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Published in:
Ibis

DOI:
[10.1046/j.1474-919X.2004.00255.x](https://doi.org/10.1046/j.1474-919X.2004.00255.x)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2004

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Komdeur, J., Piersma, T., Kraaijeveld, K., Kraaijeveld-Smit, F., & Richardson, D. S. (2004). Why Seychelles Warblers fail to recolonize nearby islands: Unwilling or unable to fly there? *Ibis*, 146(2), 298-302.
<https://doi.org/10.1046/j.1474-919X.2004.00255.x>

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Why Seychelles Warblers fail to recolonize nearby islands: unwilling or unable to fly there?

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The Seychelles Warbler *Acrocephalus sechellensis* is a rare island endemic which, from 1920 to 1988, occurred only on Cousin Island (29 ha) in the Seychelles. Despite the saturated nature of this population and the possibility of obtaining higher reproductive success on new nearby islands, inter-island dispersal by Seychelles Warblers is extremely rare (0.10%). We test the hypothesis that Seychelles Warblers show an adaptation typical for island birds: a low-cost reduced-size flight apparatus. We compared the anatomy of the flight apparatus (wing shape, wing loading, skeletal parts and musculature) of Seychelles Warblers with that of three closely related migratory *Acrocephalus* species (Eurasian Reed Warbler *A. scirpaceus*, Australian Reed Warbler *A. australis* and African Reed Warbler *A. baeticatus*). Seychelles Warblers do not differ from the migratory warblers in pectoral mass and skeletal attachment area relative to body mass, wing shape and wing loading. Seychelles Warblers show the morphological structures required for sustained flight, but may have the behavioural reluctance to cross what they may regard as extensive bodies of water.

The evolution of flight was a major innovation for birds and insects, permitting them to exploit habitats previously unavailable, to avoid terrestrial predators and to forage in three dimensions and over very large areas. However, some species of bird and insect have subsequently lost their 'morphological' flight capacity (e.g. Diamond 1981, Livezey 1992a, 1992b, Trewick 1997) or have become 'psychologically flightless' – e.g. refusing to fly across water despite flying readily over land (Willis 1974, Diamond 1981, Raikow 1985, Mayr & Diamond 2001). The majority of flightless species live on islands with low resource availability and without mammalian predators. As the capacity to fly is costly (Greenewalt 1975, Weber & Piersma 1996), the loss of flight may be a consequence of selection for reduced energy expenditure

in the face of intraspecific competition for food, or because the benefits of flight (namely predator escape) no longer apply in these habitats (e.g. Roff 1990, 1994, Wagner & Liebherr 1992, McNab 1994a, 1994b).

The Seychelles Warbler *Acrocephalus sechellensis* is a rare island endemic, which occurred on several islands in the Seychelles (Oustalet 1878; Diamond 1980) until anthropogenic disturbance in the 20th century reduced them to just one population on Cousin Island (29 ha) (Collar & Stuart 1985). This population, consisting of approximately 100 breeding pairs and 120 surplus birds, in 100 territories each year (Komdeur 1992, Richardson *et al.* 2002), has been monitored for the last 20 years. Habitat saturation has led to co-operative breeding in this species (Komdeur 1992), whereby individuals help with the breeding attempts of a breeding pair rather than breeding independently (Richardson *et al.*

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2002, 2003). Consequently, a substantial proportion of adults never acquire a breeding territory (29%; Komdeur 1991) or produce offspring (12%; D.S. Richardson unpubl. data). In 1988 and 1990, respectively, new populations of Seychelles Warblers were established by moving 29 birds to both Aride Island (68 ha, 9 km from Cousin) and to Cousine Island (26 ha, 1.6 km from Cousin). These translocations were highly successful, with the founder populations expanding to a combined population of c. 1750 individuals by 1996 (Komdeur 2003).

The presence of suitable islands nearby means that dispersal to other islands would pay greatly in fitness terms. Here we determine the extent to which birds voluntarily dispersed between the neighbouring islands of Cousin, Cousine and Aride. We also assess whether the flight performance and dispersal of Seychelles Warblers is physiologically or behaviourally constrained.

