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## Influence of habitat on the foraging behaviour of the Mediterranean horseshoe bat, *Rhinolophus euryale*

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In a previous study on habitat use by *Rhinolophus euryale* in an Atlantic area (Northern Iberian Peninsula), this bat species foraged exclusively in woodland, including both native deciduous woodland and exotic plantations. As the study was carried out in a landscape that was profoundly altered by industrial forestry, we predicted that in a better preserved landscape this species would select smaller feeding areas located at closer distances from the roost, according to the optimal foraging theory, and would use almost exclusively the preferred habitat, i.e., native deciduous woodland. To test these hypotheses, we radiotracked 14 *R. euryale* from the largest known breeding colony of northern Iberian Peninsula and determined their habitat selection, spatial foraging pattern, and hunting behaviour. Our predictions on habitat selection, as well as on the foraging site size and on commuting range were confirmed. *Rhinolophus euryale* used almost exclusively native deciduous woodland, and hedgerows were positively selected. We suggest that the richness of tree species in hedgerows provides a high prey availability sustained in time and space. Our findings show that habitat disturbance constitutes a major cause of decline for *R. euryale* in the study area.

**Key words:** *Rhinolophus euryale*, habitat changes, foraging behaviour, management

### INTRODUCTION

Rhinolophids show clear adaptations to forage in clutter, such as their peculiar echolocation system and their wing morphology (e.g., Schnitzler *et al.*, 1985; Norberg and Rayner, 1987; Emde and Menne, 1989; Jones and Rayner, 1989; Neuweiler, 1989; Emde and Schnitzler, 1990; Schnitzler and Kalko, 1998; Kingston *et al.*, 2000). Their flight is slow and very manoeuvrable, highly specialised to hunt within or close to vegetation. According to these features, rhinolophids primarily forage in broadleaved forests, as well as in other seminatural wooded

habitats (Neuweiler *et al.*, 1987; Crome and Richards, 1988; Jones and Morton, 1992; Duvergé and Jones, 1994; Schofield, 1996). Their hunting behaviour is also flexible, including hawking, flycatching and gleaning (e.g., Neuweiler *et al.*, 1987; Jones and Rayner, 1989; Pavey, 1998). So far, few studies have dealt with habitat selection in *R. euryale* (Russo *et al.*, 2002; Aihartza *et al.*, 2003). Brosset *et al.* (1988) described the landscape surrounding 83 roosts in France but gave no clear contribution to the knowledge of this species' habitat selection. The first radio-tracking study was conducted in southern Italy by Russo *et al.* (2002)

during the breeding season. The study area was characterized by a Mediterranean landscape, dominated by farmland, woodland and olive groves. This investigation highlighted the importance of broadleaved woodland as the main foraging habitat for *R. euryale*, whereas conifer plantations were negatively selected, and the foraging range observed around the roost fitted fairly well to the morphofunctional model proposed by Jones *et al.* (1995).

In a study conducted in spring in an Atlantic landscape of northern Iberian Peninsula, *R. euryale* also foraged exclusively in woodland (Aihartza *et al.*, 2003), including not only native deciduous woods, but also exotic plantations of eucalyptus (*Eucalyptus globulus*) and Monterey pine (*Pinus radiata*). Moreover, the foraging range of the colony observed was much larger than that expected for the species following the model by Jones *et al.* (1995). It was suggested that the study area, largely covered with exotic plantations, was suboptimal for the species (Aihartza *et al.*, 2003). This statement was also supported by the large size of individual feeding areas, the quite large use of (negatively selected) pine plantations, the rarity of native deciduous woodland, and the absence of the colony during the breeding season.

According to the optimal foraging models (see, for example, Krebs and Davies, 1984; Stephens and Krebs, 1986), the range a bat needs to occupy to satisfy its energetic demands would depend on habitat suitability. Optimal habitat conditions are expected where higher population densities occur or/and where individuals meet their highest energetic needs, i.e., in habitats used by large breeding colonies. We predict that in optimal habitat conditions the size of individual feeding areas of *R. euryale* are smaller and their overlap larger than those found by Aihartza *et al.* (2003), and the distance to feeding areas from the roost fits that

predicted by morphofunctional models (Jones *et al.*, 1995). Furthermore, where the most preferred habitats (deciduous woods) are well-represented, *R. euryale* is expected to reject unfavourable habitats such as exotic plantations.

