SOME OBSERVATIONS ON NESILLAS ALDABRANUS, THE ENDANGERED BRUSH WARBLER OF ALDABRA ATOLL, WITH HYPOTHESES ON ITS DISTRIBUTION

By
C. Hamrler, K. Hambler and J. M. Newing

ISSUED BY
THE SMITHSONIAN INSTITUTION
WASHINGTON, D. C., U.S.A.
MAY 1985
CONTENTS

INTRODUCTION .............................................................................................................. 1

I: RECENT OBSERVATIONS .......................................................................................... 2
  1) Observations .............................................................................................................. 2
  2) Discussion of recent observations ............................................................................ 3

II: THE HABITAT OF N. ALDABRANUS ...................................................................... 5
  1) New observations on the vegetation of western Ile Malabar ............................... 5
  2) Review of features of the classic habitat ............................................................... 6
     a) Extremely dense vegetation ................................................................................. 6
     b) Large stands of Pandanus tectorius ................................................................. 7
     c) Abundant Dracaena reflexa ............................................................................... 8
     d) Absence of tortoises and goats ................................................................. 8
        i) Numbers ...................................................................................................... 9
        ii) Distribution ............................................................................................... 9
        iii) Impact .................................................................................................. 10
  3) New hypotheses on the habitat of N. aldabranus .............................................. 11
     3.1) Other peculiarities of the Gionnet region ...................................................... 11
        e) Relatively high rainfall ............................................................................... 11
        f) Relatively species-rich flora ....................................................................... 12
     3.2) Synthesis of features of the classic habitat .................................................. 12
        g) Predicted micro-climate with high relative humidity .............................. 12
        h) Predicted high invertebrate food supply ............................................ 13
  3.3) Predicted distribution of N. aldabranus ......................................................... 13

III: CONSERVATION OF N. ALDABRANUS .............................................................. 15

SUMMARY .................................................................................................................... 16

ACKNOWLEDGEMENTS .............................................................................................. 17

REFERENCES .............................................................................................................. 17
**NOTES:**

G.S.A. denotes Gionnet Study Area

O.S.A. denotes Opark Study Area

P.G.S.A. denotes Anse Petit Grabeau Study Area

.... denotes east/west extent of Study Area

A20 shows position of numbered post on coastal 'A' path

\[\} \text{ shows approximate position of vegetation transect within penetrable mixed scrub}\]

Note correct position of Anse Cèdres Opark
SOME OBSERVATIONS ON NESILLAS ALDABRANUS, THE ENDANGERED BRUSH WARBLER OF ALDABRA ATOLL, WITH HYPOTHESES ON ITS DISTRIBUTION

By

C. HAMBLER,* K. HAMBLER AND J. M. NEWING

INTRODUCTION

Nesillas aldabranus Benson and Penny, the Aldabran Brush Warbler, is endemic to Aldabra atoll, Republic of Seychelles. It is considered the world’s rarest, most restricted and most highly threatened bird (Collar and Stuart 1985).

This paper presents relatively recent observations of N. aldabranus, and considers the features of its habitat which may be involved in the very restricted distribution of this species on Aldabra. Testable hypotheses are presented which could form the basis of future work on this species, and which might help in efforts to conserve it.

The warbler was discovered in 1967 (Benson and Penny 1968), and as much of the atoll had already been sampled by mist-netting it was evident at that time that the species was not distributed throughout Aldabra. Extensive searches by R. P. Prüfs-Jones, between July 1974 and Feb. 1977, revealed five individuals; all were within a 50 m wide, 2 km long strip along the northern coast of western Ile Malabar near Gionnet (see Fig. 1). This strip will be called the Gionnet region, and the vegetation within it the classic habitat of N. aldabranus. No warblers have ever been seen away from their classic habitat, but it was hoped that the little-known southwestern region of Grande Terre might support a population; however, it is now known that the mixed scrub in the SW is dissimilar to that at Gionnet (Cowx 1980, D. McC. Newbery pers. comm. and personal observation) and limited searches with call playback revealed no warblers (C. Peet pers. comm.; personal observation 1983). It is thus considered unlikely that a population of N. aldabranus exists elsewhere than on Ile Malabar.

The population of the warbler was estimated to be at most 25 individuals in 1977, based on knowledge of behaviour and extrapolation into the extent of likely habitat (Prüfs-Jones 1979). The habitat considered suitable was that similar to the mixed scrub near the coast in the Gionnet region, and was thought to extend to ca. 1 km west of Anse Grand Grabeau.

* 14 Yew Tree Avenue, Bradford BD8 OAD, England.
The classic habitat was considered to have four features which, taken in conjunction, made it distinct from other areas of the atoll (Prŷs-Jones 1979). These were:

a) extremely dense, closed-canopy vegetation, with a considerable leaf litter/soil layer beneath;

b) large, dense stands of almost pure Pandanus tectorius;

c) a high abundance of Dracaena reflexa;

d) a total absence of both tortoises (Geochelone gigantea Schweigger) and goats (Capra hircus L.)

In this paper we review these four features, considering recent observations of the warbler and using selected data from a study we made of the composition and architecture of the mixed scrub of Ile Malabar (which will be published separately).

We report here some observations on the warbler and related subjects made by the Animal Ecology Research Group, Oxford, Expedition to Aldabra (on Aldabra 2 Aug. to 26 Sept. 1981), the Southampton University Expedition to Aldabra (11 July to 15 Sept. 1982) and the Cambridge Aldabra Rail and Brush Warbler Expedition (19 July to 24 Sept. 1983).

1. RECENT OBSERVATIONS OF N. ALDABRANUS

1) Observations

Observations of the warbler up to 1977 are given in Benson and Penny (1968) and Prŷs-Jones (1979). Since R.P. Prŷs-Jones left Aldabra in 1977 there have been, to our knowledge, four definite records of N. aldabranus and a number of observations of birds thought to be of this species. These records are listed in Table 1. It has been pointed out by R.P. Prŷs-Jones (pers. comm.) that very occasionally vagrant warblers of other species may be found on Aldabra, and that although the long calls of N. aldabranus are distinct from the vocalisations of other indigenous birds (O.E. Prŷs-Jones, pers. comm.), confusion might conceivably arise with such vagrants; therefore, only good visual records can be treated as certain.

We describe some of the recent observations in detail below:

In 1981, whilst walking along uncut transects, C. Hambler and T.C. Guilford heard a very distinctive call, subsequently identified by comparison with taped calls as almost certainly that of N. aldabranus. The site was in thick mixed scrub about 250 m east of Anse Petit Grabeau, and about 100 m inland close to vegetation dominated by Pemphis acidula. The call, lasting about two seconds, comprised a series of clicks in rapid succession; the frequency of clicking increased in the middle of the call, which was thus described non-phonetically as a "rattle, chirr, rattle". This may be the alarm call described by Penny as a harsh "chirrr" and by Diamond as a short, scolding chatter (in Benson and Penny, 1968).

