Individual variations of male mating tactics in Egyptian mongooses (*Herpestes ichneumon*) : can body mass explain the differences ?

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Summary. – The social behaviour and mating tactics of four male Egyptian mongooses (*Herpestes ichneumon*) of different body mass in Doñana National Park (Southwestern Spain) were studied using radio-tracking. The biggest male exhibited polygynous behaviour, maintaining contacts with at least 4 females, but spending little time with each one of them (4 % per day), whereas a smaller male exhibited monogamous behaviour, maintaining contact with only one female with whom he spent more time (29 % per day). Data on two other males (one bigger and another smaller) suggested they could be included in each one of the previously described patterns, respectively. Body mass appeared to be the only factor explaining the variations in social behaviour and mating tactics of these Egyptian mongoose males.

Résumé. – Les comportements sociaux et systèmes d'appariement de quatre mangoustes Ichneumon (*Herpestes ichneumon*) mâles ont été étudiés par radio-pistage dans le Parc National de Doñana (sud-ouest de l'Espagne). Le mâle le plus grand a adopté un système de type polygame en s'associant avec au moins quatre femelles mais ne passant que peu de temps avec chacune d'entre elles (4 % par jour). Un mâle de plus petite taille a adopté un système de type monogame et était associé avec une seule femelle avec laquelle il passait une plus grande proportion de son temps (29 % par jour). Des données sur deux autres mâles, (l'un de grande et l'autre de petite taille) suggèrent que ces derniers peuvent être rattachés à l'un ou l'autre des types comportementaux décrits. La masse corporelle semble être le seul facteur responsable de la variabilité des comportements sociaux et d'appariement des mangoustes Ichneumon mâles.

INTRODUCTION

Analysis of intraspecific variations, especially at the individual level, in social behaviour and the ecological and phenotypic characteristics affecting it, are important to understand in detail the evolution of a particular strategy (Gosling 1986, Clutton-Brock 1988, Lott 1991). Male mating tactics in mammals may be different both between populations and between individuals in a given population (Clutton-Brock 1988,

Lott 1991). Differences have been mainly related to demography, social status, habitat characteristics and food resources (e.g., Schawagmeyer and Brown 1983, Sandell 1986, Zabel and Taggart 1989, Alvarez *et al.* 1990), but rarely to male phenotypic characteristics (but e.g., see Schawagmeyer and Brown 1983, Clutton-Brock *et al.* 1988). Here I describe in detail the variations of social behaviour and mating tactics (number of females contacted and mate guarding intensity) of four free-ranging males of a diurnal species of Carnivora at Doñana National Park, the Egyptian mongoose, *Herpestes ichneumon* (Palomares and Delibes 1992a), and relate the observed patterns to male body mass variations.

This mongoose displays a polygynous mating system in Doñana National Park, with males being territorial and females having overlapping ranges, although not for their core areas; core areas of females are unevenly distributed in relation to patches of optimal habitats for mongooses (those with higher density of vegetation and food resources), and male ranges include one or more of these optimal habitat patches inhabited by females (Palomares and Delibes 1993). Mating takes place between February and June in the area (Palomares and Delibes 1992b).

STUDY AREA AND METHODS

The study was carried out from September 1987 to September 1989 in a 35 square kilometer area of Coto del Rey, inside Doñana National Park, Southwestern Spain (appr. 37° 9' N, 6° 26' W). Coto del Rey is almost completely forested by pines, *Pinus pinea*, and eucalyptus, *Eucalyptus* sp, with undergrowth mainly of *Halimium halimifolium* (Cistaceae). Patchily distributed throughout the area, are small natural streams, where *Fraxinus* sp, *Populus alba*, and *Pistacia lentiscus* predominate, and associations of exclusively *P. lentiscus* at places with a higher ground water table.

Sixteen adult mongooses (six males and 10 females) were trapped, weighed and equipped with radio-collars containing tip switches to distinguish activity from inactivity (see Palomares and Delibes 1992c, for details). Out of six adult males, one removed his radio-collar and another was illegally killed by poachers, 2 days and 8 days after the attachment, respectively. Therefore good information was only available from four of them (H002, H003, H007, and H010; Fig. 1). Of 10 females, three were radio-tracked between September 1987 and July 1988 for 82 days on average (range = 27-163), and seven between October 1988 and September 1989 for 70 days on average (range = 7-206) (Fig. 1). All females were radio-tracked in the same place as males. Another adult female despite of not being caught and radio-tagged, was kept under control because her two cubs were radio-tagged and tracked between September 1987 and January 1988. I performed frequent visual contacts of both young, and in 12 out of 15 sightings, the female was with them. Thus, I assumed that the spatial behaviour and contacts of this adult female with males were similar to those of her radio-tracked cubs (H001 in Fig. 1).

The males' home ranges structure was determined by estimating their sizes (minimum convex polygon method; Hayne 1947) and the size and number of centers of maximum activity or core areas (50 % harmonic mean method, Dixon and Chapman 1980). Each individual was radio-located on foot once during daylight (activity period), and again at dawn or dusk (resting period of mongooses; Palomares and Delibes 1992a). In total, 434 male locations were obtained (Fig. 1).

