

# Population size and habitat associations of the Long-tailed Ground-roller *Uratelornis chimaera*

NATHALIE SEDDON and JOSEPH A. TOBIAS

## Summary

The Long-tailed Ground-roller (*Uratelornis chimaera*) is a globally Vulnerable, restricted-range species of dry forests in south-west Madagascar. We studied a population in 1997–2000, finding that nest-building was relatively synchronous and that pairs preferentially nested next to open areas, such as driveable tracks. By searching for trackside nests and for footprints, we conducted surveys throughout the known range of the species. Total transect coverage was 153 km, along which we encountered a minimum of 28 breeding pairs. By dividing the transects into 41 randomly distributed survey strips, each 1.2 km in length and 200 m broad, we intensively sampled an area of 9.84 km<sup>2</sup>. Using transect data, we made a tentative estimate of 5.7 mature adults km<sup>-2</sup>, from which we estimated a global population of 21,092 individuals, based on our calculation from satellite imagery that 3,706 km<sup>2</sup> of suitable habitat remained. By comparing habitat data at points with and without ground-rollers we found that, contrary to previous statements, they prefer lower stature or degraded habitats, and have no direct association with the endemic cactus-like tree *Didierea madagascariensis*. We used a novel census technique to provide the first quantitative data on population size, population density, breeding behaviour and ecology in the Long-tailed Ground-roller, or any member of the family Brachypteraciidae, information that is crucial to the design of effective conservation programmes.

## Introduction

The ground-roller family Brachypteraciidae (Order Coraciiformes) contains five bird species endemic to Madagascar, all of which are highly secretive and poorly known (Langrand 2001). Because of the ongoing destruction of Madagascar's forests, the family is of exceptional conservation importance: three of its constituent species are classified as Threatened (BirdLife International 2000). One of these, the Long-tailed Ground-roller *Uratelornis chimaera*, belongs to the only monotypic genus in the family. It is sexually monomorphic, socially monogamous, and nests in long burrows dug at an angle into flat sand (Langrand 2001, Tobias and Seddon 2003). Although mainly diurnal, it sometimes sings and feeds in darkness, somewhat like a *Rhinoptilus* courser (Appert 1968, Langrand 2001, pers. obs.). It lives singly in the dry season, in pairs after the first rains (October–November), and in small family groups containing 1–4 juveniles after fledging, mostly in November–February (Langrand 2001, pers. obs.).

Unlike the genera *Atelornis* and *Brachypteracias*, which are relatively widespread in the rainforests of eastern Madagascar, the Long-tailed Ground-roller is restricted to semi-arid deciduous forest in south-west Madagascar; it occurs in a coastal strip 30–60 km wide and 200 km long between the Fiherenana and Mangoky rivers, an area known as the Mikea forest (Seddon *et al.* 2000). Analysis of all published material until 1966 (mainly Oustalet 1899, Ménégau 1907, Bangs 1918), resulted in the conclusion that, within the confines of this range,

the distribution of the species coincided with that of woodland containing *Didierea madagascariensis*, an endemic cactus-like tree (Appert 1968). Because its range was supposedly more restricted than that of the Subdesert Mesite *Monias benschi* (the only other bird species endemic to the same tract of habitat), the ground-roller was assumed to be “more specialized” than the mesite (Collar and Stuart 1988). More recently, Langrand (2001) stated that it tolerates “slightly degraded forest” as long as it has deep leaf-litter and sandy soil. Indeed, a loose sandy substrate is essential to the species as it cannot dig its nesting burrows in rocky ground or firmer soil.

No quantitative assessments of habitat choice or population size have been undertaken for the Long-tailed Ground-roller, and there are conflicting accounts of its rarity. It was reported to be fairly common early in the twentieth century (Ménégaux 1907, Rand 1936), but by the 1950s it was becoming rare at Lac Ihotry (Griveaud 1960). It was then described as “extremely rare” in the 1960s (Petter 1963), and finally “one of the rarest birds in the world” (Appert 1968). A subsequent survey resulted in the conclusion that “the total population between Tuléar [= Toliara] and Lac Ihotry, i.e. the total global range, is not more than 500 pairs, and nearer 250 pairs with an 80% probability” (Milon *et al.* 1973). It was thus thought to have “seriously declined” (King 1977), until further fieldwork led to the more optimistic judgement that “in areas of undisturbed habitat it is common, and may even be termed locally abundant, particularly in areas of dense *Didierea* woodland” in the Ifaty/Mangily area (Collar and Stuart 1985). On the basis of this information, the Long-tailed Ground-roller is classified as Vulnerable according to IUCN criteria (BirdLife International 2000).

The species is exceptionally difficult to study and census because it is inconspicuous away from active nest-sites, and extremely secretive outside the breeding season (Langrand 2001). Indeed, some of the variation in previous survey results can be explained by seasonal fluctuations in detectability. Playback of vocalizations regularly fails to elicit a response and the species rarely sings after dawn (Tobias and Seddon 2003), therefore vocalizations do not provide a useful tool for assessing population size (cf. Tobias and Seddon 2002a). The best means of detecting the species is by searching for footprints and nest-holes; its nest-burrow entrance is distinctive and conspicuous, particularly as it is preferentially sited in open sand on the edge of small clearings or tracks, and its footprints are easily identified with practice (Tobias and Seddon 2002b).

