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Seychelles warblers: complexities of the helping paradox

Jan Komdeur, Terry Burke, Hannah Dugdale, and David S. Richardson

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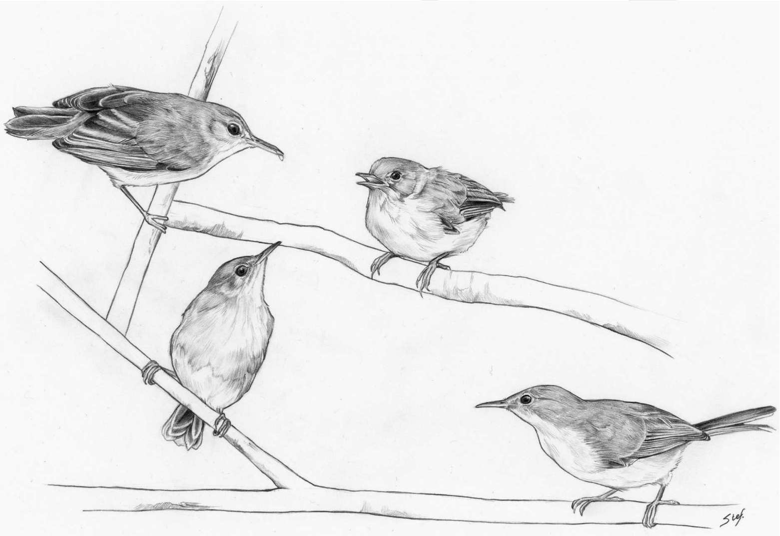

Introduction

The Seychelles warbler (*Acrocephalus sechellensis*), a passerine endemic to the Seychelles archipelago, is a facultatively cooperative breeder that lives either in pairs or small groups. Breeding groups normally consist of a dominant pair and one to three subordinates, although up to nine have been observed. Subordinates can be of either sex, and are often offspring that have delayed dispersal and remained in their natal territory (Komdeur 1992; Richardson et al. 2002; Eikenaar et al. 2008, 2010). By the 1960s the last remnant population of this then critically endangered species was confined to Cousin Island (Figure 12.1). Subsequent conservation actions, including the restoration of forest habitat and the establishment of new populations through translocations, have provided unique opportunities to study the evolutionary ecology of cooperative breeding in this species.

We have followed the entire world population of the Seychelles warbler since our study started in 1981. In

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Figure 12.1. (a) Cousin Island, with Cousine Island in the distance. Photograph by David Richardson. (b) Seychelles warblers feeding a nestling. Photograph by Danny Ellinger. See plate section for color figure.

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1997, however, we increased the intensity of work on Cousin and since then nearly all individuals, including fledglings, have been captured, ringed, blood sampled, sexed, and monitored for breeding and status. Molecular tools have been used to assign the sex and genetic parentage of young birds and to determine levels of relatedness between individuals. In addition, a comprehensive set of behavioral, life history, and annual fitness parameters have been recorded for nearly all individuals, providing important opportunities for assessing changes in social behavior. The lack of interisland dispersal (Komdeur et al. 2004a), combined with sampling of the entire population, provides a rare opportunity to monitor the survival, reproduction, and lifetime fitness of all individuals within the population.

Our long-term research program into cooperative breeding, hand-in-hand with conservation actions, has created an experimental system in which we can attempt to unravel the factors that alter the cost-benefit trade-offs of cooperative breeding. Over time, this system has become proof of the power of the experimental methods and of the corrective value of long-term studies, where iterative examination with longer-term data sheds new insights on short-term findings. Here we detail various findings that have allowed us to uncover how changing social and ecological factors influence the form and function of reproductive competition and cooperation in the Seychelles warbler. We also outline how molecular genetic tools have given us a better understanding of the species' cooperative breeding system and the selective factors that favor switching between different forms of cooperative and independent breeding.

Distribution and conservation

The Seychelles warbler is a small (13–19 g) passerine endemic to the Seychelles archipelago in the Indian Ocean (Safford and Hawkins 2013; Figure 12.2). In the 1870s this species was recorded on the islands of Mahé, Marianne, Félicité, and Cousine (Oustalet 1878; Figure 12.2). It probably also occurred historically on most of the Seychelles islands, which made up a single large island during the last ice age (Collar and Stuart 1985). This assumption is supported by the large effective population sizes estimated for the pre-bottleneck Seychelles warbler population using museum samples from the 1800s (Spurgin et al. 2014).

The destruction of natural habitat for the planting of coconut trees (*Cocos nucifera*), along with the introduction of mammalian predators in the early 1900s, resulted in the warbler's extirpation from nearly all the islands where they previously occurred. Only on Cousin Island, which remained free of predators (Collar and Stuart 1985), did the warblers survive, with only 26–50 individuals remaining between 1940 and 1967 (Crook 1960; Loustau-Lalanne 1968; Spurgin et al. 2014). Cousin Island was purchased by a consortium led by BirdLife International (then the International

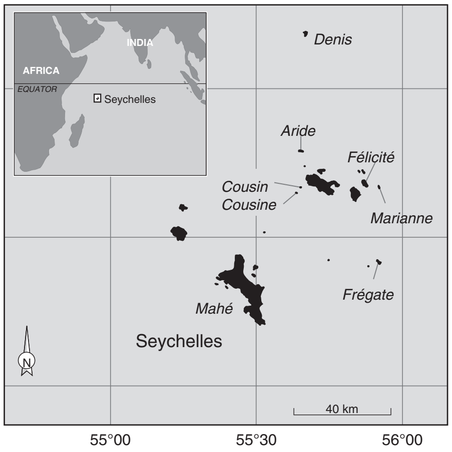

Figure 12.2. The location of the Seychelles in the Indian Ocean (inset) and the inner granitic islands in detail, including Cousin (0.29 km²), Cousine (0.25 km²), Aride (0.68 km²), Denis (1.42 km²), Félicité (2.68 km²), Frégate (2.19 km²), Marianne (0.96 km²), and Mahé (154 km²).

Committee for Bird Protection) in 1968 and designated as a nature reserve to save the Seychelles warbler from extinction. Habitat restoration was successful and, by 1982, much of Cousin was again covered with native forest (Bathe and Bathe 1982). As a consequence, the warbler population recovered and since 1982 has been at a carrying capacity of about 320 adults inhabiting around 110 territories that cover all but the bare rock areas of Cousin (Figure 12.3). This ratio of birds to territories also means there has been a considerable surplus of (unpaired) adult birds on the island since the point of saturation (Komdeur 1992; Brouwer et al. 2009, 2012).

