

# Estimating population size in the subdesert mesite (*Monias benschi*): new methods and implications for conservation

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## Abstract

The subdesert mesite, a terrestrial non-passerine bird endemic to the Mikea Forest of southwest Madagascar, is currently classified as globally threatened (category: Vulnerable). However, accurate assessment of threat in accordance with the IUCN Red List criteria (A, B and C) requires data on effective population size, area of habitat occupied and rate of decline, none of which is available for this species. Here we present the first empirical estimates of its population size using five complementary methods, three incorporating data on territory size and two using data gathered during call-playback surveys conducted throughout its entire global range. Estimates vary from 98,000 to 152,000 individuals, with the most reliable possibly being that generated by distance sampling (115,000). This figure is more than an order of magnitude greater than the only published estimate of <10,000 individuals. By analysing data on forest cover change, we estimate the population of the subdesert mesite to have declined by, at most, 10% in three generations. Although the rate of deforestation in 1994–1999 is double that calculated for 1962–1994, it is deemed unlikely that the population will decline by 20% over the next three generations. As such the species fails to meet criterion A. Although the subdesert mesite's range and area of occupancy are small, they are not fragmented and do not comprise fewer than 10 locations. Consequently, this species does not meet criterion B. Further, the species fails to meet criterion C, for which a maximum of 10,000 mature adults is required. According to IUCN (2000 Red List of Threatened Species) this species should therefore be downlisted in status. We discuss why it still warrants conservation attention and suggest the need for modifications to the criteria thresholds in relation to basic information about the ecology and taxonomic distinctness of species. © 2002 Elsevier Science Ltd. All rights reserved.

**Keywords:** Conservation status; IUCN Red List; Madagascar; Population estimate; subdesert mesite

## 1. Introduction

Given that resources for biodiversity conservation are limited it is vital that species are ranked according to the extinction risk they face (Burgman et al., 1993; Akçakaya et al., 2000; BirdLife International, 2000; IUCN, 2000). In order that this ranking procedure be objective, the World Conservation Union (IUCN) Species Survival Commission developed the Red List criteria (IUCN, 1994; 1996; 2000) to set a global standard against which risks can be evaluated. These criteria define a set of categories to which species are assigned on the basis of the apparent size of (and declines in) population

and/or geographic range (IUCN, 2000). If species are to be correctly assigned to a particular threat category, it is imperative that as accurate an estimate as possible be made of their population sizes, ranges and rates of decline. It is these parameters that are the most common source of 'uncertainty,' and thereby misjudgment of species' conservation status (Akçakaya et al., 2000).

The subdesert mesite (*Monias benschi*) is a cooperatively breeding terrestrial bird endemic to southwest Madagascar in part of the South Malagasy spiny forests Endemic Bird Area (Stattersfield et al., 1998). It belongs to a monotypic genus within the Mesitornithidae, a family endemic to the island of Madagascar that has variously been associated with columbiforms, galliforms and passerines, but is now considered a member of the gruiforms (Lowe, 1924; Livezey, 1998). However, this ancient family's taxonomic placement continues to be

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debated, and some authors consider it to be sufficiently distinct to warrant its own order (see discussions in Sibley and Ahlquist, 1990; Evans et al., 1996; Houde et al., 1997). The classification of the subdesert mesite as globally threatened in the 'Vulnerable' category (Collar et al., 1992; BirdLife International, 2000; IUCN, 2000) was a reasonable if precautionary assessment given the absence of hard data on effective population size, area of occupancy or decline in these parameters. Incorporating a recent estimation of the total extent of available habitat and its apparent rate of destruction (Seddon et al., 2000), we reassess the subdesert mesite's population size and conservation status using a variety of traditional and novel techniques. In so doing we establish a baseline against which future estimates can be compared.

The long-term viability of a population is not merely a function of its size. A large number of inter-related factors including demography, environment and behaviour determine the probability that a species will go extinct (Gilpin and Soulé, 1986; Waite and Parker, 1996; Anthony and Blumstein, 2000). A key determinant of population viability is genetic diversity (see reviews in Burgman et al., 1993; Parker and Waite, 1997; Durant, 2000) and the best predictor of whether a population can maintain genetic variability is effective population size ( $N_e$ ) (Parker and Waite, 1997). This metric essentially calibrates the influence of genetic drift in a real population to that in an ideal population with random mating, equal sex ratio, discrete generations and constant size (Wright, 1931). Many empirical studies suggest that the rate of loss of genetic variation from populations can be considerable even when the census population is large, in other words that  $N_e$  falls well below  $N$  (see Burgman et al., 1993). The factors primarily responsible for this observation are population fluctuations, unequal sex ratios and high variance in reproductive success (Nunney, 1993). Recent work has shown a significant male-bias in the adult sex ratio of the subdesert mesite (Seddon, 2001). Further, the species appears to have a variable mating system that includes polyandry, with the consequence that a certain proportion of the population may be excluded from reproduction, and variance in reproductive success is likely to be high (Seddon, 2001). Although a variety of models incorporating genetic and demographic factors have been developed for estimating  $N_e$  (e.g. Nunney and Elam, 1994; Waite and Parker, 1996), even the most minimal of these requires ecological data that are lacking for the subdesert mesite. Nonetheless, given the importance of  $N_e$  in assessment of extinction risk, we provide rough estimates using the data available.

Whether or not the subdesert mesite is classified as Vulnerable depends largely on one's interpretation of the Red List criteria and the degree of pessimism with which future habitat loss is predicted. As it happens, the species is a marginal case, and therefore this study

throws light on the process by which conservation status is assessed and in doing so illuminates some possible opportunities for improvement.

## 2. Methods

### 2.1. Study area and study species

This study was conducted as part of a 3-year investigation into the ecology of the subdesert mesite, a cooperatively breeding bird endemic to the semi-arid Mikea Forest of southwest Madagascar (Seddon, 2001). We carried out fieldwork at a site known as Pointe Kilometre 32 (PK32, a distance marker on Route 9 north of Toliara; the 200 ha site has its mid-point at 23°04'57S, 43°37'15E) and along eight transects in the Mikea Forest north of Manombo (Fig. 1). The Mikea Forest was estimated recently to cover a maximum of 3706 km<sup>2</sup> (Seddon et al., 2000), including 116 km<sup>2</sup> of secondary vegetation that has regrown since 1962; we use the overall figure in our calculations because secondary habitats were occupied by the species (but see Section 4). Seddon et al. (2000) give a detailed description of the vegetation and climate of the area.

Subdesert mesites breed year-round and acquire adult plumage by c.3 months (Seddon, 2001; Seddon et al., in press). Therefore, although most juveniles of >3 months were identified at PK32, it was difficult to distinguish young from adults during the transect surveys. For the sake of consistency, in all calculations we take 'number of adults' to include all birds with adult plumage.