To test these hypotheses, firstly we determined (1) habitat selection in relation to composition and structure of vegetation patches, and (2) spatial foraging pattern in the largest known breeding colony of *R. euryale* for northern Iberian Peninsula. Secondly, so as to investigate the influence of habitat quality on the foraging behaviour of *R. euryale* we compared our results with those by Aihartza *et al.* (2003), and hence the present study site was chosen within the same geographical area of that examined in this latter paper — 57 km apart — and both studies were conducted in the same season (Racey and Swift, 1985; Shiel *et al.*, 1999). In this way, any observed difference between the two investigations was likely to reflect differences in habitat composition and quality. We also provide new observations on the hunting behaviour of this species.

## MATERIALS AND METHODS

### Study Area

The study area is located in the Karrantza Valley, in the western part of the Basque Country (northern Iberian Peninsula). It is characterised by a warm humid Oceanic climate, an elevation range of 200–855 m a.s.l. and steep hilly slopes. Unlike most of the Atlantic region of the Basque Country, Karrantza Valley is not industrialised and forestry is only incipient, with few plantations of Monterey pine and eucalyptus. Cattle-breeding is thus the most important human activity, and consequently pastures and meadows predominate, interspersed with a large hedgerow network and deciduous woodland. Woodland consists mainly of oak *Quercus robur*, ash *Fraxinus excelsior*, chestnut *Castanea sativa*, and hazel tree *Corylus avellana*. Hedgerows include willow *Salix atrocinerea*, hazel tree *C. avellana*, bramble *Rubus ulmifolius*, maple *Acer campestre*, blackthorn *Prunus spinosa*,

hawthorn *Crataegus monogyna*, and also isolated trees. In limestone outcrops young holm oaks *Quercus ilex* form dense and impenetrable woods with climber species such as *Smilax aspera* and *Rubia peregrina*.

### The Colony

The colony roosted in a limestone cave situated at 334 m a.s.l. At least 65 *R. euryale* use this cave during the winter as a hibernaculum, but most of them congregate between mid-April and mid-June to breed. Parturitions occur mainly between mid-June and mid-July, with a population peak recorded in mid-August of up to 600 bats (Aihartza, 2001). During the present study, 364 bats were counted from photographs taken inside the roost. The cave was also used by other species through the year, including several *R. ferrumequinum* in spring and winter, several *R. hipposideros* in winter, and near 200 *Myotis emarginatus* in the breeding season (Aihartza, 2001).

### Bat Trapping, Tagging and Tracking

Captures were conducted between 3 and 13 May 2001 under license by the Regional Council of Biscay. The bats were caught with a 2 × 2 m harp trap (Tuttle, 1974) as they returned to the cave. Each subject was identified, sexed, and its forearm length and body mass were measured. Fourteen bats, 7 males and 7 females with no apparent signs of gestation, were fitted with 0.55 g radiotransmitters (PipII, Biotrack Ltd., Dorset, UK). After trimming off the hair between the scapulae with scissors, the transmitters were attached using Skinbond surgical adhesive (Smith and Nephew, Largo, Florida, USA). The weight of the transmitter and the adhesive was on average 6% of the body mass. After tagging the bats were released into the cave.

Radio-tracking was carried out by car and on foot using four radio-receivers (1000-XRS, Wildlife Materials, Carbondale, USA, and FT-290R2, Andreas Wagener Telemetrieanlagen, Köln, Germany) and hand held three-element Yagi antennas. Each night, the first fix was obtained 15–20 minutes after emergence in order to allow the bats to commute to their foraging grounds. To avoid pseudo-replication, locations were taken at least every 15 minutes. The locations were mainly determined with the homing-in method, which often allowed us to see the bats tracked. When locations were taken by triangulation, two or more observers coordinated by two-way radio to ensure simultaneous bearings (White and Garrot, 1990). Behaviour displayed was observed visually

against distant streetlights, moonlight or using a spotlight. Emergence time was also recorded.