From the series of locations, I also obtained the percentage of times when males were together with different radio-tracked females (i.e., in the same resting site when locations regarded inactive individuals, and within 0-10 m of each other when locations regarded active individuals). Besides, more information was obtained from 12 periods of 12-14 hours each of intensive tracking (Fig. 1) from sunrise to sunset undertaken on foot and at a short distance (30-100 m) from the animals, without disturbing them (Palomares 1990). Detailed information on male spatial position (every 15 or 30 minutes), activity and resting time, distance travelled, and contacts with females were obtained in these tracking periods. Several sightings of radio-tracked individuals also provided useful information.

Similar sampling was undertaken for females, with 796 isolated locations and 21 periods of 12-14 hours each of intensive tracking (Fig. 1).

Fig. 1. - Adult Egyptian mongooses radio-tracked between September 1987 and September 1989 for at least 7 days in Coto del Rey (Doñana National Park, Southwestern Spain). Tracking periods (lines), number of locations (on the right of line) are given for each individual.

RESULTS

Social behaviour and mating tactics of adult male mongooses were inferred from their home range structure, spatial behaviour, and frequency of contacts with females.

Home range structure and number of females contacted.

Male territory size and number of core areas were different for each male and positively correlated with body mass, though only the first correlation was significant ($r_s = 1$ and 0.95 , $P < 0.001$ and 0.1 , $n = 4$; Tab. 1).

H002 (the biggest male) shared his home range with at least four females (H101, H102, H106 and the mother of H001), and 5 out of his 6 core areas overlapped with core areas of these females as well. He was located together with H102, H106, and H001's mother (Tab. 1; note on Fig. 1 that he did not share tracking period with H101). On the other hand, H007 (a smaller male) shared his home range with five females (H110, H114, H117, H118), but his 2 core areas only overlapped with H110's core area. H007 shared tracking period with four of these females (H110, H114, H116, and H117; see Fig. 1), but he was only located together with H110 (the same with

which he shared his core areas; Tab. 1). Also, H007 was trapped 4 months later than H110, but during all this time he was frequently observed with her. The data from H003 and H010 data suggests that they could exhibit a behaviour similar to H007 and H002's respectively (Tab. 1). While H003 male had a small home range with only 2 core areas shared with one female (H106) with which he was frequently located, H010 male had a large home range with 5 core areas, which suggests he maintained relationships with several females.

TABLE 1. — Body mass (kg), territory size (km²), number of core areas or centers of maximum activity (NCMA) and relationships maintained with females by four Egyptian mongoose males at Doñana National Park, Southwestern Spain, 1987-1989.

a Number of females with which males were detected together during series of isolated locations. The number of females with which radio-tracking was simultaneously undertaken is given between brackets.

b Number of times when each male was located together with females. Total series of isolated locations with possibility of locating male-female together are given between brackets.

c Number of times on which males were observed with any females during travelling (observations with less than 3 hours between them were removed). Number of radio-tracking days is given between brackets.

d Time spent and distance travelled by H002, H007, and H010 males with females for 6, 4 and 2 days of intensive tracking, respectively. Percentages with regard to total daily activity time and total daily distance travelled by males are given between brackets, and the standard deviations and ranges are given below.

Male	Body mass	Territory size	NCMA	N ^o females detected ^a	Locat. ^b	Direct observ. ^c	Time ^d (min)	Distance ^d (m)
H002	3.70	6.82	6	3 (3)	16 (228)	2 (207)	16 (4%) 30, 0-75	12 (1%) 29, 0-71
H010	3.48	3.59	5	0 (0)	-	0 (46)	0	0
H007	3.22	3.13	2	1 (4)	38 (81)	7 (64)	114 (29%) 98, 0-225	869 (15%) 769, 0-1870
H003	2.80	0.55	2	1 (1)	6 (29)	1 (24)	-	-

Mate guarding intensity by males.

H007 male (the smaller one) was more often located (47 %, *n* = 81 locations) and more often directly observed (11 %, *n* = 64 observations) with H110; he was observed spending more time (114 min, *n* = 4 days) and travelling greater distances (869 m, *n* = 4 days) during foraging with H110 than H002 male did with females within his range (7 %, *n* = 228; 1 %, *n* = 207; 16 min, *n* = 6; 12 m, *n* = 6, for the same parameters, respectively; Table 1). During intensive tracking periods, male H002 (the bigger one) was found only once resting in the same den as a female before starting his daily activity, but he did not resume contact with the female in a nocturnal resting den, at the end of his daily activity. In contrast, in all 4 intensive tracking days of H007, he was found resting with the same female (H110) before starting activity, and on 3 occasions both animals used the same den at the end of their daily activity. H003 male was frequently

located with H106, and during one intensive 12-hours tracking period of this female they spent 43.3% of their activity time together. On the contrary, H010 was never observed accompanying any females.

