Group living, breeding behaviour and territoriality in the Subdesert Mesite *Monias benschi*

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In 1997–2000 we studied a population of Subdesert Mesites *Monias benschi* consisting of 35–68 adults comprising 32 groups of two to nine birds (modal group size of four). The study population was significantly male-biased in 1999 but not in 1997 or 1998. Overall, both sexes were philopatric, but when dispersal (or eviction) occurred, it appeared to be female-biased. Over 40% of groups contained more than two adult males, whilst < 15% contained more than two adult females. Whilst there was no evidence of behavioural dominance by females, intrasexual aggression within groups was observed only amongst females. In contrast to other birds occupying the same habitat, breeding in mesites was not tied to rainfall, and occurred throughout the year. Each breeding unit constructed several nests every year, only one of which was used. All adult males and at least one adult female co-operated to raise one or two clutches of one or two eggs per year. Males and females contributed equally to incubation. Chick production and chick survival were not related to group size or territory size. Groups defended large, permanent, and multipurpose territories and all group members contributed to territory defence. Territory size was positively correlated with the number of males in groups, but not with overall group size. Territories were tightly packed with very few areas unoccupied. Transect surveys conducted throughout the narrow geographical range of this species revealed its presence in a range of semi-arid habitat types. Small groups were more likely to be detected in intact, high-stature forest, whilst large groups were more likely to be detected in low-stature forest containing numerous spiny, xerophytic trees *Didierea madagascariensis*.

This study was conducted as part of a three-year investigation into the ecology of the Subdesert Mesite *Monias benschi* (Fig. 1), a group-living insectivorous gruiform bird endemic to Madagascar (Seddon 2001). The Subdesert Mesite belongs to a monotypic genus in the family Mesitornithidae that it shares with two other species, the White-breasted Mesite *Mesitornis variegata* and the Brown Mesite *Mesitornis unicolor* (Evans *et al.* 1996). All three are anatomically adapted to flight (Lowe 1924), but are mainly terrestrial and only fly to reach elevated roost sites or as an antipredator response. They are 30–32 cm long, weigh 110–170 g, their carriage is horizontal and they have thick coverts beneath long broad tails (Evans *et al.* 1996). Although both *Mesitornis* species are sexually monomorphic, the Subdesert Mesite is

dichromatic: the breast and throat of females is extensively rufous while that of males is white with black crescents (Evans *et al.* 1996).

The Subdesert Mesite is restricted to a coastal strip of semi-arid forest 30–60 km wide and 200 km long between the Fiherenana and Mangoky rivers in south-west Madagascar, an area known as the Mikea Forest (Seddon *et al.* 2000). Its distribution within this narrow geographical range has been described as 'extremely local' (Rand 1936) and it has been classified as Vulnerable according to the IUCN Red List criteria (BirdLife International 2000). Prior to this study, the species was reported to live in groups (Lavauden 1931, 1932, Rand 1936, Appert 1968, 1985, Steinbacher 1977), although there was no information about the size and spacing of territories. Information about habitat requirements was scant: whilst it had been described as 'catholic in choice of habitat, primarily requiring areas with dense leaf-litter'

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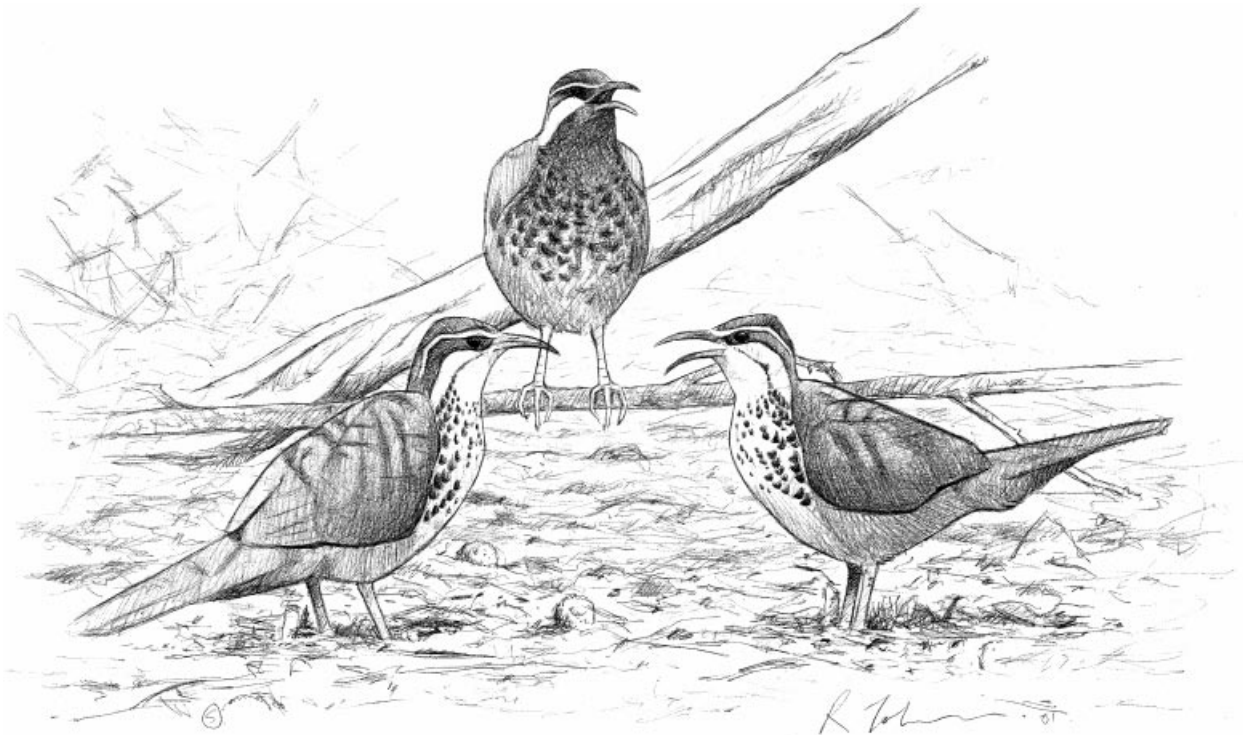Email: ns10003@com.ac.uk

Figure 1. Subdesert Mesite by Richard Johnson, reproduced with permission of the artist. The figure shows a perched female and two males engaged in a co-ordinated chorus.

(Collar & Stuart 1985), no quantitative assessment had been undertaken. Similarly, there was confusion over the social system: Rand (1936) cited the numerical preponderance of males in groups as evidence of polyandry (see also Ligon 1999), but Appert (1968, 1985) assumed polygyny having observed a nest attended by two females and a single male. Such reports indicated the existence of an unusual social system that was worthy of further investigation.

On the basis of data gathered in the Mikea Forest in 1997–2000 we present the first detailed description of the population structure, reproductive behaviour and spacing system of the Subdesert Mesite. Mainly using radiotelemetry data gathered in 1999, we investigated territorial interactions between neighbouring groups and examined changes in territory size in relation to breeding. In order to determine the species' habitat preferences we conducted surveys along transects positioned throughout its entire global range.

METHODS

During three five-month field seasons (September to January) in 1997–2000, we studied Subdesert

Mesites at two sites: PK32 (23°04′57″S, 43°37′15″E, 200 ha), and Mangily (23°07′09″S, 43°37′30″E, 120 ha) and along eight transects in the Mikea Forest north of Manombo (Fig. 2). Detailed descriptions of these sites are given in Seddon *et al.* (2000).

Population structure and social organization

Mesites were caught using 18-m two- or four-shelf mist-nets. We played taped male song to attract them to the general area, then herded them into the net with varying degrees of success. Using this technique, 102 individuals were trapped in 147 h of netting. Birds were given individual combinations of two to four coloured plastic leg rings.