The flight apparatus of the Seychelles warbler does not differ from that of other long-distance migratory *Acrocephalus* warblers (Komdeur et al. 2004a). Nonetheless, interisland dispersal is virtually nonexistent. During the 28 years of this study only six individuals were recorded to have crossed the sea between islands. Given the low probability of any new warbler populations establishing by themselves, and the vulnerability of a single small population, four new populations were established by translocation of birds from Cousin to the islands of Aride and Cousine in 1988 and 1990, respectively (29 individuals each time; Komdeur 1994a), Denis in 2004 (58 individuals; Richardson et al. 2006), and Frégate in 2011 (59 individuals; Wright et al. 2014; Figure 12.2). In contrast to the food limitation observed on Cousin, where a shorter breeding season was the norm, warblers on the new islands experienced higher food availability and initially bred year-round (Komdeur et al. 1995). This resulted in an initial increase in annual productivity of up to ten-fold compared to the population on Cousin (Komdeur 1996a). As each population increased, productivity declined, presumably because of the increased density of the population (Brouwer et al. 2009). Most recent population sizes are estimated at 210 warblers on Cousine in 2007 (van de Crommenacker and Richardson 2007), 1850 on Aride in 2003 (Orchard 2004), 300 on Denis in 2013 (J. van de Woude, unpubl. data), and 80 on Frégate in 2013 (Teunissen 2013) (Figure 12.4). The world population of Seychelles warblers is now estimated at 2750 adult birds across five islands and the conservation status of the Seychelles warbler has been reduced from endangered to vulnerable (IUCN 2013).

Natural history: Seychelles warblers

Territoriality and breeding biology

The Seychelles warbler is socially monogamous, and paired dominant birds often remain with the same partner on the same breeding territory for life (Komdeur 1992; Richardson et al. 2007). The pair bond can last up to 14 years (S. A. Kingma, unpubl. data). Seychelles warblers are largely insectivorous, mainly gleaning invertebrate prey from the undersides of leaves. As such, resource abundance, a major aspect of territory quality, can be evaluated by estimating the number of invertebrates on the undersides of leaves and extrapolating from this to estimate prey abundance according to the amount of foliage in each territory (Komdeur 1992; Brouwer et al. 2006). On Cousin, prey abundance has been measured monthly on each territory during the main breeding periods (June to September) for most years since 1987; the same technique has been used to measure prey abundance in

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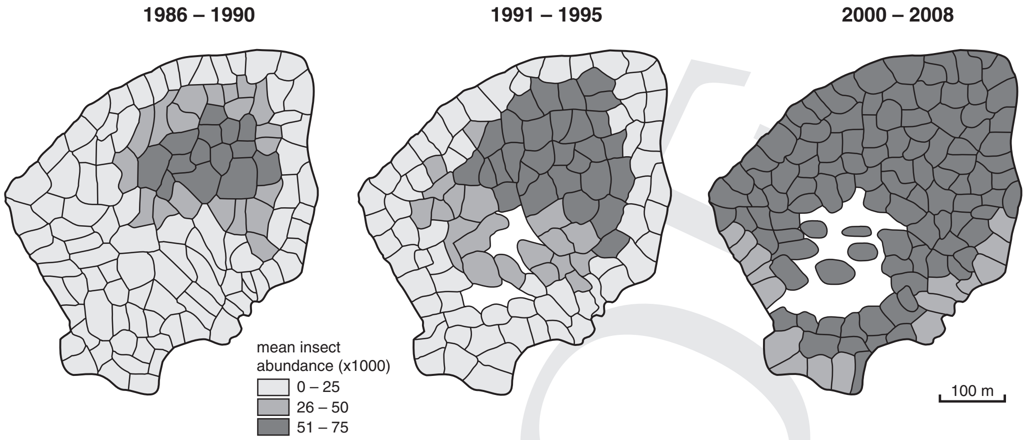

Figure 12.3. Cousin Island outline with Seychelles warbler territories drawn in and mean insect abundance present in each territory during the periods 1986–1990 (from Komdeur 1992), 1991–1995, and 2000–2008 (J. Komdeur, unpubl. data).

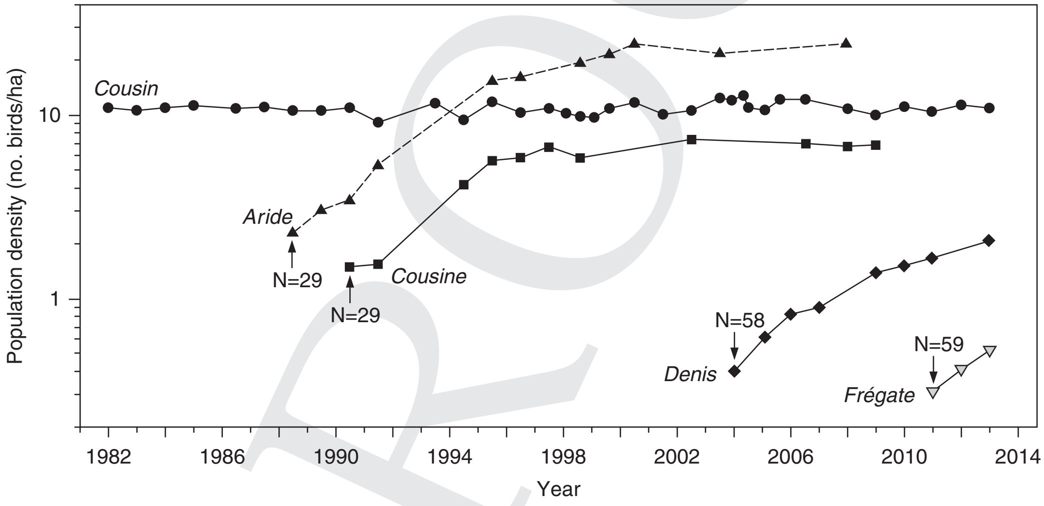

Figure 12.4. Temporal fluctuations in the population density (*ln* scale) of Seychelles warblers on Cousin (saturated), Aride (census focused on the accessible plateau area of 5.2 ha; saturated), Cousine (saturated), Denis (increasing phase), and Frégate (increasing phase) islands. Arrows with sample sizes (*N* birds) indicate the introduction of birds to each island. Initial densities differ both because of the different numbers of birds introduced and large differences in the sizes of the islands (Cousin: 0.29 km^2, Aride: 0.68 km^2, Cousine: 0.25 km^2, Denis: 1.42 km^2, Frégate: 2.19 km^2). Figure updated from Brouwer et al. (2009).

various years on the other islands since their populations were founded. Our results show that insect food supply is highly seasonal and that warblers time their breeding such that the production of nestlings is synchronized with the periods of highest prey abundance (Komdeur 1996a) with peaks of nest building between May and August and again, to a lesser extent, between December and February.

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Most breeding pairs and groups produce one clutch per year (Komdeur 1996a), with clutches normally consisting of just one egg, although ~13% of nests contain two or three eggs (Richardson et al. 2001). Incubation, which is by the female, lasts 17–19 days, and nestlings are fed by both sexes for 18–20 days prior to fledging, and then for up to four months before reaching independence. This is an extremely long period of dependence; no other known passerine has a six-month period of dependence. Indeed, the mean fledging period for other passerines is only about one tenth as long (Bennett and Owens 2002). Nonetheless, first-year survival is relatively low: 61% of fledglings survive the first year compared to an annual survival of 84% in adults (Brouwer et al. 2006). Like many other tropical bird species, the Seychelles warbler is long-lived, with an average life expectancy of around five years once they reach adulthood and a maximum recorded lifespan of 17 years (Barrett et al. 2013).

