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Sex-driven differences in Egyptian mongoose's (*Herpestes ichneumon*) diet in its northwestern European range

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Abstract Sexual dimorphism in carnivores can result from, or induce, variations in diet and foraging behaviour between individuals of different sexes. Sex-driven behavioural changes in feeding habits may also result in a reduction in intraspecific competition for resources, avoiding dietary overlap by concentrating on different prey sizes/types. We therefore evaluated the variation in feeding habits of both males and females of an invasive and range expanding southern European carnivore, the Egyptian mongoose (*Herpestes ichneumon*), through gut content analysis of road or predator-control killed animals. The analysis of 59 gut samples, collected in Portugal, revealed that northwestern populations of mongooses prey mostly upon mammals [especially lagomorphs, percentage of biomass (PB)=44%], reptiles (PB=28%) and arthropods (PB=2% but percentage of occurrence=35%). However, females seem to focus mainly on reptiles (PB=51%) and mammals (PB=38%), whilst males consume mostly mammals (PB=75%). The results suggest that this variation maybe a result of sexual dimorphism (since some variation is documented in a few Egyptian mongoose's skull measures, namely condylobasal length and canine diameter), with males shifting their diets to prey from which they can obtain more energy. Females seem to be focused on predating lighter animals, probably females or juveniles, a fact that has important game management implications.

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Introduction

Sex-driven variation in diet and foraging behaviour has been observed in many mammalian carnivore species (e.g. Kvitek et al. 1993; McDonald et al. 2000). These variations are usually perceived as a mechanism to reduce intraspecific competition, with both sexes avoiding dietary overlap by concentrating on different prey sizes/types (e.g. Birks and Dunstone 1985). On the other hand, these sex-specific behavioural changes result in, and are a result of, some degree of sexual dimorphism (Thom et al. 2004). In many carnivore species, females are smaller than males, being suggested that this difference is due to divergent selective pressures where smaller females have a higher fitness since they need less energy for survival, channelling the surplus of energy into reproduction (Begg et al. 2003). Inversely, larger males are usually favoured in competition (Dayan and Simberloff 1996).

The pattern of dietary variation between sexes has been particularly documented for mustelids, with a recognised trend where bigger males consume larger prey than the smaller females (Moors 1980). In southwest Scotland, mink (*Mustela vison*) males preyed mostly upon lagomorphs, whilst females concentrate in fish and crustaceans (Birks and Dunstone 1985). Weasels (*Mustela* spp.) in Sweden (Erlinge 1981), as well as in Portugal (Santos-Reis 1990), also showed sex-related differences in prey consumption. However, this pattern is not consistent since other species, such as the honey badger (*Mellivora capensis*), do not reveal any intersexual differences in diet preferences in spite of its marked sexual dimorphism in size (Begg et al. 2003).

Less attention, however, has been devoted to the study of sex-specific intersexual feeding habits of non dimorphic carnivore species where it can be anticipated that physiological features, as those associated with reproduction, could influence the energetic demands and therefore result in different feeding strategies between sexes (Dayan and Simberloff 1996). One such example is the Egyptian mongoose, (*Herpestes ichneumon* L., 1758). The Egyptian mongoose is an African mesocarnivore that invaded Europe in the nineteenth century (Delibes 1982; Dobson 1998). This species' northern-most distribution range includes the Iberian Peninsula (Mitchell-Jones et al. 1999) where it is still expanding its range (Borralho et al. 1996; Palomo and Gisbert 2002). Northwestern populations, which include the study area, are not sexually dimorphic in relation to macro-biometrics (e.g. weight, body and head lengths; Rosalino et al. 2005b), but do show some skull variation (micro-biometrics, e.g. condylobasal length), as has been detected by Dayan et al. (1989) and corroborated for a Portuguese population by Clamote (1997).

In southwestern Spain, where the single study on Spanish European mongoose population metrics was carried out, slight intersexual difference in weight was observed (Palomares 1990). However, this may be the result of the combined effect of two factors: high abundance of wild rabbit and the presence of Iberian lynx (*Lynx pardinus*), which makes Doñana National Park a unique system whose results may not be applied elsewhere. This protected area used to hold one of the highest densities of wild rabbits in the Iberian Peninsula, and these represent up to 71% of the consumed biomass by mongooses throughout Spain (Delibes et al. 1984). Females could be using the surplus of energy, obtained by preying upon rabbits, in reproduction instead of enlarging body size, and males could use it for territory patrol and defence activities that benefit from a larger body size. This is particularly important since in this area, the mongoose faces the presence of a predator, the Iberian lynx (*L. pardinus*), which is known to negatively affect mongooses' occurrence and behaviour (Palomares et al. 1998).

