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Inter-island transfers and population dynamics of Seychelles Warblers *Acrocephalus sechellensis*

JAN KOMDEUR

Summary

In the 1950s the Seychelles Warbler *Acrocephalus sechellensis* was a highly threatened single-island endemic species with a population of 26 individuals confined to Cousin Island in the inner Seychelles. Following long-term management of Cousin, the population steadily recovered to around 300–360 birds. In order to give the species the security of additional breeding populations, some warblers were successfully transferred to the islands of Aride and Cousine in September 1988 and June 1990 respectively. During the three years after the transfer to Aride and the first year after the transfer to Cousine, mean territory quality (measured as insect prey available) on these islands was significantly higher than that on Cousin, leading to higher reproductive success per territory and survival of juveniles and adult birds. In November 1991, all transferred birds were still alive, and 205 young had fledged successfully, bringing the total warbler population to c.585 birds. By then there was enough suitable space still remaining on Aride and Cousine for young birds to establish territories and the rise in warbler numbers is expected to continue. The successful establishment of three self-sustaining and viable breeding populations has ensured that the Seychelles Warbler is no longer a globally threatened species.

Introduction

The Seychelles Warbler *Acrocephalus sechellensis* (Oustalet 1878) is a small (15 g) insectivorous bird, endemic to the Seychelles Islands in the Indian Ocean. It was recorded as long ago as 1870 on Marianne and Cousine (Oustalet 1878; Figure 1); odd records have been reported from Mahé and Félicité and there is some confusion as to whether the original Cousine record may have been in error for Cousin (Collar and Stuart 1985). The species was certainly present on Cousin in 1938 but was by then considered rare (Collar and Stuart 1985). Between 1910 and 1920 the islands of Marianne, Cousine and Cousin were planted with coconuts *Cocos nucifera*, leaving very little suitable natural habitat for the warblers, resulting in the disappearance of the species from Marianne and Cousine. In 1959, the total population was 26 individuals, entirely confined to Cousin Island (29 ha; at 4° 20′ S 55° 40′ E) (Crook 1960; Figures 1 and 2).

In 1968 Cousin was purchased for the International Council for Bird Preservation (ICBP, now BirdLife International) with the express aim of saving the warbler: the coconuts were cleared, the original *Pisonia* forest was allowed to regenerate and the warbler staged a dramatic recovery. By 1982, the Cousin

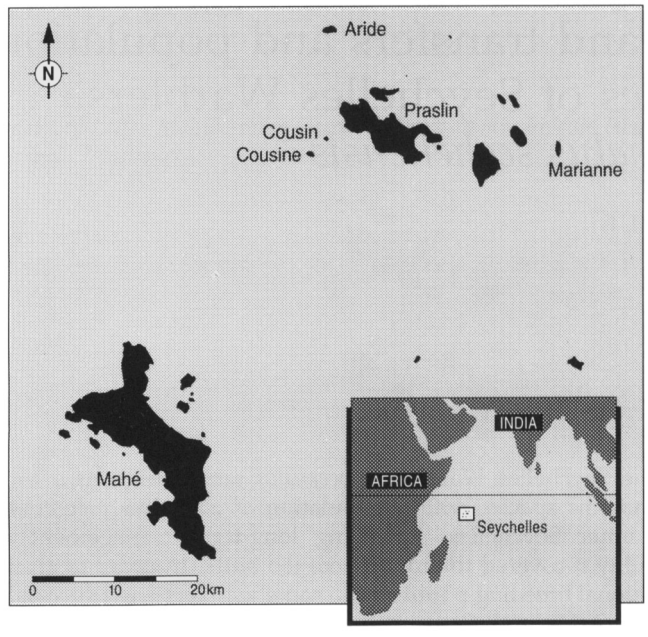

Figure 1. Map showing the Seychelles islands. Populations of Seychelles warblers on Cousin, Aride as place of first transfer (23–29 September 1988), and Cousine as place of second transfer (29 June–1 July 1990).

Figure 2. Aerial photograph of Cousin Island.

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population had grown to nearly 320 birds on 115 breeding territories (Bathe and Bathe 1982). Since then numbers of both birds and territories have fluctuated around that level, indicating that the warbler population has reached carrying capacity. Since 1973 many young birds were unable to establish new breeding territories and delayed dispersal and cooperative breeding became prevalent (Komdeur *et al.* 1991, Komdeur 1992). Young warblers frequently remained on their natal territories and acted as helpers, aiding in territorial defence, predator mobbing, nest-building, incubation (only females) and feeding dependent young of their parents. Fortunately alien predators, such as cats and rats, have never found their way onto the island. The introduction of these species would create by far the greatest threat to the future of the warblers.

On Cousin the reproductive rate is low, resulting from delayed onset of breeding (3.9 years), small clutch-size (normally one), and low recruitment rate (0.32 young per pair). This need not be a severe problem if the pressures placed on reproduction are only temporary, since warblers are long-lived. Mean adult survival is 83.5%, giving a mean adult life expectancy of 3.9 years (the length of time after which 50% of the population alive at one year will have died; Komdeur 1991). They can therefore tolerate periods of low recruitment. However, they are particularly vulnerable to factors which lead to increased adult mortality and/or prolonged reduction in recruitment.

In order to give the species the security of more breeding populations, two other islands were selected for the establishment of new warbler populations (Figure 1). Aride (68 ha; 4° 13′ S 55° 44′ E, 9 km north of Cousin) is a nature reserve owned and run by the Royal Society for Nature Conservation (RSNC). Aride had no potential competitors with Seychelles Warblers and possessed an unexploited resource base of appropriate insect prey, so a successful translocation of 29 colour-ringed adult warblers (16 males and 13 females) was carried out between 23 and 29 September 1988. All birds survived the transfer and, at the beginning of October 1988, 13 territories were established on Aride. Successful nesting started in most territories within a few weeks, and in some territories within three days, of release. The first young on Aride (twins) hatched four weeks after the transfer. During the next six months, birds on Aride had access to 21.1 times more food per unit area than birds on Cousin and mean number of annual recruits produced per pair was 16.3 times higher. In March 1989 all transferred birds were still alive and 26 young had fledged successfully, bringing the total Aride population to 45 birds (see Komdeur *et al.* 1991).

