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Migratory movements of *Miniopterus schreibersii* in the north-east of Spain

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This article analyses information gathered between 1984 and 1995 relating to the seasonal movements of *Miniopterus schreibersii* (Kuhl, 1819) in the north-east of Spain. The recapture rate of banded different individuals is 32.5% and the total recapture rate is 53.4%. Ninety five different trajectories have been reported. The bats cover an average distance of 120 km between their hibernation sites and summer roosts. The longest longevity recorded here is almost 10 years. Localities where *M. schreibersii* was observed were grouped by seasonal use pattern and according the species biological cycle. Two new hibernation sites, seven new breeding sites and sixteen new equinoctial sites have been discovered in this study. From the verified flight trajectories, the distribution of shelters and the ethological characteristics of the species, the most probable migration path have been established.

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Introduction

Miniopterus schreibersii (Kuhl, 1819) is a migratory bat, having a relatively fast flight, whose seasonal displacement distances vary widely, sometimes surpassing 300 km (Balcells 1962, Roer 1967, Griffin 1970, van der Merwe 1975, Aellen 1983). This species moves between summer roosts, commonly located in areas rich in food resources, and winter quarters, whose main features are high relative humidity and rather low and constant temperatures (Balcells 1962, 1964, Serra-Cobo 1989). Between these two kinds of localities the species stops in temporary spring and autumn shelters, called equinoctial roosts (Serra-Cobo 1989, Serra-Cobo and Balcells 1991). The males start to fly before the females in all the hibernation cavities. However, for the migrations from equinoctial refuges towards summer cavities the females fly out first, in the middle of spring (Serra-Cobo *et al.* 1987, Serra-Cobo 1989). By the end of summer the females and the young bats are the first to arrive at the equinoctial autumn roosts, where they are later joined by males (Balcells 1962, 1964). By late autumn or, dependent on climatic variations, early winter the females are the first to fly towards the winter quarters (Serra-Cobo *et al.* 1987).

This paper analyses information gathered from 1984 to the autumn of 1995. Some of the data have already been published by Serra-Cobo and Balcells (1991), who supplied information mainly on cavities near the Catalan coast and connections between them. This paper was a great advance on the older papers by Balcells (1962, 1964), which dealt exclusively with the movements of the hibernating population of only one cavity, Daví pothole (Fig. 1: No. 37). The present study analyses a much larger amount of data (most unpublished), and covers a much larger territory, and because of that provides a wider aspect of the subject. This paper shows the use and function of the different shelters by *M. schreibersii* in their seasonal movements. It also shows the complex relationships and interchanges which take place amongst the colonies of different shelters. Likewise, data are supplied on the longevity of *M. schreibersii* and the distances travelled by it between winter and summer shelters. This information allows definition of the most probable migratory paths of the species in the north-east of Spain, and is very important to any plan of protection of shelter cavities. Moreover, knowledge of the movements of the species in the north-east helps in the building of models and allows study of migratory habits of the species in other parts of Spain (for instance in Aragón). Emphasis is also put on the methodology used, which provides an efficient method for gathering data.

Material and methods

Our study on the migrations of *M. schreibersii* is based on banding and recovery of individuals. At the beginning of the present study, while carrying out sampling in refuges chosen at random, we found it very difficult to locate colonies of *M. schreibersii*. Thus, the planning of field work was developed from previous studies of the area in order to concentrate effort in zones most likely to provide information. Before each field trip the topographic map of the area was studied, and different features noted: the type of relief, the closest known shelter, the orientation of valleys, the proximity to lakes, ponds or reservoirs, marshes, and the sea, the distance to known roosts and the time of year that these are used. With these features in mind small areas could be delimited where the probability of finding *M. schreibersii* was high for a given time of year. Geomorphological and, if possible, environmental details of caves and other cavities within the area were then obtained from the literature, maps and from speleological groups. In this way the length and depth of caves, the size and situation of the rooms and corridors, the way the cave was formed, the size of entrance, the temperature, the relative humidity, the air flow and the presence of bat guano were recorded. Normally the data were sufficient to allow the selection of cavities and the best times of year to visit them. This selection, and the frequent visits to caves, allowed high recapture rates and hence much information was obtained from relatively few bandings.

