Opportunistic feeding of the Egyptian mongoose, Herpertes ichneumon, (L.) in Southwestern Spain

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OPPORTUNISTIC FEEDING OF THE EGYPTIAN MONGOOSE, *HERPESTES ICHNEUMON,* (L.) IN SOUTHWESTERN SPAIN

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Predators are often classified as opportunistic (those which take prey according to their abundance in the field, e.g., Jaksic *et al.,* 1981 ; Mcckraken & Hansen, 1987) or selective (those which take the most profitable prey, e.g., Korpimäki, 1985 ; Steenhof & Kochert, 1988). Although it is possible to infer the feeding behaviour of a predator from its trophic spectrum (Emlen, 1968), it is necessary to have information on prey abundance to classify a predator as opportunistic or selective (Griffiths, 1975 ; Bozinovic & Medel, 1988 ; Jaksic, 1989). Although prey availability is the most appropriate measure to relate with consumption rates, it is very difficult to assess objectively, and therefore prey abundance appears to be the only feasible substitute (Jaksic, 1989 ; Doncaster *et al.,* 1990).

The Egyptian mongoose, *Herpestes ichneumon,* eats many prey species (Stuart, 1983 ; Delibes *et al.,* 1984 ; Palomares & Delibes, 1991a, 1991b), which, according to Emlen (1968), would indicate a typical generalist behaviour. However, no study has compared the rates of prey consumption with prey abundances in the field. In this paper, the diet of this species is analyzed in relation to seasonal and local variations in prey abundance in Doñana National Park. The diet was studied through faecal analysis (Reynolds & Aebischer, 1991) in three areas containing the same prey species but at different densities, and during the two main seasons (wet and dry). Consumption rates of the main prey were then compared with the available data on relative abundances on each area and season.

STUDY AREA

The study was carried out between November 1985 and July 1989 in 3 selected areas of Doñana National Park (37° 10′ N 6° 23′ W) with different characteristics of landscape and vegetation : Lagunas, Vera and Coto del Rey. This Park is situated on the West bank of the Guadalquivir River mouth (south-western Spain). It is a flat area where three main biotopes can be distinguished : the marsh, the dunes and the matorral (Fig. 1). Detailed information on the characteristics of these biotopes can be found in Rogers & Myers

(1980). The climate is Mediterranean sub-humid, with an annual rainfall of 500-600 mm. The annual distribution of rains determines a wet season from November to April and a dry season from May to October.

