

DENSITY AND BREEDING BIOLOGY OF THE BARN OWL *TYTO ALBA* (AVES, TYTONIDAE) ON THE TROPICAL ISLAND OF MAYOTTE

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Abstract. *Tyto alba* is widely distributed on Mayotte, an island group of 374 km² in the Comoro archipelago. The species was studied in August 1996 (dry season) and December 1997/January 1998 (wet season). Territorial response was high in December/January, and there were fledged young in August, indicating that breeding starts in the wet season and young fledge during the dry season. The species was inventoried at the beginning of the breeding season by using playback of calls during point-transect counts. Breeding densities were high, estimated at ca. 1.03 to 2.75 territories/km², based on three different methods of calculation. Possible sources of error are discussed, but this method will most likely produce useful results in other situations where Barn Owls respond well to playback. Breeding sites were mainly cavities in trees, but cliffs and, more rarely, buildings were also used. Breeding success seemed low : 1.62 young fledged per nest.

Key words : Barn Owl, *Tyto alba*, population, density, breeding biology, Mayotte, Comoros

INTRODUCTION

The Barn Owl *Tyto alba* (Scopoli, 1769) is a cosmopolitan species. In temperate regions it is rare and declining in many places, and generally ranks highly as a nature conservation priority. It is also much used as a bioindicator for habitat quality (BUNN *et al.*, 1982; SHAWYER, 1987). The Barn Owl is widespread in the tropics, where it is the most important nocturnal avian predator on many tropical islands. It can be beneficial to man as an agent to control commensal rodents, or it can be undesirable as an important threat to endemic animals or seabirds (HEIM DE BALSAC, 1965). In regions such as Malaysia its proliferation was stimulated in oil palm monocultures, resulting in successful rodent control (LENTON, 1984; BASRI WADID *et al.*, 1986; DUCKETT, 1991). However, its introduction to some islands in the Indian Ocean (*e.g.* granitic Seychelles), in order to achieve the same goal, resulted in catastrophic predation on seabirds (PENNY, 1974), rather than rodent control. In the nearby Comoros (including Mayotte), where it occurs naturally, it does, however, feed to a very large extent (over 90%) on commensal rats (LOUETTE, 1996; ERVYNCK *et al.*, 1998).

Accurate knowledge of Barn Owl density, and monitoring of its population are needed on Mayotte, in order to evaluate, and possibly enhance and exploit its rodent control

potential. Being a nocturnal bird, standard techniques to estimate bird densities (BIBBY *et al.*, 1992) do not apply. In this paper we discuss the application of a combination of techniques to estimate the density of Barn Owls, and we investigate some aspects of its breeding biology on Mayotte.

Mayotte, the easternmost group of islands in the volcanic Comoro archipelago, covers 374 km² (Fig. 1), attains a maximum altitude of 660 m, has fertile soils and, in 1991, had ca. 94,500 human inhabitants (BOLE & CIBARD, 1994), living mostly at the coast. Shifting cultivation and forest reserves alternate with coastal villages and mangrove tracts; some badlands occur on eroded slopes. There is a marked gradient of rainfall in relation to altitude (RAUNET, 1992).

The subspecies *hypermetra* (BUNN *et al.*, 1992) of the Barn Owl, considered as a synonym of *affinis* (BENSON, 1960; LOUETTE, 1988) is known from all the Comoro islands. Observations prior to our 1996-1998 study are sparse, however. BENSON (1960) and FORBES-WATSON (1969) mentioned the species from the small annex islet of Pamandzi. LOUETTE (1988) confirmed that location, and also noted its presence at Dzaoudzi and Mamoudzou, and added that it is no doubt distributed widely on «Grande Terre». BENSON (1960) indicated that this species is partly diurnal on Mayotte, because he observed owls at the airport of Pamandzi: one at mid-day, two others hunting over grassland an hour before sunset, and another seen on the ground devouring some prey at the same time. LOUETTE (1988) also noted Barn Owls active on Mayotte during the day. Most observations by BENSON (1960) were from forested regions, but LOUETTE (1988) observed the species also in inhabited environments. There are no breeding data available from the Comoros. Based on its nesting behaviour elsewhere, LOUETTE (1988) mentioned that the species might use cavities, cliffs and buildings.