Because of this success, Cousine Island (26 ha; at 4° 19′ S 55° 39′ E) was studied to assess its suitability for a third warbler population. Cousine is a privately owned, rat-free island most of which (19 ha) is in a nearly natural state, its native woodland having recovered as swiftly as that on Cousin. Remarkably, even though Cousine is only 1.6 km south-west of Cousin, no warblers were known to have reached it on their own during at least 20 years prior to their introduction (Diamond 1980, G. Souffe verbally 1990).

This paper describes the ecological studies carried out prior to, during and after the translocations and documents the subsequent establishment of the new populations, by comparing the survival and recruitment of Seychelles Warblers over seasonal intervals up to August 1993 on the saturated Cousin

Island and on the unsaturated islands of Aride and Cousine. Documentation and dissemination of the results of this study will help similar programmes to benefit from the approaches taken and experience gained.

Methods

Study area and study population

The warblers were studied simultaneously from September 1988 to November 1991 on Cousin and Aride, and on Cousine from June 1990 to November 1991. On Cousin all 115–123 groups of warblers (300–360 birds) were studied from September 1988 to June 1990, 39 groups (139–151 birds) from June 1990 to June 1991, and 35 groups (89–103 birds) from July to November 1991. On Aride 13–43 groups (29–180 birds) were studied from September 1988 to November 1991. Additional monitoring of the warbler population on Aride was conducted by the wardens, volunteers, and myself during a visit in August 1993. On Cousine an additional 12–16 groups (29–43 birds) were studied from June 1990 to June 1991, and 10 groups (25–35 birds) from July to November 1991. The average yearly percentage of birds that were individually colour-ringed was 70% on Cousin, 74% on Aride and 90% on Cousine.

General methods and data collection

On Cousin, Aride and Cousine, as many young as possible were colour-ringed. On Aride and Cousine, twice a month a considerable time was spent quartering the island to locate dispersing birds and to plot new territories using a portable tape-recorder with a continuous loop cassette of male song to attract birds. As the three islands have the same habitat types and are very close to each other, I have employed matched pairs statistical tests to test the differences in habitat quality and warbler breeding activity between these islands. When not specified in the text, values of statistical tests are reported in the legends of figures or tables.

Transfer of Seychelles Warblers to the islands of Aride and Cousine

Between 23 and 29 September 1988, a successful translocation of 29 colour-ringed Seychelles Warblers took place to Aride Island, a journey of around 45 minutes by motor-boat. The birds were released at three different sites (see Figure 4a); two in high- and one in medium-quality habitat, measured in terms of vegetation and insects present (see section on territory and island quality in this paper and Komdeur *et al.* 1991).

In mid-June 1990 all Seychelles Warbler territories on Cousin were checked for breeding birds and birds undergoing moult, in order to select adult individuals for the transfer to Cousine. From 29 June to 1 July 1990, trapping took place from 05h00 to 08h00 and from 15h30 to 17h00, in four localities. At each locality a mist-net and a portable tape-recorder with a continuous loop

cassette of male song was used to attract birds. If possible, experienced breeding pairs (which had held a territory and bred at least once) were caught. The birds were weighed immediately after catching. To prevent aggression between territorial birds, each bird was kept in a separate 15 × 15 × 20-cm cardboard transfer cage, well-ventilated, but dark inside in order to keep the birds inactive, thus reducing stress and energy loss. A stick trellis, 1 cm above the floor of each box, was also provided to allow the birds to perch inside. Birds were then taken to the laboratory, colour-ringed, weighed again and sexed by measuring weight and wing length (Komdeur 1991), and transferred immediately. Twenty-nine adult warblers (15 males and 14 females) were transferred to Cousine by motor-boat, a journey of about 15 minutes. The cardboard cages were kept secure in a wooden carrying cage and placed on a thick foam mattress to absorb shocks in a rough sea. Immediately on landing, the birds were taken to their release sites: one high- and one medium-quality site (see Figure 4b). Birds belonging to the same territorial group were always released at the same sites. Before release, birds were again weighed and water was provided by throwing buckets of water over the vegetation within a few metres of the cages.

The effects of the transportation were assessed by weight changes of birds during captivity, and by survival and behaviour in subsequent weeks.

Breeding activity and dispersal of offspring

All territories were checked for breeding activity and the presence of colour-ringed birds, every seventh day on Cousin and Aride, every fourteenth day on Cousine. If a colour-ringed bird was missing from its territory, the rest of the island was searched for it; if it was not found it was assumed to be dead, since no movement of individuals between islands was ever recorded.

Breeding status was assessed by following each female continuously for 30 minutes and recording at 30-second intervals whether she was nest-building, incubating, or feeding young. The minimum number of records of these behaviours per 30-minute interval was two (Komdeur 1991). All nests were checked for clutch-size, sometimes with the help of a long stick and angled mirror. Observations on nest-building, incubating, and feeding young were made for three hours. Feeding observations started in the second week after hatching and were repeated every three weeks until the young died or reached independence.

Territory and island quality

Territory and island quality can theoretically be measured in terms of, for example, availability of nest sites, density of predators or food availability. On the three islands nest sites had no consistent features (within the same territory nests were found from 1 m to as high as 20 m) and were apparently abundant. Adult Seychelles Warblers lack natural predators, and nest-predators (Seychelles Fodies *Foudia sechellarum*, which are weaver birds endemic to the Seychelles, and two endemic skinks *Mabuya wrightii* and *M. sechellensis*), were evenly distributed over the islands (Brooke and Houston 1983, Owen 1986). As the warblers are insectivorous, taking 98% of their insect food from leaves

(Komdeur 1991), territory and island quality depend on the amount of insect prey available, which in turn depends on the amount of foliage present. The only other insect-eating birds present on the islands were the Seychelles Fody and the endemic Seychelles Sunbird *Nectarinia dussumieri*. Territory quality (*tq*) and island quality (*iq*) were measured as:

$$tq = a\sum_{x=1}^{12}(c_x i_x) \qquad iq = \sum_{x=1}^{12}(c_x i_x)$$

where a is mean annual territory size (hectares), c_x is mean foliage cover for plant species x in a territory and on the island (measured at various sites of 50 × 50 m each), and i_x is mean insect totals for plant species x per unit leaf area (1 dm^2) in a territory and on the island.