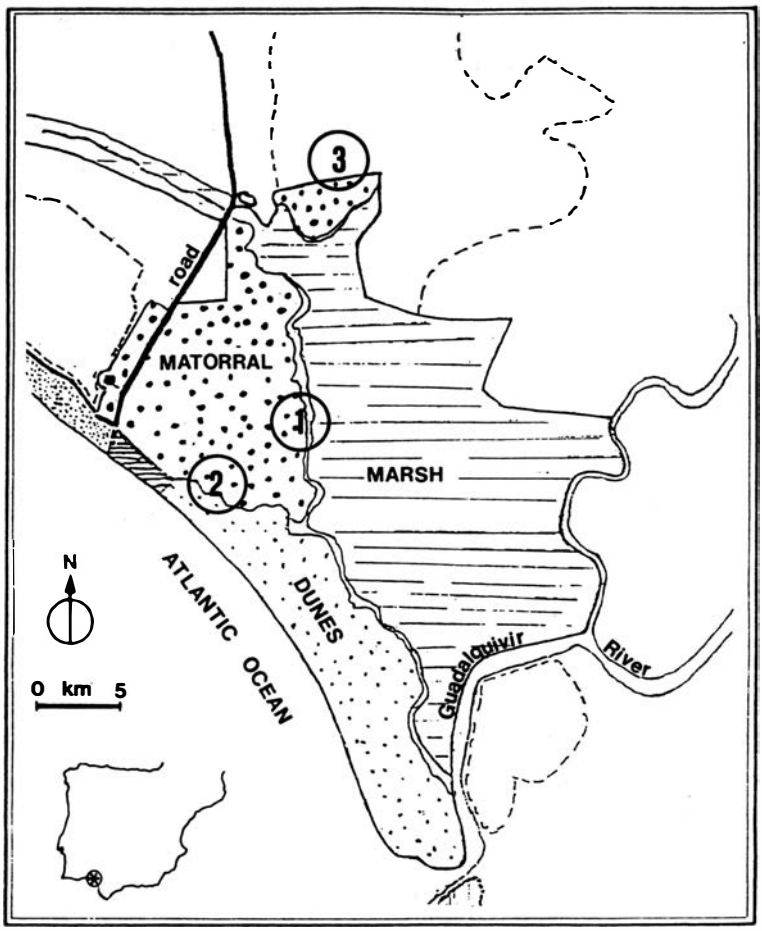

Figure 1. — Sketch map of the Doñana National Park with the location of the three study areas: (1) Vera, (2) Lagunas, and (3) Coto del Rey. Doñana National Park limits are shown by a continuous line. Other protected areas are indicated by discontinuous lines.

The study area locations and their relevant characteristics are: (1) Vera, situated in the center of the Park, where the marisma and the matorral biotopes overlap, determining a relatively moist zone throughout the year, with *Phragmites* sp., *Typha* sp. and *Juncus* sp. dominating in the most humid sites ; (2) Lagunas, situated in the mid-southern area of the Park, between the dunes and the matorral biotopes, characterized by the presence of permanent small lakes ; (3) Coto del Rey, situated at the northern end of the Park and characterized by plantations of

pines, *Pinus pinea,* and eucalypts, *Eucalyptus* sp., and the presence of patches of *Pistacia lentiscus,* as well as small streams bordered by abundant *Fraxinus* sp., *Populus alba, P. lentiscus* and *Rubus* sp. The linear distances between study areas were ca. 15 km between Coto del Rey and Vera, 3 km between Vera and Lagunas, and 18 km between Coto del Rey and Lagunas (Fig. 1). All of 30 radio-tracked mongooses (3 in Vera, 3 in Lagunas, and 24 in Coto del Rey) remained close to the areas in which they were trapped, using ranges of about 3 km^2 (Palomares, 1990). Therefore, it can be assumed that each study area was used by different individuals.

METHODS

The mongoose's diet was obtained by analysis of 428 faeces : 60 collected from Lagunas between November 1985 and December 1986 ; 190 collected from Vera between November 1985 and December 1986 ; and 178 collected from Coto del Rey between December 1986 and July 1989.

Overall diet was estimated from the frequency of occurrence of prey types in each faecal sample, and percentage of consumed biomass for each one of the following prey categories : small mammals, rabbits, birds, amphibians, reptiles, insects > 5 mm, eggs, crustaceans, gastropods, vegetables and carrion. Percentage of consumed biomass was obtained by using correction factors which transform the dry undigested matter in the faeces to fresh biomass consumed by mongooses. Details on methods can be found in Palomares & Delibes (1990, 1991a, 1991b). Significant differences in frequency of occurrence among areas were detected by the Friedman two-way analysis of variance by ranks (Siegel, 1956). Once general significant differences were detected between areas, the Bonferroni confidence intervals to control the experimentwise error probability at $p = 0.05$ was used to test significant differences between areas for each prey group (Neu *et al.,* 1974 ; Byers *et al.,* 1984). Niche breadth for each area was calculated by Levins (B) index (Levins, 1968), using data on frequency of occurrence.

The relationship between ranking of frequency of occurrence and relative abundance of prey in the field was analyzed only for the most frequently consumed prey species (excluding insects). Abundances of these prey species by season (dry and wet) and area were obtained from published studies or from communications of people carrying out research on them. The use of published studies was considered valid because I principally investigated local variations related to habitat compositions (which have remained stable for several years in our study area), and seasonal differences (which generally are greater among seasons than among years in a Mediterranean environment ; e.g., see, Beltrán, 1991, for rabbits). The analysis involved two comparisons : (1) the ranks of seasonal abundance in the field and the ranks of frequency of occurrence for each prey species in the diet, calculated from the number of occurrences per total faecal sample, were compared in every study area independently ; (2) the ranks of consumption (by frequency of occurrence) and abundance of each prey were compared among areas, for the overall data, and for each season independently. Data were considered adequate to perform comparisons between consumption and abundance ranks for every prey if previously significant differences in the frequency of occurrence were shown among seasons and areas ($p < 0.05$) by the Bonferroni confidence intervals.

