Parent presence, delayed dispersal, and territory acquisition in the Seychelles warbler

C. Eikenaar,[a] D.S. Richardson,[b] L. Brouwer,[a] and J. Komdeur[a]
[a]Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands and [b]Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

The presence of parents in the natal territory may play an important, but often overlooked, role in natal dispersal and the consequent acquisition of a territory. Living with parents in a territory may confer a fitness advantage to subordinates through, for example, the nepotistic behavior of the parents or indirect benefits gained by helping to raise nondescendent kin. When a parent is replaced by a stepparent, such advantages are reduced or disappear and, as a result, subordinates may disperse. Subordinates that disperse after parent replacement may be constrained in their timing of dispersal, which could have negative fitness consequences. In the cooperatively breeding Seychelles warbler, we show that when a parent was naturally replaced or experimentally removed and subsequently replaced by a stepparent from outside the territory, subordinates were more likely to disperse than when both parents remained in the natal territory. Furthermore, subordinates dispersing from territories in which one or both parents had been replaced were less likely to acquire a breeder position than subordinates dispersing when both parents were still on the natal territory. Our findings suggest that the presence of parents in the natal territory may promote delayed dispersal and facilitate the eventual acquisition of a breeder position outside the natal territory. Our results support the idea that the prolonged parental care, which long-lived species are able to provide, may have selected for family living. *Key words: Acrocephalus sechellensis*, delayed dispersal, indirect benefits, parent replacement, territory acquisition. *[Behav Ecol 18:874–879 (2007)]*

Family living occurs in a wide range of vertebrate taxa and usually results from the delayed dispersal of independent offspring (Emlen 1995; Russell 2004). For example, in 18.5% of all oscine passerines, individuals live in family groups (Cockburn 2003). That individuals within populations differ in how long they delay dispersal has been the focus of considerable research attention. Most studies have dealt with this question from the offspring point of view and have concluded that offspring should disperse when the benefits of breeding elsewhere outweigh the benefits of remaining in the natal territory (e.g., Stacey and Ligon 1987, 1991; Dobson et al. 1998). However, some authors have argued that although subordinates may prefer to remain philopatric, dominants may force them to disperse because subordinates may compete with dominants over resources or matings (Gayou 1986; Cockburn 1996; Russell 2004). Similarly, sibling rivalry could lead to dispersal of weaker siblings when staying is the preferred option (Ekman et al. 2002).

From either point of view, the identity of the dominants on the natal territory could play an important role in dispersal decisions. When a parent dies or disappears, an offspring may inherit the breeder position (e.g., Brown JL and Brown ER 1984) or an immigrant could fill the vacancy (e.g., Koenig et al. 1998). Inheritance of a breeder position eliminates natal dispersal, whereas the replacement of a parent with a stepparent could result in increased natal dispersal for the following reasons. First, the benefits of remaining in the natal territory will be reduced if parents give preferential treatment to their offspring, benefits which would not be provided by stepparents (Ekman et al. 1994; Ekman and Griesser 2002). Furthermore, in cooperative-breeding species, future indirect kin benefits, which could be gained by helping to increase the parents' reproductive success, will be smaller (or nonexistent)

after a parent is replaced by a stepparent. Also, although individuals living in larger groups may have increased survival (group augmentation, e.g., Woolfenden 1975), stepparents may force unrelated subordinates to disperse because they may perceive them as competitors for mates or food (Hannon et al. 1985; Goldstein et al. 1998). Parent replacement may therefore lead to natal dispersal, which could negatively affect the subordinates' fitness, because individuals that are forced to disperse may have lower survival (Green and Cockburn 2001; Griesser et al. 2006) and lower reproductive success (Ekman et al. 1999) than individuals that can delay dispersal.