The breeding system

Seychelles warbler territories are normally occupied by a single dominant pair-bonded male and female. However, about 30% of territories contain subordinate males and/or females that are sexually mature birds lacking a suitable independent breeding opportunity (Komdeur 1992; Richardson et al. 2002, 2007). This is demonstrated by the fact that birds transplanted to previously uninhabited islands immediately breed independently rather than becoming helpers or subordinate cobreeders. Furthermore, vacancies created in the source population by the translocation of breeders are filled immediately by subordinates from other territories (see "Indirect fitness benefits to subordinates").

Female subordinates normally remain on their natal territory, while ~25% of male subordinates move to a new territory to take up a subordinate position (Richardson et al. 2002). In any given breeding attempt, approximately 44% of subordinate females lay eggs within the dominant pair's nest, while only 15% of subordinate males sire offspring within the group (Richardson et al. 2001); we define such birds as "subordinate cobreeders." The remaining subordinates that have not successfully reproduced (either by siring young or laying eggs) may help to raise the chicks, either by aiding in nest building (mainly females), incubation (females), guarding the clutch (mainly males), or provisioning (males and females) (Komdeur 1994b; Richardson et al. 2003a, 2003b); we define these birds as "helpers" in that breeding attempt. Subordinates that neither help nor breed successfully are defined as "nonhelping subordinates."

There is no evidence of egg dumping; females (subordinate or otherwise) do not lay eggs in extra-group nests. Similarly, male subordinates never gain paternity outside the group (Richardson et al. 2002). However, extra-group paternity is common, with about 44% of offspring fathered by dominant males from other territories (Richardson et al. 2001; Hadfield et al. 2006). Populations also include a variable, and difficult to define, number of floaters of both sexes that have failed to find a breeding or subordinate position and wander over the island without residing in a territory (Komdeur and Edelaar 2001; Eikenaar et al. 2008).

The costs and benefits of cooperative breeding

In most species the inferred fitness benefits from helping are substantially lower than those from breeding independently. Consequently, cooperative behavior is generally considered to be a suboptimal fitness strategy (Emlen 1982; Lessells 1991; Dickinson et al. 1996; Dickinson and Hatchwell 2004). Therefore, in order to understand its evolution it is important to know what determines when and where cooperative breeding behavior occurs. With this in mind, the route to cooperative breeding may best be viewed as a two-step process: first, the decision by an individual to forgo independent breeding and become a subordinate in a group, and second, the decision by a subordinate to help the dominants to raise offspring (Emlen 1982). The first step is usually attributed to the existence of ecological constraints on independent breeding, such as a shortage of breeding territories or mates (the "ecological constraints" hypothesis; Emlen 1982, 1991), combined with the benefits of remaining in the natal group (the "benefits of philopatry" hypothesis; Brown 1978;

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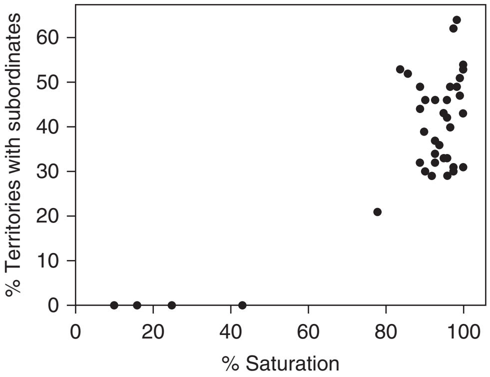

Figure 12.5. The percentage of territories with subordinates in relation to habitat saturation in a given year for the Seychelles warblers on Cousin Island between 1959 and 2013. Habitat saturation was measured as the number of territories present in that year divided by the maximum number of territories recorded in a year ($N = 121$). Figure amended from Komdeur et al. (2008).

Stacey and Ligon 1987, 1991; Ekman et al. 2004; Covas and Griesser 2007). The second step is attributable to a variety of potential fitness benefits, both indirect and direct (Stacey and Koenig 1990; Dickinson and Hatchwell 2004).

In the Seychelles warbler, cooperative breeding was first observed in 1973, when the population of adult birds started to be greater than the number of breeding positions available on territories. At this point, most, but not all, suitable breeding habitat on Cousin was occupied (Komdeur 1992). Interestingly, however, cooperative breeding occurred well before the island was completely saturated (Figure 12.5), indicating that factors other than habitat saturation per se also influence cooperative breeding.

Group living

Early on in our study, young independent males dispersed more often and earlier from their natal territories than young independent females (Komdeur 1996b). This was thought to be because females are usually born on higher-quality territories than males (Komdeur et al. 1997, see "Sex allocation"), and as there is a positive correlation between the length of time for which independent offspring delay dispersal and the natal territory quality, females ended up delaying dispersal longer than males. This sex-bias in dispersal behavior disappeared later in the study, however, apparently as a result of females starting to disperse earlier, rather than males delaying dispersal longer (Eikenaar et al. 2007, 2010).

We suspect that temporal changes in demography, most likely higher reproductive output per territory due to improved and less variable habitat quality, rather than differences in local density or social conditions, caused the observed changes. In particular, the change in male dispersal behavior coincided with a change in spatial food resource availability. Early on, mean insect numbers were highest in the center of the island and decreased gradually toward the coast (Figure 12.3), but with the restoration of the coastal vegetation insect numbers there increased significantly (Komdeur and Pels 2005). Consequently, the proportion of high-quality territories on the island increased (van de Crommenacker et al. 2011), even though the total number of territories, and Seychelles warblers, has remained similar (Brouwer et al. 2009). Given this change in food abundance across a more or less stable population and the concomitant increase in the quality and reproductive output of territories over the years (Komdeur and Pels 2005), we suspect that food-related fitness consequences drive the dispersal behavior of males, although further work is needed to confirm this.

Helping behavior

Helping is not an inevitable consequence of group living. Both within and among cooperatively breeding species, considerable variation exists in whether, and to what extent, individuals help. Furthermore, helping in many species is biased with respect to the subordinate sex. In most cooperatively breeding birds, male-biased delayed dispersal and helping is the norm (Cockburn 1998; Berg et al. 2009; Cornwallis et al. 2009). Seychelles warblers were originally thought to be an exception in that females were more likely to delay dispersal

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and become subordinate helpers/cobreeders than males, with 88% of subordinates being female helpers/cobreeders in 1986–1990 (Komdeur 1996b). As mentioned above, this bias toward helpers being females decreased over time to 68% in later years (Richardson et al. 2002) and subsequently disappeared altogether (Eikenaar et al. 2010).

Additionally, a small proportion of birds (14% of females and 3% of males) became subordinates, usually for the second time, after being deposed as dominant breeders. Many of these (68% of the females) were observed to actively help kin and are therefore termed “grandparent helpers” (Richardson et al. 2007). These observations suggest that helping is not a stable trait, but rather a plastic response to local conditions. The key, then, is to assess and understand how different costs and benefits, to both the helpers and the helped, interact to determine this variation.