On 1 Sept. 1983 at ca. 5 p.m. a chak sequence (Prŷs-Jones 1979) was heard three times by one of us (K.H.) in a thick Pemphis acidula bush, beside the northernmost pebble beach on the Malabar side of Passe Gionnet; several attempts were made to find this bird again in the following week,
including use of call playback and squeaking, but with no success.

On 2 Sept. in the early afternoon we heard two chak sequences between posts A28 and A29 on the coastal path at Gionnet. These calls, each lasting about 4 seconds, were probably the "machine-gun chatters" described by Prës-Jones (1979) as being given rarely, in excitement. The calling bird was seen, and it approached us--possibly attracted to squeaking. It did not respond to call playback and examined us from a distance of about a metre, before moving off and feeding in the scrub. The bird bore a single ring, on the right leg, so must have been one of the four birds ringed as adults in 1974; the colour ring on the left leg has been lost. Details of ringed birds are given by R.P. Prës-Jones (1979--for colour rings, and pers. comm.--for metal rings).

A warbler with a single ring, as above, was seen (by C.H.) around post A29 on 4 Sept., and between post A27 and A28 on 6 Sept. As other birds might have lost colour rings, we cannot be sure that the same individual was involved in each case.

In all the September 1983 sightings the bird was observed feeding actively; it appeared in good condition and was not in moult. In the sightings on 1 and 4 September the bird took many food items too small to identify, and was seen several times to hang beneath twigs and stems while pecking at the underside of leaves--such hanging behaviour was not observed by R.P. Prës-Jones (pers. comm).

2) Discussion of recent observations

The recent observations are interesting mainly because of the extreme rarity of N. aldabranus; although they add little to what is already known of the species, any information is worth examining in case attempts can be made to save the bird, or as the last records of a species becoming extinct.

At least one of the birds ringed between 16 April 1974 and 17 Dec. 1974 survived in 1983, indicating that an age of at least 9 years can be reached. This is not exceptional for a small tropical bird (Prës-Jones and Diamond 1984). A mean life expectancy of 8.9 years is given for the Seychelles brush warbler (Acrocephalus sechellensis) by Diamond (1980), and individuals of that species have been observed engaged in breeding behaviour at 10 years old (V. Wood, per. comm.) with some surviving to at least 11 years (H. Owen, pers. comm.).

The bird(s) we saw on 2, 4, and 6 Sept. 1983 showed an initial interest in us, and then wandered off feeding; in the latter two sightings, squeaking and call playback were not used to attract the bird, and indeed in the first sighting of a bird on 2 Sept., we were not even seeking the bird when it first appeared near us. We had the distinct impression that the bird spontaneously approached people as they moved noisily through the vegetation on the path. It is therefore interesting that curiosity and tameness have been noted in the probable ancestor of N. aldabranus: the polytypic N. typica of Madagascar and the Comoro Islands (Rand 1936; Benson 1960). It is possible that when approaching in "curiosity" the bird is seeking disturbed invertebrates--perhaps also why
Nesillas is a common member of parties of mixed species on Grande Comoro (Benson 1960). As will be discussed later (Section II, 3) invertebrate abundance or activity may be crucial to the distribution of *N. aldabranus*.

All of the records of *N. aldabranus* fall within the Gionnet region, with the notable exception of that from near Anse Petit Grabeau in 1981, which is some 9 km east of the nearest previous record. As this record was of voice only, it is subject to the reservation mentioned above. The isolated observation of *N. aldabranus* here would present many interesting possibilities, but information on the species is so limited that interpretation is virtually pure speculation. It suggests that the warbler can at least survive in habitat not previously considered suitable. However, virtually nothing is known of dispersion in this species, other than that it may account for periods when individuals "vanished" from the study area at times between 1974 and 1977 (Prŷs-Jones 1979).

It is unlikely that a "sizeable" population (i.e. one as large as that of the Gionnet region in the 1974-1977 period) could have escaped detection in the Anse Petit Grabeau to Anse Malabar area, as this area has been visited many times on various research and management projects. We visited the area of the 1981 record in 1983, and used call playback and squeaking without result. If a population did exist there it would be less likely to be discovered if it were more than about 50 m inland, away from the coastal path, in more dense and less visited vegetation.

Our exploration of the Anse Petit Grabeau area in 1981 and 1983 revealed a mosaic of mixed scrub and patches of *Pemphis*, with the mixed scrub being closer in composition to "Malabar Mixed Scrub" than to "Gionnet and Polynnie Mixed Scrubs" (vegetation classification after Gibson and Phillipson 1983). Unless other observations of the warbler are made in the Anse Petit Grabeau region, or east of Opark, we believe there are insufficient grounds to include the vegetation in this region as suitable habitat for a population of *N. aldabranus*.

The nest we discovered west of Opark presents the possibility of the Gionnet population of *N. aldabranus* extending to Opark inlet, which would be consistent with the observations on vegetation discussed in Section II 1 below.

There are not enough data to compare the size of the population of warblers near Gionnet in the early 1980's with that in 1974-1977. The species is difficult to observe, and responds less readily to call playback in the dry season when our visits were made (R.P. Prŷs-Jones, pers. comm.). The recent infrequency of observations does not give an indication of a change in abundance, which could have occurred without detection. We discuss in the next section changes in the vegetation on Ile Malabar since the 1970's, which lead us to suggest that the maximum likely population is about half that previously estimated, without assuming a change in the real density of the species.
II. THE HABITAT OF *N. ALDABRANUS*

1) New observations on the vegetation of western Ile Malabar

The critical factor in assessing the likely distribution limits of *N. aldabranus* on Ile Malabar is the distance to which habitat that is considered suitable extends east along the northern coast of the island. Various differences in the species composition of the mixed scrub vegetation of eastern and western Ile Malabar have already been described (Newbery and Hill 1981; Gibson and Phillipson 1983). A change occurs from the Gionnet type of mixed scrub to the more extensive Malabar type, but the details of the transitional zones were not known. Certain species of plants are exceptionally abundant in the NW of Aldabra ("northwestern species": Gibson and Phillipson 1983), and the frequencies of such species decline in the eastern region of Ile Malabar; we investigated this decline in 1983, using uncut transects marked on Fig. 1, to try and discover how mixed scrub suitable for the warbler graded into apparently unsuitable types.

Preliminary analysis of our results on the densities of plant species in the mixed scrub reveals that for a number of species there is a sharp decline in abundance in a particular section of the island: the Opark area. At this site there is an interruption of the coastal cliff, with a bay about 100 m wide which extends about 200 m inland before narrowing into a mangrove creek. As far as we could tell, this separates the mixed scrub belts along the northern coast on either side.