In addition to the community interactions, mongooses also interact with humans. Frequently, game managers perceive mongooses as one of the carnivore species that causes higher damage on co-occurring small game species [e.g. partridge (*Alectoris rufa*), wild rabbit, coturnix (*Coturnix coturnix*)], and predator control is often an active management prescription to control mongooses' density. However, this perceived negative impact of mongooses over small prey species is not supported by empirical scientific data (e.g. Santos et al. 2007). Nonetheless, these interactions granted mongooses the status of game species in Portugal (Decret-Law N° 202/2004, 18 August) being actively hunted.

In this study, we aimed to investigate sex-related Egyptian mongooses' feeding habits in an expanding area of their European range: central and southern Portugal. On the basis of the results of previous studies in Spain (Palomares and Delibes 1991; Palomares 1993), we predict a generalist feeding spectrum, with diversified food items composing the diet of both sexes. Moreover, assuming the character displacement observed by Dayan et al. (1989), we believe that robustness of male skulls may also constrain prey selection. These results will be extremely helpful to understand the species' feeding preferences and design adequate population management actions.

Materials and methods

Study area

The biological material used in our study was collected in southern and central Portugal (37°56′ N–40°40′ N, 6°54′ W–8°30′ W; Fig. 1), ranging from the coastal region to

Fig. 1 Location in Portugal of the collected mongooses' corpses from road kills and game reserves management practices from which gut contents where collected

mountainous areas, with altitudes reaching 1,500 m above sea level.

Biogeographically, the study area is included both in the Mediterranean Region (Mediterranean Ibero–Atlantic Superprovince), characterised by a climate with low or null rainfall in summer, and in the Eurosiberian region (Atlantic Superprovince), where the summer arid period is null or light, never exceeding two dry months (Costa et al. 1998). Landscape is highly diversified and includes regions with Mediterranean vegetation, such as cork (*Quercus suber*) and holm (*Quercus ilex*) oak woodlands and scrubland, pine (*Pinus* spp.) and eucalyptus stands (*Eucalyptus* spp.), agricultural areas and olive (*Olea europaea*) yards.

Field and laboratory methods

Between January 2003 and March 2007, adult Egyptian mongoose carcasses (more than 1.5 years old; Azcón and Duperón 1999) were collected for analysis, mainly from road kills and game reserves predator control practices. Animals were necropsied, sexed and aged (according to tooth wear; Harris 1978; Palomares and Delibes 1992) and stomachs and intestines removed; skull measurements could not be taken since most of it were destroyed (consequence of road kill or gun shot). Gut contents were posteriorly analysed according to standard analytical procedures (e.g. Rosalino et al. 2005a). Invertebrate and vertebrate non-digested body parts and vegetable remains were used to identify consumed prey and estimate the minimum number of individuals/fruits eaten (e.g. number of teeth, seeds, etc.; Madureira and Ramalhinho 1981; Brom 1986; Barrientos 1988; Teerink 1991; our own collection). Identifiable undigested remains were dried and weighted to obtain each prey group dry weight and categorised into seven food categories: mammals, birds, reptiles, amphibians, arthropods, molluscs and fruits.

Data analyses

Data were expressed as percentage of occurrence [PO = (number of individuals or fruits of the same species or taxonomic group×100)/(total number of consumed items)] and as percentage of fresh weight biomass intake [PB = (ingested biomass of the same species or taxonomic group×100)/(total consumed biomass)]. PO estimations were based on the sum of the minimum number of individuals/fruits identified in each gut. For calculations of consumed biomass (PB), we applied specific correction factors to each prey group dry weights (digestibility coefficients; Palomares and Delibes 1990). For mongooses' untested resources, we used the coefficients determined for other sympatric carnivore species: galliforms and amphibians—common genet (*Genetta genetta*; Palomares

and Delibes 1990); arthropods, *Rubus* spp., *Vitis vinifera* and *Pyrus bourgaeana*—Eurasian badger (Revilla 1998; Rosalino et al. 2003). The effect of random sampling error was accounted for by estimation of the 95% confidence limits for PO and PB values of each food item made by a bootstrap simulation process (1,000 repetitions; Reynolds and Aebischer 1991). The bootstrap simulation was performed using Data Pilot 1.03, free software (Two Pilot, Chicago, USA).