In the present study the number of banded bats has only been 2007 in 11 years. The majority of these (1330) belong to the hibernating groups of the Daví pothole, the Puig d'en Mar pothole (No. 46) and Querant Gran d'en Paús (No. 55). The remaining 677 were banded in summer and equinoctial roosts to complete the study of seasonal movements. In all, 150 visits were made to bat colonies. Banding and recapture data were input to a database to facilitate analysis.

Localities where *M. schreibersii* was observed were grouped by seasonal use pattern and the species biological cycle, as follows: hibernation quarters, equinoctial roosts (which can be linked to spring or autumn journeys), summer roosts for males (where adult males dominate), summer breeding roosts (females and young dominating) and accidental findings corresponding to isolated travelling animals. Some localities were not classified because of the lack of relevant information. Movement between wintering and equinoctial colonies was quantified only for one trajectory, that between the Daví pothole and the Castanya mines (No. 32), these localities being the most accessible and well known. Seven visits were made to the mines and 14 to the pothole, enough to estimate the minimum proportion of animals moving from winter shelters to spring roosts. The great effort invested in visits to hibernation quarters (14 to Daví pothole, 6 to Puig d'en Març pothole, 7 to Querant Gran d'en Paús), allowed quantification of the minimum proportion of animals using the same hibernation shelter during two successive winters, and the exchanges between the three hibernation quarters. The minimum proportion of bats using the same equinoctial roost during two consecutive springs or during a spring and the following autumn, have also been calculated in Castanya mines.

From the observed trajectories and from those previously published (Balcells 1962, 1964, Nadal *et al.* 1968), which have also largely been verified here, the main migratory paths of *M. schreibersii* in the north-east of Spain have been established. This has been supported by information on the physiographic features of the area and from the spatial distribution of shelters.

Results

The methodology of this study has been shown to be efficient, and has allowed not only the definition of species movements and territory use, but also has enabled us to find new shelters. The recapture rate of different individuals is 32.5%, (652 bats) whilst the total recapture rate, including repeated recaptures is 53.4% (1082 recaptures). Two animals were recaptured seven times, eight were recaptured six times and 13, 26, 59, 130, and 414 were recaptured five, four, three, two and one times respectively. Ninety five different trajectories have been reported, five of these already reported by Balcells (1962, 1964). These results contrast with those by former authors, who obtained a much smaller recapture rate using different methods. For instance, Balcells (1962, 1964) reported 18 different trajectories within Spain and confirmed 9 more across the French-Spanish border. Paz *et al.* (1987) obtained a total recapture rate of 14.6% (12.4% of banded bats), and reported 28 distinct trajectories.

Fig. 1 shows the relationships between the populations of the north-east of Spain and south-east France. Fig. 2 shows the recorded trajectories in north-east Spain and their links to the Daví winter pothole. Fig. 3 summarises the paths linked to the three hibernation caves, emphasising the colonies of Querant Gran den Paús and of the Puig d'en Març pothole.

The longest recorded movement was 270 km (measured as a straight line between banding and recapture spots). However, if the bat followed the migration paths shown in Fig. 4, the journey could have been of up to 356 km. The trip was

