).

After being caught using mistnets each bird previously unrung bird was individually colour-ringed using a unique combination of three colour rings and a British Trust for Ornithology metal ring. For all birds the length of the right tarsus was measured to the nearest 0.1mm using a vernier calliper. However, because some birds were ringed as chicks and not caught and measured again after fledging, tarsus size was not available for all birds in this study. Blood samples (ca 15 µl) were collected by brachial venipuncture and stored in 100% ethanol at room temperature. Molecular sexing using the polymerase chain reaction (PCR) method devised by Griffiths et al. (1998) was used to confirm the sex of each ringed individual. Using observations of individual warblers and territory boundary disputes between groups, territories were mapped in detail in all years of the study. During the breeding seasons, all territories were checked for the presence of warblers at least every two weeks. For all individuals, the status (primary or subordinate) and territory of residence were determined in each year during the peak breeding season (June–August) and from 1997–1999 and 2003–2006 also during the minor breeding peak (December–February). As inter-island dispersal is extremely rare (Komdeur et al. 2004a) warblers that were missing from their territory and never seen afterwards were presumed to have died.

**Foraying behaviour and routes to territory ownership**

In August 2004 three six month old subordinates were also radio tagged. In August 2004 and September 2005 we fitted 0.35 g Holohil radio transmitters to a total of eight yearling subordinates (five males and three females). Transmitters were positioned a centimetre above the preengland by gluing them onto a few back feathers that were cut just above the feather base. After tagging the yearlings were tracked continuously during all daylight hours (6am – 6 pm) for two consecutive days, whereas the six-month -olds were located each hour during three successive days. Birds were tracked at close range using a handheld Icom receiver and Yagi antenna. Ad lib foraying data consisted of incidental catches and observations of subordinates outside their resident territory, that result from the extensive catching and behavioural observations that are part of the routine fiedwork. These observations were used to estimate at what age subordinates make extra-territory forays.
Seychelles warblers may acquire a territory through a number of different routes. They may remain on the natal territory and leave only to occupy a foreign breeding vacancy, alternatively inherit a breeding position on the natal territory or bud off part of the natal territory (males only, Komdeur and Edelaar 2001). Alternatively they may leave the natal territory and, before settling as a breeder, join another group (defined as staging) or become a floater; a bird that roams over the island without having a resident territory (Komdeur and Edelaar 2001). Only primary breeders were regarded to have achieved territory ownership.

Breeder removal experiment
In 2004, the translocation of 58 Seychelles warblers from Cousin Island to the unoccupied Island of Denis (131 ha.) for conservation reasons provided the opportunity to undertake a breeder removal experiment. The translocation happened just prior to the breeding season (the first nesting attempt occurred on 24th of June). In the two weeks before the first removals, all territories were thoroughly searched in order to ascertain the status and territory of residence of as many individuals as possible. The 58 individuals were caught over two separate periods (the mornings of the 29th and 30th of May and a period covering the evening of the 11th of June and the subsequent morning) and translocated by helicopter. Among the translocated birds were 17 primary females and 20 primary male breeders. In ten territories the primary breeding female was removed, in 13 the primary breeding male and in 7 both primary breeders (hereafter all termed experimental territories). After removals, each experimental territory was thoroughly searched twice a day for 15 minutes during three 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 behaviour (e.g. fighting and singing) at the time of sighting. Daily searches ceased after three weeks, due to time constraints, however, ad lib observations were made over the next three months in territories in which no new replacement breeder(s) for the removed birds were observed.

Data analyses
We compared the tarsus length and age of birds that passively or actively gained a territory (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). To investigate the effect of age on territory acquisitions, we determined the age at which birds dispersed and occupied a primary breeder position for the first time. Because not all individuals were ringed in the nest the exact age of some birds was unknown. We did, however, always know in which breeding season each individual was born. With breeding seasons six months apart, individuals could be assigned to belong to age classes six months old, 12 months old, 18 months old, etc. In the analyses of age at dispersal
and first territory acquisition, we set the age to six months when individuals could be assigned to have dispersed / first occupied a primary breeder position in the season after they fledged, to 12 months when they dispersed / first occupied a primary breeder position two seasons after they fledged, etc.