METHODS

Seychelles Warblers were studied on Cousin Island from 1981 to 2001, on Aride Island from 1988 to 2001 and on Cousine Island from 1990 to 1997. Data were based on adult birds, at least 8 months of age, uniquely marked with three colour-rings and a British Trust for Ornithology ring. To quantify movements of warblers between islands, as many birds as possible were resighted and/or (re)captured on each island, each year. The total pool of ringed warblers, from which individuals could have dispersed to other islands, amounted to 1195 for Cousin, 636 for Aride and 93 for Cousine. Each individual bird was included only once in our estimate. All birds ('surplus' birds and those which had a breeding territory when first seen) were included in the pool, as each bird has at least one opportunity to disperse in its life before it manages to gain a breeding territory.

We compared anatomical and morphological measurements of two freshly dead Seychelles Warblers with freshly dead birds of three closely related migratory *Acrocephalus* species (Leisler *et al.* 1997): one African Reed Warbler *A. baeticatus* (Eising *et al.* 2001), one Australian Reed Warbler *A. australis* (Schodde & Mason 1999) and four Eurasian Reed Warblers *A. scirpaceus* (Cramp & Brooks 1992). Morphological measurements of live birds and anatomical measurements of freshly dead birds were made on individuals in non-moulting, non-breeding, non-migration (overwintering) phases. We measured the length of the wing, tarsus, bill (exposed culmen)

and total head (head and bill) of each bird. The following organs were dried at 50–60 °C and measured for dry mass: stomach (including proventriculus), heart, lungs, liver, the entire intestine, kidneys and the pectoral muscle complex from both sides of the sternum (for details of the method see Piersma *et al.* 1996). Six skeletal dimensions were measured: 'A' (length of the keel), 'B' (maximum height of the keel), 'C' (length from the keel to the end of the coracoid), 'D' (width of the sternum), 'E' (length of the sternum) and 'F' (posterior tip of the keel and the anterior end of the coracoid; see also Piersma *et al.* 1984). We used the biplot technique to compare the linear dimensions and dry mass values of the different organs of the four warbler species (SYSTAT 10; SPSS 2000). The length of the vectors and the degree to which they share direction reveal the correlation between the different body dimensions or body parts.

Wing loading measurements (following Pennycuik 1989) were made on 30 randomly selected adult Seychelles Warblers (15 males and 15 females of three age classes: 1–2 years [$n = 5$], 3–4 years [$n = 5$] and > 4 years [$n = 5$]), 14 Eurasian Reed Warblers, one African Reed Warbler and five Australian Reed Warblers: body mass (M , to the nearest 0.1 g); wing span, from one wing tip to the other with the wings spread horizontally (b , to the nearest 0.1 mm); wing area (S , in cm^2) – the area of both wings, fully spread out, including the area of body between the wing roots. Wing shape was calculated as b^2/S (dimensionless) and wing loading (W) as M/S (g/cm^2).

RESULTS

Seychelles Warblers were not observed on the islands of Aride and Cousine in the 7 and 9 years, respectively, before translocation. During the 20 years of study, none of the 1288 birds (1195 from Cousin and 93 from Cousine) was caught on Aride, and none of the 636 birds present on Aride was caught on Cousin or Cousine. Nevertheless, two instances of inter-island displacements have been recorded. A female, ringed as a nestling on Cousin in 1994 and observed as a helper on her natal territory from 1995 until 25 April 1996, was caught on 5 May 1996 on Cousine. She paired up on Cousine, and by July 1997 had produced a fledgling. A male ringed as a nestling on Cousin in 1988, and translocated from Cousin to Cousine in 1990, was found back on Cousin in 1991 and bred there for 8 years. Overall, dispersal rate was extremely low; of 1924 birds, only