There are many differences in the density, architecture, and species composition of mixed scrub near Gionnet and Anse Petit Grabreau (Hambler et al. in prep.), but our most significant discovery is that some such differences are evident on opposite sides of Opark, despite the relatively short length of coastline involved. We illustrate this vegetation change in Table 2, in which selected species only are included; there are other plant species which do not follow the same trend, but we consider the species listed in the table are particularly useful in the context of a habitat change which might limit the warbler, and certain of these species are discussed in more detail in the following sections. The differences in vegetation across Opark, but particularly the dramatic decline in *Dracaena reflexa* and *Tarenna supra-axillaris* gave the very distinct impression that Gionnet-type mixed scrub ends at Opark.

It is probably not possible to determine how long there has been a difference in the vegetation on the opposite sides of Opark; the possibility that it is of recent origin cannot be excluded. We know of no studies of the vegetation in this area prior to our own in 1983. It is possible that the substrate is different west of Opark (which is an exceptional feature on the coastline), but a map of the geology of Aldabra (Braithwaite et al. 1973) does not suggest this; moreover, the topography of the Gionnet region is not thought peculiar (Thorpe and Stoddart 1969). We suggest that the vegetation differences across Opark may be partly the result of the activity of large herbivores, as discussed in Section II 2 d.
We now review individually features of the classic habitat, and its extent.

2) Review of features of the classic habitat

Although the combination of the four features listed in the Introduction is probably unique to Gionnet, it remains to be explained why this combination of features might be important to *N. aldabranus* whilst other unique habitats on Aldabra are apparently unsuitable.

a) Extremely dense, closed-canopy vegetation, with much litter and soil. "Dense" is a somewhat relative and ambiguous term in the context of vegetation, and is often used as a general description of the combined influences of rooted-plant density and architectural features such as abundance of twigs, leaves, etc.

The mixed scrub near Gionnet has been described as "dense tall scrub about 15 feet high, in places almost forest" (Fosberg in: Benson and Penny 1968), and as "extremely thick mixed scrub."... with exceptional "thickness of twigs and canopy right down to ground level" (Gibson and Phillipson 1983).

In 1983 we sampled mixed scrub on Ile Malabar, examining the densities of rooted woody plants, the height of the vegetation and the number of twigs of different sizes at various heights. The results of this study will be published elsewhere, but the general conclusion was that the scrub at Gionnet was not unique in its general density, but it is probably more consistently dense throughout the Gionnet region, with fewer of the more open areas found in mixed scrub elsewhere on Ile Malabar. There was a more obvious difference in the architecture of the mixed scrub near Gionnet than in the density of rooted plants: the abundance of *D. reflexa* and *Pandanus* spp. produced stands of vegetation which were locally extremely dense, as these plants have a rather different growth form to the other shrubs and trees (see illustrations in Fosberg and Renvoize 1980).

A rough relative measure of the density of the scrub is the ease with which it can be penetrated by people in a straight line without cutting. "Pemphis scrub" (Gibson and Phillipson 1983) is virtually impenetrable, and the bulk of the vegetation of Ile Malabar is *Pemphis*, which grades into mixed scrub along the northern part of the island. Using this measure, density increases inland away from the northern coast; we were able to penetrate an average of 225 m due south from the northern coast in the Gionnet Study Area, but 350 m in the Grabeau Study Area. In the Grabeau area and to the E the denser scrub is generally further inland. *N. aldabranus* does not appear to use the densest scrub (*Pemphis*).

The mixed scrub of Ile Malabar is heterogenous in many respects, and it is possible to find local areas with physical densities similar to that near Gionnet further east; the vegetation of Ile Polymnie is also very dense locally.

We sampled the height of the vegetation twice every 5 m of our transects for the first 100 m from the northern coast. The mean heights...
and standard deviations for the Gionnet study area were: 0 to 50 m: mean 3.38 m, s = 1.04; 50 to 100 m: mean 2.77, s = 1.02. For the Grabeau area: 0 to 50 m: mean 1.90 m, s = 1.67; 50 to 100 m: mean 2.51 m, s = 1.06. This shows a highly significant (p< 0.001) decrease in the height of the mixed scrub over the first 100 m from the coast near Gionnet, and a significant (p< 0.01) increase in the same distance in the Grabeau area; for the full 100 m, Gionnet scrub is significantly taller than that near Grabeau (p< 0.001), but this is due to the difference in the most northerly section. These data suggest a habitat change inland, and to the east.

N. aldabranus may inhabit the most consistently dense and tall mixed scrub on Ile Malabar; Ile Polymnie appears rather similar, but requires study. Although this appears the least unusual feature of the classic habitat, it is worth noting that N. typica on Madagascar prefers thick vegetation (Milne-Edwards and Grandidier 1879; Rand 1936) although it is not confined to it (Benson 1960).

The depth of soil and leaf-litter at Gionnet is not unique on Ile Malabar (pers.obs.) but an unusual shallow organic type is present (Trudgill 1979), which may be important.

b) Large, dense stands of almost pure Pandanus tectorius. Pandanus stands were considered to be clearly associated with N. aldabranus from general observation of the birds (R.P. Prŷs-Jones, pers. comm.), and the plant is used as nest material and as a site for nesting (Benson and Penny 1968). However, the high use the warbler makes of Pandanus spp. at Gionnet may be purely facultative, and we believe there is insufficient evidence that the distribution of N. aldabranus is in any way related to the distribution of this plant. Prŷs-Jones (1979) presents some data suggested to support such an association, but we believe that the single quantitative measure that he uses (linear abundance) is not sensitive enough to give an accurate comparison of the amount of Pandanus at various sites. We found it impossible to quantify Pandanus abundance with any single measure, as the growth form of this large plant produces stands which differ considerably in height, shape, orientation and "solidness", reflecting the number of leaves and stems and the arrangement of stems.

Pandanus spp. would be available to N. aldabranus in the mid and eastern regions of Ile Malabar (and throughout much of Aldabra), but it is clear from journeys by boat along the northern coast of Ile Malabar that there is considerably more Pandanus in the western regions; the dominance by the species of the Gionnet vegetation has been noted by Gibson and Phillipson (1983) as exceptional. Some P. aldabrense was found near Gionnet in 1983 (F. Friedman, pers. comm.), but it is probably rare on Ile Malabar (C W.D. Gibson, pers. comm.).

A possible direct relationship between Pandanus and the warbler might be that the plant provides physical protection against predation of the nests by rats (Rattus rattus) (Prŷs-Jones 1979). We suggest a possible indirect importance of Pandanus in the habitat of N. aldabranus: the structure and height of these plants might provide some form of shelter on both a large scale in the Gionnet region, and on a
micro-environmental scale within the stands. This will be discussed further in Section II 3.

c) A high abundance of Dracaena reflexa

The particularly high abundance of D. reflexa was considered by Fosberg to be the only ecological peculiarity of the vegetation in which the warbler was first found (Benson and Penny 1968). The dominance of the Gionnet vegetation by this species (and by P. tectorius) is one of the characters Gibson and Phillipson (1983) note as exceptional compared with other Aldabra vegetation. D. McC. Newbery (pers. comm.) also considers the abundance of D. reflexa to be a particularly notable peculiarity of the classic habitat.

