

DISTRIBUTION, POPULATION SIZE AND HABITAT USE OF THE RÉUNION MARSH HARRIER, *CIRCUS M. MAILLARDI*

VINCENT BRETAGNOLLE

CEBC-CNRS, 79360 Beauvoir sur Niort, France

THOMAS GHESTEMME

SEOR, Muséum de Saint-Denis, 1, rue Poivre, 97400 Saint-Denis, La Réunion, France

JEAN-MARC THIOLLAY

Laboratoire d'Ecologie, ENS, 46, rue d'Ulm, 75005 Paris, France

CAROLE ATTIE

79360 Vaubalier, France

ABSTRACT.—On Réunion Island, Indian Ocean, the only surviving resident raptor is the endemic Réunion Marsh Harrier, *Circus m. maillardi*. It has been considered conspecific with the Madagascar Marsh Harrier (*C. m. macroceles*) but a reanalysis of the classification of both is needed. A survey was carried out on the island in 1997–98 and the breeding population was found to be no larger than 100 pairs, mostly concentrated in forested areas at mid-elevations (300–700 m) and down to sea level, but rarely above 1200 m. The distribution of pairs was clumped with as many as 8 pairs within a 10 km² patch, and mostly concentrated in low degraded native woodlands on steep slopes. Foraging habitats were more diversified and were widely distributed from coastal wetlands to cultivated fields, forest and upper montane vegetation. Breeding was apparently not synchronized among pairs but egg laying occurred primarily from December–March. The Réunion Marsh Harrier must be considered as Threatened, although its distribution has apparently not declined between 1976–98.

KEY WORDS: Réunion Marsh Harrier; *Circus m. maillardi*; Indian Ocean; population size, habitat use.

Distribución, tamaño de población y uso de habitat de *Circus m. maillardi*

RESUMEN.—En las Islas Reunión, Océano Indico, la única ave rapaz residente es *Circus m. maillardi*, la cual ha sido considerada como *C. m. macroceles*, al respecto, una revisión de la clasificación de estas dos es requerida. La investigación realizada en la isla entre 1997–98 encontró que la población reproductiva no era mayor de 100 pares, concentrados en áreas boscosas en elevaciones medias (300–700 m) descendiendo hasta el nivel del mar, raras veces sobre los 1200 m. La distribución de las parejas fue aglomerada, se encontraron hasta 8 parejas dentro de un parche de 10 km², casi siempre concentradas en áreas de bosque nativo degradadas en pendientes inclinadas. Los hábitos de forrajeo fueron mas diversos, ampliamente distribuidos desde los humedales costeros hasta áreas cultivadas, bosques y vegetación montana de altura. La reproducción no fue sincronizada entre parejas, esta ocurrió desde Diciembre a Marzo. *C. m. macroceles* debe ser considerado como amenazado, aunque su distribución aparentemente no ha declinado entre 1976–98.

[Traducción de César Márquez]

Within the group of large harriers (i.e., the Marsh Harrier *aeruginosus* complex, *sensu* Sibley and Monroe 1990), detailed information on their ecology is only available for *aeruginosus* in Europe (review in Clarke 1995), *approximans* in Australasia (review in Marchant and Higgins 1993) and to a lesser extent for *ranivorus* in Africa (see Simmons

1997). The biology of the Réunion Harrier is very poorly known, except for its morphology and molt (Nieboer 1973) and some aspects of its breeding biology (Clouet 1978).

Réunion Island (2515 km², maximum 50 × 70 km) is larger, more forested and has a lower human population density than the other two Mas-

carene Islands (Mauritius and Rodrigues) in the Western Indian Ocean. Both Mauritius and Réunion Islands have only one raptor still surviving, a kestrel and a harrier, respectively (Sinclair and Langrand 1998). The Madagascar Marsh Harrier (*Circus maillardi*), hereafter called the Réunion Harrier, is now the only raptor breeding on Réunion. There is some controversy with regard to its taxonomic status and it is currently divided into two well-marked subspecies, *C. m. maillardi* (Réunion) and *C. m. macrosceles* (Madagascar and Comoros) (Howard and Moore 1980), but the Réunion population may well deserve full specific status. The population size of the Réunion Harrier on Réunion was previously estimated at 200–300 pairs (Clouet 1978, Barré et al. 1996), but no standardized surveys were used to obtain these estimates. In earlier times, the species was considered to be abundant (Dubois 1672, in Barré et al. 1996), although no measure of abundance or relative abundance was provided.

We undertook a survey to assess the current status, population size and trends of the Réunion Harrier and to identify its conservation needs. This paper provides the first comprehensive account of the harrier on Réunion. Based on censuses carried out in 1997–98, we provide a provisional distribution map and a current population estimate for the whole island. We also summarize available data on the habitat use and breeding period, based on unpublished information gathered between 1987–98.