MATERIAL AND METHODS

Questionnaire and field inventory

BIBBY *et al.* (1992) recommended two separate methods for the inventory of Barn Owls in Europe, both with the bird in its territory as the counting unit. On the one hand, they suggested the use of questionnaires on the bird, and on the other hand, the rigorous search for nests at potential nesting sites (*e.g.* useful buildings) in the survey area. However, since we lacked information on the breeding period or the breeding habitat of Barn Owls on Mayotte, we combined the questionnaire method with other inventory techniques.

In August 1996 local people were questioned. During the presentation of a stuffed specimen, we asked standard questions of a representative number of persons in 55 villages, distributed over the whole island. These questions concerned their knowledge about the presence of the Barn Owl in their neighbourhood: preferred habitat, nesting site and nesting period, population trends, and human impact on the species. We also searched for nesting sites ourselves, in restricted areas near Dembeni and M'rereni. During daytime, we checked all trees for possible cavities, owl droppings and the presence of pellets. Each nesting site, discovered from the presence of young owls or by the accumulation of pellets, was described (situation, species of tree, height and dimensions of the cavity).

Point counts

A point-transect-count technique was tested in August 1996, and repeated in December-January 1997/98. During the counts we used playback of Barn Owl vocalisations from a cassette player. In western Europe, the species is reputed to react poorly to this sound (HUSTINGS *et al.*, 1985), but SMETS (pers. comm.) observed some cases of good response in central Belgium at the beginning of the breeding season, particularly with newly established pairs and in situations of high density. In Mayotte, Barn owls did respond quite well. Playback has also been used elsewhere for the inventarisation of other owl species (*e.g.* LYNCH & SMITH, 1984; SOLHEIM, 1986; VAN NIEUWENHUYSE & NOLLET, 1990; KOWALSKI *et al.*, 1991). Calls were played at night during five minutes, from points at 500 m intervals along roads and tracks, between 1900 h and 2300 h. The chosen distance of 500 m between points was based on the size of territories reported in the literature. Each playback included calls of the male, the female, and young (copied from PALMER & BOSWALL's bird songs cassettes); playback was repeated three times for one minute, while three observers watched (using torchlight frequently) and listened for a possible response during two more minutes after playback.

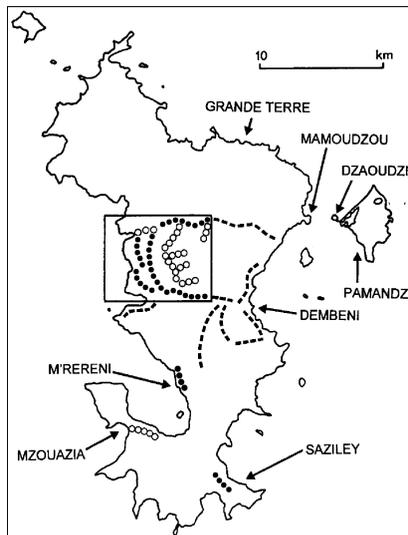


Fig. 1. – Position of the point-count transects on Mayotte. Dashed lines : counts in 1996. Open circles : counts in 1997/1998. Filled circles : counts in both years. Inset : the west-central study sector.

In 1996, counts were concentrated in the central part of the island (Fig. 1). In 1997/98, the west-central region (inset) was chosen as a restricted study area because of its comparatively dense network of roads and tracks. Outside this sector, counts were made in 1997/98 along other transects as follows : on the ridge near Saziley (south-eastern peninsula), a dry area with the vegetation dominated by Baobabs *Adansonia digitata*, near Mzouazia (south-west), a dry area dominated by *Albizia lebeck* trees, and near M'rereni (western coast), an area under intense cultivation.