Indirect fitness benefits to subordinates

For helpers to gain indirect benefits their activities must result in a net benefit to those they help (Hamilton 1964). In the Seychelles warbler, the presence of helpers on high quality territories with high prey abundance increases the number of young produced on a territory: the removal of helpers, from groups with one helper on high-quality territories, resulted in lower reproductive success for the breeding pair compared with control pairs (Komdeur 1994b). A later study demonstrated that the total amount of provisioning to nestlings significantly affects fledging success and first-year survival. Importantly, this improvement was correlated with the number of birds actually helping, not with the total number of birds in the territory including nonhelping subordinates (Brouwer et al. 2012). Furthermore, cross-fostering of nestlings between territories confirmed that it is the number of helpers in the territory where they are reared that determines the survival of offspring, thus ruling out the possibility that offspring quality is confounding the helper effect. Overall, the number of fledglings produced on a territory per breeding attempt increases by 18% for each helper present, even after excluding direct subordinate parentage (Richardson et al. 2002).

Since Seychelles warblers can breed independently in their first year, why do some individuals become subordinates? Individuals that remain as subordinates in high-quality territories and later breed there have higher lifetime fitness than those that disperse from high-quality territories at one year of age and breed in lower-quality territories. Breeding pairs without helpers on high-quality territories produce on average 0.85 fledglings each year compared to only 0.19 fledglings on low-quality territories. Furthermore, a helper on a high-quality territory can increase the dominant pair’s reproductive success by 0.77 fledglings from 0.85 to 1.62 fledglings per year, about four times the output from the low-quality territories. This increase, and the fact that subordinates are normally helping their parents, means that subordinates increase their own indirect benefits by remaining as helpers (Komdeur 1992).

At the time these results were published we assumed that all female helpers were nonbreeding helpers. Later work indicated that these "helpers" included both true nonbreeding helpers and subordinate cobreeders (Richardson et al. 2001). To the extent that these birds were actually cobreeders, they would have gained even greater fitness benefits by remaining with their parents.

We were able to experimentally verify the importance of territory quality to cooperative breeding by creating new breeding opportunities when removing breeding adults for translocation to new islands. Initially, in the source population, the breeding vacancies created were filled by subordinates from territories of equivalent or poorer quality, never by subordinates from superior territories, for which helping remained a better option than breeding (Komdeur 1992). On the new islands, initially all translocated individuals bred as independent pairs. However, after a few years, when all the high-quality areas were occupied, individuals again chose to help on high-quality territories rather than to breed independently on low-quality territories. These results support both the benefits of philopatry (Stacey and Ligon 1987, 1991) and the ecological constraints hypotheses (Emlen 1982, 1991), which differ only in the emphasis they place on the costs of leaving versus the benefits of staying (Komdeur 2003).

Cooperatively breeding species are often long-lived, have stable and strong natal philopatry, and a relatively long period of extended parental care during which they associate with family members (Stacey and Koenig 1990; Emlen 1991; Arnold and Owens 1998; Hatchwell and Komdeur 2000; Cornwallis et al. 2009). Most subordinates become helpers after delaying dispersal from their natal territory. In such situations, conditions exist that may assist subordinates to gain indirect fitness benefits through helping: first, since parents are long-lived, helpers on their natal territories will be caring for subsequent related offspring, and second, the extended care period may allow subordinates ("ego") to develop a simple rule: help any individual ("*b*") that fed ego when ego was a nestling to raise *b*'s subsequent broods, as *b* is likely to be ego's parents. However, in groups where individuals differ in how related they are to each other and to the brood because of high turnover of breeders or infidelity, direct kin discrimination will be required if potential helpers are to maximize their indirect benefits.

In the Seychelles warbler, males more often become subordinates on nonnatal territories than females and so subordinate males are no more related to the groups' nestlings than one would expect by chance (Richardson et al. 2002). Female subordinates are, therefore, more related to the nestlings than male subordinates. Thus, the kin-selected benefits of helping are more important for female subordinates. Even within the sexes, however, levels of relatedness and the amount of helping vary substantially within and among subordinates. Female subordinates that gain parentage in the nest appear to assess this fact accurately and always provision (Richardson et al. 2003a, 2003b). For nonparent female subordinates, provisioning is positively correlated with their genetic relatedness to the nestlings and thus their potential indirect fitness gain (Figure 12.6).

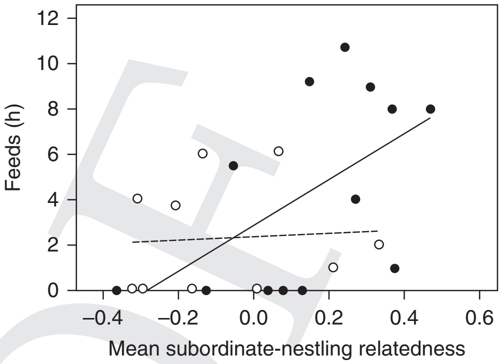

Figure 12.6. Provisioning rates by subordinate female (filled circles) and male (empty circles) nonparents in relation to relatedness between the subordinate and the nestling. There is a positive relationship between provisioning and subordinate–nestling relatedness for female subordinates (solid line; $F_{1,11} = 4.82$, $P = 0.05$, $R^2 = 0.31$) but not for male subordinates (broken line; $F_{1,8} = 0.04$, $P = 0.86$, $R^2 = 0.00$). From Richardson et al. (2003a).

In contrast, male subordinates rarely obtain paternity in the brood that they help (Richardson et al. 2001) and are usually less related to the nestlings. These males provision considerably less than subordinate females and their contribution is not influenced by their relatedness to the nestling (Richardson et al. 2003a, 2003b).

Relatedness between subordinates that remain in their natal territory and nestlings is lower than one would theoretically expect for first-order relatives (mean $r = 0.13$). This occurs for two reasons: first, males from outside the group are responsible for siring about 40% of offspring (Richardson et al. 2001; Hadfield et al. 2006). This extra-group paternity dramatically reduces the degree of relatedness between subordinates and the offspring they may help, as only 36% share the same father, even if the same male remains dominant in the territory across their birth years. Second, subordinate females commonly lay an egg within the dominant's nest (44% successfully produce offspring in a breeding season; Richardson et al. 2002). Thus, the offspring, including those now acting as subordinates, in a territory with multiple females may have different mothers, both within and between breeding seasons. The consequently reduced relatedness between subordinates and the helped nestlings (mean $r = 0.16$; Richardson et al. 2003b) means that the indirect benefits of helping are relatively small, and substantially less than was expected before we were able to assess relatedness directly using molecular techniques.

Surprisingly, despite these complications, subordinate females appear to possess a mechanism for inferring their kinship to nestlings and direct help toward those to which they are related. With its long period of parental care, kin discrimination is based

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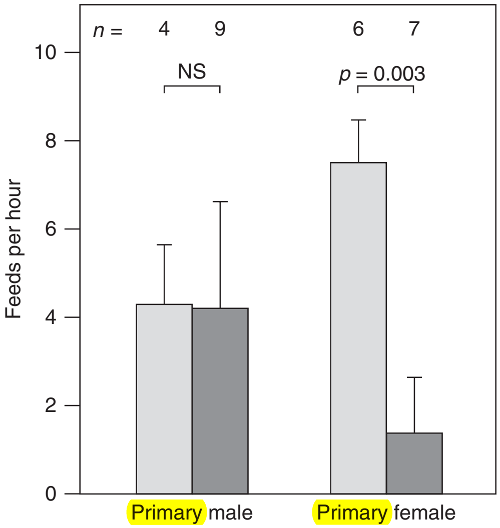

Figure 12.7. Mean provisioning (± S.E.) by subordinate female nonparents in relation to the presence (light gray bars) or absence (dark gray bars) of their putative parents (primary males $t_{11} = 0.02$; females $t_{11} = 3.71$). *n* denotes sample size. From Richardson et al. (2003a).

on association and is achieved through learning the identity of parents. The subordinate female's provisioning of the nestlings is best predicted by the continued presence of the dominant female – her putative mother – that raised her. Because the putative mother's continued presence reliably indicates a subordinate's relatedness to the nestling (Richardson et al. 2003a, 2003b), the use of this cue is effective in maximizing the indirect benefit that subordinates gain from their efforts (Figure 12.7).

