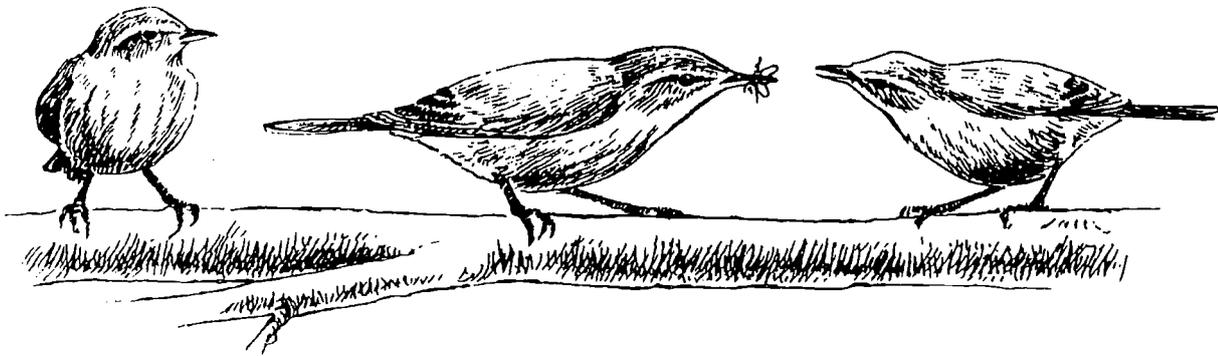# Benefits of helping in a saturating environment: the Seychelles Warbler on Aride.

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Summary

1. For the cooperatively breeding Seychelles Warbler (*Acrocephalus sechellensis*), the decision to help is a trade-off between costs and benefits, which is influenced by the environment. The newly founded and increasing population of Seychelles Warblers on Aride Island provides us with a prime example of a developing cooperative breeding system. Territories on Aride differ in quality (measured in terms of food availability), and warblers prefer territories of high quality for breeding. As higher quality habitat was being saturated by territorial warblers, helping behaviour started to occur on high quality territories because the fitness returns for delayed dispersal and helping were larger than for independend breeding. With an increase in groupsize, some birds established new territories in medium quality habitat. When medium habitat reached saturation, new helpers were found on territories of medium quality.

2. As the population increased, average territory quality declined. Territories decreased in size and new territories became smaller and were situated in habitat of lower quality As a consequence, reproductive success of the warblers declined (lower breeding frequency and smaller brood size). Currently, breeding activity on Aride is synchronised with breeding activity on Cousin, on which breeding is determined by season, indicating seasonal effects on breeding on Aride as well.

3. Reproductive success declined, probably because the food availability declined with a decreasing territory size. This view is confirmed by the present separation of reproduction and moult (both energetically costly activities) in females, as on Cousin. Initially after the establishment of the warbler population on Aride, the birds were able to breed and moult at the same time. However, feeding rates (which are negatively related to food availability) have not changed over the years.

4. Breeding vacancies of high quality were more often filled by birds helping on that territory (residents) than by non-helping birds born outside the territory (non-residents). Furthermore, new territories were more often founded by birds from adjacent territories (sometimes helping) than by non-helping birds from other territories. This happened a few years after the transfer, at a higher population density. As a helping resident has a higher probability to obtain a high quality territory than a non-helping non-resident, it will have a higher reproductive success.

5. In the absence of habitat saturation, establishment of new territories did not affect the size of existing adjacent territories. In males, the size of the newly established territory was independent of its natal territory. However, females born in adjacent territories founded smaller territories than females originating from non-adjacent territories. If a male originated from a territory adjacent to this new territory, this natal territory was similar in size to the average size of adjacent territories from which no founder originated. In contrast, adjacent territories from which the foundress originated were larger than adjacent territories from which the foundress did not originate. (It is unknown why the sexes differ in these respects).

6. For 18 out of 23 former helpers, no breeding vacancies of high quality were present at the time of helping. These birds helped on their natal territories. The behaviour of the other 5 helpers is best explained by the gaining of (breeding) experience as high quality breeding vacancies were present (n=3) or the birds helped unrelated young outside the natal territory (n=2). Helping experience has been reported to have a strong positive effect on future reproductive success, when the helper has become a breeder.

7. A direct effect of relatedness on helping probability could not be detected due to a high degree of incestuous matings and hence low levels of variation in relatedness between helpers and young. However, two types of observations are consistent with kin selected helping behaviour: 1) females which were replaced as breeders remained on the territory and helped their daughters' young, 2) territories were a breeder was replaced by an unrelated bird, significantly more (all) offspring dispersed than in territories without such a replacement.

8. For the first time in the Seychelles Warbler, group dispersal (of siblings, followed by successfull breeding) was observed. This might be induced by the high reproductive rate, and thus the formation of large family groups.

9. Helping probability is the same for both sexes, and the sex ratio of 20 young sexed in the nest is not skewed on the coastal plain. This in contrast to the situation on the fully saturated Island of Cousin. When sexed at independence, more females were present on high quality territories, and females were more prone to helping. It seems that the production of female offspring is an adaptive behaviour of the parents in order to have helpers the next breeding season, and enjoy a higher reproductive success.

1. Introduction

1.1. Theoretical background of cooperative breeding

Cooperative breeding is a reproductive system in which one or more members of a social group provide care (usually food-provisioning) to young that are not their own offspring. In birds, these aid-givers may be either non-breeding (usually called helpers) or co-breeders who share reproduction with other group members of the same sex.

The existence of helpers at the nest has been known for quite some time (Skutch 1935), but cooperative breeding has only been studied into more detail during the last three decades. This was mainly due to the lack of an adequate theoretical framework in which the evolution of the apparently altruistic (and therefore non-adaptive) behaviour of helpers could be understood (Stacey & Koenig 1990). Until then, all reports on cooperative breeding animals were dismissed as 'abberations', together with more clear examples of mix-ups, like the Northern Cardinal (*Cardinalis cardinalis*) that fed goldfish in a pond (Welty 1975 in: Stacey & Koenig 1990).

A first attempt to understand the mechanism of cooperative breeding in an evolutionary context was made by Wynne-Edwards (1962). His interpretation was that after assessing a low food availability, cooperative breeding would be the best strategy for the population. Such behaviour seemed to require a kind of group selection for its evolution, otherwise a trait of forfeiting reproduction would be selected against if other individuals did reproduce. At that time, mechanisms by which group selection could occur were not well understood.

Shortly thereafter Hamilton (1964) and Maynard Smith (1964) developed the theory now referred to as kin selection, and laid a firm basis upon which the empirical study of cooperative breeding could begin. The quintessence of their work is that the number of gene copies in the next generations ('fitness') is not only determined by producing own offspring ('direct') but augmented through the reproduction of relatives ('indirect'). Any action undertaken by a helper that increases the reproductive output of their relatives, increases the helpers' fitness. If the benefits of helping (b: the increase in number of relatives) times the relatedness of the extra offspring (r) exceeds the costs of helping (c), helping will be evolutionary stable (Hamilton's rule: br-c > 0). If not, helping behaviour is selected against. The development of this theory resulted in the starting of a number of long-term studies on cooperative breeding by the mid '70s (Stacey & Koenig 1990), which by now have extended the knowledge and idea's explaining mechanisms of cooperative breeding.

Cooperative breeding

Why stay

Two artificially seggregated explanations why young birds should delay dispersal and remain on their natal territory have been discussed.

The **ecological constraints theory** focusses on the (lack of) possibilities for a helper to disperse and breed successfully, and the costs associated with it. Many constraints have been identified, such as lack of suitable or acceptable breeding habitat or mates, or low survival and reproductive rates of individuals that did disperse. If waiting for a breeding vacancy is best done in the natal territory, dispersal should be delayed.

The **benefits of philopatry theory** does not stress the costs of dispersal, but the benifits of staying, because of differences in territory quality. Staying in the natal territory may increase the chance to obtain a territory of higher quality by the inheritance of the natal territory or by filling a vacancy in a nearby territory of similar quality. An advantage of residents over non-residents of the chances to 'win' a vacancy has been noted recently in several species (Emlen, in: Krebs & Davies 1991).

These two explanations for delayed dispersal however are not contradictory, but complementary, as has been argued by Emlen (1991) and Komdeur et al. (1995a). Each individual should choose the best option available. If benefits of staying outweigh benefits of dispersal and possibly even breeding on it's own, a bird should stay. But no benefits of philopatry will result in delayed dispersal, however high they may be, if the benefits of breeding elsewhere are higher. As Emlen (1994) already stated: "The distinction over whether constraints or benefits currently play the major role in maintaining any particular case is unimportant to the larger issue of identifying the ecological factors that predispose one species or population towards delayed dispersal and family formation and another towards dispersal and early breeding or floating".

Why help

If a young bird stays in its natal territory, why should it help in the rearing of non-descendent kin? A number of adaptive hypotheses has been formulated (Emlen 1991), grouped under 4 captions:

-helping enhances survivorship: helping is a payment for access to recources, and helping increases the benefits a living in a large group,
-helping enhances future probability of breeding: a helper demonstrates its parental abilities, and a larger group outcompetes other groups for territory area,
-helping increases the helpers reproductive success: a helper gains parenting experience, and helping gains the helping services of the recipients in future breeding attempts,
-helping increases indirect fitness: the production of non-descendent kin increases through increased survival of parents and the increased production due to helping of related young.

In this report, some benefits of helping will be discussed: obtaining a territory, gaining breeding experience and increasing indirect fitness. These were studied in the Seychelles Warbler (*Acrocephalus sechellensis*).

1.2. The Seychelles Warbler

The Seychelles Warbler is a 15 cm long insectivorous passerine, member of the genus of Reed Warblers. It is historically known from Marianne (where now extinct) and Cousin Island (29 ha): an island in granitic Seychelles (see map 1). In 1967 the world population numbered only 26 birds on Cousin. Therefore the island was purchased by the International Council for Bird Preservation (ICBP) in 1968, who managed it as a nature reserve. Management activities included the removal of Coconuts, and allowing regeneration of a more natural vegetation. This has resulted in a spectacular recovery of the warbler population to about 320 birds and 115 territories in 1982. Since then, both the population remained around this level and had probably reached the island's carrying capacity.

In 1988 resp. 1990 two populations of the Seychelles Warbler were founded on Aride (68 ha) and Cousine (26 ha) (Komdeur 1994a). Since the translocation of 29 birds to each of the islands, the populations now number about resp. 350 and 110 individuals (Peter Carty, pers. comm. and own estimate), and numbers are still increasing on both islands.

The warbler is greenish-grey on the upperparts, and pale yellowish-grey on the underparts. Juveniles are similarly colourred. The iris is grey-blue in juveniles, and changes via grey-brown to the brown-red of the adults (after 11 months). Males are on average larger than females: body mass, winglenght and tarsus differ significantly between the two sexes, but overlap in all measurements exists and not all birds can be sexed using these measurements (Komdeur 1991a). However, the behaviour also differs. Males more often raise their crest during interactions, and females behave more submissive. Only males mount the females and only females display juvenile wing-flapping behaviour. Females are also sole incubators. Its diet mainly consists of insects: 99.8% of all identified prey were insects. These are taken from leaves (98.2%), mainly from the underside (95%)(Komdeur 1991a).

The warbler is year-round territorial, and territories are defended by song and physical contact. Once paired, a warbler will remain in the same territory for life. Additional resident birds may be present for a number of years in a territory, and these birds are engaged in many social interactions with the other residents, and aid in territory defence and sometimes reproduction. If so, they usually help the dominant breeder pair in raising the chicks. But sometimes they become joint-nesters, sharing reproduction with the dominant breeder pair. It's assumed that these additional birds are mature offspring of at least one of the (former) breeders, and they may disperse after a number of years but sometimes stay their entire life on their natal territory. On Cousin only 2% of the population consists of floaters: non-territorial, non-breeding males (Komdeur 1991a).

Breeding may occur in almost any month, but peaks twice a year on Cousin: from June through August, and a smaller peak from December through February (see fig. 1). The timing of reproduction is linked to the maximum food availability for the young (Komdeur 1995b). The cup-like nests are build in trees from 1-20 m, mainly by females, and are constructed in forks or supported by large leaves. Up to 4, but usually one egg is laid in the nest (average clutch size 1.13). Only females incubate for 18 days, and during this time the

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male or any helpers may guard the nest to avoid predation by Skinks (*Mabuya sechellensis* and *M. wrightii*), Bronze Gecko (*Aeluronyx sechellensis*) and Seychelles Fodies or Toq-toqs (*Foudia sechellarum*). The nestling spends on average 19 days in the nest, and it takes another 3 months before the young are independent. During this period both sexes feed the young. Independent young remain on their natal territories until they are full-grown after about 11 months. After that, some remain but others disperse. In females, dispersal always led to breeder status, but males could become non-territorial floaters (Komdeur 1991a).

Yearly survival is high in adults: 83.5%. A hatchling has a 36% survival to the age of 1, a yearling 80% to the age of 2. Floaters do worse: only 10% of floating yearlings reached the age of 2.
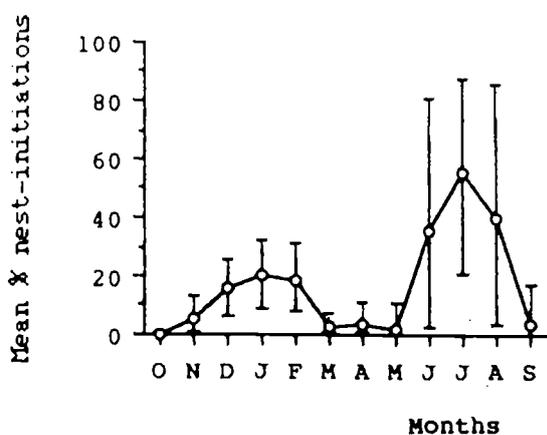
Fig. 1. Percentage of territories with nest-initiations each month, average of January 1986-September 1990 (n=470) (from Komdeur 1991a).

Factors affecting helping behaviour in the Seychelles Warbler

Several factors influence the behaviour of potential helpers: kinship, territory quality and habitat saturation.

-kinship: indirect fitness of helper is the product of two terms: 1: the number of extra, non-descendent young produced by a breeding pair entirely due to the helper's effort, 2: the degree of relatedness between donor and recipient. For example, if a helper helps a non-related breeder pair, its indirect fitness component will be 0. In the absence of other

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benefits of helping, helping non-relatives will be altruistic, and selected against. A positive effect of putative relatedness between potential helpers and the recipient was found on the proportion of birds to become helpers, and the intensity of help given (Komdeur 1994c).

-territory quality: on Cousin, territories differ in quality. Territory quality depends on insect prey available and amount of foliage present. It was measured as the yearly sum of the monthly product of mean foliage cover and mean number of insects per unit leaf area for every plant species present, times the mean annual territory size. Nest sites (see Appendix 7.1.), predators, water availability etc. are evenly distributed over the island and do not influence territory quality. Territory quality, divided into low, medium and high, had a positive effect on foraging efficiency, and hence on reproductive success (no. of yearlings produced) and adult survival.

The presence of helpers was of positive effect on the reproductive success of a warbler pair in high quality territories (HQT), but of negative effect in low quality territories (LQT), which was confirmed by removal experiments (Komdeur 1994b). The negative effect of helpers on the reproductive success of a warbler pair in a LQT is probably due to reproductive and food competition. For an adult offspring, the trade-off between staying/helping and dispersing/breeding will be influenced by quality of the natal and vacant territories.

Offspring stayed longer and helped more often in their natal territory with increasing territory quality. Increasing territorial quality will increase both direct fitness as indirect fitness of a helper. Komdeur (1992) has shown that it is advantageous for a bird in a HQT to refrain from occupying a vacancy in a medium quality territory (MQT) resp. LQT if a HQT vacancy is expected within 6 resp. 11 years. A bird in a MQT should not disperse to occupy a LQT-vacancy if a vacancy in a MQT is expected within 9 years.