The aim of the current study is 2-fold. First, we examine how the replacement of a parent with a stepparent affects the natal dispersal decisions of yearling subordinate Seychelles warblers, *Acrocephalus sechellensis*. Previous studies indicate that there are costs of group living for dominants in the Seychelles warblers (Komdeur 1994; Ridley et al. 2003; Brouwer et al. 2006) and that inheritance of breeder positions is rare (Komdeur 1992; Eikenaar et al. forthcoming). We therefore expect that yearling subordinates disperse more often from territories in which a parent is replaced than from territories in which the parents remain. Second, we assess how parent replacement and consequent dispersal affects territory acquisition. The timing of natal dispersal may be viewed as a decision making problem. After parent replacement, subordinates may be more constrained in their choice of when to disperse than subordinates living in territories in which both parents were present. Unconstrained offspring may be able to wait on the natal territory for an opportunity to disperse directly into a breeder vacancy, whereas constrained individuals probably have to search for vacancies while floating through the population. Therefore, we expect yearling subordinates dispersing from the natal territory after the replacement of one or both parents to be less successful in acquiring a breeder position elsewhere than subordinates dispersing when both parents are still on the natal territory. We use both natural and experimental situations to test our predictions.

METHODS

Study species and population

The Seychelles warbler is a small passerine endemic to 4 small islands in the Seychelles. This study was carried out on Cousin Island (29 ha.) in the Seychelles. The population of Seychelles warblers on Cousin has been relatively stable since 1982 with 105–120 territories, and, except for a barren rocky outcrop in the center of the island, all habitat is occupied. Seychelles warblers defend all-purpose territories year round (Komdeur 1992), and off-island dispersal is virtually absent (Komdeur et al. 2004). The Seychelles warbler is a facultative cooperative-breeding species that lives either in pairs or groups—which normally consist of a primary pair and one or more offspring that have delayed dispersal and remained in the natal territory as subordinates (Komdeur 1992, 1994). Annual survival of adults is high (84%) and equal for the sexes (Brouwer et al. 2006). Natal dispersal distance is female biased (Eikenaar et al. forthcoming), but during the period 1995–2006, there was no sex bias in dispersal rate (Eikenaar et al. forthcoming; this study). Some subordinates become helpers and assist their parents in raising nondescendent kin, whereas other subordinates stay on the natal territory without engaging in helping behavior (Komdeur 1992; Richardson et al. 2002; Richardson, Burke, and Komdeur 2003). Breeding vacancies, which usually result from the death of a breeder, are typically taken by subordinates from outside the territory (Komdeur 1992; Eikenaar et al. forthcoming). Subordinates prospect for breeder vacancies by making forays from the natal territory (Eikenaar et al. forthcoming).

Offsprings were either ringed in the nest or were caught as dependent fledglings on the natal territory within 6 months of fledging. On Cousin Island, young never dispersed before 6 months of age (Komdeur 1996; Eikenaar et al. forthcoming), and parentage analysis has shown that offspring caught within 6 months after fledging were always still in their natal territory (Eikenaar et al. forthcoming). 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 method devised by Griffiths et al. (1998) was used to confirm the sex of each ringed individual.

In most years, all territories were mapped in detail. For all color-ringed individuals, the status (primary or subordinate) and territory of residence were determined in each year during the peak breeding season (June–September) and in some years also during the minor breeding peak (January–March). The primary male and female were defined as the dominant, pair-bonded male and female in the territory. All other birds, old enough to disperse (>6 months old), resident in the territory were defined as subordinate. During fieldwork periods, all territories were checked at least once every 2 weeks. As interisland dispersal is extremely rare (0.1 %, $n = 1924$; Komdeur et al. 2004), warblers that were missing from their territory and not found on other territories were assumed to have died.

Dispersal after parent replacements

The first year natal dispersal patterns of all subordinates between 6 and 12 months old, ringed between 1995 and 2002 and in 2004, were determined. When both of their parents were color ringed, we also know whether the parents survived and stayed on the territory or if they died and were replaced by a stepparent during this year. The subordinate's parents were defined as the primary male and primary female present in the territory when the subordinate was born (Komdeur 1991; Richardson et al. 2002). Although this definition does

not always match the genetic relatedness (Seychelles warblers have 40% extrapair paternity and joint nesting occurs; Richardson et al. 2001), it probably does represent the off-springs' perception of who their parents are. The effect of natural parent replacements on dispersal decisions was assessed by comparing the dispersal behavior of subordinates from territories in which one ($n = 23$) or both ($n = 3$) parents were replaced with the dispersal behavior of subordinates from territories in which both parents remained ($n = 128$). Only the dispersal pattern of yearlings was used, as the inclusion of older subordinates would lead to pseudoreplication; older subordinates still living on the natal territory would already have been included in the analysis as yearlings.