Results were analysed globally and by sex. The representativeness of the analysed sample was tested, after randomisation, by plotting the cumulative frequency of resource items against increase in sample size (Mason and Macdonald 1980). Dietary sexual differences were tested by a modified chi-square test (Simpson et al. 1960) using the Yates' correction for continuity and the Bonferroni correction for adjusting the level of statistical significance. Food diversity was evaluated using the Shannon–Wiener index (H') and the Evenness index (J'; Krebs 1989). The trophic niche overlap was assessed by the Morisita index (C) when resources were expressed as number of individuals and by the Horn's index (R) when consumed biomass was used, as suggested by Krebs (1989). Intersexual Shannon–Wiener index values were compared by the Hutcheson t test (Zar 1999).

All analyses were performed using the statistical package SPSS 14.0 for Windows, Release 14.0.0 (Chicago, USA) at a significance level of 0.05.

Results

A total of 59 Egyptian mongooses carcasses containing undigested gut remains were analysed, mainly concentrating in the winter/spring period (Table 1); 33 were males and 26 females, showing no intersexual sample size differences ($\chi^2=0.831$, $df=1$, $p=0.362$). Moreover, the cumulative frequency of resource items seems to indicate that male, female and total sample sizes are sufficient to characterise mongooses' diet, since the cumulative frequen-

Table 1 Seasonal samples sizes

Sex	Season	Sample number
Male	Winter	19
	Spring	13
	Summer	1
Female	Winter	13
	Spring	11
	Summer	2

Winter: January, February and March; Spring: April, May, June; Summer: July, August and September

cy reaches an asymptote with 15, 12 and 29 gut samples, respectively.

Overall, in western Iberian Peninsula and during the wet period, Egyptian mongooses feed mainly upon mammals, which constitute more than 60% of the ingested biomass and one third of the eaten prey (Table 2). Within the mammalian species preyed, lagomorphs (rabbits and hares) played an important role, since they account for more than 43% of PB. Reptiles were the second most consumed prey group, with especial reference to the Montpellier snake (*Malpolon monspessulanus*). Arthropods are only important in terms of the number of prey, since they account for 35% of all prey. Nevertheless, mongoose diet present some degree of diversity (H'=0.67; J'=0.79).

Intersexual variation in feeding habits was more evident in terms of ingested biomass than in number of consumed prey. Diet diversity, in terms of biomass, was significantly higher in females (H'_{males}=0.34; $H'_{females}$=0.48; t=−2.005, df=2296, p=0.023; J'_{males}=0.50; $J'_{females}$=0.57), with reptiles, fruits and mammals being the most relevant food

categories explaining such differences (Table 3). Reptiles (χ^2=354.285, df=1, p<0.01) and fruits (χ^2=144.615, df=1, p<0.05) were significantly more preyed by females, and among mammals, lagomorphs were the most important prey (PB=32%). Inversely, males prey mostly on mammals, which account for more than 75% of PB (χ^2=10276.700, df=1, p<0.001), especially lagomorphs that correspond to half of all consumed biomass. Additionally, amphibians were also slightly more consumed by males (χ^2=391.561, df=1, p<0.01). Nonetheless, and despite the observed differences between number of consumed items in each prey category (Table 2), no statistically significant variation was observed in the diet diversity index (H'_{males}=0.60; $H'_{females}$=0.69; t=−0.541, df=175, p=0.294) nor for each of the consumed prey category (all p>0.05).

These results are confirmed by the trophic niche overlap assessment, which revealed a high diet similarity in terms of prey numbers (C=0.97) but a low overlap (R=0.38) in terms of prey ingested biomass.