In the Seychelles Warbler males and females may have different costs and benefits related to dispersal/helping, indicated by differences in behaviour. Females are much more prone to stay and help, and females only disperse to territories with breeding vacancies, whereas some males become floaters (1991a). Possibly in response to this, the sex ratio is extremely skewed between HQT and LQT: in HQT 80% of all produced yearlings is female, whereas in LQT this is only 20%. The mechanism (primary sex ratio or differential mortality) by which this skew is achieved are not yet clear.

-habitat saturation

Since the translocation, the populations on Aride and Cousine have increased dramatically, and numbers are still increasing on both islands.

Mean monthly temparature, monthly rainfall and monthly rainfall frequency did not differ between the islands during August 1989-November 1991 (Komdeur 1991a). Vegetation cover and -composition are highly similar, and only local differences exist in species abundance and cover. Overall, the islands are very much the same. However, differences in

food availability do exist between the islands: Aride has on average 3.4 times as much insects as Cousin, whereas Cousine has 1.8 as much as Cousin. The seasonal pattern of food availability was the same for all three islands (fig. 2)(Komdeur 1995b). It is concluded that the islands only differ in absolute food availability, but are similar in other respects (Komdeur 1995b).

This similarity of the islands makes it to a certain extent possible to view the populations of Cousine and Aride as growing populations with a developing cooperative breeding system similar to the one on Cousin. During the transition from a non-cooperative to a cooperative breeding system, the effect of any parameters on the individual behavioural strategies may be more individually detectable than in a stable population, as its effect may more clearly interact with time and space.

The most pronounced difference between a growing and a stable population, is the level of habitat saturation (occupation of habitat by territorial birds). In an unsaturated habitat, high quality habitat will be available and all fullgrown offspring will disperse. As the population increases, vacant HQT will become scarcer and later absent. The offspring from HQT will be the first to be confronted with a shortage of acceptable vacancies (or in other words: their habitat is fully saturated), and will be the first to refrain from dispersal.

Territory quality is affected by insect availability per unit vegetation area, vegetation cover and territory size. Insect availability per unit vegetation area and vegetation cover are constant between years (Komdeur 1995b). However, territory size may change with an increasing number of warblers. Consequently, the costs and benefits of staying/helping versus dispersing/breeding may change likewise. Therefore, the study of cooperative breeding must be viewed in this dynamic context. The first part of the results section will present the population dynamics and the various effects of population growth on individuals and reproduction, and discuss its effects on potential helpers. The results of this first section will help interpret the results concerning helping benefits presented in the second part of the results section.
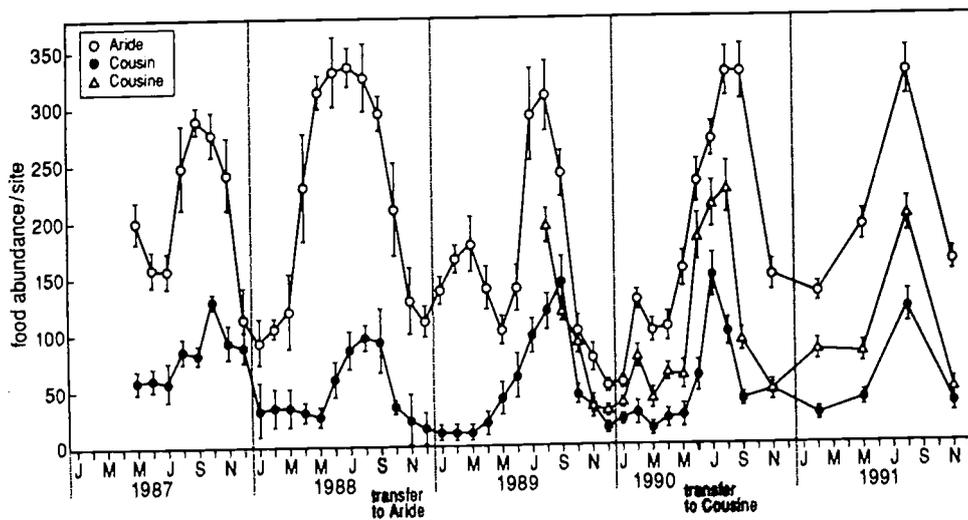
Fig. 2. Monthly food abundance (± SE) of Aride, Cousin and Cousine (January 1987-November 1991) (from Komdeur subm. Biol. Rhythms).

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2. Methods

2.1. Study populations

On Aride, the warbler population has been studied intensively from September 1988 to the end of 1993. After that, with numbers increasing each year, mainly birds on the plateau were followed: about 90 birds on a 5.2 ha coastal flat area. This area is of higher habitat quality, and was occupied first by the warblers after the transfer (map 2). At present, about 80% of the birds on the plateau are ringed with unique colour combinations, for individual recognition. I studied the Aride plateau population from 20th February to 15th June 1995, except between 1st May untill 4th June.

Warblers on Cousine were studied from June 1990 till November 1991. After that, only short visits have been paid to the population. Almost 50% of the birds is colour ringed. In 1995, I studied the population from 1st May untill 25th May.

2.2. Warbler census and territory mapping

Much time was allocated to the accurate mapping of territorial birds and territory borders.

On Aride, three subsequent surveys were carried out, with particular focus on unclear territory borders in the last survey. Typically, the whole plateau and the fringing hill parts were covered. Every 50 meters, some minutes were spent playing a loop tape with warbler song, and attracted warblers were identified. Special attention was paid on interactions between the birds (socializing or aggression), in order to allocate every bird to the right territorial group. If the tape failed to attract any warblers, periods of silence, "pishing-noises" and tape playing were alternated, which sometimes successfully attracted warblers. As the birds are easily attrackted to the observer, a fair idea of territory borders was obtained. This type of survey was repeated once a month. Additional observations were added on the maps.

On Cousine, the same type of survey was conducted on the whole of the island, but only once. For results of the Cousine population, see Appendix 7.3..

2.3. Moultscores

During the surveys, tail moult was scored as absent (all tail feathers present) or present (at least some tail feathers missing or growing) for all individual, adult warblers.

2.4. Breeding observations

Every three weeks, potentially breeding females were followed during thirty minutes. Within this time, a female engaged in nestbuilding, breeding or feeding would have led the observer to the nest or chick (Komdeur 1991a). Potential breeders are defined here as mature females which are often socializing with other group members. Usually the oldest and dominant female reproduces, but sometimes other females also do, either by separate or by joint nesting. When a nest or chick was found, a two-hour protocol was made. For every bird

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present in the territory, it was scored how much time was allocated to nestbuilding, incubating and guarding (closer than 2.5 m to the nest), and how often the chick was fed. Breeding and feeding observations were done in the second week after laying resp. hatching and every third week thereafter until independence. All protocols were done between 8.00 and 18.00, when activity of the birds is constant (Komdeur 1991a).

2.5. Feeding observations

As feeding rate is inversely correlated to food availability (Komdeur, Bullock & Laboudallon 1989), it can be used as an estimate for individual food availability. Feeding rate is defined as the average number of pecks during 30 seconds. Previous data have been collected on Aride and Cousin. Of 6 individuals, a hundred protocols of 30 seconds were made. This year continuous protocols were made, with a duration of 50 minutes (equivalent to a hundred half minute protocols). On both islands 6 individual bird were followed. When visible, the bird was timed with a stopwatch. The number of pecks (both successful and unsuccessful) were recorded, mostly using binoculars, and after the bird had been visible for 50 minutes, feeding rate was calculated as the total number of pecks divided by a hundred.

2.6. Blood sampling and analyses of blood samples

A blood sample was taken of as many individual birds as possible, in order to establish the relatedness between all group members and a chick. As birds have DNA in their red blood cells (contrary to e.g. mammals), the collection of a little blood will suffice. Adults were trapped with mistnets. These nets were placed in fly-paths or preferred foraging sites, were sufficient shade and cover was availabe. Often, warbler song was played nearby the nets for a few hours a day to attract the birds. The nets were checked regularly.

Caught birds were ringed, measured and weighed. A few drops of blood were taken from the brachial vein in the wing using a single-use syringe, or, in case of nestlings, from the tarsus. The blood was stored in a dimethyl-sulphuroxide (DMSO) solution (25 volume % in a 4 M natrium chloride solution). Samples were stored in a refridgerator when possible. In this report, only results from samples collected by Jan Komdeur and Lars Gabrielsen on Aride in 1993 are used.

In 1993 and 1994 immature birds were caught on the Aride plateau, and subsequently sexed with Polymerase Chain Reaction (PCR) by Jan Komdeur. Of all birds caught in 1993, genetic variability and relatedness was determined by Anique Kappe (in prep.).

2.7. Historical data

Since the introduction on Aride, the birds and there breeding biology were followed on a weekly basis until early 1994. Whenever possible, chicks were ringed. Furthermore, the island was checked for territory boundaries, new territories and floating birds on a more or less regular basis. This intensive scheme was relaxed in January 1994, when observations were done every two weeks. Since August 1994, only once a month 10 minutes were spent

within the bounderies of 10 selected plateau territories,and group members and begging young were recorded. Active nest searches were stopped.

Relevant data collected in advance of my stay were used in the analyses. Additional information was available from visits in 1993 and 1994 by Jan Komdeur.

2.8. Analyses of helping benefits
A) Territory inheritance and establishment

One of the benefits of delayed dispersal might be the increase in the probability to obtain a breeding vacancy (i.e. become a breeder), either in the natal territory or nearby. If helping further increases these probabilities, this must be viewed as a benefit of helping. It was analysed whether the vacancies on or nearby the natal territory are more likely to be obtained by residents and/or helpers than expected if random occupation occurs. Only birds of which the natal territory is known were included in the analysis.

With one exception, changes in breeder(s) (after a vacancy occured) have only been noted in those territories founded before January 1992. Only vacancies after this date, when 11 territories were present on the plateau, have been regarded. The exact number of potential competitors for a vacancy from each territory is not known. But it is assumed that territories will not differ much in this respect, and at least all territories produced several fledglings each year. Therefore the number of candidates for a vacancy will be proportional to the number of territories present. If vacancies are occupied at random, it is expected that 1 out of 11 vacancies is occupied by a resident bird (a bird from the territory with a vacancy). The other 10 vacancies will be occupied by birds from one of the other 10 plateau territories. This estimate is very conservatively biased, as offspring of newly founded plateau territories and hill territories also contribute to the pool of competitors for vacancies.

The same effects of residency and helping were analysed for newly founded territories on the plateau. Staying and helping might increase the probability to successfully found a new territory on or adjacent to the natal territory. It is expected that the likelihood that the birds of a newly founded territory were born in an adjacent territory, is proportional to the number of adjacent territories divided by the total number of plateau territories.

In order to interpret the fitness consequences of the founding of a new territory for both founders and adjacent birds, it is important to know how new territories originate: is empty habitat occupied or is a part of the natal/adjacent territory budded off?

Territory size of 12 new territories (founded after January 1992) was determined. Both male and female founders were classified as born on adjacent territories, non-adjacent or unknown territories. Unknown and non-adjacent birds were lumped, as unknown founders are most likely born on territories outside the plateau (as the plateau birds were intensively ringed) and therefore by definition non-adjacent birds.

For the nearest old territory (founded before January 1992), territory size before and

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after the founding of a new adjacent territory, and the change in size, was calculated. Change in territory size was also expressed as a relative measure: the change in size divided by the size before the new territory was founded. Also, the combined area of the old and new territory after the new territory was founded was calculated.

B) Breeding experience

Since the first helper was observed in 1990, 23 helpers have been recorded as 'helper at the nest' in the past. Some of these helpers have been retraced, either at the same or another territory. The fate of a (former) helper might indicate what advantages or disadvantages are linked to helping.

C) Effect kinship on helping

The effect of kinship on helping is analysed with putative kinship. This was estimated by observations of courtship and nest attendance, and age and dominance of present adults. It is assumed that all birds present on a territory and younger than the dominant pair are offspring of former breeders. For birds of known descent, this was true for 91 % (20 out of 22).

2.9. Statistics

Several statistical methods were used, using Statistix 4.0 or calculated by hand.

Relations between variables were tested using lineair regression. If a non-lineair effect of a variable was expected, its square or higher terms were included. Multiple regressions were performed in a stepdown procedure: variables were omitted from the regression equation in order of significance (least significant first), until all variables included in the equation were significant or the larger model explained significantly more variance than the smaller model. For non-normally distributed variables, non-parametric testing was performed (Spearman rank-correlation). Variables which consisted of proportions or percentages, were analysed with logistic regression, or arc-sine transformed.

Differences in means between samples were analysed using ANOVA (F-tests) or, in case of two smaller samples, t-test.

Associations were usually determined by calculating X^2, corrected for continuity in case the data were discrete. In one case the (highly comparable) G-test was applied for reasons of comparison with the original analysis. For data distributed in a 2*2 contingency table, Cochran's corrected X^2 was calculated; in smaller samples Fisher's exact probability was calculated. If the probability of an event (p) could be expressed as 1 minus the chance of an alternative event to happen (q), the binomial test was used for smaller samples.

Relative differences in quality between territories will exist, influencing dispersal and helping behaviour. In some of the following analyses, it is tried to correct for possible but unknown differences in quality between plateau territories by encorporating territory size (the larger the territory, the more food available) and -age (older territories in preferred habitat).

3. Dynamics of the warbler population on Aride

3.1. Results

3.1.1. Population increase

Starting with only 29 birds in september 1988, the population has increased dramatically, almost doubling each year in the initial 2 years (fig. 3 and 4). The significant quadratic term indicates a decelerating growth. If the analysis is repeated excluding the last two data points (being somewhat abberant, and the last one is an estimate), the quadratic term remains significant (p=0.0005).

Habitat on the plateau is of higher quality than outside the plateau. Fig. 3 and 4 show the gradual increase in numbers on the plateau and the hill. Both subpopulations display reduced growth, but to a much greater extent on the plateau.
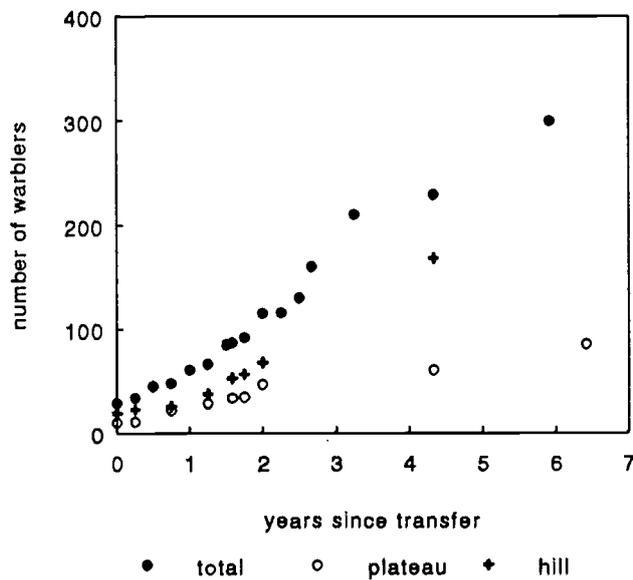
Fig. 3. Number of warblers on Aride since the transfer, on the plateau (0), outside the plateau (+) and the whole of the island (●).

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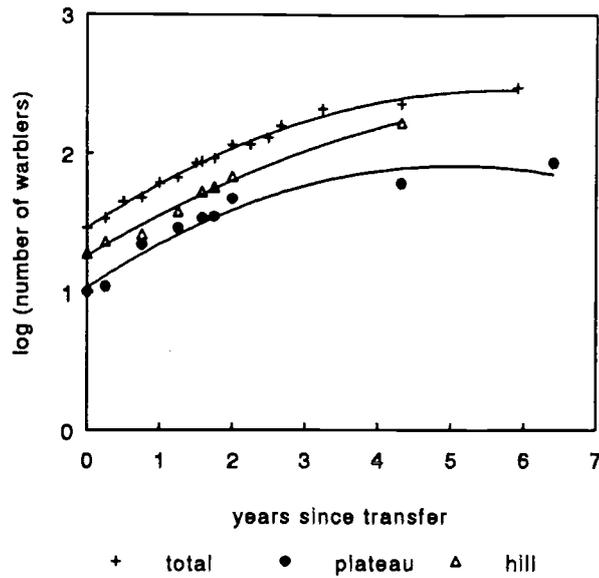
Fig. 4. Number of warblers (log transformed) on Aride since the transfer, on the plateau (●) (linear regression: log(W)=1.03+0.029*T-2.38E-4*T², T: p=0.0004, T²: p=0.004, R²=0.95, with W= number of warblers, and T=time in months since the transfer), outside the plateau (▲) (log(W)=1.26+0.026*T-1.40E-4*T², T: p=0.0003, T²: p=0.005, R²=0.99) and the whole of the island (+) (log(W)=1.46+0.029*T-2.10E-4*T², T: p<0.0001, T²: p<0.0001, R²=0.99).