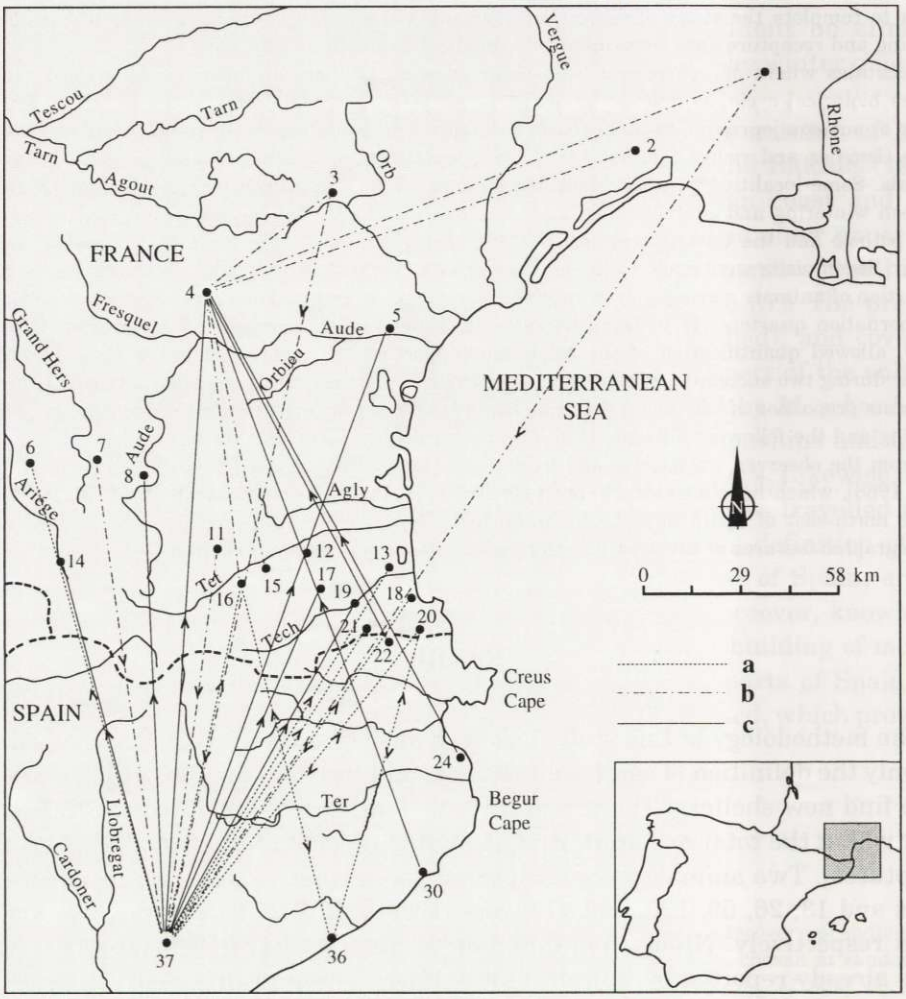

Fig. 1. Verified trajectories between *M. schreibersii* colonies of north-east Spain and south-east France. (a) Trajectories verified using recapture data from France of bats banded by Balcells (1962, 1964). (b) Trajectories verified using data from bats banded in France (Heymer 1964, Terrisse 1964, Salvayre 1980). (c) New trajectories verified in this study.

made by a female migrating in mid-spring from the Vall d'en Rubí cave (No. 48) to the Frare caves (No. 24). The journey took less than three and half months. The length of trajectories of *M. schreibersii* in north-east Spain and south-east France, between winter and summer shelters vary between 23 and 251 km, with an average of 120 km and a standard deviation of 71.17 km (n = 16). The distances have been calculated using the six migratory paths described in this paper.