### 2.2. Estimation of population size

The population size of birds can be estimated using a variety of methods (reviewed in Ralph and Scott, 1981; Bibby et al., 2000; Buckland et al., 2000), each of which has its limitations. The choice of method depends upon the behaviour and habitat of the species in question, and is critically important as variations in output can strongly affect threat classification (Burgman et al., 1999). We used five complementary techniques (A–E later).

#### 2.2.1. Intensive territory mapping

A traditional approach involves mapping and calculating the size of territories of individuals at a particular study site (reviewed in Ralph and Scott, 1981; Bibby et al., 2000). The population density calculated at this site can be translated into a crude estimate of total population size if the area inhabited by the species is known. However, not only is accurate measurement of territory size difficult, but the technique also assumes that the study site is representative of the entire area inhabited

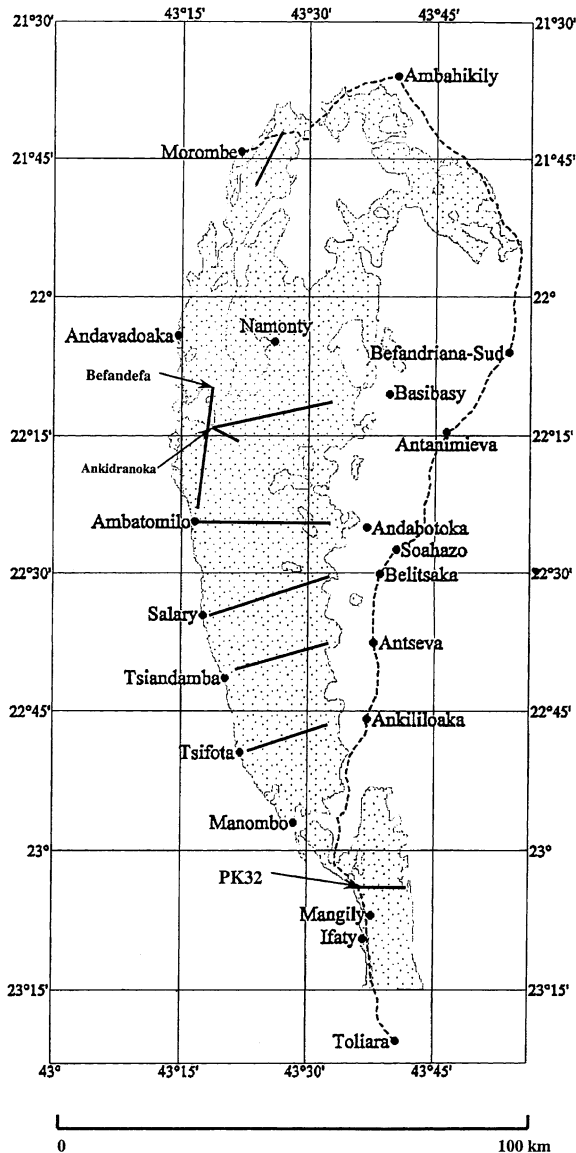


Fig. 1. Global range of the subdesert mesite (outlined in grey) annotated with the position of the nine tracks (straight lines) used to conduct playback surveys; the road (Route National 9, dashed line) used to access the tracks; the main villages and towns in the region and the study site, Pointe Kilometre 32 (PK32).

by the species. Ideally, estimates thus derived should be compared with those generated using data gathered during surveys carried out in a variety of key habitat types throughout the species' range. Birds can be surveyed in this way through casual encounters either along transects or during timed counts at survey points (Bibby et al., 2000). As chance encounters with subdesert mesites are scarce, the territory mapping method is likely to underestimate population size; this problem arose in studies of the related white-breasted mesite (*Mesitornis variegata*) (Hawkins, 1994).

As part of our investigation into the subdesert mesite's spacing system (Seddon et al., in press), we measured territory size in 11 colour-ringed groups

comprising 40 subdesert mesites between September 1999 and January 2000 (Fig. 1). During 4–7 h semi-continuous focal watches we recorded the location of groups containing one radio-tagged individual; we then mapped territories using the Macintosh programme *WildTrak* version 1.2 (Todd, 1992), drawing minimum convex polygons (MCPs; Southwood, 1966) around registrations made whenever a group moved > 25 m (or every 20 min). For seven of the radio-tagged groups for which there were sufficient data, territory size reached an asymptote at a mean ( $\pm$ SE) of  $71 \pm 6$  registrations. For the purpose of this study, however, territory size was defined as the area encompassed by a MCP drawn around 95% of the registrations obtained for groups for which we had more than 170 registrations. We then calculated the population size of subdesert mesites in three ways:

(A) Following Kelsey and Collins (2000) we simply divided the total area of suitable habitat (i.e. 3706 km<sup>2</sup>) by mean territory size ( $0.12 \pm 0.02$  km<sup>2</sup>,  $n=7$  groups) and then multiplied this by the mean number of adults per territory (i.e. 4.31,  $n=83$  groups).

(B) We divided the total number of individuals with adult plumage in the seven study groups by the area encompassed by their territories and multiplied the figure by 3706 km<sup>2</sup>. Both these methods assume that territories are discrete and non-overlapping (Bibby et al., 2000). Given that there is minor overlap between territories in the south of the site (see Fig. 2) this assumption is violated.

(C) To control for the territory overlap problem, we placed three 1-km<sup>2</sup> quadrats over a map of territories in the study site in such a way as to cover as much of the site as possible (Fig. 2) and calculated the population of each quadrat by multiplying the proportion of each territory embraced by the quadrat with the number of individuals occupying the territories. We estimated population size by multiplying the mean population density of the quadrats by the total amount of habitat remaining. For those groups with insufficient registrations to calculate territory size accurately (i.e. P5, P11, P12 and P14), we estimated the proportion of their territories embraced by the quadrat by dividing the area falling within the quadrat by the mean territory size derived from groups with adequate registrations (this also applies to the calibration method; see E later).

These methods assume that there are no 'floaters' in the population and as such could underestimate the population size. However, in the subdesert mesite this assumption is valid as, with rare exceptions, all birds in the population live in groups (Seddon, 2001).