Categories of response

Response of Barn Owls to playback of their vocalisations was classified in the following five categories :

1. *Presence of a pair*

Two adult owls were heard and/or seen during the count. The distinction between partners could sometimes be made from their behaviour (both birds present without mutual aggression but with a co-ordinated reaction in vocalisation and while flying about the playback spot), or from their vocalisations.

2. *Presence of two individuals not belonging to the same pair*

Either two males were present simultaneously, being recognised by mutual aggression, or two individuals were present which could not be assigned to one pair, according to their behaviour.

3. *Presence of a single individual*

In most cases, at each point, only a single owl responded. A distinction was made between early and late reaction and between strong and weak reaction. The intensity of the response varied from flying towards the tape and perching silently, to flying about repeatedly during the entire counting period in search of the source of the sound, while calling regularly.

4. *Presence of the same individual at different points*

In a number of cases, it was clear that the same individual responded at consecutive points. A bird could respond at one point and subsequently follow the observers to the next point (then first calling at a distance, from the direction of the previous point, followed by calls emitted progressively closer by, eventually approaching the second point).

5. *Presence of juveniles*

A number of juveniles were encountered, sometimes in groups, producing the characteristic begging call. They were also recognised by their plumage, which is more yellowish than in adults, especially on the throat and breast. Sometimes the adults were also seen nearby. A number of nests were found on subsequent visits during the day near spots where fledged juveniles had been recorded.

Calculations of density

The point counts in the west-central sector enabled us to attempt an estimate of the density of the Barn Owl population on Mayotte. Three methods were used :

1. The number of territories found, divided by the total surface studied, gave an estimate of the (minimal) density (D_1).

2. From evidence in the field (*e.g.* birds responding at two consecutive points 500 m apart and a number of field tests of audibility of calling juveniles), we concluded that birds responded from distances of up to 250 m. Dividing the number of territories by the sur-

face inventoried as such (points with a radius of 500 m), we obtained a second measure of density (D).

3. Finally, we used the nearest-neighbour-distances (NND). The mean NND of the (presumed) centres of territories was considered as the average diameter of the territories. If they were adjoining and covering the entire study area, the (maximal) density could be estimated.

RESULTS

Questionnaire and field inventory

For the detailed results of the questionnaires see LOUETTE *et al.* (1996). It is sufficient to mention here that the Barn Owl is known in 54 of the 55 villages of Mayotte. It is observed mostly around the perimeter of the village (15 times), in rural habitats (13 times), and infrequently in forests (five times). Most persons (21) named trees as the main nesting site, two indicated buildings, and one person indicated cliffs. Few persons (six) had (contradictory) ideas about the breeding period. Fourteen out of 15 informants indicated a declining population. In 10 out of 12 villages, people were convinced that humans, especially children, catch and kill Barn Owls, because they are widely considered to be a 'harbinger of evil'.

In the neighbourhood of Dembeni (on nearly 350 ha), 336 potential nest trees (310 Mango *Mangifera indica*, 11 West Indian Almond *Terminalia catappa*, eight Kapok *Ceiba pentandra*, six *Erythryna* sp., one Baobab) were investigated for signs of Barn Owl presence. We observed a nest in one Mango, pellets under another one and droppings under three more trees.

In M'rereni we checked 318 *Erythryna*, four Mango trees, and three West Indian Almonds, but found only one pellet.