Here we present the first empirical estimate of population size and habitat preferences in the Long-tailed Ground-roller, using a comprehensive transect survey conducted throughout its global range. In doing so we establish a baseline by which its conservation status can be objectively assessed, and against which future estimates can be compared.

## Methods

We spent three 5-month field seasons (September–January, 1997–2000) studying the Subdesert Mesite (Seddon *et al.* 2003), mainly at a site 32 km north of Toliara, south-west Madagascar (Point Kilométrique 32 or PK32: 23°04′57S, 43°37′15E). During this time we regularly encountered ground-rollers, and recorded data opportunistically.

### *Location and identification of nests*

Nest-cavities of this species are distinctive, especially as no similar-sized burrow-digging bird or animal lives in the Madagascan spiny forest (or Mikea forest). The cavities used by sympatric snakes are all much smaller in diameter and distinctly different in design. Burrows of Long-tailed Ground-roller slope at an angle into flat sand, through which a tunnel continues for at least a metre to the nesting chamber. By searching for these nests at PK32, and by tracking focal individuals during the breeding season, we ascertained that pairs with breeding territories

situated along a straight track through the study site usually excavated their nests adjacent to the track itself (see below). It was always possible, even during brief surveys, to identify active nests by the collection of fresh footprints around the entrance.

### Transects

To estimate the population size of this species we carried out transect surveys between 28 November and 13 December 1999 along nine straight tracks (Fig. 1): Tsifota–Ankililoaka (c. 20 km); Tsiandamba–Antseva (c. 25 km); Salary–Belitsaka (c. 25 km); Ambatomilo–Andabotoka (c. 25 km); Ambatomilo–Befandefa (c. 10 km); Ankindranoka–Basibasy (c. 20 km); Ankindranoka–Vorehe (c. 3 km); east of Morombe (c. 10 km); and PK32–Mikoboka Plateau (c. 15 km). These tracks traverse the global range, running from its easternmost limit to its westernmost, and distributed from its northernmost extremity to its southernmost. This system of tracks thus provides relatively complete coverage for an animal with such a large range. Our transects were divided into 41 survey strips, each 1.2 km in length and separated by 2–3 km. We accessed the starting point of each strip using a vehicle, but each strip was surveyed entirely on foot. To minimize disturbance and maximize the chance of encountering birds, a period of 5 minutes was left between switching off the vehicle's engine and commencing the survey. We stress that the tracks used as transects are straight, narrow (4 m wide), sandy tracks constructed for the purpose of oil exploration. They run through pristine or near-pristine habitat for much of their length, and in most cases trackside degradation and vehicle traffic is nil.