STUDY AREA

Réunion Island (21°15'S, 55°30'E) is a volcanic island, 2–3 million years old. It is 165 km from Mauritius, the nearest island, and 700 km east of Madagascar (Fig. 1). Most of the island is mountainous and steep. Three large and deep cirques (caldeiras), Mafate, Cilaos and Salazie, surround the highest peak (Piton des Neiges, 3069 m). An active volcano (Piton de la Fournaise, 2631 m) in the southeast is the second highest summit. Coastal lowlands are now totally cultivated or urbanized. Below 1300 m, degraded native forest is restricted to the steepest slopes. The mean annual rainfall is highest on the eastern (windward) side of the island, increasing from 3 m on the coast to 8–12 m between 1300–1900 m elevation and decreasing above 2000 m elevation (Barcelo 1996). Precipitation declines markedly on the eastern (leeward) side, down to 1 m on the southwestern coast. The mean annual temperature decreases from 24–26°C in the lowlands to 12°C around 2000 m elevation where frost is frequent in winter (June–August). Major cyclones occur every 5–10 years during the hot rainy season (December–April), but tropical storms with heavy rainfalls are of almost yearly occurrence.

The island was discovered in the 16th century and was

heavily deforested with human population growth. Massive extinctions, including 22 bird species, occurred from the early stages of colonization due to hunting pressure, introduced mammals (rats, cats, goats and pigs) and habitat destruction (Barré et al. 1996). Intensive agriculture, sprawling urbanization and construction of a dense road network are still affecting the remaining natural habitats. The native flora comprises 750 species, but 1100 additional taxa have been introduced, some of which are invading natural forest remnants (MacDonald et al. 1991). At most 55 000 ha of forest remain (Cadet 1980, Doumenge and Renard 1989, Dupont 1990) on 22% of the island area and consist of almost none of the former western dry woodlands, <1% of the original lowland mixed forest, 60% of the montane forest and 80% of the high altitude vegetation.

Five major natural habitats have been recognized (Rivals 1952, Cadet 1980, Barré et al. 1996; Fig. 1): (1) dry savanna woodland and semi-sclerophyllous forest on the coastal lowlands has almost entirely been replaced by cultivation, urbanization and introduced vegetation; (2) humid lowland mixed evergreen forest ("Bois de Couleur des Bas"), originally covered the eastern lowlands up to 800–900 m and the western side from 750–1100 m, is now largely degraded with remnants having a dense understory, dominated by an open canopy 6–15 m high; (3) upland wet mixed evergreen forest ("Bois de Couleur des Hauts"), from 800–1900 m in the east and from 1100–2000 m in the west, is richer in epiphytes and tree ferns; (4) montane forest, between 1600–2000 m, is dominated by large *Acacia heterophylla* ("Tamarins de Hauts") that are taller (15–20 m) and larger (<1.5 m dbh) than trees in mixed evergreen stands; the understory is locally rich in native bamboos (*Nastus borbonicus*), giant heath (*Philippa montana*) and stands of screwpines (*Pandanus montanus*), (5) high heath and shrubs above the tree line are 1–2 m tall and can be very dense. We also recognized the following five heavily modified habitats that are dominated by exotic vegetation; (6) monospecific exotic tree plantations of *Cryptomeria* spp., *Pinus* spp. and *Eucalyptus* spp., (7) dry derived savannas and shrubby areas mostly in the western lowlands on abandoned fields; (8) cultivated areas, often large fields of sugarcane but sometimes with more diversified crops with tree rows, woodlots and orchards; (9) urban and suburban areas, including associated gardens, roads and tourist resorts; and (10) wetlands such as coastal ponds and marshes or lakes in the mountains that are highly restricted and modified by exotic vegetation and deforested surroundings.

METHODS

We conducted a comprehensive survey aimed at locating every territorial pair of Réunion Marsh Harrier. Because of the landscape heterogeneity and a perceived uneven distribution of the species, we avoided making a population estimate that relied on extrapolations from a limited number of sample areas. Instead, we surveyed most areas of natural and semi-natural vegetation and searched, as far as possible, most potentially suitable breeding habitats for harriers. This was based on our previous experiences on Réunion and the dense network of roads, forest tracks, mountain trails and viewpoints that allowed an adequate coverage of otherwise seemingly in-

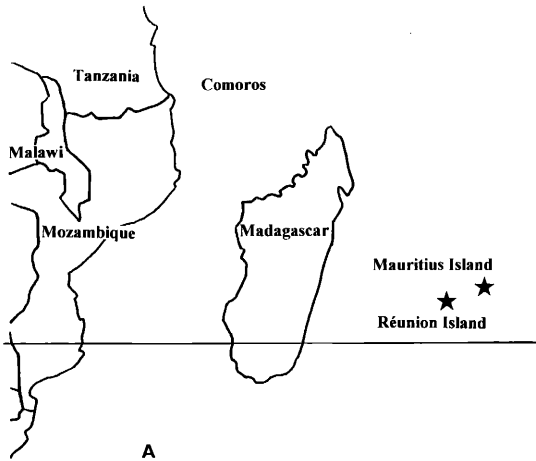


Figure 1. (A) Location of Réunion Island.

accessible areas. Observations on harriers were made during surveys from a network of 111 lookouts sampled under good weather conditions between 0700–1800 H from 23 October 1997–15 May 1998, and reported on a map using a grid of 2×2 -km squares with each square searched for >1 hr and, if possible, >2 hr. Additionally, two extensive surveys (14 December and 29 March) were conducted by as many as 14 observers who simultaneously recorded the number, sex, movements and behavior of all individual harriers seen within contiguous areas from separate lookouts over a full day. The first survey method covered the most suitable areas of habitat. From each site, an area of about 3 km^2 was surveyed using 10×42 binoculars. Because of the low-flying behavior of harriers, the movements of all individuals were drawn on 1:25 000 topographical maps, using prominent landmarks. Surveys were conducted most often with two people. Therefore, we obtained an estimate of the minimum number of pairs present within a well-defined area around each lookout. In order to avoid possible double counts of the same pair on adjacent squares, we only counted those pairs whose core territory fell within the survey square.