We estimated the numbers of mesites at the study sites by using distinctive plumage characteristics to distinguish the sexes and estimate age (Seddon 2001). We counted the number of individuals of each sex in each of the study groups at monthly intervals. A group was defined as a cohesive collection of individuals that shared a common territory, foraged together and co-operated over territory defence and in the care of young. Within- and between-seasons
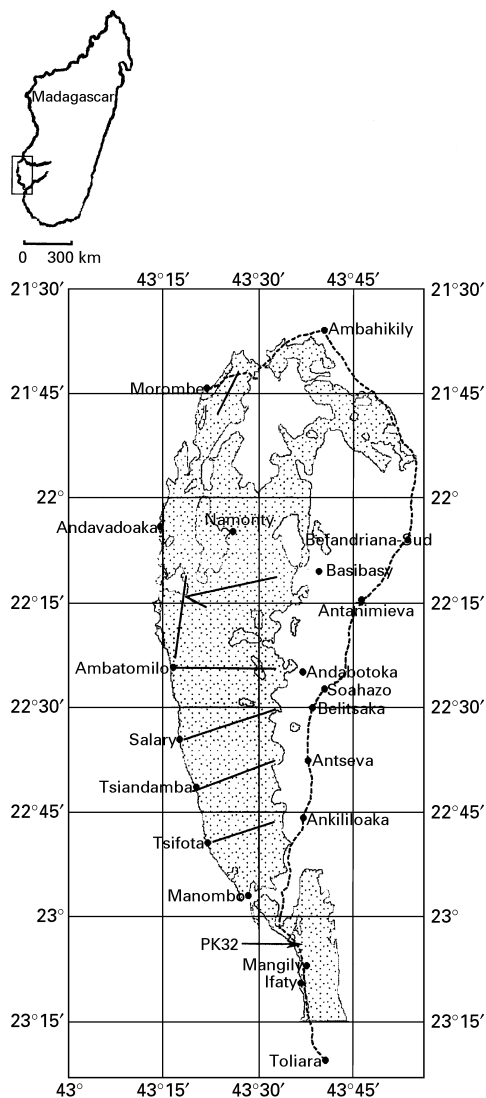
Figure 2. The global range of the Subdesert Mesite (the Mikea Forest, outlined in grey) annotated with the position of the main study sites (PK32 and Mangily), the tracks (fine straight lines) used to conduct vegetation and playback surveys and the road (thick dashed line) used to access the Mikea Forest. The names given refer to important villages and small towns.

group size and composition changed. In order to minimize pseudoreplication in calculations of group size and sex ratio, groups were defined as unique if new individuals accounted for more than 50% of the group.

Behavioural observations

In 1997–98 and 1998–99, groups were located by active systematic searches, chance encounters along forest trails, by listening for distinctive vocalizations

(Seddon 2001) or by finding and following characteristic tracks made in the sand (Tobias & Seddon 2002a). In 1999–2000, we also used radio-transmitters to locate groups. Every few days we followed groups semicontinuously at a distance of 15–30 m from dawn (*c.* 05:00 h) to 11:00 h and from 16:00 h to dusk (*c.* 19:00 h), avoiding the hottest part of the day when conditions were unbearable and mesites were generally inactive. Even after weeks of tracking, mesites showed no signs of habituation, and this sustained nervousness precluded the collection of detailed behavioural data. The behaviour described here is based largely on a total of 260 h of focal watches (range: 12–80 h per group, $n = 8$ groups) in 1999–2000.

Breeding behaviour

Breeding was extremely inconspicuous and despite the use of radio-tags, no copulation and very little nest-building was observed in 18 months of fieldwork. We recorded the position and structure of each nest, and we checked newly constructed nests every 2–3 days, remaining at a distance of at least 10 m in order to avoid disturbing any birds in the vicinity. All four nests located in the process of being constructed were abandoned. During focal watches on active nests (conducted at > 10 m from dawn to dusk) we recorded the duration of incubation bouts for each group member.

By taking biometrics and studying the plumage of birds of known age it was possible to estimate the age and hence approximate hatching dates for young Subdesert Mesites produced less than 3 months before early September 1998 and 1999 (Seddon 2001). In order to compare the timing of mesite reproduction to that of other bird species at PK32, we recorded approximate dates (within 7 days) of hatching in 30 species for which nests were found and monitored regularly. Together, these species encompassed a broad range of foraging guilds.

Territory mapping

In October 1999–January 2000 we used 1.0-g TW-4 radio-transmitters with whip-antennae (from BIOTRACK Ltd) powered by 2.0-g mercury cells (Ag393), which gave lifespans of *c.* 84 days. We attached transmitters to one member of each of 10 groups. Packages were attached to the heaviest individual captured and represented a mean ± se of 2.22 ± 0.02% and 2.10 ± 0.09% of the mean body mass of males ($n = 3$) and females ($n = 7$), respectively,

well below the recommended maximum of 5% of body weight (Aldridge & Brigham 1988). Transmitters were attached with a backpack harness so that they sat in the interscapular region on the back of the bird (Godfrey 1970, Kenward 1987, Hill *et al.* 1999). Standard non-abrasive Teflon ribbon was threaded through plastic tubes firmly glued to the sides of the transmitter package and looped beneath the wings and over the shoulders to form a simple, permanent harness. It was not possible to tie or glue the transmitter to the tail feathers (as in other studies of terrestrial birds, e.g. Jansen 1999) as the rectrices are rather loosely attached and tend to be ejected when the birds are stressed. Once transmitters had been attached, the birds were allowed to acclimatize for at least a week before data were collected.

Radio-transmitters were located using a portable receiver (TRX-1000S, from Wildlife Materials Inc., Carbondale, IL, USA) and a hand-held, collapsible three-element Yagi aerial (BIOTRACK Ltd, Wareham, UK). The signal range was 100–150 m in dense forest. Signals were tracked until the birds were visible or their contact calls and/or alarm calls were audible. Effort was made not to disturb groups, which usually meant remaining at a distance of 15–20 m. Once groups had moved on from a fix, observers walked to the point, the exact position of which could be identified by tracks. Registrations were recorded either as co-ordinates (using a Garmin 2-plus GPS) or as bearings from fixed stations, such as path-markers, whose GPS points had already been measured.

We attempted to obtain registrations for each group distributed evenly from dawn (*c.* 05:00 h) to 11:00 h and from 16:00 h to dusk (*c.* 19:00 h), a time period encompassing the main activity periods of mesites. Registrations were gathered from four sources: visual encounters with colour-marked groups following active searches or chance encounters; sets of fresh (< 1 day old) tracks; radiotracking data; and contact calls or songs. Fixes from chance visual encounters and radiotracking data were taken every 20 min. This frequency was based on the observation that it was possible, although unlikely, for birds to reach any other location in their territory within 20 min, groups having been observed to walk or occasionally fly from one side to another in < 15 min. Sets of tracks were considered independent if located ≥ 25 m apart. Following detection of songs, groups were tracked down to sight so that the precise location of the group could be recorded, and this point represented a single fix. If it was then possible to follow groups, fixes were taken every 20 min.

We describe the ranges of each group as territories because they were more or less restricted and exclusive areas within which a group moved when performing routine activities (foraging, vocalizing, reproducing, caring for young and roosting) and which were defended against intruders. The large size of mesite territories, the relatively dense understorey and the low rate of singing meant that birds were extremely difficult to locate. In 1997 and 1998, it was not possible to gather sufficient registrations to quantify seasonal changes in territory size and configuration, so we have drawn minimum convex polygons (MCPs: Southwood 1966) around registrations from the entire field season. We used at least 70 registrations to create each map (see below), which gave 84.7 ± 2.6% of the final territory size (as determined from graphs of cumulative area against number of registrations for nine groups for which we recorded 150 or more total registrations in a season).

In 1999–2000, registrations were derived from daily 4–7-h-long semicontinuous focal watches of groups containing at least one radiotagged individual. We obtained sufficient fixes for seven groups in order to compare their territory size and configuration for the whole season. We also had sufficient fixes for these groups to split the data by month and breeding period (at least 65–70 fixes for each category). Breeding was defined as the period during which eggs were incubated, plus a 10-day period during which adult mobility was constrained by that of the precocial chicks.

Using WILDTRAK version 1.2 (Todd 1992), we constructed MCPs either around all visual-, track- and song-registrations (vts MCPs), around radiotracking fixes only (rt MCPs), or around all registrations (100% MCPs). Only those registrations that were unequivocally identified to a specific group were used to define territory limits. One hundred percent MCPs are likely to overestimate territory as they include outliers and hence incorporate large areas of the territories which are very rarely used (Harris *et al.* 1990). We therefore also calculated the area within which 95% of all the registrations fell (95% MCP).