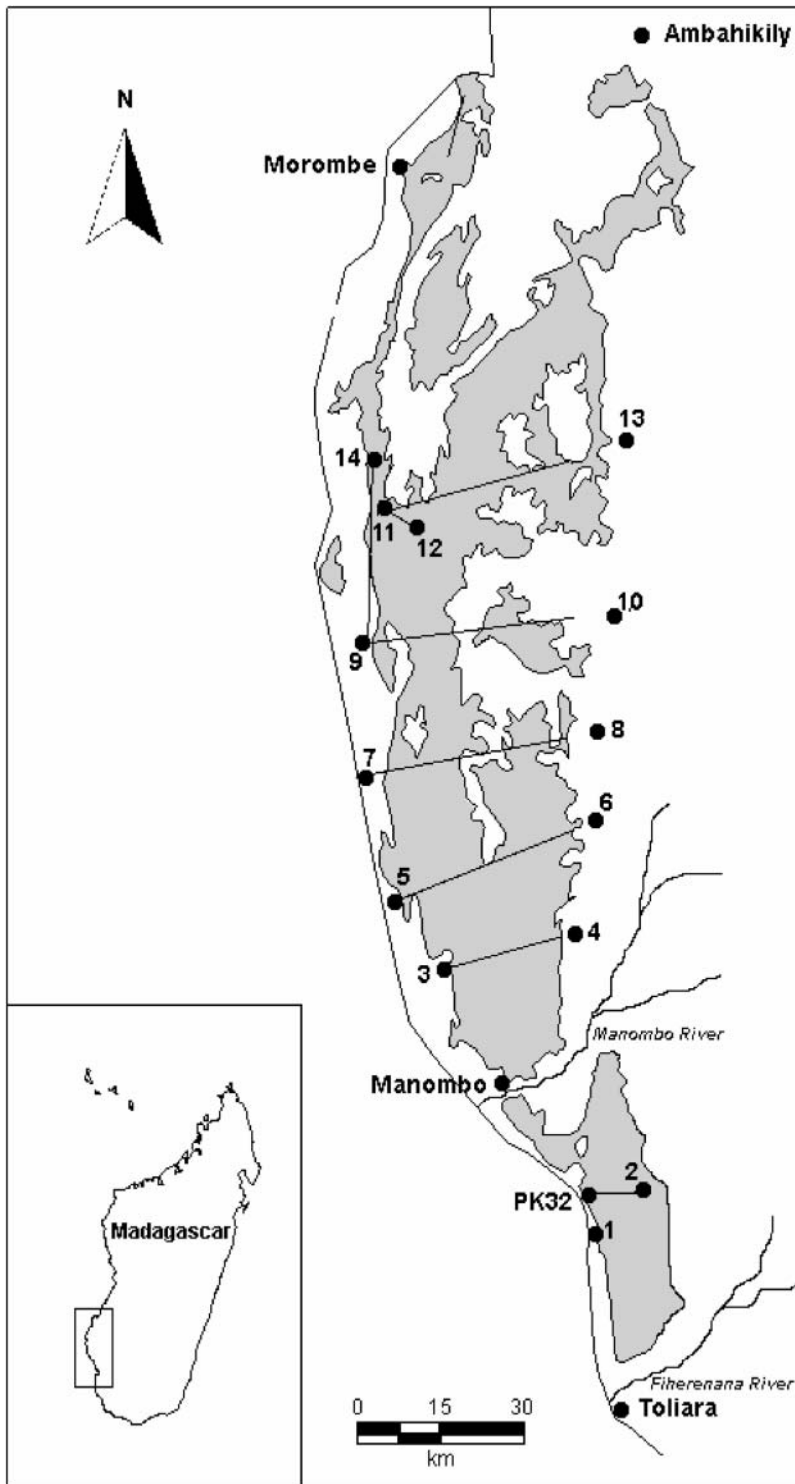
We located ground-rollers along these strips by listening for vocalizations and searching for footprints, nest-burrows, or evidence of nest-building. Given that breeding in the species is highly seasonal (nest excavation is possible only after the wet season begins in October), we timed transects to coincide with a period when most (or all) pairs had built at least one nest. Despite intensive searching we never found a nest facing towards vegetation, and thus we are confident that a very high proportion, if not all, trackside nest entrances were visible from the transect (see Results). As nest chambers from previous years invariably collapse during the dry season (pers. obs.), all nests were certain to have been excavated during the current breeding season. As we searched for nests only along tracks, however, any burrows situated within the forest were missed. At PK32 we found that breeding pairs within 100 m of tracks always left footprints along the track itself (usually at dawn, dusk, or during the night). For these reasons, we assumed that pairs whose territories were centred within 100 m of the track were very likely to have left evidence of their presence in the form of nests, or otherwise as footprints.

We treated an encounter as pertaining to a breeding pair only if we found a nest, or a cluster of nests. If there was a gap of > 100 m between nest clusters we assumed that more than one pair was involved. In all cases, quantification of the number of pairs involved was straightforward as the active and speculative nests of individual pairs were typically clumped along a short stretch of track.

To estimate population density, we took the area of each survey strip to be 0.24 km<sup>2</sup> (i.e. 1,200 m × 200 m), and the total area of available habitat within the range of the species to be 3,706 km<sup>2</sup> (Seddon *et al.* 2000; see below). We divided the population of each survey strip by its area (0.24 km<sup>2</sup>), to generate a population density per square kilometre. We then multiplied this density by the amount of available habitat to produce an estimate of total population size. Repeating this process for all survey strips gave us 41 population size estimates, from which we calculated a mean estimate with 95% confidence intervals.

### Validity of assumptions

The accuracy of our estimate relies on the validity of four major assumptions: (1) that habitat quality and population density in transect strips was representative of the total habitat area; (2)



that most nesting pairs of Long-tailed Ground-rollers whose territories were centred within 100 m of the tracks built at least one of their nest-tunnels at the edge of the track, or left footprints on the track itself; (3) that breeding territories did not extend beyond the limits of the 200 m wide strip, and (4) that the figure we use for the global range is accurate. We deal with these four issues in turn.

(1) If Long-tailed Ground-rollers prefer trackside habitats our extrapolation will tend to overestimate population size. However, given the sparse, deciduous nature of the forest, extra light at gaps makes little difference to the understorey, and thus habitat along tracks is indistinguishable from habitat away from tracks. At PK<sub>32</sub>, ground-roller footprints were regularly found > 1 km from tracks. There is thus no reason to suppose that the recently built tracks we used as transects have influenced the distribution of the species.