Point counts

In 1996, owls were recorded at 21 out of 134 points (15.6%); in 1997/98 at 52 out of 135 (38.5%). The comparison of the number of positive and negative points along the transects counted in both years shows no significant relationship ($X^2 = 0.20$, $p > 0.50$). The density analysis was restricted to the data obtained in 1997/98 in the west-central study sector (Fig. 1). Here, owls were recorded at 44 out of 107 counted points (41.1%). The counting points with a pair were always considered as territories. Those with one adult were considered as territories if they were not already situated in a territory covered by neighbouring points (Fig. 2). In a number of cases, two adjoining positive recording points were included in a single territory. Very few cases left us undecided. Fig. 3 shows the position of the (presumed centres of) territories in the west-central sector as deduced from the data in Fig. 2. In an attempt to extrapolate the data from this sector to the whole island of Mayotte, the counts in Saziley, M'rereni and Mzouazia were used (LOUETTE, 1998). It is interesting that, from the ridge of Saziley in August 1996, no response of Barn Owls was obtained, but in December-January 1997/98, five counting points yielded six territories there.

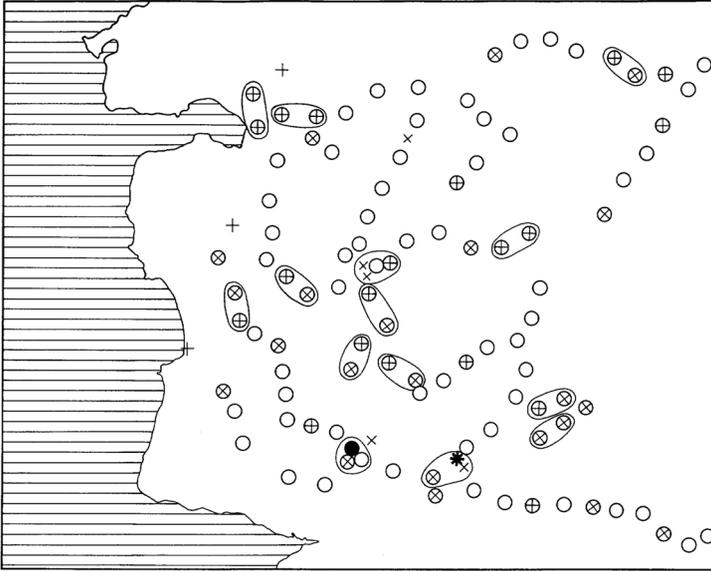


Fig. 2. – The west-central study sector on Mayotte. Results at each counting point in 1997/1998 during the transects (encircled): open circles : no response ; + : poor response ; x : heavy response ; filled circle : response of a pair. A few observations outside the transects added (not encircled ; asterisk : response of a pair). In ellipses : adjoining points, presumed to have yielded responses from (a bird of) the same pair.

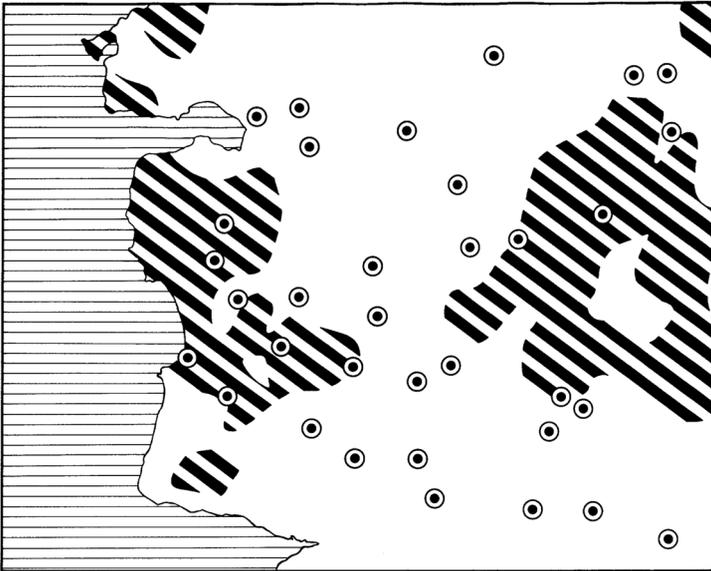


Fig. 3. – The west-central study sector on Mayotte. Forested areas shaded. Stippled circles : presumed centres of territories.