**EXPERIMENTAL DATA**
The effect of subordinate sex, competitor density and presence of subordinates on the time until occupancy of experimental vacancies was analysed using a GLM. Time between the creation and the occupancy of experimental vacancies was expressed in days and was log-transformed prior to analysis. Competitor density was measured as the number of subordinates of the same sex as the removed breeder, living within two territory widths of the experimental vacancy (two widths being the median distance dispersed in the experiment). The presence - in the experimental 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 occupied.

Komdeur (1992) showed that the quality of the natal territory influenced settlement decisions; e.g. young born in high quality territories only occupied breeder vacancies in high quality territories. In our breeder removal experiment, we compared the quality of the territories of origin and settlement for individuals that occupied a vacancy outside their resident territory. Territory quality in terms of insect prey availability was measured as described by Komdeur (1992).

The effect on territory acquisition of proximity to vacancies, subordinate age, size and sex, parent removal, and the degree of competition were analyzed using a multi-level mixed modelling procedure in MlwiN (Rasbash et al. 2004). For each subordinate, proximity was expressed as the average distance (in territory widths) between the resident territory and all the same-sex vacancies within seven territory widths around the resident territory. This radius was chosen, because for both sexes it was the maximum dispersal distance that was observed in the experiment. Since the experimental vacancies were created in two rounds ten days apart, individuals occupying 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. Age was expressed using the earlier described age classes. Because young have never been observed to disperse within six months off fledging on Cousin (Komdeur 1996) individuals that fledged in the last breeding season before the translocation (and hence were only about four months old) were excluded from the analyses.

In the Seychelles warbler the sexes differ in size, therefore tarsus values were centred around the population mean for the individuals own sex by subtracting the mean trait value from the individuals’ trait value. Parent removal was defined as when a primary breeder(s) was removed from the subordinate’s territory. The level of local com-
petition over breeder vacancies for each subordinate was estimated as the number of same-sex subordinates present in the focal subordinate’s own and adjacent territories. In the MlwiN analyses, the binary response variable was whether or not a subordinate occupied an experimental vacancy. Territory identity was included as the level two unit of variation and subordinate identity as the level one unit of variation, because in five occasions two, not just one, same-sex subordinates lived in the same territory at the time of the experiment. Model selection was based on the backward method, in which non-significant terms ($P > 0.05$) were removed from the model in order of least significance. Only subordinates for which the resident territory immediately prior to the experiment was known were included in the analyses. Since breeder dispersal is rare (1.3% of breeders dispersed on average each year, Eikenaar et al. 2008), we excluded primary breeders as competitors in the analyses on factors affecting territory acquisition.

**Results**

**Foraying behaviour**

The radio-telemetry data suggested that the extra-territory foray rate of subordinates was low. During 116 hours of continuous radio-tracking of eight one-year old individuals (five males and three females), only six forays were observed. This indicates an individual foray rate of less than one foray per week during daylight hours. The observed forays lasted between 5 and 30 minutes and foray distance was limited to one or two territories away from the natal territory. The short distances of forays suggest that the familiarity of young with their surroundings decreases with distance from the natal territory.

The position of each of the three six-month old radio-tagged subordinates was determined 34 times. The subordinates were never located outside their natal territory. Ad lib foray data, however, revealed that six-month olds sometimes did engage in extra-territory forays. Of all female forays 12.5% were by six-month olds, 50% were by one-year olds and 37.5% by older females (out of a total of 32 observed forays). For males these percentages were 11.6%, 39.5% and 48.9% ($n = 43$).