(2) At first glance, the idea that ground-rollers will select a trackside nest-site in preference to a secluded nest-site seems unlikely, but there are several pieces of evidence to support our assumption. At PK<sub>32</sub>, four out of five breeding attempts in a 3-year period involved nest-burrows sited next to the track. This amounted to 10 out of 11 (91%) nests. Our intensive fieldwork at this study site, including prolonged focal watches of individual ground-rollers in the breeding season, allows us to state with certainty that we did not miss any breeding pairs, nor did we miss any speculative nest-sites. Our assertion is not that most Long-tailed Ground-rollers nest along undisturbed tracks, merely that pairs occupying territories bisected by such a track tend to site their nests adjacent to it. If we have overestimated the propensity of ground-rollers to nest along tracksides, our population estimate will in turn be an underestimate. Conversely, if ground-rollers move their territories as well as their nests towards tracksides, then our estimate will exaggerate the population size of this species. However, the latter seems unlikely as there was no evidence of competition for trackside territories: many survey strips located in suitable habitat lacked evidence of ground-rollers, and one pair at PK<sub>32</sub> nested within the forest, despite the availability of space along the track.

(3) If breeding territories extended beyond the limits of the 200 m wide strip, our calculations will tend to overestimate population size. This contention can be discounted as anything but a minor issue because prolonged focal watches of pairs through the nesting period at PK<sub>32</sub> indicated that their home ranges at that time were relatively small (they never ventured more than 100 m from the nest). Moreover, neighbouring pairs were found nesting only c.150 m apart on three occasions.

(4) To generate an estimate of remaining forest cover in the entire global range of the species we interpreted two 1999 SPOT satellite images (03120723-36587 and -28090) using ISODATA automatic classification in conjunction with field reference data gathered in 1998–2000. Mapping vegetation cover and type from satellite imagery and field data involves numerous potential sources of error and it is unlikely that our absolute figure for forest cover is accurate, especially as it is now more than 5 years old. However, employing careful analysis of satellite imagery in an earlier study, we calculated a margin of error in our forest cover estimate of 5%, and rate of forest loss of less than 1% per annum (Seddon *et al.* 2000), thus our forest cover datum provides a good baseline figure from which to estimate a global population. Further details of the mapping and analysis process are presented in Seddon *et al.* (2000).

---

Figure 1. The location of Madagascar relative to Africa and the global range of the Long-tailed Ground Roller (the Mikea Forest, in grey). The position of PK<sub>32</sub> is indicated, as are the nine tracks (fine straight lines) used to conduct vegetation and playback surveys. Names of villages are: 1, Mangily; 2, Mikoboka; 3, Tsifota; 4, Ankililoaka; 5, Tsiandamba; 6, Antseva; 7, Salary; 8, Belitsaka; 9, Ambatomilo; 10, Andabotoka; 11, Ankinranoka; 12, Vorehe; 13, Basibasy; 14, Befandefa.

### Habitat associations

We used Discriminant Function Analysis (DFA) to examine the relationship between habitat variables and the occurrence of Long-tailed Ground-rollers. Vegetation was surveyed at a total of 212 points. Of these, 205 were derived from five points positioned at 300 m intervals along each survey strip, with seven points added where ground-rollers were encountered between survey strips. Thus, 205 points (97%) were positioned at random, i.e. with no bias towards locations with ground-rollers present.

Although survey points were placed centrally in the track, we ignored the track itself during our vegetation surveys. To achieve this we assumed the central point was located at the adjacent edge of the track, and surveyed a semi-circle of habitat 10 m in radius. By repeating this process on both sides of the track, we effectively surveyed two semi-circular areas, and then pooled the data. Our ability to detect birds was not affected by the quality of the habitat (e.g. amount of leaf-litter cover), because the sandy tracks on which we looked for evidence of ground-rollers were generally devoid of vegetation. In each survey area the same person estimated: (1) percentage leaf-litter cover; (2) depth of leaf-litter (in cm); (3) maximum and modal visibility at 0.5 m above the ground (in m); total number of four characteristic tree species, namely (4) *Euphorbia* spp.; (5) *Didierea madagascariensis*; (6) baobabs *Adansonia fony*; and (7) "Farafatse" *Givotia madagascariensis*; (8) maximum and modal canopy height; and (9) number of trees with diameter at breast height (dbh) > 20 cm. High scores for variables (6) to (9) were indicators of intact habitat (Seddon *et al.* 2000).

DFA was used to assess whether the vegetation data could be used to discriminate between survey points with evidence of ground-rollers and those without. A survey point was scored as having evidence of ground-rollers if we detected their presence within 100 m of the point. We justify this on the grounds that (1) in the majority of cases the survey point will have fallen within the territory of the birds detected, and (2) the habitat was very homogeneous. When carrying out DFA we included all variables simultaneously, using group size to calculate prior probabilities, and *F*-tests (Wilks' Lambda) to examine whether the overall discriminant model was significant. To rank the importance of the discriminating variables by total correlation, as well as the relative importance of each variable on the discriminant function, we calculated the Pearson correlation between a given independent variable and the discriminant scores associated with a given function (Statsoft 2003). To test the generality of the classification we used cross-validation to estimate error rates. By generating a discriminant function by withholding one observation at a time, and then classifying that observation (Bard *et al.* 2002, Westcott & Kroon 2002), this method controls for the bias involved in constructing discriminant functions with the same observations that they are then used to classify (Statsoft 2003). Prior to this analysis, data were checked for normality using Kolmogorov–Smirnov tests; data on percentage leaf-litter cover were arcsine transformed, while data on number of tree species and total number of large trees were square-root transformed.