D. reflexa is generally uncommon on Aldabra; its distribution follows a "Northwest and Groves" restriction pattern (Gibson and Phillipson 1983). It is most abundant in Gionnet type mixed scrub, in which Gibson and Phillipson found it to be about ten times as frequent as in the vegetation in which it was next most abundant (Gionnet and Polymnie mixed Pemphis); Ile Polymnie mixed scrub is very similar to that at Gionnet, with the important exception that D. reflexa is far less abundant. Ile Picard has very local and limited stands of D. reflexa, and the Groves area of woodland on Grande Terre has a few plants of this species.

In our Gionnet study area we found that D. reflexa is common from the northern coast to at least 200 m inland, and is present more than 200 m inland here and W of Opark. It is noteworthy that the "Z" path, a transect which crosses Ile Malabar due south from the Gionnet region, is not representative in this respect, since it suggests the belt of high abundance of D. reflexa extends only 50 m inland from the coast (Prŷs-Jones, 1979: Appendix 2). This is an anomaly produced by the Anse Porchê beach, behind which the path starts; this beach and bay occupy an area which would have been mixed scrub if the coastline had been straight; atypical plant species and human disturbance here are further complications. We found D. reflexa with high abundance, in thick stands, immediately W of Opark, and it is probable that it is present in similar quantity throughout the mixed scrub/mixed Pemphis between Opark and Passe Gionnet.

The northwestern distribution of D. reflexa (with certain other plants) may be explained by their sheltered position relative to the dry, salt-laden SW trade winds (Gibson and Phillipson 1983). The leaf surface of D. reflexa is not protected against high water loss (D. McC. Newbery, pers. comm.) and the species appears better adapted to the wetter parts of Aldabra. This will be discussed further in Section II 3.

N. aldabranus is known to spend considerable time foraging in stands of D. reflexa, although there is not sufficient evidence to demonstrate selective use of this plant (Prŷs-Jones 1979). We predict that detailed study would confirm such an association, since we predict certain invertebrates will favour the moist micro-environment this plant is likely to provide; this will also be expanded in Section II 3.

d) The absence of tortoises and goats

The Gionnet region, and Ile Polymnie, are unusual in that local
populations of the endemic giant tortoise and feral goats have recently been very low or absent (Bourn & Coe 1978; pers.obs.). These large herbivores may indirectly influence the distribution of N. aldabranus and so we present here evidence of population changes in these species which we suggest are of significance.

i. Numbers

Tortoises were reduced to very low numbers by exploitation before this century, and populations easily accessible from the settlement at Ile Picard were virtually exterminated; their numbers recovered rapidly this century when exploitation declined (Stoddart and Peake 1979). The population of tortoises on Ile Malabar was estimated to be about 2000 in the early 1970's (Bourn and Coe 1978), whilst there is not thought to be a population on Ile Polymnie (C.W.D. Gibson pers. comm.).

Goats were introduced to Aldabra before 1890, and their total population has suddenly increased alarmingly; in 1977 the total number was estimated to be 500 to 600 (Gould and Swingland 1980), but in 1982 it was estimated at 2560 ± 560 (Newing et al. 1984). The population on Ile Malabar was estimated to be 200 to 250 in 1976 (Gould 1979), and that of Ile Malabar east of Anse Grande Grabeau was estimated to be 289 ± 30 in 1982 (Newing et al. 1984). In 1983 we found fewer goats at the eastern end of Ile Malabar than in 1982, but more in the Anse Malabar/Anse Petit Grabeau area than in 1981. Given the distribution records below, these figures show a population increase and spread on Ile Malabar since 1976.

ii. Distribution

Tortoises were probably present throughout the length of Ile Malabar before their exploitation, and were probably particularly reduced in the more accessible western areas of the island. Fieldwork in 1972-74 suggested that tortoises were distributed in mixed scrub from the eastern tip of Ile Malabar to about 5 km E of Opark (Bourn and Coe 1978). Studies of goats between 1976 and 1977 suggested these also occurred over this range (Gould and Swingland 1980), i.e. up to Anse Petit Grabeau. No signs of goats or tortoises were found in brief explorations up to about 2 km W of Anse Petit Grabeau, nor near Anse Cédres Opark in 1975-76 (I.R. Swingland, pers. comm.). Brief visits to Opark between 1974 and 1977 revealed no signs of these animals (R.P. Prës-Jones 1979). Although Seychellois guides and workers think both goats and tortoises were present around Opark in the middle of this century (H. Charles, E. Constance and R. La Fontaine, pers. comm.), the numbers of large herbivores W of Anse Petit Grabeau must have been very low up to 1977.

In 1981 several goat and tortoise faeces were found about 1 km W of Anse Petit Grabeau (C.H., pers. obs.), and in 1983 we discovered goats and tortoises were present in numbers far too high to have been overlooked, up to the eastern bank of Opark. Tortoises were found throughout the Opark study area--i.e. up to 500 m W of Opark, but we could find no signs of goats W of Opark. The present western distribution limits of tortoises and goats are not clear, although we found no signs of them up to 2 km E of Gionnet. It is likely that there are more tortoises than goats W of Opark: the number of goats would have to be very low since no faecal pellets were found near the coast. There is an unconfirmed report that four tortoises were observed near Gionnet Camp in early 1983 (P.Bijoux,
pers. comm.). Our observations suggest very few large herbivores were present W of Opark in 1983.

It is clear that there has been a considerable increase in the numbers of both goats and tortoises in the western region of Ile Malabar, particularly E of Opark. This increase is likely to be a result of migration from more eastern regions, with continuous populations from Opark to Passe Houarseau. In 1983 we found that three of the tortoises examined near Anse Cédres Opark had disk marks indicating they had moved from the Anse Malabar region (some 7 km away) since 1974 (Bourn and Coe 1978), and tortoises and goats were evident throughout the Grabau study area in 1983. One tortoise nest was found near Anse Cédres Opark in 1983, but the smallest tortoises we found were about 10 to 15 years old—also suggesting movement was more important than reproduction in the population increase E of Opark.

Opark inlet is dry at low spring tides, and it is easy to cross on foot, small bays on each side providing points where access to and from the land surface is possible; the western bank is the more difficult to ascend and penetrate. The inlet may provide a relatively large obstacle to the movement of large herbivores on Ile Malabar, but there seems to be no absolute barrier, and it is possible that they could move round the inlet to the south. Although these herbivores may not favour the thick vegetation W of Opark, we believe it is only a matter of a few years before they cross the inlet in significant numbers.

iii. Impact

Tortoises and goats—the only large herbivores on Aldabra—may be responsible for some of the vegetation patterns on the atoll; however, the origins of most patterns are complex (Newbery and Hill 1981; Gibson and Phillipson 1983). It is useful to consider their potential impact on the habitat of N. aldabranus, by examining their distribution and behaviour in relation to the limits to the likely habitat of the warbler.