Table 2 Diet of the Egyptian mongoose in Portugal

Food item	N	W (g)	PO	PB	Food item	N	W (g)	PO	PB
Mammals	51	2,348.5	28.65	62.52	Arthropods	62	84.5	34.82	2.26
Crocidura russula	2	43.2	1.12	1.15	O. Aranea	1	1.7	0.56	0.05
Talpa occidentalis	2	95.7	1.12	2.55	C. Crustacea[a]	2	4.6	1.12	0.12
O. Lagomorpha	20	1,640.4	11.24	43.73	C. Chilopoda	2	13.4	1.12	0.36
Microtus cabrerae	1	22.8	0.56	0.61	F. Gryllidae	1	1.6	0.56	0.04
Microtus sp.	11	292.7	6.18	7.80	F. Gryllotalpidae	5	9.2	2.81	0.25
Apodemus sylvaticus	3	58.8	1.69	1.49	F. Acrididae	3	16.5	1.69	0.44
Rattus rattus	2	8.8	1.12	0.23	O. Ortoptera NI	6	2.5	3.37	0.07
Rattus norvegicus	1	152.2	0.56	4.06	O. Hymenoptera NI	2	Vest.	1.12	Vest.
Mus sp.	4	27.2	2.25	0.72	O. Lepidoptera NI	1	0.2	0.56	Vest.
C. Mammalia NI	5	6.7	2.81	0.18	F. Cetoniidae	4	7.2	2.25	0.19
Birds	19	78.8	10.68	2.19	F. Trogidae	3	2.1	1.69	0.06
O. Galliformes	3	49.8	1.69	1.33	F. Chrysomelidae	1	1.0	0.56	0.03
O. Charadriiformes	1	0.5	0.56	0.01	F. Tenebrionidae	1	0.1	0.56	Vest.
O. Columbiformes	3	0.6	1.69	0.02	F. Cerambycidae	1	0.5	0.56	0.01
O. Passeriformes	4	11.5	2.25	0.39	F. Carabidae	10	12.4	5.62	0.33
C. Aves NI	8	16.4	4.49	0.44	F. Scarabaidae	2	1.6	1.12	0.04
Reptiles	30	1,040.5	16.87	27.75	F. Silphidae	1	1.7	0.56	0.05
Podarcis sp.	3	110.0	1.69	2.93	O. Coleoptera NI	12	7.3	6.74	0.20
Psammodromus sp.	14	254.3	7.87	6.78	Arthropod NI	4	0.9	2.25	0.02
F. Lacertidae NI	3	6.56	1.69	0.18	Molluscs	1	0.6	0.56	0.02
M. monspessulanus	2	576.8	1.12	15.38	Fruits	5	32.9	2.81	0.88
Sub-O. Serpentes NI	4	89.25	2.25	2.38	*Vitis vinifera*	3	30.0	1.69	0.80
C. Reptilia NI	4	3.6	2.25	0.10	*Pyrus* sp.	1	2.6	0.56	0.07
Amphibians	7	148.2	3.94	3.95	*Rubus* sp.	1	0.3	0.56	0.01
Bufo sp.	1	23.4	0.56	0.62	Carrion	3	17.0	1.68	0.45
Rana sp.	3	105.4	1.69	2.81	*Ovis aries*	1	8.6	0.56	0.23
C. Amphibia NI	3	19.4	1.69	0.52	O. Ciconiformes	2	8.4	1.12	0.22

N number of prey individuals consumed, *W* weight of individual items, *PO* percentage of occurrence, *PB* percentage of consumed biomass, *NI* non-identified

[a] *Procambarus clarkii*; *Vest.* vestigial

Table 3 Egyptian mongoose's diet, by sex, in Portugal, with the estimated 95% confidence limits (95% CL) for the percentage of occurrence (PO) and percentage of consumed biomass (PB) values (bootstrap simulation)

	Males		Females	
	PO (95% CL)	PB (95% CL)	PO (95% CL)	PB (95% CL)
Mammals	34.36 (30.60–43.94)	75.10 (69.12–89.28)	22.22 (18.18–30.00)	37.50 (31.48–73.34)
Birds	14.11 (12.12–14.57)	1.99 (1.26–2.23)	11.11 (10.00–11.36)	4.02 (1.80–4.15)
Reptiles	12.13 (9.55–13.39)	15.87 (7.77–19.50)	22.22 (21.97–22.50)	51.33 (21.96–56.46)
Amphibians	5.05 (1.91–5.74)	5.18 (0.25–7.14)	2.47 (0.00–3.79)	1.45 (0.00–1.62)
Arthropods	34.36 (32.48–35.70)	1.86 (1.44–2.00)	34.57 (31.82–37.50)	3.02 (2.90–3.09)
Molluscs	–	–	1.23 (0.00–2.27)	0.05 (0.00–0.06)
Fruits	–	–	6.17 (0.00–10.61)	2.63 (0.00–3.14)
Carrion	2.11 (0.00–3.05)	0.65 (0.00–0.90)	1.23 (0.00–2.00)	0.06 (0.00–0.08)