We also used a survey method based on a grid of 577 (4 km^2) squares that covered the entire island. From 8 December 1997–22 January 1998, we sampled as many squares as possible. Observations were made from the most suitable viewpoint and crossed by foot or car. We considered a square to be completely surveyed if at least 60 min of continuous observation time were spent at a central point in the square, or if the total observation time for the square was ≥ 1 hr with periods of >20 min of continuous observation in the same area. Many of these squares were sampled for >2 hr. Also, during the same breeding season (September 1997–March 1998), we surveyed an additional 105 squares, some of them not previously sampled. Using such criteria, 331 (2×2 km) squares were surveyed and the minimum number of pairs in each of them was assessed. Two pairs were considered to be different if they were seen at least once

simultaneously. Many other squares were crossed opportunistically but they were not adequately or fully surveyed because of a lack of time, inappropriate weather conditions or because they were unsuitable for breeding harriers (totally urbanized, cultivated or above treeline).

Because we focused on the identification and localization of breeding or potentially-breeding pairs, we excluded observations of individual foraging birds. The following criteria were thus used in all census methods to classify the degree of breeding evidence: a possible breeding pair was a pair of adults flying together that showed no particular breeding behavior or a single adult that performed nuptial displays; a probable breeding pair was a pair that showed territorial defense behavior, usually an adult chasing an individual of the same sex, or even talon grasping, two adults of opposite sexes that displayed together, or one in the presence of the other or adult females that gave solicitation to passing adult males; a certain or confirmed breeding pair was one with one or more young following an adult carrying a prey with persistent begging calls, an adult bringing prey or nest material to a potential nest site, prey transfer between males and females, the occupied nest was found or an empty nest was found with a pair nearby.

All observations (irrespective of sampling methodology) were plotted on a digitized map of Réunion Island using a Geographical Information System (ARCVIEW 3.b software; Environmental Systems Research Institute Inc. 1996). A grid was superimposed on the island GIS map dividing it into 577 (2×2 km) squares whose limits crossed habitat types randomly. Among them, 85 squares overlapped the coastline and included a variable proportion of sea area. When a nest site was not precisely located and the record overlapped the limits of two squares, it was assigned to a single and most appropriate square.

Data sets obtained by the two survey methods were treated separately, but used together for estimating the distribution of population on the island. Observations from lookouts were first mapped on the island grid. We then lumped all data to produce two kinds of maps. The first summarized searching/sampling effort by giving each square a sampling status (i.e., not sampled, sampled by the first method, sampled by the second method or sampled by both methods). The second map was a general distribution map of the species. Using these maps, we determined the breeding status of harriers in each square using the highest recorded status by any of the methods.

For abundance estimates, we reported data from the two methods in each square. When harriers were observed in a given square, we summed the number of possible, probable and confirmed territorial pairs. When there were two different pairs in the same or adjacent squares, they had to have been seen simultaneously to be tallied. This meant that, if a square was surveyed using two different methods, we used the maximum number of pairs given by one method.

RESULTS

Surveys and Coverage of Réunion Island. A total of 384 squares (66.6%) were adequately surveyed. Because 43 additional squares were unsuitable for

