Resting ecology and behaviour of Egyptian mongooses (*Herpestes ichneumon*) in southwestern Spain

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(With 3 figures in the text)

Nocturnal and siesta resting ecology and behaviour of 24 Egyptian mongooses were studied. Mongooses mainly used underground dens (rabbit warrens and badger setts) and thickets in both periods. Tree hollows were occasionally used. Twenty-one individuals used 338 different nocturnal resting sites on 672 occasions. Mean number of resting sites per individual was 16.1, though resting sites used by each individual increased when sample size did. Mean re-use rate was 1.99 nights/site. The majority of nocturnal resting sites were only used once, and very few more than five times. Nocturnal resting sites used two or more times were significantly more often inside than outside home range core areas, whereas resting sites used once were significantly more often outside than inside. Mean distance between consecutive nocturnal resting sites was different among classes of individuals, and annual variations were detected. Eighteen mongooses used 133 different resting sites on 171 occasions during siesta periods. Mean number of different sites used and re-use rate were 7.4 and 1.29, respectively. Types of resting sites used during siesta periods changed throughout the year with underground dens predominating in summer. Re-use rates remained constant for the whole year. The impacts of social structure and summer high temperatures on mongoose resting behaviour are discussed.

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Introduction

Detailed studies on carnivore resting sites have been carried out in recent years (e.g. Bock, 1988; Buskirk *et al.*, 1989; Hellgren & Vaughan, 1989; Weber, 1989; Skinner, Skinner & Harris, 1991). They have proved useful to the understanding of distribution patterns and to the planning of conservation measures for carnivores. Herein, we studied several aspects of resting ecology and

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behaviour of Egyptian mongooses, *Herpestes ichneumon* L., in Doñana National Park, southwestern Spain. Additionally, the importance of social structure and of summer high temperatures on Egyptian mongoose resting behaviour were considered.

Mongooses are diurnal in Doñana, with a continuous nocturnal resting period (from one hour before sunset to two hours after sunrise on average) and one or several short resting periods or siestas during the rest of the day (Palomares & Delibes, 1992a). Characteristics and use of resting sites during nocturnal and siesta periods were investigated separately.

Previous information about the resting ecology and behaviour of Egyptian mongooses is limited to comments of Valverde (1967) and Ben-Yaacov & Yom-Tov (1983), who stated that mongooses use rabbit warrens and dens amongst vegetation as resting sites. Also, Palomares & Delibes (1990) reported on winter resting sites of three radio-tracked female Egyptian mongooses.

Study area and methods

The study took place at Coto del Rey (Northern Doñana National Park, southwestern Spain; 37° 9' N, 6° 26' W). Coto del Rey is characterized by forested lands of pines, *Pinus pinea*, and eucalyptus, *Eucalyptus* sp., with undergrowth mainly of *Halimium halimifolium*, some small natural streams, where mixtures of *Fraxinus* sp. and *Populus alba*, *Pistacia lentiscus* and *Rubus* sp. predominate, and associations of exclusively *P. lentiscus* at places with higher ground water level.

The climate is Mediterranean subhumid, with mild, wet winters and hot, dry summers. Annual rainfall generally ranges between 500 and 600 mm. The coldest and hottest months during the study were January 1989 and July 1988, with mean temperatures of 9.3 °C and 26.0 °C, respectively. The study area is flat, with sandy ground. More detail about the study area can be found in Rivas-Martínez *et al.* (1980).

Twenty-four mongooses (12 adult females, 7 adult males, 2 young males, and 3 young females) were captured with box-traps between September 1987 and September 1989, and equipped with radio-collars containing tip switches (Wildlife Materials, Inc., Carbondale, Illinois). Age was estimated by body mass and dentition (Palomares & Delibes, 1992b). Except for 5 individuals which were tracked for less than 1 week, the mongooses were tracked for an average of 87 days (range = 24–251).

Each individual was located once during daylight, and again during the night, dusk, or dawn, using the homing technique (Mech, 1983) without disturbing them (Palomares, 1990). A nocturnal resting site corresponded to a location of a mongoose inactive between 16:30 and 10:30 solar hour. All locations of inactive individuals between 10:30 and 16:30 h were considered as siesta sites. The exact position of animals ($n = 673$ and 171 for nocturnal and siesta periods, respectively) and the characteristics of resting sites ($n = 427$ and 63 for nocturnal and siesta periods, respectively) were noted. Inactive animals were distinguished from active animals by tip switches of the radio-collars (see, e.g. Garshelis *et al.* (1982) for a description of tip switches).