We compared the response of Barn Owls between dirt tracks (excluding one which supported intense traffic) and tar roads (LOUETTE, 1998). During both years, no significant difference in Barn Owl response could be detected between the two road types (1996: $X^2=0.69$, $p>0.30$; 1997/98: $X^2=0.20$, $p>0.50$).

Calculations of density

From the data of 1997/98, the different methods resulted in the following estimates:

1. D_t

The total surface in the west-central sector amounts to 33 km². The number of territories was 34. The corresponding (minimal) density was 1.03 territories per km².

2. D_c

The counting points (circles with a diameter of 500 m) represented a studied surface of $107 \times 0.1962 \text{ km}^2 = 20.9 \text{ km}^2$, yielding 34 territories. This corresponds to 1.62 territories per km².

3. NND

The mean NND was 647 m, which gave an average territory size of 0.363 km² (if hexagonal-shaped). This corresponded to a (maximal) density of 2.75 territories per km².

With a mean NND of 647 m and 34 territories on 33 km², the territories were distributed regularly ($P = 0.00023$; test for significance of departure of the observed NND from the expected NND for a randomly distributed population density via the «standardized normal deviate» – WRATTEN & FRY, 1980). Because the mean NND was considerably larger than the distance between counting points, there was no interference with the quality of the test.

Choice of nesting place

Table I lists the 20 nesting sites found on Mayotte. All nests were situated in a cavity: 16 in trees, two in buildings and two in cliffs. Of the 16 tree nests, five were in an *Erythrina*, four in a Mango, four in a West Indian Almond, two in a Baobab, and one in a Takamaka *Calophyllum inophyllum*. The cavity was, in general, high in the tree, but its dimensions varied strongly. The depth of the cavity varied from 2 cm to 2 m. In the former, the nest was simply made on an open platform in the trunk. The most aberrant nest was found in an old Baobab tree with a hollow trunk and large, hollow roots. The nest was actually situated about 1.5 m beneath ground level.

The trees containing a Barn Owl nest were situated mainly in a rural environment, near villages, frequently in valleys near water courses. Probably because of the difficulty of finding them, we located no nests in forests. The counts indicated however that the birds were present in this habitat as well, and Fig. 3 suggests that the density was no less in forests.

One nest in a building was situated on the garret, just under the roof. The entrance was about 50 cm in diameter. The two nests in cliffs were about 6 m and 20 m above the ground

TABLE I
Description of the Barn Owl nests found on Mayotte in 1996 and results of their control in 1997/1998 (plus two additional nests of 1997/1998)

Dates	1997/1998	Localities	Nest support	Cavity dimension in cm	Height above ground in m	Number of adults present in 1996	Number of juveniles present in 1996	Occupied in 1997/1998 ?
27 VII	19 XII	Musicale plage	Baobab		5/6	2	1	no
29 VII	19 XII	Mramadoudou	<i>Erythryna</i>	20 x 25	4	2	2	no
29 VII	19 XII	Mtsanga Sakouli	Baobab	150	1,5	2	1	1 ad
30 VII	20 XII	Pointe Mahabou	Cliff	rock crevice	20	2	2	no
30 VII	21 XII	Sohoa plage	WIA (1)		2	2	2	no
30 VII		Barakani	Mango	25-35 x 150	3/4			
30 VII	24 XII	Ongojou	Mango	35 x 100	4		2	no
31 VII	27 XII	Bouyouni	<i>Erythryna</i>	30 x 150	7			no
31 VII		Hamjago	Garret	Ø 50	3		1	
1 VIII		Sada-Doujani	Roof		3,5			
1 VIII	28 XII	Mouanatrindri	Takamaka	30 x 80	5			(2)
1 VIII	19 XII	Kani-Be	WIA		9/10	1	1	1 ad
1 VIII	19 XII	Nyambadao	WIA				2	no
7 VIII	9 I 98	Mavingoni	<i>Erythryna</i>	30 x 100	5	2	3	no
10 VIII	24 XII	Combani	<i>Erythryna</i>	30 x 100	8		2	no
13 VIII	21 XII	Sohoa	Mango	20 x 30	5	1	1	no
15 VIII	9 I 98	Tsararano	<i>Erythryna</i>	50 x 30	6	1	2	no
19 VIII	19 XII	M'lamamani	Mango	Ø 25	8/10		1	no
	17 XII	Dzaoudzi	Cliff	rock crevice	5/6			no
	23 XII	Chembenyumba	WIA	30 x 30	5			no