**Routes to territory ownership**

In total, 191 (87 females and 104 males) natural acquisitions of a primary breeder position by a subordinate with known dispersal history were recorded. Table 4.1 presents the numbers of subordinates with known dispersal history that followed the different routes to primary breeding positions. For both sexes, the predominant route was the passive acquisition of a vacancy outside the natal territory that resulted from the death of a primary breeder. Although most birds (69.1%) occupied a vacancy directly from the natal territory, some became a floater or a subordinate in another group (staging) prior to acquiring their own territory (table 4.1).
Active territory acquisition appeared to be a strategy predominantly followed by males. During our study period 20 completely new territories formed, of which six were created by males budding off part of their natal territory (Table 4.1). The other 14 territories also seemed to be initiated by males, because only male subordinates were observed to foray from their natal territory to the exact locations where they later created new territories ($n = 4$). In 15 instances (six females and nine males) of territory acquisition the previous breeder was observed again the next breeding season, usually in another territory. In these instances it was unclear whether territory acquisition was active (displacement of the previous breeder) or passive (the previous breeder left after a divorce).

There was no evidence that males engaging in active territory acquisition were phenotypically superior to those that engaged in passive territory acquisition; tarsus length was similar between the two groups (mean ± S.D.: active acquisition = $25.9 ± 0.76$ mm ($n = 18$) and passive acquisition = $25.7 ± 0.78$ mm ($n = 74$); $T$-tests: $t = −0.95$, $P = 0.35$). Furthermore, age of first territory acquisition was not different between these two groups (median age: active acquisition = 2 years ($n = 20$) and passive acquisition = 2 years ($n = 84$); Mann-Whitney $U$: $Z = 0.43$, $P = 0.99$). Therefore all males were pooled when comparing 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 = 1.5 years for both males and females, Mann-Whitney $U$: $Z = -0.85$, $P = 0.40$ and $n = 191$), and the majority of males and females dispersed within two years of fledging (figure 4.1). Females did acquire a territory for the first time at a significantly younger age than males (median age: females = 1.5 years and males = 2 years, Mann-Whitney $U$: $Z = −2.25$, $P = 0.03$ and $n = 191$; figure 4.2). Individuals acquiring a territory by dispersing directly from the natal territory into a breeder vacancy 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: from natal territory = 1.75 years and alternative route = 2 years, $Z = −3.55$, $P < 0.01$ and $n = 104$; females: median ages: from natal territory = 1.5 years and alternative route = 2 years , $Z = −3.67$, $P < 0.01$ and $n = 87$). The age at which birds acquired a territory for the first time did not depend on tarsus length ($F_{1,167} = 0.50$ and $P = 0.48$).

### Table 4.1

The percentages of male and female subordinate Seychelles warblers that followed the different routes to a primary breeding position, 1995 – 2006. Total natal dispersal events males, $n = 104$ and females, $n = 87$.

<table>
<thead>
<tr>
<th>Route to Primary Breeding Position</th>
<th>Males $n = 20$</th>
<th>Females $n = 84$</th>
<th>Total $n = 104$</th>
</tr>
</thead>
<tbody>
<tr>
<td>From natal territory</td>
<td>64.4</td>
<td>74.7</td>
<td>69.1</td>
</tr>
<tr>
<td>From staging territory</td>
<td>7.7</td>
<td>6.9</td>
<td>7.3</td>
</tr>
<tr>
<td>Floating</td>
<td>18.3</td>
<td>16.1</td>
<td>17.3</td>
</tr>
<tr>
<td>Territory budding</td>
<td>5.8</td>
<td>-</td>
<td>3.1</td>
</tr>
<tr>
<td>Territory inheritance</td>
<td>3.8</td>
<td>2.3</td>
<td>3.1</td>
</tr>
</tbody>
</table>

*Note: The percentages are rounded to one decimal place.*
Breeder removal experiment

**Occupation of experimental breeder vacancies**

Of the 37 experimental breeder vacancies, six (3 territories where both primary breeders were removed) were lost to the experiment because the primary breeders in an adjacent territory expanded their own territories and took over the entire vacant territory. These take-overs were observed two, five and six days after breeder removals. Of the remaining 31 experimental breeder vacancies two remained vacant for more than three months and were not therefore considered here. The territory of residence just prior to the experiment was unknown for two of the 29 individuals that oc-
ocupied the experimental vacancies (hereafter termed occupiers). Of the remaining 27 occupiers, 26 were subordinates and one was a primary breeder that abandoned its previous territory to occupy an experimental vacancy. Of the 26 subordinates, 19 occupied an experimental vacancy outside their resident territory and seven ‘inherited’ a vacancy on their resident territory.