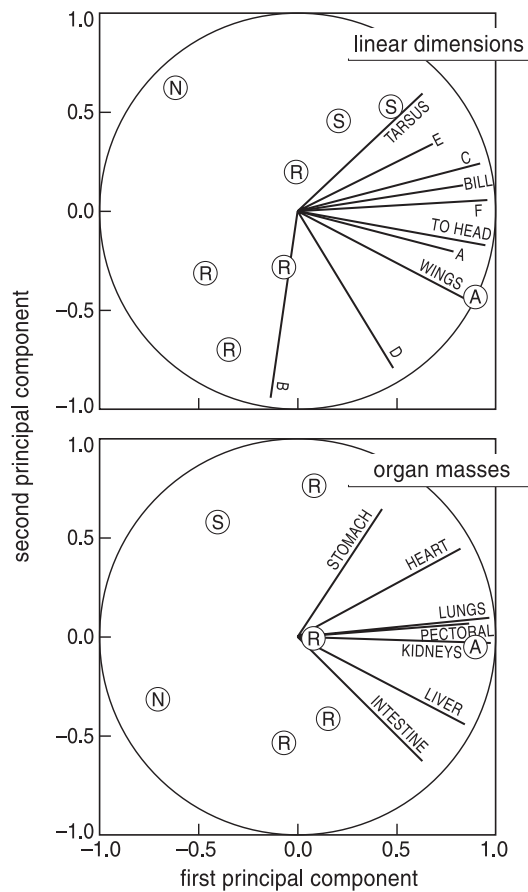


Figure 1. Relationships between the linear dimensions and organ dry masses of eight *Acrocephalus* warblers of four different species (S = Seychelles Warbler, R = Eurasian Reed Warbler, A = Australian Reed Warbler and N = African Reed Warbler). For linear dimensions, the first principal component is usually interpreted as the size variable, whereas the second principal component is the shape variable. The lengths of the vectors indicate R values (i.e. the variance explained by the two components), whereas the angle between two vectors gives the degree of correlation between them (thus, orthogonal vectors represent variables that are uncorrelated). The relative size of any variable of any bird can be read by projecting the individual datum on the relevant vector. For example, in the top graph, the African Reed Warbler ('N') has a relatively short wing, and the Australian Reed Warbler ('A') a relatively long wing.

two (0.10%) have been observed to fly between islands and, in both cases, this was between Cousin and Cousine (0.16%, 1288 birds).

The biplot (Fig. 1a) indicates that most of the linear dimensions of *Acrocephalus* warblers are closely correlated, but that the skeletal dimensions sternum width ('D') and keel height ('B') stand apart. Although Seychelles warblers have relatively long tarsi,

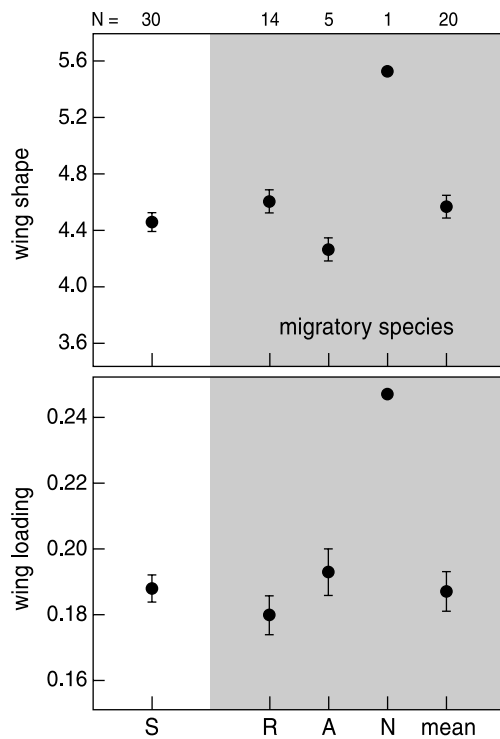


Figure 2. Mean wing shape (dimensionless) and mean wing loading (g/cm^2) of four different species of *Acrocephalus* warblers. For abbreviations see Fig. 1 (N denotes sample size).

sternum ('E') and coracoïd ('C'), their size ('A') and shape ('F') do not differ from those of the other warbler species. They are intermediate between Reed Warblers and Australian Reed Warblers in size and between Reed Warblers and African Reed Warblers in shape (the second principal component). The conclusions are similar in respect of organ mass (Fig. 1b). The organs of the Seychelles Warbler relate in scale to each other in a similar way as they do in Eurasian Reed Warblers. With regard to the pectoral muscles, the Seychelles Warbler is intermediate between the African Reed Warbler and the other reed warblers. Stomach and heart are relatively large in the Seychelles Warbler.