The amount of foliage in each territory and at each site was measured using a transect method. In each territory and site the transect was 250 m long, subdivided into straight subtransects plotted 25 m apart from each other and facing north from one territory or site boundary to the other. Every 5 m the presence or absence of foliage and the plant species were noted in the following heights: 0–0.75 m, 0.75–2 m, 2–4 m, and at 2 m intervals thereafter. Total foliage cover for plant species x (c_x) was the total number of cases of presence of foliage at all heights along the transect. To assess prey availability (i_x) in each territory and at each site, the upper- and under-sides of 50 leaves per plant species (12 dominant species) were searched for insects. Insect density was assessed for plant species by measuring the area of 250 leaves at 50 random sites on the island (five leaves per site).

Every three months (between 15th and 29th) the quality of all territories under study was assessed simultaneously, on Cousin and on Aride from September 1988 to June 1991, and on Cousine from June 1990 to June 1991. In September and November 1991, the quality of 10 randomly chosen territories (out of 25) on Cousin, and four territories and two control areas on Cousine was assessed. Territories were divided into three categories: low- (*tq* = 0.0–15.0), medium- (*tq* = 15.1–30.0), and high-quality (*tq* = 30.1–45.0).

Each month (between 15th and 29th) island quality of Cousin and Aride was studied from May 1987 to June 1990, and quality of Cousine from August 1989 to June 1990. Insects and vegetation were monitored simultaneously on Cousin and Aride, and on Cousine at a later stage at 67, 28, and 20 randomly chosen sites, respectively.

Results

Suitability of Cousine Island for Seychelles Warblers

Between August 1989 and June 1990 the quality of Cousine averaged 1.7 times higher than that of Cousin (mean *iq* ± SE: 89 ± 17.5 vs. 52 ± 17.5; paired-sample *t*-test: $t = 3.57$, $df = 10$, $P < 0.005$), but 0.6 as high as that of Aride Island (mean *iq* ± SE: 155 ± 25.4; paired-sample *t*-test: $t = 4.97$, $df = 10$,

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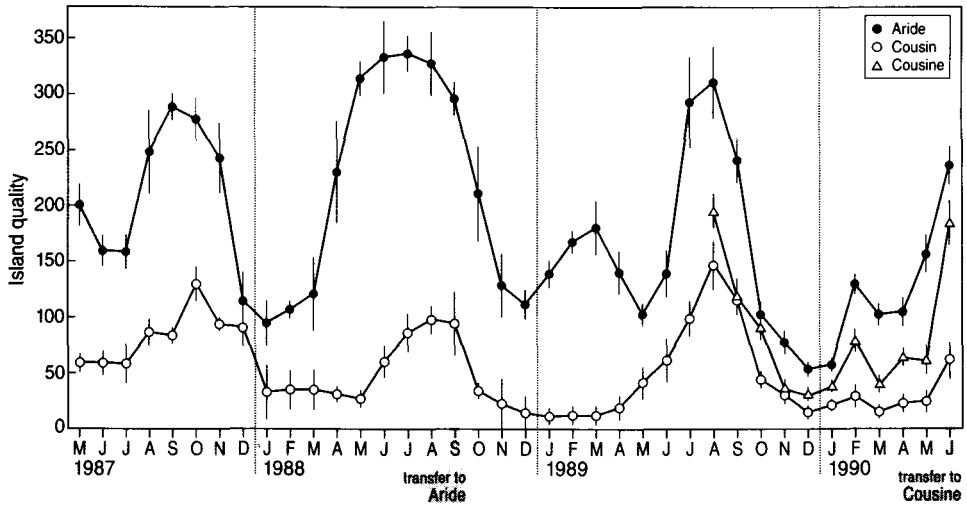

Figure 3. Monthly island quality (± SE) of Aride Island, Cousine Island and Cousin Island (May 1987–June 1990).

$P < 0.001$) (Figure 3). The seasonal pattern of change in island quality of Cousine was synchronous with that of Cousin and Aride (Spearman rank correlation: $r = 0.81$, $df = 9$, $P < 0.005$ and $r = 0.92$, $df = 9$, $P < 0.001$, respectively). Cousine was therefore judged to be suitable for the establishment of a third population.

Effect of release-site quality on settling pattern of Seychelles Warblers

The transferred birds swiftly accepted their new habitat on Aride and Cousine, formed pairs with their original or new mates and began establishing territories within days, and in some cases hours, of being released (Figure 4). At the beginning of October 1988, 13 high-quality territories were established on Aride; 11 were occupied by pairs and two by single males. The other five birds were seen wandering all over the island on their own. At the beginning of July 1990, 12 high-quality territories were established on Cousine; eight were occupied by pairs and four by single males. The other nine birds were seen wandering over the island on their own.

The distribution pattern of territories immediately following the transfers to Aride and Cousine (October 1988 and July 1990, respectively) showed that the birds released at high-quality release sites had settled close to the high-quality release points, whereas none of the birds released at medium-quality sites settled close to the release point; they moved about and established high-quality territories far away from the release site (Figure 4). By comparing the pattern of territories around high- and medium-quality release sites immediately following the transfers, it emerged that significantly more birds, both males and females, had settled close (<200 m) to a release point when this was situated in a high-quality area (Table 1).