### Data Analysis

Fixes were mapped in the field on georeferenced orthophotograph layouts, and then stored in a Geographic Information System (Arcview 3.2. ESRI, California, USA). We used digital cartography for all spatial analyses. We determined habitat availability within a Minimum Convex Polygon traced around the overall fix sample. Five habitat categories were classified according to dominant plant species: pasture, holm oak wood, pine plantation, eucalyptus plantation and deciduous wood. Furthermore, the habitats were also categorized according to structure and shape of patches: hedgerow, mature woodland and isolated tree. We defined 'isolated' any tree or small group of trees (1–5 individuals), which were at least 10 m apart from other trees. The 'used' proportion was expressed by calculating the percentage of fixes falling in each habitat category. Foraging areas were defined using all individual locations. Vegetation type and structure was confirmed by field surveys.

Pearson's  $\chi^2$ -test was used to determine the independence between usage and availability, and Bonferroni confidence intervals were applied to assess the statistical significance of the selection upon each category (Manly *et al.*, 1993). Significance was set at  $P < 0.05$ . Significance of differences between the size of individual foraging areas recorded in this work and previous data observed by Aihartza *et al.* (2003) was checked by Mann-Whitney *U*-test.

## RESULTS

### Habitat Use and Selection

We obtained data from 13 individuals, seven males and six females (Table 1). One tagged female was never detected following release. During 16 tracking nights 204 locations were obtained. Deciduous woodland was the most used habitat type (199 locations, Table 2). Only 4 locations were found in pinewood and all of them corresponded to one individual during two foraging bouts of 30 min. each. Only one fix was assigned to holm oak wood, but the bat foraged on the edge close to a hedgerow. We never recorded a bat foraging in eucalyptus plantation or over pasture. Bats used deciduous

TABLE 1. Sex, tracking data, and spatial use data of the 13 radiotracked bats

Code	Sex	Tracking period	No. of nighths tracked	No. of locations	Foraging area (ha)	Mean flown distances (km)
81	Male	3–16 May	6	16	20.3	3.8
110	Male	13–22 May	8	15	10.4	0.5
128	Female	13–18 May	4	14	23.7	1.1
143	Male	13–20 May	4	15	118.3	0.7
164	Female	3–22 May	5	14	7.5	0.7
182	Female	13–19 May	4	10	13.2	0.8
195	Male	3–22 May	9	17	17.3	0.6
242	Male	3–13 May	5	14	6.1	1.1
348	Male	3–22 May	5	22	89.3	1.8
388	Male	3–21 May	5	18	50.7	0.7
424	Female	3–22 May	9	26	142.6	2.4
433	Female	13–18 May	4	12	14.7	0.8
482	Female	13–17 May	3	11	21.2	2.1

tree structures in different proportions, hedgerows being the most visited, followed by mature woods and isolated trees (Table 2). Of 61 locations in mature deciduous wood, 10 (16.4%) were on wood edge, though in the other cases no discrimination was possible.

Habitats were not used according to availability ( $\chi^2 = 76.97$ ,  $d.f. = 2$ ,  $P < 0.05$ ; Table 2). Deciduous woodland including the three structural categories was positively selected, whereas pine and holm oak wood were negatively selected (Table 2). Eucalyptus plantation as well as pasture were not used and thus were negatively selected. Because habitat types other than deciduous woods were marginally used, we focused the selection analysis on deciduous

vegetation structures. The use of different deciduous structures did not depend on availability ( $\chi^2 = 10.23$ ,  $d.f. = 2$ ,  $P < 0.05$ ). Hedgerows were positively selected, mature woods were used less than expected, and isolated trees were opportunistically used (Table 2).

Emergence

Bats emerged on average 32 min. after sunset ( $SD = 6.75$ ,  $n = 66$ ) between the 8th and the 21st of May. A male exhibited an unusual behaviour as it emerged once 1 min. after sunset, 8 min. after sunset in two cases, and 15 min. after sunset on average. The bats emerged both solitarily or in small groups of up to five individuals. Before

TABLE 2. Selection of habitats classified according to vegetation type and structure by 13 *R. euryale* ( $P < 0.05$ )

Habitat	Used proportion ( $O_i$ )	Available proportion ( $\pi_i$ )	Bonferroni confidence intervals		Selection
			Lower	Upper	
Vegetation type					
Pinewood	0.020	0.11	-0.004	0.043	Negative
Holm oak wood	0.005	0.20	-0.007	0.017	Negative
Deciduous wood	0.975	0.69	0.950	1.001	Positive
Vegetation structure					
Hedgerow	0.573	0.486	0.489	0.657	Positive
Mature wood	0.306	0.418	0.228	0.385	Negative
Isolated tree	0.121	0.096	0.065	0.176	Opportunistic

leaving the roost, the bats flew inside the cave by the entrance and in some cases after emerging for a short flight of a few seconds they returned to the cave. Once emerged, linear features such as hedgerows and wood edges were used, and the flight was very close and parallel to vegetation. Radio-tagged bats flew directly to their foraging sites as soon as they emerged.