### 2.2.2. Extensive playback surveys

As an alternative, we used playback of calls to estimate population size. This method has proved particularly effective in determining the presence of otherwise

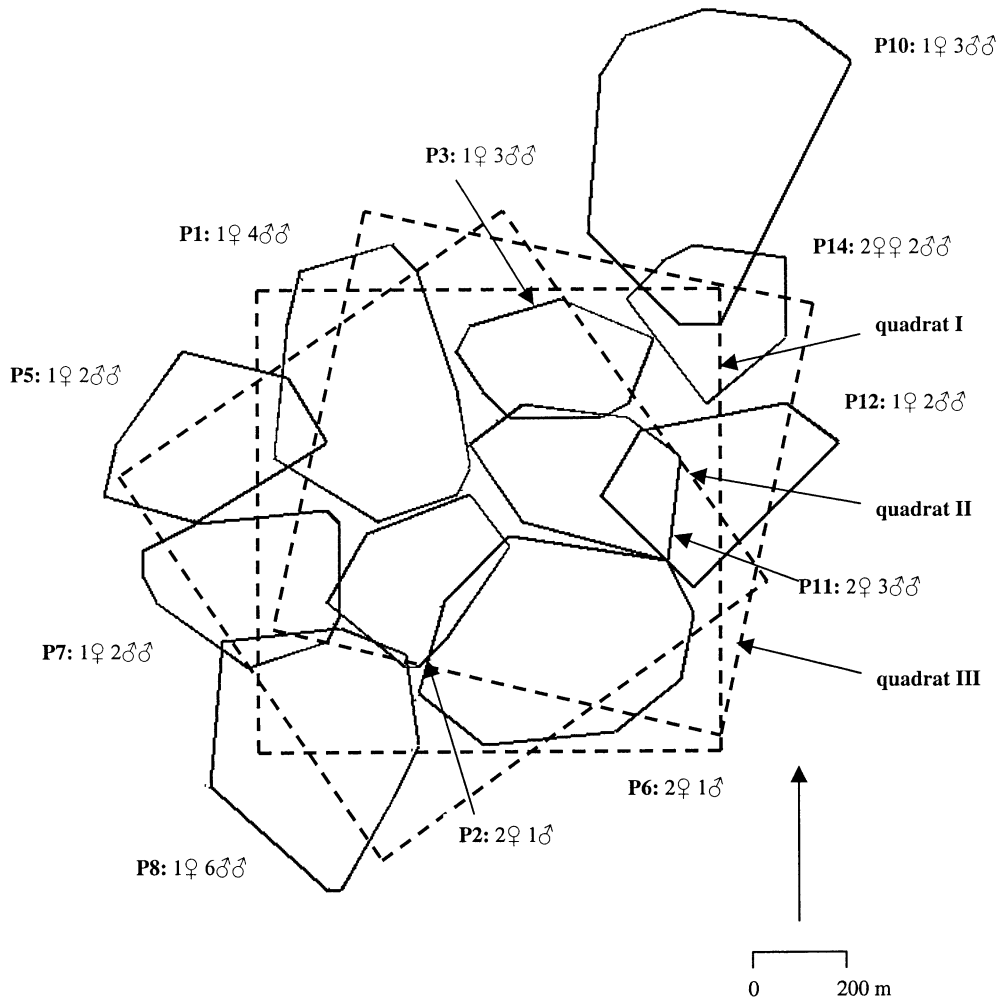


Fig. 2. Map illustrating mesite territories at PK32 and the position of the three quadrats used to estimate population density by method (C). Territories are defined by minimum convex polygons drawn around 95% of registrations gathered in September 1999 to January 2000 for all groups except P5, P11, P12 and P14 for which all registrations were used. Group compositions are given and include adults plus any known juveniles with adult plumage.

elusive birds (Glahn, 1974; Marion et al., 1981; Gibbs and Melvin, 1993; Legare et al., 1999), and allowed estimation of population density in white-breasted mesites with relative ease (Hawkins, 1994). Two factors favoured the use of playback surveys for censusing the subdesert mesite. First, the species is generally highly responsive to playback (Seddon, 2001). Second, it was logistically feasible to conduct systematic surveys along linear transects traversing the entire global range of the species owing to the presence of a series of long and perfectly straight tracks constructed by an oil company whilst prospecting in the 1960s. We use two techniques to analyse the resultant data.

(D) First we estimate population density using distance sampling (Buckland et al., 1993; Bibby et al., 2000), a highly effective method that has been applied to several threatened species, e.g. Madeira laurel pigeon (*Columba trocaz*) (Oliveira et al., 1999) and Montserrat oriole (*Icterus oberi*) (Arendt et al., 1999). It assumes

that distance is the main factor influencing detection of animals.

Playback surveys were carried out in the Mikea Forest between 28 November and 13 December 1999 along eight transects (see 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); Ankidranoka–Basibasy (c.20 km); Ankidranoka–Vorehe (c.3 km); and east of Morombe (c.10 km). These transects were divided into 40 survey strips each 1.8 km in length and separated by 2–3 km. Playback was conducted at five points positioned at 300-m intervals along each survey strip (Fig. 3). This distance was chosen because in the prevailing calm conditions subdesert mesite songs were clearly audible only up to c.300 m away, as judged by walking away from singing radio-tagged groups of known location and from loudspeakers broadcasting songs at a natural sound intensity. Further, radio-tagged