Discussion

Whilst our results indicate that northwestern populations of Egyptian mongooses tend to have a generalist feeding behaviour (corroborating the results of Palomares 1993), they also show a considerable consumption of rabbits and, to a lesser extent, of reptiles (see also Delibes et al. 1984). Moreover, the presented data also suggest a pattern of sex-specific feeding habits: males subsist preying mostly upon mammals (especially lagomorphs), whilst females have a more diversified diet, focusing more on reptiles and fruits. Although both genders have similar hunting tactics, involving intensive search which may favour a more generalist feeding behaviour (Palomares 1990), intersexual variation in the diet of northwestern populations of Egyptian mongooses may be the result of two concurrent factors: (1) males need to have higher energy inputs to compensate energetic costs of defending and patrolling larger core areas (Palomares 1994) and (2) females need to compensate the costs of reproduction by consuming less costly prey (e.g. lower handling time—fruits), in light of their plausible lower hunting success of more profitable prey, such as rabbits.

Our results suggest that males take advantage of a highly profitable resource for mesocarnivores: lagomorphs. Most likely, the majority of the eaten lagomorphs were wild rabbits (*Oryctolagus cuniculus*), since the greater size, escape speed, strength and non-fossorial habits of hares (*Lepus granatensis*) are likely to decrease their predators' probability of capture (Birks and Dunstone 1985). Wild rabbits' fossorial habits make them vulnerable to underground predation and kill (Birks and Dunstone 1985), especially when persecuted by mesocarnivores with a fusiform body shape, short legs and claws adapted to excavate, such as the Egyptian mongoose (Palomares 1990). This behaviour was confirmed by Palomares (1993) who reported that rabbits were usually captured in groups of two inside warrens.

Although mongooses show no body size dimorphism (Rosalino et al. 2005b), a more detailed analysis of several skull features related to feeding mechanics show some degree of sexual dimorphism. Clamote (1997), through the analysis of 37 mongoose skulls (25 females and 12 males) collected in similar locations as ours, found that males had significantly larger skulls (zygomatic width, rostral length and mandibule height, with a mean male/female index of 1.03, 1.04 and 1.03, respectively) and longer canines (mean male/female index: superior=1.09; inferior=1.06). Usually, it is accepted that larger skulls will have larger muscles and, consequently, larger bite strength (Wiig 1986). This feature, together with larger canines, which are usually used for display, territorial defence, dismembering carcasses and, more important, killing prey through neck bite (Valkenburgh 1989), will increase hunting success of male mongooses in capturing larger prey, such as rabbits, when compared to females.

Alternatively, since females are usually assumed to have higher energetic demands, due to pregnancy, lactation and cub rearing (Oftedal and Gittleman 1989), it would seem plausible to infer that due to the time period of data collection (Table 1), they should focus on more energetically profitable prey, such as lagomorphs. However, our findings do not corroborate this. We think that although energetic costs associated with reproduction are higher for females, demands are seasonally restricted, whereas males have a constantly higher need of energy, especially because of the larger territories they need to patrol and mark (Palomares 1990; Begg et al. 2003). This would result in a shift of males feeding behaviour towards bigger prey, which their skull characteristics allow to hunt more successfully. To compensate some limitations on hunting larger prey (smaller skulls and more fragile canines), females focused on less energy profitable, but less energy-consuming prey items, such as reptiles and fruits, reducing consequently the intraspecific competition (Dayan and Simberloff 1996).

Moreover, although no differences were detected in the PO of rabbits consumed both by males and females, the higher importance of rabbits to males (higher PB) seems to indicate that females are predating lighter animals, probably females or juveniles.

These sex-specific differences in diet may have implications at the prey community level, especially in what concerns wild rabbits as a game species, and should be taken into account when game management plans are being delineated in mongoose distribution areas.

Although we are aware of some potential source of bias in our study, mainly due to the extent of the study area and timeframe analysed, we also believe that our results are of interest for the understanding of the feeding patterns of this carnivore in its European range, particularly in what concerns the main finding of the paper (the variation of the diet of males and females) which is a specially novel approach. Future research should be designed to improve our knowledge on the effect of resource spatial structuring on mongoose sex-specific prey consumption and potential "cascading" impacts on the community.

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