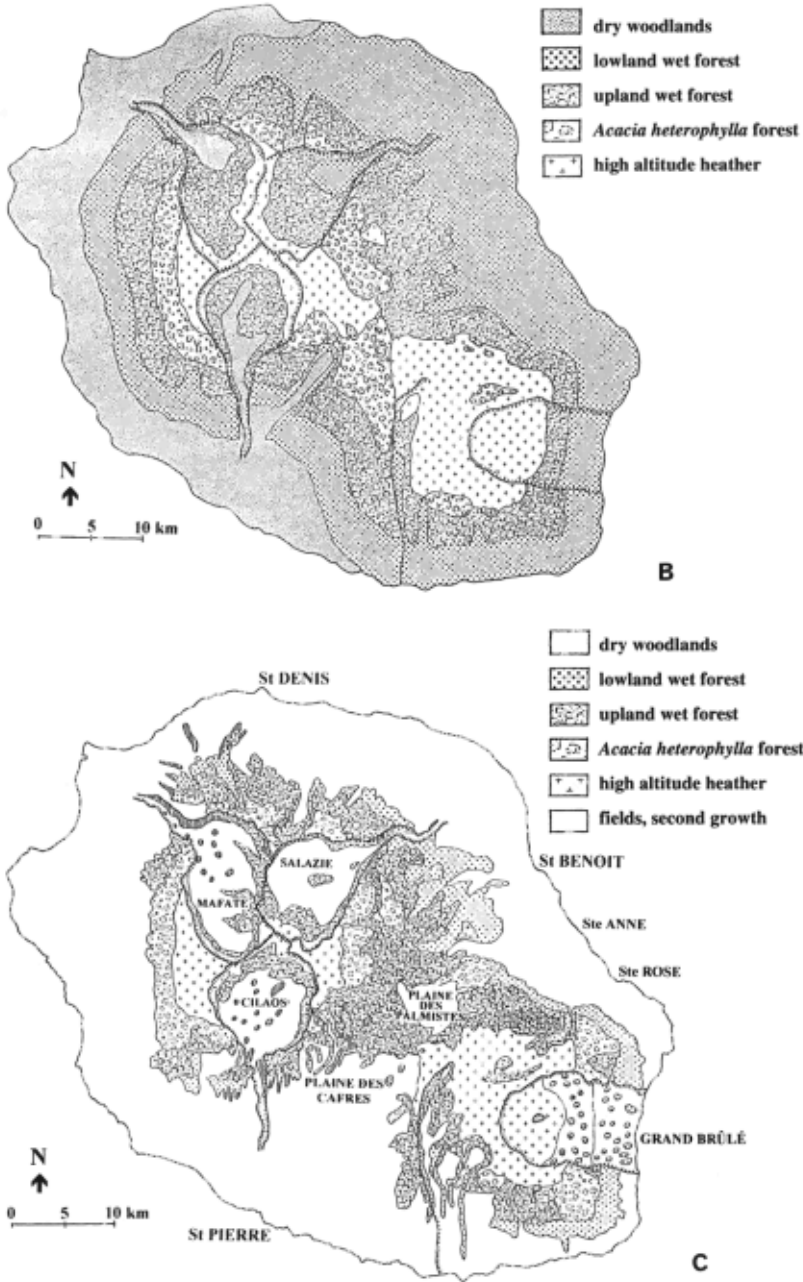


Figure 1. Continued. (B) Reconstructed distribution of natural vegetation before human colonization. (C) Current distribution of main vegetation types.

harriers, our combined survey covered 75% of Réunion Island. Surveys based on 2-hr observations from lookouts provided data on 108 squares ($N = 111$ lookouts), while the method based on surveys

of squares resulted in 111 squares with >1 hr of observation and an additional 196 squares with a shorter census (Fig. 2). The least surveyed areas were two of the three cirques which were known

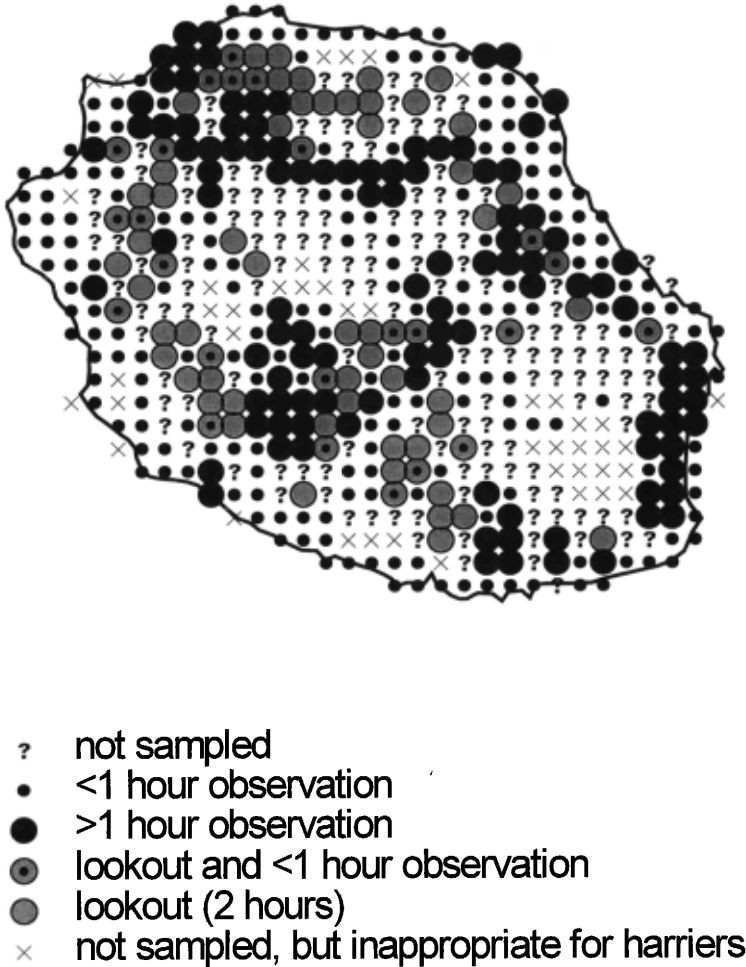


Figure 2. Harrier survey sampling sites.

to contain very few harriers and a heavily forested area in the east of the island where harriers were probably scarce due to the vegetation structure.

Distribution Pattern of Réunion Harriers. Overall, harriers were distributed throughout the island, with no marked preference for any region (Fig. 3). Pairs were irregularly spaced with large areas where they were absent as breeders. There were six areas where as many as 7–8 pairs were aggregated (e.g., within a 8-km segment of a valley with a density of 5–7 pairs over 16 km² [Fig. 3, see Clouet 1978 for density estimates]). Surprisingly, harriers were rare within the three large cirques with no more than 2–3 breeding pairs in each although they were abundant at the entrances of the cirques. The bottom of these cirques were rather

flat and heavily populated but their surrounding steep slopes could provide suitable breeding sites for harriers. Overall, most pairs were concentrated in the lower valleys, mostly along gullies, canyons and other steep areas, a tendency which is also apparent in some breeding seabirds.