The effect of experimental removal and subsequent replacement was investigated as a side effect of the translocation of birds from their territories as part of the long-term Seychelles warbler conservation plan. About a month prior to the start of the breeding season of 2004 (on the 29th and 30th of May and 12th of June), a total of 58 Seychelles warblers were captured and translocated from Cousin Island to Denis Island (144 ha). Among the birds translocated were 17 primary females and 20 primary male breeders (in 10 territories the primary breeding female was removed, in 13 the primary breeding male, and in 7 both primary breeders). The translocation provided a situation in which we could experimentally test the idea that parent replacement triggers natal dispersal and that these dispersers make nonoptimal dispersal decisions. In territories in which one or both primary breeders were removed, daily visits, lasting 15 min, were made for 3 weeks to check for new breeders. We compared the dispersal decisions of subordinates from the territories in which a parent was replaced (removal group) with subordinates from territories in which no attempt was made to remove parents (control group). The presence of subordinates within specific territories was assessed by checking all territories just prior to the experiment. If a subordinate permanently left the natal territory and was seen elsewhere in the population within a month of the experiment, it was defined as having dispersed. All subordinates located just prior to the experiment were resighted within a month of the experiment.

For logistical reasons related to the conservation objectives of the translocation, in some of the territories in which a breeder was removed, the subordinates were also translocated. Furthermore, 4 subordinates filled the newly created breeder position in their own natal territory and so could not be used. Additionally, in some of the removal territories, no subordinates were present. This left 7 experimental territories, in which a parent was eventually replaced by a new primary bird, that also contained a color-ringed subordinate native to the territory. In 3 of these territories, the breeding male was removed, in 2 the breeding female, and in another 2 both breeders. In 37 control territories, a color-ringed subordinate was present. The average distance, in territory widths, to same-sex vacancies created in the experiment did not differ between subordinates from the removal and subordinates from the control group (5.4 and 5.7 territory widths, respectively, $Z = -0.47$, $P = 0.64$; Mann–Whitney U-test).

Settlement after dispersal

After dispersing, subordinates could 1) gain a primary breeder position by occupying the position of a breeder that died or was removed in the experiment, 2) gain a primary breeding position by setting up a completely new territory (males only: Komdeur and Edelaar 2001; Eikenaar et al. forthcoming), 3) become a floater; birds that float around the island in search of a territory (Komdeur and Edelaar 2001),

and 4) become a subordinate in a territory other than where it was born.

For the nonexperimental situation, the status, in relation to dispersal, of offspring was determined a year after fledging. We compared dispersal from territories in which at least one breeder was replaced with dispersal from territories in which both original breeders remained. In the experiment, we compared the dispersal status of individuals in the removal and control groups both a month and a year after the experiment.

Data analyses

Previous work on the Seychelles warbler, using data gathered from 1985 to 1990, has shown that subordinate sex and quality of the natal territory affect dispersal; males dispersed earlier than females, and dispersal was delayed longer with increasing territory quality (TQ) (Komdeur 1992, 1996). Also, offspring born in very low–density populations, created by the transfer of warblers from Cousin to unoccupied islands, dispersed earlier than offspring born on Cousin (Komdeur 1992). Therefore, the effect of these 3 factors (offspring sex, TQ, and density) on dispersal decisions was taken into consideration (along with the effect of parent replacement) in the analysis of the present long-term data set (1995–2004). Furthermore, we assessed the effect of group size on dispersal as this has been shown to effect reproductive success (Komdeur 1994) and survival (Brouwer et al. 2006). Territory quality, in terms of insect prey availability, was measured as described by Komdeur (1991, 1992, 1994). The components of TQ values are insect density per square decimeter leaf area, vegetation abundance scores, and territory size. TQ was measured in the peak breeding season of 1999 and in 2003 and 2004. For subordinates born between 1995 and 2000, TQ values of the 1999 measurement were used. For subordinates born after 2000, TQ was the average of the 2003 and 2004 measurements. For each subordinate, population density was expressed as the number of territories on Cousin Island in the year of fledging. Group size was expressed as the maximum number of independent individuals in the group during the subordinates' first year of life. Using the multilevel mixed modelling procedure in MlwiN (Rasbash et al. 2004), dispersal was fitted as the binary response variable using the logit link function. As some birds that fledged in different years came from the same territory, territory was included as the level 2 unit of variation and subordinate as the level one unit of variation. Model selection was based on backward elimination of nonsignificant terms, assessed by the Wald statistic.