Habitat associations

We used multivariate statistics to examine the relationship between the vegetation and the occurrence, size and adult composition of mesite groups. We gathered data from 28 November to 13 December 1999 along eight transects north of Manombo (Fig. 2). The transects were divided into 40 survey

blocks, each 1.2-km long and separated by 2–3 km. Vegetation was surveyed at five points positioned at 300-m intervals along each block. Within a 10-m radius of each point we estimated: (1) percentage leaf litter cover and (2) depth of leaf litter; (3) modal canopy height; (4) maximum and modal visibility at 0.5 m above the ground; (5) number of *Euphorbia* spp. trees; the total number of three common tree species, namely (6) spiny *Didierea madagascariensis* (7) baobabs (bottle trees) *Adansonia* spp., and (8) 'Farafatse' *Givotia madagascariensis*; (9) maximum canopy height, and (10) number of trees with diameter at breast height (dbh) > 20 cm. High scores for variables (7)–(10) were good indicators of relatively intact habitat (Seddon *et al.* 2000).

At each survey point we used a Sony SRS-58 loudspeaker to broadcast two 30-s mesite songs. The speaker was held by one observer at *c.* 1 m above the ground and slowly and evenly rotated through 360 degrees. At the beginning of each broadcast, the sound pressure level (SPL) was adjusted to 65 dB at 15 m in front of the loudspeaker (the SPL of natural songs: Seddon 2001). Playback was carried out in calm conditions at 06:00 h–11:00 h and 13:00 h–19:00 h. There was no significant variation across hourly sampling periods in the mean number of groups responding per playback (ANOVA: $F_{1,12} = 0.891$, $P = 0.557$). At each point, we recorded the number of groups contacted (with or without playback) and where possible the number of individuals with adult plumage in the group. When groups approached the loudspeaker we ascertained their size and composition. A total of 15 min was spent at each point ensuring that all group members had been accounted for. Occasionally group size might have been underestimated as incubating birds may not have approached playback. However, over a sample of 69 groups the potential for this factor to confound the results is likely to have been small (see Tobias & Seddon 2002b).

Statistics and sampling

We used Discriminant Function Analysis (DFA) to examine the transect data. We assessed whether it was possible to use the vegetation data to discriminate between points at which small groups were observed and those at which large groups were observed. A small group was defined as one comprising four or fewer adults, i.e. a breeding pair and one or two of its latest offspring. A large group was one comprising at least five adults including individuals

in addition to a pair and its latest offspring. Regardless of the habitat type, large groups were no more likely to be detected than small groups as mesites produced loud alarm calls on perceiving observers irrespective of their own group size. When more than one group was observed we included these shared survey points in each group (5/69 points). Prior to this analysis, data were checked for normality using Kolmogorov–Smirnov tests and data on percentage leaf-litter cover were arcsine transformed (Seddon 2001). We present the results from the DFA using simultaneous and stepwise inclusion of variables. In order to show whether differences in the multivariate data sets of the classes of survey points are statistically significant we give values for Wilks' Lambda. We show the discriminant function scores of the survey points and test the statistical differences between them using unpaired *t*-tests. To decipher the ecological meaning of the discriminant function axes, we list those variables which have correlation coefficients with the discriminant function of > 0.20 (Hedderson 1987).

In other analyses non-parametric tests were used because sample sizes were small. We pooled data from all study sites and across seasons in order to obtain a sufficiently large sample to test statistical significance. Sample sizes were too small to test for differences in group size and structure between the sites, but pooling of these data was justified given the fact that the habitat was more or less identical and contiguous, the sites being only 6 km apart. All statistical tests are two-tailed and are corrected for ties where appropriate. All means are given ±1 se.

Ethical note

The capture and radiotagging of mesites was conducted under licence from the Ministère des Eaux et Forêts in Madagascar. To ensure that the tags did not impinge on the birds' welfare, only healthy individuals were selected: these were defined as strong, heavy birds (> 150 g) with fresh, intact plumage. Following release, no adverse effects were recorded on roosting, flight, health, territorial ownership, nest construction, incubation or defence of young (Seddon 2001).

RESULTS

Population structure

Of a population of 35–68 Subdesert Mesites, 52%, 76%, and 50% were colour-ringed in 1997, 1998

Table 1. The structure of the adult population of Subdesert Mesites studied in 1997–2000. In 1999, the sex ratio deviated significantly from 1:1 at PK32, north of Manombo and overall.

Location	Date	Males	Females	Total	Sex ratio (males per female)	χ^2_1
Mangily	December 97	11	10	21	1.10	0.04
	December 98	10	7	17	1.43	0.53
PK32	December 97	6	8	14	0.75	0.29
	December 98	27	24	51	1.13	0.18
	December 99	34	17	51	2.00	5.67*
N. Manombo	December 99	177	128	305	1.38	7.87**
Overall†	December 99	211	145	356	1.46	12.24***

†Includes combined data from PK32 and north of Manombo in December 1999.
Chi-squared: *$P < 0.02$, **$P < 0.01$, ***$P < 0.001$.

Table 2. Mean ± se (and range, number of groups) of adult mesite group sizes and compositions at three sites in the Mikea Forest in mid-December 1997, 1998 and 1999. In 1999 there was no significant difference in mean group size between PK32 and those north of Manombo (Mann–Whitney U-tests: group size: $U = 358$, $n_1 = 14$, $n_2 = 69$ groups, $P = 0.12$). However, within-group sex ratios were significantly more male biased at PK32 ($U = 303$, $n_1 = 14$, $n_2 = 69$ groups, $P = 0.026$).

	Group size			Group sex ratio (males per female)		
Location	1997	1998	1999	1997	1998	1999
Mangily	4.2 ± 0.4 (3–5, 5)	4.3 ± 1.4 (2–8, 4)	–	1.10 ± 0.19 (0.5–1.5)	1.29 ± 0.17 (1.0–1.67)	–
PK32	3.5 ± 0.6 (2–5, 4)	4.3 ± 0.5 (2–8, 12)	3.6 ± 0.23 (2–6, 14)	1.00 ± 0.36 (0.33–2.0)	1.15 ± 0.22 (0.33–3.0)	2.21 ± 0.32 (0.5–5.0)
North of Manombo	–	–	4.4 ± 0.2 (2–9, 69)	–	–	1.49 ± 0.09 (0.33–4.0)
Overall	3.9 ± 0.4	4.3 ± 0.5	4.3 ± 0.2	1.06 ± 0.18	1.19 ± 0.17	1.61 ± 0.10

and 1999, respectively. These comprised 27 unique groups at the main study site, PK32, and five groups at Mangily. In addition, 69 groups encompassing 305 individuals were encountered along eight transects located north of Manombo. Table 1 shows the population structure at the three sites.

There were no consistent patterns of movements within and between groups between seasons and we found that both males and females dispersed (Seddon 2001). Of all birds banded in 1997 and 1998 only six dispersed to known territories. The remainder either stayed on the same territory (22/35 in 1998 and 9/27 in 1999) or dispersed to unknown territories and/or died. Given the uncertain fate of a substantial proportion of the study population, it is not possible to quantify dispersal. However, it is interesting that the majority (66.7%, 10/15) of the lone and presumably dispersing individuals observed were adult females.

Social organization

The sex ratios in groups of Subdesert Mesites observed were not significantly biased in any year (Table 2). However in 1999, groups at PK32 were significantly more male-biased than those encountered north of Manombo. The modal adult group size was four; the most frequently encountered group composition was three males and two females, with pairs ranking second, and groups of two males and two females ranking third. Whilst 42.6% of groups encountered contained three or more adult males, groups containing more than two adult females were scarce, together accounting for 13.9% of groups recorded.