Little or no data were available for 150 squares but many of them were unsuitable for harriers. Breeding harriers were absent from another 343 squares (60% of the island area). Possible breeders were found in 20 squares, probable breeders in 46 squares and confirmed breeders in 18 squares (Fig. 4). The rather low numbers in the latter category were due to our late searching effort during the fledging and postfledging periods (>3 mo, Clouet 1978). During this period, we observed many pairs

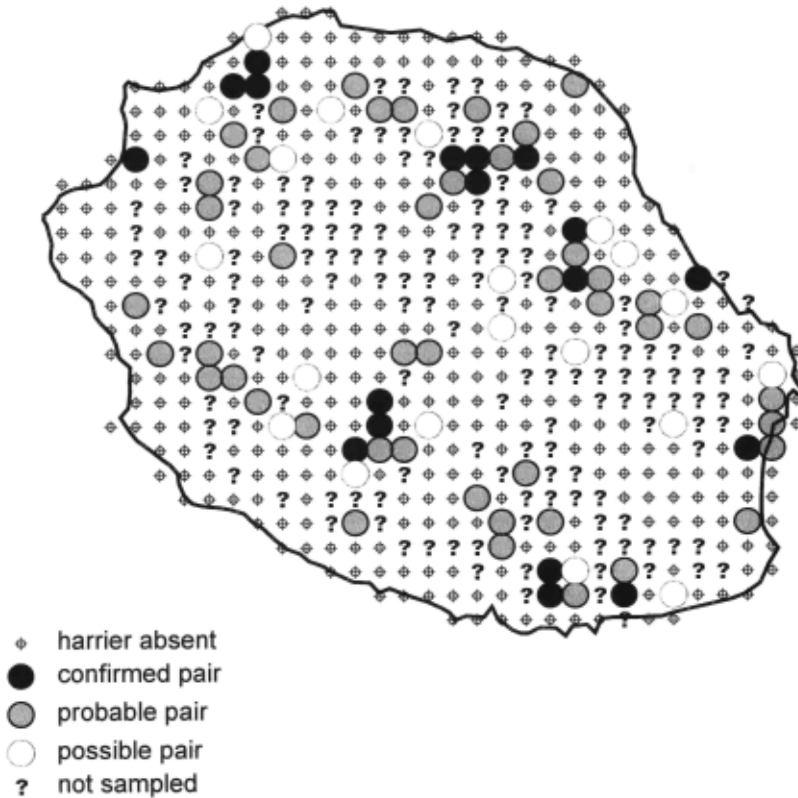


Figure 3. Harrier breeding distribution on Réunion Island according to the highest breeding status recorded per square.

feeding flying young and possibly outside their breeding territories. We treated these as probable breeders.

Population Size. Lumping possible, probable and certain pairs and using data from the two methods, 62 squares had a single pair, 19 squares had two pairs and 3 squares had three pairs for a total of 109 pairs. They were divided into 21 confirmed breeding pairs, 28 probable pairs, 33 family groups not belonging to any of the two former categories and 27 possible pairs (in most cases single males displaying). Nearly half of the 150 squares not adequately surveyed were in cirques or in dense natural forests and were unlikely to be used by harriers. Using the mean density estimate in squares actually sampled, we estimated that <20 pairs would have been found in the 80 unsurveyed squares. Therefore, the total estimated population could be as high as 125–130 pairs (21 confirmed, 28 probable, 33 additional families and up to 50 unconfirmed pairs). A more conservative estimate

would place the current breeding population of Réunion Harriers at about 100 pairs.

Breeding Habitat. Confirmed breeding pairs of harriers were distributed from 0–1200 m elevation, and up to 1800 m if probable breeding pairs and possible dispersing families were added. Overall, about 75% of pairs were below 800 m elevation and 25% were between 800–1600 m (Table 1). Most were concentrated between 300–700 m (Fig. 5), with a median altitude of 500 m ($N = 49$, $\bar{x} = 650 \pm 396$ m \pm SD). We could not test for a statistical preference for mid- to low-elevation breeding ranges because of difficulties associated with assessing the availability of areas at each elevation. However, harriers clearly avoided high altitudes (>1200 m) for breeding, but there was no evidence that they selected a particular level below this limit.

Because most habitat types had a limited altitudinal distribution, there was a strong correlation between habitat choice and elevation range (Table