3.1.2. Feeding rates

In 1988, feeding rates of 6 non-breeding, non-moulting birds were scored on both Aride and Cousin (Komdeur, Bullock & Laboudallon 1988). This was repeated in 1995. See table 1 for an overview of results.

In 1988, birds on Cousin had a higher feeding rate than birds on Aride. In 1995 feeding rates on both islands were somewhat lower than in 1988, probably due to seasonal or observer effects, but did not significantly differ between the years. In 1995, the difference between the islands was still present, and the difference in feeding rates between the islands was of the same magnitude: 0.70 pecks/30 sec. in 1988, 0.78 pecks/30 sec. in 1995.

Table 1. Feeding rates of 6 non-breeding, non-moulting females on Aride and Cousin, in 1988 and 1995 (mean ± standard deviance), and results of t-tests.

	1988	1995	t-test
Cousin	3.30±0.25	3.07±0.64	t=0.8, n.s.
Aride	2.60±0.23	2.29±0.35	t=1.8, n.s.
t-test	t=5.0,p<0.001	t=2.6,0.02<p<0.05	

3.1.3. Territory size and -quality

Territory size was evaluated as a function of time (with which population increase/habitat saturation will be related). Of all plateau territories, average territory size decreased with 526 m² per year (6.8% of the initial size)(fig. 5). In the 6.7 years past, the average territory size has decreased with 45.6%.
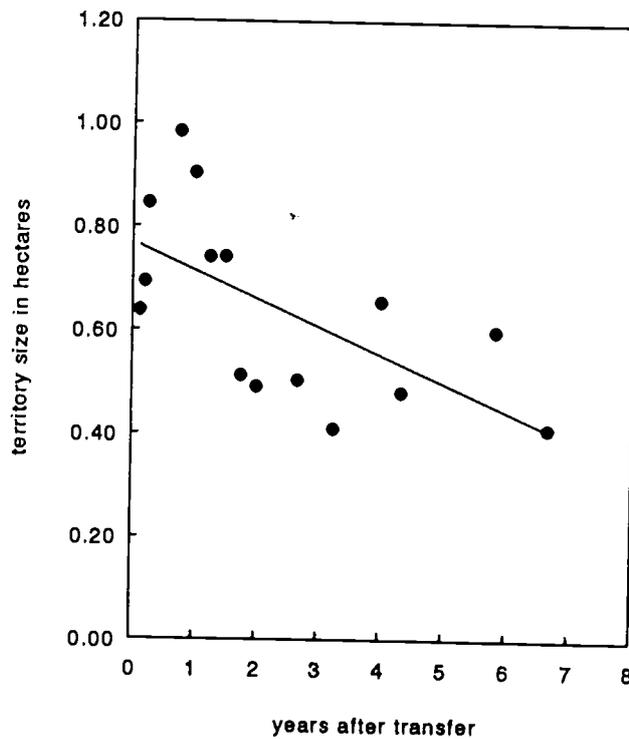
Fig. 5. Average territory size (in hectares) of all Aride plateau territories since the transfer (4≤n≤12) (linear regression: territory size=0.77-0.053*number of years since transfer, p=0.02, R²=0.37).

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This differed however between territories of different age. Only the territories initiated after the transfer decreased in size in time, and were 44.4% of their initial size (fig. 6). Territories founded 12 resp. 24 months after the transfer did not change in size, but the former territories were larger than the latter in 1995 ($F_{1,45}=5.75$, p=0.02)(fig. 6). The territories founded shortly after the transfer were very large, but at present those territories are smaller than the ones founded after a year, and have the same size as the ones founded after two years ($F_{2,9}=6.77$, p=0.02 and Newman-Keuls test at p<0.05).
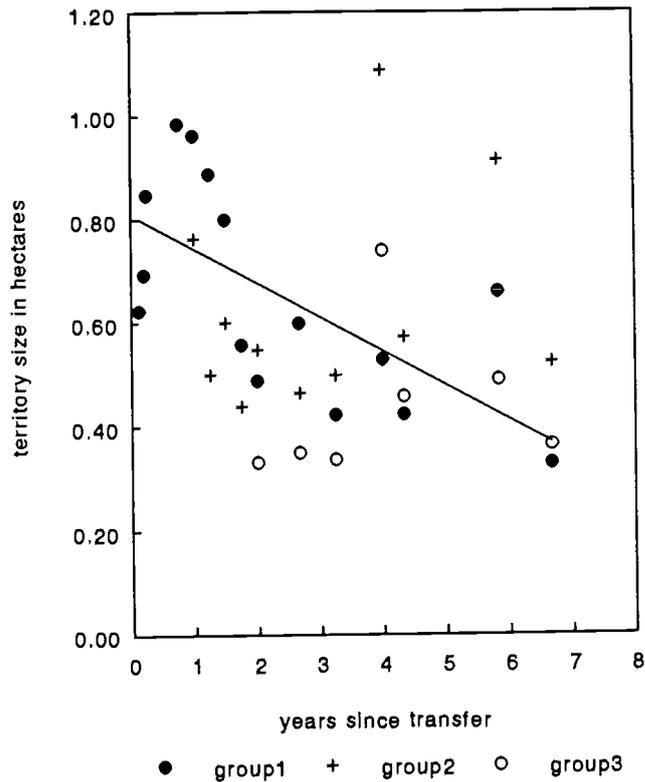
Fig. 6. Average territory size (in hectares) of Aride plateau territories founded in the first year (●) ($1 \leq n \leq 5$) (linear regression: size=0.81-0.066*years since transfer, p=0.002, $R^2=0.13$), second year (+)($1 \leq n \leq 4$) (p=0.65) and third year (○) ($1 \leq n \leq 3$)(p=0.57) since the transfer.

The decrease of territory size in time is less obvious for individual territories: 2 of the 5 initial founded territories decreased significantly in time, and none of the later founded territories. The two territories with decreased size currently have a group size of 2, the other three territories have a larger group size. Group size (2 versus larger than 2) seemed to be correlated with the probability of a territory to have decreased in size (exact probability test, p=0.055).

A decrease in territory size in time is not entirely explained by group size. On average, territory size still decreased in time after the two territories with current group size 2 are excluded, and if the first three months (when territory boundaries still had to be fixed) were excluded (p=0.006, R²=0.20). Therefore, the size of the initial 5 territories decreased in time, interacting with group size. In sections 4.1.A) and 4.2.A) the formation and size of new territories is presented and discussed.

The effect of the population increase on territory quality is not easily assessed, as there are no data available on food availability based on individual territories. Territory quality is a function of size and food availability. This means that the quality of the territories founded in the first year, has decreased on average by 50 %. Territories founded in the second year after the transfer, are at present larger than older territories, but it is unlikely that territory quality is higher. The territories founded after 2 years are both small and most likely settled in habitat of lower quality. Territory quality of Aride plateau territories is difficult to compare with territory quality on Cousin. Both lower food availability (± 5 times lower) and smaller territory size (± 4 times smaller) contribute to a 20-fold lower average territory quality on Cousin. Compared to Cousin, on the plateau of Aride a LQT has to be smaller than 0.04 ha (20*20 m), and a MQT between 0.04 and 0.09 ha (30*30 m). At present, the smallest territory on the plateau is 0.19 ha. However, relative differences in quality between territories will exist, influencing dispersal and helping behaviour.

3.1.4. Breeding activity

In a saturated environment as on Cousin, the warblers show a very distinctive breeding activity pattern (see fig. 1 and introduction). This breeding activity is positively related with rainfall frequency and negatively with temperature in the same month (Komdeur 1991a). Insect numbers are highly correlated with rainfall frequency and temperature two months before. By immediate respons in breeding activity to temperature and rainfall frequency, the birds have most food available to them when it is most needed, early during the fledgling stage.

On Cousin, breeding is constrained in the periods with lower food availability. On Aride however, food has been found to be more abundant than on Cousin throughout the year (Komdeur 1995b). In the absence of other inhibitors and physiological constraints, a high food availability overruled climatic inhibitors of reproduction (Komdeur 1995b). After the transfer, the newly arrived warblers started nesting soon (within the first weeks) and maintained high levels of breeding activity throughout the year, for at least the first 4 years. Fig. 7 gives the breeding activity since the transfer.
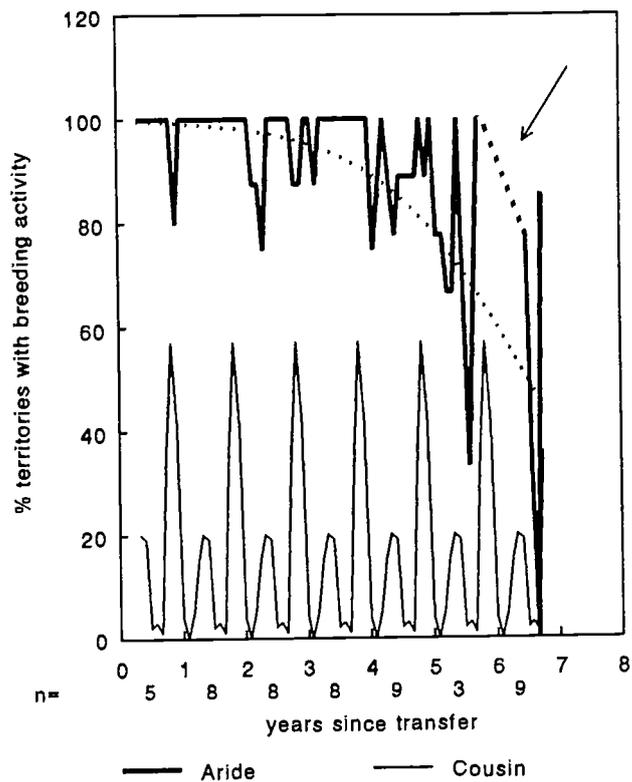
Fig. 7. Monthly percentage of territories with breeding activity since the transfer on Aride plateau (logistic regression, $\ln(p/1-p) = 5.66-0.87x$, with p=proportion territories with breeding activity, x=months since transfer, $p < 0.0001$) and monthly percentage of territories with breeding activity on Cousin (average from January 1986-September 1990, $n = 470$, data from Komdeur 1991a) (The arrow denotes a period when breeding activity is not known).

Breeding activity has been high and virtually uninterrupted until the end of 1992. Since then breeding activity decreased, and varied more and more between months. There was a negative relationship between breeding activety and number of years since the transfer. For the first time since the transfer, an absence of breeding activity was observed at the end of April 1995. Monthly breeding activity on Aride in each individual year since the transfer did not show a relation with average monthly breeding activity on Cousin (logistic regression, range p-values 0.08-0.78), except in 1995 (p=0.03).
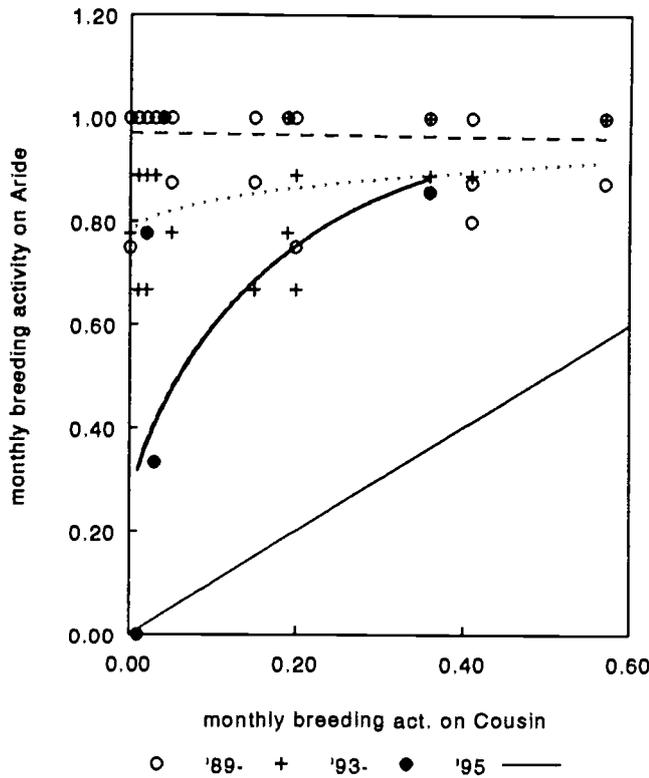
Fig. 8. Relation between monthly proportion of territories with breeding activity on Cousin (average from January 1986-September 1990, data from Komdeur 1991a) and monthly proportion of territories with breeding activity on Aride, in 1989-1992 (O)(5 ≤ n ≤ 8) (logistic regression: p=0.75), in 1993-1994 (+) (3 ≤ n ≤ 9)(p=0.19) and 1995 (●) (n=9)(ln(p/1-p)=-1.282+0.09x, p=proportion of territories with breeding activity on Aride, x=arcsine-transformed proportion of territories with breeding activity on Cousin (average from January 1986-September 1990 (data from Komdeur 1991a), p=0.03) (1995 own data, other Aride data from data files). Also plotted is the relation Y=X.

Fig. 8 depicts the relationship between monthly breeding activity on Aride and Cousin, for three subsamples: 1989-'92, '93-'94 and 1995. With time progressing, the relationship more and more resembles the breeding activity pattern of Cousin. The three groups significantly differ in elevation (p<0.005), and the 1995 data almost significantly interact with Cousin monthly breeding activity. The larger model, including the group differences and the interaction between Cousin monthly breeding activity and 1995 Aride monthly breeding activity, fits the data almost significantly better ($F_{1,65}$=3.984, p=0.06) than the smaller model, not including group and interaction effects.