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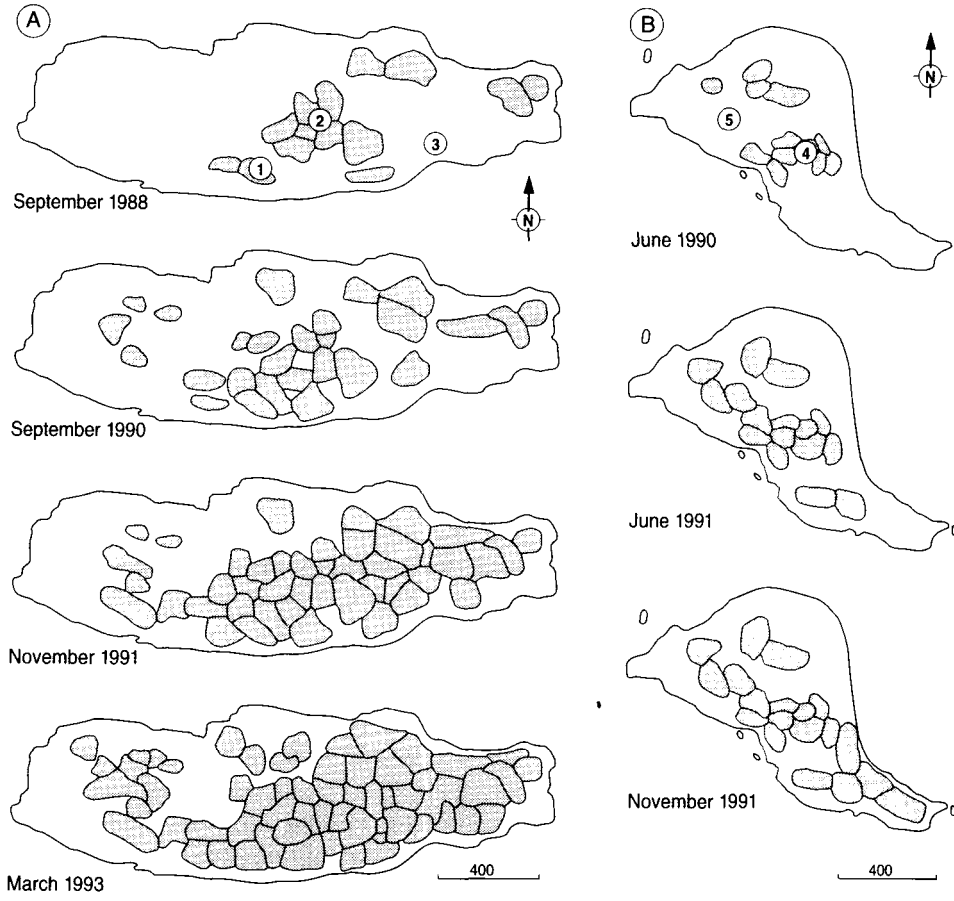

Figure 4. Seychelles warbler territories (a) on Aride Island in September 1988 (at the time of transfer), in September 1990, in November 1991 and in March 1993 (Taylor and Dixon 1993), and (b) on Cousine Island in June 1990 (at the time of transfer), in June 1991 and in November 1991. Numbers refer to release-sites: 1, 2 and 4 are of high quality; 3 and 5 of medium quality.

Breeding activity following the transfers

As on Aride, successful nesting on Cousine started in most territories within a few weeks, and in one territory within three days, of release. The first young on Cousine was hatched three weeks after the transfer, one week earlier than on Aride. Comparing breeding activity on Aride and Cousin for the three years and two months after the transfer (Figure 5), Aride birds showed on average 2.9 times more breeding activity than Cousin birds (paired-sample t-test: $t = 10.36$, $df = 37$, $P < 0.001$). The seasonal pattern in the percentage of territories with breeding activity on Aride was not correlated with that on Cousin ($r = 0.19$, $df = 36$, $P = 0.242$). A minimum of 64% of pairs bred on Aride in October 1988 and a maximum of 90–100% of pairs were breeding from January 1989 to November 1991. Over the same period the percentage of breeding pairs on Cousin varied from 0% (October and November 1988 and June 1989) to 96%

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Table 1. Effect of release-site quality on settling pattern of Seychelles Warbler males and females on the islands of Aride and Cousine immediately after the transfers (September 1988 and June 1990, respectively; see also Figure 4).

	Release-site quality	Distance between release-site and territory		*n*	*P*-value
		<200 m	>200 m		
Aride					
Male	High (1)	2	0	2	
	High (2)	6	0	6	<0.001
	Medium (3)	0	5	5	
Female	High (1)	1	1	2	
	High (2)	5	0	5	<0.05
	Medium (3)	0	4	4	
Cousine					
Male	High (4)	8	0	8	
	Medium (5)	0	4	4	<0.01
Female	High (4)	5	0	5	
	Medium (5)	0	3	3	<0.05

Statistical significance of comparisons determined by chi-square contingency analysis. Numbers in parentheses refer to release-sites indicated in Figure 4.

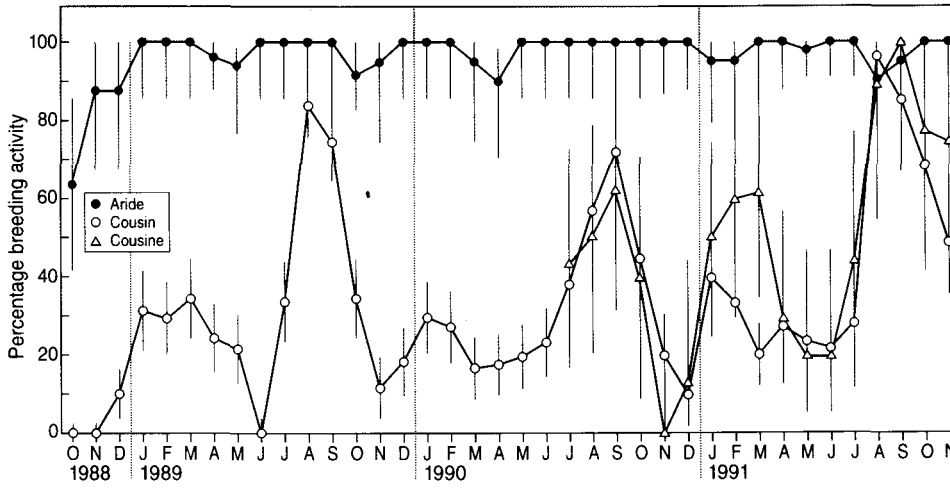

Figure 5. Percentage territories with breeding activity (nest-building, incubating or feeding young) each month (± 95% confidence limits) on the islands of Aride, Cousin and Cousine. Mean breeding activity on Aride and Cousin (October 1988 to November 1991): 97% (mean n = 21) and 34% (mean n = 82), respectively. Mean breeding activity Aride, Cousin and Cousine (July 1990 to November 1991): 98% (mean n = 19), 44% (mean n = 38) and 49% (mean n = 12), respectively.

(August 1991 only). On Cousin birds undergo a pre-breeding moult; of all the possible monthly moulting and breeding activity combinations, the only significant correlation found was between the percentage of territories with nests and the percentage of moulting birds two months earlier (r = 0.68, df = 52, $P < 0.001$). On Aride, birds were able to moult and breed at the same time. Comparing breeding activity on the three islands for one year and five months

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following the transfer to Cousine (Figure 5), Cousine birds showed the same breeding activity as Cousin birds ($t = 1.50$, $df = 16$, $P = 0.153$), but half that of Aride birds ($t = 8.53$, $df = 16$, $P < 0.001$). There appeared to be two annual peaks of breeding activity in the populations on Cousin and Cousine; one in August–October and another in January–March. The seasonal pattern in the percentage of territories with breeding activity on Cousine was synchronous with that on Cousin ($r = 0.83$, $df = 15$, $P = 0.001$).