Breeding behaviour

Timing of reproduction
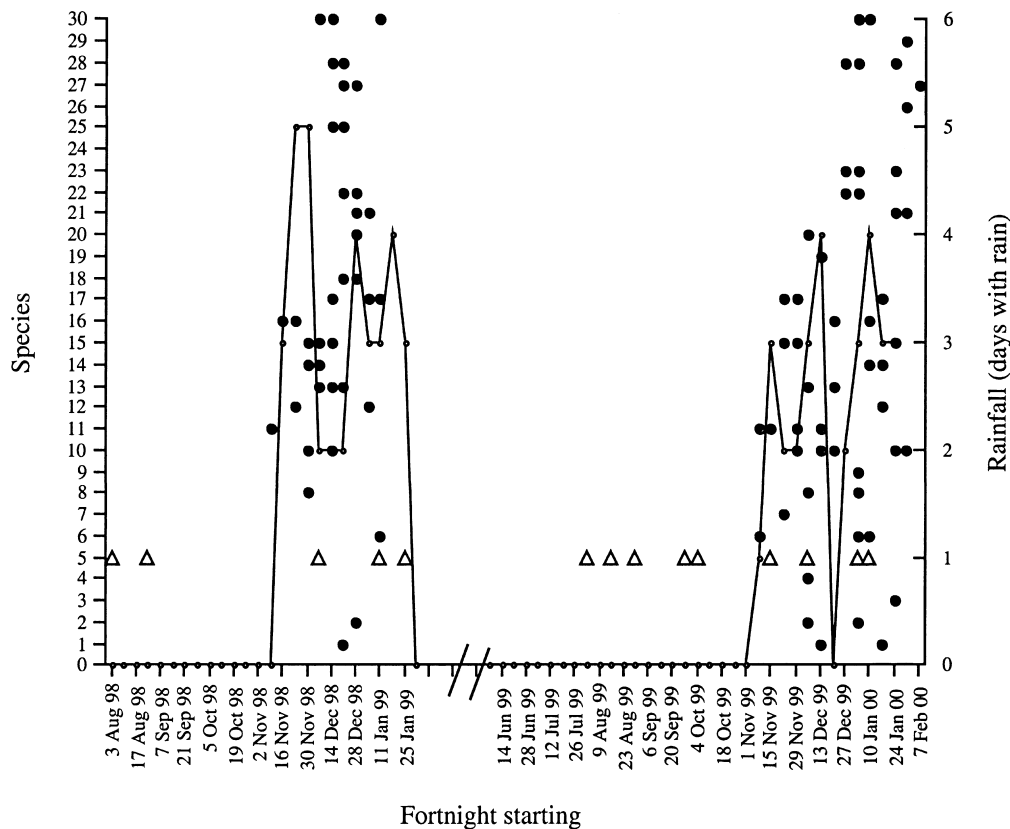Figure 3 illustrates the hatching dates of Subdesert Mesites along with those of 30 other bird species

Figure 3. Timing of reproduction in mesites (triangles) relative to rainfall (fine solid lines) and breeding in other bird species (solid circles) across a broad range of foraging guilds. Species: 1, *Polyboroides radiatus*; 2, *Buteo brachypterus*; 3, *Accipiter francesii*; 4, *Falco newtonia*; 5, *Monias benschi*; 6, *Turnix nigricollis*; 7, *Streptopelia picturata*; 8, *Coracopsis madagascariensis*; 9, *Cuculus rochii*; 10, *Coua olivaceiceps*; 11, *Coua cursor*; 12, *Coua cristata*; 13, *Caprimulgus madagascariensis*; 14, *Uratelornis chimaera*; 15, *Copsychus albospecularis*; 16, *Upupa marginata*; 17, *Terpsiphone mutata*; 18, *Newtonia brunneicauda*; 19, *Newtonia archboldi*; 20, *Neomixis tenella*; 21, *Neomixis striatigula*; 22, *Nectarinia souimanga*; 23, *Leptopterus viridis*; 24, *Leptopterus chabert*; 25, *Falculea palliata*; 26, *Calicalicus madagascariensis*; 27, *Xenopirostris xenopirostris*; 28, *Dicrurus forficatus*; 29, *Foudia madagascariensis*; 30, *Ploceus sakalava.* Data are from PK32 in 1998, 1999 and 2000.

(in 17 families) at PK32 in 1998–99. Reproduction across a broad cross-section of bird taxa appears to be tied to rainfall, there being a conspicuous pulse of hatching from mid-November to mid-January in both years. In contrast, only 46.7% (7/15) of known mesite clutches hatched during these pulses.

Nest building
Of the 24 nests located in 1997–2000, only nine contained eggs. Nests were loosely woven platforms of twigs, *c.* 15 cm in diameter and *c.* 5 cm deep, with a very shallow cup in which to place the eggs. They were adorned with variable quantities of fresh lichen and were positioned at a mean of 1.6 ± 0.1 m above the ground (range: 1.1–2.0 m). Of the nests found, 37.5% (9/24) were in *Securinegina perrieri*, 33.3% (8/24) were in *Commiphora simplicifolia*, 16.7%

(4/24) were in *Euphorbia stenoclada*, 8.33% (2/24) were in vine-tangles, and one (4.17%) was in *Commiphora humbertii*. Mesites reached their nests by walking up a gently sloping branch or by flying directly (contra Appert 1968 who stated that they needed 'natural ramps' to access nests). Nests were constructed 4–6 weeks before laying and were located close to the centres of groups' home ranges: the mean distance of nests from their nearest border was 87.9 ± 9.0 m (*n* = 14 nests, six groups). A mean of 2.9 ± 0.5 nests was recorded per group per breeding season (range: 1–5) for seven groups whose territories had been searched systematically. The number of nests constructed per breeding attempt was strongly and positively correlated with the number of males in the group but only weakly with the number of females (Spearman rank correlations,

Table 3. Percentage of incubation carried out by those observed incubating in each of seven groups in 1997–2000. There was no significant difference between the principal male and female incubators in total number of daylight hours spent incubating (Wilcoxon-signed rank test: $T = 19$, $N = 7$ groups, $P = 0.23$). In the table N refers to number of hours. Cases where there were no individuals in a particular category are denoted by a dash (–).

Group	Month/ year	Diurnal incubation (05:00–19:00 h)								Diurnal + nocturnal incubation (00:00–24:00 h)					
		♀₁	♀₂	♂₁	♂₂	♂₃	♂₄	♂₅	N	♀₁	♀₂	♂₁	♂₂	♂₃	N
M11	11/97	62.7	0	37.3	–	–	–	–	14.5	37.1	0	62.9	–	–	24.5
P7	12/98	28.8	0	71.2	–	–	–	–	18.5	–	0	–	–	–	–
P12	01/98	45.9	0	30.9	23.2	–	–	–	18.8	–	0	–	–	–	–
P12	10/99	50.9	–	33.8	15.3	–	–	–	88.1	28.3	–	63.1	8.5	–	158.1
P3	12/99	35.9	–	32.2	25.1	6.8	–	–	104	25.6	–	41.3	18.1	15.0	184
P2	12/99	66.0	0	33.0	–	–	–	–	26.5	37.6	0	62.4	–	–	46.5
P8	01/00	18.4	–	32.4	20.7	17.4	7.3	3.7	54.5	–	–	–	–	–	–
Mean		44.1	0	38.7	21.1	12.1	7.3	3.6		32.2	0	57.4	13.3	15.0	
± se		± 6.6		± 5.5	± 2.1	± 5.3	± 4	± 7		± 3.1		± 5.4	± 4.8		

$n = 8$ groups: males: $r_s = 0.994$, $P = 0.009$; females: $r_s = 0.606$, $P = 0.060$). The only bird encountered building a nest was a male. The mean distance of multiple nests from the centre of the range they delimited was 36.2 ± 0.8 m.

Incubation and care of young

Mesites laid clutches of one ($n = 1$) or two eggs ($n = 8$). Of these 17 eggs, one never hatched and was presumably infertile. Within a week of laying, eggs weighed 15.8 ± 0.2 g and were 36.9 ± 0.5 mm in length and 27.6 ± 0.3 mm in width ($n = 7$ eggs from four clutches), and the mean clutch mass as a percentage of female mass was $20.7 \pm 0.4\%$ ($n = 4$). We cannot give a precise incubation period as the exact time and date of laying was not known for any group (groups tended to abandon newly constructed nests when we found them). However, for two groups whose eggs were found 4 and 3 days after empty nests were located, the incubation periods were 21–25 and 24–27 days, respectively. Incubation was carried out by all adult males and at least one adult female per group (Table 3). The second and probably subordinate females in four groups were not observed incubating. No juveniles contributed to incubation but some males incubated before they were 1 year old.