In contrast, the continued presence of the dominant male that raised the subordinate is not used to determine when to help. From an evolutionary perspective this makes sense because the high frequency of female infidelity means that the continued presence of the same dominant male does not predict reliably that subordinates are related to the nestling.

Cross-fostering experiments focusing on breeding pairs without female helpers have confirmed that the subordinate's decision to help is based on the identity of the female parent, rather than a direct assessment of her relatedness to the nestling. For nestlings that later became subordinates, their decision to help was associated only with the continued presence of the dominant female (their putative mother) irrespective of whether the subordinate was cross-fostered, and therefore regardless of their actual genetic relatedness to that female (Figure 12.8).

It is clear, however, that the cue just outlined will only work for subordinates that were raised in a territory without female helpers present. It remains to be investigated whether and how subordinates that were raised in groups of multiple females discriminate kin. For example, if mothers provide more food than helpers, then the subordinates might base their decision to help on the continued presence of the female that fed them the most. Alternatively, since both the breeding and helping females within a group are often related (Richardson et al. 2002), the subordinate may help to feed the nestling if either potential mother remains present, as this will still indicate subordinate–nestling relatedness, although to a lesser degree.

Even after taking into account subordinate–nestling relatedness, considerable variation in the extent of helping behavior remains unexplained (Richardson et al. 2002). To gain a full and accurate picture of the role of indirect benefits in helping, the costs of helping, and not just the benefits, need to be considered. In the Seychelles warbler, helping appears to be costly and condition dependent. Female subordinates that help have lower body mass at the end of the season than female subordinates that do not help (van de Crommenacker et al. 2011). Consequently, body condition has a positive effect on an individual's decision to help: only those individuals that are in good condition prior to the breeding season will help. Results such as these in the Seychelles warbler and in other species such as meerkats (*Suricata suricatta*; Russell et al. 2003; Chapter 17), suggest that helpers may be only using energy that is surplus to their requirements. If this is true, are there any actual costs of helping? Unless the proximate costs lead to a reduction in future survival and fitness, there may not be any ultimate cost of helping. So, by refining their helping decisions based on their condition, helpers may be able to obtain an indirect benefit at little or no long-term cost.

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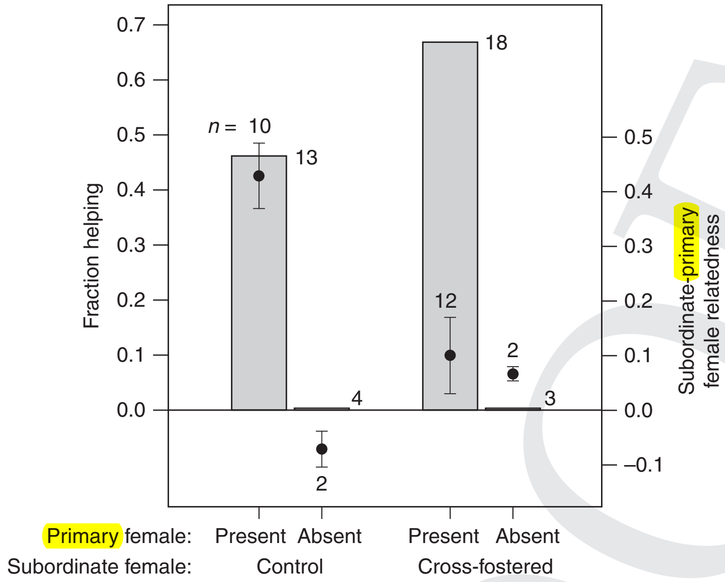

Figure 12.8. The fraction (gray bars) of control and cross-fostered female subordinates that helped to feed nestlings during their second year of life in relation to the continued presence of the primary females and primary foster females ($\chi^2 = 1.3$, d.f. = 1, $P = 0.25$), and in relation to the new primary females that replace the primary (foster) females that raised the subordinates (absent). Only those subordinates that could have been helpers, that is, where nests with young were present in their natal territory, were included ($N = 38$ individuals). Circles indicate mean relatedness of subordinates (± S.E.) to the primary females and primary foster females that raised the subordinates and were still present on the territory (present; $t_{20} = 3.48$, $P = 0.002$) or to new primary females that replaced the primary (foster) females that raised the subordinates (absent). n denotes the number of subordinates. From Komdeur et al. (2004b).

Direct fitness benefits of helping

It has been suggested that only 10% of the variation in helping behavior can be explained by indirect benefits (Griffin and West 2002). Thus indirect fitness benefits alone are unlikely to fully explain this phenomenon. An alternative explanation is that helpers may increase their own survival and future reproduction by cooperating with others. Here we do not consider all the various possible ways that subordinate individuals might improve their direct fitness, but instead focus on those that appear to be important in the Seychelles warbler system.

Acquisition of parentage

As discussed earlier, female subordinate Seychelles warblers often gain parentage within their own group by laying an egg in the dominant bird's nest (Richardson et al. 2001). In contrast, male subordinates rarely gain parentage. As a result, the direct fitness benefits gained through parentage by female subordinates are over three times higher than those gained by male subordinates (Figure 12.9). Importantly, in both sexes the direct benefits of helping are up to six times higher than the indirect benefits when direct breeding benefits were included. This suggests that direct benefits are more important in the maintenance of cooperative breeding in the Seychelles warbler than are indirect benefits.

Accumulation of breeding experience

By helping to raise the dominant birds' offspring, subordinates may gain breeding experience, allowing them

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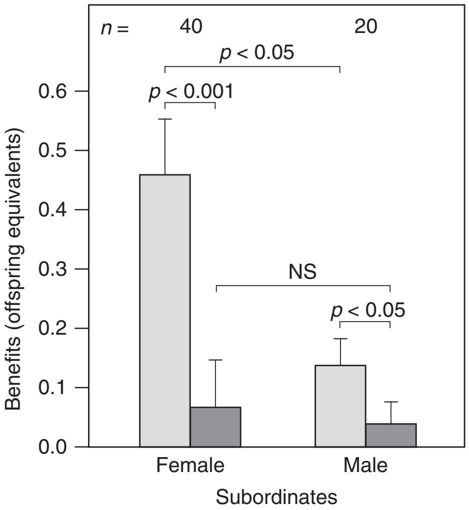

Figure 12.9. Fitness benefits (± S.E.) of cooperative breeding gained by female and male subordinates (1997–1999). Both female and male subordinates gain significantly higher direct (pale columns) compared to indirect (dark columns) breeding benefits (female: $z = 4.22$, males: $z = 2.39$). Direct breeding benefits were significantly higher in females than in males ($z = 2.29$), but there was no significant difference between the sexes in indirect benefits ($z = 0.21$). n denotes sample size. From Richardson et al. (2002).