In each of the three years (October 1988–September 1989; October 1989–September 1990; October 1990–September 1991) following the transfer to Aride, the production of offspring per territory on this island was significantly higher than that on Cousin (Table 2). The increase in reproduction can be attributed to three factors: (1) higher number of nesting attempts per territory (on average 2.8 times as many); (2) higher percentage of nests in which a clutch was laid (1.4×), and consequently higher number of nests with clutch per territory (4.6×); (3) higher survival of fledglings to one year of age (2.8×), and consequently a higher number of one-year-old young produced per territory. In addition, young fledged four to five days earlier and, during the two years following the transfer, mean clutch-size was almost twice as high. Hatching and fledging success were not significantly higher on Aride. Taken together, the production of yearlings per territory was on average 11.3 times higher on Aride. Annual adult survival (the probability of surviving to the next year, starting at the age of one year) was also significantly higher on Aride (Table 2). The higher breeding output of Aride birds is no doubt related to the 15.9 times higher quality of Aride compared with Cousin (Table 2).

Despite the same breeding activity by warblers on Cousine and Cousin (Figure 5), the production of offspring per territory on Cousine in the first year (July–November 1990) following the transfer was significantly higher than that on Cousin (Table 3). This was mainly due to the much higher number of nests built per territory (2.4 times as many). Percentage of nests with clutch, clutch-size, hatching success, mean number of days nestlings spent in the nest, and fledging success were all slightly, but not significantly, higher on Cousine. In addition, fledgling survival to one year of age was more than twice as high on Cousine. Taken together, these factors resulted in a five times higher production of yearlings. Adult survival was also significantly higher on Cousine (Table 3). Mean territory quality on Cousine was 3.4 times higher than that on Cousin (Table 3).

During the same period in the second year (July–November 1991), adult birds survived significantly better, but the reproductive output per warbler territory on Cousine was similar to that on Cousin (Table 3). The number of nest-building attempts per territory, and the number of nests resulting in clutch, pulli, and fledglings, were the same. Moreover, on both islands hatching success and survival of nestlings to fledging were the same. These results are in agreement with the fact that the quality of territories on Cousine for warblers had declined (Table 3). With an expanding population more territories were established within the high-quality areas leading to complete occupation of this area in the first place, and to smaller, and thus lower-quality territories in the second place. As a consequence birds spread into poorer habitat (see next section).

Table 2. Comparison of annual adult survival, breeding performance (±SD) of Seychelles Warblers and territory quality on the islands of Aride and Cousin during the first (October 1988–September 1989), the second (October 1989–September 1990) and the third year (October 1990–September 1991) following the transfer.

	Aride	Cousin	*P*-value
October 1988–September 1989	(*n* = 11)	(*n* = 49)	
Annual adult survival	100 (29[a])	80.3 (117[a])	<0.025
Nest-building attempts			
Per territory	5.55 ± 1.55	1.93 ± 1.06	<0.001
Total	61	95	
Nests with clutch (%)	88.5	64.2	<0.005
Number of nests with clutch			
Per territory	4.91 ± 1.17	1.24 ± 0.99	<0.001
Total	54	61	
Mean clutch-size	1.85 ± 0.52 (20)	1.00 ± 0.00 (55)	<0.005
Clutches hatched (%)	70.4	69.7	NS
Number of nests with pulli			
Per territory	3.46 ± 1.08	0.76 ± 0.82	<0.001
Total	38	37	
Mean no. days to fledge	14.0 ± 0.87 (26)	18.8 ± 1.35 (22)	<0.001
Nestlings fledged (%)	76.3	83.8	NS
Number of nests producing fledglings			
Per territory	2.64 ± 0.80	0.63 ± 0.71	<0.001
Total	29	31	
Fledglings reaching one year of age (%)	100.0	29.0	<0.001
Number of yearlings produced			
Per territory	2.64 ± 0.80	0.19 ± 0.17	<0.001
Total	29	9	
Mean territory quality	327 ± 31.2 (11)	15.5 ± 10.3 (49)	<0.001
October 1989–September 1990	(*n* = 18)	(*n* = 49)	
Annual adult survival	100 (36[a])	83.3 (132[a])	<0.025
Nest-building attempts			
Per territory	5.22 ± 1.49	1.67 ± 0.99	<0.001
Total	94	82	
Nests with clutch (%)	87.2	58.5	<0.001
Number of nests with clutch			
Per territory	4.56 ± 1.04	0.98 ± 0.75	<0.001
Total	82	48	
Mean clutch-size	1.75 ± 0.40 (24)	1.00 ± 0.00 (48)	<0.005
Clutches hatched (%)	67.1	64.6	NS
Number of nests with pulli			
Per territory	3.17 ± 0.95	0.63 ± 0.69	<0.001
Total	57	31	
Mean no. days to fledge	14.1 ± 0.77 (29)	19.1 ± 1.15 (22)	<0.001
Nestlings fledged (%)	78.9	77.4	NS
Number of nests producing fledglings			
Per territory	2.50 ± 0.84	0.49 ± 0.58	<0.001
Total	45	24	
Fledglings reaching one year of age (%)	100.0	33.3	<0.001
Number of yearlings produced			
Per territory	2.50 ± 0.84	0.16 ± 0.16	<0.001
Total	45	8	
Mean territory quality	288 ± 32.2 (18)	17.3 ± 14.2 (49)	<0.001

Table 2—cont.