Because samples were small, we used Fisher's exact test to 1) assess whether, in the nonexperimental situation, dispersal decisions after maternal replacements differ from dispersal decisions after paternal replacements, 2) examine the effect of experimental parent replacement on dispersal decisions. We used Chi-square test to assess whether the chances of acquiring a breeder position were different between dispersers from territories with parent replacement and dispersers from territories in which both parents remained. Subordinates with unknown status after dispersal were excluded. Probabilities are 2 tailed in all tests.

RESULTS

Dispersal after natural parent replacements

Subordinates were significantly more likely to disperse within their first year of life when either one or both parents were replaced by a new dominant from another territory compared with when both parents survived and stayed on the natal territory (Table 1 and Figure 1). The near-significant interaction

Table 1

Model summaries examining dispersal decisions of subordinate Seychelles warblers ($n = 154$) in relation to natural parent replacement, quality of the natal territory, group size, subordinate sex, and population density

Explanatory variables	$\beta \pm$ standard error	χ^2	df	P
Constant	6.32 ± 4.25	2.22	1	0.14
Parent replacement	2.66 ± 0.64	17.50	1	<0.001
Quality of natal territory	0.10 ± 0.07	1.87	1	0.17
Group size	-0.29 ± 0.20	1.96	1	0.16
Subordinate sex (male)	0.78 ± 0.45	3.0	1	0.08
Sex (male) $\times$ parent replacement	1.88 ± 0.98	3.65	1	0.06
Population density	-0.07 ± 0.04	3.53	1	0.06

between subordinate sex and parent replacement suggested that the likelihood of dispersal was higher for male than female subordinates (Table 1 and Figure 2). In the 3 territories in which both breeders were replaced, all subordinates dispersed (Figure 1). Excluding these 3 territories from the analyses did not change the results (not shown). The proportion of subordinates that dispersed when a father was replaced seemed higher than when a mother was replaced (Figure 1). This difference was, however, not significant ($P = 0.414$, Fisher's exact test). The quality of the natal territory and group size did not affect the dispersal likelihood of yearling subordinate warblers. Expressing TQ per individual (TQ divided by group size) did not change the results. The likelihood of dispersal as a yearling tended to decrease with increasing population density (Table 1).