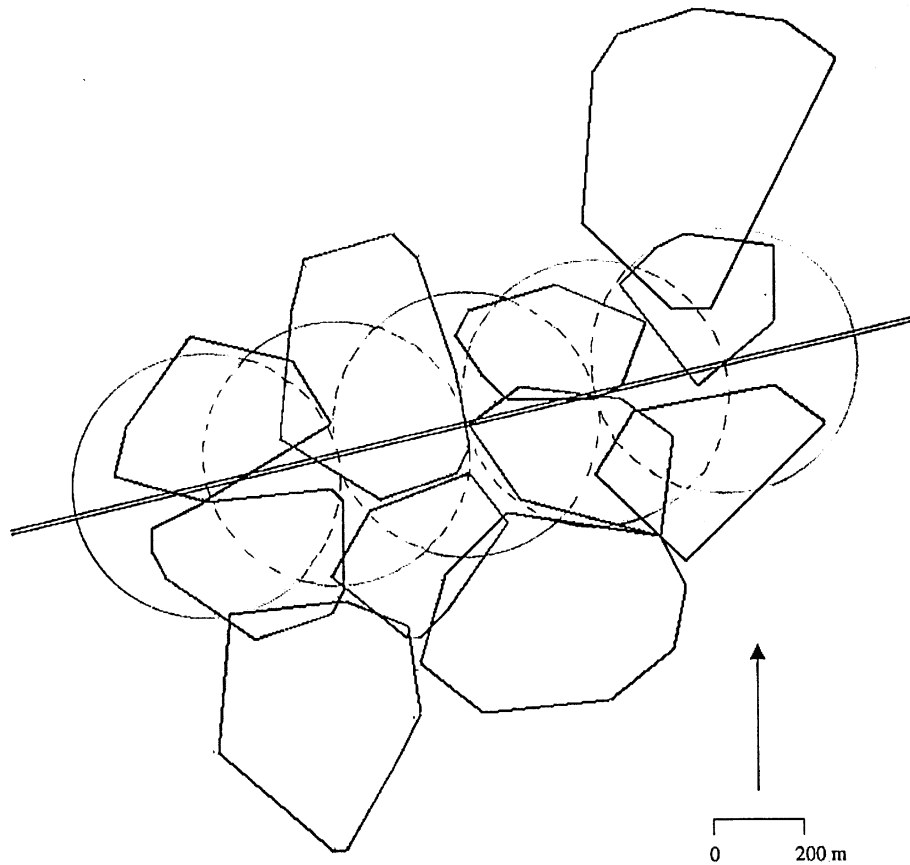


Fig. 3. Map illustrating the area sampled by playback at PK32, as defined by five overlapping circular zones of response with radii of 300 m. The sample area has been superimposed on a map of mesite territories in order that the size of the population sampled can be calculated and used to estimate population size with Eq. (1) (method E). Territories are defined by minimum convex polygons drawn around 95% of registrations gathered in September 1999 to January 2000 for all groups except P5, P11, P12 and P14 for which all registrations were used. Refer to Fig. 2 for group names and compositions.

groups were never noted responding to playback (or to their neighbours' songs) when  $> 300$  m away. Playback was carried out in calm conditions at 06:00–11:00 and 13:00–19:00. There was no significant variation across hourly sampling periods in the mean number of groups responding per playback (ANOVA:  $F_{12, 106} = 0.891$ ,  $P = 0.557$ ), nor was there any difference between the number of groups responding early in the morning (06:00–09:00) and later (09:00–11:00) (unpaired  $t$ -test,  $t = 0.79$ ,  $n_1 = 42$ ,  $n_2 = 55$ ,  $P = 0.43$ ,  $df = 95$ ).

At each survey point, we tried to locate groups by their vocal responses to a 30-s recording of a male sub-desert mesite solo song broadcast through a Sony SRS-58 loudspeaker. The latter was held by one observer at c.1 m above the ground and slowly and evenly rotated through  $360^\circ$  (starting and ending at north, read from a wristwatch compass). Using the volume control on the cassette recorder, the sound pressure level (SPL) was kept at a constant 65 dB at 15 m in front of the loudspeaker (the SPL of natural songs: Seddon, 2001). This was verified using a Tandy sound level meter (on slow setting) held by a second observer for the first few seconds of each presentation. When a group responded it

was located as quickly as possible by this second observer who took care not to disturb the birds.

In addition to locating groups, playback was conducted in order to investigate the function of sub-desert mesite songs. For this reason, once groups had been located by sight and a period of three minutes had elapsed, a second playback was carried out using one of five different recordings: female solo, male solo, pair-duet, small chorus and large chorus chorus (see Seddon, in press, for descriptions of these song types). At each point, we recorded the number of groups contacted (with or without playback), the radial distance from the survey point to the position of the group(s) prior to any movement in response to observers or playback (see below) and, where possible, the number of individuals in the group. A total of 15 min was spent at each survey point.

The population size of the sub-desert mesite was then estimated using *DISTANCE* version 3.5 (Thomas et al., 1998). Comprehensive explanations of distance sampling procedure are given in Buckland et al. (1993) and Lloyd et al. (1998), and a more detailed account of selecting models to fit our data is given by Seddon

(2001). Large distances are complex to model and the additional terms required increase the variance of the slope of the detection curve. For this reason, Buckland et al. (1993) suggest that roughly 10% of observations should be truncated prior to application of the models. We found that truncation of data at 150 m removed 34.5% of groups detected, but improved data quality in several ways (Table 1). First, truncation at this distance ensured that there was no overlap in the areas sampled at successive points. Second, groups detected within this area were less likely to have moved in response to playback at a previous point. Third, distance measurement is likely to have been much less accurate beyond 150 m (see below). And finally, whilst most groups detected within this distance (75.6%; 59/78) were actually observed, only 24.4% (10/41) of groups detected over 150 m away were observed. We assigned all unobserved groups a size of 4.3 adults, this being the mean value calculated from all unique study groups plus all groups clearly observed along transects in 1999 ( $n=83$ ); there was no significant difference between group sizes in the study site versus the transects (Seddon et al., in press). Table 1 compares the AIC and GoF  $P$ -values of models applied to truncated and non-truncated data. Goodness-of-fit tests revealed that no model fitted the non-truncated data particularly well: the  $P$ -values are significant in all but the hazard-rate model (Table 1). When the models were fitted to truncated data not only were the AIC values all very similar, but the GoF test generated non-significant  $P$ -values for all models; the best fit was achieved by the half-normal key with one hermite polynomial adjustment (see Seddon, 2001, for graphs of the detection functions fitted to actual distance data).

Population density and size were estimated by treating all groups detected as clusters. Such an analysis assumes that (1) probability of detection is independent of cluster size, and (2) that cluster sizes are estimated without bias at all distances (Buckland et al., 1993). The first assumption was met as large groups were no more likely to respond to playback than small groups (Seddon, 2001). The likelihood of violating the second assumption was minimised by truncating the data at 150 m (see earlier).

To generate an unbiased density estimate with distance sampling, three major assumptions must be met (Buckland et al., 1993). (1) Survey points must be positioned randomly with respect to the distribution of birds. Points were positioned at regular intervals (avoiding clearings) along nine straight tracks originally constructed for the purpose of oil prospecting. As such the survey points pass through the forest at regular intervals irrespective of forest type or terrain; given the general uniformity of the habitat, they were very unlikely to pass exclusively through regions with abnormally high or low population densities (see Fig. 1). (2) The probability of detecting groups at 0 m equals one. It is extremely unlikely that birds at each survey point will have been missed as subdesert mesites always give loud and prolonged alarm calls clearly audible up to 15–20 m away. Even if dense vegetation precluded visual detection of groups close to the survey point, we are confident that they will have been detected using playback given the observation that all study groups  $\leq 25$  m from the loudspeaker responded to playback of songs (Seddon, 2001). As subdesert mesites rarely foraged on the tracks themselves (c.3 m wide), the track area was ignored and the closest points on each side were treated as 0 m. (3) All birds must be detected at their initial location; accurate estimates of the radial distance from the survey point to this location must be made. While groups located visually within 10 m of the survey point invariably moved away from the observer, they moved noisily and slowly and it was possible to memorise their original position. Groups detected by playback were located as quickly as possible after they had started to sing. A more accurate estimate of initial distance was then made by counting paces back to 0 m, the position of which was marked in the sand; we are confident that these measurements will have been accurate to within 5 m.