	Aride	Cousin	*P*-value
October 1990–September 1991	(*n* = 15)	(*n* = 35)	
Annual adult survival	96.7 (30[a])	78.8 (85[a])	<0.05
Nest-building attempts			
Per territory	5.27 ± 1.20	2.11 ± 0.81	<0.001
Total	79	74	
Nests with clutch (%)	73.4	59.5	<0.025
Number of nests with clutch			
Per territory	3.87 ± 1.35	1.26 ± 0.41	<0.001
Total	58	44	
Mean clutch-size	1.25 ± 0.43 (20)	1.11 ± 0.33 (9)	NS
Clutches hatched (%)	75.9	72.7	NS
Number of nests with pulli			
Per territory	2.93 ± 1.31	0.91 ± 0.40	<0.001
Total	44	32	
Mean no. days to fledge	15.1 ± 0.70 (10)	19.0 ± 0.58 (6)	<0.001
Nestlings fledged (%)	90.9	84.4	NS
Number of nests producing fledglings			
Per territory	2.67 ± 1.04	0.77 ± 0.46	<0.001
Total	40	27	
Fledglings reaching one year of age (%)	100.0	44.4	<0.025
Number of yearlings produced			
Per territory	2.67 ± 1.04	0.34 ± 0.24	<0.001
Total	40	12	
Mean territory quality	213 ± 38.2 (15)	19.4 ± 15.2 (10)	<0.001

Figures in parentheses are number of observations.
[a] Number of bird years.
Statistical significance of comparisons determined by chi-square contingency analysis (percentage data) or two-tailed *t*-test. NS denotes $P > 0.05$.

Dispersal of juveniles on the islands of Aride and Cousine

During the three years and two months following the transfer to Aride and the one-and-a-half years following the transfer to Cousine, there was still enough suitable habitat left on Aride and Cousine for young birds to establish new territories (Figure 4). During the two years following the transfer to Aride and the first year following the transfer to Cousine, all the offspring initially produced by translocated birds left their natal territories significantly earlier than young on Cousin (Table 4). Juveniles left their natal territories on Aride and Cousine on average 5.8 times earlier than on Cousin Island (Table 4). Unlike young hatched on the new islands, Cousin juveniles from the highest-quality territories stayed in their natal territory for on average 43.2 months ($n = 20$). On Aride and Cousine, between the time of leaving and pair formation, young were seen wandering all over the island. The offspring sex ratio on both islands at that time was not biased (female : male on Aride 1.01 : 0.99, n = 79; on Cousine 1 : 1, $n = 6$), so all young birds were able to find a mate. They all paired and established territories of their own within one year, and bred on average 5.8 times earlier than young on Cousin (Table 4). All 105 young (91 and 14, respectively) were able to establish a breeding territory of similar quality to their natal territory (mean quality of breeding vs. natal territory ± SD on Aride:

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Table 3. Comparison of annual adult survival, breeding performance (mean ± SD) of Seychelles Warblers and territory quality on the islands of Cousine and Cousin during the first five months in the first year (July–November 1990) and the first five months in the second year (July–November 1991) following the transfer.

	Cousine	Cousin	*P*-value
July–November 1990	(*n* = 10)	(*n* = 39)	
Annual adult survival	100 (29[a])	81.3 (75[a])	<0.05
Nest-building attempts			
Per territory	2.00 ± 0.67	0.85 ± 0.56	<0.01
Total	20	33	
Nest with clutch (%)	85.0	78.8	NS
Number of nests with clutch			
Per territory	1.70 ± 0.71	0.67 ± 0.31	<0.001
Total	17	26	
Mean clutch-size	1.13 ± 0.33 (8)	1.09 ± 0.29 (22)	NS
Clutches hatched (%)	47.1	46.2	NS
Number of nests with pulli			
Per territory	0.80 ± 0.51	0.31 ± 0.27	<0.001
Total	8	12	
Mean no. days to fledge	18.8 ± 0.43 (4)	19.0 ± 1.35 (12)	NS
Nestlings fledged (%)	87.5	83.3	NS
Number of nests producing fledglings			
Per territory	0.70 ± 0.46	0.26 ± 0.25	<0.001
Total	7	10	
Fledglings reaching one year of age (%)	85.7	40.0	<0.05
Number of yearlings produced			
Per territory	0.60 ± 0.44	0.12 ± 0.21	<0.001
Total	6	4	
Mean territory quality	53.2 ± 5.2 (10)	15.6 ± 10.3 (39)	<0.001
July–November 1991	(*n* = 10)	(*n* = 35)	
Annual adult survival	100 (26)	80.3 (80)	<0.05
Nest-building attempts			
Per territory	1.10 ± 0.30	1.17 ± 0.45	NS
Total	11	41	
Nests with clutch (%)	90.1	85.4	NS
Number of nests with clutch			
Per territory	1.00 ± 0.34	1.00 ± 0.48	NS
Total	10	35	
Clutches hatched (%)	90.0	74.3	NS
Number of nests with pulli			
Per territory	0.90 ± 0.30	0.74 ± 0.44	NS
Total	9	26	
Nestlings fledged (%)	100	84.6	NS
Number of nests producing fledglings			
Per territory	0.90 ± 0.30	0.63 ± 0.48	NS
Total	9	22	
Mean territory quality	41 ± 8.9 (4)	20.9 ± 19.2 (10)	NS

Figures in parentheses are number of observations.

[a] Number of bird years.

Annual adult survival = $(b/a)^{12/n}$, where a = number of ringed brids present in early July, b = number of ringed birds still present in late November and n = 5 (the number of months between counts in July and November).

Statistical significance of comparisons determined by chi-square contingency analysis (percentage data) or two-tailed *t*-test. NS denotes $P > 0.05$.

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Table 4. Age of dispersal and first breeding of Seychelles Warblers, and percentage of territories with helpers on the saturated Cousin Island (C; 1986–1991) and the unsaturated islands of Aride (A; October 1988–September 1990) and Cousine (C^e; June 1990–June 1991).

	Aride	Cousine	Cousin	*t*-test (A–C)	*t*-test (C^e–C)
Age young disperse (months)	4.0 ± 0.7 (n = 85)	4.2 ± 0.9 (n = 14)	23.3 ± 16.4 (n = 93)	P< 0.001	P < 0.001
Age first breeding (months)	8.1 ± 0.9 (n = 61)	8.3 ± 0.8 (n = 4)	47.3 ± 15.8 (n = 44)	P < 0.001	P < 0.001
Territories with helpers (%)	0.0 (y = 2)	0.0 (y = 1)	25.5 (y = 6)	P < 0.001[a]	P < 0.001[a]

n, Number of individuals; y, number of years; t-values represent comparisons between the unsaturated island and Cousin Island.
[a] t-Test was calculated using arcsine transformations.