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3.1.5. Occurrence of twins

Fig. 9 gives the percentage of twins for all successful nests (nests with at least one fledgling) after the transfer. This percentage is decreasing steadily. Territory quality may be a confounding variable, and the analysis was repeated for the first occupied territories (n=5), and all other territories, seperately. The decrease in twins in time is not significant for the old territories, and nearly significant for the newer territories (fig. 10). This is probably due to low sample size. The percentages of the 5 old territories are highly correlated to the percentages of the whole dataset (Spearman rank correlation: rs=0.99), indicating that the proportion of twins decreased in time for the average territory.
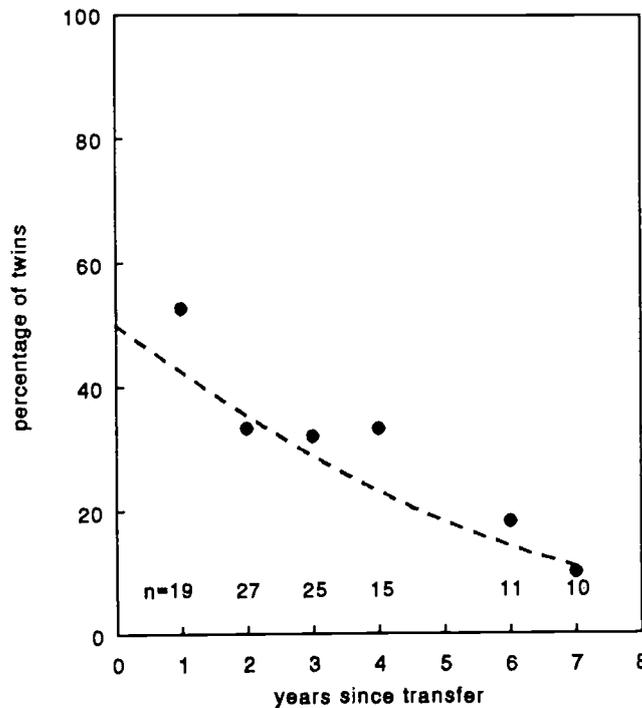
Fig. 9. *Yearly percentage of twins of all fledglings of Aride plateau territories since the transfer (logistic regression:* $\ln(p/1-p) = -0.299x$, *p=proportion broods with twins,* $x=years$ *since transfer,* $p=0.02$) *(data from Aride data files and own data).*
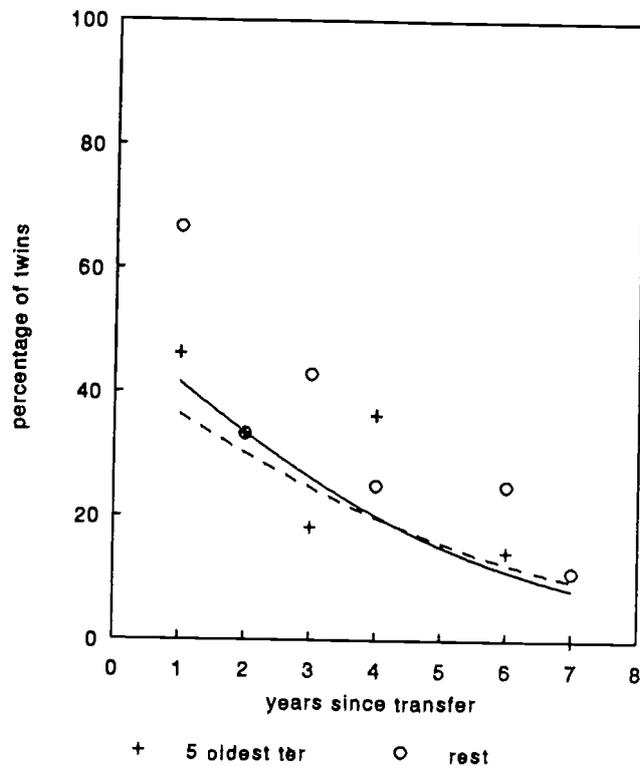
Fig. 10. Yearly percentage of twins of all fledglings of Aride plateau territories, divided in territories founded in first year (+) (logistic regression: p=0.15) and after the first year (0) (ln(p/1-p)=-0.344x, p=proportion broods with twins, x= years since transfer, p=0.054) since the transfer (data from Aride data files and own data).

3.1.6. Timing of moult

During this study, moult and breeding were clearly separated in females. In April, 0 out of 7 breeding females were moulting, wereas 17 out of 19 non-breeding females were moulting (Fisher exact test: p=0.00005). In June, with most females breeding, the situation had not reversed. 0 out of 20 breeding females were moulting, and 2 out of 3 non-breeders were moulting (p=0.01).

Males did not separate moult and breeding. In April 2 out of 4 breeders moulted, and 11 out of 18 non-breeders moulted (p=0.38). In June, there were no moulting males, and only 3 out of 21 birds were not breeding (p=1.0).