When more than one group responded to playback (22/200 of survey points), or when the vegetation was too dense to penetrate without disturbing the birds, initial distance was estimated by ear. Before carrying out fieldwork, we practised estimating distances to a loudspeaker broadcasting subdesert mesite song at a

Table 1  
Model selection for estimation of population size of subdesert mesite

Model (key + adjustment)	$w = 300$ m					$w = 150$ m				
	No. parameters	AIC	$\chi^2$ GoF	df	$P$	No. parameters	AIC	$\chi^2$ GoF	df	$P$
Uniform + cosine	2	-163.7	7.93	2	0.02	1	-169.4	0.42	2	0.81
Uniform + polynomial	4	-165.2	–	–	0.02	0	-166.3	3.49	3	0.32
Half-normal + hermite	1	-152.3	20.8	3	0.00	1	-166.5	0.61	2	0.74
Hazard-rate + cosine	2	-163.4	4.38	2	0.11	2	-167.1	0.62	1	0.43

All models have been fitted to ungrouped distance data with two different truncation values ( $w$ ). The goodness-of-fit (GoF) statistic is given for all models with sufficient degrees of freedom, the best of which have the lowest values of Akaike's Information Criterion (AIC). The closer the GoF  $P$ -value is to 1, the better the fit of the model to these data.

natural SPL (c.65 dB). In addition to these ‘tests’, 10 months of prior field experience in finding vocalising groups enabled us to estimate initial distance with an accuracy of  $\pm 10$  m for distances  $< 150$  m.

Movement of groups towards or away from the survey point prior to singing in response to playback would lead to a misjudgment of initial distance. Based on the fact that vocal responses by white-breasted mesites to a second playback were no closer than those given to the first, Hawkins (1994) concluded that prior movement must be minimal (although the possibility that groups moved before first singing was not excluded). In contrast, subdesert mesites moved considerably between playback trials, but observations made during focal watches and playback experiments at PK32 indicated that movement prior to first singing was rare (Seddon, 2001). Groups moved up to 20 m towards (or away from) playback whilst singing, but most movement occurred immediately afterwards. On the few occasions when prior movement was recorded, it involved single birds. As single birds were detected by playback at survey points on only two occasions, any underestimation of their initial distance is unlikely to have influenced the overall population size estimate. However, group positions were memorised at the onset of singing rather than at the end and, for groups detected within 150 m of the survey points, it was usually possible to inspect tracks to confirm the initial distance: changes in track configuration and direction between foraging and singing states were quite easy to detect (Tobias and Seddon, 2002).

(E) The relationship between the number of animals responding to playback and those actually present is influenced by factors such as sex and breeding status (e.g. Ogotu and Dublin, 1998; Legare et al., 1999). To correct for the partial response of the sampled population, we devised a calibration based upon the responses of a colour-ringed, radio-tagged population of known size. Playback was also conducted at 300-m intervals along a 1.8-km segment of the track running through the centre of the PK32 study site (Fig. 3). Six repeats were carried out at 05:30–07:30 on 25 November 1999, 07:30–09:30 on 12 December 1999, 09:30–11:30 on 14 December 1999, 13:00–15:00 on 16 December 1999, 15:00–17:00 on 30 December 1999 and 17:00–19:00 2 January 2000. In this analysis, the total sampling area consisted of 40 1.8-km strips (excluding PK32) scattered throughout the Mikea Forest (Fig. 1). The area sampled per survey strip (five overlapping circular zones of response with radii of 300 m) covered 0.971 km<sup>2</sup>. We superimposed this area onto a map of territories at PK32 (as defined by 95% MCPs) and calculated the proportion of each group’s territory falling within a 300-m radius of the five survey points (Fig. 3). The probability that groups within the sampled area would respond to playback was calculated by dividing the mean number of groups to respond over the six trials by

the total number of groups calculated to fall within this area. We then estimated the population size of subdesert mesite in the Mikea Forest using the following equation:

$$A \left( \sum_{i=1}^{40} (n(1/p)g)/a \right) \quad (1)$$

where  $A$  is the total area estimated to be occupied by mesites (i.e. 3706 km<sup>2</sup>),  $n$  is the number of groups detected from each survey strip,  $p$  is the probability of detection,  $a$  is the area surveyed per strip (i.e. the area encompassed by the circles in Fig. 3: 0.971 km<sup>2</sup>), and  $g$  is mean group size.

### 2.3. Effective population size ( $N_e$ )

When the adult sex ratio deviates from parity,  $N_e$  can be estimated from  $4p(1-p)N$  where  $p$  is the proportion of males in a population of size  $N$  (Nunney, 1993). However, when there is variation in the number of progeny per individual,  $N_e$  will be further reduced and can be calculated using the variance in the number of progeny per generation per individual (Burgman et al., 1993, p. 239), or basic demographic data such as survival rate and the mean and variance of adult lifespan (see Nunney and Elam, 1994). In the absence of these data we provide only very approximate estimates for two alternative mating systems representing the opposite extremes found in the species (Seddon, 2001). At one extreme, reproductive skew is maximal and only one pair of birds breeds per group (monogamy). At the other extreme, reproductive skew is at a minimum: given that maximum clutch size is apparently two, two males and two females might breed per group (polygynandry). By incorporating this information into the above equation, we find that  $N_e$  can be estimated using:

$$4(p_m p_{bm})(p_{bf}(1-p_m))N \quad (2)$$

where  $p_m$  is the proportion of males in the population (as derived from the population sex ratio of 1:1.38, Seddon, 2001),  $p_{bm}$  and  $p_{bf}$  are the proportion of males and females breeding per year, and  $N$  is the total census population size. Under a monogamous mating system  $p_{bf}$  and  $p_{bm}$  are 1/2 and 1/3, respectively, whilst under a polygynandrous mating system they are 2/2 and 2/3, given that the modal group comprised two adult females and three adult males (Seddon, 2001).

