SEASONALITY, POPULATION STRUCTURE AND BREEDING ECOLOGY OF THE SEYCHELLES BRUSH WARBLER *ACROCEPHALUS SECHELLENSIS*

A.W. DIAMOND

SUMMARY

DIAMOND, A.W. 1980. Seasonality, population structure and breeding ecology of the Seychelles Brush Warbler *Acrocephalus sechellensis*. *Proc.IV Pan-Afr.orn.Congr.* 253-266.

This species is now restricted almost entirely to Cousin Is., a reserve owned and managed by the British Section of I.C.B.P. Its appearance and more especially its voice support the view that it should be assigned to the *Acrocephalus gracilirostris* species group (Hall & Moreau). Brush Warblers are highly territorial (average territory size 0,225 ha), living in groups of two to five of variable composition, but always with at least one bird of each sex. Since Cousin was acquired by I.C.B.P. the Brush Warbler population has increased steadily at a rate of about six territories per year, apparently in response to an increase in suitable habitat as native woodland has been allowed to regenerate in the old coconut plantation. The number of colour-ringed birds in an intensively studied 1,4 ha area has decreased slightly, having apparently reached maximum density. Recruitment here (5,2% per year) was less than one quarter of that calculated for the population as a whole (22,7%). Adult mortality was 10,7% per annum, giving mean life expectancy of 8,9 years. The population usually breeds twice a year, once each in wet and dry seasons, apparently using rainfall frequency to predict peak abundance in insect food. As the still increasing population approaches the carrying capacity of the island, this continuing study promises results of considerable biological interest.

INTRODUCTION

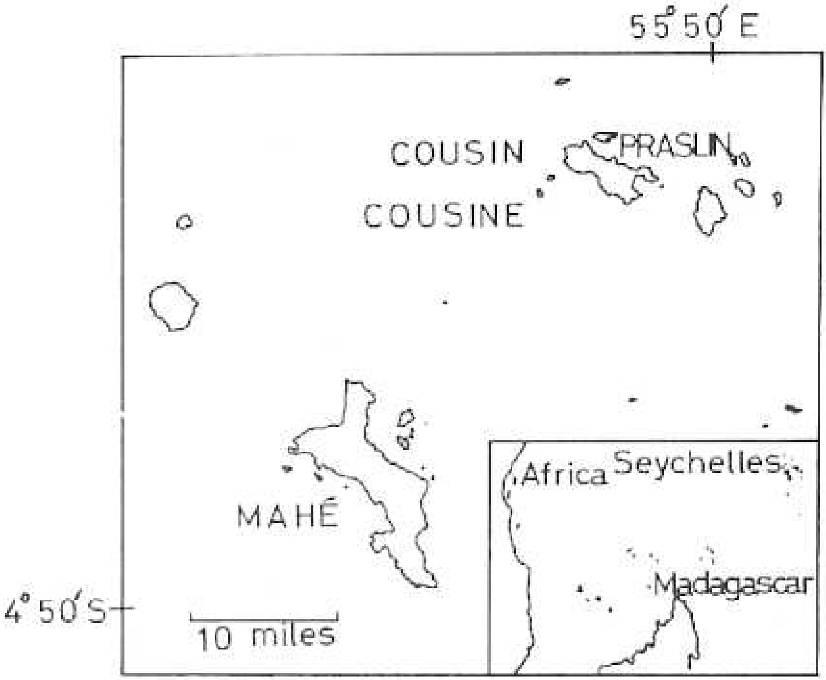
The Seychelles Brush Warbler *Acrocephalus sechellensis* is one of two species that constituted the genus *Bebrornis*, restricted to remote islands in the western Indian Ocean. *A.rodericana* of Rodrigues is described by Cheke (in press). *A.sechellensis* formerly inhabited Marianne as well as Cousin in the Seychelles, but is now confined to Cousin and Cousine; about 99% of the world population lives on Cousin. At one time described as one of the rarest birds in the world (Vesey-Fitzgerald 1940), there were only about 50 birds in 1963 (Gaymer *et al.* 1969). In 1968 Cousin Island was bought by the British Section of the International Coucil for Bird Preservation, who have managed the island as a nature reserve (Percy 1970). Management has been directed towards increasing the habitat for the warbler (Diamond 1975) with spectacular success, the population rising to nearly 300 by 1975. This paper describes three aspects of a two-year study of breeding ecology and feeding behaviour, designed to provide information on which to base future management policy. The study is continuing, and will be described in full elsewhere.

Cousin (04°20'S, 55°40'E) is small (28 ha) granite island, 2 km west of the northern end of Praslin, the nearest large island (Fig. 1). The southwestern part is a granite hill (69 m), barren on the south and east but more densely vegetated on the north and west slopes. The northeastern half of the island is flat coastal plain, locally called 'plateau', of phosphatic sandstone; the whole plateau was planted with coconuts *Cocos nucifera* between about 1910 and 1920, and it is in this overgrown plantation that most of the warblers live. A detailed description of the island is given by Diamond (1975).

METHODS

Habitat use and seasonality in breeding and feeding behaviour were investigated in all the land birds of Cousin (Diamond & Lloyd, in prep.). Once a month I walked slowly along each of two fixed routes, passing through all the island's habitats, once in each three-hour period from 0600 to 1800, and recorded the following data: species of plant on which bird first seen, feeding method, height, diameter of perch, type of prey, and breeding activity. For the latter, singing and carrying nest material were recorded, but for the warblers the most useful measure was the number of chicks heard giving the persistent and far-carrying begging call that is given throughout the post-fledging dependence period of two to three months. This study continued for the 20 months of May 1973 to December 1975, and gave information on the warbler population as a whole.

Figure 1. Map showing main Seychelles islands mentioned in text. Inset: position of Seychelles in relation to Madagascar and Africa.