All statistical tests were carried out using SPSS (version 11.01; Hedderson 1987); means are reported  $\pm$  SD unless otherwise stated; all *P*-values are two-tailed and corrected for ties where appropriate.

## Results

### Placement of nests

During the transect survey we found 35 nests, all of which faced away from vegetation: the distance from nest entrances to the nearest vegetation directly in front of the nest (mean  $\pm$  SE: 4.74  $\pm$  0.29 m) was invariably longer than the distance between nest entrances and the nearest vegetation directly behind (0.89  $\pm$  0.08 m; *t* = 12.6, *df* = 34, *P* < 0.0001). This difference reflects the fact that nests were almost always constructed so that the entrance faced directly

across the track. We defined the ground immediately above the burrow as being 'behind' the nest entrance.

Each pair excavated 1–6 nest chambers in the breeding season. When speculative nest-chambers were involved, these were always situated within 50 m of other nests built by the same pair. Pairs with territories centred further than c.100 m from the track nested in deeper forest, usually by narrow paths or small openings, and were not easily found.

### Population size

We found evidence of Long-tailed Ground-rollers at 23 new localities for the species including 22 of the 41 transect strips surveyed (Fig. 2). Evidence was usually in the form of sightings, recently constructed nest-cavities (35 in total, of which 31 were complete or well-advanced) and sets of fresh footprints. During the transect surveys, we encountered the species on 39 occasions, 28 of which involved confirmed breeding pairs. Taking all survey strips into account we estimated the mean population density to be 5.7 mature individuals  $\text{km}^{-2}$  (95% confidence intervals = 2.6–8.8), and the global population to be 21,124 individuals (95% confidence intervals = 9,487–32,687).

### Habitat associations

We found evidence of active pairs of Long-tailed Ground-rollers at 46 of the 212 points at which we sampled vegetation. We found that points with ground-rollers were best discriminated from those without by the habitat variables modal canopy height, maximum canopy height and extent of leaf-litter cover, all three of which had correlation coefficients with the discriminant function (DF) of  $> 0.5$  (Table 1). The descriptive DF thus generated had an Eigenvalue of 0.64 and was strongly significant (Wilks'  $\lambda = 0.85$ ,  $\chi^2_{11} = 32.8$ ,  $P = 0.001$ ). The overall degree of discrimination was high at 81.2%, with cross-validation correctly classifying 76.1% of survey points. This is significantly higher than expected by chance ( $\chi^2_1 = 5.07$ ,  $P < 0.05$ ). Overall, we found that ground-rollers were least likely to occur in high-stature forest, with a good cover of leaf-litter and numerous large trees (Fig. 3).

## Discussion

By counting trackside nests of the Long-tailed Ground-roller during transect surveys we estimated that 21,124 (9,487–32,687) mature individuals survive in the wild. Further, we argue that our assumptions, and the associated sources of error, do not invalidate this result, especially as they tend to work in opposite directions and thereby reduce each other's effects. If anything, the figure is probably an underestimate because we were more likely to miss pairs than to count pairs twice; if we had used our primary study site as a transect strip, for example, we would have encountered only four out of five pairs (80%). Therefore, regardless of the exact size of the population, it clearly far exceeds the published estimate of 1,000 mature individuals (Milon *et al.* 1973), and although our lowest estimate (9,487) falls slightly below a more recent estimate of  $< 10,000$  mature individuals (BirdLife International 2000), the true number of adults is likely to exceed this figure. The degree of uncertainty attached to several variables – notably the estimated extent of habitat, the proportion of excavated nests detected, and the size and distribution of breeding territories – means that our calculation is crude. Nonetheless, the result does provide strong evidence that the global population estimate should be revised upwards.

The perceived rarity of the species is easily explained: outside nesting periods it is so inconspicuous that it was once thought to migrate to unknown winter quarters (Collar and Stuart 1985). To overcome this problem we searched for nests and timed our surveys to coincide with the few weeks when this species is most conspicuous. Fortunately, given its nesting habits,

we are certain to have detected a high proportion of pairs in each survey strip. Detectability will have declined with increased distance of territories from the track, but to correct for this bias it would have been necessary to use distance sampling methods. These methods, which may have generated a more accurate population assessment, were impractical given the dense, thorny