Although the 'dominant' male and female contributed equally to diurnal incubation, incubation bouts were of significantly greater duration for females than for males (5.7 ± 0.9 vs. 2.8 ± 0.3 h; Mann–Whitney U-test: $U = 39.5$, $n_1 = 12$, $n_2 = 5$, $P = 0.008$). However, females were only twice observed incubating overnight. When data for nocturnal incubation were included, there was no significant difference in mean bout length between the sexes (6.9 ± 0.9 vs. 6.1 ± 0.9 h; $U = 136$, $P = 0.687$). We assumed that there were no switchovers at night as on all 18 occasions (involving four groups) the individual incubating at dusk was the same as that observed on the nest prior to sunrise the following day.

Hatching was almost synchronous at the one nest where it was observed, with two chicks hatching within 2 h of each other between 06:30 h and 08:30 h on 15 November 1999. The similarity in biometrics of paired chicks suggested that synchronous hatching was usual (Seddon 2001). The chicks remained in the nest for up to 24 h after hatching. At one nest we were able to observe during this period, only the male of a pair fed the young (six feeds in 8 h). Once chicks had dropped to the ground all group members appeared to defend them cooperatively. This was observed in nine different groups on 15 occasions and involved the same ritualized behaviour, including an elaborate distraction display mainly involving males (Seddon 2001). When foraging with their young, mesites were extremely vigilant and any slight disturbance incited this display, making it difficult to quantify social behaviour during this time. In the one group that we could observe during this period, all group members (one female and three males) fed an 8-day-old chick. On the only occasion when a group with chicks was observed roosting, both young birds rested under the wings of a single adult male.

For the 20 groups that we knew attempted to breed in September–January 1997–2000, overall mean chick production was 1.5 ± 0.2 per group. For

Table 4. Territory size estimates (in hectares) for 1997–98, 1998–99 and 1999–2000 for those mesite groups with at least 70 registrations, i.e. groups in which asymptotes were achieved in plots of territory size vs. number of registrations. MCP: minimum convex polygon, vts: registrations derived from visual encounters, tracks and songs; rt: registrations derived from radio-tracking data. Core areas are derived from song, nests and roost registrations, the total number of which are given in parentheses. P- and M-prefixes denote study groups at PK32 and Mangily groups, respectively.

Group	1997–1998 MCP (vts)	1998–1999 MCP (vts)	1999–2000 MCP (vts)	1999–2000 MCP (rt)	1999–2000 100% MCP	1999–2000 95% MCP	1999–2000 Core area
P1	8.72	14.38	11.77	17.45	17.80	14.63	10.96 (28)
P2	4.73	4.47	7.07	3.22	7.49	5.59	2.33 (12)
P3	–	4.12	9.93	9.65	11.28	6.78	5.03 (20)
P6	3.97	7.56	14.26	17.03	18.94	16.48	12.23 (25)
P7	–	4.01	8.44	10.57	11.57	9.78	5.95 (11)
P8	–	–	14.50	9.41	15.65	13.21	3.97 (10)
P10	–	–	15.95	18.10	21.38	18.18	11.70 (19)
M7	5.65	–	–	–	–	–	–
M8	4.02	4.02	–	–	–	–	–
M9	5.68	5.90	–	–	–	–	–
M10	7.88	7.83	–	–	–	–	–
M11	3.51	–	–	–	–	–	–
Mean ± se	5.52 ± 6.70	6.54 ± 1.25	11.70 ± 1.27	12.21 ± 2.09	14.87 ± 1.87	12.09 ± 1.82	7.45 ± 1.54

those 12 distinct groups that produced chicks, the mean number (and percentage) of chicks surviving more than 4 weeks was 1.5 ± 0.1 per group (84.7 $\pm 6.6\%$). Neither the number of offspring produced nor the number surviving per group was related to group size, number of males per group, number of females per group or territory size estimated using 'vts' MCPs (Spearman rank correlations: chick production: r_s-values: -0.12 to 0.01, $n = 20$, *P*-values: 0.75–0.97; chick survival: r_s-values: 0.18–0.40, $n = 12$, *P*-values: 0.19–0.61).

Territoriality

Territory defence

The Subdesert Mesites studied lived in multipurpose territories and it is likely that territories were occupied and defended permanently, especially given the evidence for year-round breeding. Six groups containing at least one individual from the preceding year were found in approximately the same locations in September 1998 as in January 1998, and five such groups were found in roughly the same locations in October 1999 as in January 1999.

All mesites occupying a territory helped to defend it, with adults apparently defending against same-sex intruders. Following a direct encounter, birds moved together from their more scattered foraging positions and gave a communal song or songs with a long mean ($\pm$ se) duration of 240 ± 56 s ($n = 10$

groups). In all but two observed events, when groups finished singing there were short scurrying chases and the intruders retreated irrespective of their relative group size. When intruders did not retreat the interaction escalated into prolonged running song contests and fights between opposing birds.

Comparison of territory size estimates

Estimates of mean territory size for the 1999–2000 season varied from 11.7 ± 1.3 ha to 14.9 ± 1.9 ha depending on the method used and the source of registrations used in the calculation (Table 4). There were no significant differences between the estimated MCPs drawn around registrations derived only from visual encounters, tracks or songs ('vts MCP'), those using fixes taken whilst radiotracking ('rt MCP'), and those using 95% of all registrations (95% MCPs; Friedman test: $\chi^2 = 0.28$, $n = 7$, $P = 0.87$).

Correlates of territory size

There were no significant correlations between territory size and the number of adults in the group for the seven groups for which we collected sufficient registrations in 1999–2000, whether using 100% or 95% MCPs (100% MCPs: $r_s = 0.24$, $P = 0.55$; 95% MCPs: $r_s = 0.72$, $P = 0.13$; Spearman rank correlations, $n = 7$). Given that one sex may be more active than the other in territory defence, we investigated whether territory size was related to the number of males or females in a group, but no significant correlations were found
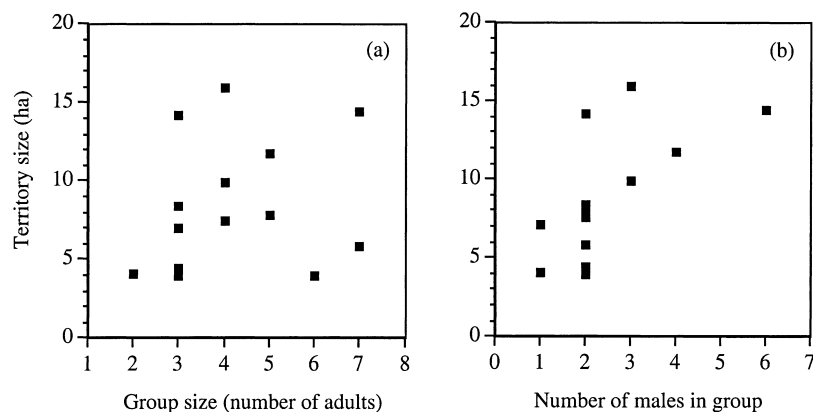
Figure 4. Scatterplots depicting the relationship between territory size and (a) the number of adults in a group and (b) the number of males in a group. Although there was no significant relationship between overall group size and territory size (a), the number of males in a group was significantly positively correlated with territory size (Spearman rank correlations, $n = 14$: group size: $r_s = 0.26$, $P = 0.344$; number of males: $r_s = 0.68$, $P = 0.014$).

(r_s-values: 0.61–0.36, $n = 7$, P-values: 0.13–0.37). This lack of significance may be an artefact of small sample sizes, and so we increased the sample by incorporating data into the analysis from different groups studied in 1998–99 (Table 4). We used 'vts MCP' territories from 1999 to 2000 to ensure these territory sizes were comparable to those estimated for groups in 1998–99 when radiotelemetry was not employed. Again, although there was no significant relationship between territory and overall group size, there was a positive correlation between territory size and number of males in a group (Fig. 4).

Changes in territory size and configuration
Figure 5 illustrates the overall pattern of mesite territories at PK32 in October 1999–January 2000 for 11 study groups. When considered over the whole season, territories were tightly packed with very little habitat unoccupied. In 1999 there was a decline in territory size over three periods: 10 October–20 November 1999, 21 November–22 December 1999 and 23 December–14 January 2000 (Fig. 6). Territory size also declined during breeding in three radiotagged groups: breeding territories constituted 41.3%, 40.4% and 71.2% of non-breeding territories.

During 1999–2000 there was very little change in the position of each group's territory and only minor changes were detected in boundary location. The extent to which neighbouring groups overlapped each other's territories varied between groups (mean: 4.94 ± 1.52%, range: 0.20–28.0%, $n = 10$ neighbouring groups) and declined from September–December 1999 (Seddon 2001).