In addition, territorial behaviour, population dynamics and the cycles of marked individuals were studied intensively in a small (1,4 ha) study area. This was in dense *Morinda citrifolia-Pisonia grandis* woodland on the plateau (Fig. 2), bordered and crossed by cut paths 1,5m wide, marked with consecutive numbers painted every 5 m. Mist nets were set up on these paths in a random rotation, and the warblers caught were colour-banded, weighed, measured, scored for visible subcutaneous fat and examined for primary moult and incubation patch, using the same techniques that Diamond (1974) used in Jamaica. Netting activity was reduced when all the warblers had been banded, but some netting was carried out in most months to provide data from recaptures, and special efforts were made to catch fledged young and unmarked birds that appeared in the area. The entire area was checked approximately weekly and the position of each bird noted by reference to the numbers on the paths, and regular searches were made for nests. The routine fixed walks around the island, and checks of the study area, provided the bulk of the information on the behaviour of the population as a whole, and of the marked sample of the population, respectively. Casual observations were also made elsewhere, especially around the house and laboratory where many of my other activities were concentrated, and are referred to as appropriate.

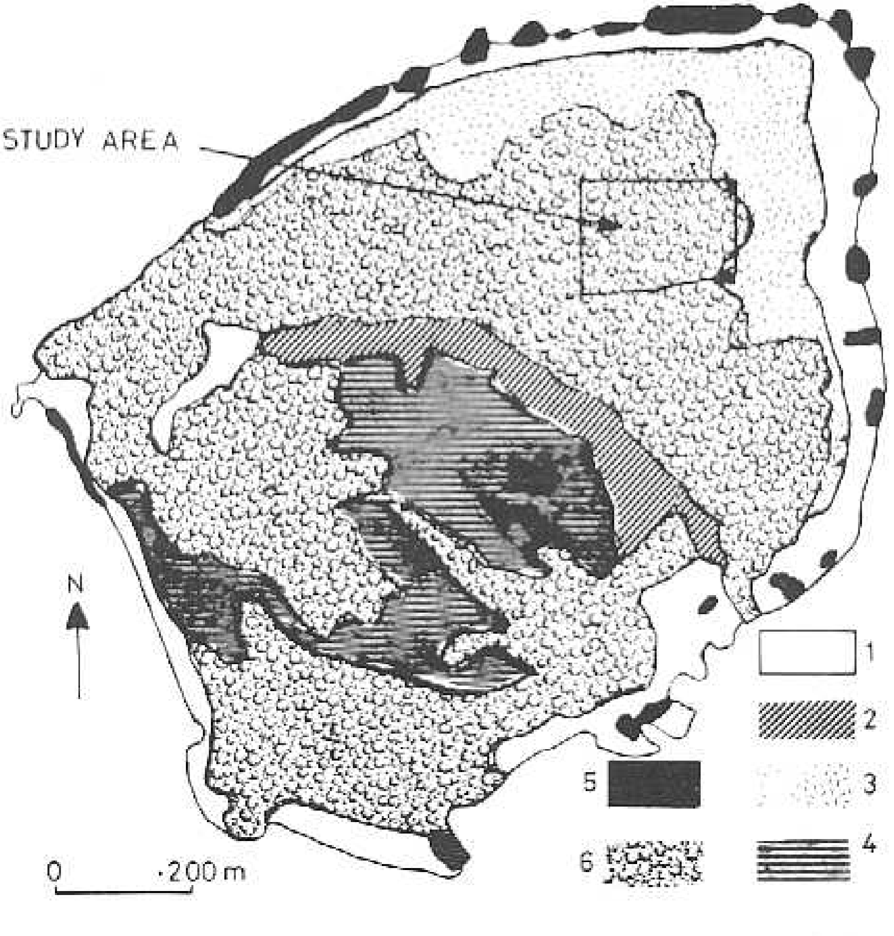
Seasonal variation in insect food supply was measured by sampling flying insects using a water trap with baffles (Southwood 1971:199) at ground level, set out fortnightly for 24 hours.

SPECIES DESCRIPTION

MORPHOLOGY, WEIGHTS AND MEASUREMENTS

The Seychelles Brush Warbler is a fairly large old-world warbler (Sylviidae), in the field usually appearing greyish or brownish green above, paler below, with pale lores and eye-ring of variable contrast. The tail is relatively long, the bill long and stout, the legs and feet slateblue. The light streaking on the breast of some individuals — not only juveniles as Gaymer *et al.* (1969) suggested

Figure 2. Simplified vegetation map of Cousin Island, showing location of warbler study area. Vegetation types: 1. Herbs. 2. Fruit trees and vegetables. 3. Open woodland regenerating near coast. 4. Herbs on hill slopes. 5. *Casuarina* groves. 6. Closed scrub, woodland and forest, chiefly *Morinda, Pisonia, Ficus, Euphorbia* and planted *Cocos*. (Greatly simplified from Diamond (1975)).



— seems to be due to feather arrangement rather than pigmentation. The eye is grey-brown or grey-blue in juveniles, red-brown in adults.

Weights and measurements are given in Table 1. Males were on average significantly larger than females in all dimensions except bill length. Relatively few individuals could be sexed; in any pair only the smaller bird developed an incubation patch and this was assumed to be the female. Only birds that were paired to a bird known to have developed a brood patch, were sexed as males. Many breeding units contained more than two birds and here only the female could be sexed, which accounts for more birds having been sexed as females than as males.