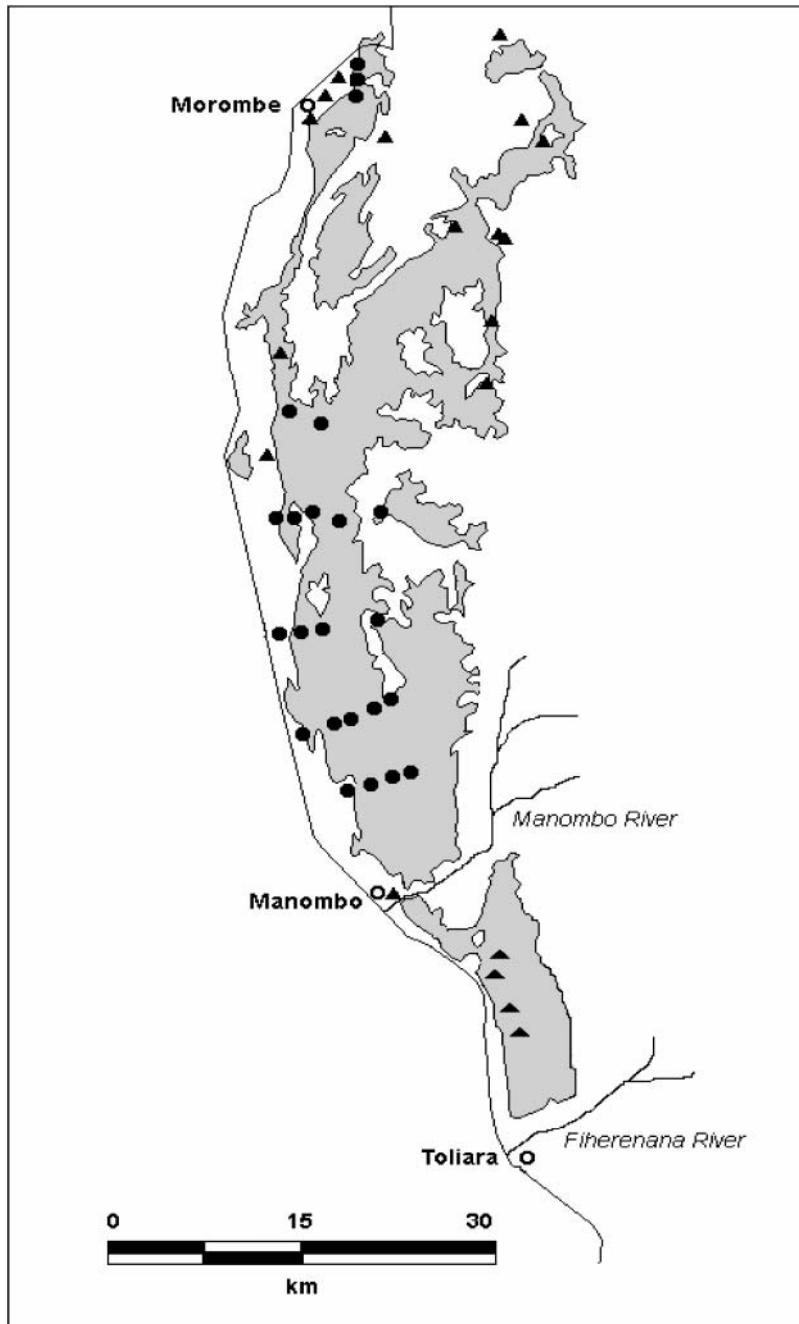




Table 1. Pooled within-groups correlations between habitat variables and standardized discriminant functions separating survey points with and without evidence of Long-tailed Ground-rollers.

Direction of correlation	Variable	Coefficient
Positive (no evidence of Long-tailed Ground-rollers)	Modal canopy height	<b>0.630</b>
	Maximum canopy height	<b>0.558</b>
	Leaf-litter cover	<b>0.512</b>
	Number of <i>Adansonia</i> spp.	0.350
	Maximum visibility	0.324
	Modal visibility	0.298
	Number of <i>Euphorbia</i> spp.	0.276
	Number of large trees	0.245
Negative (evidence of Long-tailed Ground-rollers)	Depth of leaf-litter	0.028
	Number of <i>Didierea madagascariensis</i>	-0.260
	Number of <i>Givotia madagascariensis</i>	-0.070

Variables are grouped according to the sign of their correlation. Points with evidence of ground-rollers are associated with high scores for variables with negative coefficients; points without are associated with high scores for variables with positive correlations. Correlation coefficients  $> 0.5$ , denoted in boldface, made a significant contribution to the discrimination.

habitat. Our method of searching for nests thus represents the most direct and workable approach to assessing and monitoring the status of the species.

The predilection of Long-tailed Ground-rollers for nesting at tracksides is poorly understood and worthy of further study. It is possible that in placing nests at the edge of openings in dense forest an advantage is conferred in terms of visibility, or ease of escape, or else because the substrate in these areas is relatively uncluttered with fallen debris and leaf-litter, and therefore easier to excavate. Undoubtedly, adults are at their most vulnerable to predators while nesting, especially as it is easy to dig them out of the sand, and it might be that this danger has shaped their nest-site preferences. Whatever the underlying reasons, the placement of nests provides a clue that can be used to survey the population.