Occupancy of breeder vacancies seemed to be on a first-come-first-served basis. First, in none of the 15 minutes searches \((n = 159)\) of the experimental territories were fights or disputes observed. Second, in all except one of the 20 (10 male and 10 female) times an individual from another territory took the position the first non-resident individual observed in the territory was the individual that became the new breeder. The median time to occupation of these 20 breeder vacancies was 3.5 days (range 1–20 days). Table 4.2 shows which factors influenced the time until occupation of the experimental vacancies. Male vacancies were occupied slightly faster than female vacancies (median: male = 2 days and female = 4 days). The time it took for a vacancy to be occupied was negatively related to the presence of a subordinate in that territory of the same sex as the removed breeder. Occupation time did not depend on competitor density.

Of the 20 individuals that left their resident territory to occupy a breeder vacancy, eight moved to a territory that was of higher quality than their territory of origin, two moved to an equal quality territory and ten moved to a lower quality territory.

### Table 4.2. The effects of competitor sex, presence of a subordinate of the same sex as the removed breeder, and competitor density on time to occupation of experimental breeder vacancies \((n = 20)\). The final model is in bold.

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>(\beta \pm SE)</th>
<th>(F)</th>
<th>d.f.</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Competitor sex</td>
<td>-0.34 ± 0.16</td>
<td>4.57</td>
<td>1</td>
<td>0.048</td>
</tr>
<tr>
<td>Subordinate presence</td>
<td>-0.49 ± 0.19</td>
<td>6.59</td>
<td>1</td>
<td>0.021</td>
</tr>
<tr>
<td>Competitor density</td>
<td>-0.06 ± 0.04</td>
<td>2.65</td>
<td>1</td>
<td>0.12</td>
</tr>
</tbody>
</table>

**FACTORS INFLUENCING TERRITORY ACQUISITION**

Table 4.3 shows which factors influenced a subordinate’s chance of occupying a breeder vacancy in the experiment. The number of same-sex competitors present in the focal or adjacent territories did not influence the chance of territory acquisition, nor did subordinate size or any of the other interactions.

The age of the subordinate did affect territory acquisition and the significant interaction between sex and age indicated that the effect of age differed between the sexes. We therefore analysed the effect of age on territory acquisition separately for the sexes. For males there was a positive relation between their age and the likelihood
of territory acquisition ($\beta \pm \text{s.e.} = 1.86 \pm 0.62, \text{Wald} = 9.1, \text{d.f.} = 1, \text{P} = 0.003$, figure 4.3). For females age did not affect the chances of territory acquisition ($\beta \pm \text{s.e.} = 0.15 \pm 0.55, \text{Wald} = 0.76, \text{d.f.} = 1, \text{P} = 0.78$, figure 4.3). The experimental removal of a primary breeder tended to increase the chance that the subordinate within that territory would gain a breeding position. This was probably the result of territorial inheritance after the removal of the primary breeder in a subordinate’s territory. When subordinates that inherited an experimental breeder position were excluded from the analysis, breeder removal did not explain variation in territory acquisition ($\beta \pm \text{s.e.} = –0.66 \pm 0.75, \text{Wald} = 0.79, \text{d.f.} = 1, \text{P} = 0.39, n = 53$). The proximity of the subordinates’ territory to same-sex vacancies positively influenced their chances of

![Figure 4.3](image_url)

**Figure 4.3.** The probability that 10–12 months, 1–2 and 2–3 year old subordinate male and female Seychelles warblers occupied a breeder vacancy in the breeder removal experiment. Males $n = 34$ and females $n = 26$.