VOICE

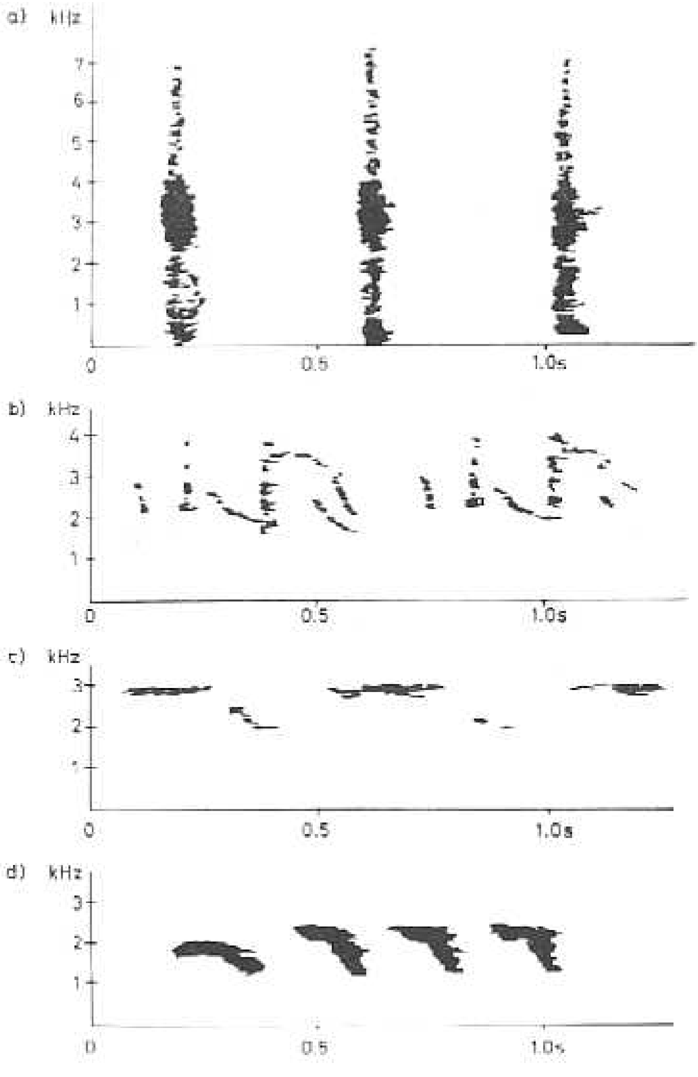
Brush Warblers have a short melodious song of simple whistled phrases repeated several times, with substantial individual variation. In addition a low, fast warbling was occasionally heard, often from young birds but sometimes from adults, which may be a subsong. The main calls are a harsh

TABLE 1. Weights (g) and measurements (mm) of adult Brush Warblers.

	Weight			Wing Length			Bill length			Tarsus length		
	n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.
Males	43	16,8*	0,79	9	67,7*	1,50	8	14,6	0,40	8	24,8*	1,29
Females	25	15,0*	1,12	12	65,2*	1,08	12	14,5	0,66	10	23.0*	0,59
Unsexed	26	16,4	0,96	14	67,9	2,44	17	14,5	0,73	16	24,1	1,38
All birds	—	—	—	—	—	—	37	14,5	0,63	—	—	—

*Significant difference between sexes (t-test, $p<0,001$)

Figure 3. Diagrammatic sonagrams of warbler calls. a) alarm calls, in response to playback. b) 'meeting' calls. c) &d) song phrases from two different birds.



nasal alarm call and a very low rapid twittering that I named the meeting call because birds often gave it on coming into close contact, but subsequently I also heard it from birds that were apparently alone. Juveniles from fledging until they become independent (two to three months later) have a single wheezy begging call that is repeated endlessly until the bird is fed.

Diagrammatic sound spectrographs of two song prases and alarm and meeting calls are shown in Fig. 3.

The alarm calls cover a wide frequency range, 0,08-8,0 kHz, are very short (c.0,075 s) and have an emphasised frequency higher than that of the song, between 2,5 and 4,0 kHz. (3a). This pattern is typical of calls given by passerines in response to stationary predators; the wide frequency band and the sharp beginning and end enable the call to be easily located (Thorpe 1961), and serve to attract conspecifics to the site. Warblers give this call in response to people, egg predators such as skinks, to other bird species (e.g. Seychelles Fody *Foudia sechellarum*) coming too close to the nest, or other warblers transgressing the territorial boundary. This call thus resembles, in structure and context, the 'mobbing' call of passerines that are at risk from aerial predators. I heard no call similar to the usual 'alarm' call of such species, with a narrow frequency range and indefinite start and end to the note. This may be because Cousin lacks the aerial predators that would elicit such a call. The only call that might have these acoustic properties (wide frequency range, difficult to locate) is the begging call of the dependent fledged young, which I found hard to locate, but I did not taperecord this call.

The meeting call is very quiet and therefore hard to record but seems to consist of two components: a short sharp call about 1,5 to 4,0 kHz, with a slurred descending call running from the top of this frequency range to the bottom, the two components together lasting about 0,19s. (3b).

The songs, from different individuals, differ slightly in phrase length (0,36s and 0,15s) and the degree of separation of the pure tone-like component from the slurred descending note, but have similar frequencies of about 1,9 to 2,7 kHz in one case, 1,1 to 2,4 kHz in the other. (3c,3d). These frequencies fall in the range 1,6-2,5 kHz that Morton (1975) found to attenuate least in tropical forest.

DISTRIBUTION AND AFFINITIES

The species was first described as *Ellisia sechellensis*, by Oustalet (1877) from specimens collected by de l'Isle on Marianne Island in February 1876. Lantz collected further specimens on Marianne in 1877 and described the species as being 'rare on Ile Cousine' (Oustalet 1878). Cousine is 2 km from Cousin, and Gaymer *et al.* (1969) thought Lantz had confused the two, but there is no reason to suppose that he did. Lister collected one on Cousin in 1888 (Benson 1971) and Didier collected three there in 1905 (Jouanin 1962). Thus there are definite past records from only Cousin, Cousine and Marianne. It was however overlooked on Marianne even by the assiduous E. Newton, who recorded all the other species there, so it may well have been overlooked elsewhere in the Seychelles. Penny (1974) stated that it was reintroduced to Cousine about 1960, but gave no evidence for this. Lloyd (pers.comm.) found three there in 1972; I found none on several visits in 1973 and 1974, but in December 1974 found one singing and caught another showing a brood patch several hundred metres away. The present population of Cousine can only be one or two pairs at most; thus nearly 99% of the world population is confined to Cousin.

Oustalet (1877) considered the species more closely related to *Ellisia* (now *Nesillas*) *typica* of Madagascar than to *E.* (now *Bebrornis*) *rodericana* of Rodrigues, but he had no specimen of the latter for comparison. Sharpe (1883) combined the Seychelles and Rodrigues specimens in one new genus, *Bebrornis*. Some recent authors (Jouanin 1962, Bourne 1968, Gaymer *et al* 1969) have combined *Bebrornis* with *Nesillas*, a genus otherwise confined to Madagascar, the Comores and Aldabra, while Benson (1960) also merged them but later (Benson & Penny 1968, 1971) suggested they should remain separate pending further information. My field experience of both *Bebrornis* spp. and of *Nesillas typica*, *N.mariae* and *N.aldabranus* leaves no doubt that the two genera are quite distinct and should not be merged. Vocal differences between the genera, and similarities within them, are particularly marked.