3.1.7. Sex ratio

Of the 170 young born on Aride between the introduction and July 1993, 50 have been sexed at the adult stage. Cumulative sex ratio of the young started out very skewed: a 100 % females (fig. 11). This skew quickly disappeared, and within one year after the transfer the cumulative sex ratio stabilized at about 50 %.

```
n(per)=  4 5  6  3        19      5       7

n(cum)=  4 9  15 18       37      42      49
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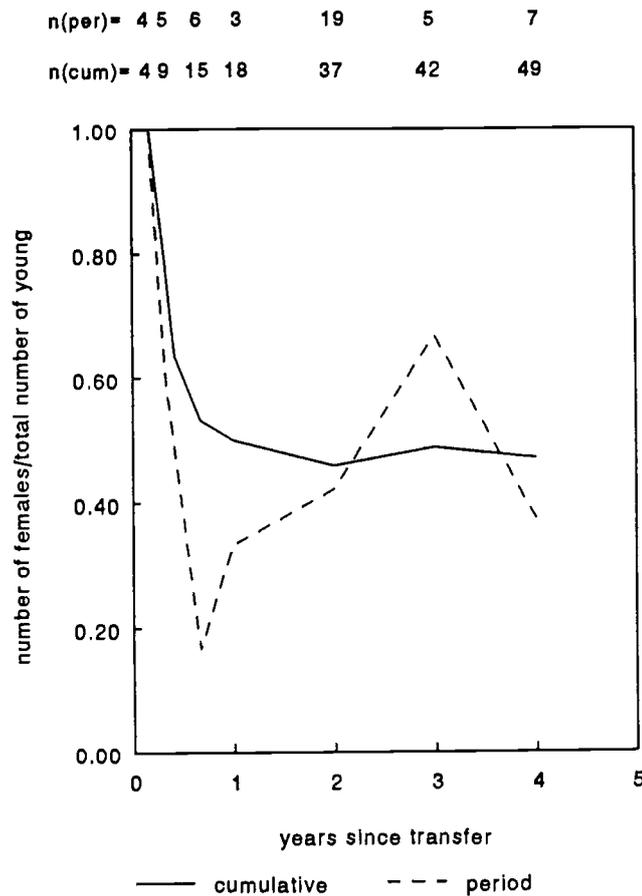

Fig. 11. Cumulative and periodic sex ratio (♀♀/(♂♂+♀♀)) of all sexed Aride fledglings since the transfer (data from Aride data files).

Using sex ratio data of seperate periods, and pooling periods with too little data, sex ratio seemed skewed in the first year after the transfer ($X^2=5.68$, $0.05<p<0.10$). Mostly females were produced just after the transfer (7 out of 9 in the first 4 months, binomial test: $p=0.09$), followed by a male skew (7 out of 9 in the next 8 months, binomial test: $p=0.09$). After that, sex ratio was not skewed (15 females out of 31 young, $X^2=0.0$, n.s.) (fig. 11).

In 1993, 5 out of 11 immatures sexed with PCR were male (binomial test, n.s.). In

1994, 5 out of 9 immatures were male (binomial test, n.s.). Lumping the two years yielded the same result: 10 out of 20 immatures were male (binomial test, n.s.).

Within territories, sex ratio did not differ (all n.s.). Territories with only male offspring, only female offspring and territories with offspring of both sexes did not differ in average territory size ($F_{2,6}=0.34$, $p=0.72$), present group size ($F_{2,6}=0.36$, $p=0.71$), age of territory ($F_{2,6}=1.51$, $p=0.29$) and number of months with helpers ($F_{2,5}=0.89$, $p=0.47$). There was no relation between territory sex ratio (number of males/total number of offspring) and average territory size, present group size, age of territory and number of months with helpers, or any combination of these variables (logistic regression, all p-values >0.05). These results did not change if only territories with more than one offspring were used ($n=5$).

3.2. Discussion and conclusions on the dynamics of Aride

Conditions on Aride have been very favourable to the warblers, as is shown by the steep population increase. However, already after a few years this increase slowed down.

Several aspects indicated a decrease in habitat conditions for the birds over the years. Breeding activity is no longer independent of season, the percentage of fledgling twins decreased almost to zero, and moult is recently separated from reproduction in females, as is the usual situation on Cousin for all aspects. This is a striking difference with the past situation on Aride. In the first year after the transfer, breeding was continuous, many twins were born and moult was not separated from reproduction (Komdeur et al. 1990).

These effects of the population increase on individuals are probably caused by a decrease in food availability to the individual, as all activities (breeding, feeding twins, moulting) are related to high energy expenditure (Drent & Daan 1980, Lindström et al. 1993). However, food availability for a single bird does not seem to be a function of bird density. Feeding rates still differed between the islands, but not between the years with little and many birds on Aride. It is concluded that food availability is mainly a function of island characteristics.

The observed slowing down of population growth is most likely linked to a decrease in reproductive success. Both breeding activity and the percentage twins were shown to decrease in time and this will result in less fledglings, (although this could not be shown for the plateau territories in the first 5 years after the transfer ($p=0.73$)). Most likely, a decrease in reproductive success is causally related to a decrease in average territory quality. With more birds present, all high quality habitat will be occupied, leaving habitat of lower quality. On Aride, the plateau is richer in food and this area was occupied first by the warblers (Jan Komdeur pers.comm., and map 2). Also, this area showed a much more obvious decrease in population growth due to saturation of the habitat, indicating a preference for this area.

More important, territory quality is related to size of the territory. The territories settled within a year after the transfer have more than halved in size, and newly settled territories are much smaller than the first settled territories. Both effects have led to a

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decrease in average territory quality of more than 50%. Both the proportion of twins and breeding activity were positively related to average yearly territory size (fig. 12).
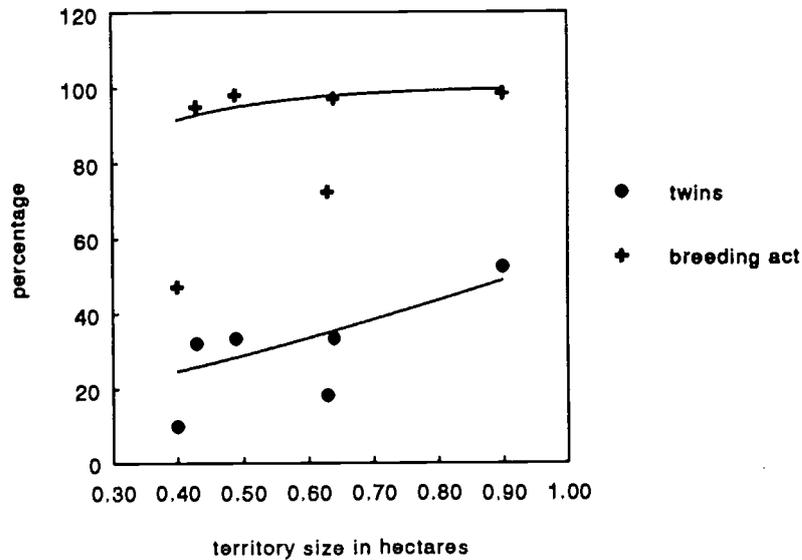
Fig. 12. Relation between yearly average territory size of all Aride plateau territories and yearly percentage of twins of all fledglings of Aride plateau territories (logistic regression: $ln(p/1-p) = -1.98 + 2.15x$, $p = 0.066$) resp. yearly average percentage of plateau territories with breeding activity $(+)(ln(p/1-p) = 5.89x$, $p = 0.002)$ (data on twins and breeding activity from Aride data files and own data, sample sizes as in fig. 6,7 and 9).

The lack of a skew in sex ratio of all plateau young or in the sex ratio of offspring of individual territories, indicates that parents do not (seem to) optimize fitness by adjusting the sex ratio of their offspring due to sex differential dispersal- and helping behaviour. Several explanations are possible, all indicating that the value of either sex to the parents is the same. The possible explanations are discussed with the (circumstantial) evidence from the Aride population.

1- there are still many vacancies for young birds, and both sexes have equal fitness expectations when either dispersing or helping. On Aride, the population is still increasing, and vacancies are still present. These vacancies will be of lower quality than natal territories, but possibly still sufficiently high (for some individuals) to justify dispersal over long-term staying (compare Komdeur 1992),

2- helping does not influence reproductive success of the parents. On Aride, the reproductive success of the warblers has dropped with the increase in numbers. In that case (worse breeding conditions), it is likely that helpers at the nest will be beneficial,

3- male and female have the same value as helpers to the parents.

On Aride, the effect of the sex of a helper on reproductive success of the parents is

unknown. However, the sex ratio of 14 sexed helpers was 0.57 (8 females out of 14 birds). This differs from the average sex ratio of 0.886 among helpers on Cousin ($X^2 = 10.78$, df=1, $0.001 < p < 0.005$), but not from an equal sex ratio ($X^2 = 0.07$, df=1, $0.70 < p < 0.90$). The probability of helping increases with age (Komdeur 1991a), and most male helpers were quite young. This indicates that the sex ratio of helpers nears equity, like the sex ratio of all immatures. This indicates that helping is as beneficial to males as it is to females, and a skew in offspring sex ratio is not advantagious to the breeder pair.

The effect of a partial habitat saturation on the behaviour of a potential helper is not easily assessed. On the one hand, areas of vacant habitat are becoming scarcer, smaller and of lower quality, decreasing the benefits of dispersal. On the other hand, indirect fitness (a major benefit of staying and helping) is also decreasing: reproductive success per helper in the natal territory decreases with a decrease in territory quality, and an increase in group size.

Komdeur et al. (1995a) (fig. 13) reviewed the occurence of helping on Aride. At first, exclusively HQT were settled. When all high quality habitat was occupied, two years after the transfer, MQT were settled, while at the same time first helping was observed on HQT. Both the number of MQT and the number of HQT with helpers increased, the latter up to a 100 %. After another year, virtually all medium quality habitat was occupied and LQT were fouded, while at the same time helping was observed in MQT. It became a common phenomenon in the years thereafter, with the number of LQT still increasing.
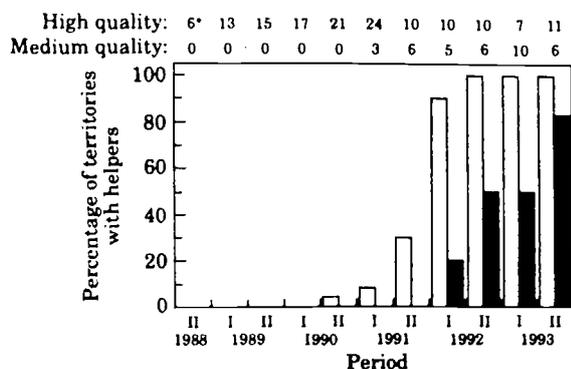
Fig. 13. Percentage of high- (open bars) and medium-quality (closed bars) territories with helpers on the unsaturated Aride island (I: January-June; II: July-December; 1988-1993). Top figures are number of territories which could have had helpers, because potential helpers and nests with young were present (*potential helpers from six territories on Cousin, which were transferred to Aride with their parents) (from Komdeur et al. 1995).

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This indicates that, due to changes in quality of available habitat, some birds stay and help, while others disperse and breed. Costs and benefits of either strategy probably vary between individuals.

Not much is known from the birds which have dispersed away from the plateau. But a more detailed analysis of the history of the plateau territories, their breeders, and remaining helpers and non-helpers might indicate the fitness benefits of birds that stay and help.
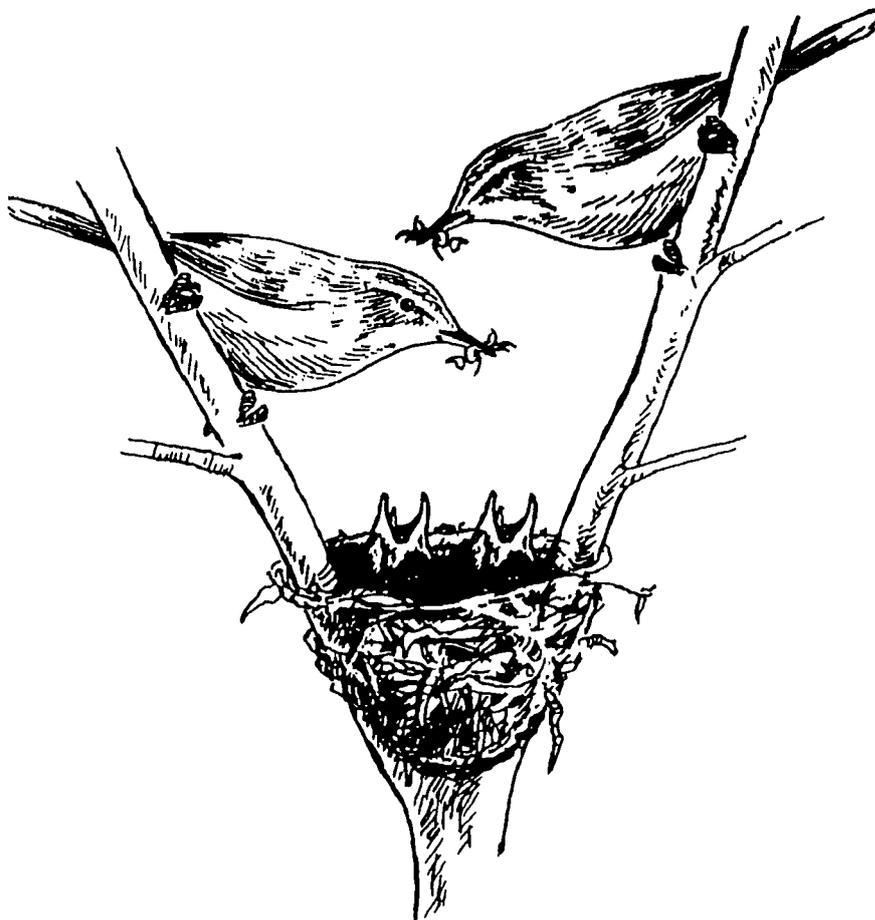
4. Helping benefits

4.1. Results

A) Territory inheritance and establishment

The probability to occupy a vacancy differed between resident and non-resident birds: of the 7 vacancies, 3 were taken by a resident (corrected for continuity, $X^2 = 5.53$, $0.01 < p < 0.025$). All resident birds that occupied a vacancy had been helpers, and none of the non-residents that occupied a vacancy was recorded to be a helper (exact probability test: $p = 0.03$).

Territories founded before January 1992 shared territory borders with 2.36 other territories. There was no difference between the probability of a bird of an adjacent territory or an immigrant bird to found a new territory ($n = 6$, $X^2 = 0.85$, $0.25 < p < 0.5$). Territories founded after January 1992 shared on average 2.5 borders with adjacent territories. A bird of an adjacent territory had a significant higher probability than an immigrant bird to found a territory ($n = 11$, $X^2 = 8.28$, $0.001 < 0.005$). This seemed true for both male and female ($0.05 < p < 0.1$, with $n = 4$ for males, $n = 7$ for females). Of the new territory founders of adjacent territories, 29% had been helper previously. None of the immigrant founders had been helper. This difference was not signficant (exact probability test, $p = 0.40$).

Territory sizes differed between territories founded in the first, second, third, and fourth or later years ($F_{3,19} = 5.70$, $p = 0.006$). Territories founded in the second year were larger than all other categories. The remaining three categories were undistinguishable in size (Newman-Keuls test, $p > 0.05$).

Within territories founded after January 1992 (fourth year and later), there was no difference in size between territories founded by males from adjacent territories and territories founded by males from elsewhere ($F_{1,9} = 0.01$, $p = 0.94$). However, newly founded territories with females from non-adjacent territories were larger than newly founded territories with by females from adjacent territories ($F_{1,9} = 4.87$, $p = 0.06$).

These differences in the effect of origin on size of the new territory between males and females effects were also found in the size of the old territory adjacent to the newly established one.

- Territories with adjacent new territories founded by males from adjacent versus non-adjacent territories did not differ before ($F_{1,7} = 0.99$, $p = 0.35$), did not change ($F_{1,4} = 1.34$, $p = 0.31$ and $F_{1,10} = 0.04$, $p = 0.85$ resp.) and did not differ after new territories were founded ($F_{1,7} = 0.46$, $p = 0.46$).

- Territories with adjacent newly founded territories with females from adjacent territories versus non-adjacent territories differed before the new territories were founded ($F_{1,7} = 11.47$, $p = 0.01$), but did not change in size ($F_{1,6} = 0.30$, $p = 0.60$ and $F_{1,8} = 1.92$,

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p=0.20 resp.). However, these changes in size differed between territories with newly founded adjacent territories with females from adjacent territories versus non-adjacent territories ($F_{1,7}=6.64$, p=0.04). After the new territories were founded, territories with adjacent newly founded territories with females from adjacent versus non-adjacent territories differed even more in size than before ($F_{1,7}=13.4$, p=0.008).

There was a strong correlation between change in size and the relative change in size (Spearman rank correlation: r=0.98, p<0.001). Therefore, relative changes in old territory size differed between territories with newly founded adjacent territories with females from adjacent versus non-adjacent territories (Mann-Whitney, U=17.5, 0.05<p<0.1).

The difference in the change in size between old territories with adjacent newly founded territories with females from adjacent or non-adjacent territories (0.09 hectares), is about the same as the difference in size between newly founded territories with adjacent or non-adjacent females (0.12 hectares). This indicates that founding a new territory with a female from an adjacent territory increases territory size, and this increase is at the expence of the size of the adjacent old territory. Indeed, there is no difference in total size of old plus new territories, between pairs with new territories founded by adjacent or non-adjacent birds (males: $F_{1,7}=0.03$, p=0.86; females: $F_{1,7}=2.25$, p=0.18).

Fig. 14 gives a graphical representation of territory sizes before and after the founding of a new territory.

B) Breeding experience

In table 2 the status of 23 former helpers on the plateau are summarized.

Table 2. Present status of former helpers on the plateau.

status	male	female	not sexed	total
breeder in natal territory	1	3	-	4
breeder in new territory	1	2	-	3
breeder in old territory	-	1	2	3
helper natal territory	3	1	-	4
missing ±	1	1	7	9
total number of birds	6	8	9	23
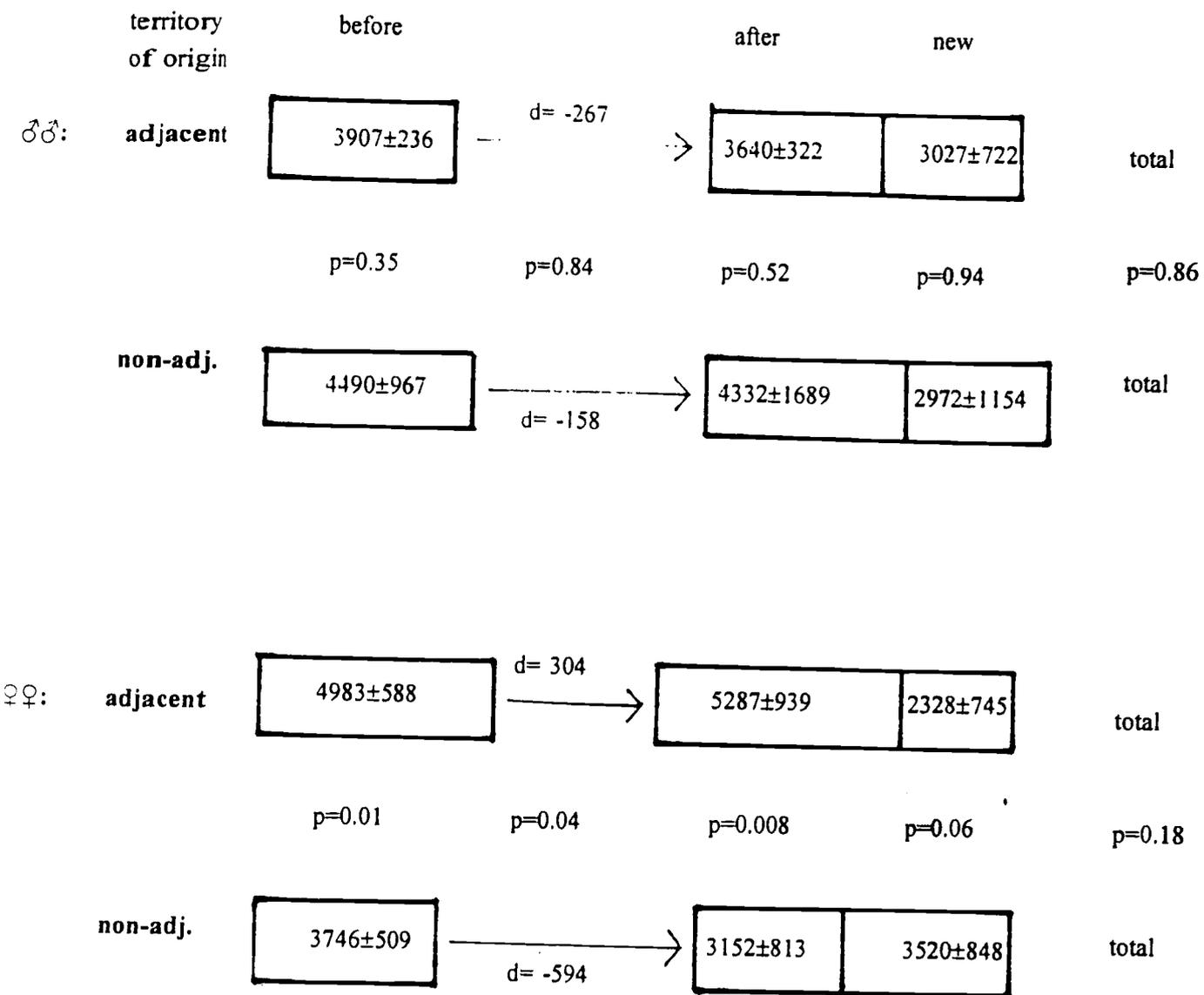
Fig. 14: old territory size before, change in size (d) of old territory, and size of old and new territory after the founding of a new territory, by a male or female from an adjacent or non-adjacent territory. Size (mean±sd) in m². Statistical differences between (changes in) sizes and size of old and new territory combined are given. Lenght of box on scale: 6 cm= 10,000 m² (1 hectare).