Re-use rates of resting sites (total number of resting periods divided by the number of different resting sites) for both nocturnal and siesta periods were estimated. Additionally, linear distance between resting sites used consecutively and spatial location (inside or outside home range core areas) were measured for nocturnal resting sites. Mongoose individual home ranges and core areas were estimated by minimum convex polygon (Macdonald, Ball & Hough, 1980) and 50% harmonic mean (Dixon & Chapman, 1980) methods, respectively, when at least 20 locations were available.

Data were analysed by classes of individual (adult females, adult males and young) and seasons (2-month periods). To test significant differences, we used chi-squared (χ^2) analysis of contingency tables when data were frequencies, and ANOVA for distances between consecutive resting sites. The 'Exact Test' of Wells & King (1980), using a hypergeometric distribution, was used when frequencies prevented the use of χ^2 analysis. Distances were transformed as $\log(1 + x)$ for the analysis. A standard Z was used to test differences between proportions of use of each type of resting site (Zar, 1984).

Results

Nocturnal resting

Characteristics of resting sites and frequency of use

Mongoosees were detected in three general types of resting site, which, by decreasing frequency of use, were: underground dens, thickets and tree hollows (Table I). The relative importance of each type of resting site was the same for each class of individual (Table I). Underground dens were significantly more often used than thickets and tree hollows (all $Z_s > 7.0$, all $P_s < 0.0001$), and thickets were significantly more used than tree hollows (all $Z_s > 4.0$, $P_s < 0.0001$) for all males, females and young.

Underground dens ($n=305$) were never excavated by mongooses. They used rabbit warrens (59.7%), badger setts (39.0%), and a disused irrigation ditch (1.3%). The badger sett most often used was simultaneously inhabited by badgers, *Meles meles*, with apparently no interference (Palomares, 1991). Thickets ($n=115$) comprised brambles, *Rubus* sp. (45.2%), *P. lentiscus* (33.0%) and mixed thickets of different shrubs and climbing plants (21.7%). Mongooses entered tree hollows ($n=7$) from tunnels between roots on four occasions, or by climbing 2 m on three occasions.

The three main types of resting sites were similarly used throughout the year (Table II).

Number of resting sites per individual, re-use rates, and spatial location

Twenty-one individuals used 338 different nocturnal resting sites on 672 occasions (Table III). The mean number of different resting sites used per individual was 16.1 (S.D. = 12.2, $n=21$, range = 2–53). There was a significant positive correlation between number of sampled nights and number of used resting sites ($r^2=0.71$, $P<0.0001$; $y=4.64+0.358x$), indicating there was no stabilization in the number of resting sites used by mongooses, at least in this study.

Mean number of nights per resting site or re-use rate was 1.99 (Table III). Differences in re-use rates between classes of individuals were not significant ($\chi^2=5.494$, $d.f.=2$, $P=0.0641$; Table III).

By analysing in greater detail the patterns of use of nocturnal resting sites by the eight most

TABLE I
Frequency of use of each resting site type during nocturnal and siesta resting in adult female, adult male and young Egyptian mongooses in Doñana National Park. Percentages are given in parentheses

Type of resting site	Females	Males	Young	Overall
Nocturnal				
Underground dens	173 (72.7)	77 (64.2)	55 (80.9)	305 (71.4)
Thickets	63 (26.5)	38 (31.7)	13 (19.1)	114 (26.9)
Tree hollows	2 (0.8)	5 (4.2)	0 (0.0)	7 (1.6)
Siesta				
Underground dens	26 (60.5)	8 (53.3)	1 (20.0)	35 (55.6)
Thickets	17 (39.5)	7 (46.7)	4 (80.0)	28 (44.4)
Tree hollows	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)

TABLE II

Bimonthly use of nocturnal and siesta resting sites (U. dens = underground dens, Thic. = thickets, and Tr. hol. = tree hollows) of Egyptian mongooses in Doñana National Park from September 1987 to September 1989. Sample sizes (n) for each two months are given