RESULTS

1. *Overall diet for each area*

The Friedman test detected significant differences between areas in frequency of occurrence for overall prey categories (χ^2 = 20.06, d.f. = 10, p = 0.0287). Insects, reptiles, and small mammals constituted the most consumed groups (> 40 %) for Lagunas ; birds and small mammals for Vera ; and rabbits and insects for Coto del Rey (Fig. 2). Niche breadth was largest for Lagunas, followed by Vera and Coto del Rey (B = 3.707, 3.619 and 2.717, respectively), indicating that diet was more specialized in the latter area, where rabbits predominated, than in Lagunas and Vera. In the comparisons between every two areas for each prey group, significant differences were also detected for all prey categories, except for eggs. The largest differences were for birds, rabbits, small mammals, and amphibians (Fig. 2). Diet in Coto del Rey was similar for each study year (Palomares & Delibes, 1991b), which justified pooling the data.

The prey categories contributing the largest biomass to the diet were reptiles for Lagunas, birds for Vera, and rabbits for Coto del Rey (Fig. 2). Among areas, the largest differences were observed in rabbits, birds and amphibians. Small mammals and reptiles had similar importance in all areas. Insects, eggs and crustaceans were always little represented (never exceeding 6 %).

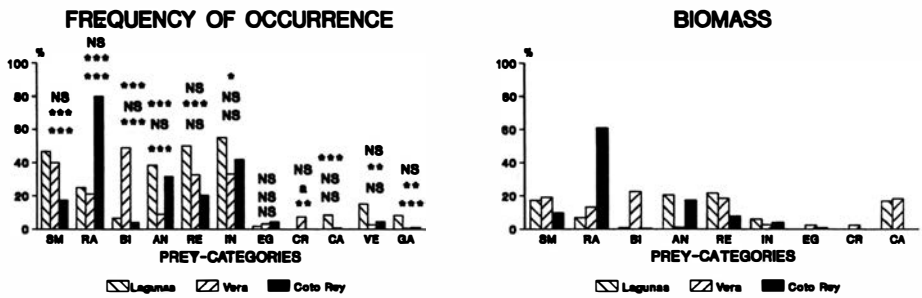

Figure 2. — Egyptian mongoose diet in three areas of Doñana National Park as given by frequency of occurrence and percentage of consumed biomass of each prey category. SM = small mammals ; RA = rabbits ; BI = birds ; AN = amphibians ; RE = reptiles ; IN = insects ; EG = eggs ; CR = crustaceans ; CA = carrion ; VE = vegetables ; GA = gastropods. For frequency of occurrence, the results of statistical compararisons by the Bonferroni confidence intervals between Lagunas and Vera, Lagunas and Coto del Rey, and Vera and Coto del Rey are given above each prey category from top to bottom, respectively. ns not significant, *** $p < 0.001/2\,k$; ** $p < 0.01/2\,k$; * $p < 0.05/2\,k$ where k = number of prey categories ; « a » indicates a frequency of occurrence of 0 for both areas.

The most frequently consumed prey species were the 12 enumerated in Appendix 1. Excluding insects, they represented 46 %, 63 % and 79 % of all items detected for Lagunas, Vera and Coto del Rey, respectively (also see Palomares & Delibes 1991a, 1991b).

2. *Relation between prey consumption rates and abundance*

At Doñana, the abundance of the prey species used in this analysis was always greater during the wet season, except for reptiles which were more active during the dry season (Table I). The comparison of the ranks of abundance in the field and prey occurrence in the diet, when some significant seasonal differences were noticeable for prey consumption rates (see Table I), led to the following results: At Vera, *Crocidura russula* and *Mus spretus* were consumed more frequently in their season of greater abundance, whereas ducks, *Anas* spp., and skinks, *Chalcides chalcides,* were taken more frequently when they were less abundant. At Coto del Rey, rabbits, spadefoots (*Pelobates cultripes*), small *Psammodromus* sp., and skinks, were consumed more frequently when they were more abundant (Table I).