Females and males status seems to differ: females are mostly breeding, males are mostly helping. This difference however is not significant (exact probability test, p>0.15), therefore all birds are lumped. Moreover, any difference will be primarily due to the age of the males (the older females have attained breeder status after having helped for some time).

Of the helpers, status of 39 percent is unknown. These birds might be dead, but it is very much possible that they are looking for vacancies or are breeding outside the plateau. 17 Percent of the plateau helpers is still present as a non-breeder in the natal territory. These are all birds ringed after July 1993, and most birds are less than 2 years old. Probably, some of these birds will change in status in the future: either take over a vacancy nearby or disperse. 13 Percent has occupied a breeding vacancy in a territory outside the plateau. 17 Percent has taken over their natal territory and are now the dominant breeder (as shown before in section 4.1.A), of resident birds only helpers have been able to take over the natal territory). The final 13 percent are breeders now in new territories: 1 male founded a territory adjacent to the natal territory (with a female from another adjacent territory), 1 female occupied a vacancy in an adjacent new territory, most likely created by a male of unknown origin, and 1 female occupied a vacancy in a new territory outside the plateau.

C) Kinship and helping

Of 29 potential helpers (independent birds with nests or dependent young present in the same territory), 10 displayed some kind of helping behaviour (34%). Surprisingly, 2 out of 6 birds less than a year old helped: one of 4.2 months old and one of 4.4 months old.

Stepdown logistic regression of helping probability showed no significant effect of helper sex, territory size, territory age, number of recipients and relatedness (all p-values > 0.66). Age had a positive effect on helping status (age scored as <1 year, 1 year, 2 years, >2 years) (fig. 15).
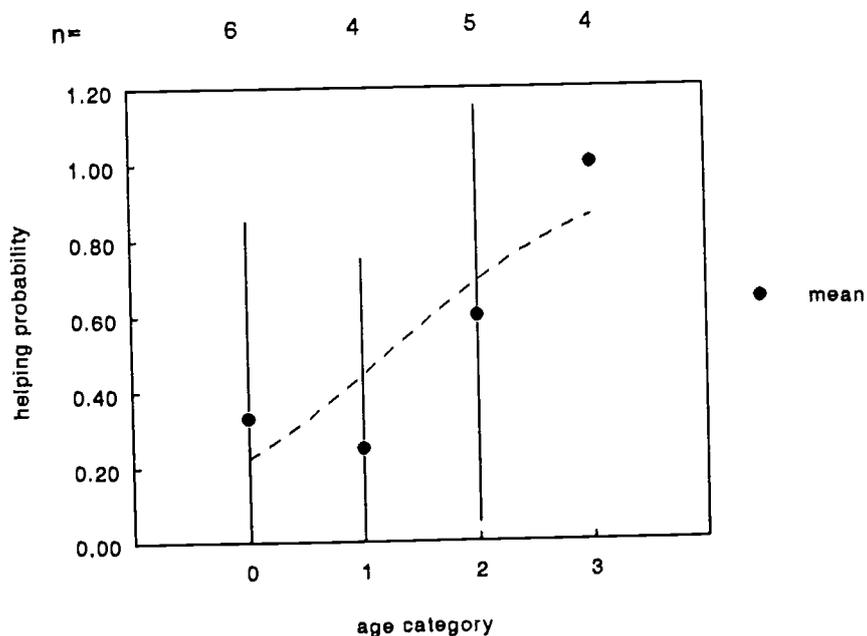
Fig. 15. Effect of age category (0=less than a year, 1=one year, 2=2 years, 3=older than two years) on the probability to be a helper (logistic regression: ln(p/1-p)=-1.251+1.025x, proportion of potential helpers helping, x= age category, p=0.047)(data from 1995, only birds with helping possibilities included).

Time spent incubating did not differ between helpers with relatedness 0.5 or 0.25 to the nestling ($F_{1,1}=1.31$, $p=0.46$). Also, number of feeds to the nestling did not differ between helpers with relatedness 0.5 or 0.25 to the nestling ($F_{1,3}=0.01$, $p=0.92$). Time spent incubating and number of feeds did not differ between helpers differing in other variables: age, sex and age of territory (Anova, all p-values >0.20), but all sample sizes were very small.

4.2. Discussion on helping benefits

A) Territory inheritance and establishment

The effect of differences in female origin on territory sizes is not an artefact. Effects were found on both territory size of the newly founded territories, as on territory size of the old adjacent territory, both before and after the founding of the new territory. These effects are independent of each other and leave little room for coincidence.

This is quite surprising. Komdeur (1991a) states that males initiate new territories first, and afterwards obtain mates, which enhances the growth of the newly established territory. Possibly the female plays a larger role in territoriality than realized before. In this study, more details on this subject are lacking.

Budding (the founding of a new territory starting on the natal territory) had virtually no effect on the size of the natal territory. On Cousin, this was not the case: initially budding happened at the expense of the natal territory size. Later on, neighbouring territories lost ground as well (Komdeur 1991). This indicates that the habitat on Aride was not yet fully saturated, and vacant habitat could be occupied. It is expected that in the future, when the Aride population has reached carrying capacity, increasing or founding a territory will have an effect on adjacent territories.

In females, territories with budding were larger than territories with an adjacent new territory founded by immigrant birds. One explanation could be that the dominant, territorial birds of a large territory 'allow' one or more of their offspring to found a new territory, starting on the natal territory. Birds from smaller territories are less inclined to do so, e.g. for reasons of competition, but are unable to defend a larger area, and immigrants will found new territories. In a saturating habitat, it will be advantageous to promote own offspring as territory owners of a potential new territory over immigrant birds, if the own territory is large. For a small territory, any new territory adjacent to the own territory will be disadvantageous.

Unfortunately, it is not possible to quantify fitness consequences of either behavioural strategy. There are hardly any data on the reproductive success of the newly founded territories, because these were not recognized until recently, and fledgling production was attributed to the older adjacent territories. Also, the reproductive success of offspring that have occupied territories away from the natal area, is not recorded any more. In general, the occupation of a high quality territory on the plateau by offspring from an adjacent territory

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is expected to be beneficial to the fitness of the offspring, and therefore to the parental fitness.

B) Breeding experience

There are two explanations possible for the 13 % of the former helpers that were first helping and later occupied empty habitat:

1- the habitat wasn't 'empty' in a strict sense, but new territories were created at the cost of others, and only after the vacancies existed could the helpers occupy them. This explanation can not be falsified, although earlier analyses showed very limited and no significant effects of founding a new adjacent territory on territory size of adjacent older territories, indicating that founding a new territory was relatively easy.

2- by helping, breeding experience increases, and experience has a positive effect on future reproductive success, enough to justify a delay in own reproduction. There is supporting evidence.

Two birds (9% of all helpers) were seen helping young in **adjacent** territories. If the relatedness between birds transfered from Cousin is assumed to be negligible and unknown to newborn helpers, the relatedness between the donor and the recipient is 0.25 (chick was aunt of helper), and 0.0 resp. The first helper dispersed afterwards and is now breeding outside the plateau, the second helper is still present in the natal territory. This helping behaviour indicates that even in the presence of low relatedness, helping could be beneficial. Expressed as Hamiltons rule (br-c > 0): helping exists, even though the benefits*relatedness are small and the sum of benefits*relatedness minus costs of helping is possibly even negative. Although costs of helping might be low (but see discussion), it is likely that other benefits, not included in Hamilton's equation, are present, enough to cause helpers to help outside the natal territory. Of the adaptive hypotheses presented in the introduction, only the increase in future reproductive success through increased breeding experience seems likely.

The occupation of empty habitat after a period of helping, and the helping of young of low relatedness on adjacent territories, strongly indicate a benefit of purely the act of helping. The only likely adaptive benefit of this behaviour is gaining breeding experience. In this study, no further data on the effect of helping experience on reproductive success are available.

In the same population, Komdeur (1995c) has shown a positive effect of helping on reproductive success. The reproductive success of birds with previous helping experience in the first year of breeding is as high as the reproductive success of birds with previous breeding experience. Inexperienced bird have a lower reproductive success in the first year of breeding. These effects are mainly caused by the better quality of the nest, and the allocation of more time to incubation (female) and nest guarding (male). Previous experience had a positive effect on mate fidelity. Both effects increase reproductive success when breeding, after the period of helping.

C) Kinship and helping
-Helping probability
Of all factors included in the analysis of helping probability, only age signficantly explained part of the variation. The same effect of age on the probability of helping was found on Cousin (Komdeur 1991a).

On Cousin only 3 out of 65 helpers helped in their first year, on Aride already 2 out of 6 birds younger than a year helped (exact probability test: p=0.09). None of these 6 birds have reached the age of one yet, and more birds might start helping in their first year of life. This will have a further effect on the difference in helping probability in the first year of life of potential helpers between Cousin and Aride. A difference in helping probability in the first year of life (when birds are immature and probably not physically capable of breeding) indicates a difference in the benefits (of various kinds) and costs (mainly determined by the environment as there are no cost of sacrificed independent breeding) between the islands. Compared to Cousin, on Aride the costs of helping are probably reduced because of a higher food availability. Several benefits will be increased. Probably a major one is indirect fitness, as the birds on Aride still produce more fledglings per territory than on Cousin.

There was no effect of relatedness on helping probability. Sample sizes were small (of 29 potential helpers only 10 were active helpers, and all but two potential helpers had a relatedness of 0.5), reducing the power of the analysis. On Cousin a large effect of kinship on helping was found. Unrelated birds never helped, and the same birds reduced the period of helping with 50 % if relatedness to the recipient decreased from 0.5 (full-sibs) to 0.25 (half-sibs)(Komdeur 1994c).

Size and age of the territory were included in the analysis as possible quality measures of the territory. Larger territories might be better, and the habitat where the first territories were founded were probably preferred. Both factors did not significantly explain a part of the variance. The same conclusion can be reached with data from Komdeur 1994c. Controlled for sex and relatedness, there was no significant difference between the proportions of helpers of medium and high quality territories (all corrected $X^2=0.0$, n.s.).

It is surprising to find that sex had no effect on helping probability. On Aride, 42.9 percent of all sexed helpers was male, and this is probably even an underestimate. Most protocols were done at nests in the building/breeding phase, when females are more likely to be scored as helpers. There is a difference in the proportion of male helpers between Cousin and Aride: on Cousin, 21 out of 184 helpers were male (Komdeur 1991a), on Aride 3 out of 7 helpers were male (exact probability test, p=0.044). However, controlling for relatedness, data of Komdeur 1994c also show no difference in helping probability between two and three year old males and females, when medium and high quality territories are lumped (corrected G (for r=0.5)=0.282, df=1, 0.50<p<0.75), corrected G (for

r=0.25)=0.035, df=1, 0.75<p<0.90). This indicates that the proportion of males of all helpers on Cousin is not influenced by the inclination of males to help (the proportion of males of all potential helpers), but by the skewed sex ratio of potential helpers. On Aride, this skew in sex ratio among potential helpers is absent (5 males of 12 sexed potential helpers: X^2=0.08, df=1, 0.75<p<0.90).

In contrast to this explanation, data from Komdeur 1991a do give a difference in helping probability between males and females. Of 29 two and three year old females, 24 were helper, and only 16 out of 40 two and three year old males helped (corrected X^2=47.85, df=1, p<0.001). A possible explanation for this descrepancy, is that in the latter sample birds from LQT are included, whereas the first sample consisted only of birds from MQT and HQT. It is possible that only in the LQT a difference in helping probability between the sexes exists. On the plateau of Aride, LQT are probably absent, and no effect of sex on helping probability is found.

-Helping intensity
No effects of relatedness, age, sex and territory size on helping intensity were found. This is due to sample sizes, and no conclusions can be drawn from the results. Komdeur (1994c) showed a large effect of relatedness on helping intensity: the same individuals reduced their helping efforts with 75% if their relatedness decreased from 0.5 (full-sibs) to 0.25 (half-sibs).

Apart from the relation between helping occurence and -intensity and relatedness, other observations support the hypothesis that helping can (partly) be explained by the positive effect of helping on the indirect fitness component.

First, in at least two territories (15 % of all territories with potential helpers), the dominant females are replaced by one of their daughters as the dominant breeder. This was indicated by the analysis of bloodsamples obtained in 1993 (analysis by Anique Kappe), and supported by field observations in 1995. These replaced females were both very active helpers at the nest, and shared incubation and feeding with the new dominant female. It is difficult to imagine other options open to the old females (maybe occupying a vacancy in another/lower quality territory). But it is somewhat amazing and in agreement with the indirect fitness hypothesis to see replaced breeders invest their energy in the last years of their life in rearing offspring of related birds.

Second, during three months of fieldwork in 1995, in 2 territories vacancies arose. One was filled by a male from a nearby territory, the other by an unringed bird of unknown origin. In both cases, all offspring that had stayed on the natal territory until then (1 resp. 2 or 3 unringed birds), disappeared. On all other territories with no such replacements and a groupsize larger than two, at least some (but usually all) offspring stayed (n=12, Fisher exact probability test, p=0.011). This is most likely a behavioural strategy of the offspring, and not a forced dispersal by the new breeder. Aggressive interactions between breeders and their or former breeders' offspring present in the territory were never observed (Komdeur