Dispersal after experimental parent removals

The parent removal experiment confirmed the role of parent presence on dispersal decisions; subordinates were more likely to disperse from the natal territory when a parent was experimentally removed and subsequently replaced by a step-parent than when both parents stayed ($P = 0.007$, Fisher's exact test; Figure 3). After experimental removal of one or both parents, 5 of the 7 subordinates (71.4%) dispersed within a month of the experiment. All 5 subordinates that dispersed from an experimental territory were observed
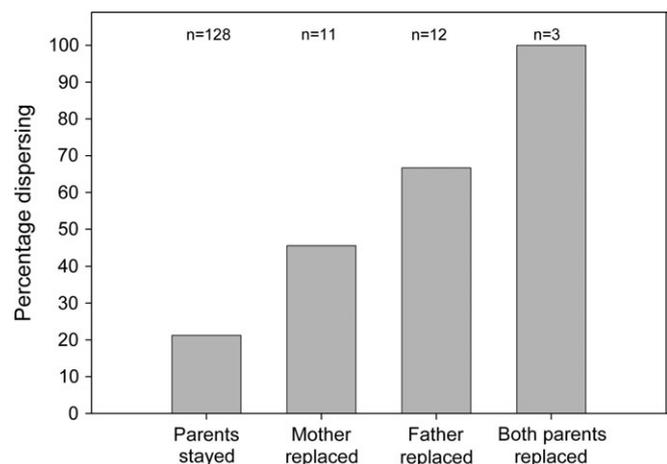
Figure 1
The percentage of subordinates that dispersed within a year when both parents survived and stayed in the territory or when the mother, the father, or both the parents were replaced by stepparents.
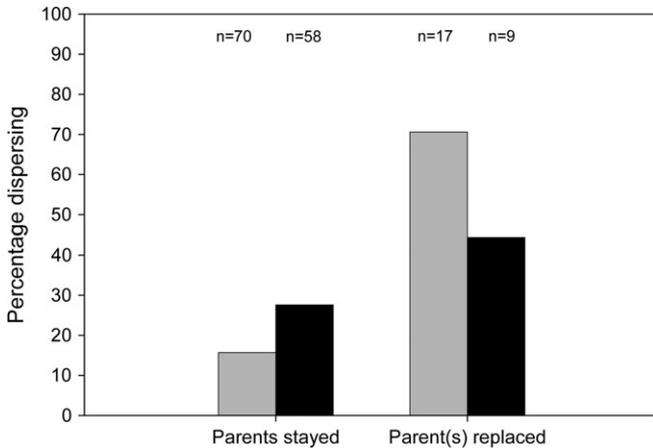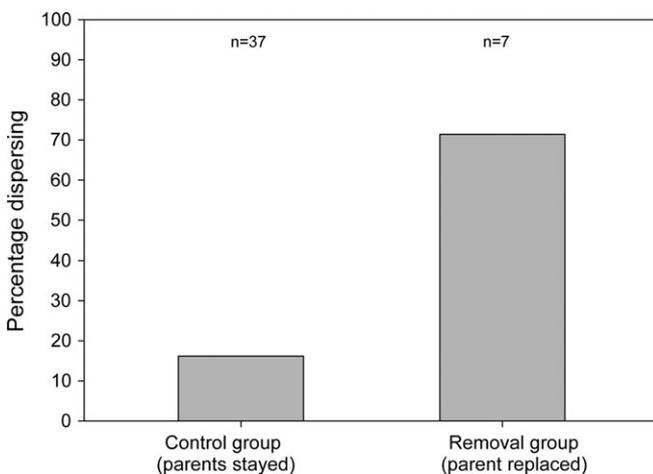
Figure 2
The percentage of male (gray bars) and female (black bars) subordinates that dispersed within a year when both parents survived and stayed in the territory compared with when at least one parent was replaced by a stepparent.

Table 2

The number and percentage (in brackets) of dispersers with their status 1 year after fledging

Status dispersers 1 year after fledging	Parents replaced	Parents stayed
Occupy breeder vacancy	4 (25)	18 (66.6)
Create new territory	2 (12.5)	1 (3.7)
Float	4 (25)	3 (11.1)
Subordinate in other territory	6 (37.5)	4 (14.8)
Unknown	0 (0)	1 (3.7)
Total	16	27

Dispersal was either from territories in which one or both parents were replaced or from territories in which both parents stayed.

within their natal territory directly (1–2 days) after a parent was removed, so dispersal did not appear to be due to the immediate disturbance associated with us catching and removing the parent. In the control group, 6 of the 37 subordinates (16.2%) dispersed within a month of the experiment.

Settlement after dispersal

The status of all nonexperimentally induced dispersers a year after fledging is presented in Table 2. Subordinates dispersing from territories containing both parents often occupied a breeder position outside their natal territory. However, the majority of subordinates that dispersed from territories in which one or both parents were replaced did not gain a breeder position. Instead, most of these became floaters or subordinates in a territory other than the one in which they were born. As a result, subordinates dispersing from territories containing both parents more often occupied a breeder position a year after fledging than subordinates

dispersing from territories in which one or both breeders were replaced ($\chi^2 = 5.20$, degrees of freedom [df] = 1, $P = 0.023$). The proportion of dispersers that survived until 2 years after fledging was not different between the 2 groups ($\chi^2 = 1.88$, df = 1, $P = 0.17$).