Traylor (in Benson & Penny 1971, and pers.comm.) suggested that *Bebrornis* was derived from *Acrocephalus*, which is a successful coloniser of islands in the Pacific and off west Africa.

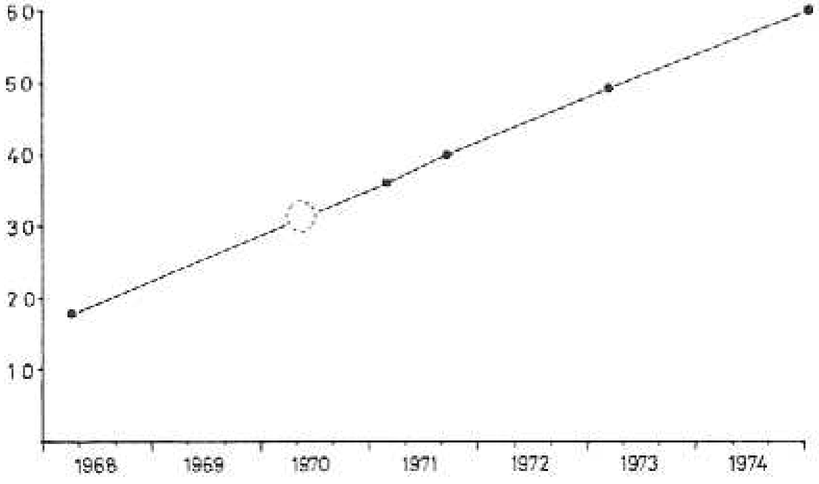
Bebrornis differs from typical *Acrocephalus* in several respects: wide bill, pale-edged rectrices, long distal primary; characters that are shared with the *Acrocephalus gracilirostris - rufescens* species group formerly separated as *Calamocichla*. Hall & Moreau (1970) pointed this out and suggested *Bebrornis* might also be a member of this group. Limited field experience of *A. gracilirostris* suggests its close similarity to *Bebrornis*, particularly with respect to voice, and there seems no longer any good cause to regard *Bebrornis* as anything other than an island form of *Acrocephalus*, and it is so treated here.

POPULATION DYNAMICS

Island population census

Brush Warblers are highly territorial, and defend their territories by song. The most convenient census method was therefore to walk slowly round the island, either imitating the song by whistling or playing back recorded songs, and mapping the localities of the birds which responded. At least two people were needed, one to keep track of birds in a territory while the other located the owners of the adjacent one, to ensure that birds were not counted twice. A check on this method, carried out in the study area where the territories were known and all the birds colour-ringed, showed that some birds were missed but all the territories detected. This method was first used by D. Lloyd in 1971 and has been in use ever since. Earlier counts, by P. Lousteau-Lalanne in 1968 and M.J. Penny in 1970, were of birds not territories and the census method was not stated. In plotting the change in population (Fig. 4) I have assumed that the mean number of detected birds per territory was the same then as in January 1975 (i.e. 2,3).

Figure 4. Increase in number of territories with time. Open dotted circle encloses area of uncertainty of 1970 census.



Census work was done on established paths, to minimise disturbance to other species, and so is incomplete. To check the proportion of territories detectable from paths, the 1973 census was complete, i.e. we left the paths when necessary and so covered the whole island. This showed that 50,5% (49/97) of the territories were detected from paths. In plotting population changes with time (Fig. 4) I have, for consistency, used only those territories detectable from paths: the full census results are given in Table 2.

Census results

Between 1968 and 1975 there was a linear increase in the number of warbler territories (Fig. 4). The rate of increase was equivalent to 6.2 territories per year. In a population expanding into a

TABLE 2. Census results.

					Total number of territories	
Month	Year	Authority	Source	Total number of birds	Detectable from paths	Not detectable from paths
April	1968	P. Lalanne	Lalanne 1968	42	18[1]	—
June	1970	M.J.Penny	Penny 1970	67*	29[1]	—
Feb/Mar	1971	D. Lloyd	Lloyd 1971[2]	—	36	6
Sept	1971	"	"	—	40	10
Mar/Apr	1973	D. Lloyd & A.W. Diamond	This study	—	49	48
Jan	1975	A.W. Diamond & J.R. Wilson	"	138	60	—

* Penny (1974) gives 85 birds. I have used his earlier figure as it is the original source and so likely to be more reliable. Both figures include fledged young.

[1] Estimated from the total number of birds, using the average 2.3 birds per territory found in 1975.

[2] Copies of Lloyd's maps were used to extract the data, rather than using the figures he gave. Counts of territories not detectable from paths in 1971 are incomplete.

newly-colonised habitat a logistic pattern of increase would be expected; on Cousin, it seems that the birds have been responding instead to a steady increase in the available habitat which supplied an equal number of new territories each year. Unfortunately vegetation changes have not been measured quantitatively so the point cannot be established beyond doubt, but regeneration of woodland has certainly proceeded without interruption since 1968 and the pattern of increase in the warbler population strongly suggests it is linked to this increase in available habitat.

The census unit has been the territory; individuals may have followed a different pattern of increase. Only since the establishment in 1973 of the study area of marked individuals has it been possible to detect this. Over the 20 months study of this area the mean number of birds per territory declined from 2.8 to 2.3, the number of territories increasing from 10 to 11. Using this latter figure, the number of birds at the time of the 1975 census (60 territories counted from paths, 59 estimated off paths) is estimated as 274, excluding recently fledged young.

STUDY AREA SAMPLE

Within the study area, the number of adults decreased from 28 on 30 September 1973 to 25 on 31 December 1974, whereas the population over the whole island increased by about 12% over the same period. Thus the population dynamics of the birds in the study area were not typical of the whole population; the chief difference seemed to be in reduced breeding output in the study area, but there are no quantitative data from outside the study area to confirm this.

Recruitment

In the study area, nine chicks were fledged in 11 territories containing an average of 26 adults during the 20-month study, equivalent to approximately a 20.8% production per year. Four of these fledged more than one year before the end of the study; of these, only one is known to have survived that year. The other three are thought to have died but may possibly have moved out of the area and evaded subsequent detection, though this is very unlikely. Assuming they did die, juvenile survival is 25%, reducing the recruitment rate to 20.8 x 0.25 = 5.2%.