It is possible that the relative abundance of some plant species in the NW of Aldabra is related to the degree of exploitation of tortoises in these areas. However, exclosure experiments suggest that it is unlikely that release from grazing pressure alone would result in vegetation like that of Ile Polymnie (Gibson et al. 1983), nor like the similar Gionnet region.

In view of the dramatic vegetation differences across Opark, it is interesting to consider the known diets of the two herbivores. D. reflexa is a particularly important species to examine, as are other common species of the Gionnet mixed scrub which show a marked decline across the inlet.

Tortoises will readily eat D. reflexa (Grubb 1971) and are likely to damage it physically. However, they have not eliminated it on Ile Picard, or in the Groves, and are co-existing with it W of Opark (although they were found to be favouring stands of the species, judging by their faeces). Euphorbia pyrifolia and Tarenna spp. are considered unpalatable species for tortoises (Grubb 1971). It is thus unlikely that tortoises alone are responsible for the change across Opark.
Goats are capable of exploiting most vegetation types on Aldabra, and both graze and browse (pers.obs.). Although previously less dominant (Gould and Swingland 1980), goats are now having a striking impact on the vegetation of Aldabra, and on Grande Terre 36% of the scrub cover of some regions has been lost since 1978, particularly those species most palatable to goats (Newing et al. 1984). On eastern and middle Ile Malabar goats are now beginning to degrade vegetation (pers. obs. 1983). Goats are reported to take D. reflexa "more than occasionally" in studies of their food preferences on Ile Ficard (Stevenson 1972); E. pyrifolia is a "preferred" food; Tarenna supra-axillaris and T. verdcourtiana, however, are not eaten at all frequently (but might be indirectly affected by scrub degradation).

It is probable that goats are involved in the vegetation change across Opark, but they cannot be considered entirely responsible, as some less palatable species show a decline across the creek, whilst some preferred food plants (such as Polysphaeria multiflora) did not decline greatly. It is likely that a "natural" decline in "northwestern" plant species on Ile Malabar has been exaggerated by goats.

We conclude this review of the likely significance of tortoises and goats to the distribution of N. aldabranus by suggesting that large herbivores may adversely modify the vegetation by selective removal of some plant species and by opening up the scrub cover; this may have restricted the range of N. aldabranus in the past. We suggest that the west/east decline in certain plant species across Opark and the decline in large herbivore numbers (particularly goats) in the reverse direction is not coincidental. The absence of large herbivores is probably a key feature of the classic habitat, but not the most important.

3) New hypotheses on the habitat of N. aldabranus

3.1) Other peculiarities of the Gionnet region
Although the Gionnet to Opark mixed scrub region appeared subjectively distinctive to us, it is hard to single out the characteristics which gave this impression. The four features reviewed above are each fairly obvious at Gionnet, but they do not provide sufficient information to explain the limits of the population of the warbler. Other areas on Aldabra possess combinations of these features, apparently without supporting warblers, and although it is possible the birds do not occupy all suitable habitats on Aldabra, it is instructive to consider other characteristics of the Gionnet region which add to its distinctiveness. These features will be labelled: e) and f).

e) Relatively high rainfall
A feature of the northwest of Aldabra that has recently been confirmed is that it receives a relatively high rainfall; several years of records from rain-gauges at up to 14 sites around Aldabra have been compiled by Stoddart (1983), and these are sufficient to detect some trans-atoll variations in rainfall in the study period (1973-1981) although some sites lack records in some years.
The NW of Aldabra generally receives a higher mean annual rainfall than the other regions of the atoll. In the NW, Anse Var (on Ile Picard) received the overall highest mean annual rainfall (1567 mm); Gionnet received the second highest (1448 mm) and the highest mean annual rainfall in three out of the seven years for which records are available (in 1976, 1979 and 1981); Anse Var received the highest mean annual rainfall in two of the four years for which records are available (in 1978 and 1980). The rainfall in the NW and at Gionnet is also relatively high in the driest six months of the year (June to November), and in this period Gionnet receives a consistently high rainfall—no months with a mean rainfall of zero. The more easterly areas of Ile Malabar received a lower overall mean rainfall in the driest six months than did Gionnet and the NW (Stoddart 1983, figure 17).

Gionnet is probably not exceptional in its local rainfall, relative to the rest of the NW, but we consider the high rainfall it receives throughout the year to be an important link in the range of features which lead to the selective use of Gionnet by the warbler. Rainfall may be directly or indirectly important to *N. aldabranus*, particularly as in the dry season there is very little standing fresh water other than puddles after rain. Aldabra is relatively arid by comparison with other habitats used by Nesillas species, with the exception of *N. typica lantzii* of the subdesert in the SW of Madagascar. It is possible that Aldabra is a marginal habitat for Nesillas, in terms of water balance as in the dry season such a small island might provide fewer opportunities to acquire water (directly or in food) than do parts of the SW of Madagascar.

f) Relatively high species richness of the flora
The mixed scrub of Gionnet has a notably rich woody flora (D. McC. Newbery, pers. comm.; Gibson and Phillipson 1983). It is again not unique—the floras of Iles Picard and Polymnie are richer—but this may contribute to the quality of the habitat near Gionnet directly (e.g. through structural diversity) or indirectly (e.g. through herbivorous invertebrates see Frith 1979).

3.2) Synthesis of features of the classic habitat
We now combine the known features of the classic habitat ("a" to "f") with some predicted features ("g" and "h" below) to produce a general theory which may explain the restricted range of *N. aldabranus* on Aldabra.