The parent removal experiment produced similar results to the natural replacements; subordinates dispersing from territories containing both parents occupied a breeder position a month after the experiment more often than subordinates dispersing from territories in which one or both breeders were replaced ($P = 0.015$, Fisher's exact test). One month after the experiment, of the 6 subordinates that dispersed from the control group, 4 had filled experimental vacancies, one had filled a nonexperimental vacancy that coincidentally opened during the experiment, and one had become a joint nester in another territory. Their status was the same a year after the experiment. Of the 5 subordinates that dispersed after experimental removal of one or both parents, 4 had become floaters, whereas one had filled an experimental breeder vacancy. A year after the experiment, 2 of the 4 floaters had occupied a breeder position, one was still floating, and one had died.

DISCUSSION

Seychelles warbler subordinates were more likely to disperse from the natal territory when a parent died and was replaced by a stepparent than when both parents remained in the natal territory. Enhanced dispersal after parent replacement may be the consequence of a decrease in the kin benefits that results from group living, such as decreased future indirect fitness benefits derived from helping to raise nondescendent kin (e.g., Richardson, Burke, and Komdeur 2003; Richardson, Komdeur, and Burke 2003) or the loss of nepotistic behaviour toward offspring (e.g., Ekman and Griesser 2002). Our results indicate that the enhanced dispersal after parent replacement was not the result of a decrease in indirect fitness benefits derived from helping. Instead our results suggest that Seychelles warbler parents are nepotistic in that they tolerate their mature offspring remaining on the territory, which allows natal dispersal to be delayed.

Because the Seychelles warbler is a cooperative breeder, decreased future indirect fitness benefits could trigger dispersal after a parent is replaced by an unrelated stepparent. Because of the high incidence of extragroup paternity (ca., 40%; Richardson et al. 2001), subordinates will, on average, be less related to the primary male than to the primary female. The replacement of a primary female will, therefore, result in a larger decrease of future indirect fitness gains for subordinates than the replacement of a primary male. Seychelles warbler subordinates have been shown to be able to discriminate between maternal and paternal replacement in relation to the

Figure 3
The percentage of subordinates that dispersed within a month from territories in which no parent was removed (control group) and from territories in which a parent was experimentally removed and subsequently replaced by a stepparent (removal group).

degree of help they provide at the nest (Richardson, Burke, and Komdeur 2003; Richardson, Komdeur, and Burke 2003). Because we found no difference in the likelihood of dispersal after maternal compared with paternal replacement, decreased future indirect fitness benefits of helping seem less likely to have caused the observed dispersal. Furthermore, the replacement of a parent with a stepparent tended to be more likely to cause dispersal for male than for female subordinates. This does not support dispersal as a result of decreased indirect benefits because the decrease is probably more important for females than males, as females are more likely to help (Komdeur 1996). Instead, we suggest that the stepparent has more reason to force male, rather than female, subordinates from its territory. The logic behind this is that the stepparent could gain fitness benefits if a female subordinate engages in joint nesting (laying in the same nest as the dominant female—which frequently happens in the Seychelles warbler; Richardson et al. 2002). Furthermore, a dominant male could gain additional paternity with the subordinate female (Richardson et al. 2001, 2004), and a dominant female could benefit from sharing incubation with the subordinate female, which may decrease both energetic costs and egg predation risk. That stepparents have reasons to evict unrelated subordinates follows from previous studies on the Seychelles warbler that indicate that costs of group living do exist. Removal experiments in medium-quality territories showed that the presence of 2 or more subordinates reduces the reproductive success of the breeding pair (Komdeur 1994). Furthermore, irrespective of TQ, birds living in larger groups have lower survival probabilities than birds living in small groups (Brouwer et al. 2006), contrary to the concept of group augmentation. Finally, a theoretical study on population regulation suggested that helpers usually produce insufficient benefits to unrelated dominants and should, therefore, usually be evicted (Ridley et al. 2003). The idea that stepparents evicted unrelated subordinates from the territory is supported by the observation that the 5 subordinates that dispersed from an experimental territory were all still seen in their natal territory after the parents were removed but before a new breeder arrived. The absence of a parent in itself did not, therefore, seem to be reason enough to disperse. This pattern was also reflected in the observation that 4 subordinates "inherited" an experimental breeder vacancy. Contrary to the idea of parental tolerance is the observation that subordinates are sometimes tolerated by dominants who are not their parents (Table 2). This in itself does not, however, exclude the possibility that, besides tolerating nonbreeders on the territory, Seychelles warblers provide other benefits to their offspring that unrelated immigrants do not receive.