Recruitment in the population as a whole must have been considerably higher, since the population increased by about 12% per year, (Table 2). If adult mortality is assumed to be the same in the study area and the whole population (10.7% per year), then recruitment in the population as a whole can be estimated as 10.7 + 12.0 = 22.7% per year, or over four times that in the study area. Territories averaged 57% larger outside the study area and the increased crowding within study area territories may have accounted for this reduced recruitment.

Mortality

Of 28 adults that had been ringed by 30 September 1973 and were seen regularly thereafter, at least 24 were certainly still alive at the end of December 1974. Adult mortality is thus 14,3% over 16 months, equivalent to 10,7% per year. Using the formula $s = 2-m/m$, where s = mean adult expectation of life and m = mortality (Lack 1954), mean annual adult life expectancy is 8,9 years.

The annual adult mortality of about 11% is similar to that recorded for other tropical forest passerines (Snow & Lill 1974, Fogden 1971) and considerably less than the 35-50% found in passerines that winter in the tropics but breed at higher latitudes (Roberts 1971, Nisbet & Medway 1972, Diamond & Smith 1973).

Emigration and immigration

For the population as a whole these factors can be ignored, since almost the whole population lives on the one island, but the measures of recruitment and mortality refer to the study area and there may have been movement in and out of there. However there seems to be little movement of adults once they have established territories; none of the birds ringed in the study area and subsequently seen regularly within it was found in a thorough search of the surrounding area during the 1975 census, although two birds that had been ringed in the study area but not resighted there were found some distance away. Movement into the study area is harder to detect since, unless all chicks can be ringed before they become independent (which was not possible), an unringed bird appearing may have been fledged within the study area.

POPULATION DISPERSION

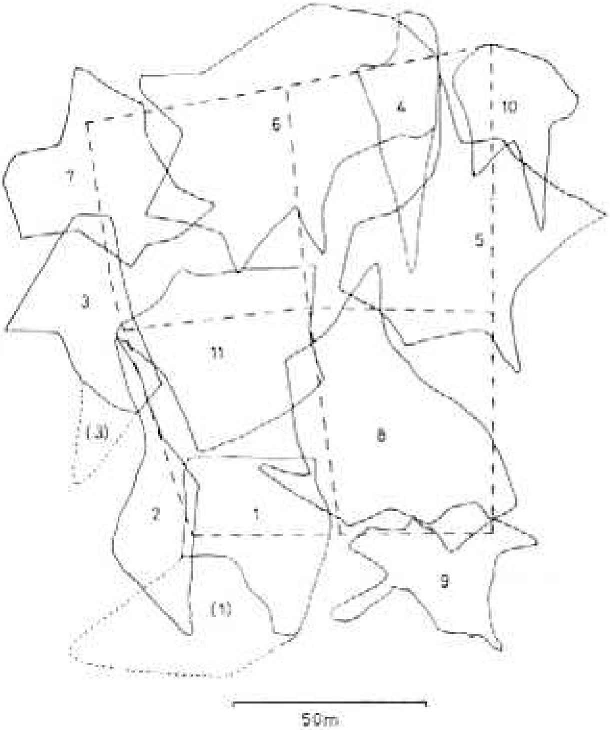
TERRITORY SIZE

Eleven territories were partly or wholly contained within the study area. Of these, six were considered to have been delimited reasonably accurately by plotting the observations of colour-marked birds (Fig. 5). The area of the territory was taken as that enclosed by a line joining the outermost positions at which birds were seen, forming a polygon (Stanger & Falls 1959), excluding observations that were unusually far from others. The concept of the 'observation-area curve' (Odum & Keunzler 1955) could not be used here because observations of marked birds were too infrequent, but territory size was not related to the number of observations so this source of error is unlikely to be important. The mean area of the territories of 18 birds, based on a mean of 46 observations per bird, was 1522 m^2 (s.d.424, range 916-2184). Males seemed to have slightly larger home ranges than females (1734 ± 310; 1451 ± 409, respectively), but the difference was not significant ($t = 1,46$, $p < 0,1$). There was no relation between the size of a group's territory and the number of birds defending it, which ranged from two to five.

The mean territory size in the study area, 0,15 ha, is the smallest recorded for any passerine. The nearest recorded figure, 0,2 ha, is for the American Redstart *Setophaga ruticilla* (Ficken 1962, Schoener 1968) which is a migrant and so holds the territory only during the breeding season. The Brush Warbler holds its territory all the year round, so the small size is even more remarkable. Warblers are more densely distributed in the study area than elsewhere; the average territory size, estimated by dividing the area of the island by the number of territories, is about 0,225 ha. The only other territories measured were the two which included the house and laboratory in open coastal vegetation with few trees. These covered approximately 1,7 and 1,9 ha, or more than ten times the average size of territories in the forest.

If we take the mean territory size in the study area as the minimum that could be maintained, the maximum number of territories that the island can hold is given by the area of the island divided by this territory size, i.e. 28/0,15 = 187 territories. This is probably an overestimate, since much of the hill is bare rock or herbaceous vegetation unsuitable for warblers. At a very rough estimate two-thirds of the island may ultimately be covered with forest in which the birds might maintain territories of this size, so the maximum number of territories may be recalculated as 187 x 0,67 = 125, with perhaps five to ten on the hill, an island total of 130-135 territories, so there is room for very few more territories unless territory size is compressed still further. Brief observations in November 1976 suggested that there may still be plenty of room for increasing the number of birds

Figure 5. Approximate boundaries of warbler territories in study area. Dotted lines: enclose observations in areas irregularly sampled. Dashed lines: footpaths. Solid lines: approximate territorial boundaries. Numbers correspond to group numbers in Figure 6.



per territory (one that held three birds in 1975 held eight in November 1976), so the population may continue to grow substantially even after the maximum number of territories is reached.