Habitat associations

At the 200 points at which playback was conducted and vegetation sampled, 119 groups were detected, of which the exact size and composition was ascertained for 69 groups comprising 305 individuals. The surveys confirmed that mesites are widespread within their narrow geographical distribution. They were recorded in (a) very low-stature, sparse coastal scrub within 1 km of the coast, (b) high-stature, relatively dense, dry forest up to 40 km further inland and (c) in degraded forest and regenerating scrub at the edge of maize fields. However, none was recorded in burnt forest.

Overall, small groups were more likely to be detected in intact, high stature forest, whilst large groups were more likely to be detected in low stature forest containing numerous spiny, xerophytic trees *Didierea madagascariensis*. Specifically, the differences between survey points at which small groups were recorded and those at which large groups were recorded were significant for the 11 habitat variables (Wilks' Lambda = 0.732, $df = 10$, $P = 0.044$). When these variables were simultaneously included in the analysis, the discriminant function scores of survey points at which small groups were located were significantly lower than those of points at which large groups were recorded (unpaired t-test: $t = -5.06$, $df = 68$, $P < 0.0001$; Fig. 7). When the variables were entered into the analysis in a stepwise fashion only two (number of large trees and number of xerophytic trees *Didierea madagascariensis*) were included in the discriminant function. There was a
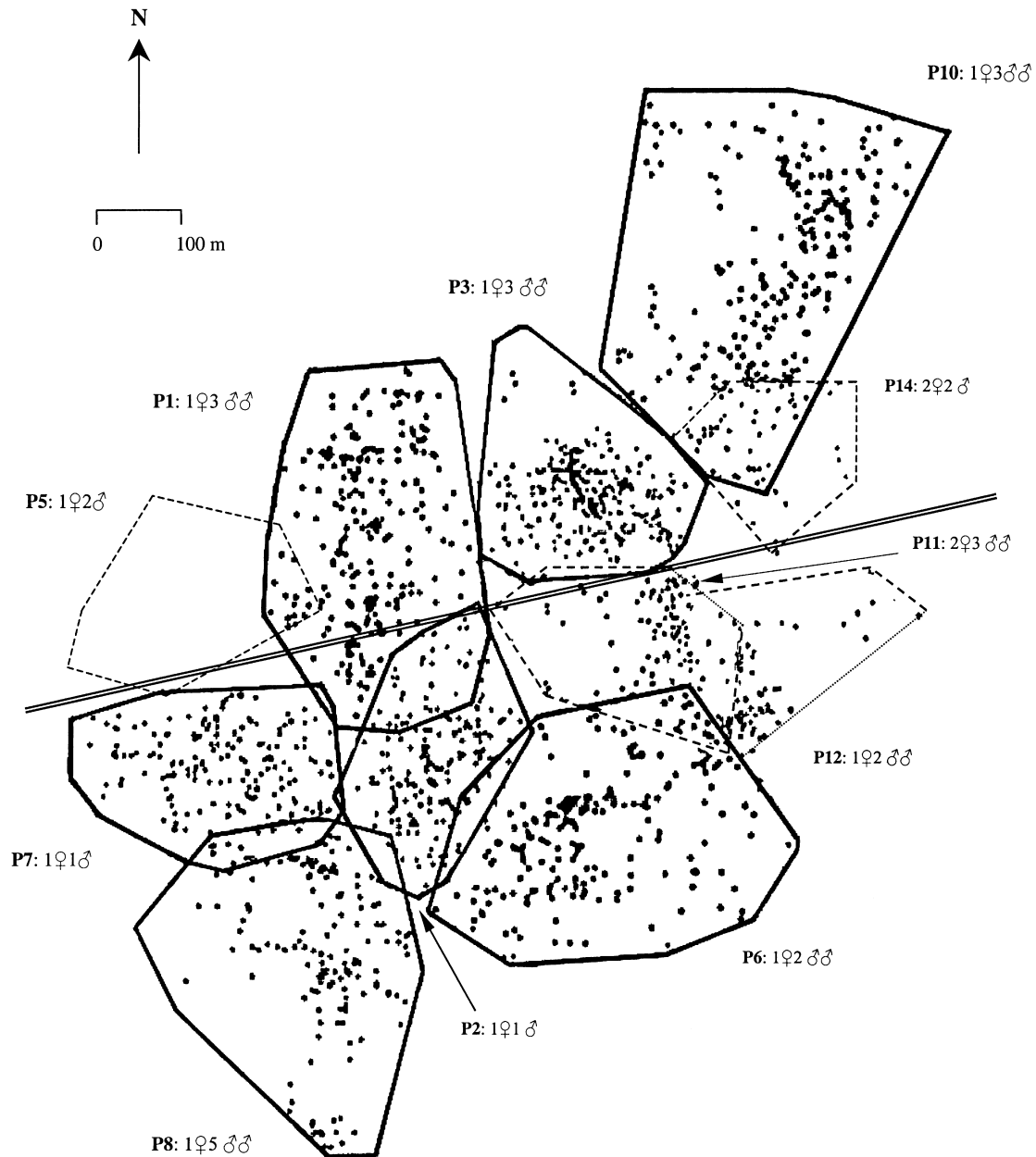
Figure 5. The overall configuration of the territories of the main study groups at PK32 in September 1999 to January 2000 as defined using 100% MCPs drawn around all registrations gathered during this period. Territories for P5, P11, P12 and P14 were drawn using only 50, 64, 74 and 60 registrations, respectively, and are therefore defined by dashed lines. A double line shows the track from which the site was accessed.

significant difference in data for these two variables between points at which small and large groups were recorded (Wilks' Lambda = 0.86, *df* = 1, *P* = 0.006). The scores generated by this discriminant function also differed significantly between the groups of survey points (*t* = −3.38, *df* = 68, *P* = 0.001). Table 5 lists the variables that made important contributions

to the functions generated by both analyses. Whilst the function generated by the simultaneous inclusion of variables accurately classified 76.4% of the 69 survey points, the function generated by the stepwise method correctly classified 68.1% of the survey points. This suggests that although the addition of variables other than number of large trees and
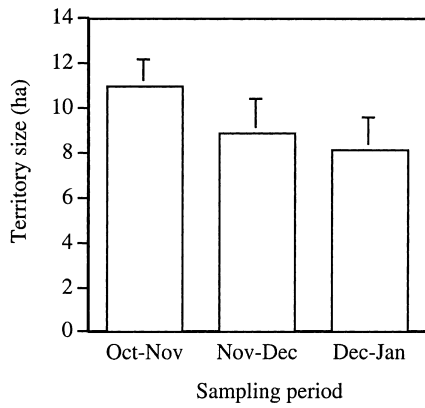
Figure 6. Histograms depicting the size of mesite territories with respect to month for seven radiotagged study groups 1999–2000. Territory size varied significantly across the three months of study (Friedman test: $\chi^2_2 = 6.0$, $P = 0.050$). Bars show mean ± se, with sample sizes given above.

D. madagascariensis did not greatly increase the discriminatory power, other variables were important in determining the occurrence of the two classes of groups. The correlation coefficients generated by both analyses are similar, suggesting that the discriminant function illustrated graphically in Figure 7 is relatively robust.