to be more productive when they achieve a breeding territory of their own in the future (Komdeur 1996c; Hatchwell et al. 1999). In the Seychelles warbler, this idea was tested by translocating similar-aged females and males with different breeding and helping experience. On the new islands, newly formed pairs, where one partner only had helping experience and the other had breeding experience, produced their first fledgling as fast as pairs in which both partners were experienced breeders, and significantly faster than pairs consisting of an inexperienced breeder with no helping experience and an experienced breeder (Komdeur 1996c). Inexperienced females took more than a year to produce a first fledging, but only four months when they had helping experience. Females with either helping or breeding experience built stronger nests that were less prone to be blown away by wind, and spent more time incubating, resulting in higher hatching success than for inexperienced females. Once the previously inexperienced birds fledged young themselves, they were then able to produce a second fledgling in the same time as experienced birds, suggesting that they had by then learned all the necessary skills.

In this study, we presumed that all the female helpers were nonbreeders and that all dominant females had bred. However, our later work indicated that 44% of helper females in territories with genotyped offspring were assigned maternity, so it is likely that some of the female helpers included were subordinate cobreeders. Either way, this study shows that the females that gain breeding experience as subordinates do better when subsequently breeding as a dominant for the first time than females without breeding experience. Given that some "helping" females may have been cobreeders, however, it does not unequivocally demonstrate that "helping" females do better as a breeder as a result of the experience or skills gained from their behavior.

Territorial inheritance

Helping may lead to higher status within the group and, hence, greater success when competing for a territory after the death of its owner of the same sex as the helper (Zack 1990; Koenig et al. 1992; Balshine-Earn et al. 1998; Leadbeater et al. 2011). Alternatively, helping can result in higher productivity and thus a larger group size, which may make the group more competitive compared to neighboring groups. If the group then increases the size of its territory by outcompeting neighboring groups, the helper may eventually be able to take over a portion of the territory as its own breeding territory (Emlen 1991).

In the Seychelles warbler, territory inheritance is rare and not linked to helping: of the 219 monitored subordinates, only 3.7% (five males and three females) inherited their natal territory (Eikenaar et al. 2008). However, of the males that remained on their natal territory as subordinates, 78% budded off a small portion of the territory for themselves without having ever been a helper (Komdeur and Edelaar 2001). Those males that did help never budded off part of the territory and never inherited a breeding territory after the death or experimental removal of the dominant male (Eikenaar et al. 2008).

Territory inheritance is therefore almost exclusively linked to budding, and not helping, and even then only accounts for about 4% of cases of territory acquisition.

That it is only male subordinates that are able to bud off a new territory may be because male subordinates gain fewer fitness benefits from helping than female subordinates (Figure 12.9). Plus, if helping is costly in terms of condition, males may do better by refraining from helping and instead harboring their resources to mount a challenge to bud off part of a territory and expel intruders.

Pay-to-stay

This hypothesis proposes that individuals that do not help are punished and may be evicted from the territory (Gaston 1978; Balshine-Earn et al. 1998). Importantly, the "resources" that the helpers are paying to get access to are not necessarily food. For example, where subordinates join and help in a group other than their natal group, the goal of helping may be to form social or breeding relationships with nonkin (Croft et al. 2004). This could well be one of the reasons why, in the Seychelles warbler, males – the sex that gains lower fitness benefits from helping on the natal territory than female subordinates – often disperse to become subordinates on nonnatal territories, while females normally remain on their natal territory as subordinates (Richardson et al. 2002). If this is true, the fitness benefits to subordinate males on nonnatal territories should be higher than those to males on natal territories; this remains to be tested.

Group augmentation

Helping may result in the production of more individuals, causing the group to grow larger. This may increase the survival chances of all individuals in the group, because larger groups are better at competing with other groups or deterring predators (Kokko et al. 2001; Clutton-Brock 2002, 2009). Under this scenario, helpers not only gain benefits for themselves, but also benefit other individuals in the breeding group.

In the Seychelles warbler, helpers have both a short- and long-term effect on offspring fitness: the number of helpers in a territory is positively associated with both the offspring's chances of reaching adulthood and its late-life survival as an adult (Figure 12.10). Importantly, larger group size per se does not appear to be beneficial to adults, as individuals living in larger groups had lower survival probabilities than those living in small groups (Figure 12.11). Predation of warbler eggs and nestlings occurs, but adult warblers suffer virtually no predation pressure on Cousin Island; therefore competition for food is the most probable cause of this reduction in adult survival with increasing group size.

Overall, however, the negative effect of increasing group size on individual survival may be counterbalanced by a gain in the reproductive success of subordinates (Richardson et al. 2002). For example, in larger groups, female subordinates may have a higher chance of becoming cobreeders, although this remains to be investigated. Finally, lower survival benefits in larger groups may form an additional selection pressure on subordinates to help rear related offspring in order to gain a compensatory benefit (at least for female subordinates) or to disperse and join a smaller group to offset the negative effects of increasing group size as an adult.

Sex allocation

In the Seychelles warbler, the advantage of having helpers depends on territory quality. Helpers are beneficial for dominant birds on high-quality territories because they improve the reproductive success of breeding pairs. Unassisted dominant females on high-quality territories maximize their fitness by biasing the sex ratio of eggs to females (Figure 12.12) thus producing a greater proportion of female offspring that are likely to become helping subordinates in subsequent years (Komdeur 1996b, Komdeur et al. 1997). When the group includes helping female subordinates, the dominant birds not only gain an increase in their own productivity, but also gain the indirect benefits associated with subordinate females breeding (Richardson et al. 2002). In contrast, unassisted dominant females on medium-quality territories produced sex ratios around parity, and on low-quality territories, where the presence of subordinates is costly for breeding pairs because of competition for food, unassisted dominant females maximize

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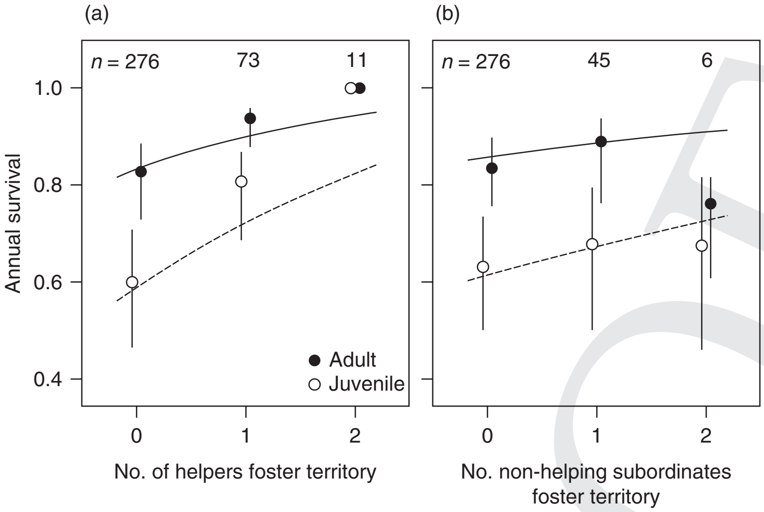

Figure 12.10. Annual adult and juvenile survival probabilities (± S.E.) in relation to (a) the number of helpers in the rearing territory, and (b) the number of nonhelpers in the rearing territory. *n* denotes the number of individuals that were monitored for survival in their first year of life and subsequently for annual adult survival. From Brouwer et al. (2012).