TABLE I

Abundance ranks (« + » greater, « − » lower) of twelve prey species of mongooses for each season (dry = DRY, wet = WET), and occurrence frequency of each in the mongoose diet for each study area and season.

Probability (p) of the comparisons between occurrence frequencies for each season in a same area using the Bonferroni confidence intervals is given. « ns » not significant; *** $p < 0.001/2k$; ** $p < 0.01/2k$; * $p < 0.05/2k$, where k is equal to the number of prey species.

	ABUNDANCE		LAGUNAS			VERA			COTO DEL REY		
	DRY	WET	DRY n = 30	WET n = 30	P	DRY n = 87	WET n = 103	P	DRY n = 39	WET n = 139	P
Oryctolagus cuniculus	−	+	30.0	23.3	ns	16.1	25.2	ns	76.9	90.6	**
Crocidura russula	−	+	10.0	23.3	ns	3.4	16.5	*	0.0	2.9	ns
Rattus sp.	−	+	6.7	0.0	ns	5.7	8.7	ns	0.0	2.9	ns
Mus spretus	−	+	6.7	6.7	ns	2.3	47.6	**	15.4	9.4	ns
Bubulcus ibis	−	+	0.0	0.0	ns	5.7	6.8	ns	0.0	0.0	ns
Anas sp.	−	+	0.0	6.7	ns	28.7	8.7	**	0.0	0.0	ns
Psammodromus sp.	+	−	40.0	23.3	ns	11.5	5.8	ns	25.6	7.2	*
Chalcides chalcides	+	−	13.3	3.3	ns	4.6	22.3	**	12.8	0.7	**
Natrix sp.	+	−	3.3	6.7	ns	8.0	8.7	ns	0.0	0.0	ns
Pelobates cultripes	−	+	20.0	50.0	ns	2.3	1.0	ns	15.4	51.8	***
Sus scrofa	−	+	10.0	3.3	ns	2.3	14.6	ns	0.0	0.0	ns
Procambarus sp.	−	+	0.0	0.0	ns	12.6	2.9	ns	0.0	0.0	ns

It was not always possible to rank the abundance of each prey species between our three study areas. This was possible (at least at one area in relation to the other two) for all prey species, except for spadefoots, when considering overall diet; for all the prey species except for *Rattus* sp., *Mus spretus* and spadefoots during the dry season; and for all the prey species except for *Rattus* sp., cattle egrets (*Bulbucus ibis*) and spadefoots during the wet season (Table II). On the other hand, significant differences of prey consumption rates between areas were detected for all the prey species except for *Rattus* sp. when all data were

pooled ; only for rabbits, ducks, small lizards and spadefoots during the dry season ; and for all the prey species except for *Rattus* sp., skinks and crayfishes (*Procambarus* sp.) during the wet season (see Table II). The comparison of the ranks of abundance in the field and occurrence in the overall diet showed that rabbits, mice, cattle egrets, ducks, small lizards, and crayfishes were consumed more frequently where they were more abundant, whereas shrews, skinks, grass snakes (*Natrix* sp.) and wild boar (carrion) were consumed less frequently wherever they were the least abundant (Table II). During the dry season, rabbits, ducks and small lizards were consumed more often in the areas of greater abundance (Table II). Finally, during the wet season, rabbits, mice, small lizards and wild boars (carrion) were consumed more frequently wherever they were more abundant, whereas skinks, ducks and *Natrix* sp. were taken less frequently where they were scarcer (Table II). As a rule, when comparisons were possible, ranking of prey consumption always coincided with rankings of prey abundance (Table II).

TABLE II

Occurrence frequency (from 1 to 3 in decreasing order), and relative abundance ranks (also from 1 to 3) of more important prey species in the mongoose diets for each study area and by seasons.