DISCUSSION

This study has confirmed that the Subdesert Mesite is a group-living bird that co-operates over territory defence and in the raising of young. Table 6 compares the basic characteristics of the Subdesert Mesite's ecology and breeding behaviour with those of other well-studied co-operatively breeding birds that forage terrestrially and/or inhabit arid environments. The Subdesert Mesite shares numerous important features with these other group-living birds, indicating that it is a typical co-operative breeder.
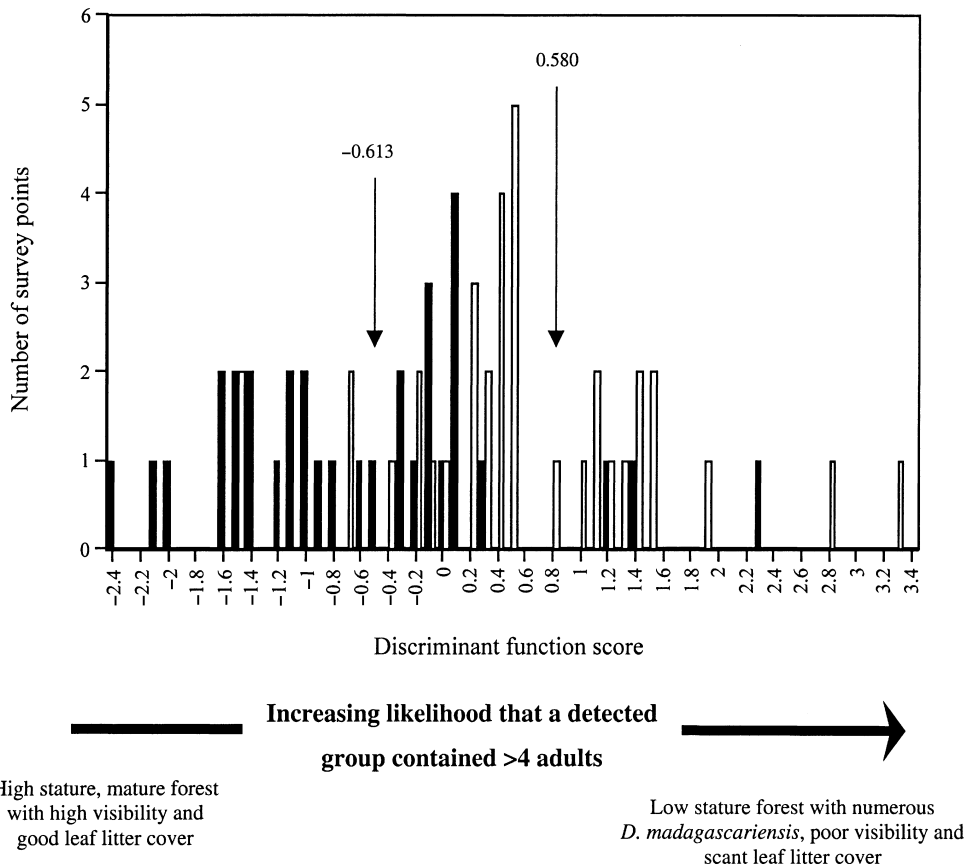

Figure 7. The distribution of discriminant function scores produced by the simultaneous inclusion of habitat variables for survey points at which small groups of subdesert mesites were recorded (solid bars, *n* = 33) and those at which large groups were recorded (open bars, *n* = 36). Arrows mark group centroids.

Table 5. Correlation coefficients between habitat variables and the discriminant function separating survey points at which small groups of Subdesert Mesites were recorded and those where large groups were recorded. Variables are grouped according to the sign of their correlation with the function for both the simultaneous and stepwise inclusion of variables. Points at which small groups were recorded were associated with high scores for variables with negative coefficients, but points at which large groups were recorded were associated with high scores for variables with positive coefficients (Fig. 6).

		Correlation coefficient	
Direction of correlation	Variable	Simultaneous	Stepwise
Negative	Number of large trees	−0.414	−0.620
Occurrence of small groups	Modal canopy height	−0.395	−0.409
	Maximum canopy height	−0.368	−0.300
	Maximum visibility	−0.285	−0.193
	% cover of leaf litter	−0.209	−0.097
	Number of *Euphorbia* spp.	−0.130	−0.282
Positive	Number of *D. madagascariensis*	0.501	0.750
Occurrence of large groups			

The study population's sex ratio was male biased to an extent that is comparable to that recorded in other species (e.g. Pukeko *Porphyrio porphyrio* and Galapagos Mockingbird *Nesomimas parvulus*). Historical records of male-biased sex ratios in Subdesert Mesite populations (Rand 1936) suggest that the bias recorded in 1999 was not a local or recent phenomenon. This bias may result from greater female mortality during diurnal incubation (see below) and/ or during dispersal. In mesites, although both sexes appear to disperse, two observations suggested that dispersal (or eviction) might be more common in females: first, groups rarely comprised more than two adult females, and secondly, birds encountered singly were more frequently female than male. Female biased dispersal has been reported in other co-operative breeders (see Stacey & Koenig 1990), including at least four in Table 6.

The mean group size in the Subdesert Mesite is close to that found in the Galapagos Mockingbird, and the range of group sizes recorded in mesites matches exactly those reported in the Galapagos Mockingbird, Arabian Babbler *Turdoides squamiceps* and White-throated Magpie-jay *Calocitta formosa*. In common with all species in Table 6, except the White-throated Magpie-jay, mesite groups usually contained multiple males. Without the results of a genetic study (this work is currently in progress), we cannot know whether these groups contain monogamous pairs assisted by mature male offspring that fail to disperse from their natal territory or else coalitions of males that have either stayed on territory to breed, jointly taken over a territory or joined single males. Interestingly, interactions amongst males

seemed relatively harmonious and such equanimity is surprising given the small clutch size: a dominant male may jeopardize his certainty of paternity by tolerating extra males. The prevalence of multimale groups hints that genetic costs may be offset by the benefits of maintaining peaceful male alliances such as improved survival or reproductive success through sharing incubation and co-operating to defend chicks, or through dilution and vigilance effects. In contrast, as in Pale-winged Trumpeters *Psophia leucoptera* and Grey-crowned Babblers *Pomatostomus temporalis*, groups rarely contained more than two adult females. The scarcity of multi-female groups may result from enforced and/or voluntary dispersal by mature females. Eviction of adult females occurs in Pale-winged Trumpeters where tolerance of males, but not of females, is thought to relate to the observation that adequate territory defence depends on the males. The same might also be true of mesites, given that territory size was positively correlated with the number of males. Alternatively, this asymmetry may arise because, although males can share paternity without increasing clutch size above the optimal, females must lay to reproduce (Chao 1997, Vehrencamp 2000). Clutch size in the Subdesert Mesite is two, and the large size of the eggs relative to the nest and adults' brood patches may mean that no more than two can be incubated simultaneously. In this case, dominant females cannot concede reproduction and they may evict females to avoid reproductive conflict.

In mesites, all adult males and at least one adult female shared incubation and care of the young. Such division of labour is found in all but three

Table 6. Comparison between the basic ecology and breeding behaviour of the Subdesert Mesite and other group-territorial co-operatively breeding birds that forage on the ground and/or occur in arid habitats.

Species	Main habitat[a]	Foraging niche	Adult sex ratio ($\male/\female$)	Dispersing sex	Group size: mean (and range)	No. breeding females per group	Social organization	Mating system	Who helps raise young?	Key references
Subdesert Mesite *Monias benschi*	Semi-desert forest/scrub	Terrestrial insectivore	1.46	♀?	4.3 (2–9)	1?	Multi-♂ 1–2 ♀♀	?	Dominant ♀ + all ♂♂	Seddon (2001)
Pale-winged Trumpeter *Psophia leucoptera*	Lowland rainforest	Terrestrial frugivore	1.3	♀♂	7 (4–13)	1	Multi-♂ 1–2 ♀♀	Polyandry[c]	Dominant ♀ + all ♂♂	Sherman (1995)
Pukeko *Porphyrio porphyrio*	Range of wetland habitats	Terrestrial herbivore	1.00–1.07	♂♀	2.8, 4.5, 7[b] (2–12)	1–2	Multi-♂ multi-♀	Polygynandry	All group members	Craig and Jamieson (1990)
Tasmanian Native Hen *Gallinula mortierii*	Short pasture near water	Terrestrial herbivore	1.11–1.37	♂♀	2.6 (2–5)	1	Multi-♂ +/or multi-♀	Variable	All group members	Ridpath (1972); Goldizen et al. (1998)
Galapagos Mockingbird *Nesomimas parvulus*	Scrub woodland	Terrestrial insectivore	0.75–2.13	♀	4.2 (2–9)	1–4	Multi-♂, multi-♀	Monogamy + polygyny	All group members	Curry and Grant (1990)
Grey-crowned Babbler *Pomatostomus temporalis*	Open Acacia + Eucalyptus woodland	Arboreal + terrestrial insectivore	1.18	?	3.8, 6[b] (2–11)	1	Multi-♂ 1–2 ♀♀	Monogamy[c]	All group members[d]	King (1980)
Arabian Babbler *Turdoides squamiceps*	Desert	Terrestrial omnivore	1	♀	5.5 (2–9)	1–4	Multi-♂ multi-♀	Variable	All group members	Zahavi (1990)
Stripe-backed Wren *Campylorhyn chus nuchalis*	Savanna, open woodland	Arboreal insectivore	1.2	♀	3.9 (2–10)	1	Multi-♂ multi-♀	Monogamy + polyandry	All group members	Rabenold (1990), Piper & Slater (1993)
White-winged Chough *Coracorax melanorhamphos*	Dry sclerophyll woodland	Terrestrial insectivore	1.05	Neither	6 (2–20)	1	Multi-♂ multi-♀	Variable	All group members	Rowley (1978), Heinsohn et al. (2000)
Florida Scrub Jay *Aphelocoma coerulescens*	Open scrub land	Arboreal insectivore	0.76–1.38	♀	3.0 (2–8)	1	Multi-♂ multi-♀	Monogamy	All group members[d]	Woolfenden & Fitzpatrick (1990)
White-throated Magpie Jay *Calocitta formosa*	Dry, semiopen woodland	Arboreal insectivore	0.92	♂	5.3 (2–9)	1	Multi-♀ 1–2 ♂♂	Monogamy[c]	All group members[d]	Langen (1996)