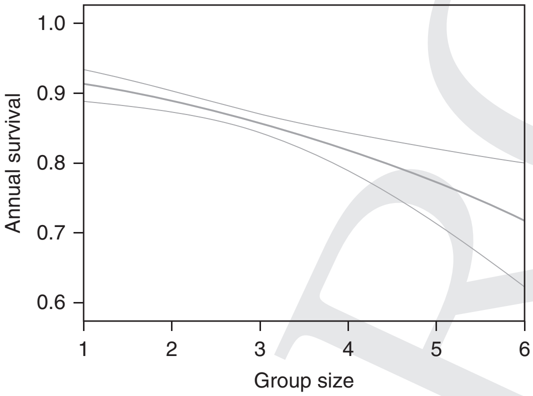

Figure 12.11. Adult survival (± 95% confidence interval) probabilities for an average year (thick lines) in relation to average group size inhabited as an adult. From Brouwer et al. (2006).

their fitness by biasing the egg sex-ratio toward males (Figure 12.12), thus producing a greater proportion of male offspring that will disperse from the natal territory and avoid competing for food with the breeding pair.

This ability to bias the sex ratio, and its link to territory quality, was confirmed during the establishment

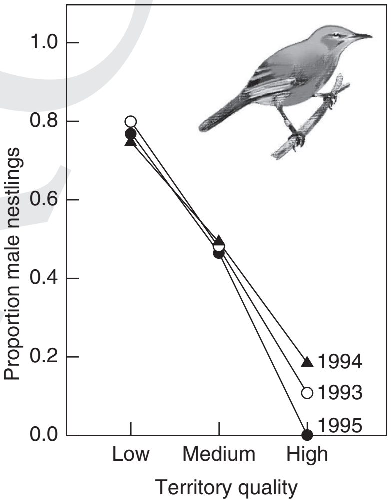

Figure 12.12. Sex ratio of nestlings produced by pairs in relation to quality of breeding territory (low-, medium- and high-quality territories; 1993–1995). Young were hatched from one-egg clutches only. No additional young were present on the territory. From Komdeur et al. (1997).

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of a new population on Aride Island. Breeding pairs that were transferred from low- to high-quality territories switched from producing 90% sons to producing 85% daughters. Breeding pairs that were switched between high-quality territories showed no change in sex ratio, producing 80% daughters before and after the switch (Komdeur et al. 1997). Sex-specific embryonic mortality between egg laying and hatching can be ruled out, because the sexes of dead embryos were not biased toward the less adaptive sex (Komdeur et al. 1997, 2002).

We have been able to experimentally confirm the differing fitness consequences of unassisted breeding pairs producing daughters or sons on high- and low-quality territories, respectively. Young nestlings were cross-fostered between unassisted breeding pairs on high- and low-quality territories that were feeding a nestling of the putatively adaptive sex. Pairs breeding on high-quality territories that were allocated foster daughters gained significantly higher inclusive fitness benefits than those raising foster sons, whereas the reverse was true for pairs breeding on low-quality territories (Figure 12.13). These findings provide strong evidence that sex allocation in the Seychelles warbler is adaptive to the breeding pair.

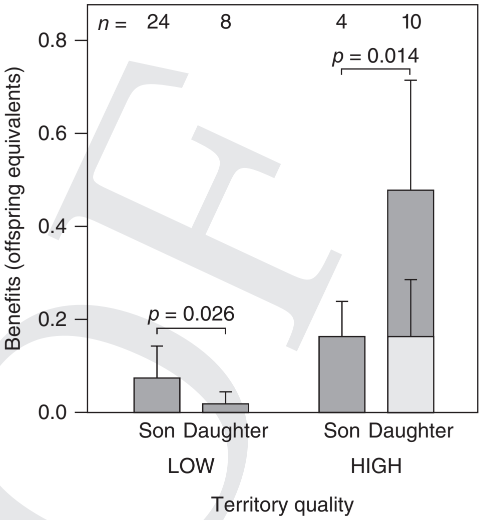

Figure 12.13. Inclusive fitness benefits accrued to focal breeding pairs by producing sons or daughters (1985–1986) on low- and high-quality territories. Fitness benefits (± S.D.; indirect = dark columns, direct = pale columns) were expressed in terms of additional number of yearlings produced by the focal breeding pair through help of their first-generation offspring. The dispersal tactics and reproduction of all first-generation offspring were recorded throughout their lives. *P* values for differences between sons and daughters were determined by two-tailed Mann–Whitney *U* test. *n* denotes number of breeding pairs. Analyses from Komdeur (1998).

An alternative route to cooperative breeding

In cooperative breeding species helpers are often younger, pre-reproductive individuals that have not yet acquired an independent breeding position (Brown 1987; Cockburn 1998; Koenig and Dickinson 2004; West et al. 2007). In a few long-lived mammalian species, however, older post-reproductive individuals have been documented to provide kin-directed cooperative behavior (Packer et al. 1998; Pavelka et al. 2002). In the Seychelles warbler, we found that some dominant breeders, mainly females, were deposed from their breeding position (Richardson et al. 2007). Importantly, the new dominant females that replaced them were more closely related to the deposed females than one would expect by chance (mean $r = 0.29$); indeed, they are often their daughters. Some of these deposed females left the territory to become floaters, but 68% remained as subordinate females if, apparently, the quality of the territory was sufficiently high to support another subordinate. Of the demoted subordinates, 64% became helpers for the new dominant female. As of yet, no clear direct benefits have been identified as being gained by these deposed females. It is clear, however, that by helping these new, related dominant females to reproduce, they can gain indirect benefits (Richardson et al. 2007).

In the few other species (including humans) where post-reproductive helping occurs, the cessation of reproduction by older females appears to be a strategy linked to senescence (Packer et al. 1998; Pavelka et al. 2002). This does not appear to be the case in Seychelles warblers. Dominant breeders do not become

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subordinates as part of a strategy linked to a senescent reduction in their own reproductive output. Indeed many demoted individuals are substantially younger (average age 5.2 years; Richardson et al. 2007) than the age at which reproductive senescence occurs (from age 8 years onward, Hammers et al. 2012).

The observation that adults that have lost a dominant breeding position help their younger relatives is important because this represents an alternative route to cooperative breeding. Becoming a helper is not necessarily an effective strategy for all adult females challenged by a rival, however. The effectiveness of the strategy depends on the degree of relatedness between the demoted female and the new dominant female.

A recent study suggests that an alternative response might be available. If a female dominant allows a subordinate related female helper to cobreed in the same nest she will gain indirect fitness benefits comparable to a demoted nonreproducing female that becomes a helper (Hammers et al. 2012), but in addition the dominant female gains the direct fitness benefits from laying her own egg. For a dominant female it would then be better to allow another subordinate female to become a joint-nester than to be demoted and instead help a new unrelated or less-related dominant female. It remains to be investigated why this does not always happen and why some females become demoted helpers and not cobreed while others adopt the joint-nesting strategy.