287 ± 39.4 vs. 281 ± 37.3; paired-sample t-test: t = 0.43, df = 90, P = 0.589; on Cousine: 47.9 ± 6.2 vs. 47.6 ± 7.7; paired-sample t-test: t = 0.69, df = 13, P = 0.50).

With a range of habitat qualities available, it was predicted that the best should be occupied first, with overflow into poorer habitats once the best habitat was saturated (Davies and Houston 1984). On Aride, only high-quality territories were occupied until June 1990 (Figure 6a). Thereafter, the number of these territories remained constant, and so the high-quality habitat seemed to be saturated. Territories were subsequently established in medium-quality habitat until September 1991, and in low-quality habitat from November 1991 onwards (Figure 6a). From November 1991, the number of high-quality territories declined owing to the disintegration of high quality territories, resulting in a higher number of medium-quality territories within the high-quality area. In November 1991 a new breeding pair defended and budded off part of two territories in the high-quality area. Subsequently a new territory was formed, at the expense of the other two territories, resulting in three medium-quality

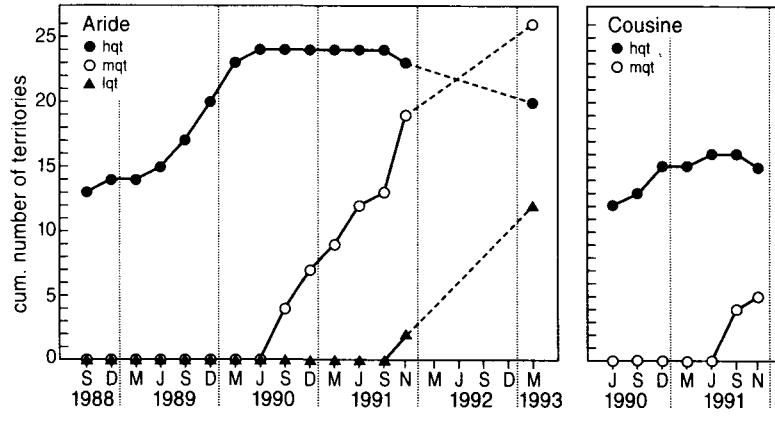

Figure 6. Effect of territory quality on dispersal by Seychelles warblers on the islands of (a) Aride and (b) Cousine (hqt, high-quality territory; mqt, medium-quality territory; lqt, low-quality territory).

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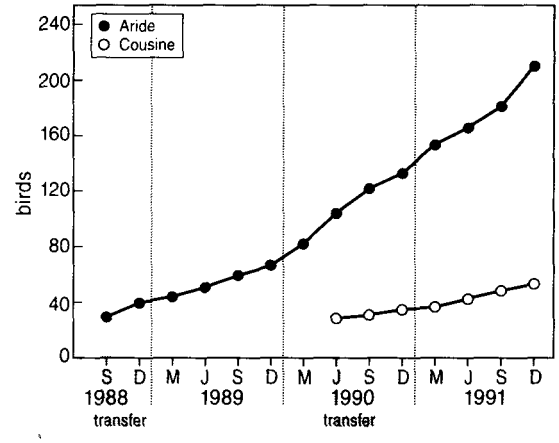

Figure 7. Increase in Seychelles Warbler numbers on Aride since September 1988 ($y = 4.58x + 8.39$; $r = 0.99$, $df = 12$, $P < 0.001$) and on Cousine since June 1990 ($y = 1.37x + 25.60$; $r = 0.99$, $df = 5$, $P < 0.001$).

territories within the high-quality area. In March 1993 two high-quality territories had been transformed into six medium-quality territories (Taylor and Dixon 1993; Figure 6a). On Cousine, only high-quality territories were established until June 1991 (Figure 6b). Thereafter, with the high-quality area being fully occupied, new territories were established in both medium-quality and high-quality habitat by taking over part of the existing territories. In November 1991 two breeding pairs established territories in the high-quality area at the cost of two existing territories, resulting in four medium-quality territories (Figure 6b).

In October 1990, two years after the transfer, three one-year-old young on Aride born on high-quality territories were found to have stayed on their natal territories as helpers, even though there was still abundant space for them to establish territories in lower-quality areas (Figure 4). After that time, helping on high-quality territories on Aride has become more common. In September 1991, one year and four months after the transfer, the first helper on Cousine was observed. This was a 13-month old bird, born on a high-quality territory, which helped its parents defending the nest and territory, and feeding twins. Since the first observations of helping activity, other young born on high-quality territories have begun to stay as helpers on Cousine, while there was still abundant space for them to establish territories in lower-quality areas (Figure 4). These results were not biased by a shortage of mates, as the offspring sex ratio at the time of cooperative breeding was equal males and females (sex ratio Aride 1.08 : 0.92, $n = 50$; sex ratio Cousine 0.8 : 1.2, $n = 9$).

Increase in Seychelles Warbler numbers on the islands of Aride and Cousine

During the three years and three months following the transfer to Aride and the one year and five months following the transfer to Cousine, birds on both islands showed increased reproductive rates compared with the population on Cousin (Figure 7). The mean annual population growth on Aride was signific-

antly higher than that on Cousine; slopes of the two regression lines in Figure 7 are significantly different ($t = 8.94$, $df = 17$, $P < 0.001$).

In November 1991, three years and three months after the transfer to Aride, all transferred birds were still alive and 181 young had fledged successfully, bringing the total Aride population to 210 birds (Figure 7). In the same month, one year and five months after the transfer to Cousine, all transferred birds were still alive and 24 young had fledged successfully, bringing the total Cousine population to 53 birds (Figure 7).

Discussion

Evaluation of the transfer method

There is a minimum weight below which Seychelles Warblers will die (Komdeur *et al.* 1991), so it is clearly vital that the handling of birds, and total time in captivity, are kept to an absolute minimum to prevent their weight falling below this critical level. On average the birds in this study spent just over three hours in captivity. The minimum known survival weight, defined as the lowest weight of known birds on Cousin Island still alive, is 14.6 g for males and 12.6 g for females (J. Komdeur, unpublished data). All birds survived the transfers and were released before they reached the minimum weight. Male and female warblers caught for transfer to Cousine weighed respectively 7.0% and 7.1% more than birds of the same sex caught for transfer to Aride: mean weight ± SD (n) males: 16.8 ± 0.58 (16) vs. 15.7 ± 0.41 (15) g; females: 15.1 ± 0.50 (13) vs. 14.1 ± 0.68 (14) g; both differences being significant (males: $t = 6.06$, $df = 29$, $P < 0.001$; females: $t = 4.33$, $df = 25$, $P < 0.001$). This extra weight is possibly an insurance against the forthcoming energy-demanding period of breeding from June onwards (the transfer to Aride occurred just after the breeding season).