[a]Habitat as described in key references; [b]multiple figures derive from different study sites; [c]cases where no genetic data are currently available; [d]cases where only dominant female incubates.

species listed in Table 6 and, given the high costs of care, such sharing may lower the mortality of breeders. Female mesites undertook more diurnal incubation than males, perhaps incurring higher risks given the large number of potential diurnal predators (i.e. raptors and carnivores) in the Mikea Forest. Therefore, although males and females invest equally in terms of hours, the cost to the female may be greater, a factor that may be related to her certainty of a genetic stake in the clutch.

Territoriality

Whilst several studies of co-operative breeders reveal a positive correlation between group size and territory size (e.g. Jansen 1999), others find negative or no relationships (e.g. Koford *et al.* 1990). In mesites, between-group variation in territory size was not related to group size, perhaps because territories may be larger than needed to supply food. As such, a pair's territory might support additional birds without any increase in size. Alternatively, territories may be large because they are defended year round and thus have traditional boundaries, which limits the ease with which new territories could be squeezed between those already existing. It is unlikely that between-group variation in mesite territory size reflected local differences in habitat quality as the soil and vegetation at PK32 was relatively homogenous.

Timing of reproduction and habitat associations: why delay dispersal?

The presence of birds of < 3 months of age in September 1998 and 1999 revealed that groups produced clutches at the height of the dry season. This conclusion is endorsed by records of a nest containing two eggs on 3 March 1995 (H. Kahl *in litt.* 1995) and of a juvenile male in June 1931 (Lavauden 1932). In contrast to all other bird species in the same habitat, reproduction in mesites is not tied to rainfall (contra Collar & Stuart 1985 and Evans *et al.* 1996). Therefore, mesites are able to access food that remains plentiful in the dry season, such as termites and buried invertebrate larvae. Of all species observed in the Mikea Forest, only mesites dig in the sand for food (Seddon 2001). An ability to access buried food may delay dispersal and thereby promote sociality, if buried invertebrates are more easily found by groups and/or if this foraging skill takes time to develop (as in White-winged Choughs *Coracorax melanorhamphos*; Heinsohn 1991). Restricted

breeding in other terrestrial birds (i.e. Running Coua *Coua cursor*, Green-capped Coua *Coua olivaceiceps* and Long-tailed Ground Roller *Uratelornis chimaera*) may relate to the fact that these species do not have bills adapted for digging, but instead feed on insects and small reptiles that are abundant in November–January (pers. obs.).

Relatively intact habitat characterized by numerous large trees, high maximum and modal canopy height, good visibility at < 0.5 m above the ground and high percentage of leaf litter cover was more likely to be occupied by pairs or small family groups. In contrast, large groups were more likely to be detected in relatively disturbed habitat where *Didierea madagascariensis* were numerous, large trees were few, canopy height reduced and leaf litter cover low. In habitat with the latter characteristics, there may be direct advantages to remaining in natal territories and forming alliances with conspecifics. Such advantages may relate to predation, to which mesites are particularly vulnerable on three main accounts. Firstly, they are relatively weak and slow fliers, which makes them vulnerable to predators such as hawks (Accipitridae). Secondly, as ground-dwelling birds they are at risk from terrestrial mammalian predators such as the Fosa *Cryptoprocta ferox*. Finally, their gleaning and probing foraging mode means that they are constantly on the move and hence relatively conspicuous. Therefore, group living may reduce an individual's chance of being preyed upon through dilution or increased vigilance effects (Roberts 1996). However, large groups may also incur the cost of increased predator attraction and increased competition for food (e.g. Lima *et al.* 1999). The balance between these costs and benefits could be influenced by the structure of the habitat, the amount of food it provides and the degree of protection from predation it affords. This may be reflected in the result that smaller groups were located in areas with a higher modal canopy height and with a relatively open understorey. Both these features are likely to reduce predation pressure and therefore the size of groups.

The importance of life-history traits such as low adult mortality and low productivity in encouraging delayed dispersal has recently been emphasized (Arnold & Owens 1998, 1999, Hatchwell & Komdeur 2000). There are no data on adult mortality in the Subdesert Mesite, but annual productivity, at least, is low. It is likely that these life-history traits reduce the turnover of breeding opportunities and act in concert with ecological factors, such as high

Table 7. Summary of key differences and similarities in the basic ecology and breeding behaviour of the three species of mesite. Data for White-breasted Mesite are taken from Hawkins (1994), and for Brown Mesite from Evans *et al.* (1996).

	Subdesert Mesite	White-breasted Mesite	Brown Mesite
Habitat	Open-canopy dry forest and coastal scrub	Closed-canopy dry forest and rainforest	Closed-canopy rainforest
Foraging mode	Digs in sand	Gleans in leaf litter	Gleans in leaf litter
Territories	6–18 ha, stable	2–15 ha, stable	Small, temporary (?)
Breeding	Year-round	Rainy season only	Rainy season only
Clutch size	1–2	1–3	1 (?)
Group size	2–9	2–4	2
Social system	Multimale, multifemale groups	Pairs plus recent offspring	Pairs
Mating system	Variable (?)	Monogamy[a]	Monogamy[a]
Sex differences	Dichromatic	Monomorphic	Monomorphic

[a]No genetic study has been carried out.

predation pressure and habitat saturation, to promote delayed dispersal and hence group-living in this species.

Does phylogeny or ecology determine delayed dispersal and co-operation in mesites?

Cockburn (1998) stated that 'it is now clear that complex co-operative systems are often not the product of local ecological constraints but may be deeply seated and ancestral characteristics of many important avian clades'. In common with several other gruiform birds (e.g. Pukeko, Pale-winged Trumpeter and Tasmanian Native Hen *Gallinula mortierii*), the Subdesert Mesite breeds co-operatively. Although the monophyly of the Gruiforms is regularly contended (reviewed in Livezey 1998), it is possible that co-operation is ancestral in this order (as proposed for the parvorder Corvida: Cockburn 1996).

By way of assessing the relative importance of phylogenetic, life history and ecological constraints in promoting delayed dispersal, it is instructive to compare the basic ecology of all three species of mesite (Table 7). This comparison implicates the role of local ecology over phylogeny or life-history characteristics. The observation that breeding in White-breasted and Brown Mesites is restricted to the rainy season (Evans *et al*. 1996) implies a seasonal food resource. Such seasonal breeding is common amongst organisms inhabiting tropical wet forests, despite the common perception that these forests are stable and aseasonal environments (Wikelski *et al.* 2000). In accordance with this, the Brown Mesite appears not to hold fixed territories,

but instead performs altitudinal migrations, breeding at lower elevations in the wet season, at least in parts of its range (Evans *et al*. 1996). Although the White-breasted Mesite inhabits stable territories, they are smaller than those of the Subdesert Mesite. The smaller territory size of *Mesitornis* spp. may result in a less saturated habitat in which dispersal is less constrained, breeding vacancies plentiful and group living scarce. Alternatively, differences may relate to the structure of the habitat rather than the food resource it provides. In particular, the closed canopy forest inhabited by *Mesitornis* spp. may provide greater cover from predators and thereby reduce incentives for remaining in or joining a group. Long-term field studies and experimental work on all three species are necessary to test these ideas.

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