**Table 4.3.** Model summaries examining occupation of experimentally created breeder positions by subordinate Seychelles warblers ($n = 60$) in relation to sex, age and size of the subordinate, its proximity to vacancies, breeder removal from the subordinate’s territory and the degree of competition. Summaries derived from the binomial response mixed-modelling procedure in MLwiN. The final model is in bold. Non-significant interactions are not presented.

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>$\beta \pm \text{SE}$</th>
<th>$\chi^2$</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex (female)</td>
<td>4.67 ± 1.86</td>
<td>6.29</td>
<td>1</td>
<td>0.012</td>
</tr>
<tr>
<td>Age</td>
<td>2.34 ± 0.73</td>
<td>10.20</td>
<td>1</td>
<td>0.001</td>
</tr>
<tr>
<td>Proximity</td>
<td>–1.12 ± 0.51</td>
<td>4.89</td>
<td>1</td>
<td>0.027</td>
</tr>
<tr>
<td>Sex (female) x age</td>
<td>–2.16 ± 0.96</td>
<td>5.10</td>
<td>1</td>
<td>0.024</td>
</tr>
<tr>
<td>Size</td>
<td>–1.18 ± 0.89</td>
<td>1.00</td>
<td>1</td>
<td>0.32</td>
</tr>
<tr>
<td>Competition</td>
<td>–0.06 ± 0.54</td>
<td>0.38</td>
<td>1</td>
<td>0.54</td>
</tr>
<tr>
<td>Breeder removal</td>
<td>–1.12 ± 0.68</td>
<td>3.09</td>
<td>1</td>
<td>0.08</td>
</tr>
</tbody>
</table>
acquiring an experimental breeder position (table 4.3). However, of the 20 experimental vacancies occupied by individuals from other territories, 11 (five female and six male vacancies) were not by the subordinate bird that lived closest to the vacancy. In fact, in 10 of these 11 occupations more than one (median = five) same-sex subordinates lived closer to the vacancy than the eventual occupier. In males the ages of these occupiers were higher than the median ages of these non-occupiers (Wilcoxon signed ranks: \( Z = -2.03, P = 0.04, n = 6 \)). This suggests that for male subordinates being older than your competitors is more important to occupy a breeder vacancy than living very close to such a vacancy. For females, the median ages of these non-occupiers were not different from the ages of the occupiers (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 main route to territory ownership for male and female Seychelles warblers was the passive acquisition of a breeder vacancy outside the natal territory. Active territory acquisition through the creation of new territories seemed to be a strategy predominantly followed by males. In 15 (nine males and six females) instances of territory acquisition the previous breeder was observed again, after the new breeder settled. Ten (five males and five females) of these previous breeders were observed as primary breeders on another territory the next season. These breeders most likely dispersed after a divorce, because displacement by a subordinate would imply these breeders to be weak competitors, that would probably not have succeeded in re-establishing as a primary breeder. This suggests that these 10 instances of territory acquisition were passive. The remaining five instances of territory acquisition may have been active, which fits the idea that active acquisition is mainly a male strategy. To locate breeder vacancies young warblers engaged in exploratory forays. Foray rate was low (estimated one foray per week), especially when compared to foray rates observed in Acorn woodpeckers, *Melanerpes formicivorus* (more than one foray per hour, Hooge 1995). Although foray distances observed in the current study were restricted to one or two territories away from the natal one, ad libitum observations show that young warblers sometimes also engage in long-distance forays (Eikenaar, unpublished results). Males and females dispersed at the same age, but males were older than females when acquiring a territory for the first time. Beside analyzing natural data, we performed a breeder removal experiment to assess which factors affect success in territory acquisition. Similar experiments have been conducted in quite a few bird species and revealed that territory ownership may depend on factors such as age or body mass of the competitor (e.g. Arcese 1989b; Zack and Rabenold 1989; Piper et al. 2000), site familiarity (e.g. Jakobsson 1988; Beletsky and Orions 1993; Yáber and Rabenold 2002) or chance effects (e.g. Beletsky and Orions 1993). Some studies, however,
failed to identify factors that predicted which competitors obtained territorial vacancies (e.g. Hannon and Roland 1984; Martin 1991). Because unlike most removal experiments, we created breeder vacancies for both sexes, we were able to study sex-based differences in territory acquisition.