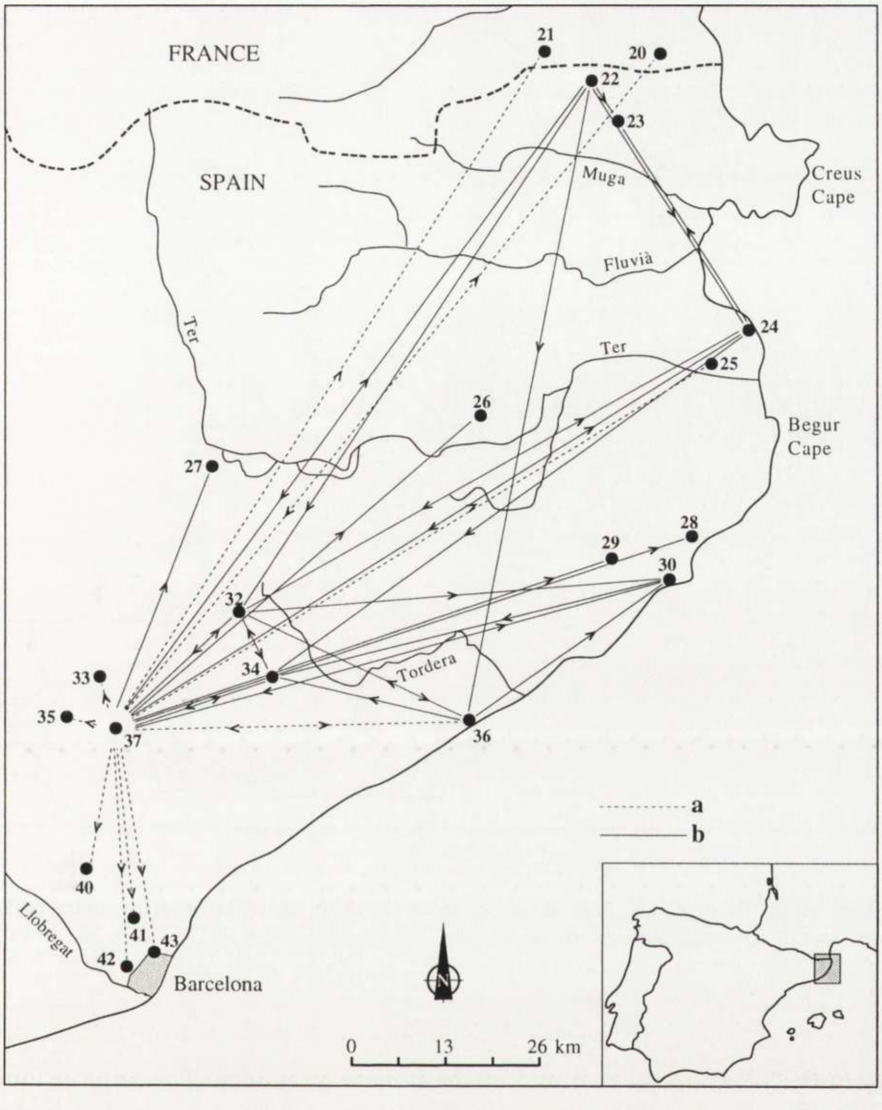

Fig. 2. Verified trajectories in the north-east of Spain and their relationships with the wintering cavity of the Daví pothole. (a) Trajectories verified by Balcells (1962, 1964). (b) New trajectories verified in this study.

The study has resulted in discovery of two new hibernation quarters, seven nursing colonies and sixteen equinoctial roosts (Table 1). Seven of the eight known breeding colonies in north-east Spain are located near dams (less than 500 m), marshes or the coast, locations where there are probably more trophic resources

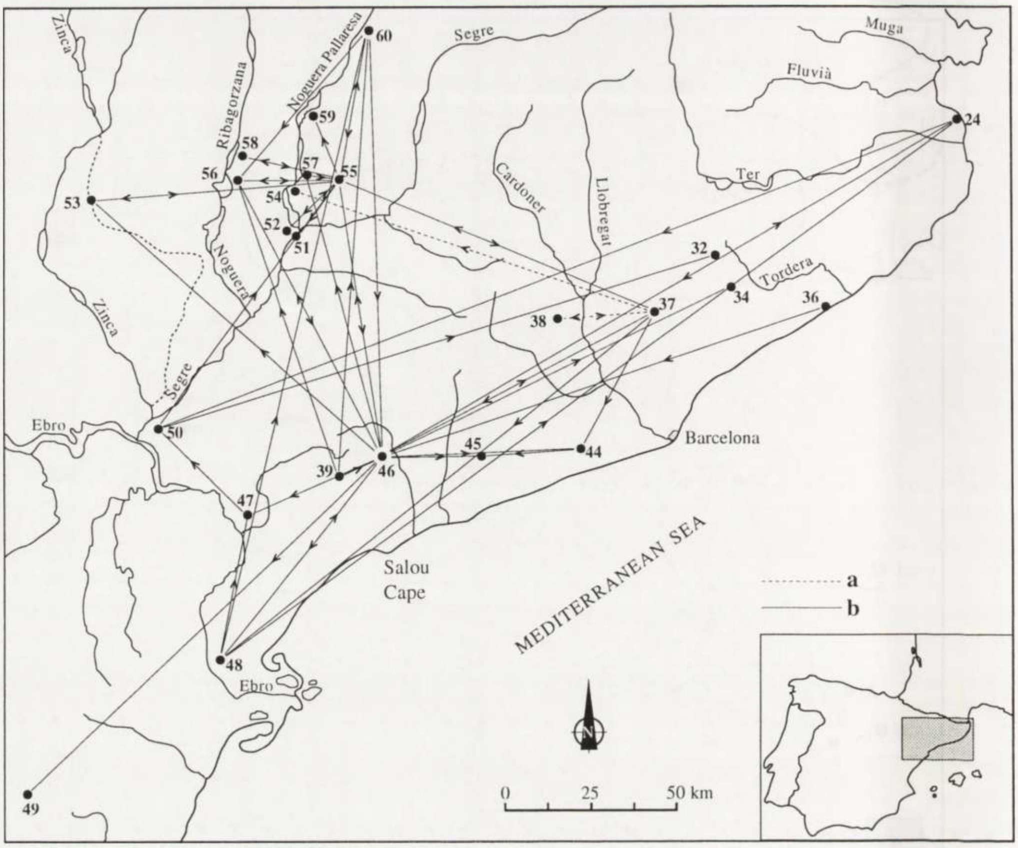

Fig. 3. Verified trajectories of *M. schreibersii* between the three Spanish wintering quarters (Nos. 37, 46 and 55) and movements related to the colonies of Querant Gran d'en Paús (No. 55) and the Puig d'en Març pothole (No. 46). (a) Trajectories verified by Balcells (1962, 1964). (b) New trajectories verified in this study.