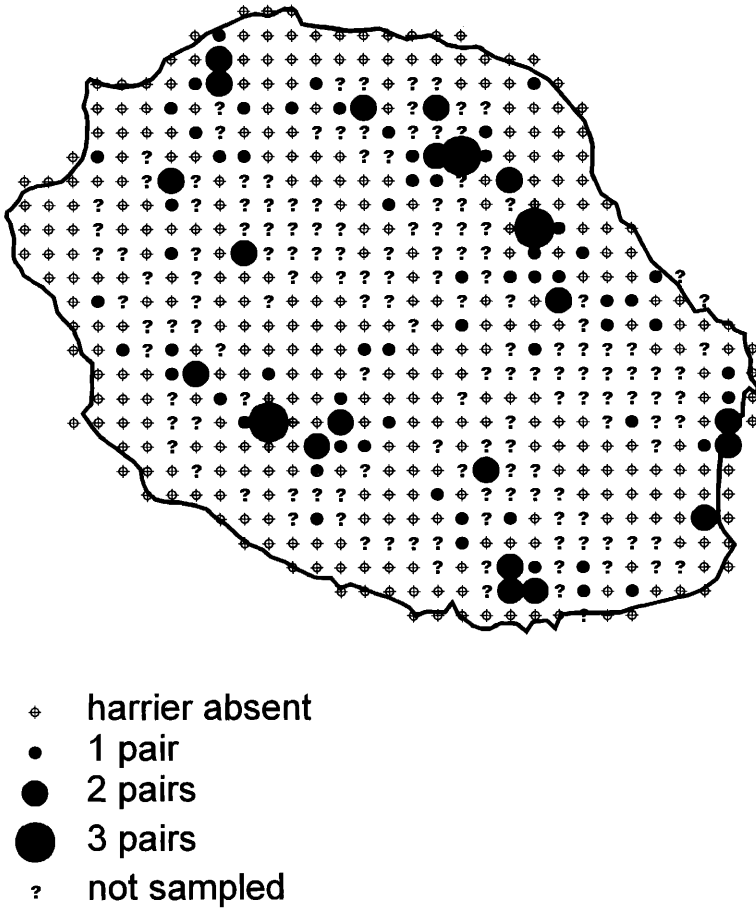


Figure 4. Harrier abundance map on Réunion Island during the 1997–98 breeding season. Number of pairs recorded per 2×2 km squares.

Table 1. Distribution of breeding pairs of the Réunion Harrier among habitat types.

HABITAT	HABITAT REFERENCE	ELEVATION RANGE	NUMBER OF BREEDING PAIRS	
			CONFIRMED	PROBABLE
Dry savanna woodland	1	<500	0	2
Lowland evergreen forest ^a	2	200–800	10	15
Upland wet evergreen forest ^a	3	800–1600	4	8
Montane <i>Acacia</i> forest	4	1600–2000	0	0
High altitude heathland	5	2000–3000	0	0
Exotic tree plantations	6	200–1400	0	0
Derived shrubland	7	100–600	4	2
Cultivated areas and pastures	8	0–1500	1	1
Urban and suburban areas	9	0–1300	0	0
Wetlands	10	0–600	2	0
Total			21	28

^a Including secondary and degraded forests.

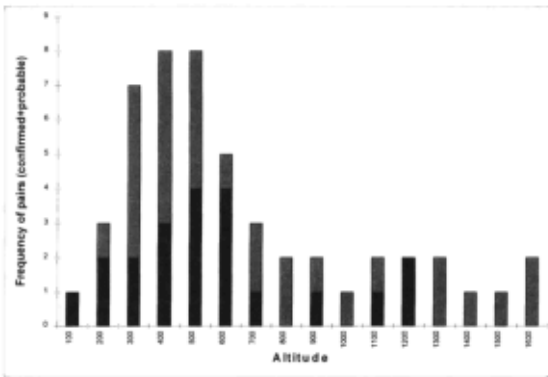


Figure 5. Altitudinal range of certain and probable pairs of Réunion Harriers during the 1997–98 breeding season.

1). Except for lowland swamp and shrubby areas, all known harrier breeding sites were in wooded areas in low, open, degraded native woodlands and were never in taller, dense forest. Nests that we found were never under a tree canopy but in open patches within forests ($N = 6$), in savanna with shrubs ($N = 12$) and in vegetation on cliffs or steep grassy slopes ($N = 10$, see Clouet 1978). No nests have ever been found or suspected to be in the widespread sugarcane fields or under primary dense forest cover.

Foraging Habitat. We pooled all independent observations of foraging harriers (predominantly males) obtained during census sessions ($N = 447$). Foraging habitats were much less restricted than nesting habitats and included almost any habitat type, except urban and suburban areas which were apparently used in historical times (Barré et al.

1996). A minor proportion (15%) of foraging harriers were recorded over open grasslands, derived savannas, roadsides, airfields and a golf course (Table 2). The majority of them used various forested areas including low native forests, open tree plantations, shrubby clearings, heathland above tree-line and woody vegetation on steep slopes (65%). The third important foraging habitat type was sugarcane fields and pastures which accounted for 20% of the records. Few harriers foraged over dense unbroken native forests, gardens, dense mature tree plantations, coastline, stony estuaries of rivers, ponds and industrial areas (<2%). A set of randomly encountered birds, including nonforaging individuals, gave an even broader distribution. In this sample, almost any habitat was occasionally flown over, except towns and mountain slopes above 2600 m, yet low or open woodlands were still favored.

DISCUSSION

According to our observations and those of Clouet (1978), males begin to perform display flights in August–September, nest building occurs from October–November onward, egg laying from January up to April and fledglings often follow parents up to October. Our surveys (October–May) covered only part of the breeding season but, because pairs of Réunion Harriers are sedentary on their territories all year round, this survey period may have only affected the proportion of confirmed compared to possible breeding pairs and not their distribution or numbers. The time we spent in survey squares was variable from 1–>4 hr. Observation time (1 vs. >2 hr) significantly affect-

Table 2. Foraging habitat of the Réunion Harrier.