### 2.4. Population decline

In order to fulfil the minimum requirements of the IUCN Red List criteria A (‘rapid population reduction’), a species must have experienced or be expected to experience a reduction in its population size of at least

20% in 10 years or three generations, past or future (see IUCN, 2000). Generation span is usually taken as  $(M-1+A)$  where  $M$  is age at first breeding and  $A$  is average adult lifespan (Waite and Parker, 1996). There are no data that enable us to ascertain values for these parameters accurately. However, as subdesert mesites develop sexually mature plumage by 3–4 months but generally disperse from groups at 10–14 months, we estimate  $M$  as one year. One year is also given as the age of first breeding in several of the subdesert mesite's close relatives, including buttonquail (Turnicidae: Debus, 1996) and rails (Rallidae: Taylor and van Perlo, 1998). The average adult lifespan of the subdesert mesite is assumed to be similar to that of medium-sized tropical rails such as white-throated rail (*Dryolimnas cuvieri*), another forest species endemic to Madagascar, which has been estimated as 5–6 years based on recoveries of ringed birds (Hamblen et al., 1993). We thus calculate generation span to be at least five years and estimate decline over 15 years. We assume that there is a linear relationship between number of individuals and area inhabited. Therefore, by calculating how much the area of occupancy has declined recently or is likely to decline, we can estimate population decline using the following equation for a simple arithmetic progression:

$$n/2(2a + (n - 1)d) \quad (3)$$

where  $n$  is the number of years over which the decline is predicted,  $a$  is the current annual rate of deforestation and  $d$  is the rate of annual increase in deforestation. Data on the extent and decline of forest cover since 1962 derive from a detailed analysis of satellite imagery (Seddon et al., 2000).

### 3. Results

#### 3.1. Intensive territory mapping

Method (A) produced a total population size of 133,000 individuals (rounded to the nearest 1000). The seven groups of radio-tagged subdesert mesites contained a total of 29 individuals and occupied an area of

0.85 km<sup>2</sup>. Thus, using method (B) the population density at the study site was calculated as 8.3 groups km<sup>-2</sup> or 34 adults km<sup>-2</sup>. These population density estimates translated into population sizes of 31,000 groups and 126,000 individuals, respectively. Using method (C) we found that a total of 6.7 groups (27.2 individuals) fell within quadrat I, 6.9 groups (27.1 individuals) fell within quadrat II, and 6.5 groups (25.2 individuals) fell into quadrat III. Thus, the mean number of groups per 1-km<sup>2</sup> quadrat was 6.7 and the mean number of individuals was 26.5. These population densities extrapolate into population sizes of 25,000 groups and 98,000 individuals, respectively (Table 3).

#### 3.2. Extensive playback surveys

At the 200 points at which playback was conducted, 119 groups were detected. The composition was ascertained for 69 of these and included 305 adults (i.e. 177 males and 128 females). Using distance sampling (method D), and applying the best-fit model to these data, we calculate a population size of 115,000 individuals (Table 2).

The number of groups calculated to fall within the area sampled by playback at the PK32 study site was 6.7 out of a total of 11 groups (Fig. 3). Over the six trials the mean number of groups responding per trial was 2.2. The probability that groups within the sampled area would respond ( $p$ ) was therefore calculated as 0.328 (i.e. 2.2/6.7). By applying this value of  $p$  to Eq. (1), we estimated population density to be 9.5 groups km<sup>-2</sup> and the total population size to be 35,207 groups. By multiplying these figures by the mean group size (4.31 adults), this method (E) generates the highest population size estimate of 152,000 adults (Table 3).

#### 3.3. Effective population size

Assuming monogamy, and using Eq. (1), we calculate  $N_e$  to lie between 16,000 and 24,000 adults. If, however, there is a more egalitarian system in which two males and two females contribute to a clutch of two eggs per year, then  $N_e$  lies between 64,000 and 99,000. Given that these two mating systems represent the opposite ends of a continuum of apparent variability in subdesert

Table 2  
Population density and population size of subdesert mesites in the Mikea Forest calculated using distance sampling

Model (key + adjustment)	Population density	95% CI of population density	Population size	95% CI of population size
Uniform + cosine	38.2	23.6–61.9	142,560	87,398–229,300
Uniform + polynomial	21.5	16.1–28.8	79,590	59,399–106,640
Half-normal + hermite	24.1	19.4–49.8	115,180*	71,960–184,370
Hazard-rate + cosine	46.3	8.8–244	171,570	32,503–905,620

The estimates derive from the four models applied to ungrouped data with a truncation distance of  $w = 150$  m. The best estimate, as derived from the best-fitting model, is marked with an asterisk.



Table 3  
Population density and total population size estimates ( $N$  and  $N_e$  rounded to the nearest 1000) of the subdesert mesite generated using five methods

Method	Population density		Total population size ( $N$ )		Effective population size ( $N_e$ )	
	Groups km <sup>-2</sup>	Adults km <sup>-2</sup>	Groups	Adults	High skew: monogamy	Low skew: polygynandry
<i>Territory mapping</i>						
(A)	8.3	35.6	31,000	(133,000)	21,000	86,000
(B)	8.3	34.1	31,000	126,000	20,000	82,000
(C)	6.7	26.5	25,000	98,000	16,000	64,000
<i>Playback surveys</i>						
(D) Distance sampling	(7.2)	31.1	(27,000)	115,000	18,000	75,000
(E) Calibration	9.4	(40.7)	35,000	(152,000)	24,000	99,000

Population size as measured by number of groups using methods (A) and (B) was multiplied by the mean group size (4.31) to translate it into total number of individuals given in parentheses; population size as measured by number of individuals in method (D) was divided by 4.31 to give a total number of groups in parentheses. The estimate derived by distance sampling uses the half-normal + hermite model and is generated by bootstrapping with 1000 iterations.

mesite's mating system, the actual value of  $N_e$  is likely to lie somewhere between these extremes (16,000–99,000).

### 3.4. Population decline

Forest cover in the range of the subdesert mesite is estimated to have declined by 12.8% in the period 1962–1999 (Seddon et al., 2000). However, rates of deforestation varied across the region and an analysis of two 1999 SPOT satellite images covering the eastern fringe of the forest indicated that cover in this area declined by as much as 25% in the same 37-year period. Even using this higher rate of deforestation (i.e. 0.78% per annum), the population is still only likely to have declined by 10% in three generations. Accelerated declines are nevertheless predicted over the forthcoming three generations. The overall rate of deforestation has increased from 0.35% per annum in 1962–1994 to 0.93% per annum in 1994–1999. If the annual rate of deforestation remains at this level, the population will have declined by 13% in 15 years. However, if the rate of deforestation increases at the same rate of increase recorded for 1994–1999 (i.e. 0.12% per annum) then, using Eq. (2), we calculate that the population will have declined by 26.1% in three generations.

## 4. Discussion

### 4.1. Total population size

Estimates of the total population size of the subdesert mesite derived using the five different methods adopted in this study are summarised in Table 3. While each method has limitations, collectively they provide a realistic range within which the true number of birds is very likely to fall.