### *Spatial Use*

The maximum straight line distance travelled from the roost to a foraging site was 4.2 km, and the average value was 1.4 km (SD = 1.06 km,  $n = 204$ ; see Table 1). Seven out of 13 bats never flew further

apart. There was not significant difference between distances travelled by males and females (Mann-Whitney  $U = 13$ ,  $n_1 = 7$ ,  $n_2 = 6$ ,  $P < 0.05$ ).

The size of individual foraging areas varied from 6.6 to 142.6 ha ( $\bar{x} \pm \text{SD} = 41.2 \pm 45.8$  ha,  $n = 13$ ; Table 1). No significant difference was found in the size of foraging areas between sexes ( $U$ -test = 22,  $n_1 = 7$ ,  $n_2 = 6$ ,  $P < 0.05$ ).

Foraging areas largely overlapped (Fig. 1), especially for bats foraging in the vicinity of the roost. We saw some cases ( $n = 10$ ) in which apart from the tagged bat other individuals were also foraging in the same area. The bats showed a high roost fidelity. Only two males moved to another cave

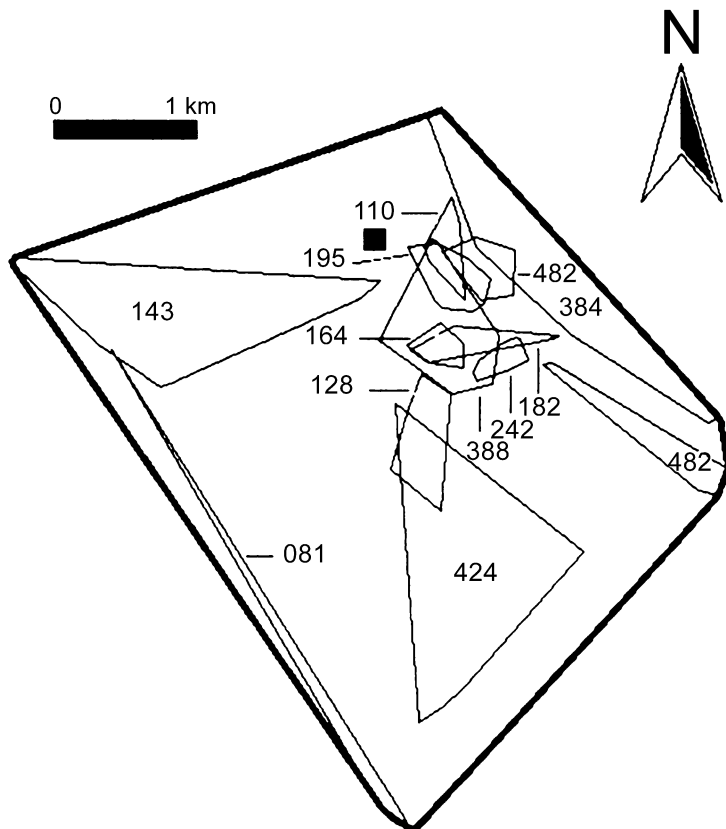


FIG. 1. Minimum Convex Polygons showing the individual foraging grounds of *R. euryale* within the total area considered as available (in bold). Each bat is identified by its code number as in Table 1. The main roost location is represented by a black square

1 km apart from the capture site, but they returned to the previous roost within a week.

### Hunting Behaviour

*Rhinolophus euryale* showed three hunting strategies (Fig. 2): (1) Continuous flight parallel to and within 50 cm from the vegetation, travelling back and forth. Bats flew along linear structures such as hedgerows and woodland edges, and also around isolated trees; (2) Flight close to the canopy, plunging themselves repeatedly into the foliage, very close to the leaves, and/or diving through the branches; (3) Perch hunting. The bat hung from a twig and after a short forward and downward flight it returned to the previous place, presumably after catching the prey.