	Nocturnal				Siesta			
	n	U. dens	Thic.	Tr.hol.	n	U. dens	Thic.	Tr.hol.
Jan.-Feb.	95	76.8	20.0	3.2	19	42.1	57.9	0.0
Mar.-Apr.	131	67.2	31.3	1.5	16	50.0	50.0	0.0
May-Jun.	46	73.9	26.1	0.0	5	80.0	20.0	0.0
Jul.-Aug.	25	72.0	28.0	0.0	2	100.0	0.0	0.0
Sep.-Oct.	49	61.2	36.7	2.1	10	50.0	50.0	0.0
Nov.-Dec.	80	77.5	21.3	1.2	11	72.7	27.3	0.0

sampled ($n > 25$ nights) individuals, it was observed that most resting sites were used only once, and very few were used more than five times (Fig. 1). In spite of using many different resting sites, the majority of individuals spent $> 50\%$ of nights in only a few sites: H002 15 sites, H007 one site, H106 seven sites, H110 and H108 three sites, H116 four sites, H001 17 sites, and H112 two sites.

Re-use rates were significantly different throughout the year ($\chi^2 = 11.22$, $d.f. = 5$, $P = 0.0471$), and were higher in the first six-month period (Fig. 2). The maximum number of consecutive nights spent in the same den for any individual was 14 for a female (she was probably breeding), during June 1988.

The same resting sites were frequently used by different individuals. This occurred simultaneously with related individuals (male-female pair bond, or parents-offspring), and with both related and apparently unrelated individuals different days or years. One resting site, a badger sett, was utilized by nine of the ten individuals which included it within their home ranges (see Palomares, 1991, for more detail).

TABLE III

Number of locations, number of different resting sites used and re-use rates (number of nights or times per site) of nocturnal and siesta periods for adult female, adult male and young Egyptian mongooses in Doñana National Park. Number of individuals sampled (n) of each sex are given

	Females	Males	Young	Overall
Night				
n	11	5	5	21
No. of location	373	174	125	672
Resting sites	165	91	82	338
Re-use rates	2.26	1.91	1.52	1.99
Siesta				
n	10	3	5	18
No. of location	97	51	23	171
Resting sites	75	42	16	133
Re-use rates	1.29	1.21	1.44	1.29

FIG. 1. Use of nocturnal resting sites for eight Egyptian mongooses sampled more than 25 times. Ordinates show the number of resting sites where each mongoose was located one or more times.

Spatial location of resting sites within home ranges was different for those used only once versus those used two or more times. Resting sites used once were located on 94 occasions (37.8%) inside core areas, and on 155 occasions (62.2%) outside them ($\chi^2 = 15.88$, $d.f. = 1$, $P < 0.0001$). Those used two or more times were located on 70 occasions (78.7%) inside core areas, and only on 19 occasions (21.3%) outside them ($\chi^2 = 43.51$, $d.f. = 1$, $P < 0.0001$).

Distance between consecutively used resting sites

Mean distance between consecutively used nocturnal resting sites was 620 m (S.D. = 650, range = 0–2758, $n = 373$). Significant differences between classes of individuals were detected

FIG. 2. Bimonthly re-use rates (night or times divided by the total number of different resting sites) of nocturnal resting and siesta sites for Egyptian mongooses. Because no significant differences were detected among classes of individuals, data from females, males and young were pooled.

($F_{2,370} = 20.24$, $P < 0.0001$). Mean distance for females was 461 m (S.D. = 526, $n = 202$, range = 0–2148), for males 920 m (S.D. = 802, $n = 114$, range = 0–2758) and for young 584 m (S.D. = 485, range = 0–1779, $n = 57$). Differences between males–females and males–young were significant ($P < 0.05$, Tukey test).

Females kept a relatively constant distance (500–600 m) between resting sites, except during May–June and July–August, when the mean considerably decreased (Fig. 3). In males, distance between consecutive resting sites was minimal in March–April (758 m) and November–December (765 m), while from May to October it averaged > 1100 m (Fig. 3). Young had similar values to females (Fig. 3).

Siestas

Characteristics of resting sites and frequency of use

Resting site characteristics were similar to those for nocturnal resting, though only underground dens and thickets were detected (Table I). Some sites were used both for nocturnal and siesta resting. Each class of individuals used siesta resting sites in a similar way ($\chi^2 = 3.01$, $P = 0.2090$; Table I). Overall frequency of use of resting sites was different with regard to nocturnal resting ($\chi^2 = 8.80$, $P = 0.0144$; Table I). Rabbit warrens (88.6% of 35 sites) and brambles (46.4% of 28 sites) were the most commonly used underground dens and thickets, respectively. Badger setts (11.4%), *P. lentiscus* (25.0%) and mixed thickets (28.6%) were also used.