The same occurrence frequency ranks were used when no significant difference between all or some areas were found using the Bonferroni confidence intervals (« o » if not between the three areas ; « + » if greater and « − » if lower in two areas in relation to the third). The same signs were used to indicate abundance in the field when the relative abundances were not known, or were similar between areas (○), or only known in one area with regard to the other two (« + » if was greater or « − » if was lower). LA = Lagunas, VE = Vera, CR = Coto del Rey.

	OVERALL						DRY						WET					
	OCCURRENCE			ABUNDANCE			OCCURRENCE			ABUNDANCE			OCCURRENCE			ABUNDANCE		
	LA	VE	CR	LA	VE	CR	LA	VE	CR	LA	VE	CR	LA	VE	CR	LA	VE	CR
O. cuniculus	−	−	1	2	3	1	−	−	1	2	3	1	−	−	1	3	3	1
C. russula	+	+	3	+	+	3	○	○	○	+	+	3	+	+	3	+	+	3
Rattus sp.	○	○	○	2	1	3	○	○	○	○	○	○	○	○	○	○	○	○
M. spretus	−	1	−	−	1	−	○	○	○	○	○	○	−	1	−	−	1	−
B. ibis	−	1	−	−	1	−	○	○	○	2	1	3	+	+	3	○	○	○
Anas sp.	−	1	−	2	1	3	−	1	−	2	1	3	+	+	3	2	1	3
Psammodromus sp.	1	−	−	1	−	−	1	−	−	1	−	−	1	−	−	1	2	3
C. chalcides	+	+	3	+	+	3	○	○	○	1	2	3	○	○	○	1	−	−
Natrix sp.	+	+	3	1	2	3	○	○	○	1	2	3	+	+	3	1	2	3
P. cultripes	+	3	+	○	○	○	1	−	−	○	○	○	+	3	+	○	○	○
S. scrofa	+	+	3	2	1	3	○	○	○	2	1	3	2	1	3	2	1	3
Procambarus sp.	−	1	−	2	1	3	○	○	○	2	1	3	○	○	○	2	1	3

DISCUSSION

In general, the mongoose staple prey were consumed more frequently when and where they were more abundant. Two statistically significant exceptions were ducks and skinks at Vera. However, a likely explanation may be found, at least for ducks. Large water bodies protect ducks against mongoose predation during the wet season, but during the dry season, as water levels recede (see Amat, 1981), ducks gather into the few remaining pools, making them more accessible to mongooses (pers. observ.). Additionally, changes in the consumption of prey, both between areas and seasons, suggest that the consumed prey were generally the most available ones, as noted by Corbett & Newsome (1987) and MacCracken & Hasen (1987).

On the whole, the most frequently consumed prey, at both Vera and the Coto del Rey during both seasons, appear to be the most profitable, and that of the highest nutritional value. Rabbits at the Coto del Rey, and birds at Vera were probably the most easily captured prey during the dry season and those which needed the shorter search time (hence the energy gain was maximized, Schoener, 1971). Furthermore, such prey probably provided a larger amount of food ; the birds taken were generally large (ducks) and the rabbits, though most of them were young (Palomares & Delibes, 1991b), were usually captured in groups of 2 to 4 inside warrens. Conversely, small mammals mostly represented by the small *Mus spretus* (12 g) predominated at Vera during the wet season. The mongooses' hunting tactics which commonly involves an intensive search (Palomares, 1990), probably favours the capture of such a high density prey at that season in this area (Camacho & Moreno, 1989). The number of captures would therefore be increased.

The dietary spectrum of the Egyptian mongoose at Doñana could be explained by both the species' hunting tactics and by its ability to quickly learn what are the most profitable prey at each time of the year and at each location. Learning when and where valuable food can be encountered (rabbits at Coto del Rey ; birds and small mammals at Vera during the dry and wet seasons) seems likely to influence the dietary choices of this species following the model proposed by Erlinge (1981) and Lucas (1983).

Prey type and prey characteristics are important for the undertanding of Carnivore social organization (Macdonald, 1983). The highly social mongooses all feed on quickly renewable prey, usually insects, whereas more solitary species feed on small vertebrates (Waser, 1981 ; Rood, 1986). Egyptian mongooses in our study area are frequently observed in pairs and family groups, whereas groups made of several adult individuals are rare (Palomares & Delibes, 1993). Their feeding habits and the slower renewal rate of their staple prey at Doñana might well explain their lack of gregariousness, as argued in Palomares & Delibes (1993).