We believe the most important and exceptional feature of the classic habitat is the high abundance of *Dracaena reflexa*. The distribution of this plant is not fully understood, and further examination of the substrate near Gionnet would be helpful. Substrate, available water and the activities of large herbivores may limit this plant's range on Aldabra; as this species is suspected to be susceptible to high transpirational water loss, we predict a likely feature of the Gionnet region:

g) Predicted micro-climate with high relative humidity and still air
We suggest that abundant *D. reflexa* will both depend on and produce a high relative humidity around the stands. This would be facilitated by a high and constant rainfall, a topographically sheltered position on the
atoll, and local windbreaks such as tall mangrove and Pandanus stands. Our subjective observations at Gionnet did suggest such a micro-climate, which might be important to the warbler in critical periods such as the dry season or when rearing young if standing water is less rapidly lost through evaporation. We predict a possible indirect importance of such a micro-climate:

h) Predicted high invertebrate food supply

Rainfall is probably related to the annual abundance and the types of insects on Aldabra (Cogan et al. 1971); local rainfall is almost certainly related to the local abundance of insects at various sites and times on the atoll (Frith 1979). Rainfall may act through increased humidity, and might act directly to increase invertebrate abundance and activity through decreased water-stresses, or indirectly e.g. through delaying leaf-fall. The classic habitat might provide diverse and numerous invertebrates for *N. aldabranus*, and this might be further increased by a rich flora (Frith 1979) and by the absence of strong winds. Spiders, winged ants and small moths are known to be eaten by *N. aldabranus*, at least occasionally in some numbers (Benson and Penny 1968). These invertebrates are not sufficiently known on Aldabra to test for an exceptional abundance near Gionnet; soil and litter arthropods do not appear exceptionally diverse or abundant near Gionnet (Spaul 1979), nor did those invertebrates sampled by Heath light traps (Frith 1979). However, neither of these surveys is comprehensive enough to support or refute our prediction: substrate is probably a major factor influencing ground-living invertebrates; the Heath trap is not a satisfactory sampling method for micro-lepidoptera (P.H. Sterling, pers. comm.) and many other groups; and Frith's trap at Gionnet was in "poor mixed scrub".

The invertebrates likely to be most significant to the warbler are those of the appropriate size range, active by day or sheltering by day in accessible places such as on bark or on leaves. We suggest the appropriate sampling method to test for feature "h" would be beating, and the dry season might be the most interesting time to compare the classic habitat with other areas. In passing, it is worth noting that there is a notorious abundance of mosquitos at Gionnet.

In concluding this synthesis, we suggest that it is significant that *Nesillas* warblers of the east and northwest of Madagascar "recherchent de préférence les endroits humides" (Milne-Edwards and Grandidier 1879). We suggest that features "a" to "h" could explain the limitation of a species of bird with very particular habitat requirements to the Gionnet to Opark mixed scrub, in addition this area of the atoll is, objectively, one of the most likely places to find a member of the genus *Nesillas* on Aldabra.

3.3) Predicted distribution of *N. aldabranus*

If we assume that the features of the classic habitat discussed above are in combination important to the warbler, we can predict the likely distribution limits to the current population. In general, we would predict that if *N. aldabranus* is present elsewhere on Aldabra, it is more likely to be in the mixed scrub in the NW--given the known (and probably related) vegetation and rainfall characteristics of that area.
The western limit to the population of the classic habitat appears to be Passe Gionnet (Prüys-Jones 1979). This is a channel about 100 m wide, of which the mixed scrub belt of the northern coast changes somewhat in character (Gibson and Phillipson 1983), probably reflecting a geological change (Braithwaite et al. 1973). Further W is the 600 m wide channel of Grande Passe, and west of this the mixed scrub is considerably different from that near Gionnet (Gibson and Phillipson 1983, and pers. obs.). Although there is considerably less D. reflexa on Ile Polymnie, we find it rather surprising that warblers have not been found there, and this island seems the most likely site for a population of the warbler outside Ile Malabar. It is possible that the absence of continuously abundant D. reflexa on Ile Polymnie breaks the vegetation into patches of suitable habitat too small to support a viable population of warblers. It is also possible that Passe Gionnet provides a barrier to voluntary movement of the warbler; it is notable that Nesillas is reported to fly poorly, and to be incapable of crossing "grands espaces d'une traite" (Milne-Edwards and Grandidier 1879).

The eastern limit of the Gionnet population seems less likely to be related to physical interruptions of the habitat; Opark inlet interrupts the mixed scrub, but Pemphis scrub behind it might permit movement round it. We suspect that a combination of the decline in rainfall to the E, and vegetation gradients, would have restricted the warbler to the western parts, and that the change across Opark marks the most likely eastern limit to the current population. Our limited sampling suggests that D. reflexa may decline slightly in abundance between Gionnet and the western bank of Opark (see Table 2), and it is likely that it declined gradually to the east of Opark before the encroachment of large herbivores. The nest found in 1983 gives hope that the warbler population does indeed reach Opark, but the probable record from near Anse Petit Grabeau in 1981 is too isolated to seriously suggest that the population extends this far east into such different vegetation.

Between Gionnet and Opark the mixed scrub belt is some 200 m wide; the species richness of the scrub, and the structural influence of Pandanus, decline inland from the northern coast. We find it surprising that N. aldabranus was not found more than about 50 m from the coast (Prüys-Jones 1979, and pers. obs.), and it would be interesting both to search intensively for N. aldabranus in mixed scrub between Gionnet and Opark, and to examine micro-climatic gradients inland from the coast within the mixed scrub; there are patches of mixed scrub between 50 and 200 m from the coast which closely resemble the classic habitat in most features (other than Pandanus stands, few of which occur more than 100 m from the coast here), and these seem the most likely marginal habitat for the warbler.

The population of N. aldabranus was estimated to be under 25 individuals if suitable habitat extended 50 m inland and 9 km along the coast from Passe Gionnet (Prüys-Jones 1979). We believe that in 1983 habitat that was closely similar to the classic one extended only to Opark, i.e. 4.5 km E from Passe Gionnet, and using the same assumptions for extrapolation the maximum likely population was about 13 individuals in 1983.
III. THE CONSERVATION OF N. ALDABRANUS

N. aldabranus is clearly endangered merely through its extremely limited distribution. It is not clear how long the population has been so small, but it is unlikely that a very small isolated population could survive long enough to become an endemic species with signs of island adaptations. It is probable that the warbler was either far more numerous and widespread on Aldabra in the past (perhaps in wetter periods of its history) or that the population is a relict of a recent colonisation by this species from an as yet undiscovered (and possibly extinct) population on another Indian Ocean island. If the former suggestion is correct we may now be witnessing the natural extinction of a species due to large-scale climatic and vegetation changes on Aldabra; long-term climatic changes are known to have occurred in the region (Stoddart and Walsh 1979; Walsh 1984) and standing fresh water has been more extensive on Aldabra in the past (Stoddart et al. 1971). In this case there is probably little that can be done to protect the species. If the population has always been restricted to a small area of Aldabra, or has been restricted at least in the last few centuries, then it is possible that Man might have indirectly influenced its abundance through the exploitation of tortoises and the introduction of goats and rats (Rattus rattus). It is possible that the warbler was able to colonise Aldabra, or temporarily flourished, because reductions in the populations of tortoises on certain islands of the atoll allowed vegetation similar to the classic habitat to expand. In the latter case, there would be more chance that the warbler could survive in the long term, provided reduction in its habitat through the encroachment of large herbivores can be prevented.