Seasonally, most resting sites were underground dens in May–June, July–August and November–December; thickets in January–February, and equal use of both in March–April and September–October (Table II).

FIG. 3. Bimonthly variations of distance between nocturnal consecutive resting sites for adult female, adult males and young Egyptian mongooses. Sample sizes, beginning from January to February, were: 21, 61, 47, 14, 34 and 25 for adult females; 37, 49, 12, 4, 3 and 9 for adult males; and 8, 0, 0, 2, 20 and 27 for young individuals. Dashed line (---) indicates that no data were available.

Number of resting sites and re-use rates

Eighteen individuals used 133 different resting sites on 171 occasions. Mean number of different resting sites used per individual was 7.4 (S.D. = 6.7, range = 2–28, $n = 18$). Again, a significant positive correlation between sample size and number of different resting sites used ($r^2 = 0.95$, $P < 0.0001$, $y = 0.058 + 0.772x$) was detected. Mean re-use rate was 1.29 (Table III). There was no significant difference among classes of individuals ($\chi^2 = 0.194$, $d.f. = 2$, $P = 0.9074$; Table III). Re-use rates for siesta and nocturnal resting sites were significantly different ($\chi^2 = 10.75$, $d.f. = 1$, $P = 0.0010$; Table III). Resting site re-use rates were similar throughout the year (Fig. 2).

Discussion

Nocturnal resting sites

Mongooses devote 75% of their daily time budget to resting (Palomares & Delibes, 1992a), so selection of resting sites that provide safety from predators (e.g. Iberian lynx, *Felis pardina* (Palomares & Delibes, 1992b)) and protection from weather is very important. Underground dens and thickets fulfil both requirements. Accordingly, the habitats where these two resting sites are frequent (small streams and associations of *P. lenticus*; Palomares, 1990) should be protected to guarantee the conservation of mongooses.

It has been shown that minimal nocturnal temperatures influence resting site selection by carnivores in cold environments (Spencer, 1987; Buskirk *et al.*, 1989; Weber, 1989). Nevertheless, mongooses of Doñana selected underground dens and dense vegetation for reasons other than nocturnal minimal temperatures, which rarely fall to 0 °C. For example, two mongooses bedded in the open with a minimal temperature of 3 °C in January, 12 km from the present study area

(Palomares & Delibes, 1990). Similarly, selection of resting site types did not vary seasonally (Table II).

Frequency of use of underground dens may be underestimated because dense thickets sometimes prevented determination of whether resting sites were above or below ground. In two instances, radio-collars removed by mongooses were found on above-ground beds made within thickets.

Some interesting conclusions about the use of resting sites can be obtained from the most sampled individuals. Few resting sites were regularly used, and sporadic resting sites on isolated nights were often used. The use of sporadic resting sites may be to reduce the cost of travelling from foraging areas to a more frequently used resting site. Intensive radio-tracking during mongoose activity periods allowed us to document several occasions when mongooses foraged far from their core areas and then selected resting sites near their foraging areas. This hypothesis is supported by the finding that spatial locations of sporadic resting sites were more frequently found out of core areas. On the other hand, a high turnover of resting sites, even for those most often used, which were commonly situated very close to one another (78.7% inside core areas), suggests that it could be a defensive strategy against parasites, such as lice (Pérez-Jiménez *et al.*, 1990). Dwarf, *Helogale parvula*, and banded, *Mungos mungo*, mongooses also seem frequently to use sporadic resting sites on isolated nights (Hiscocks & Perrin, 1991).

The annual pattern of re-use rates were different from the annual pattern of numbers of observed mongooses foraging together (Palomares & Delibes, 1993). When re-use rates were higher (March, April), almost only solitary mongooses were sighted. On the other hand, when re-use rates were lower (September, October), foraging groups of two or more individuals were often sighted. The first period coincided with mating, pregnancy and birth of mongooses (Palomares & Delibes, 1992b), and the second with both closer relationships between mother and cubs (Palomares & Delibes, 1993) and relative scarcity of rabbits (*Oryctolagus cuniculus*), the staple prey of mongooses in the study area (Palomares & Delibes, 1991; Beltrán, 1991). Fidelity to some resting sites could facilitate the meeting of males and females after foraging activities, thereby favouring mating. On the other hand, larger foraging groups (females and cubs, sometimes the male as well) might need to forage over longer distances owing to energy requirements, making it difficult to re-use the same resting site. In fact, a positive correlation exists between daily distance travelled and linear distance between consecutive resting sites of mongooses (Beltrán *et al.*, 1989).