SUMMARY

The feeding behaviour of Egyptian mongooses, *Herpestes ichneumon,* was studied in south-western Spain. Diet was analyzed from 428 faeces collected in three spatially independent areas of Doñana National Park and frequency of occurrence of the most consumed prey (N = 12) was compared with available

data on relative abundance in the field for each area and season (dry and wet). Independently for each area, these prey species were consumed by mongooses in the seasons when they were most abundant, except for two cases. In one of them the availability of the mongooses' prey was probably greater during the season of lower prey abundance. Comparing between areas, prey species were consumed more frequently in the area or areas where they were more abundant in all cases where analyses were possible. Results indicated that mongooses behave as opportunistic predators at Doñana, consuming the most abundant prey in each area and season.

RÉSUMÉ

Le comportement alimentaire de la Mangouste d'Egypte *Herpestes ichneumon* a été étudié de novembre 1985 à juillet 1989 dans trois localités du Parc National de Doñana, S.O. de l'Espagne. Le régime a été déterminé par analyse de 428 fèces collectées dans ces trois habitats. La fréquence des proies les plus communes (N = 12) a été comparée avec leur abondance dans chaque milieu et à chaque saison (sèche et humide). Dans l'ensemble, ces proies sont consommées par la Mangouste à la saison où elles sont les plus nombreuses, à deux exceptions près. Dans l'un de ces derniers cas, la facilité de capture était probablement plus grande quand la proie était moins abondante. La comparaison des trois habitats montre, là aussi, que la ou les zones où les espèces sont le plus souvent consommées sont toujours celles où ces espèces sont les plus abondantes. La Mangouste d'Egypte se comporte donc à Dañana comme un prédateur opportuniste se nourrissant en toutes saisons et dans chaque milieu des espèces-proies qui sont en plus grand nombre.

ACKNOWLEDGEMENTS

The research was supported by DGICYT (project PB87-0405). The author had a postdoctoral grant of Consejo Superior de Investigaciones Científicas. Drs. M. Delibes, S. Moreno, J.A. Donazar, F.M. Jaksic, S. Erlinge, L.K. Corbett, C.M. Herrera, and two anonymous referees kindly reviewed the manuscript and provided useful comments. N. Bustamante revised the English version.

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APPENDIX 1

Information sources used to obtain abundance ranks of the main prey species in Egyptian mongoose diet for dry (May-October) and wet (November-April) seasons, and for the three study areas inside Doñana National Park :

1. Rabbits, *Oryctolagus cuniculus :* Rogers & Myers (1980) ; Kufner (1986) ; Beltrán (1991) ; R. Villafuerte (pers. com.).
2. Shrews, *Crocidura russula :* Kufner (1986) ; Camacho & Moreno (1989) ; S. Moreno (pers. com.).
3. Rats, *Rattus* sp. : Kufner (1986) ; Camacho & Moreno (1989).
4. Mouse, *Mus spretus :* Kufner (1986) ; Camacho & Moreno (1989) ; S. Moreno (pers. com.).
5. Cattle egrets, *Bubulcus ibis :* García *et al.* (1989).
6. Ducks, Family Anatidae : García *et al.* (1989).
7. Small lizards, *Psammodromus* sp. : Mellado (1980) ; Díaz-Paniagua and Rivas (1987) ; M. Blázquez (com. pers.).
8. Skinks, *Chalcides chalcides :* Díaz-Paniagua & Rivas (1987), M. Blázquez (com. pers.).
9. Grass snakes, *Natrix* sp. : Díaz-Paniagua & Rivas (1987).
10. Spadefoots, *Pelobates cultripes :* Díaz-Paniagua (1983) ; Díaz-Paniagua & Rivas (1987).
11. Wild boars, *Sus scrofa :* Braza *et al.* (1984) ; Braza & Alvarez (1989).
12. American crayfishes, *Procambarus* sp. : Delibes & Adrian (1987) ; personal observation.