(1) WIA = West Indian Almond.

(2) Occupied by Indian Mynah *Acridotheres tristis*.

or the sea, respectively. The latter nest-site was a large ledge of some tens of m² in a sea cliff. The other was a typical cavity with an entrance of about 50 x 100 cm diameter, and extended several m deep.

Breeding success

The number of juvenile birds actively begging for food in the vicinity of the nest sites in August 1996 was an indication of the breeding success. In thirteen nests (including one in a building containing one nestling) we found an average of 1.62 fledglings (one with 3, six with 2 and six with 1).

DISCUSSION

Questionnaire and field inventory

The Barn Owl is indeed widespread on Mayotte. The local people in all regions of the island know the species very well. During our questionnaire, people led us to seven active nests. These data complete the scanty information previous ornithologists obtained during the past decades (BENSON, 1960; FORBES-WATSON, 1969; LOUETTE, 1988). These preliminary data allowed us to further investigate the species efficiently. However, random investigation of potential nest trees without prior consultation with local informants is definitely a time-consuming technique, yielding poor results.

Breeding period

During the counts in December-January 1997/98, many birds responded strongly to playback. We observed strong territorial aggression, sometimes between pairs. These observations indicated that the birds were in the pre-breeding or early breeding period. On the other hand, in August 1996, hardly any territorial behaviour was observed. The presence of fledglings, the observation of only one young remaining in the nest, and the presence of fresh pellets near nests indicated that the breeding season was then near its end. Furthermore, the occurrence of begging young decreased progressively during August: begging juveniles encountered on consecutive days in the first weeks were not found again during the last days of the month. This indicated that the last fledglings became independent by mid August. The breeding cycle of the Barn Owl in Europe spans about five months (seven for the whole population) (CRAMP, 1985; BUNN *et al.*, 1992). In Madagascar, breeding is reported from April and May (GOODMAN *et al.*, 1993). In southern Africa, the breeding period is extended, but is mainly in the cool, dry season (WILSON *et al.*, 1988; MENDELSON, 1997).

Combining our observations of both study periods, and the knowledge of the length of time Barn Owls need to accomplish their breeding cycle, we conclude that the breeding period on Mayotte starts in December-January (the beginning of the rainy season), and the last young become independent in August (in the second half of the dry season). This means that most Barn Owls have nestlings in the period April, May and June (the start of

the dry season) and that most fledglings will leave the nests in July (the middle of the dry season). (Climatological data from BATTISTINI & VERIN, 1984). Since our observations are from two different breeding cycles, the possibility remains, however, that the breeding cycle is not strictly timed but could be tuned *e.g.* to the intensity of the rainy season.

The lower responsiveness during the counts in August in comparison with December-January was due to the season. The absence of any response during the counts in Saziley in August 1996 could have been due to an earlier or shorter breeding season in the dry southern part of the island in comparison with the breeding season in the wet parts of the island.