to satisfy the high energy demand of the breeding females. The longest longevity recorded here is almost 10 years, but other authors have found higher longevities in longer studies (Gaisler and Hanák 1969, Aellen 1983). The bats use one or more equinoctial roosts in their travel from winter to summer caves. Some breeding caves may also serve as equinoctial roosts for a part of the migrating population from a winter cave, for instance Can Palomeres mines (No. 36). Individuals from a winter quarter are distributed amongst various summer roosts. Breeding colonies may include females from different winter refuges. The coastal breeding sites of the Rates-Penades cave (No. 30) and the Frare cave (No. 24), for instance, include bats from the winter caves of the Daví pothole and the Cabrespine cave (No. 4).

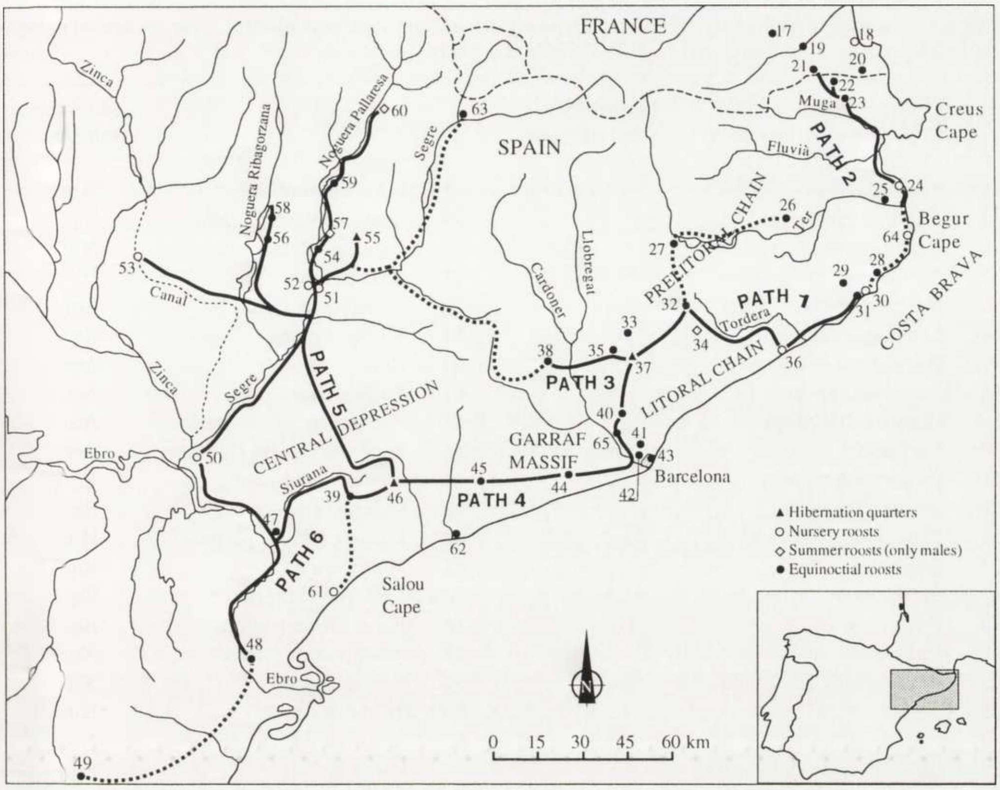

Fig. 4. Probable migratory paths of *M. schreibersii* in the north-east of Spain. Heavy lines show most likely nigratory paths. Dotted lines mean unconfirmed paths.

Of the 98 bats banded in the Frare cave, 21 were caught in Path 1, and 3 in Path 2 (Fig. 4).

Population exchanges between different hibernation quarters, within a year or in consecutive years, are shown in Table 2. Sixty one trajectories were recorded between the three Spanish wintering quarters, 40 of these being movements between the Puig d'en Març pothole and Querant Gran d'en Paús, some 100 km apart This amounts to 82% of all the trajectories recorded among the three hibernation quarters (Table 2). The minimum percentage of bats sheltering in the Daví pothole for two consecutive winters is 36.3% (from 226 bats banded along the 1985–1986 winter, 82 were recovered on the following year), while for the Querant Gran d'en Paús it is 27.5% (from 233 bats banded along the 1985–1986 winter, 64 were recovered on the following year – see Table 2).