There is some recent evidence of vegetation changes in the Gionnet region since 1968: M.J. Penny (pers. comm.) reports that in 1984 he found that the areas of mixed scrub at both ends of Ile Malabar appeared less dense, with more dead twigs and branches, than expected. This would be worth investigating further. There is also evidence that the rat population is still widespread on Ile Malabar (we saw them frequently in all study areas in 1983) and there is evidence that their impact on Ile Malabar is increasing: we found rats had stripped bark from branches of 50% of the Mystroxylon aethiopicum we examined, and a few Sideroxylon inerme bushes had also suffered damage. This stripping of bark was not apparent in the late 1970's (D.McC. Newbery, pers. comm.) nor in 1981 (pers. obs.). It is likely that rats will evolve to exploit the fauna and flora of Aldabra more seriously. Local control of rats might be possible in small areas (e.g. if a nest of the warbler were found in use) using new, highly specific poisons (I.R. Swingland, pers. comm.).

It is vital that the remaining habitat of N. aldabranus be monitored and protected. It seems likely that goats and tortoises would degrade the classic habitat; the control of goats is very urgent, and easier to justify than the control of the native tortoises. Although complete eradication of the goats would be extremely difficult (considering the history of failures in the attempts to eliminate them from other islands) it might be possible to achieve this ideal using extremely specific biological control agents such as viruses; this method was suggested to control mammalian pest species in the Galapagos (Swingland in Mitchell 1981). In the short-term, culling of goats in the Opark area, and towards
Passe Houareau, might reduce the rate at which they are spreading towards the west and the classic habitat of the warbler.

We suggest that human disturbance should be minimised between Passe Gionnet and Anse Malabar (to include the area of the 1981 record); any tourists visiting the Gionnet region should be careful to reduce the possibility that they may introduce exotic seeds or pests.

Positive measures to encourage the remaining population of N. aldabranus seem theoretically possible if our hypotheses are correct. It might be fairly easy to increase the availability of standing fresh water, using water-dispensing hoppers; this might be particularly worthwhile in the drier months. The food supply might be increased locally if barrels of water, with netting over the top, were provided before and during the breeding season. Such measures might influence other species, including potential predators and competitors of the warbler, and so would require very careful monitoring.

**SUMMARY**

No more than one individual of Nesillas aldabranus has been seen at a time in each observation of the species since 1976, and there is no proof that more than one survived in 1983 although some observations suggest that this was possible.

Records of ringed birds since 1977 include at least one seen in 1977, and three sightings of a bird, or birds, which had lost the colour ring but bore only the metal ring in September 1983. There were three sightings of the warbler in late 1983, in which the view was not good enough to see if rings were present; there were no observations of the species in 1984.

Sightings of ringed birds show one bird to have lived at least nine years by 1983.

All sightings of the species have been within the Gionnet coastal region of Aldabra Atoll. One probable record, which cannot be proven, as only the call was heard, was reported outside the classic habitat in the vicinity of Anse Petit Grabeau; this suggests it may be possible for the warbler to venture into habitat dissimilar to that at Gionnet. Exploration of the vegetation east of Gionnet revealed a very sharp decline in the abundance of certain plant species across the Opark inlet, most notably that in Dracaena reflexa. The likely extent of habitat considered suitable for a population of the warbler is thus re-defined to half its previously suggested length, so reducing the predicted maximum population of N. aldabranus to 13 individuals within the mixed scrub between Passe Gionnet and Opark. The extremely restricted range of the warbler is discussed; known, recently-confirmed and predicted features of the habitat of the species are united in a general theory which helps explain this range the abundance of Dracaena reflexa is considered the most ecologically atypical feature of the Gionnet region, and it is suggested to be no coincidence that the other exceptional feature of this region is that it is the only area of Aldabra which supports a warbler of the genus Nesillas.
The following hypotheses are presented which inter-relate the features of the habitat of the warbler and its restricted distribution:

i) **Dracaena reflexa** is a particularly important feature of the habitat of *N. aldabranus*.

ii) Relatively high rainfall and shelter from the trade winds favour *D. reflexa* at Gionnet; this plant may be restricted to the west of Gionnet by substrate changes, and to the east by large herbivores and lower rainfall.

iii) A combination of high rainfall and a particularly high degree of shelter from drying winds (due to location and tall vegetation) promote a high relative humidity in the micro-climate of the classic habitat, with the greatest humidity in and near stands of *D. reflexa*.

iv) High rainfall and a predicted high humidity are significant to the warbler for part or all of the year; these features may be important through the water requirements of the birds, or through the activity, abundance or species composition of their invertebrate food supply.

Large herbivores have spread at least 4 km west towards the habitat of the warbler since 1977. Goats are particularly likely to have degraded possibly suitable habitat, and will encroach into and degrade the habitat of the warbler unless urgently controlled. Rats still present a particularly great threat. Some positive conservation measures may be possible, and are required immediately if *N. aldabranus* is to be saved.

ACKNOWLEDGEMENTS

We were very fortunate to receive much help and encouragement from Dr C. W. D. Gibson and Dr D. McC. Newbery, both on and off Aldabra. We thank Dr R. P. Prêys-Jones and Dr I. R. Swingland for very useful comments on our work. J. A. Stevenson, F. H. Drinkwater, V. Wood and H. Owen provided valuable data, and Dr C. J. Harrison and M. P. Walters kindly examined the specimen of a nest for us. Particular thanks go to the Seychelles Islands Foundation, and we are indebted to L. U. Mole, J. Collie and the Seychellois on Aldabra for making our work possible. Many groups and individuals supported the three expeditions from which our results derive, and we are most grateful for their help and interest. We thank also the members of these expedition teams, and J. A. Hambler for vital typing.

REFERENCES


**TABLE 1. CERTAIN AND POSSIBLE OBSERVATIONS OF NESILLAS ALDABRANUS 1977 - 1985. SEE TEXT FOR SOME DETAILS**

<table>
<thead>
<tr>
<th>OBSERVER</th>
<th>DATE</th>
<th>LOCATION</th>
<th>CERTAINTY</th>
<th>NOTES ON OBSERVATION</th>
<th>REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. HAMBLER &amp; T.C. GUILFORD</td>
<td>1/9/1981</td>
<td>Anse Petit Grabeu</td>
<td>v. probable</td>
<td>distinctive call heard once</td>
<td>PERS. OBS.</td>
</tr>
<tr>
<td>K. HAMBLER</td>
<td>1/9/1983</td>
<td>Gionnet: bank of Passe Gionnet</td>
<td>v. probable</td>
<td>3 calls heard in thick bush</td>
<td>PERS. OBS.</td>
</tr>
<tr>
<td>C. HAMBLER</td>
<td>16/9/1983</td>
<td>Opark: within 150 m only slight of western bank, c. possibility: 50 m inland nest only</td>
<td>certain</td>
<td>old, fallen nest, with some similarities to nests of warbler; stored in British Museum, Tring with nests of N. aldabranus</td>
<td>PERS. OBS. AND SPECIMEN. SEE ALSO BENSON &amp; PENNY (1968)</td>
</tr>
<tr>
<td>F.H. DRINKWATER</td>
<td>7/11/1983</td>
<td>Gionnet: 'A' path c. 500 m east of Anse Porche</td>
<td>almost certain</td>
<td>description of bird seen, and of call, matches the warbler, but no ring was seen and other (remote) possibilities exist; calls heard c. 100 m and a few mins. Apart could be from 2 birds</td>
<td>F. DRINKWATER pers. comm.</td>
</tr>
<tr>
<td>F.H. DRINKWATER</td>
<td>8/12/1983</td>
<td>Gionnet: as above</td>
<td>almost certain</td>
<td>seen as on 7/11/1983</td>
<td>&quot; &quot;</td>
</tr>
</tbody>
</table>
TABLE 2