Bats showed a high fidelity to individual feeding sites and these were intensively and persistently used on different nights. Bat 81

flew as far as 4.2 km from the roost to an isolated maple tree on 5 consecutive nights. Similarly, bat 348 travelled up to 3 km to a willow hedgerow on 4 nights.

Eighty-six percent ( $n = 22$ ) of the isolated trees or small copses used occurred within 50 m from the nearest hedgerow or wood. The remaining three sites were isolated trees used by different bats, located 90, 110 and 140 m far from the nearest tree. Such trees, however, were located along linear elements such as a barbed wire fence or a stone wall. We observed three bats that night-roosted in trees in the foraging areas. There seemed to be a threshold dusk temperature of 10°C below which bats did not emerge or ceased their foraging. We also observed bats foraging in drizzle.

### DISCUSSION

Our results confirmed all the predictions about the influence of optimal habitat quality on foraging behaviour of *R. euryale*, in terms of both habitat preference and spatial foraging pattern. As expected, *R. euryale* selected the native deciduous woodland since it foraged almost exclusively in this habitat avoiding woodlands of other composition such as eucalyptus and pine plantations. These results are in accordance with Russo *et al.* (2002). Aihartza *et al.* (2003), suggested that in the case they analysed *R. euryale* must have used extensively exotic plantations because the preferred deciduous woodland was scarce in the study area. The native holm oak woodland, positively selected in southern Italy (Russo *et al.*, 2002), was avoided in northern Iberian Peninsula (Aihartza *et al.*, 2003; present study). In both studies within this latter region, however, holm oak woodland consists of young trees forming a very cluttered habitat rich in thorny and climber scrubs, where foraging bats may not be able to manoeuvre. Our results followed the predictions on

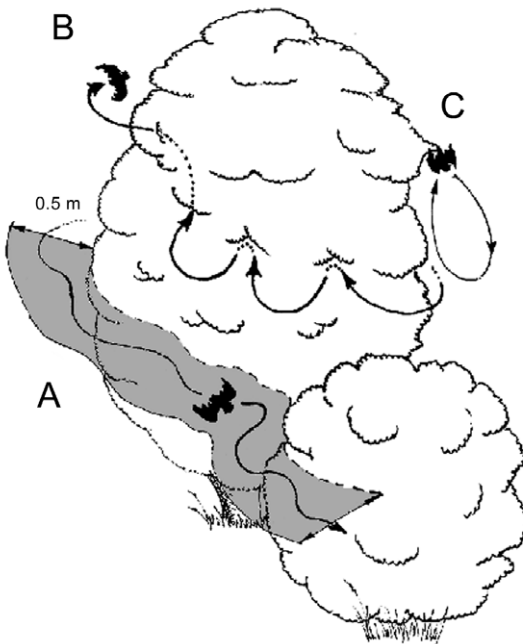


FIG. 2. Hunting strategies observed in *R. euryale*: (A) flying along woodland edge, (B) plunging into the foliage, and (C) perch hunting

spatial foraging pattern. Indeed, comparing the present study with that of Aihartza *et al.* (2003), an increase in the preferred habitats was accompanied by a reduction in size of the foraging range and a significant decrease of individual feeding areas, as well as an increase of overlap between them.

Consequently, habitat quality influences the foraging behaviour of *R. euryale*. This is consistent with the optimal foraging theory, according to which the range an animal would occupy to satisfy its energy requirements would depend on the abundance and distribution of food (Davies and Houston, 1984; Krebs and Davies, 1984; Stephens and Krebs, 1986). As a result, low insect densities would induce the bats to fly longer distances and spend more time or exploit larger feeding areas to fulfil their requirements. This relation would persist until flight costs are not paid by energy inputs, after which the habitat would become unsuitable for the species.