Choice of nesting place

In Africa, Barn Owls nest readily in rock crevices or caves, and in hollow trees, far from human habitations (ARCHER & GODMAN, 1961; WILLIAMS, 1963; SERLE *et al.*, 1977); in certain areas in Europe nesting on sea-cliffs has been reported (CRAMP, 1985). The proportion of 80% of nests in hollow trees, as found in Mayotte, is high with respect to information from Europe (BEZZEL, 1985; BUNN *et al.*, 1992; DE JONG, 1995), but probably comparable with Africa and Madagascar. The low number found in Mango trees is somewhat surprising, because this tree is the most common one over wide areas on Mayotte. However, it probably is generally a «healthy» tree, only rarely presenting cavities adequate for owl nests. Since it is mostly old trees that are hollow and represent important nesting sites, it is alarming that in some areas (*e.g.* M'rereni) they are cut and burned on a large scale for cultivation.

Breeding success

The figure of 1.62 fledglings per nest may be an underestimation of the actual breeding success. We cannot be certain that the number of juveniles observed was the number really present. Nevertheless, we probably would have heard other juveniles had they been present. They are very noisy and can be heard over large distances while begging at this stage (*pers. obs.*). If the number of juveniles observed did represent complete sets, breeding success on Mayotte is relatively low. In the different parts of Europe, mean breeding success varies between 2.7 and 5.2 young fledged (dependent on prey abundance: BAUDVIN, 1975; BRAAKSMA & BRUIJN, 1976; BEZZEL, 1985; BRUIJN, 1994; DE JONG, 1995).

Breeding density

Evaluation of the field methods

Accurately assessing the population density of Barn Owls in a tropical environment, during a period of a few weeks as a visiting researcher, is no easy matter, particularly because most owls breed in hollow trees in remote areas. Methods for inventory used *e.g.* in Europe (questionnaires of owners of potential buildings, and monitoring of known nesting sites) are of no use here. We decided to use point counts and playback. At variance with Barn Owl behaviour in Europe, response to playback was strong on Mayotte, which greatly improved the quality of our data. Potential sources of error are, however, numerous.

The population might be underestimated if not all territory-holders responded. During the pre-breeding period at the onset of the wet season, however, this seems unlikely in view of the strong and often prompt response of most birds.

Underestimation could also be the case if individuals belonging to different territories were considered to be one and the same. This error is unlikely to be important, because adjacent birds could often be recognised by their behaviour (aggressiveness, response of pairs). Overestimation due to double counting of the same individual is also unlikely. In a number of cases we were able to trace the same individual from one count point to the other. Such points therefore belonged to a single territory. If the same birds were regularly counted twice from adjacent points and later considered as belonging to different territories, we would expect our results to show a clustering of territories, which was not the case.

An overestimate due to separate registration of males and females is unlikely at this stage of the breeding cycle, when pair formation takes place. If unpaired individuals were also territorial and responded to playback, this would result in an overestimation of the breeding population. This possibility cannot be ruled out and is difficult to assess; we assume, however, that the proportion of territorial, unpaired birds is likely to be small in a high density population.

Another factor possibly interfering with the quality of the data is the noise and disturbance from traffic during observations, possibly causing observers to be distracted and owls to be scared off, but this factor was not found to be significant.

The comparison of positive and negative points indicated that the territories found were not situated at the same sites. However, at particular points it was very clear that intense response was obtained in both years. This was especially so where villages and fields alternated. Possibly villages were good beacons between territories, and in these modified habitats the number of potential nesting trees was more limited anyhow, resulting in the same sites being re-used.

Evaluation of density calculations

According to the distance at which owls still responded and at which owls could still be recorded by the observers (either visually or acoustically), part of the 33 km² of the study area was, in fact, not addressed from any of the playback points, notwithstanding the dense network of roads and tracks in comparison with the rest of the island. So the first density estimate (D_1) of 1.03 territories/km² was an underestimation.