Conclusions and prospects

Our study shows that the occurrence of group living and helping behavior in Seychelles warblers can be explained by several ecological and social variables. We discussed the fitness implications resulting from these behaviors, not only for the subordinates but also for the dominants with which they share the territory. Moreover, we also demonstrated that the expression of dispersal behavior and cooperative breeding change over time, and differently for males and females. Despite the long-term nature of our study, however, we are still left with many unresolved questions.

Understanding variation in natal dispersal between and within the sexes

Our study has demonstrated large spatial and temporal variation in the natal dispersal behavior of young Seychelles warblers. At the beginning of our study, young males dispersed from their natal territories more often than females, but later in the study both males and females showed similar natal dispersal. The observed change was the result of females starting to disperse earlier and not the result of a change in the quality of the territories on which males and females were born. We can think of several possible explanations for this change, but the most likely appears to be changes in fitness gained by females dispersing at younger ages. In the beginning of the study period (1982–1990) none of the dispersing female subordinates were observed as floaters and all settled as primary breeders (Komdeur 1992), whereas later in the study (1995–2005) 16% of dispersing female subordinates became floaters (Eikenaar et al. 2007). These floater females do not gain parentage (there is no egg dumping), and are therefore excluded from reproducing. This increase in the number of female floaters over time suggests that females have more difficulty recruiting into the breeding population and that the fitness gains from leaving the natal territory may have declined over time. If this is true, then the fitness gains from remaining on the natal territory as a subordinate must also have declined, since otherwise it is hard to explain the increased dispersal of females.

To understand the evolution of delayed dispersal, it is important to relate variation in timing of natal dispersal to inclusive fitness benefits gained over the lifetime. This would involve a comparison of fitness costs and benefits before dispersal (remaining on the natal territory as a subordinate) versus the costs and benefits after natal dispersal until death. Furthermore, experiments are needed to show a causal relationship between the timing of natal dispersal and the resultant fitness payoffs. For example, natal dispersal could be delayed by decreasing the group size in which the subordinate lives by removing individuals, or natal dispersal could be advanced by removing a parent (Eikenaar et al. 2007).

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In cases where a parent was replaced by a stepparent either naturally or because of the removal of the parent for translocation, young dispersed from the natal territory earlier but were less likely to occupy a breeding vacancy in the next year (Eikenaar et al. 2007). This may indicate that under such circumstances, subordinates cannot postpone dispersal until the best moment, but may be forced out at suboptimal times. The decision to delay natal dispersal may therefore be an adaptive strategy employed by the subordinate to wait until the chances of gaining a breeding position are high.

Furthermore, when a parent was replaced by a stepparent, the likelihood of dispersal was higher for male than female subordinates (Eikenaar et al. 2007). The logic behind this could be that the stepparent could gain fitness benefits if a female subordinate engages in joint nesting (Richardson et al. 2002). Stepparents may evict unrelated subordinates, given the costs of group living (Brouwer et al. 2006), but this counteracts the observation that a dominant pair sometimes tolerates immigrant male subordinates. To investigate parental tolerance, detailed observations on agonistic interactions between subordinates and (step)parents are required.

Understanding the evolution of variation in helping behavior between and within the sexes

Future studies should also focus on the evolutionary causes of sex-biased helping. Our study has demonstrated that female Seychelles warblers gain more direct benefits through cooperation than do males. This may explain the female bias in helping behavior observed early in the study. What, however, are the factors that drive males to disperse earlier and help less? In order to answer this question we need to know what fitness gains are made by early-dispersing males and females relative to the alternative of staying.

We can suggest several ultimate explanations for the observed sex differences:

(1) *Territory ownership is more important for males than for females.* For males, this is a near prerequisite for reproduction, whereas females can reproduce by joint nesting (Richardson et al. 2001, 2002). In other words, males should obtain a territory at the earliest age possible, because every year that a male remains a subordinate is a year with no or very limited reproduction. Given the importance of territory ownership, competition over breeder vacancies may be more intense for males than for females. This is supported by the fact that experimentally created male vacancies were occupied faster than female vacancies (Eikenaar et al. 2009).

(2) *Reduced costs of dispersing by males*. There may be fewer costs of dispersal for males than females, because males may be more readily accepted into new groups. However, it is unknown how or why group members may benefit from the presence of an immigrant male subordinate.

(3) *Higher fitness benefits to males of joining other groups as subordinates.* The higher competition for male vacancies, and the limited fitness benefits accrued from males remaining on the natal territory, might explain why a considerable fraction of males disperse and become subordinates in other groups. Males might disperse and join groups smaller than their natal group to improve their survival prospects, or they might join a group with an old dominant male to improve their chances of reproducing with the dominant female while the dominant male is still alive, or in order to inherit the territory after his death. Males may move to other groups to avoid inbreeding in their natal territory, and choose to become subordinates in groups where they are less related to the females to avoid inbreeding when the males at a later stage become dominants in these group. However, there is as yet no evidence of inbreeding avoidance (Richardson et al. 2004; Eikenaar et al. 2008). Indeed, breeding between first-order relatives is relatively frequent, resulting in >5% of all offspring, despite negative fitness effects in poor-quality seasons (Richardson et al. 2004). Clearly, we lack an understanding of what drives temporal variation in natal dispersal by males and females.

In the Seychelles warbler there is also variation among individuals in whether or not they provide help if there is an opportunity to do so, at least in females. Preliminary analyses suggest that subordinate females that help produce more fledglings over their lifetime than subordinate females that do not help. This was not due to these helping female subordinates having higher annual survival, but instead because they have higher lifetime reproductive success than nonhelping female subordinates (H. Dugdale et al. unpubl. data). Why, then, do not all subordinate females become helpers when an opportunity arises? This may be linked to their relatedness to the dominant female, as discussed earlier, but there may also be other reasons. For example, it might be that only subordinates in sufficiently high condition can afford to help. In the Seychelles warbler there is evidence that declines in condition are associated with helping, and that the expression of helping behavior is determined by body condition (van de Crommenacker et al. 2011, 2012). Up to now, condition-dependence in dispersal has rarely been incorporated into models of helping strategies (Heinsohn and Legge 1999; Russell et al. 2003; Covas and Griesser 2007; Lawson Handley and Perrin 2007).

Finally, in our studies of the Seychelles warbler we were able to estimate the direct lifetime fitness benefits – the total number of fledglings produced – as a result of helping. It is extremely difficult, however, to assess all the inclusive fitness benefits that are gained. We have a good long-term database on individual-level dispersal behavior and helping strategies, social and environmental parameters, and a genetic pedigree. But it is still a very challenging and complex task to compare an individual's potential inclusive fitness benefit from dispersal versus that gained from remaining in the group and subsequently helping, or not. This is because of hidden effects. For example, helping can also have long-term fitness effects for the offspring that have received helped (i.e., greater later-life survival; Brouwer et al. 2012), and living in groups itself can have costs irrespective of helping. Nonetheless, the unique features of the Seychelles warbler study offer the opportunity to answer this, and other, important questions.

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