The fact that no link was found with *Didierea madagascariensis* runs contrary to statements made by Appert (1968), and the fact that the Long-tailed Ground-roller appears not so much to tolerate slightly degraded habitat but to prefer it also contrasts with previous literature on the subject (e.g. Langrand 2001). It was often common in low-stature, disturbed forest, occurring (and breeding) in some extensive areas of regrowth less than 2 m tall, habitat that is avoided by Subdesert Mesites (Seddon *et al.* 2003). The Long-tailed Ground-roller therefore appears to be the less

Figure 2. Distribution of new (circles) and historical localities (triangles) of the Long-tailed Ground-roller. As the transects ended at the eastern limit of suitable habitat, the mapped localities equate to the range of the species, which is narrower in the south than the north. Of the new localities, 20 are mapped using the coordinates of the mid-point of each survey strip in which we found evidence of ground-rollers; the remaining three derive from records made outside the survey strips. We measured coordinates using a Garmin 2-plus GPS. Historical records are from Oustalet (1899), Ménégau (1907), Rand (1936), Appert (1968), Milon *et al.* (1973) and Collar and Stuart (1985). There are early specimens in the Museum National d'Histoire Naturelle, Paris, which were collected, according to their label data, at or near to Toliara, and thus outside the known range of the species. We have not mapped these as it was common practice to label specimens with the name of the nearest large town. There is thus no proof that the species ever occurred south of the Fiherenana River.

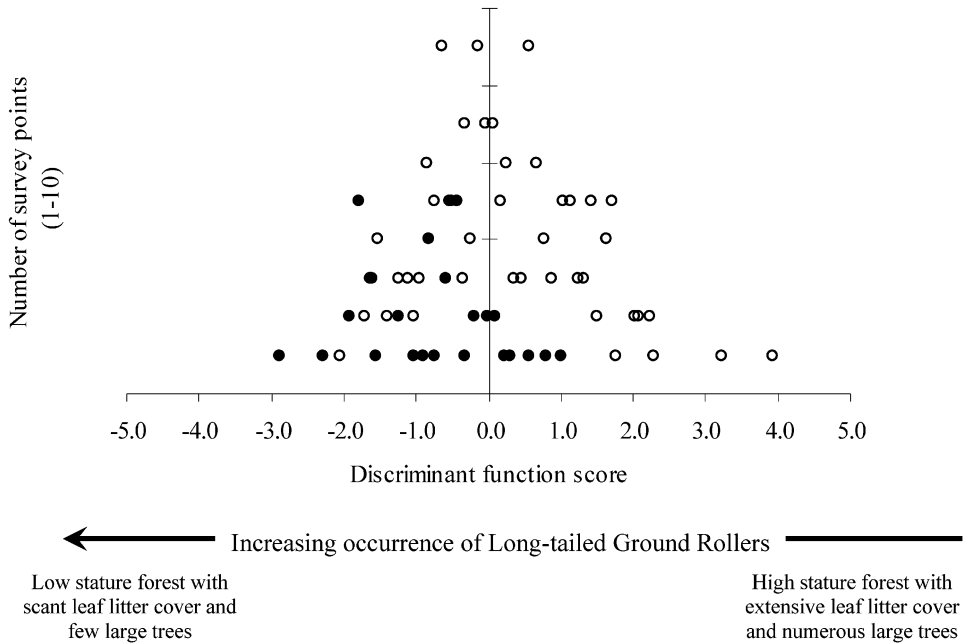


Figure 3. The distribution of discriminant function scores produced by the simultaneous inclusion of habitat variables for survey points with Long-tailed Ground-rollers (filled circles,  $n = 46$ ) and those without (open circles,  $n = 166$ ).

specialized of the two species (*contra* Collar and Stuart 1988), and certainly the better adapted to degraded habitat.

Both these endemic species avoid excessively rocky or sandy areas, but, unlike the mesite, the ground-roller is scarce in taller forest with deep leaf-litter. Presumably, it can only dig nest-burrows into soft sand, and not into firm or humic soils. In optimal habitats, the Subdesert Mesite appears to be considerably more abundant, and its total population probably exceeds 100,000 individuals (Tobias and Seddon 2002a), partly because it lives in groups rather than pairs. This disparity notwithstanding, it is possible that the mesite is more highly threatened than the ground-roller simply because it fares poorly in degraded or secondary habitat.

Having shown that the Long-tailed Ground-roller is almost certainly more common than once assumed, and capable of surviving in degraded habitat, does it warrant treatment as a Threatened species? Using a strict application of the precautionary principle to invoke a population size of 9,487 mature birds, this species would qualify as Vulnerable simply because its habitat is declining. However, the data presented above suggest that a global population estimate of 20,000 mature individuals is more reasonable, in which case, as with the Subdesert Mesite, the species only qualifies for Threatened status if we predict a rapid population decline. Given that over 16% of the original forest cover has declined since 1962, and the annual rate of deforestation is increasing by 0.93% per annum (Seddon *et al.* 2000, Tobias and Seddon 2002a), this prediction seems plausible. Indeed, although Long-tailed Ground Rollers appear to prefer slightly degraded forest, they do not occur in habitat that has been completely deforested. Moreover, both *Uratelornis* and *Monias* are monotypic, possibly ancient genera, restricted to the same small area of forest, where habitat is being rapidly destroyed (Seddon *et al.* 2000). Appropriate conservation measures are required to ensure their long-term survival.