In all calculations the area inhabited by the subdesert mesite is taken as 3706 km<sup>2</sup>. However, this figure may be an overestimate for two reasons. First, it is assumed that there was no deforestation in 1994–1999 outside the area covered by the 1999 SPOT satellite image (Seddon et al., 2000). Observations made whilst accessing transects indicated that forest has been cleared outside this region, for example in the areas just south of Morombe, around Befandefa and in particular between Ifaty and PK32 (see Seddon et al., 2000). Second, it is possible that some of the area is unoccupied. Although we were able to access a large proportion of the species' range (Fig. 1), in November and December 1999 the region between Lake Ihotry and the Namonty wetland was inaccessible owing to severe waterlogging. Some of this area is inundated annually (B. Forgeau, personal communication) and it is thus possible that the subdesert mesite is scarce or even absent where this is the case. All estimates may consequently be exaggerated by a few thousand birds.

The most critical assumption of the mapping method is that territories are discrete and non-overlapping (Bibby et al., 2000). Fig. 2 illustrates the configuration of the seven territories used in this analysis, and overlap of 95% MCPs appears to be minimal at least over the four months of study. Nevertheless, there is some overlap between territories in the south of the site. While some of this is probably a result of drift in territory position over time, methods (A) and (B) may slightly exaggerate population density. Method (C) was designed to overcome this problem and, as predicted, produced a lower and possibly more realistic estimate of population density. However, all three mapping methods are limited insofar as they assume that the habitat at PK32 is representative of the whole area inhabited. Whereas the dry forest at PK32 matches the main type of vegetation growing in the Mikea Forest (Seddon et al., 2000), subdesert mesites were also found in coastal

scrub, higher-stature open dry forest and areas of sand and sparse vegetation. It is possible that the size and configuration of territories will have varied greatly between these vegetation types.

Using the distance sampling method (D), the best-fit model generated a population estimate of 115,000 individuals which is comparable to that generated by methods (A) and (B). According to the GoF test, the model fits these data quite well and the density estimate it has produced may be reasonably accurate. It might be a slight overestimate as it was not possible completely to rule out the possibility that groups moved prior to singing on a minority of occasions. However, the fact that the outcome is relatively similar across these three methods lends robustness to the results.

The calibration method (E) produced the highest estimate of population size. Care was taken to avoid habituation of groups at PK32 and only a slight decline in the responses of study groups was detected in September to December 1999 (Seddon, 2001). However, it is possible that these groups were more reticent than elsewhere, having been subject to playback during experiments prior to the trials. This would result in an overestimate of true population size.

#### 4.2. *Effective population size ( $N_e$ )*

Provided that a population has not experienced any major fluctuations in size (e.g. Vucetich et al., 1997), its social system will influence its effective population size ( $N_e$ ), and thereby its persistence through time (Komdeur and Deerenberg, 1997; Parker and Waite, 1997; Durant, 2000; Anthony and Blumstein, 2000). The variability of the subdesert mesite's social system and the lack of genetic data made it impossible to predict accurately the relationship between  $N_e$  and  $N$ . In some groups there is likely to have been high skew in reproductive success, with only the dominants breeding monogamously. In others, a more egalitarian system may have prevailed and subordinates may have bred. In the former scenario,  $N_e$  was calculated to be  $0.2N$  and in the latter it was  $0.6N$ . The true relationship might be expected to fall somewhere between these two extremes, and this is indeed likely for demographic reasons. Waite and Parker (1996), for example, emphasise the importance of the relationship between age at first breeding ( $M$ ) and average adult lifespan ( $A$ ). They show that there is an asymptotic convergence of  $N_e$  on  $0.5N$  as generation span ( $M-1+A$ ) increases. As already described,  $M/A$  is likely to be small in the subdesert mesite, and as such  $N_e$  may be close to  $0.5N$ . However, in order to estimate  $N_e$  accurately, good data on demography and variance in reproductive success are required (e.g. Nunney and Elam, 1994; Parker and Waite, 1997); in their absence the figures presented in Table 3 should be treated as provisional.

#### 4.3. *Conservation status of the subdesert mesite*

Species are assigned to a particular threat category on the basis of their effective population size, the extent and/or occupancy of their range and rates of decline in these factors (IUCN, 2000). The threat codes for the subdesert mesite once stood at A2b; B1+2c,e; C1; C2b (Collar et al., 1992). What has this study indicated about the validity of these codes and what conclusions can be drawn regarding the conservation status of the species?

##### 4.3.1. *Criterion A: population reduction*

In order to fulfil this criterion a population must either have experienced a reduction of >20% over the last 10 years (or three generations) or is expected to do so over the same time-scale in the future. It is unlikely that the subdesert mesite population has experienced such a decline in three generations (15 years) given our finding that the area of occupancy has only declined by 12.8% in the last 40 years. However, the area of occupancy is estimated to decline by 13% over the next 15 years if rates of deforestation remain the same, and by 26% if they increase at the current annual rate. It is, of course, difficult to predict how the rate of deforestation will change. Although current rates are likely to increase given mounting pressures on the forest, they are unlikely to grow at the same annual rate because most accessible forest has already been exploited and substantial improvements in the local infrastructure would be necessary to enable access to and exploitation of the remainder; moreover, most of the forest standing on cultivable soil has already been lost, while much of the forest left standing is unlikely to be cleared for agriculture, for the time being at least (see Seddon et al., 2000). Thus, a 20% population decline in three generations is unlikely, and as such the subdesert mesite fails to meet criterion A. This of course depends on how freely we apply the precautionary principle advised by IUCN (2000), this being one area in which subjectivity tends to compromise the consistent assessment of conservation status across species (see Collar, 1999).

##### 4.3.2. *Criterion B: small extent of occurrence or area of occupancy*

The subdesert mesite occurs in a region of c.5000 km<sup>2</sup> and the area they occupy is currently estimated as 3706 km<sup>2</sup>, although this is likely to be an overestimate (see above). A continuing decline in both extent of occurrence and area of occupancy is anticipated, but the range is not severely fragmented and does not consist of fewer than ten locations (Seddon, 2001; Seddon et al., 2000). IUCN (2000) define a location as 'a geographically or ecologically distinct area in which a single event (e.g. pollution) will soon affect all individuals of the species present' and '...which usually, but not

always, contains all or part of a subpopulation of the taxon, and is typically a small proportion of the taxon's total distribution'. Given the geographical and ecological distinctness of the Mikea Forest as a whole (reviewed in Seddon et al., 2000), subdesert mesites could be considered to occur in one location only. However, if we strictly apply this definition, a single event is unlikely to affect the entire Mikea Forest. In this way, the species does not occur in a 'location' as such but in a single continuous area, and it therefore does not fulfil Criterion B1.

#### 4.3.3. Criterion C: small and declining population

For inclusion in this category, a species must number fewer than 10,000 sexually mature individuals. This study has revealed that, even using effective rather than absolute estimates of population size, the number of subdesert mesites remaining exceeds this minimum value by a factor of 10–15. The assignment of threat code C to the species by Collar et al. (1994), on the basis of available information and the precautionary principle, was therefore incorrect. This highlights the difficulties involved with estimating numbers of and assigning threat status to poorly known elusive species such as the subdesert mesite.