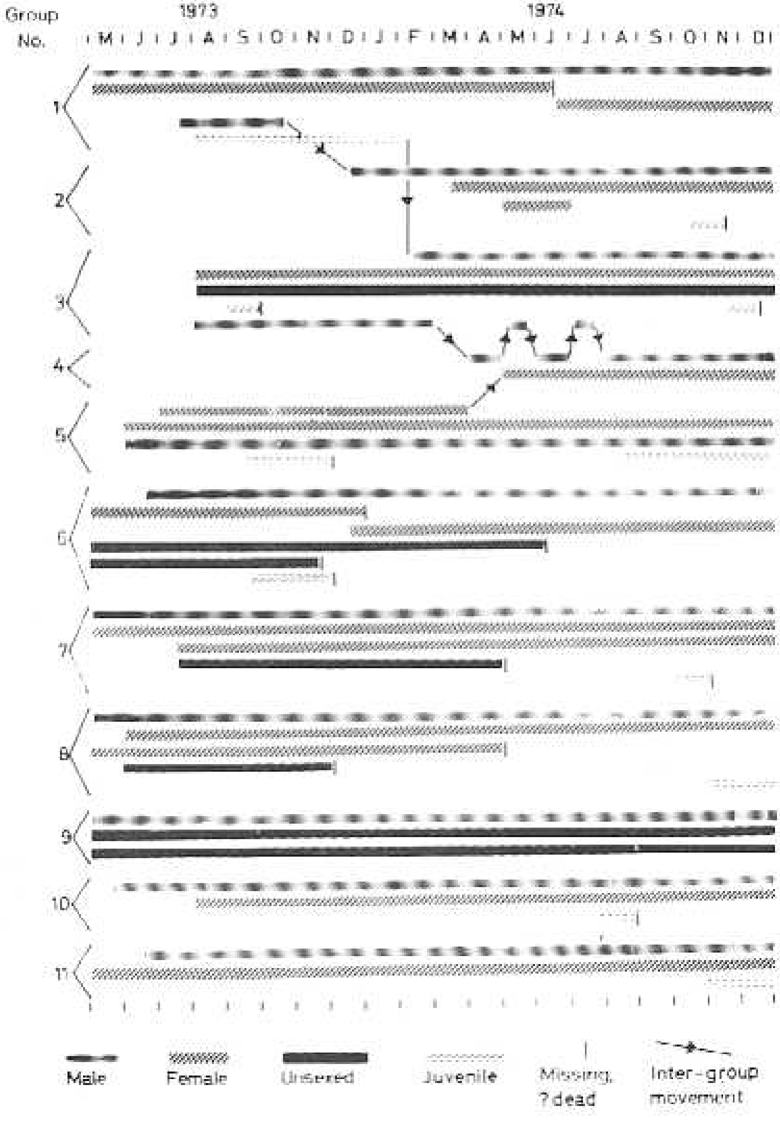
GROUP SIZE AND COMPOSITION

The composition of groups throughout the study is shown in Figure 6. In the eleven groups there was a mean of 2.7 birds per group, excluding recently fledged young.

Three groups (9,10,11) remained of constant composition throughout the study, two of them producing chicks in 1974. Two groups (7 and 8) changed only by the loss of apparently fullgrown birds (that may, nevertheless, have been juveniles at the beginning of the study), almost certainly due to death: one group decreased from four to three and the other from four to two, each also producing one chick during the study. Group 6 lost two fully-grown birds within two months but gained another in the same period: they later lost another so decreased from four to two but involved five birds in all. In four of the remaining five groups, birds changed groups or formed new ones. In group 3 a male, fledged six and a half months previously by group 1, entered the group and at the same time an apparently established male left to join a female, that had been a regular 'helper' (see below) in group 5, to from a new pair (4). Group 1's male helper also left to join group 2 whose composition was not well known because their territory was only just included in the study area. Group 1 also lost an adult female, which was replaced at once by a female of unknown origin.

The composition of the 11 groups can be arranged in four apparently distinct categories:
a) pairs: a male and a female that were seen consistently together in a territory where other birds were rarely or never seen. (Groups 4, 10, 11; and, temporarily, 1,2,5,6,8).

Figure 6. Composition of groups in study area, 1973-74.



b) pair plus helper: male and female seen consistently together; a third bird seen regularly in the territory, often alone, except when the pair nested, when the third bird was seen regularly at the nest or feeding the fledged chick and was clearly a 'helper' in the usual sense (Fry 1972). Only two groups were of this type, and in both the helper confined its assistance to only one part of the breeding cycle. In group 1 the helper (a male) probably shared in incubation, but certainly not in feeding the young; this bird later moved to an adjacent territory where it paired and raised young. In group 5 the helper was a female, and took no obvious part in breeding until the chick fledged, when it supplied nearly a quarter of the feeds given to the chick. This bird later paired with a male from group 3 that may itself have been a helper (although this group was too little observed to be sure) and formed group 4.

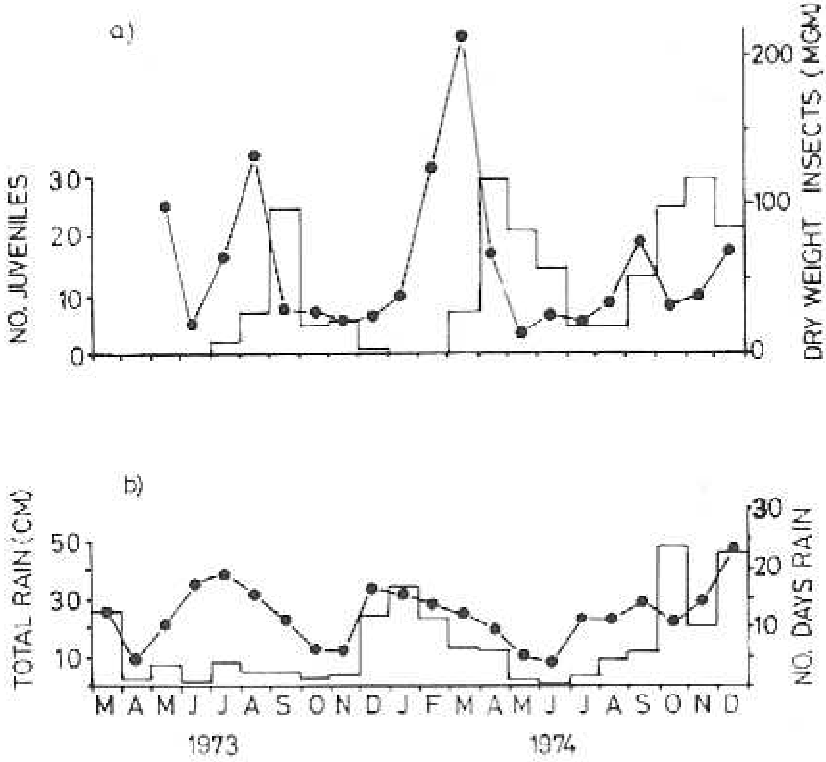
c) Trio: in group 9, and latterly in group 7, three birds were seen about equally often in the territory, no two birds associating together more frequently. They differed from the previous category in the lack of any obvious association between any two of the individuals.