Table 1. Locations. Migratory functions: Hib. – hibernation, Acc. – acidental, Nur. – nursery, Eq. – equinoctial, S.m. – summer males. * The newly discovered locations.

No.	Locations	Migratory function	No.	Locations	Migratory function
1	Feés cave		34	Can Nadal mine*	S.m.
2	Sambuc cave		35	Castellsapera pothole	Eq.
3	Bézelle cave		36	Can Palomeres mines	Nur.
4	Cabrespine cave	Hib.	37	Daví pothole	Hib.
5	Narbonne	Acc.	38	Pouetons pothole	Eq.
6	Les Morts cave		39	Rufino cave*	Eq.
7	Herm cave		40	Rubí	Acc.
8	Pierre Lys cave		41	Vallvidrera	Acc.
9	Château de Salses		42	Fontsanta	Acc.
10	Perpinyà	Acc.	43	Sant Gervasi de Cassoles	Acc.
11	Inquentades caves		44	Esquerrà pothole*	Eq.
12	Montou I cave		45	Vallmajor cave	Eq.
13	Elne	Acc.	46	Puig d'en Març pothole*	Hib.
14	Ospitalet pothole		47	Molar mines*	Eq.
15	Sirach cave		48	Vall d'en Rubí cave*	Eq.
16	Fullà cave	Hib.	49	Forat de Cantallops*	Eq.
17	Calmeilles cave		50	Mequinença mines*	Nur.
18	Château des Templiers	Nur.	51	Escaleta cave*	Nur.
19	Cêret	Acc.	52	Tabac cave*	Nur.
20	Pouade cave	Eq.	53	Almunia de San Juan*	Nur.
21	Château de la Bellegarde	Eq.	54	Forat de l'Or	Eq.
22	Roc Colom mine*	Eq.	55	Querant Gran d'en Paús*	Hib.
23	Capmany bunkers*	Eq.	56	Cova Negra de Corçâ	Eq.
24	Frare caves*	Nur.	57	Muricecs cave	S.m.
25	Bellcaire d'Empordà	Acc.	58	Cova Colomera*	Eq.
26	Bora Tuna cave*	Eq.	59	Gourp cave*	Eq.
27	Carnús cave*	Eq.	60	Saverneda cave	S.m.
28	Platja d'Aro	Acc.	61	Llop de Mar cave*	Nur.
29	Santa Cristina d'Aro	Acc.	62	Altafulla bunker*	Eq.
30	Rates-Penades cave	Nur.	63	Carradan cave	Eq.
31	Sant Féliu de Guíxols	Acc.	64	Begur cave*	Nur.
32	Castanya mines*	Eq.	65	Molins de Rei mines*	Eq.
33	Cueva Simanya	Eq.			

From the 233 bats banded in the Daví pothole during the winter of 1985, 76 were recaptured in the Castanya mines in spring of 1986, thus giving a recapture rate of 32.6%. The minimum percentage of *M. schreibersii* using the equinoctial refuge of Castanya mines during two consecutive springs was 40%, 48 of the 120 bats banded in 1985 being recaptured in 1986. Fidelity to the roost between the spring and the following autumn is much lower: of the 119 bats banded during spring of 1986 only five (4.2%) were recaptured during the autumn of that year.

Table 2. Population exchanges between different hibernation quarters within a year or in consecutive years. n – No. of bandings.

		From					
	Season	Querant Gran d'en Paús		Puig d'en Març pothole		Daví pothole	
	(Winter)	Winter 1985–86 n = 233	Winter 1986–87 n = 87	Winter 1985–86 n = 543	Winter 1986–87 n = 17	Winter 1984–85 n = 226	Winter 1985–86 n = 233
To Q. G. Paús	1985–86	0	–	8	–	1	1
	1986–87	64	0	21	0	0	2
P. Març	1985–86	0	–	0	–	1	0
	1986–87	1	0	16	0	0	0
	1987–88	11	9	52	3	0	0
Daví	1985–86	0	–	4	–	82	0
	1986–87	1	0	1	0	1	19

Table 3. Representative movements for the interpretation of *Miniopterus schreibersii* migrations in the north-east of Spain.