HABITAT CATEGORY	TIME SPENT (HOURS)	NUMBER OF CONTACTS	% OF CONTACTS	RECORDS PER HOUR
Dry savanna or shrubby woodlands	32	24	5.4	0.75
Wet mixed evergreen forest	31	38	8.5	1.23
Secondary native forest	91	88	19.7	0.97
Montane <i>Acacia</i> forest	11	0	0	0.00
High altitude heathland	>10	2	0.4	0.20
Exotic tree plantations ^a	61	199	44.5	3.26
Cultivated areas (including pastures)	57	90	20.1	1.58
Urban and suburban areas	>10	0	0	0.00
Wetlands	11	6	1.3	0.55
Total	>314	447	100	

^a Including heavily degraded forests.

ed the probability of detecting the presence of harriers in a given square ($\chi^2 = 81.7$, $df = 1$, $P < 0.001$), but there was no relationship between observation time and number of pairs detected on squares ($\chi^2 = 0.5$, $df = 1$, $P > 0.05$). This suggested that observation time had little effect on our surveys. Therefore, we are confident that potential bias due to our methods is limited, and that the data provide a realistic estimate of both distribution and population size.

Overall, harriers were distributed throughout the island, with no marked concentration in any part of it. The current distribution probably reflected more the influence of human disturbance than true habitat preferences. Their preferred habitat occurred on rather steep and forested slopes, away from human settlements. Such characteristics are most often found along rivers, especially at cirque entrances. This suggested a currently significant level of human persecution, despite the harrier's fully protected status.

The total population in 1998 was estimated to consist of 400–600 individuals with <100 breeding pairs, although this was a conservative estimate. Uncertainties about the true population size resulted from the large proportion of birds in adult plumage which did not exhibit territorial or sexual behavior. A more accurate estimate of the breeding population size might be made if we had a better understanding of the social and breeding behavior of this species.

None of the previous estimates of the Réunion Harrier population were based on systematic searches. Therefore, estimates of the population ranged from 130–300 breeding pairs (Clouet 1978, Cheke 1987, Barré 1988, Barré et al. 1996). Our population estimate cannot be compared to previous ones because it was derived from the first complete and reliable survey of the island. Nevertheless, based on the map given by Cheke (1987) and an unpublished map (M. Clouet pers. comm.), neither the overall distribution of the harrier, nor the areas with highest densities have shown any detectable change between 1978–98. Based on 17th-century accounts (Dubois, *in* Barré et al. 1996), the Réunion Harrier was probably much more abundant than today. Habitat losses and faunal impoverishment following human colonization most likely caused its early decline although shooting probably played a significant role. There is no conclusive evidence showing that the harrier population has declined significantly during the last 25 yr,

despite higher population estimates at a time when its recently protected status was enforced very little. Human persecution still takes place but may be currently decreasing, and formerly cultivated or grazed areas are now abandoned, thus increasing areas of suitable habitat. Urbanization and road construction are still increasing but they occur mostly in lowlands and areas that have long been deforested and already out of the harrier's range.

Aggregation of nesters in a few areas may be due to a lack of territorial behavior of harriers away from the immediate vicinity of their nests. It exhibits a broad range of foraging habitats, a variety of hunting techniques and an eclectic prey choice, including birds, introduced mammals and some reptiles, amphibians and grasshoppers (Clouet 1978, Cheke 1987, pers. obs.). This wide niche breadth and adaptability are typical of most island birds when compared to their continental counterparts, including tropical raptors (Thiollay 1993, 1997). Nevertheless, prey abundance and accessibility are likely to be major determinants of hunting habitat selection.

Until the 16th century, the island was almost completely covered with forest. The relatively short rounded wings of the Réunion Harrier probably are an adaptation to hunt in rather dense vegetation and its relatively long middle toe is typical of a bird specialist, probably a necessity when terrestrial mammals were absent and medium-sized lower vertebrates were uncommon (Nieboer 1973). Today, large birds have disappeared but introduced rodents (*Rattus*, *Mus*), insectivores (*Tenrec*, *Suncus*), reptiles (*Calotes*, *Chameleo*, *Phelsuma*), toads (*Bufo*) and frogs (*Ptychadena*) are abundant (Probst 1997). Most of them are probably more difficult to find and catch in forests than were the once numerous pigeons and parrots (Barré et al. 1996). This may explain why this harrier tends to avoid closed canopy forest and to favor lower vegetation and more open woodlands in spite of its apparent morphological adaptation to forest. Nevertheless, it remains much more of a forest bird than any of the 12 other species of harriers in the world (del Hoyo et al. 1994).

The population of Réunion Harriers is precariously small by genetic, demographic and conservation standards. It is currently the smallest population of any native and nonmarine bird species on Réunion. It is also one of the rarest raptor species in the world and its population is now even lower than that of the fast-recovering population of the

Mauritius Kestrel (*Falco punctatus*), once the most endangered raptor in the world (Collar et al. 1994, del Hoyo et al. 1994). There is good evidence to upgrade its taxonomic status to the full specific level, distinct from the Madagascar Harrier. As a taxon of its own, and according to IUCN criteria (Collar et al. 1994), it may well deserve Endangered status because of its small population size, small range and current factors threatening its long-term survival. Although the population appears to be currently stable, this does not mean that it is at full carrying capacity and/or that carrying capacity is not declining through habitat loss or disturbance and degradation. Human population growth and economic development are very high on Réunion and the species is threatened by human persecution both from shooting and loss of breeding and foraging habitats, by increased urbanization and road construction and frequent cyclones, heavy rains and wildfires during the breeding season.