## Acknowledgements

N.S. was supported by a studentship from the Natural Environment Research Council, UK. We are indebted to the Ministry of Water and Forest (Antananarivo) for their permission to conduct research, and to Parc Botanique et Zoologique de Tsimbazaza and Projet ZICOMA (BirdLife International) for support. We also thank N. Davies and J. Ramanampamonjy for their advice, B. Forgeau for logistical assistance and O. Langrand for comments on an early draft of this manuscript.

## References

- Appert, O. (1968) Zur Brutbiologie der Erdracke *Uratelornis chimaera* Rothschild. *J. Ornithol.* 109: 264–275.
- Bangs, O. (1918) [Vertebrata from Madagascar.] *Aves. Bull. Mus. Comp. Zool.* 61: 489–511.
- Bard, S. C., Hau, M., Wikelski, M. and Wingfield, J. C. (2002) Vocal distinctiveness and response to conspecific playback in the spotted antbird, a Neotropical suboscine. *The Condor* 104: 387–394.
- BirdLife International (2000) *Threatened birds of the World*. Cambridge, U.K.: BirdLife International.
- Collar, N. J. and Stuart, S. N. (1985) *Threatened birds of Africa and related islands*. Cambridge, U.K.: International Council for Bird Preservation.
- Collar, N. J. and Stuart, S. N. (1988) *Key forests for threatened birds in Africa*. Cambridge, U.K.: International Council for Bird Preservation (Monogr. 3).
- Griveaud, P. (1960) Une mission de recherche de l'I.R.S.M. au Lac Ihotry (S. E. Morombe, Province de Tuléar). *Naturaliste Malgache* 12: 33–41.
- Hedderon, J. (1987) *SPSS made simple*. Belmont, California: Wadsworth Publishing Company.
- King, W. B. (1977) *Endangered birds of the world: the ICBP bird Red Data Book*. Washington, D.C.: Smithsonian Institution Press.
- Langrand, O. (2001) Family Brachypteraciidae (Ground-rollers). Pp. 378–388 in J. del Hoyo, A. Elliott and J. Sargatal, eds. *Handbook of the birds of the world*, VI. Barcelona: Lynx Edicions.
- Ménégaux, A. (1907) Liste des oiseaux rapportés en 1906 par M. Geay, du sud-ouest de Madagascar. *Bull. Mus. Natn. Hist. Nat.* 13: 104–113.
- Milon, P., Petter, J.-J. and Randrianasolo, G. (1973) *Faune de Madagascar, 35: Oiseaux*. Tananarive and Paris: Orstom and CNRS.
- Oustalet, E. (1899) Note sur le mâle de l'*Uratelornis chimaera*. *Bull. Mus. Natn. Hist. Nat.* 5: 280–282.
- Petter, J.-J. (1963) The serious situation in Madagascar. *ICBP Bull.* 9: 95–96.
- Rand, A. L. (1936) The distribution and habits of Madagascar birds. *Bull. Am. Mus. Nat. Hist.* 72: 143–499.
- Seddon, N., Tobias, J. A., Yount, J. W., Ramanampamonjy, J. R., Butchart, S. and Randrianahana, H. (2000) Conservation issues and priorities in the Mikea Forest of south-west Madagascar. *Oryx* 34: 287–304.
- Seddon, N., Tobias, J. A. and Butchart, S. H. M. (2003) Group-living, breeding behaviour and territoriality in the Subdesert Mesite *Monias benschi*. *Ibis* 145: 277–294.
- Statsoft (2003) *Statistica for Windows*. Tulsa, Oklahoma: Statsoft Inc.
- Tobias, J. A. and Seddon, N. (2002a) Estimating population size in the subdesert mesite (*Monias benschi*): new methods and implications for conservation. *Biol. Conserv.* 108: 199–212.
- Tobias, J. A. and Seddon, N. (2002b) Reading the sand: identifying bird tracks in Madagascar's spiny forest. *Afr. Bird Club Bull.* 9: 12–15.
- Tobias, J. A. and Seddon, N. (2003) Vocalizations and display in the Long-tailed Ground-roller *Uratelornis chimaera*. *Wilson Bull.* 115(2): 193–196.
- Westcott, D. A. and Kroon, F. J. (2002) Geographic song variation and its consequences in the golden bowerbird. *The Condor* 104: 750–760.

NATHALIE SEDDON\*

*Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK  
(present address: Edward Grey Institute of Field Ornithology, Department of Zoology,  
University of Oxford, South Parks Road, Oxford, OX1 3PS, UK).*

JOSEPH A. TOBIAS

*BirdLife International, Wellbrook Court, Girton Road, Cambridge, CB3 0NA, UK (present  
address: Edward Grey Institute of Field Ornithology, Department of Zoology, University of  
Oxford, South Parks Road, Oxford, OX1 3PS, UK).*

*\*Author for correspondence; e-mail: [nathalie.seddon@zoo.ox.ac.uk](mailto:nathalie.seddon@zoo.ox.ac.uk)*

Received 30 August 2005; revision accepted 14 March 2006