The relationship between annual pattern of re-use rates and foraging group size suggests the importance of social structure in the resting behaviour of Egyptian mongooses. Further evidence for this relationship was that different individuals used the same resting sites. Social organization of mongooses is characterized by frequent contact between related individuals (Palomares & Delibes, 1993). Therefore, the use of the same resting sites can facilitate interchange of information and meeting of family groups. In fact, although no significant differences were detected, mongooses were located more often together during nocturnal resting than during foraging (Palomares, 1990).

Unrelated mongooses used the same resting sites on different dates. A first interpretation of this behaviour suggests that suitable resting sites were scarce in the study area. This could be the case for a particular resting site such as the heavily used badger sett, where mongooses could find an optimal microclimate (see Bock, 1988). Nevertheless, underground dens and thickets are very abundant in the study area (Palomares & Delibes, pers. obs.; Rivas-Martínez *et al.*, 1980). Other factors may be involved. Mongooses place their faeces mainly at latrines around the most commonly used resting sites (Palomares, 1990), thus unrelated individuals might, from resting

sites, obtain information on social status, reproductive state, and maybe identity and physical condition of competitors (Gorman & Trowbridge, 1989).

Distance between consecutive resting sites throughout the year was different between males, and females and young (Fig. 3). From May to August, the main birth season (Palomares & Delibes, 1992b), females rested in the same sites or moved short distances, whereas males increased the distance between consecutive resting sites. Relationships between males and females were looser in this period (Palomares & Delibes, 1993). Young presented similar values to females, as expected because they frequently accompanied their mothers. Again, different social roles reflected different resting behaviour in each sex.

Siestas and differences with nocturnal resting

Resting sites selected for siestas were similar to those selected for nocturnal resting, but the pattern of use was different. Re-use rates were also different for both periods, and furthermore, siesta re-use rates changed very little throughout the year (Fig. 2). Since, on average, mongooses devote only one hour daily to siestas as opposed to 17 hours for nocturnal resting (Palomares, 1990; Palomares & Delibes, 1992a), results were predictable.

Also, important bimonthly variations in frequency of use of each type of siesta resting site (underground dens and thickets) were detected, but not for nocturnal resting sites. During the summer, mongooses considerably increased the use of underground dens during siestas, maybe as a behavioural thermoregulatory strategy, since maximum temperatures in summer can exceed 40 °C in our study area. Inside underground dens, daily surface temperature fluctuations disappear (Reichman & Smith, 1990) and this may help mongooses to avoid diurnal heat (see, e.g. Golightly & Ohmart, 1983; Kuntzsch & Nel, 1990). However, with the lowering of temperatures at night, a strong selection for resting sites may not be necessary.

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REFERENCES

- Beltrán, J. F. (1991). Temporal abundance pattern of the wild rabbit in Doñana, SW Spain. *Mammalia* **55**: 591–599.
- Beltrán, J. F., Aldama, J., Palomares, F., Servin, J. & Delibes, M. (1989). Optimization of radio-tracking effort to estimate daily distance travelled by wild carnivores. *Int. Theriol. Congr.* No. 5.
- Ben-Yaacov, R. & Yom-Tov, Y. (1983). On the biology of the Egyptian Mongoose, *Herpestes ichneumon*, in Israel. *Z. Säugetierk.* **48**: 34–45.
- Bock, V. W. F. (1988). Untersuchungen zur Lage und zum Mikroklima von Dachsbauen (*Meles meles*). *Z. Jagdwiss.* **34**: 141–152.
- Buskirk, S. W., Forrest, S. C., Raphael, M. G. & Harlow, H. J. (1989). Winter resting site ecology of marten in the central Rocky Mountains. *J. Wildl. Mgmt* **53**: 191–196.
- Dixon, K. D. & Chapman, J. A. (1980). Harmonic mean measure of animal activity areas. *Ecology* **61**: 1040–1044.
- Garshelis, D. L., Quigley, H. B., Villarrubia, C. R. & Pelton, M. R. (1982). Assessment of telemetric motions sensors for studies of activity. *Can. J. Zool.* **60**: 1800–1805.
- Golightly, R. T., Jr & Ohmart, R. D. (1983). Metabolism and body temperature of two desert canids: coyotes and kit foxes. *J. Mammal.* **64**: 624–635.
- Gorman, M. L. & Trowbridge, B. J. (1989). The role of odour in the social lives of carnivores. In *Carnivore behaviour, ecology and evolution*: 47–88. Gittelman, J. L. (Ed.). London: Chapman & Hall.