Based on morphofunctional criteria, Jones *et al.* (1995) predicted that the foraging range for a bat such as *R. euryale* should be of 1.5 km from the roost. That value closely matches our results and is also very similar to that recorded in southern Italy (Russo *et al.*, 2002). In contrast in a suboptimal landscape Aihartza *et al.* (2003) observed a mean foraging distance of 5.5 km and a maximum of 10 km. In fact, individual foraging areas in our study were significantly smaller than in Aihartza *et al.* (2003: table 4) ( $U$ -test = 16,  $n_1 = 7$ ,  $n_2 = 13$ ,  $P < 0.05$ ). Values close to or above 10 km have been recorded for bat species with a high aspect ratio (Barclay, 1989; Shiel *et al.*, 1999; Barclay *et al.*, 2000) or with a low aspect ratio but a large size (Arlettaz, 1995). Bats similar in size or in aspect ratio to *R. euryale*, however, travel shorter distances (e.g., Racey and Swift, 1985; Adam *et al.*, 1994; Duvergé and Jones, 1994; Entwistle *et al.*, 1996; Bontadina *et al.*, 1999). As

Jones *et al.*'s (1995) model does not take into account habitat quality constraints, it is probably only applicable to optimal habitat conditions.

In our study, we could not observe whether *R. euryale* hunted by gleaning. We confirm, however, the use of flycatching, as suggested by Russo *et al.* (2002). This hunting strategy is typical for *R. ferrumequinum* (Jones and Morton, 1992; Duvergé and Jones, 1994; Lugon, 1996), but not for *R. hipposideros*, which may both feed on the wing and glean (Jones and Rayner, 1989; Schofield, 1996). Nevertheless, in agreement with Russo *et al.* (2002), we observed *R. euryale* flying along linear elements such as hedgerows, treelines or woodland edge. *Rhinolophus euryale* flew closer to the foliage than *R. ferrumequinum* (Duvergé and Jones, 1994; Bontadina *et al.*, 1995; Jones *et al.*, 1995), probably because the former is favoured by a smaller wing loading and wingspan (i.e., by a higher manoeuvrability in clutter) than the latter. Likewise, *R. hipposideros* forages in cluttered environments such as woodland and uses extensively riparian habitats, hedgerows and tree lines (McAney and Fairley, 1988; Jones and Rayner, 1989; Schofield, 1996; Bontadina *et al.*, 1999; Motte and Libois, 2002). Tree formations showing a high area/volume rate (hedgerows and even isolated trees) were then the preferred spatial structures by *R. euryale*. Beyond morphofunctional clues, food supply influences different aspects related to foraging behaviour (Bradbury and Vehrencamp, 1976a, 1976b; Barclay, 1991). Racey and Swift (1985) also deduced that the foraging habitat of pipistrelles *Pipistrellus pipistrellus* was determined by insect abundance. In this sense, the high tree species diversity shown by hedgerows might guarantee a continuous prey supply spread out along time and space. Thus, we think that both structure and species richness are key

factors which can determine the habitat quality and hence the spatial foraging pattern for *R. euryale*.

*Rhinolophus euryale* has suffered a serious regression all along Europe but especially in the Eurosiberian region of its distribution range. In France a population decline of about 70% was recorded between 1940 and 1980, with a slow recovery up to 1987 (Brosset *et al.*, 1988). The Czechoslovak population showed also a clear decline (Horáček, 1984), and the Spanish one, of ca. 30.000–35.000 individuals, has shown a slow decreasing trend across its range, and especially in the central area (Paz and Alcalde, 2000). Roost disturbance, uncontrolled ringing and intensive use of organochlorine pesticides have been blamed for this decline (Brosset *et al.*, 1988; Stebbings, 1988; Palmeirim and Rodrigues, 1992). Our data stress that changes in natural habitats may be an important factor causing the decline of this species, as some authors suggested (Stebbins and Griffith, 1986) and recent data in southern Italy support (Russo *et al.*, 2002). In fact, not only did the disappearance of several breeding colonies in the Basque Country since the 1960s (Aihartza, 2001) correspond to an increase in roost disturbance, but also with a loss of hedgerows and deciduous woodland and a spread of pine plantations. The transformation of the seminatural Atlantic landscape into extensive industrial forestry may have seriously reduced habitat suitability for *R. euryale*.

We agree with Russo *et al.* (2002) that the maintenance of a significant hedgerow network and a large mixed woodland cover consisting of native deciduous species is crucial for the survival of *R. euryale*. Interestingly, our results suggest that even relatively small areas, as far as well preserved, may harbour large bat colonies. Focusing conservation efforts such as habitat restoration or preservation on these areas could be thus achieved at quite low financial and

social costs. To help develop conservation measures, further research is needed to determine seasonal changes in habitat use and to assess the minimum availability of the preferred habitat needed by breeding colonies.

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