Throughout the year, H007 was also the most often located with a female, H002 the least, and H003 showed intermediate values (Fig. 2). For all three males, an increasing degree of contact with females was observed in January-February (early mating season), and a reduction in March-April (the time of first births).

Fig. 2. — Bimonthly variations of number of times that H002, H003 and H007 males were located together with adult females in Doñana National Park, Southwestern Spain, between September 1987 and September 1989. Sample sizes are given between brackets.

DISCUSSION

Within a general polygynous mating system, different rates of inter-individual relationships were found in territorial Egyptian mongoose males living in the same area. The biggest H002 male defended a larger territory, which included several spatially independent females' core areas, and was linked with all these females, though he spent little time with each one of them. On the other hand, the smaller H007 male defended a smaller territory, which only included the core areas of one female, the only one with which he was linked, but, on the contrary, he spent a lot of time with her. Both tactics included contacts out of the mating period, as well as during it, but relative individual rates of contacts were constant in each time. Data from H010 and H003 males suggests that they could be included into each pattern respectively.

The obtained results also suggest that generalization about male-female relationship and mating behaviour in radio-tracked animals should be considered with caution when data concern only spatial behaviour. In fact, our spatial data from male H007

suggested that he was linked to five females; actually, intensive radio-tracking revealed that he was linked only to one.

Some studies have pointed out that some ecological aspects can produce variation of male behaviour, even locally (see Introduction). This does not appear likely for the male mongooses here studied. Population characteristics appeared constant between the two study years (Palomares and Delibes 1992*b*), therefore, differences in resource holding or sex ratio should not influence the mating tactics of each male. On the other hand, all the males studied had apparently the same spatial behaviour (all of them were territorial; Palomares and Delibes 1993). Space availability and quality (habitat composition) for each male, and the mongooses' diet in both years were similar (Palomares and Delibes 1991), which suggests (Zabel and Taggart 1989) that food resources were similar as well. The opportunist feeding habits of mongooses in the area lend further support to this (Palomares 1993). So, the physical differences between individual males (body mass in this case, perhaps related with age), and their potential as factors affecting intrasexual competition appears to be the main factor capable of explaining the differences found in spacing behaviour and contacts with females among the studied males. Despite the fact that the sample size is too small to reach a reliable conclusion, the results suggest that the relationship between male social behaviour and body mass might exist in carnivores. More studies of Egyptian mongooses and other carnivores would be necessary to confirm the hypothesis proposed here.

The bigger males were favoured in intraspecific competition, as they monopolized a higher number of females. If a direct relationship between number of monopolized females and offspring production is admitted (e.g. see Clutton-Brock *et al.* 1988, Parker *et al.* 1988), it would indicate that a phenotypic factor (body mass) affects reproductive success in males of a polygynous carnivore. Although in several species of animals reproductive success has been related to body size (e.g. Schwagmeyer and Brown 1983, for the ground squirrel, *Spermophilus tridecemlineatus*; Lawrence 1987, for milkweed beetle, *Tetraopes tetraophthalmus*; Howard 1988, for bullfrogs, *Rana catesbeiana*, and woodfrogs, *Rana sylvatica*), it has rarely been shown in carnivores (see Clutton-Brock 1988, for a review).

Results also appear to indicate that unfavoured males for intrasexual competition (smaller ones) exhibit a greater mate guarding behaviour than bigger ones both in and out of the mating period. This can be an adaptative process of smaller males to compensate for their lower access to females: 1) Males with a greater mate guarding behaviour will have a greater probability of assuring paternity; and 2) they could increase their final reproductive success (offspring recruitment) by protecting female and offspring against predation and assisting the female in feeding offspring. An observation which is compatible with this hypothesis was obtained when H007's pregnant female was favoured with male presence when an Iberian lynx, *Felis pardina*, tried to chase them (Palomares and Delibes 1993). H007 fought with the lynx, while the female escaped. On the other hand, since medium-sized prey like rabbits, *Oryctolagus cuniculus*, are shared by all members of the family group and there exists evidence that cooperative hunting increases adult rabbit captures (Palomares 1990), it can be expected that the presence of a male helps in the feeding of offspring. Owing to these same advantages, it may be hypothesized that a monogamous behaviour which includes parental investment of her partner (always that male territory supports offspring rearing) should also be adaptative for females, because they may obtain some benefits that are not otherwise obtainable, and thus, increase their own reproductive success. Again, future research focused on this topic, could confirm this hypothesis.

ACKNOWLEDGEMENTS

The research was supported by Dirección General de Investigación Científica y Técnica (project PB87-0405). The author had a postdoctoral grant of Consejo Superior de Investigaciones Científicas. Drs. M. Delibes, T. Redondo, D. F. Lott., T.H. Clutton-Brock, M. Sandell and an anonymous referee kindly reviewed previous drafts of this manuscript and N. Bustamante the English version. X. Lambin translated the French summary.

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