**Slow occupation of experimental vacancies**
Many of the experimental breeder vacancies remained vacant for several days, sometimes even weeks, after the removal of the original breeder(s). This does not appear to be an artefact of the experiment as such slow occupation of breeder vacancies sometimes also occurs naturally within this population (C. Eikenaar, pers. obs.). These results contrast with findings in other cooperative breeders where vacancies are rapidly filled (e.g. Pruett-Jones and Lewis 1990; Russell and Rowley 1993), and seems strange given the permanent surplus of independent non-breeders seen in the Seychelles warbler population. It is possible that potential occupiers were slow to discover breeder vacancies as a result of the low foray rate. However, in our experiment the time lag between the opening and filling of a breeder vacancy did not depend on competitor density as would be expected if the rate of vacancy occupation depended on the foray rate. Furthermore, most territories in which a breeder position remained vacant for longer than one day had one or more potential occupiers living in adjacent territories. These subordinates would probably not even have had to leave their territory to notice the vacancy. This suggests that other factors contributed to the slow rate of occupation of experimental vacancies. In a similar removal experiment in Acorn woodpeckers, Hannon et al. (1985) showed that replacement was delayed substantially in groups containing helpers of the same sex as the removed bird. They argued that this was caused by subordinates attacking potential replacements. In agreement with these findings, we found that the time until occupation of a breeder vacancy was greater when a subordinate of the same sex as the removed breeder was present in the territory. However, since such subordinates were present in only five of the 20 territories in the analysis, this can not be the whole explanation. When parental investment is extensive, breeders are expected to exhibit choosiness in finding their mates, especially when pairing for life (Trivers 1972; Parker 1983; Shellmann-Reeve 1999). Because in Seychelles warblers, parental investment is high in both sexes and pair bonds usually are for life (Komdeur 1991; 2003), ‘widowed’ breeders may have been choosy about replacement mates. This may have contributed to the slow occupation of breeder vacancies. Contradicting choosiness about replacement mates, occupancy of breeder vacancies seemed to be on a first-come-first-served basis. We may, however, have missed rejections of candidate replacements if these occurred rapidly and without overt conflict.

**Age and territory acquisition**
We observed that females were younger than males when occupying a territory for the first time (median age: females = 1.5 and males = 2). 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 occupied a breeder position by inheriting or budding off part of the natal territory. Furthermore, some individuals that did disperse did not immediately occupy a breeder position, but first became a floater or a subordinate in a staging territory. Individuals of both sexes which followed these alternative routes occupied a breeder position at an older age than birds dispersing directly from the natal territory into a breeder vacancy. As more males occupied a breeder position through an alternative route than females (36% and 25%, respectively) this led to the difference in the age of the sexes when first acquiring a breeding position.

The explanation above can not, however, explain why young males were less able to acquire a territory than young females in our experiment. It seems improbable that this pattern resulted from a sex difference in prospecting behaviour, because in both sexes young individuals (six to 12 months old) were observed to engaged in extra-territory forays. It seems more likely that this sex difference is the result of sexual selection, i.e. males facing more intense intra-sexual competition for mates than females, or female choice for certain male characteristics (Trivers 1972). In the Seychelles warbler the degree of intra-sexual 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 primary female (Richardson et al. 2001; 2002). Competition over breeder vacancies may therefore be more intense in males than in females. Furthermore, because of the promiscuous breeding system of this species (40% of young are extra pair, Richardson et al. 2001), there probably is greater variation in reproductive output in males, which should consequently compete fiercer for mates 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 may usually be out competed by old subordinate males. Because we never observed fights or disputes in territories where there was a vacant breeder position, male-male competition was probably indirect, possibly through an age-related increase in a subordinate’s familiarity with its surroundings. The idea that competition for territory ownership is more intense in males than females is supported by the observation that, in our breeder removal experiment, male vacancies were occupied faster than female vacancies. An alternative explanation for this observation could be that there were more male (34) than female (26) subordinates at the time of the experiment, whereas the number of vacancies was the same for the sexes. This does not, however, seem likely, because time until occupation of experimental vacancies did not depend on the number of potential occupiers living around these vacancies.