During the transfer to Aride, males lost on average 0.9 g, females 1.0 g (respectively 5.7% and 7.1% of body weight). The weight loss of birds during the relatively short transfer to Cousine was on average 0.6 g for males and 0.5 g for females. Owing to the higher weights at catching and to the relatively short captivity time, the release weight of males and females after the transfer to Cousine was on average 1.3 g (16.2 vs. 14.9 g) and 1.2 g (14.5 vs. 13.4 g), respectively, higher than that of birds released on Aride. Moreover, release weight of males and females on Cousine was even higher than catching weight in 1988 before transfer to Aride.

Generally, it is advisable to start a transport before rather than after the breeding season, because the birds are in a much better condition: body weight of the same seven breeding females on Cousin before and after the breeding season in 1989 was 15.2 g and 14.0 g respectively (paired-sample t-test: $t = 8.35$, $df = 6$, $P < 0.001$). This aspect of the study is consistent with the inter-island transfer of New Zealand Black Robins *Petroica traversi*, where the main advantage of transfers prior to the breeding season was a reduced loss of birds (Flack 1977).

The transfers of Seychelles Warblers showed that the transferred birds will settle as close to the release point as possible when the surrounding habitat is of high quality; otherwise they move about and settle further away. Owing to

the relatively small size of Aride and Cousine, all the birds released in medium-quality or better habitats were able to find a mate and establish territories. However, in cases when birds are transferred in smaller numbers or to larger areas, it would be advisable to release the birds in high-quality habitats; otherwise they may move about and/or fail to form pairs and reproduce. The inter-island transfer of New Zealand Black Robins also found that the transferred birds settled as close to the release point as possible when the habitat was suitable (Flack 1977).

Effect of territory quality on reproduction and survival

Even on a small island like Cousin, the quality of territories (measured as amount of insect prey available) varied significantly. Territory quality was shown to be significantly associated with foraging efficiency of warblers; birds on high-quality territories not only spent less time foraging but still had higher foraging success (mean pecks after which the bird was seen swallowing food per half-minute) and caught more prey of high calorific value than birds on lower-quality territories (Komdeur 1991). An increase in foraging efficiency presumably affects the amount of energy which can be allocated to reproduction without incurring additional survival costs. Overall, the number of young fledged and survival of both juveniles and adults were significantly related to territory quality (Komdeur 1991). Because gross differences in territory quality cause variation in reproduction and survival, they also significantly affect the fitness of a bird, measured in terms of the number of young produced in a lifetime.

During the three years after the transfer to Aride and the first year after the transfer to Cousine, mean territory quality on these islands was significantly higher than that on Cousin, leading to higher reproductive success per territory and survival of juveniles and adult birds. Another cause of higher adult survival could be age-specific survival rates; annual survival on Cousin Island improved up to age six and deteriorated after age seven (Komdeur 1991). The current populations on the islands of Aride and Cousine may have higher annual survival rates because they are young; in August 1993 all the warblers on Aride and Cousine, except those survivors of the 29 founder birds, were under 5.5 and 3 years old, respectively. All young birds were able to establish high-quality territories and to breed within their first year of life. During the second year, however, more territories were established within the high-quality area, leading to habitat saturation within this area and to smaller territories (and hence to declining territory quality) at a later stage. Thereafter, new territories began to be established in the unsaturated medium-quality habitat. As a consequence, mean territory quality on Cousine declined and ultimately approached the levels found on Cousin territories, and reproductive output per territory and survival of birds declined to become the same as those on Cousin. On Aride, during the third year after the transfer, mean territory quality was still higher than that on Cousin, and in the fourth year new territories began to be established in low-quality habitat, owing to saturation of medium-quality habitat. However, once all areas have been filled and territories have become smaller and declined in quality because the warblers have less space for foraging, I expect that repro-

ductive output per territory and survival of birds on Aride will be the same as on Cousin.

The future of the Seychelles Warbler

In December 1991, all but one transferred birds were still alive and 205 young had fledged successfully on the new islands, bringing the total warbler population on the three islands to c.585 birds. By then the new populations had still not reached their maximum. As there is enough suitable space still remaining on Aride and Cousine for young birds to establish territories (areas still unoccupied: 35.8 ha and 18.0 ha, respectively) and mean territory size on saturated Cousin Island is very small (0.25 ha), the rise in warbler numbers is expected to continue for the future. However, a warbler census carried out by transect on Aride in January 1993 estimated 239 birds (Taylor and Dixon 1993), suggesting that warbler numbers had already begun to reach a plateau. As there was still suitable habitat unoccupied on the island in March 1993, the transect method may have underestimated the number of warblers. Nevertheless, given the presence now of three healthy breeding populations, the Seychelles Warbler is no longer a globally threatened species and should be listed as out of danger in the next edition of *Threatened birds of Africa and related islands* (Collar and Stuart 1985).

This study has provided some lessons for other translocations which have not (yet) succeeded. Translocations are conservation tools which may be employed when the parent population is declining or has reached carrying capacity. It is not enough simply to release rare bird species on other islands and gamble on their survival without conducting proper research beforehand. The decision to undertake a translocation should be based on a series of "feasibility" assessments (e.g. the bird's ecology, current threats and suitability of the new place for the species involved). Releases should take place only when the habitat is capable of sustaining a viable population and the original constraining factors no longer operate. The birds should be of optimal quality in terms of breeding behaviour and health (e.g. non-moulting) and they should be released and monitored according to sound strategies and criteria. Assessment and adjustments of the programme should be made periodically after initial releases, and documentation of the programme should be published.

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JAN KOMDEUR
BirdLife International, Wellbrook Court, Girton Road, Cambridge, CB3 oNA, U.K. and National Environmental Research Institute, Department of Wildlife Ecology, Kalö, Grenåvej 12, 8410 Rönde, Denmark.
Address for correspondence: *Department of Zoology, University of Melbourne, Parkville 3052, Victoria, Australia.*