d) More than three: In group 3 there was a period of about five months after a male had joined the group, while another male was vacillating between this and group 4, in which there were intermittently four birds in the group. Group 6 contained between two and four birds at different times, and five in all during the study period. Groups 7 and 8 both involved four birds for most of the time, though by the end of the study they contained only three and two respectively.

Pairs of course consisted of a male and a female: of the two known helpers, one was of each sex. Of the trios, group 7 contained one male and two females, and group 9 one male with two birds that were not sexed certainly but whose dimensions suggested they were one of each sex. All the larger groups contained at least one bird of each sex but many birds were necessarily unsexed (see Methods). There seems therefore to be no consistent relationship between the size of a group and its sexual composition, except that each group always contained at least one bird of each sex.

SEASONALITY

Figure 7. Seasonality of warbler reproduction in relation to food supply and rainfall. Solid circles: a) dry weight of insects caught in water trap (mean of 2 24-hr. samples per month), b) number of days on which at least 0.1 mm. rain recorded, corrected to 30-day month. Histogram: a) monthly total number of juveniles heard calling on routine fixed walks. b) total monthly rainfall. Note that the measure of breeding activity is the calling activity of fledged young, and so falls about two months after laying (see text).

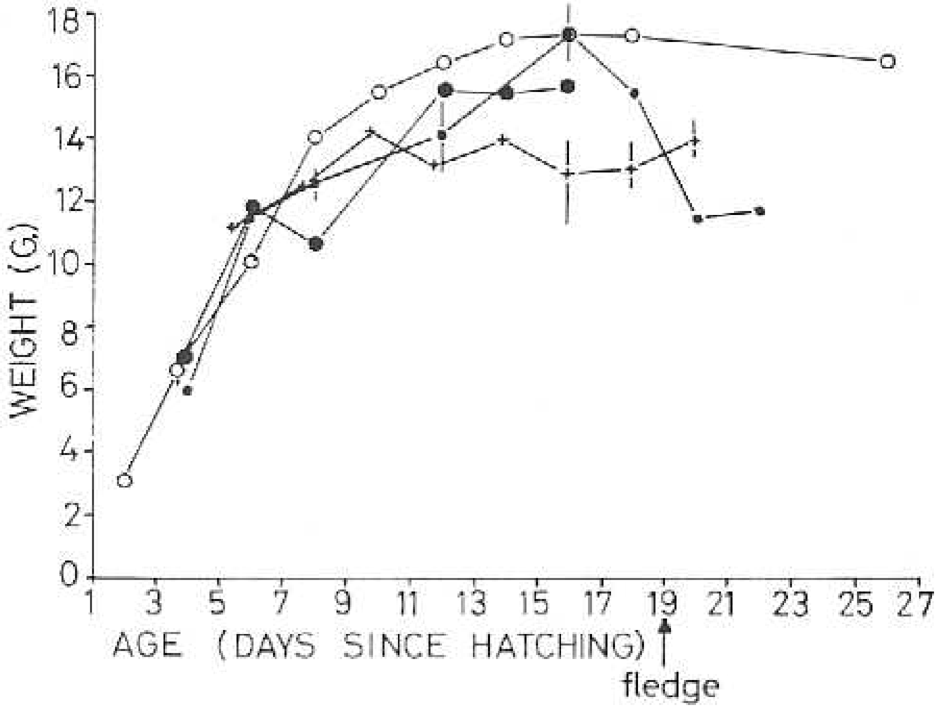


In the four and a half years for which records have been kept Brush Warblers have bred twice each year except in 1973 when they bred only once. The eight breeding intervals in the population ranged from 5 to 9,5 months, mean 6,9 months. Comparison of approximate laying periods with the total amount of rain, and with rainfall frequency (the number of days per month that 0,1 mm or more rain was measured) shows that laying periods were related more closely to frequency than to total amount of rainfall. Some laying periods (e.g. Sept/Oct 1971, June 1973) fell during a period of very low rainfall; but all laying periods occurred shortly after a rise in rainfall frequency.

Until food supply was measured, as it was in this study, it was very difficult to explain the breeding peak that occurs in most years during the dry season (June-Sept). However my records of rain and insect abundance (Fig. 7) show that although rainfall is low during the dry season, rain falls often enough — though in very small quantities — to raise insect abundance to a level allowing the warblers to breed. In the three breeding periods covered by this study, juvenile calls peaked about one and a half months after the maximum insect abundance; a juvenile probably calls most vigorously at three to four weeks old, and the fledging period is 18 days, so the peak food supply occurs approximately at the main hatching period.

A multiple regression of insect dry weight against rainfall amount and frequency showed that:
(i) neither amount nor frequency of rain were correlated with insect abundance in the same month, or the next month, but were positively correlated with insect dry weight two months later ($r = 0{,}53$, 19 df, $p < 0{,}01$, for each);
(ii) both amount and frequency of rain combined accounted for 43% of the variation in insect dry weight two months later ($r = 0{,}67$, 19 df, $p < 0{,}01$), whereas each rainfall parameter separately accounted for only 28%;
(iii) amount and frequency of rain were so highly intercorrelated ($r = 0{,}62$, 18 df, $p < 0{,}01$) that the effect of each on insect dry weight could not be separated statistically. This is probably because the very high values of all three measures coincide in the wet season and are sufficient to outweigh

Figure 8. Growth in weight of warbler chicks in different seasons. Vertical lines show ranges. Small dots = dry season 1973. Large dots = dry season 1974. Circles = wet season 1973-4. Plus signs = wet season 1974-5 — All twins.



statistically the numerically minor, but biologically significant, relationship between rainfall frequency and insect abundance in the dry season. Visual inspection of Fig. 7 shows that rainfall frequency is the only rainfall measure that can account for the dry-season insect peak, despite the statistical evidence that rainfall amount is equally important.