ACKNOWLEDGMENTS

We are grateful to M. Clouet for providing many unpublished notes and maps. We also thank J.M. Probst who contributed additional information, E. Fortier who shared fieldwork, M. Lecorre and members of the Société d'Etudes Ornithologiques de la Réunion for organizing simultaneous harrier counts over large areas and to F. Thiollay who assisted with most of the surveys and helped with typing successive drafts of the manuscript. We thank M. Bechard, M. Pandolfi and an anonymous referee for improving a previous draft. This work was supported by a grant from Réunion (Régional Council), European Community (FEDER) and French Ministry of Environment (DIREN-Réunion), for the study and conservation of terrestrial birds on Réunion.

LITERATURE CITED

- BARCELO, A. 1996. Analyse des mécanismes hydrologiques en domaine volcanique insulaire tropical à relief jeune. Apports la connaissance du Bilan Hydrique. Massif du Piton de la Fournaise (Ile de la Réunion). Thèse de Doctorat Hydrologie, Université de Montpellier II, France.
- BARRÉ, N. 1988. Une avifaune menacée: les oiseaux de La Réunion. Pages 167–196 in J.C. Thibault and J. Guyot [EDS.], Livre rouge des oiseaux menacés des régions françaises d'Outremer. International Council for Bird Preservation, Saint-Cloud, France.
- , A. BARAU AND C. JOUANIN. 1996. Oiseaux de la Réunion. Editions du Pacifique, Paris, France.
- CADET, T. 1980. La végétation de l'Isle de la Réunion. Imprimerie Cazal, Saint-Denis, Réunion.
- CHEKE, A.S. 1987. The ecology of the surviving native land birds of Réunion. Pages 301–358 in A.W. Diamond [Ed.], Studies of Mascarene Island birds. Cambridge Univ. Press, Cambridge, U.K.
- CLARKE, R. 1995. The Marsh Harrier. Hamlyn, London, U.K.
- CLOUET, M. 1978. Le busard de maillard, *Circus aeruginosus*, de l'Isle de la Réunion. *O.R.F.O.* 48:95–106.
- COLLAR, N.J., M.J. CROSBY AND A.J. STRATTERSFIELD. 1994. Birds to watch 2. The world list of threatened birds. Birdlife International, Cambridge, U.K.
- DEL HOYO, J., A. ELLIOTT AND J. SARGATAL. 1994. Handbook of the birds of the world. Vol. 2. Lynx Edicions, Barcelona, Spain.
- DOUMENGE, C. AND Y. RENARD. 1989. La conservation des systèmes forestiers de l'Isle de la Réunion. IUCN, Cambridge, U.K.
- DUPONT, J. 1990. Cartes de végétation de la Réunion. Srepen, Saint-Denis, Réunion.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE, INC. 1996. Redlands, CA U.S.A.
- HOWARD, R. AND A. MOORE. 1980. A complete checklist of the birds of the world. Academic Press, London, U.K.
- MACDONALD, I.A.W., C. THEBAUD, W.A. STRAHM AND D. STRASBERG. 1991. Effects of alien plant invasions on native vegetation remnants on La Réunion (Mascarene Islands, Indian Ocean). *Environ. Conserv.* 18:51–61.
- MARCHANT, S. AND P.J. HIGGINS. 1993. Handbook of Australia, New Zealand and Antarctic birds. Vol. 2. Oxford Univ. Press, Melbourne, Australia.
- NIEBOER, E. 1973. Geographical and ecological differentiation in the genus *Circus*. Dissertation, Free Univ., Amsterdam, Netherlands.
- PROBST, J.M. 1997. Animaux de la Réunion. Azalées Editions, Saint-Denis, Réunion.
- RIVALS, P. 1952. Etude sur la végétation naturelle de l'île de la Réunion. Travaux du Laboratoire Forestier de Toulouse, V, 3 sections. Vol. I. Faculté des Sciences de Toulouse, Toulouse, France.
- SIBLEY, C.G. AND B. MONROE. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven, CT U.S.A.
- SIMMONS, R.E. 1997. The African Marsh Harrier. Pages 236–237 in J.A. Harrison, D.G. Allan, L.G. Underhill, M. Herremans, A.J. Tree, V. Parker and C.J. Brown [EDS.], The atlas of southern African birds. Birdlife South Africa, Johannesburg, South Africa.
- SINCLAIR, I. AND O. LANGRAND. 1998. Birds of the Indian Ocean islands. Struik, Cape Town, South Africa.
- THIOLLAY, J.-M. 1993. Habitat segregation and the insular syndrome in two congeneric raptors in New Caledonia, the White-bellied Goshawk, *Accipiter haplochrous*, and the Brown Goshawk, *A. fasciatus*. *Ibis* 135:237–246.
- . 1997. Distribution patterns and conservation of bird community and raptor populations in the Andaman archipelago. *Ecography* 20:67–82.

Received 1 April 1999; accepted 7 October 1999