Sex	Location and date of ranging	Location and date of recaptures			
		1st	2nd	3rd	4th
M	Daví 15 Dec 1984	Castanya 31 Mar 1986	Can Nadal 10 Aug 1986	Castanya 26 Oct 1986	
F	Daví 15 Dec 1984	Castanya 4 May 1986	Can Palomeres 22 Jun 1986		
F	Castanya 23 Mar 1985	Rates-Penades 8 Jul 1985	Daví 2 Mar 1986	Castanya 4 May 1986	
M	Castanya 13 Apr 1985	Daví 16 Feb 1986	Castanya 23 Mar 1986	Frare 26 Jul 1986	Daví 23 Sep 1986
F	Can Palomeres 16 Jun 1985	Rates-Penades 22 Jul 1985	Daví 16 Feb 1986	Castanya 15 Mar 1986	Rates-Penades 2 Jul 1986
F	Daví 2 Mar 1986	Castanya 15 Mar 1986	Rates-Penades 2 Jul 1986	Can Nadal 10 Aug 1986	
F	Frare 26 Jul 1986	Can Nadal 9 Nov 1986	Castanya 16 Nov 1986	Daví 23 Nov 1986	

Table 3 shows some representative movements which are useful for interpretation of the migrations of the Daví pothole population towards north-east. Possible migratory paths used by *M. schreibersii* are shown in Fig. 4.

Discussion

Migratory movements of *M. schreibersii* are not so long as those of other bat species. For instance, movements over 1000 km long have been recorded for *Nyctalus noctula* (Schreber, 1774), *Myotis mystacinus* (Kuhl, 1819) and *Pipistrellus nathusii* (Keyserling and Blasius, 1839) in Europe, and *Tadarida brasiliensis mexicana* (De Saussure, 1860) in America (Sluiter and Heerdt 1966, Panyutin 1968, Gaisler and Hanák 1969, Strelkov 1969, Heise and Schmidt 1979, Aellen 1983, Brosset 1990, Peterson 1990), but the longest distance recorded in this study was only 270 km (356 km if deviations from a straight line are accounted for).

Our results (53% recaptures and 95 different trajectories) show that there is no need to band large numbers of bats to obtain good recapture data and thus information about the migrations of *M. schreibersii*. What is needed instead, is a detailed study of the area to be surveyed, a good banding plan and a thorough monitoring of the colonies.

Population exchange between winter quarters

Although many of the bat population of a winter quarter of *M. schreibersii* returns year after year to the same wintering site, there are intra- and interannual exchanges between wintering colonies (Table 2). Sometimes the change of winter quarter is a consequence of environmental perturbations, occasionally dramatic. For instance, in the summer of 1986 a fire burnt the surroundings of the Puig d'en Març pothole. Local people cleared the area of half-burnt firewood and threw all the waste material into the pothole. The entrance of it was partly blocked, and consequently during the following winter only 350 bats were counted there, instead of the 4000 found in that site the previous year. In contrast, the number of bats wintering that year in the Querant Gran d'en Paús (at 100 km distance) increased sharply, adding about 3000 animals to the previous years census. It is clear from recapture data that this increase, was in large part due to the arrival of animals from Puig d'en Març. The number of individuals in the Daví pothole colony did not change that winter although the distance to the Puig d'en Març pothole was similar. But topographic features of the intervening terrain are quite different, the area between the Puig d'en Març pothole and the Daví pothole being much more rugged than the area between Querant Gran d'en Paús and the Puig d'en Març pothole. Therefore, it seems to be the nature of the terrain to be crossed which determines the choice of a path in the roost switch.

Migratory paths

The high number of verified trajectories and the high recapture rate allow the definition of migratory paths with some confidence. These paths are described in the following sections.

Path 1. An important part of the colony wintering in the Daví pothole migrates towards the Castanya mines, in the Montseny massif (Fig. 4). From there the bats move towards the coastal refuge of Can Palomeres mines (No. 36). The journey to the coast follows the upper part of the Tordera valley, maybe with a stop at the Can Nadal mine (No. 34; many males stay at this site during the summer). The bats probably also use the lower part of the Tordera valley to reach the coast (Fig. 4). In Can Palomeres a breeding group is formed by late spring, but other individuals continue to move northwards along the coast, and contribute to the breeding colonies of Rates-Penades cave (No. 30) and Frare caves (No. 24). This last part of the path, between the two latter caves, has been marked in Fig. 4 by a dotted line, because exchanges between the caves have not been verified. If, as believed, the Rates-Penades cave serves as a temporary stop, the time spent in it by migrating bats would be very short, and hence verification is difficult. The existence of this path, however, seems probable, given the distribution of *M. schreibersii* refuges in the Costa Brava and the recapture in the Frare cave of bats coming from Daví or Castanya. At the end of summer and during the autumn the bats return to the Daví pothole by the same path (Table 3). Path 1 is the best known migratory path for the species in Spain.