- Hellgren, E. C. & Vaughan, M. R. (1989). Denning ecology of black bears in a southeastern wetland. *J. Wildl. Mgmt* **53**: 347–353.
- Hiscocks, K. & Perrin, M. R. (1991). Den selection and use by dwarf mongooses and banded mongooses in South Africa. *S. Afr. J. Wildl. Res.* **21**: 119–122.
- Kuntzsch, V. & Nel, J. A. J. (1990). Possible thermoregulation behaviour in *Giraffa camelopardalis*. *Z. Säugetierk.* **55**: 60–62.
- Macdonald, D. W., Ball, F. G. & Hough, N. G. (1980). The evaluation of home range size and configuration using radio tracking data. In *A handbook on biotelemetry and radio tracking*: 405–424. Amlaner, C. J. & Macdonald, D. W. (Eds). Oxford: Pergamon Press.
- Mech, L. D. (1983). *Handbook of animal radio-tracking*. Minneapolis: University of Minnesota Press.
- Palomares, F. (1990). *Ecología y organización social del meloncillo, Herpestes ichneumon, L., en el Parque Nacional de Doñana*. PhD thesis, University of Granada, Granada.
- Palomares, F. (1991). Use of active badger sett by Egyptian mongooses, *Herpestes ichneumon*, in southwest Spain. *Z. Säugetierk.* **56**: 119–120.
- Palomares, F. & Delibes, M. (1990). Habitat preference of large grey mongooses, *Herpestes ichneumon*, in Spain. *Acta theriol.* **35**: 1–6.
- Palomares, F. & Delibes, M. (1991). Dieta del meloncillo, *Herpestes ichneumon*, en Coto del Rey, Norte del Parque Nacional de Doñana. *Doñana Acta vert.* **18**: 187–194.
- Palomares, F. & Delibes, M. (1992a). Circadian activity patterns of free-ranging large gray mongooses, *Herpestes ichneumon*, in southwestern Spain. *J. Mammal.* **73**: 173–177.
- Palomares, F. & Delibes, M. (1992b). Some physical and population characteristics of Egyptian mongooses (*Herpestes ichneumon* L. 1758) in southwestern Spain. *Z. Säugetierk.* **57**: 94–99.
- Palomares, F. & Delibes, M. (1993). Social organization in Egyptian mongooses: group size, spatial behaviour, and interindividual contacts in adults. *Anim. Behav.* **45**.
- Pérez-Jiménez, J. M., Soler-Cruz, M. D., Benítez-Rodríguez, R., Ruiz-Martínez, I., Díaz-Lopez, M., Palomares-Fernández, F. & Delibes-de Castro, M. (1990). Phthiraptera from some wild carnivores in Spain. *Syst. Parasit.* **15**: 107–117.
- Reichman, O. J. & Smith, S. C. (1990). Burrows and burrowing behaviour by mammals. *Curr. Mammal.* **2**: 197–244.
- Rivas-Martínez, S., Costa, M., Castroviejo, S. & Valdes, E. (1980). Vegetación de Doñana (Huelva, España). *Lazaroa* **2**: 1–189.
- Skinner, C., Skinner, P. & Harris, S. (1991). An analysis of some of the factors affecting the current distribution of badger *Meles meles* setts in Essex. *Mamm. Rev.* **21**: 51–65.
- Spencer, W. D. (1987). Seasonal rest-site preferences of pine martens in the northern Sierra Nevada. *J. Wildl. Mgmt* **51**: 616–621.
- Valverde, J. A. (1967). Estructura de una comunidad Mediterránea de vertebrados terrestres. *Monogr. Estac. biol. Doñana* **1**: 1–219.
- Weber, D. (1989). The ecological significance of resting sites and the seasonal habitat change in polecats (*Mustela putorius*). *J. Zool., Lond.* **217**: 629–638.
- Wells, H. & King, J. L. (1980). A general 'Exact test' from $N \times M$ contingency tables. *Bull. Sth Calif. Acad. Sci.* **79**: 65–77.
- Zar, J. H. (1984). *Biostatistical analysis*. 2nd edn. New Jersey: Prentice-Hall Int. Inc.