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>DIST.</th>
<th>PAL.</th>
<th>STUDY AREA AND TRANSECT NUMBER (SEE FIGURE 1)</th>
<th>GIONNET</th>
<th>W. OPARK</th>
<th>E. OPARK</th>
<th>OPARK</th>
<th>ANSE PETIT GRABEAU</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 2 3 4 5 mean</td>
<td>6 7 mean</td>
<td>8 9 mean</td>
<td>mean</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acalypha claoxyloides</td>
<td>NW,G</td>
<td>T, G</td>
<td>0 6 8 13 16 8.6</td>
<td>56 58 57.0</td>
<td>35 7 21.0</td>
<td>39.0</td>
<td>22 11 12 34 37 23.2</td>
<td></td>
</tr>
<tr>
<td>Apodytes dimidiata</td>
<td>SE</td>
<td>UT,UG</td>
<td>0 1 0 3 9 2.6</td>
<td>17 0 8.5</td>
<td>4 6 10.0</td>
<td>9.3</td>
<td>7 6 20 0 5 7.6</td>
<td></td>
</tr>
<tr>
<td>Arecastrum microphala</td>
<td>NW,G</td>
<td>G</td>
<td>27 2 4 6 1 8.0</td>
<td>4 4 4.0</td>
<td>1 0 0.5</td>
<td>2.3</td>
<td>0 2 1 0 2 1.0</td>
<td></td>
</tr>
<tr>
<td>Bals Faultia</td>
<td></td>
<td></td>
<td>8 3 5.5</td>
<td>0 0 0.0</td>
<td>2.8</td>
<td>0 0 0 0 0 0 0.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Euphorbia</td>
<td></td>
<td></td>
<td>80 48 71 54 27 56.0</td>
<td>44 8 26.0</td>
<td>0 0 0.0</td>
<td>13.0</td>
<td>0 0 0 0 0 0 0.0</td>
<td></td>
</tr>
<tr>
<td>Euphorbia</td>
<td></td>
<td></td>
<td>25 16 22 7 15 17.0</td>
<td>18 7 12.5</td>
<td>0 0 0.0</td>
<td>6.3</td>
<td>0 0 0 0 0 1 0.2</td>
<td></td>
</tr>
<tr>
<td>Acalypha</td>
<td>NW,G</td>
<td>T, G</td>
<td>0 6 19 11 22 13.6</td>
<td>28 12 20.0</td>
<td>3 10 6.5</td>
<td>13.3</td>
<td>3 3 11 2 10 5.8</td>
<td></td>
</tr>
<tr>
<td>Arecastrum</td>
<td></td>
<td></td>
<td>19 4 5 9 1 7.6</td>
<td>4 4 4.0</td>
<td>0 5 2.5</td>
<td>3.3</td>
<td>0 0 0 0 0 0 0.0</td>
<td></td>
</tr>
<tr>
<td>Ficus</td>
<td></td>
<td></td>
<td>21 4 22 11 20 15.6</td>
<td>28 22 25.0</td>
<td>12 8 10.0</td>
<td>17.5</td>
<td>15 7 11 4 6 8.6</td>
<td></td>
</tr>
<tr>
<td>Arecastrum</td>
<td></td>
<td></td>
<td>20 27 25 18 21 22.2</td>
<td>37 109 73.0</td>
<td>27 13 20.0</td>
<td>46.5</td>
<td>35 23 14 7 8 17.4</td>
<td></td>
</tr>
<tr>
<td>Arecastrum</td>
<td></td>
<td></td>
<td>94 15 41 41 48 47.8</td>
<td>93 39 66.0</td>
<td>34 34 86.5</td>
<td>56.3</td>
<td>29 12 50 14 19 24.8</td>
<td></td>
</tr>
<tr>
<td>Arecastrum</td>
<td></td>
<td></td>
<td>4 2 11 14 13 8.8</td>
<td>5 6 5.5</td>
<td>2 3 2.5</td>
<td>4.0</td>
<td>10 0 1 0 2 2.6</td>
<td></td>
</tr>
<tr>
<td>Arecastrum</td>
<td>NW,G</td>
<td>T, G</td>
<td>76 23 51 44 41 47.0</td>
<td>83 21 52.0</td>
<td>4 0 2.0</td>
<td>27.0</td>
<td>0 0 2 0 0 0 0.4</td>
<td></td>
</tr>
<tr>
<td>Arecastrum</td>
<td></td>
<td></td>
<td>12 3 8 10 4 7.4</td>
<td>34 13 23.5</td>
<td>3 2 2.5</td>
<td>13.0</td>
<td>1 0 3 0 2 1.2</td>
<td></td>
</tr>
<tr>
<td>Arecastrum</td>
<td></td>
<td></td>
<td>6 2 4 5 4 4.2</td>
<td>1 5 3.0</td>
<td>3 0 1.5</td>
<td>2.3</td>
<td>2 0 0 0 1 0.6</td>
<td></td>
</tr>
<tr>
<td>Arecastrum</td>
<td></td>
<td></td>
<td>2 1 3 0 0 1.2</td>
<td>0 1 0.5</td>
<td>0 0 0.0</td>
<td>0.3</td>
<td>0 0 4 0 0 0 0.8</td>
<td></td>
</tr>
</tbody>
</table>

The northernmost 100 m of the transects shown in Figure 1 are used in this table; each transect is 2 m wide. The origins of the transects are considered to be at random with respect to vegetation patterns within each study area. The species selected are the 15 most common species of woody plants found in these transects, plus Pandanus spp. These data are generally insufficient for statistical treatment, but are considered to illustrate patterns noted in our study.

'DIST.' denotes restriction of distribution (after Gibson and Phillipson 1983); the symbols used for distribution centres are: NW = northwest centred; G = groves; SE = southeast centred; F = F. acidula scrub.

'PAL.' denotes known palatabilities to large herbivores; the symbols used are: T = palatable to tortoises; G = palatable to goats; UT and UG denote unpalatability to tortoises and goats, respectively. Palatabilities are taken from Grubb (1971) for tortoises; and Stevenson (1982), Newing et al. (1984) and pers. obs. for goats.