Path 2. A part of the population wintering in the French Cabrespine cave migrates to the Spanish Costa Brava to breed. The Roc Colom mine (No. 22) and the Capmany bunkers (No. 23) are used as intermediate refuges by the migrating populations from the French cave to the Spanish coast and back (Figs 1, 2, 4). Given the proximity of the Roc Colom mine to the frontier pass of Banyuls it is very probable that one of the France-Spain migratory paths crosses through this pass. Another path crosses through the Perthus pass, but this may be of minor importance because of the high human presence in this touristic area. As we have banded only Spanish colonies, the migratory paths in the south-east of France are not well known, but it is probable that bats travel along the coast and follow the Aude valley until reaching the Cabrespine cave (Fig. 1). This hypothesis is supported by the distribution of the refuges of *M. schreibersii*, by the migratory pattern in the north-east of Spain and by seasonal movements previously verified in the south-east of France (Balcells 1962, 1964, Heymer 1964, Tarrisse 1964, Salvayre 1980). While some years ago the spring migration between the two countries was thought to be from south to north (Balcells 1962, 1964), new data support the contrary direction, from north to south. As reported in the studies of Balcells (1962, 1964) some bats from the Daví pothole migrate to the French breeding site of Château des Templiers (No. 18, Figs 1, 4). However, we have been unable to verify if this migration still takes place, because we were not allowed to visit the castle.

Path 3. Not all the bats from the Daví pothole migrate in a north-easterly direction in the spring, towards the Castanya mines. A part of the population goes to the equinoctial roosts of Pouetons pothole (No. 38, Fig. 4). Neither the final destination nor the remaining migratory path of these bats are known, but given the configuration of valleys near Pouetons it is probable that the bats are distributed northwards along the Llobregat and Cardoner valleys. Moreover

Pouetons lies on the migration path of the bats which change hibernation site and move between the Daví pothole and the Querant Gran d'en Paús.

Path 4. A small part of the Daví pothole colony also migrates in late winter to the lower reaches of the Llobregat river. Before arriving at the sea these bats change direction and move to the Garraf massif to the west, where they eventually arrive at the Esquerrà pothole (No. 44, Figs 3, 4). This cave is a shelter for large spring and autumn colonies, with a seasonal behaviour similar to that of the Castanya mines colony. We do not know at present the location of sites of females coming from Esquerrà but, the sea being so close, it is probable that they use small coastal cavities south of Barcelona (Fig. 4). Exchanges between the Esquerrà pothole and the Puig d'en Març pothole have been verified. It seems that these bats take Path 4 to change hibernation quarter (Figs 3 and 4).

Path 5. Some of the bats from the Puig d'en Mar pothole migrate during spring to the pre-Pyrenean valleys located to the north of the hibernation cave. During summer, most of these bats shelter in small cavities close to reservoirs (Figs 3, 4). The spring and summer distribution of the bats of the Puig d'en Mar pothole coincides in part with the distribution of bats from Querant Gran d'en Paús, also linked to pre-Pyrenean valleys. Some females, nevertheless, follow the Central Depression to the Ebro valley, arriving at the Mequinenza mines (No. 50, Figs 3, 4) to breed.

Path 6. Not all the bats from the Puig d'en Març pothole move to the pre-Pyrenean valleys. A part of the population migrates to the Siurana river arriving finally in the Ebro valley (Figs 3 and 4). Once there the bats can go up river to the breeding roost of the Mequinenza mines or down river to the cave of Vall d'en Rubí (No. 48). The individual recaptured at Forat de Cantallops (No. 49, Figs 3 and 4) and banded in Puig d'en Març, probably moved by Path 6 to the Ebro and then along the coast to the Forat de Cantallops. A part of the colony of Puig d'en Març may also supply some individuals to the coastal breeding refuges such as the Llop de Mar cave (No. 61, Fig. 4). That cave is, however, difficult to access, and the connection has not been proved.

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