When group living is costly, why do parents not always evict independent offspring from the territory? We suggest that Seychelles warblers tolerate their offspring on the territory because the costs of group living are counterbalanced by an increased chance that offspring will eventually successfully acquire a territory when they are allowed to wait on the natal territory. The enhanced dispersal observed after parent replacement suggests that when a stepparent takes the position of a parent, subordinates are unable to wait for the most opportune moment to disperse, but may be forced out earlier than they wish. If subordinates are constrained in the timing of their dispersal, this could influence their fitness through reduced survival prospects (Mulder 1995; Griesser et al. 2006) or lower reproductive success (Ekman et al. 1999). In the Seychelles warbler, primary breeders produce more offspring than subordinates (Richardson et al. 2001). Therefore, dispersing to fill a breeder vacancy should be preferred over dispersing to become a subordinate in another territory or to become a floater. In the natural situation, yearling subordinates dispersing from territories in which both parents remained were more likely to occupy a breeder position a year after fledging than subordinates dispersing from territories in which one or both parents were replaced. Furthermore, in the experimental situation, subordinates from control territories only dispersed to occupy a breeder position, whereas 4 of the 5 subordinates that dispersed after parent replacement became floaters. These results suggest that when both parents remain in the natal territory, it may function as a safe haven (Kokko and Ekman 2002) from where young can foray in search of a breeder vacancy and return to if the foray is unsuccessful. Prolonged parental care therefore seems to enhance group benefits through increasing an offspring's opportunity to occupy a breeder position. Komdeur (1992) argued that delayed dispersal in the Seychelles warbler resulted from both habitat saturation and from offspring waiting for opportunities to breed in high-quality habitat. Individuals that delay dispersal in high-quality territories, but which eventually breed there, have greater lifetime fitness than those that disperse at one year of age and breed immediately in lower quality territories (Komdeur 1992). Our results also indicate that delayed dispersal might be an adaptive life-history decision rather than "the best of a bad job" (Covas and Griesser 2007). Our study supports the idea that the prolonged parental care, which only long-lived species such as the Seychelles warblers (Komdeur 1991; Brouwer et al. 2006) are able to provide, may have selected for family living (Ekman 2006; Covas and Griesser 2007).

REFERENCES

Brouwer L, Richardson DS, Eikenaar C, Komdeur J. 2006. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. J Anim Ecol. 75:1321–1329.

Brown JL, Brown ER. 1984. Parental facilitation: parent-offspring relations in communally breeding birds. Behav Ecol Sociobiol. 14:203–209.

Cockburn A. 1996. Why do so many Australian birds cooperate: social evolution in the Corvida? In: Floyd RB, Sheppard AW, De Barro PJ, editors. Frontiers of population ecology. Melbourne (Australia): CSIRO Publishing. p. 451–472.

Cockburn A. 2003. Cooperative breeding in oscine passerines: does sociality inhibit speciation? Proc R Soc Lond B Biol Sci. 270:2207–2214.

Covas R, Griesser M. 2007. Life history and the evolution of family living in birds. Proc R Soc Lond B Biol Sci. doi: 10.1098/rspb.2007.0117.

Dobson FS, Smith AT, Gao WX. 1998. Social and ecological influences on dispersal and philopatry in the plateau pika (*Ochotona curzoniae*). Behav Ecol. 9:622–635.

Eikenaar C, Richardson DS, Brouwer L, Komdeur J. Forthcoming. Sex biased dispersal in a closed, saturated population of Seychelles warblers. J Avian Biol.

Ekman J. 2006. Family living among birds. J Avian Biol. 37:289–298.

Ekman J, Bylin A, Tegelström H. 1999. Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. Proc R Soc Lond B Biol Sci. 266:911–915.