Courtship, nest building, laying and incubation probably take about two months (incubation is known to be 18 days). Two months is also the time lag between rainfall frequency and insect abundance. The birds could, therefore, by responding to an increase in rainfall frequency (or, in the wet season, rainfall amount) time their breeding effort so that food was at a maximum when the chick hatched. Whether or not this is how they do it, it is quite clear from these three seasons' data (Fig. 7) that the birds predict changes in the food supply, rather than respond to them.

Peaks of food supply are a function of rainfall frequency, but the amount of food in each peak is evidently influenced by rainfall amount. Prolonged heavy rain — i.e. a protracted period of high-frequency rainfall — occurred towards the end of the study period, in October and December 1974. At this time two warbler nests were found which each contained two chicks, though all active nests found previously had contained only one egg or chick. The relationship suggested above, between rain, food and breeding, would attribute these doubled clutches to a prediction by the birds that the sustained heavy rain would be followed by a prolonged period of high food abundance, sufficient to raise twice the usual number of young.

Lower levels of insect abundance were recorded in the dry season than in the wet, and this difference was reflected in the growth pattern of chicks reared in the two seasons (Fig. 8). Fledging periods and wing growth were the same in these two seasons, but weight increased more slowly, and reached a lower peak, in the dry season than in the wet. The two sets of twins that appeared in the very wet period referred to above, grew at rates similar to single chicks reared during the dry season. Unfortunately these samples are too small to be tested statistically.

ACKNOWLEDGEMENTS

This work was carried out while I was employed by the International Council for Bird Preservation (British Section) as Scientific Administrator of Cousin Island. I thank I.C.B.P. for their support and for the use of the Geigy Laboratoy of Cousin Island Research Station. For help in the field I am indebted to Roby Bresson, and also to David Lloyd and Roger Wilson, my predecessor and successor respectively, for permission to use the results of our joint censuses.

REFERENCES

BENSON, C.W. 1960. The birds of the Comoro Islands. *Ibis* 103:1-106.
BENSON, C.W. 1971. The Cambridge collection from the Malagasy region. *Bull.Br.Orn.Club.* 91:1-17.
BENSON, C.W. & PENNY, M.J. 1968. A new species of warbler from Aldabra. *Bull.Br.Orn.Club.* 88:102-108.
BENSON, C.W. & PENNY, M.J. 1971. The lands of Aldabra. *Phil.Trans.Roy.Soc.Lond.* B 260:417-527.
BOURNE, W.R.P. 1968. Further notes on the birds of Rodrigues. *Ibis* 110:338-344.
CHEKE, A.S. In press. Observations on the surviving endemic birds of Rodrigues. *Ibis.*
DIAMOND, A.W. 1974. Annual cycles in Jamaican forest birds. *J.Zool.,Lond.* 173:277-301.
DIAMOND, A.W. 1975. Cousin Island Nature Reserve management plan. London: International Council for Bird Preservation (British Section).
DIAMOND, A.W. & SMITH, R.W. 1973. Returns and survival of banded warblers wintering in Jamaica. *Bird-Banding* 44:221-224.
FICKEN, M.S. 1962. Agonistic behaviour and territory in the American Redstart. *Auk* 79:607-632.
FOGDEN, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114:307-343.
FRY, C.H. 1972. The social organisation of bee-eaters (Meropidae) and co-operative breeding in hot-climate birds. *Ibis* 114:1-14.
GAYMER, R., BLACKMAN, R.A.A., DAWSON, P.G., PENNY, M. & PENNY, C.M. 1969. The endemic birds of Seychelles. *Ibis* 111:157-176.
HALL, B.P. & MOREAU, R.E. 1970. An atlas of speciation in African passerine birds. London: British Museum (Natural History).
JOUANIN, C. 1962. Inventaire des oiseaux éteints ou en voie d'extinction conserves au Muséum de Paris. *Terre Vie* 109:257-301.
LACK, D. 1954. The natural regulation of animal numbers. Oxford: Clarendon Press.
MORTON, E.S. 1975. Ecological sources of selection on avian sounds. *Am.Nat.* 109:17-34.
NISBET, I.C.T. & MEDWAY, LORD. 1972. Dispersion, population ecology and migration of Eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. *Ibis* 114:451-494.

ODUM, E.P. & KEUNZLER, E.J. 1955. Measurement of territory size and home range size in birds. *Auk* 72:128-137.

OUSTALET, M.E. 1877. *Bull.Soc.philomath.Paris* (7) 1:103.

OUSTALET, M.E. 1878. Etude sur la faune ornithologique des iles Seychelles. *Bull.Soc.philomath.Paris* (7) 2:161-206.

PERCY, LORD R. 1970. Cousin Island nature reserve in the Seychelles. *Biol.Cons.* 2(3):225-227.

ROBERTS, J.O.L. 1971. Survival among some North American wood warblers. *Bird-Banding* 42:165-184.

SCHOENER, T.W. 1968. Sizes of feeding territories among birds. *Ecology* 49:123-141.

SHARPE, R.B. 1883. Catalogue of the birds in the British Museum. 7:102-103.

SNOW, D.W. & LILL, A. 1974. Longevity records for some neotropical land birds. *Condor* 76:262-267.

SOUTHWOOD, T.R.E. 1971. Ecological methods. London: Chapman and Hall.

STENGER, J. & FALLS, B.J. 1959. The utilised territory of the Ovenbird. *Wilson Bull.* 71:125-140.

THORPE, W.H. 1961. Bird-song. Cambridge: University Press.

VESEY-FITZGERALD, D. 1940. On the birds of Seychelles. 1 - the endemic birds (land birds). *Ibis* (14)4:480-489.

Dr A.W. Diamond, Zoology Dept. University of Nairobi, P.O. Box 30197, Nairobi, Kenya.

Present address: Edward Grey Institute, Zoology Dept., South Parks Rd. Oxford OX1 3PS, U.K.