In Seychelles Warblers, wing shape and wing loading are independent of sex and age (wing shape: sex: $F_{1,29} = 1.39$, $P = 0.249$, age: $F_{2,28} = 0.00$, $P = 0.998$; wing loading: sex: $F_{1,29} = 0.80$, $P = 0.380$, age: $F_{2,28} = 0.08$, $P = 0.926$), and both measurements are similar to those recorded for the three migratory *Acrocephalus* warbler species (wing shape: Mann–Whitney test $Z = 0.98$, $n_1 = 30$, $n_2 = 20$, $P = 0.326$; wing loading: $Z = 0.378$, $n_1 = 30$, $n_2 = 20$, $P = 0.706$; Fig. 2).

DISCUSSION

This study shows that, despite the saturated nature of the established Seychelles Warbler populations and the possibility of obtaining higher reproductive success on new islands (Komdeur 1996), inter-island dispersal by Seychelles Warblers is extremely rare. The annual production of yearlings by breeding pairs that were artificially translocated to Aride or Cousine was, on average, 14 times higher than before the translocation (Komdeur 1996).

Observations indicate that the warblers have not lost the ability to fly over the distances required to recolonize islands in the Seychelles. Territorial warblers readily move within an island (Richardson *et al.* 2001) and have been observed to fly up to 2.1 km (over rocky habitat between suitable habitat) within a day (G. Castle and R. Mileto pers. comm. 1992). Radiotelemetry studies also confirmed that individuals ranged widely (J. Komdeur, V. Madson, J.M. Tinbergen and S. Daan pers. comm. 1996).

Energy conservation is proposed to be the selection pressure behind reduced flight ability and, compared with closely related flying species, flightless birds usually have smaller pectoral muscles, relative to body mass, wing shape and wing loading (Livezey 1990, 1992a, 1992b, McNab 1994b; McCall *et al.* 1998). The Seychelles Warbler does not fit the predictions of the energy conservation theory, as neither the average pectoral mass relative to body mass, the skeletal attachment area, the wing shape nor the wing loading is distinct from those of its migratory relatives. Seychelles Warblers show the morphological structures required for sustained flight, but still do not manage to disperse successfully to relatively close suitable islands. Seychelles Warblers appear therefore to have a behavioural reluctance to cross what they may regard as extensive bodies of water. This phenomenon of 'psychological flightlessness' occurs in other species that are capable of sustained flight (Diamond 1981, Raikow 1985). For example, tropical rainforest species that frequently fly over land refuse to cross water gaps of even a few hundred metres (Willis 1974).

Given the historical presence of discrete island populations of Seychelles Warbler and the vulnerability to extinction of such populations, we would not expect the Seychelles Warblers to have lost the ability or willingness to disperse across water to colonize new islands. The anatomical and behavioural bases of dispersal are subject to natural selection (Diamond 1981). Therefore, one would expect

that the ability to disperse over water and settle on nearby suitable islands (where, as shown by the translocations, individuals could gain higher fitness) should have been maintained in this species. The reluctance to do so could have developed a long time in the past when all Seychelles islands were perhaps fully occupied by warblers. Under these conditions, dispersal over water was not an adaptive strategy as all islands may have been saturated with warblers. Perhaps it is only now, after 100 years in which warblers have disappeared from all but one island, that flying across water to breed on other islands would be adaptive. The case of the Seychelles Warbler may exemplify the inability of natural selection to plan ahead.

We are grateful to Nature Seychelles for allowing us to work on Cousin Island, to P. Hitchins and J. Cadbury who arranged permission to work on Cousine and Aride, respectively, and to the Department of Environment and the Seychelles Bureau of Standards for permission to work in the Seychelles. We also thank M. Berg, J. Welbergen, R. Kats, K. Blaakmeer, C.M. Eising and the Groningen Museum (The Netherlands) for help in securing the specimens, J. van der Meer for statistical advice, and P.R. Grant, J.M. Diamond and R.H. Drent for constructive comments on the manuscript. J.K. and D.R. were supported by grants from the Australian Research Council (LARC: A19802483) and the UK Natural Environmental Research Council (NERC: GR3/1154 A), respectively, while T.P. was supported by a PIONIER-grant of the Netherlands Organization for Scientific Research (NWO).

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Received 17 December 2002; revision accepted 8 October 2003.