Ekman J, Eggers S, Griesser M. 2002. Fighting to stay: the role of sibling rivalry for delayed dispersal. Anim Behav. 64:453–459.

Ekman J, Griesser M. 2002. Why offspring delay dispersal: experimental evidence for a role of parental tolerance. Proc R Soc Lond B Biol Sci. 269:1709–1713.

Ekman J, Sklepkovych B, Tegelström H. 1994. Offspring retention in the Siberian jay (*Perisoreus infaustus*)—the prolonged brood care hypothesis. Behav Ecol. 5:245–253.

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

Gayou DC. 1986. The social system of the Texas green jay. Auk. 103:540–547.

Goldstein JM, Woolfenden GE, Hailman JP. 1998. A same-sex stepparent shortens a prebreeder's duration on the natal territory: tests of two hypotheses in Florida scrub-jays. Behav Ecol Sociobiol. 44:15–22.

Green DJ, Cockburn A. 2001. Post-fledging care, philopatry, and recruitment in brown thornbills. J Anim Ecol. 70:505–514.

Griesser M, Nystrand M, Ekman J. 2006. Reduced mortality selects for family cohesion in a social species. Proc R Soc Lond B Biol Sci. 273:1881–1886.

Griffiths R, Double MC, Orr K, Dawson RGJ. 1998. A DNA test to sex most birds. Mol Ecol. 7:1071–1075.

Hannon SJ, Mumme RL, Koenig WD, Pitelka FA. 1985. Replacement of breeders and within-group conflict in the cooperatively breeding acorn woodpecker. Behav Ecol Sociobiol. 17:303–312.

Koenig WD, Haydock J, Stanback MT. 1998. Reproductive roles in the cooperatively breeding acorn woodpecker: incest avoidance versus reproductive competition. Am Nat. 151:243–255.

Kokko H, Ekman J. 2002. Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. Am Nat. 160:468–484.

Komdeur J. 1991. Cooperative breeding in the Seychelles warbler [PhD dissertation]. [Cambridge (UK)]: University of Cambridge.

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. 1994. Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. Behav Ecol Sociobiol. 34:175–186.

Komdeur J. 1996. Facultative sex ratio bias in the offspring of Seychelles warblers. Proc R Soc Lond B Biol Sci. 263:661–666.

Komdeur J, Edelaar P. 2001. Male Seychelles warblers use territory budding to maximize lifetime fitness in a saturated environment. Behav Ecol. 12:706–715.

Komdeur J, Piersma T, Kraaijeveld K, Kraaijeveld-Smit F, Richardson DS. 2004. Why Seychelles warblers fail to recolonize nearby islands: unwilling or unable to fly there? Ibis. 146:298–302.

Mulder RA. 1995. Natal and breeding dispersal in a co-operative, extra-group-mating bird. J Avian Biol. 26:234–240.

Rasbash J, Steele F, Browne W, Prosser B. 2004. A user's guide to MLwiN. Version 2.0. London: Centre for Multilevel Modelling.

Richardson DS, Burke T, Komdeur J. 2002. Direct benefits and the evolution of female-biased cooperative breeding in Seychelles warbler. Evolution. 56:2313–2321.

Richardson DS, Burke T, Komdeur J. 2003. Sex-specific associative learning cues and inclusive fitness benefits in the Seychelles warbler. J Evol Biol. 16:854–861.

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. 10:2263–2273.

Richardson DS, Komdeur J, Burke T. 2003. Altruism and infidelity among warblers. Nature. 422:580.

Richardson DS, Komdeur J, Burke T. 2004. Inbreeding in the Seychelles warbler: environment-dependent maternal effects. Evolution. 58:2037–2048.

Ridley J, Komdeur J, Sutherland WJ. 2003. Population regulation in group-living birds: predictive models of the Seychelles warblers. J Anim Ecol. 72:588–598.

Russell AF. 2004. Mammals: comparisons and contrasts. In: Koenig WD, Dickinson JL, editors. Ecology and evolution of cooperative breeding in birds. Cambridge (UK): Cambridge University Press. p. 210–227.

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.

Woolfenden GE. 1975. Florida scrub jay helpers at the nest. Auk. 92:1–15.