Stronger intra-sexual competition for territories in males than females could have contributed to our observation that young males were less likely to acquire a territory
than young females. The occupation of a breeder vacancy 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% of extra-pair offspring, but no egg dumping, Richardson et al. 2001). Seychelles warbler females may distinguish young males from old males by their eye colour, which gradually changes from grey, through light brown to red brown during the first two years of life (Komdeur 1991; Eikenaar, unpublished data). Support for a preference for old males comes from the observation that in the three experimental territories where there were no remaining breeder females (both breeders removed) the males that occupied the vacancies were relatively young (1.5, 1.5 and 2 years compared to a median age of 2.5 years when there was a remaining breeder female). On the other hand, male vacancies tended to be occupied slightly faster than female vacancies, which contradicts the idea that females are choosier about replacement mates than males. To resolve whether choosiness about replacement mates differs between the sexes, detailed observations on interactions between ‘widowed’ breeders and potential replacement mates are required. This is challenging, because it requires 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.

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First record of Kermadec petrel *Pterodroma neglecta* for Seychelles

Cas Eikenaar
Adrian Skerrett


On 29 August 2003 Cas Eikenaar (CE) noted a medium sized seabird on the hill of Cousin Island Nature Reserve in an open patch near dense vegetation. It was very obviously different to the Audubon’s Shearwaters *Puffinus lherminieri* and Wedge-tailed Shearwaters *P. pacificus* common in the vicinity. Having taken two photographs (Fig. I-1.1), CE approached the bird in order to examine it in the hand and take more photographs. The bird moved into the vegetation where it was caught next to a Wedge-tailed Shearwater, with which it showed no aggressive interactions. In the hand, the bird proved to be very strong and could only be controlled by holding tail, wings and legs (Fig. I-1.2). As a result, with no one to assist, the underwing was not properly examined and not photographed. Following release, the bird settled next to the Wedge-tailed Shearwater, again showing no aggressive interactions. The bird could not be relocated the next day. The photographs and description were submitted unidentified to Seychelles Bird Records Committee (SBRC).

CE departed Cousin Island on 12 September 2003, returning on 20 May 2004. On 29 June 2004, what appeared to be a similar or the same bird was located at exactly the same spot as the previous year. The bird was caught and examined (Figs. I-1.3-4). With the assistance of Lyanne Brouwer, it was possible to examine the underwing and to take measurements and a blood sample. Again, details were sent to SBRC.

**Description of first bird**

Pale grey-brown to white underparts contrasting with darker upperparts and wings. Back dark; upper back to neck gradually becoming greyish brown. Paler head also contrasted with darker upperparts. Whitish patch on lores extending to above and below striking dark eye. Sturdy neck and short, thick dark bill. Area below gape and chin darker, greyish brown. Crown, hindneck and face sides darker greyish brown. Forecrown slightly darker (especially feather centres). Dark tail, tip shorter or equal to tip of wings. Did not appear weak (as far as that can be judged without previous experience of this species) and resisted with great strength upon capture.

**Description of second bird**

Appeared identical to first bird. In addition, examination of underwing revealed this was mainly dark with white patch at base of primaries and white primary shafts. White primary shafts noted on upperwing. Measurements: weight 410 g, tarsus 41.8 mm, tarsus-toe 105 mm, folded wing 30.7 cm, wing stretched 46.7 cm, undertail 120 mm, uppertail 105 mm, head + bill 80.6 mm, bill from tip of nail in straight line to furthest point of gape 33.3 mm, bill depth measured just before nasal tube 30.1 mm.