1991a, 1994c; own observations on Aride, Cousine and Cousin). The replacement of one of the parents by a non-related bird will reduce the indirect fitness benefits by half (relatedness from 0.5 for a full-sib to 0.25 for a half-sib), and possibly shift the behavioural optimum from staying and helping to dispersal with possible subsequent breeding.

However, one other adaptive hypothesis is in agreement with this observation. The occupation of an (expected) vacancy by another bird of the same sex will diminish the probability of occupying a vacancy in the natal territory in the near future. This will decrease the benefit of staying, and thereby promote dispersal. In this case, the sexes will differ in dispersal tendency. In a larger sample this hypothesis could be tested. Most likely, both a decrease in indirect fitness and a decrease in the probability to attain breeder status in the natal territory will contribute to the descision to disperse, after one of the parents is replaced by an unrelated bird.

Other helping benefits

Apart from the three benefits of helping which are presented and discussed so far, another benefit of helping was observed.

A bird of unknown sex, hatched in July 1993 on the plateau and helper in its natal territory, dispersed in October 1993. In February 1995 it was observed with 2 younger birds of its natal territory (one full-sib and one probable full-sib) and an unringed bird in a hill-territory. Usually, birds do not settle on a territory outside the natal one if they do not attain breeder status there (91% of all non-breeders of known descent were offspring of the (former) breeders). Therefore, most likely the three birds dispersed as a group and settled on either a vacant area or displaced the territory occupants. The observation of an unringed immature bird seems proof of successful breeding by one or more of the three dispersed birds, probably including the oldest one, the former helper.

Group dispersal (with possible reciprocal helping) has not been observed before in the Seychelles Warbler (Komdeur 1991a), and probably constitutes a rare behaviour (7% of all retraced helpers on Aride). In this one case, other options were limited. Earlier an older brother had budded off a part of the natal territory, and the former breeding female was replaced as a breeder by an older sister. More birds were present in the natal territory which could have acted as competitors for territory space and breeding vacancies. Even now, this territory holds most birds of all plateau territories (9 birds). Probably, the presence of many birds has facilitated dispersal as a group.

5. General discussion

Cost of helping

Discussing the behaviour of a potential helper must include the costs and benefits linked to helping. Some helping benefits have been discussed in the previous section. Costs of helping include the sacrifice of independent breeding, but also the effects of helping on the helper itself, like survival. Some helpers stop helping when the relatedness of the helper to the recipient decreases (which reduces the indirect fitness benefit of helping). This indicates that there are costs. A large cost will be the sacrifice of independent breeding. This cost will be a fixed one, only paid if a potential helper will help.

On the other hand, helpers also reduce their helping **intensity** if their relatedness to the recipient decreases. This strongly indicates that helping intensity is a trade-off between the costs and benefits of helping. In this case, linear models like Hamilton's rule (whether or not other benefits of helping are included) are not capable of explaning this observation. A model incorporating the relations between helping intensity and the costs/benefits of helping, with at least one of both being non-linear, will be more suitable for this purpose.

Corrected for age, sex and territory quality, survival (a potential non-linear cost of helping) does not differ between helpers and non-helpers (Komdeur 1994b). However, individual quality might differ between these categories, and obscure any effect of helping on survival. Identifying and quantifying additional costs of helping, aside from sacrificed breeding, would greatly improve the understanding of the behaviour of a potential helper.

Guarding behaviour

One of the few differences between the islands of Aride, and Cousin/Cousine, is the presence of Toq-toqs. These birds are very important egg-predators, and the absence of Toq-toqs on Aride might influence the guarding behaviour of the birds. In fact, in only a few protocols was guarding clearly observed. In all other cases, it was not clear whether birds were guarding or not. A lot of feeding and hardly any scanning was observed, and it proved to be impossible to accurately quantify guarding behaviour. During the one protocol of breeding on Cousine, it was very distinctive to see several birds non-stop near the nest, sitting and scanning, or at the most preening a little. During 2 hours, several Toq-toqs were chased away, and guarding seemed to be not superfluous. If a difference in predation probability does exist between the islands, this might affect both guarding intensity (a cost) and helping benefits (number of fledglings is less increased by guarding). In turn, this might affect the behavioural optimum of a potential helper, with a further complication if the sexes are influenced differently. With plans to (re-)introduce the Toq-toq to Aride (Peter Carty & Harriet Herzig pers.comm.), it will be most interesting to compare guarding intensity between the islands without and with an extra egg-predator.

Cobreeding/inbreeding

Apart from the adaptive hypotheses presented in the introduction, another may be formulated: by 'helping' a helper increases its direct fitness component through the production of **direct** descendents. In fact, the helper is not a helper any more but a cobreeder, and an increasing body of evidence suggests that many birds were mistakenly scored as helper in the past and are actually active reproducers. This will drastically alter the interpretation of their behaviour. It leads to the intriguing question if this is the result of parasitism by the 'helper' or that cobreeding is granted by the dominant breeders. Cobreeding creates an additional field of potential conflict between primary breeders and potential helpers/cobreeders, and between potential cobreeders.

Opposite to many other species, the Seychelles Warbler does not seem to show 'inbreeding avoidance'. Related birds, usually own offspring, are readily accepted as breeding partners, and were shown to have a significant higher probability to occupy a vacancy in the natal territory. This observation has several implications.

-The relatedness of the parents to the offspring increases. If a bird mates with one of it's offspring, the relatedness to the chick is 0.75 for both parents. Therefore, inbreeding increases fitness, if fitness is defined as the number of produced gene copies

-The relatedness of any resident helpers to the new offspring remains the same: 0.5. There are no direct effects of inbreeding on helping (Hamilton's rule). But helping increases the probability to obtain an incestuous vacancy on the natal territory, which increases fitness. In turn, this increases the benefits of helping. Thus, the lack of inbreeding avoidance stimulates the evolution of a cooperative breeding system

-Inbreeding may have negative effects on the condition of the offspring, as rare recessive genetic aberrations are more likely to be transmitted to the offspring by both parents. Effects of inbreeding on offspring viability in the Seychelles Warbler are currently studied. Negative effects of inbreeding on fitness will influence the trade-off between dispersal and helping for a potential helper.

-Inbreeding may have an effect on genetic variation, which could have implications for the viability of the (sub)populations. Initial analyses showed a surprisingly large genetic variation within the different island populations, and significant differences between the islands (pers. comm. Anique Kappe). The historic development of (differences in) genetic variation and the role of inbreeding are currently under study.

In the Cousin population, males are much more prone to disperse than females. Three possible explanations came to mind:

-a female is able to give more help (nestbuilding, guarding, breeding, feeding) than a male (mainly guarding and feeding) (supported by the fact that moult and breeding are separated in females but not in males, indicating a higher energy allocation to reproduction in females). The allocation of the females time and energy to helping instead of independent breeding will have a larger positive effect on its indirect fitness than for a male. This might

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shift the behavioural optimum for females from dispersal to staying and helping,

-females benefit more from the gaining of breeding experience. In both males and females helping experience increases the number of independent young of the first independent breeding attempt (Komdeur 1995c). In females, helping experience increased the production of independent young of the first reproductive with 1.0, opposed to only 0.76 in males. There was no difference between the production of independent young in the first breeding attempt by males or females with helping experience ($t=1.26$, $df=16$, $0.50<p<0.20$), but females without helping experience produced less independent young in their first breeding attempt than males without breeding experience ($t=3.01$, $df=15$, $0.01<p<0.005$) (data from Komdeur 1995c, Table 3).

-females are more likely to become cobreeders than males. Of offspring sampled on Aride in 1993, 1 out of 14 young was not fathered by the putative father, and 7 out of 16 young were not mothered by the putative mother (exact probability test: $p=0.03$) (data by Anique Kappe). Being a cobreeder in the natal, high quality territory increases fitness in multiple ways: in a high quality territory reproductive success is high, and through inbreeding fitness increases.

If the same is true for the Cousin population, this could explain the skew in sex ratio in that population. On high quality territories, reproductive success increases with the number of helpers, which are mostly females, and the fitness expectations are higher for female offspring.

If females, having XY sex chromosomes in birds, manipulate offspring sex ratio, they create their own breeding competitors. Modelling differences in fitness effects of different sex ratios between males and female parents could indicate if a conflict (different optimal sex ratio) exists between the breeding partners.

Much more data on exact relatedness and cobreeding must be collected. Combined with modelling effects of cobreeding on the fitness of all envolved individuals, this could have a very significant impact on the cooperative breeding system of the Seychelles Warbler as we know it today.

The importance of relatedness for explaining helping behaviour

Of the adaptive hypotheses presented in the introduction, only two refer to Hamilton's idea that helping increases indirect fitness. This and other studies have identified other benefits of helping, and the conclusion can be drawn that Hamilton's rule does not have to be the sole explanation for helping. In many cases positive effects of helping on future direct fitness are possible.

In order to compare the two gains (direct and indirect), Vehrenkamp (1979) derived an index that can be used to evaluate the relative importance of the two. Up till now, only a small number of species have shown to be completely 'altruistic' in the Hamiltonian sense: with only indirect fitness benefits of helping. The more usual situation is a mixture of

positive effects of helping on both indirect and direct fitness (Emlen 1990). This is true for the Seychelles Warbler.

Modelling dispersal and helping

The actions of a potential helper could be subdivided into a two-step procedure(see Introduction): 1) stay or leave, 2) help or not. However, to my opinion, a potential helper has 4 simultanious options:

      1-disperse but do not breed

      2-disperse and (try to) breed

      3-stay but do not help

      4-stay and help

The optimal choice will be determined by the costs and benefits of each. These costs and benefits might be influenced by the steepness of the habitat gradient (e.g. very little marginal habitat present), and by the social and reproductive system of the population (which is partly the outcome of the adaptation on an evolutionary scale on, again, the habitat). This makes the delayed-dispersal threshold model of Koenig et al. (1992, in: Emlen 1994) applicable, with some modifications.

The slope of each fitness curve and the fitness obtained at a certain territory quality are influenced by both habitat and competitors: if suitable habitat is restricted and saturated, the slope in the middle part of the graph will become steeper and dispersal will be limited. If fitness benefits of helping (both direct and indirect) are small (e.g. when there are already helpers present in the territory), dispersal will be more common. Every individual will estimate the fitness obtainable at the present territory quality for each strategy (helping or not), and compare this with the fitness obtained with the other strategies (breeding or not) in the new territory quality, and will adopt the behavioural strategy that maximizes fitness. No doubt, these fitness curves differ between individuals and that makes generalizations and testing of predictions more difficult, and sometimes impossible, as not all manipulatons will be possible in the field (e.g. make a floater breed in a low quality territory within the same population). But others are and there is still a lot of scope for further work, both theoretically and in the field, into identifying the importance of any parameters on the breeding system of cooperative breeders.
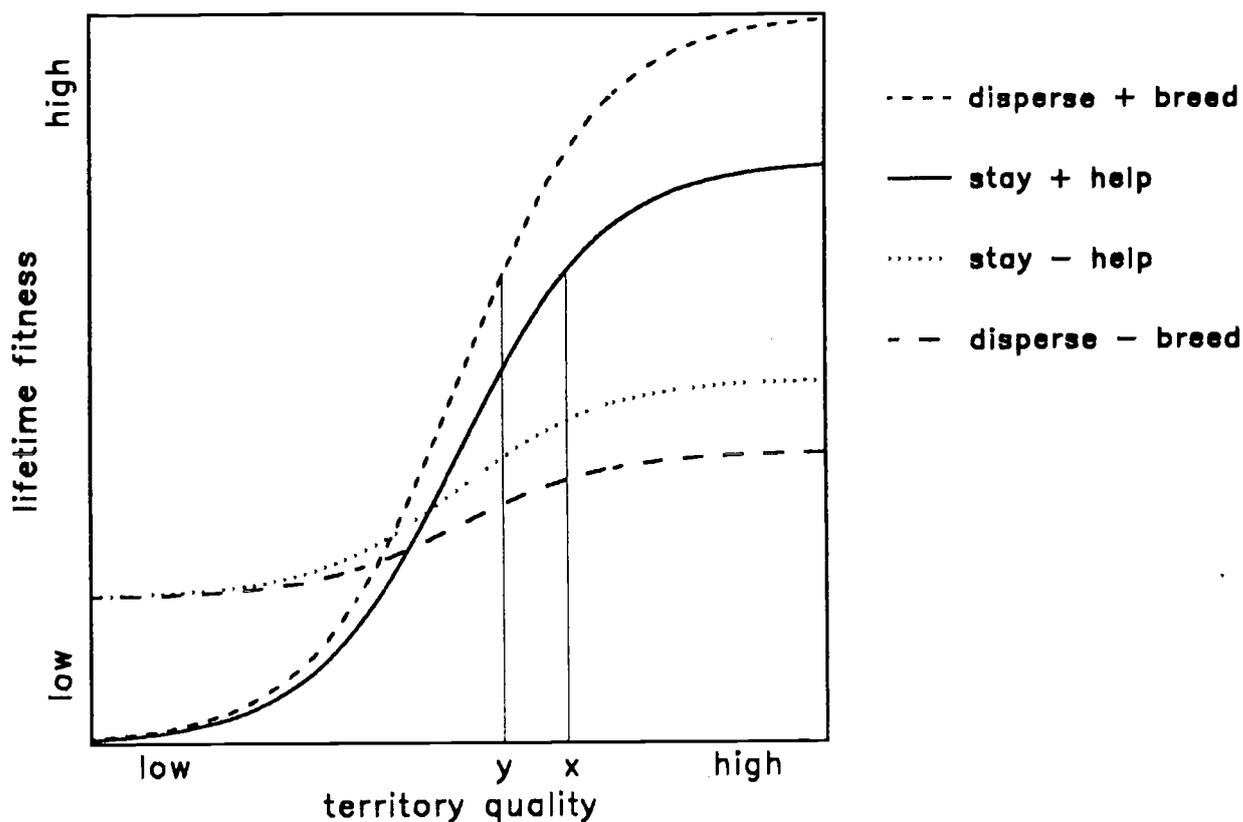