To summarise, in contrast to previous assessments (Collar et al., 1994; IUCN, 2000), subdesert mesites do not meet criteria B or C. In addition, if the annual rate of increase in deforestation stabilises or declines as expected, subdesert mesites also fail to fulfil the requirements for criterion A (*contra* BirdLife International, 2000). As such, according to the guidelines presented by IUCN (2000), this species should be down-listed to Near-threatened, or possibly even Lower Risk status. Applying the precautionary principle to invoke a minimum  $N_e$  of 16,000 and a decline rate close to the requisite, the former is probably justified.

#### 4.4. Status assessment and application of the IUCN criteria

It is often stressed that the IUCN criteria should operate in combination with additional factors (costs, feasibility etc.) and are not intended to determine conservation priorities on their own (IUCN, 2000). This is important given that 'their *consistent* application using anything less than high-quality data is unattainable' (Collar, 1999). In practice, however, classification as threatened or otherwise can have a strong influence on conservation attention and action. In cases where the collection of data for threatened species triggers their demotion from the Red List, such a move can deflect conservation funding from them and their habitat, while hundreds of other species remain 'threatened' merely owing to continuing epistemic uncertainty. Moreover, a considerable amount of research relies on analysis of the

IUCN Red List data as a tool to identify patterns of threat and priorities for conservation (e.g. Brooks and Balmford, 1996)

While it is thus clear that the criteria for inclusion in the IUCN Red List play an important role, it is also apparent that the thresholds delimited by these criteria cannot be equally appropriate for all species. While this study concludes that the subdesert mesite should be down-listed, it highlights the insensitivity of the current IUCN criteria to three factors, namely lack of data and variations in ecology and taxonomic distinctness. Although it is beyond the scope of this study to make specific recommendations, we believe that a discussion of these topics (1–3 respectively) is necessary.

(1) For a great many plant and animal species, data on population size and rate of decline are poor if not entirely absent. However, the criteria do not consider the amount or quality of data available for species and they do not enable such uncertainty to be handled consistently (e.g. Burgman et al., 1999). Uncertainty falls into two basic categories: epistemic uncertainty and vagueness (Regan et al., 2000). Epistemic uncertainty arises from incomplete data (limitations of measurement accuracy, extrapolations and so forth) and it is this that resulted in the misclassification of the subdesert mesite with respect to criteria A and C. Vagueness arises from textual ambiguity: the 'minor loopholes and grey areas' in the IUCN criteria (Collar, 1999; see Section 4.3.2), as well as poorly defined data. Recent attempts to resolve the issue of uncertainty suggest incorporating the type and extent of uncertainty into the classification process (e.g. Colyvan et al., 1999; Akçakaya et al., 2000), and software has recently been developed for this very purpose (i.e. RAMAS Red List: Akçakaya and Ferson, 1999).

(2) While taxa differ in their vulnerability to extinction (Bennett and Owens, 1997; Owens and Bennett, 2000a), there is no 'clear line that separates threatened and non-threatened species' (IUCN, 1996). A large number of ecological, demographic and genetic factors interact to determine the persistence of species through time (see Burgman et al., 1993), and as a result it is impossible to fit risk indicators into neat numerical categories. There is, for example, no minimum viable population size that has universal application (Gilpin and Soulé, 1986).

Given this degree of complexity, we might conclude that species should be subject to a population viability analysis (PVA) before they are assigned a conservation status. However, this is not a realistic option because accurate PVA requires high quality data (Coulson et al., 2001), for which there are neither resources nor time to gather for all species of concern. Even so, basic data on clutch size, home-range size, social system and current levels of protection are available for many species (see the Red Data Books: Collar and Stuart, 1985; Collar et

al., 1992; BirdLife International, 2001). Much attention has been focused on refining the Red List criteria so that they maintain integrity in the light of such data (reviewed by Mace, 2000), but they currently provide only one variable with which to differentiate between species: generation span. Bennett and Owens (1997) showed that in birds ‘increases in extinction risk are independently associated with increases in body size and decreases in fecundity’ when phylogeny is controlled for. Although generation span is related to body size and thereby to fecundity (e.g. Gaston and Blackburn, 1997) it seems unlikely that this single measure could adequately differentiate between taxa as widely divergent as hummingbirds (Trochilidae) and eagles (Accipitridae), never mind insects and ungulates. While it is of utmost importance that the criteria remain easy to apply, they might be adjusted to take greater account of these substantial differences in ecology (e.g. degree of habitat specialisation: Owens and Bennett, 2000b).

(3) The ultimate objective of conservation is the preservation of biodiversity (e.g. Mace and Hudson, 1999). The evolutionary processes by which current biodiversity arose (and on which future biodiversity depends) act on all molecular and phenotypic variation in the organic world; it is clearly important to preserve this variation (Brooks et al., 1992; Wilson, 1992; Bennett and Owens, 1997). However, all species are not equal in terms of taxonomic distinctness (Atkinson, 1989; Vane-Wright et al., 1991; Nee and May, 1997): the sub-desert mesite, for example, is more distinct than most other bird species and presumably shares comparatively few of its genes with them. Houde et al. (1997) conclude that, according to their DNA analysis, mesites are much the most extreme outlier of all the varied Gruiforme families.

The Mesitornithidae was identified by Owens and Bennett (2000a) as the top ranking family in the world with respect to ‘diversification-under-threat,’ on the basis that mesites produce small clutches compared to their closest relatives and are all currently classified as threatened according to the IUCN Red List criteria. (It is worth adding that demotion in status for the sub-desert mesite would relegate the family to third rank according to Owens and Bennett’s analysis. Clearly, caution is advisable when incorporating the IUCN threat status of poorly known taxa into analyses designed to identify conservation priorities.) In addition, the subdesert mesite has unusual and poorly understood social and communication systems compared to its relatives (Seddon, 2001). Apart from its phylogenetic isolation, therefore, the species is also phenotypically distinct.

For these reasons, the extinction of the subdesert mesite would represent a substantial impoverishment of biodiversity. If this species is down-listed, there remain many others, weakly differentiated white-eyes *Zosterops*

spp., warblers (Sylviidae) and the like, whose official claim on limited conservation funding will be greater. While both taxonomic and phenotypic distinctness have been identified as important in assessing conservation priorities (e.g. Vane-Wright et al., 1991), the IUCN criteria have not yet been modified in their light. A case can be made for increasing the degree of precaution, by relaxing the criteria used for highly distinct species.

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