According to the second method (D_2), with an effectively inventoried surface of circles with 250 m radius per counting point, only 20.9 km² were effectively inventoried, and the 34 territories represented in that case an effective density of 1.62 territories/km². In suitable habitat, this would also represent the «ecological density» (*sensu* VERHEYDEN, 1991). Along with the variation according to local circumstances (*e.g.* topography and vegetation density), there remains the problem that some individuals probably could be heard from a greater distance than others. Some might have been missed. From field observations (*e.g.* birds responding at two consecutive points 500 m apart, and a number

of field tests of audibility of calling juvenile birds), the radius of 250 m seems to be the «best possible» average in the given circumstances.

For the third method, we assume that the (mean) NND between two territories equals two times the apothem of the supposedly hexagonal territory. Indeed, all territories supposedly touch one another, without gaps in between (otherwise circles would have to be used). The mean NND was 647 m, which corresponds to a density of 2.75 territories/km², if hexagons are used. But it is probably wrong to think that the whole surface was occupied at the same rate (= density) or that one could hope to obtain a response at each point (indeed, there were quite a number of points without response). Therefore, in reality, this density estimate is probably exaggerated. A remaining problem is that the NND could only be measured with an accuracy of ca. 500 m, because the counting points were situated at that distance from each other.

The comparison of density (D) with mean NND shows the owls were spread out extremely regularly in the west-central sector. No doubt this was due to territorial activity, which in turn determines the population size to a great extent. It suggests furthermore that available nesting places and the amount of food were less important determinants of population size in this sector.

Extrapolation to the whole island

The study area is situated in the wet west-central sector of Mayotte. The few transects counted in the drier parts gave the same response rate, suggesting that densities were similar. On the Saziley peninsula, the proportion of positive points was particularly high, probably because the counts from the ridge addressed a wider landscape. On the other hand, the less successful search for nests in the near Dembeni showed that densities in parts of the island under intense cultivation were lower. The density in unbroken forest remains unknown.

With the density of the study area extrapolated to the whole island, we estimate respectively 385, 606 and 1141 territories on Mayotte, for the three methods of density estimation. Given the methodological discussion above, we estimate the total population to be between 500 and 1000 pairs, possibly near 750 pairs.

Breeding density

In western Europe, where grassland habitats tend to be fragmented, average breeding densities of between 1 and 10 breeding pairs (bp)/50 km² are the norm. They rarely exceed 12-25 bp/50 km² (OSIECK & SHAWYER, 1997). CRAMP (1985) listed some high densities in parts of Europe. In lowland Scotland 23 pairs breed per 50 km². In central Europe one pair per village is the rule. Exceptionally, in Switzerland four pairs were found in one area of one km². Indeed, locally the Barn Owl can breed in high densities, but over large areas this density flattens off. The European values are 50-100 times lower than those attained on nestbox-rich oil-palm estates in Malaysia where prey-saturated habitats are vast and contiguous (TAYLOR, 1994). It is therefore possible that the breeding density on Mayotte could have been higher previously as suggested by our informants. Nevertheless, a population density of ca. 2 bp/km² over a large surface on Mayotte is high compared with data in the literature, which mostly relates to continents and moderate cli-

mates. However, on another group of tropical islands, the Galapagos, densities of comparable magnitude have been found (DE GROOT, 1983). In general, population density seems to be regulated by the number of nesting or roosting sites (CRAMP, 1985; OSIECK & SHAWYER, 1997). This is decidedly not the case in our study area. By 1998, Barn Owls had not started to use a single one of the 11 nestboxes placed, in 1996, in the central area of Mayotte (LOUETTE, 1998). Territorial activity was the most obvious limiting factor in the investigated part of Mayotte. The high density may be due to one or more of the following factors: the near-absence of other avian predators, and the presence of abundant food supplies (commensal rats) (LOUETTE, 1999). There is no systematic destruction of Barn Owls on the island, although localised disturbance may affect the population (in villages and urban areas). Over the whole study area enough nesting sites seem to be available, but the lower density in regions under intense cultivation could be due to localised shortage of nesting sites.

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