Fig. 16. The delayed-dispersal threshold model (modified after Koenig et al. 1992). The lifetime fitness of any of the four reproductive strategies is hypothetically influenced by the quality of the territory in which it is performed. The strategies are defined for offspring after reaching independence. Disperse + breed: occupy a territory and commence with breeding. Stay + help: delay dispersal and help other birds in rearing offspring. Stay - help: delay dispersal but do not help. Disperse - breed: disperse but do not try to breed instantly ('floating'). In low quality territories, breeding impinges on fitness. In high quality territories, reproduction will increase fitness.

When reaching independence, each individual estimates the fitness in relation to the quality of the territory for every strategy. In this case, a bird born on a territory with quality X, will disperse and breed if a breeding vacancy is present in a territory with a quality higher than Y. If only territories of a quality lower than Y are present, its fitness is higher if it delayes dispersal and helpes. For this individual, the delayed-dispersal threshold is territory quality Y. The effects of other factors than territory quality influencing fitness are discussed in the text.

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7. Appendices

7.1. Nesting heights (n=30) in different tree species, Aride, February-June 1995.

Treespecies	Old nests	New nests
Pisonia grandis	4-3-10-3	10-3-12-6-2-10-3-10
Euphorbia pyrifolia	3	8-4-5-4
Calophyllum inophyllum	6	8
Citrus sp.	3	3-4
Bamboo sp.	3	4
Cordia subcordata	7	
Ficus small leaved	8	
Ficus large leaved		11-5
Coconut		9-7

7.2. List of all Birds present on Aride plateau territories, April 1995: Aride number, colour code, territory of ringing (Rterr), sex, age, present territory (Pterr: see map 3) (underlined birds are bloodsampled; xx=no Aride number given yet; ur=unringed; *=missing in June 1995; ¹=ringed in June 1995, colour codes are 'upper-lower' ring; x=metal ring; ()=colourring lost; colour-colour=split-ring, C=bird of transfer; ringed on Cousin, age x+=x or more than x years old (ringed as fullgrown adult), F=fledgling.

number	colour rings left	right	Rterr	sex	age	Pterr
182	db/bk	r/x	18	f	4+	18
220	r/x	lb/r	45	f	2+	18
228	r/x	db/db	18	m	2+	18
303	v/x	v/bk	54	f	1+	18
385	r/lb	v/x	18	f	1+	18
386	v/lb	v/x	18	-	F	18
ur	-	-	-	-	F	18
16	dg/x	db/db	C	f	8+	16
20	dg/x	r/r	c	m	8+	16
145	x	o/lg	16	f	4	16
210	lg/lg/	lg/x	16	m	3+	16
249	r/x	bk/o	16	-	1	16
243	bk/y	bk/x	16	m	2+	16

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252	r/x	w/v	16	-	1	16
<u>397</u>	db/o	v/x	16	-	1	16
<u>398</u>	bk/w	v/x	16	-	1	16
<u>xx</u>[1]	bk/r	v/x	16	-	F	16
<u>5</u>	dg/x	db/(o)	C	f	8+	4
<u>6</u>	dg/x	bk/o	C	m	8+	4
<u>217</u>	w/lb	lb/x	4	-	1	4
<u>224</u>	r/x	lg/r	4	f	2	4
<u>226</u>	r/x	o/bk	4	-	2	4
256	r/x	r/db	4	-	1	4
<u>306</u>	v/x	db/lb	4	-	1+	4
ur	-	-	-	-	F	4
<u>xx</u>[1]	v/r	v/x	4	-	F	4
65*	r-dg/x	o/y	4	m	6	37b
<u>131</u>	v/db	x	3	f	4	37b
<u>207</u>	w/v	lg/x	7	f	2+	37b
<u>213</u>	bk/dg	lg/x	4	m	2+	37b
246	r/x	lb/lb	37	-	1	37b
<u>389</u>	r/v	v/x	37b	-	F	37b
<u>xx</u>[1]	w/r	v/x	37b	-	F	37b
<u>206</u>	dg/lb	lg/x	4	f	2+	T-new
<u>205?</u>	lb/w	lg/x	4	m	2+	T-new
<u>208</u>	bk/lg	lg/x	16	f	3+	37t
<u>215*</u>	dg/r	lg/x	37	m	3+	37t
<u>323</u>	v/x	v/lg	37	m	1+	37t
<u>390*</u>	v/v	v/x	37t	-	F	37t
248	r/x	lg/o	7	m	1	37t
98*	x	lg/y	3	-	5	7west
<u>235</u>	r/x	lb/bk	7	m	2+	7west
255	r/x	db/lg	7	f	2+	7west
<u>xx</u>[1]	lg/r	v/x	7west	m	1	7west
<u>xx?</u>[1]	o/r?	v/x?	7west?	f?	1+?	7west?
<u>87</u>	x	dg/r	4	m	5	39old
<u>221</u>	r/x	v/r	45	f	2+	39old
225	r/x	o/r	45	f	2+	45
<u>322</u>	v/x	r/lg	45	m	1+	45
164	x	r-w	11	m	5+	11
<u>222</u>	r/x	v/bk	45	m	2	11
<u>320</u>	v/x	r/o	11	f	1+	11
<u>321</u>	v/x	db/v	11	f	1+	11

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ur	-	-	-	-	-	11
17	dg/x	w/(o)	C	m	8+	10
399	lb/o	v/x	10	f	1+	10
133	lb/o	y/x	23	m	4	3inl.
227	r/x	o/db	3	f	2+	3inl.
ur*?	-	-	-	-	-	3inl.
ur*	-	-	-	-	-	3inl.
ur*	-	-	-	-	-	3inl.
48	x	dg/lb	10	m	6	23
141	x	dg-r	23	f	-	23
388	w/lb	v/x	23	-	F	23
xx[1]	lb/r	v/x	23	-	-	23
146	x	v/dg	4	m	4	23gap
244	v/lb	w/x	23	f	2+	23gap
ur	-	-	-	-	-	23gap
ur	-	-	-	-	-	23gap
180	y/dg	r/x	23	f	4	39marsh
239	r/x	lg/bk	39	m	2+	39marsh
ur	-	-	-	-	F	39marsh
12	dg/x	lb/y	C	m	8+	7east
242	p/p	bk/x	5	f	2	7east
161	x	v/o	4	f	4	Jacq's
325	v/x	o/o	39	m	1+	Jacq's
ur	-	-	-	-	-	Jacq's
40	x	w/lb	10	m	6	19
50	x	db/w	3	f	6	19
ur	-	-	-	-	F	19
192	lg/y	lg/x	19	f	2	3coast
254	r/x	db/lb	19	m	2+	3coast
ur	-	-	-	-	F	3coast
253	r/x	v/lb	19	-	1	3coast
80	x	db/o	3	m	5	3gap
201	lg/db	lg/x	3	f	2+	3gap
173	lb/db	r/x	3	m	4+	23coast
212	db/dg	lg/x	23	f	3+	23coast
390	w/v	v/x	23	-	F	23coast
178	db/lg	r/x	16	m	4+	pigsty
240	r/x	lg/w	23	f	1	pigsty
324	v/x	lg/o	39	m	1+	lodge
ur	-	-	-	f	-	lodge

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7.3. The Seychelles Warbler on Cousine, 1-25 May 1995

The first weeks were spent checking the entire island, excluding the west-side of the north hill (*Pandanus* sp. stand), for territories, warblers and nests. Every 50 m. or so, a loop-tape with warbler song was played for about 1 minute. Also, inbetween song-bouts and afterwards, 'pishing' noises were made. When no warblers were attracted or noticed, the search was continued. Otherwise the birds' colourrings (if present) were read and tailmoult scored. If the bird was known or expected to be the dominant female, it was followed for 30 minutes to check for breeding activity. In case of the presence of a nest or young and more than 2 adults in the territory, a 2-hour protocol of brooding/feeding was made. On 5 days, birds were trapped using at maximum 3 mistnets and looptapes. Nets were checked regularly, and sometimes the taperecorder was switched off to renew the stimulus.

Results
Numbers
At least 77 different birds were identified, and approximately 7 more unringed birds of uncertain territorial status were encountered. Repeated visits to the same spots during this period yielded a very consistent picture. It is therefore believed that over 90% of all birds were identified in the studied area. A further 15 birds are estimated to be present on not visited parts of the island, and wanderers. This gives an estimated ppulation size of 105-110 birds. The Cousine population has almost 4-folded in 5 years.

No doubt, relative growth of the population will be less now then in the early stages of the introduction, but there is still scope for a higher population-total. Especially the southern end of the island seems underpopulated, and as the population grows, more birds will stay on there natal territory, thereby increasing the density of birds. My guess is a population total of near 250, more if the vegetation management on the plateau is successful in terms of warbler habitat.

Survival
Of the 29 introduced birds, 10 were seen. This gives an annual adult survival of 80.2% (4.83 root of 10/29). This is very close to the Cousin figure of 83.5% (Komdeur 1991). However, as adult survival was significantly higher than on Cousin right after the transfer (100%, Komdeur 1995), adult survival now must be less than 80.2 %, and is therefore, relative to Cousin, quite low. Of birds ringed in July 1994 (26), 17 were seen, which yields an annual survival of 60.7%. This however includes young birds. Those have a higher mortality rate (50.3%/year, after independence, Komdeur 1991), and therefore this figure constitutes an intermediate beween 50.3 and 80.2%.

On the other hand, it was found that many territories had 1 or more new territory owners, or other birds were missing, or the territory was missing altogether. This means that territory-occupancy is still very dynamic, which might be partially caused by a relatively high

mortality for unknown reasons. Following the remaining 10 transfer-birds (or a larger subsample of adults) might clearify if mortality is indeed higher than on Cousin. As territory owners don't disperse any more, only the 9 territories with old birds need be checked annually (or more regular). By recording groupsize at the same time, the filling-up of the habitat too can be recorded.

Groupsize

Plotting current groupsize against groupsizes of last year shows a plateauing at 4: only small groups have grown, and all groups larger than 4 last year are sized 4 now. At the moment, groupsize is 3.20-1.25 (mean plus standard deviance). This is significantly higher than groupsize on Cousin low quality territories (t-test, $t=13.9$, $df=384$, $p<0.001$), and inbetween groupsizes of medium and high territory quality (Komdeur 1991). This indicates:
1- Cousine is of better quality than Cousin, and/or
2- lower quality habitat is not yet occuped.

Reproduction

Breeding activity was 33.3%: in 24 territories (several new ones, see map 3.) 7 fedglings were seen and one nest was found, containing 3 eggs. All hatched 21/22 May, and on 25 May were still present. Breeding activity was higher than is usually the case on Cousin during the same period (20%), but did not differ significantly. Breeding and moulting were not significantly seggregated from each other ($X2=1.45$, $df=1$, $0.1<p<0.25$), which also indicates a more favourable breeding-situation than on Cousin, were moult and breeding are seggregated.

Literature:

- Komdeur, J., 1991. Cooperative breeding in the Seychelles WArbler. Thesis, Cambridge University, England.

- Komdeur, J., 1995. Transfer experiments of Seycheles Warblers to new islands: changes in dispersal and helping behaviour. Anim. Behav. 49: 695-708.

-List of all Cousine Warblers (underlined birds are bloodsampled, codes are 'upper/lower' ring, see map 4. for territories)

number	colourcode left	right	sex	age	territory 90	91	94	95
1	y/y	y/x	m	6+	6			
2	o/o	y/x	f	6+	3	1	1	1
3	db/db	y/x	f	6+				
4	lb/lb	y/x	f	6+				
5	bk/bk	y/x	f	6+				
6	r/r	y/x	m	6+	5	5		
7	v/v	y/x	m	6+		20		20
8	w/w	y/x	f	6+		14		
9	lg/r	y/x	m	6+		9	9	9
10	dg/dg	y/x	f	6+	9	10		10
11	w/bk	y/x	f	6+	5	5	5	
12	r/bk	y/x	f	6+		13		
13	lb/r	y/x	m	6+			11	11
14	db/w	y/x	m	6+				
15	v/bk	y/x	f	6+	A	9		
16	db/o	y/x	f	6+	10			
17	y/db	y/x	m	6+	8	8	8	
18	v/o	y/x	m	6+	2	1	1	
19	ow	y/x	m	6+				
20	o/bk	y/x	m	6+	B	1?		
21	o/dg	y/x	f	6+	10	10	10	10
22	r/y	y/x	m	6+				
23	bk/y	y/x	m	6+		20		
24	dg/y	lb/x	f	6+		19	19	19
25	dg/w	lb/x	f	6+	7	15		3/15
26	y/dg	lb/x	m	6+	8	8	8	8
27	r/dg	lb/x	f	6+	1			
28	r/w	lb/x	m	6+	3	14		
29	bk/dg	bk/x	m	6+		13		
30*	w/lg	r/x	m	2+			1	1
31	bk/w	r/x	m	2+			3	3/15
32*	bk/bk	r/x		1			3	
33*	bk/bk	r/x	m	2+			5	
34	lg/lg	r/x		2+			5	5
35	bk/r	r/x	f	2+			10	10

36	bk/db	r/x	f	2+		10	
37	p/p	r/x	f	2+		10	10
38	bk/p	r/x	f	2+		10	11
39	w/p	r/x		1		10	
40	p/w	r/x		1		11	9
41*	w/w	r/x		1		12	
42	lg/p	r/x		2+		12	
43	y/p	r/x		2+		12	
44	db/p	r/x	f	2+		13	
45	p/bk	r/x	m	2+		13	13c.
46	p/lg	r/x		1		14	
47	y/y	r/x	f	2+		16	sapp
48*	w/lg	r/x	f	2+		16	16
49	y/lg	r/x	m	2+		16	16
50	db/db	r/x	f	2+		16	16
51	lg/bk	r/x	f	2+		17	17
52	w/db	r/x	m	2+		17	17
53*	w/w	r/x	m	2+		18	18
54	w/y	r/x	f	2+		19	19
55	y/bk	r/x	f	2+		19	19
56	r/w	r/y/x	m	4.5+	21	21	21
57	dg/dg	r/y		4.5+	21	21	21
58	lb/lb	r/y		4.5+	10		x
59	r/r	r/y		3.5	10		
60	lb/y	r/r		3.5	13		
61	o/db	v/x		1			3/15
62	r/bk	v/x		1			16
63	r/lg	v/x		1			sapp
64	r/r	v/x		1			spoint
65	r/lb	v/x		1			sapp
66	r/v	v/x		1			sapp
67	lg/r	v/x		1			spoint
68	r/w	v/x		1			sapp
69	lb/lb	v/x		1			11
70	lb/r	v/x		1			11

*: most unfortunately, there are three pairs with identical colourrings:
- 30 & 48 (w/lg r/x)
- 32 & 33 (bk/bk r/x)
- 41 & 48 (w/w r/x)

-Territory and occupants (see map 4.)

(terr. number: Cousine warbler numbers, plus unringed, F=fledgling)

1: 2-30-ur-urF
3: 25-31-61-ur
5: 11-34
8: 26-ur-ur
9: 9-40-ur
10: 10-21-35-37
11: 13-38-69-70-urF
"12": 32 or 33-ur
13central: 45-ur
13south: ur-ur
14: fused with 12?
15: fused with 3?
16: 48-49-50-urF
17: 51-52-ur-ur
18: 53-ur
19: 24-54-55-ur-ur-urF
20: 7-ur-urF
21: 56-57
U: ur-ur-urF
V: ur-ur-urF
W: ur-ur-ur
X: 58-ur
Y: ur-ur
Z: ur-ur
Savannah point: 47-64-ur-ur-ur-ur (afterwards some ringed)
Savannah appartments: 63-65-ur-ur (afterwards some ringed)

7.4. Measurements on Turtle Doves (*Streptopelia picturata picturata* X *S. p. rostrata*)

wing	tarsus	head+bill	crowncolour	moult b	w	t	rings right
163	27.5	48.2	P-G	+	-	-	
158	29.2	49.6	G	+	-	-	
160	29.5	49.8	P-G	-	-	-	dg/w
163	29.5	51.3	G	-	-	-	
164	28.4	50.6	G	+	+	+	
164	28.8	51.6	P-G	+	-	-	
166	29.2	49.9	G	+	-	-	
162	31.7	49.2	P-G	+	-	-	
158	27.5	49	P-G	+	+	-	
165	29	49.9	G	+	-	-	b/g
158	29.3	49.3	G	+	+	+	
156	27.3	48.9	G	+	-	-	
161	28.3	50.3	B	+	-	-	

(all measurements in mm.; crown: P=purple, G=grey, B=brown; moult: b=body, w=wing, t=tail, +=present, -=absent; rings only on right leg; all birds were bloodsampled)

7.5. Measurements on Seychelles Sunbirds (*Nectarina dussumieri*)

winglenght	sex	moult body	tail	wing	site	colour rings left	right
63.0	m	+	-	-	V	o/v	-
58.5	f	-	-	-	V	o/w	-
59	f	+	-	+	V	o/lb	-
59.5	f	+	+	-	11	lb/lb	-
61	m	+	-	+	11	lb/r	-

(sites are the Warbler territories as located on map 4., no metal rings)

7.6. Measurements on Seychelles Fodies (*Foudia sechellarum*)

colourrings			moult				
left	right	sex	b	t	w	wing	tarsus
o/w	-	m	-	-	-	73	19.1
o/r	-	-	-	-	-	69.5	19.7
o/lb	-	m	+	-	+	75.5	20.8
o/db	-	-	-	-	-	70.5	19.5
o/bk	-	-	-	+	+	68	19.7
lb/lb	-	-	-	-	-	68.5	19.9
lb/r	-	-	+	+	+	67.5	20.2
o/v	-	-	-	-	-	68	20
lb/v	- *	-	+	+	+	68.5	20.4
lb/o	-	-	+	-	+	70	20.4
lb/w	-	-	-	+	-	71	20.5
lb/lg	-	m	-	-	-	72	20.1
lb/bk	-	-	+	+	+	69	19.6
w/bk	-	m	-	-	-	74	20.6
w/lg	-	-	-	-	-	72.5	20.6
w/r	-	-	-	-	+	-	20.8
w/lb	-	m	-	-	+	75	20.8
w/v	- *	-	-	-	-	71.5	19.1
w/w	-	-	-	-	-	70.5	19.1
r/v	-	m	-	-	-	72	19.9
r/w	-	m	-	-	+	73.5	19.3
r/r	-	m	-	-	-	73.5	20.3
r/lb	-	m	-	-	+	73	20.2
r/db	-	-	-	+	-	70	20.6
r/bk	-	-	-	-	-	70	20.1
lg/v	-	-	+	+	+	68.5	20.4
lg/w	-	m	-	-	+	73	20.3
lg/r	-	m	+	-	+	73.5	21
lg/lb	-	m	+	+	+	73	20.2
lg/db	-	-	+	+	+	66.5	20
lg/bk	-	m	+	-	+	73.5	20.8
lg/lg	-	-	+	-	+	72.5	20.2
w/v	- *	-	-	-	+	65.5	18.3
lb/v	- *	m	-	-	+	75	20
v/w	-	m	+	-	+	75	21.1

60

v/lb	-	-		-	-	-	64.5	19.9
v/lg	-	-		-	-	-	72	20.4
v/v	-	-		-	+	-	69	20.6
v/r	-	-		-	-	-	71.5	18.9
v/db	-	-		+	+	+	71	20.3
v/bk	-	m		+	-	+	74	19.9
bk/w	-	m		+	-	-	76	20.5
bk/lb	-	-		+	+	+	67	19.6
bk/lg	-	m		+	-	+	75	20.4
bk/v	-	-		+	+	+	67.5	20.1

(sex: only birds with some yellow on the head are sexed as males; all other birds are females/immatures/non-breeding males; all birds were bloodsampled)
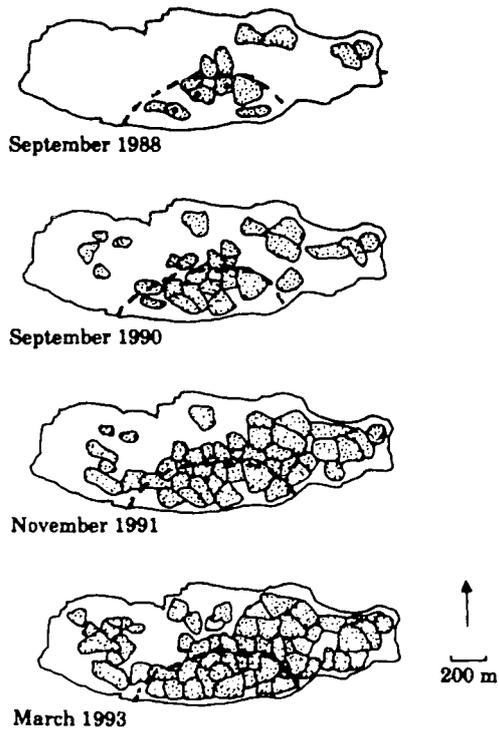
*: 2 pairs of birds received the same colourrings:
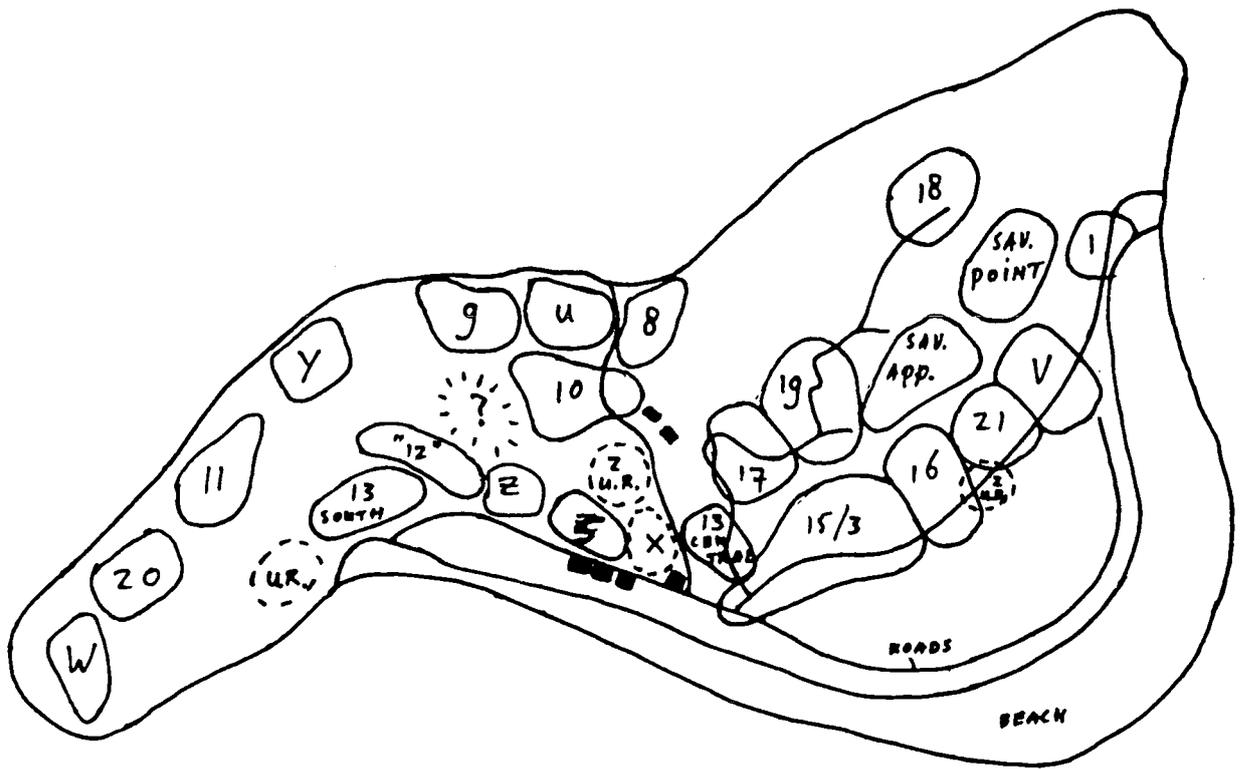
- w/v
- lb/v (one is sexed as male, the other isn't)
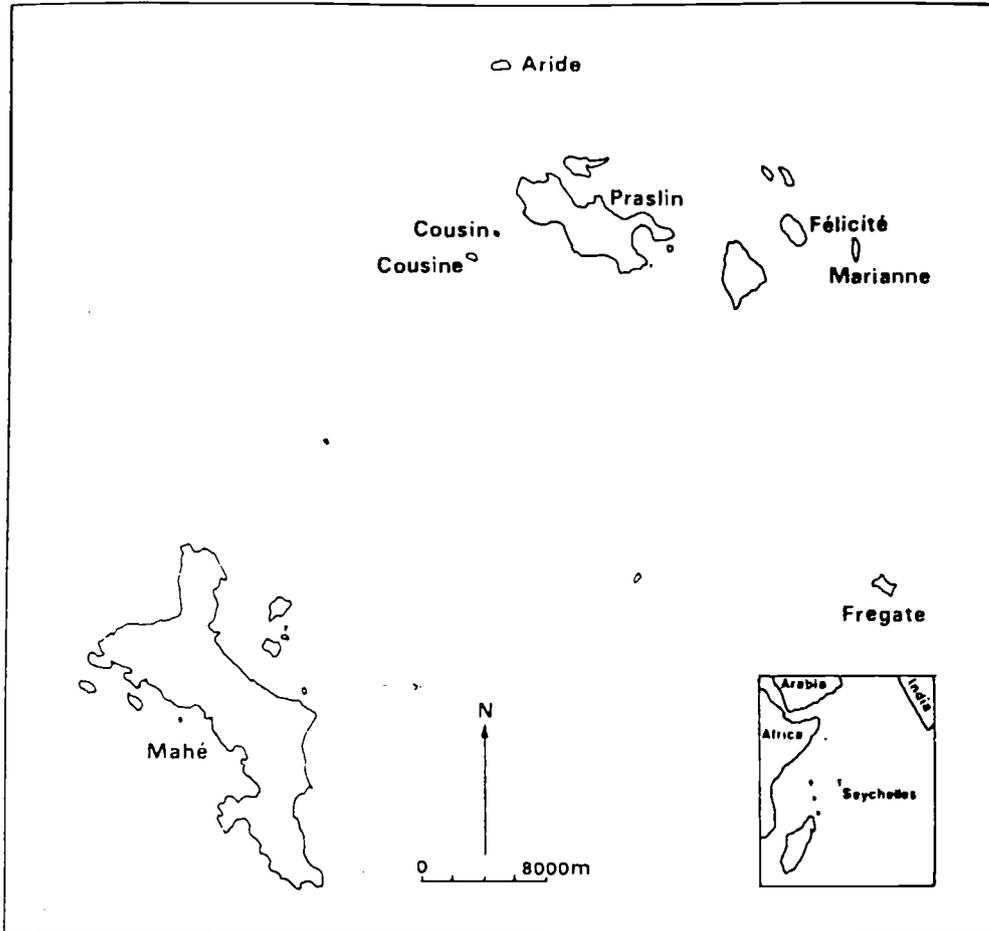
Map 1. Location of Aride Island and Cousine Island, Seychelles (from Komdeur 1991a).

September 1988

September 1990

November 1991

200 m

March 1993

Map 2. Territories on Aride, September 1988 - March 1993 (from Komdeur et al. 1995a).

Map 3. Territories on the plateau of Aride, June 1995.

Map 4. Territories on Cousine Island, May 1995.