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).
MATING TACTICS IN EGYPTIAN MONGOOSEs

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 mongoose radio-tracked between September 1987 and September 1989 for at least 7 days in Casa del Rey (Dornata National Park, Southwestern Spain). Tracking periods (in box), number of locations (on the right of five) 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 0.25, 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 H001). 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

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Le comportement social et les systèmes d'appariement de quatre mongooses (H. ichneumon) mâles ont été étudiés par radio-trage dans le Parc National de Casa del Rey, Espagne. Le plus grand a adopté un système de type polygynique en appariant quatre femelles mais ne passant que peu de temps avec chacune.

La revue par le médiateur de l'Est, en collaboration avec le Conseil international de la faune, en 1990.

Par廳の主要な目的は、エジプトのマングースによる行動と結婚戦略を研究することである。大きな男性は、4つの雌の結びつきを示し、20%の時間しか他の個体との結びつきを示さなかった。他の2匹の雄（大きさが違う）のデータも、それぞれの既述のパターンを示し、これらのエジプトのマングース雄の行動パターンを示すことが目的である。
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 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.

<table>
<thead>
<tr>
<th>Male</th>
<th>Body mass</th>
<th>Territory size</th>
<th>NCMA</th>
<th>Number of females</th>
<th>Direct</th>
<th>Time</th>
<th>Distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>H001</td>
<td>3.70</td>
<td>6.82</td>
<td>6</td>
<td>3 (32)</td>
<td>16 (228)</td>
<td>2 (207)</td>
<td>16 (48)</td>
</tr>
<tr>
<td>H010</td>
<td>3.42</td>
<td>3.59</td>
<td>5</td>
<td>0 (0)</td>
<td>-</td>
<td>0 (44)</td>
<td>0</td>
</tr>
<tr>
<td>H007</td>
<td>3.22</td>
<td>2.12</td>
<td>2</td>
<td>1 (4)</td>
<td>10 (81)</td>
<td>7 (64)</td>
<td>114 (228)</td>
</tr>
<tr>
<td>H003</td>
<td>2.80</td>
<td>0.55</td>
<td>2</td>
<td>1 (1)</td>
<td>6 (29)</td>
<td>1 (24)</td>
<td>-</td>
</tr>
</tbody>
</table>

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 2 occasions both animals used the same den at the end of their daily activity. H003 male was frequently

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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 contact with only one female; the smaller male exhibited monogamous behaviour, maintaining contact with only one female. The differences in body mass appeared to be the only factor explaining the variations in social behaviour and mating tactics of these Egyptian mongoose males.

Les comportements sociaux et systèmes d’attirage de quatre mâles d’H. ichneumon (Herpestes ichneumon) mis en évidence au cours de la présente étude (Estación Biológica doñana, CSIC, Avenida María Luisa s/n, 41013 Seville, Spain).
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).

![Graph showing monthly 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 spa-
tially 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 relation-
ship 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 1992b), therefore, differences in resource hol-
ding 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 compo-
sition) 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 opportunistic 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 affect-
ing 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, Pac-
ker et al. 1986), it would indicate that a pleiotropic factor (body mass) affects repro-
ductive success in males of a polygynous carnivore. Although in several species of ani-
imals reproductive success has been related to body size (e.g. Schagwemeyer and Brown
1983, for the ground squirrel, Spermophilus tridecemlineatus; Lawrence 1987, for
two-knobbed beetle, Tenebrio terrestris; Howard 1988, for bullfrogs, Rana cates-
beinu, 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 male guarding behaviour than bigger ones both in and
out of the mating period. This can be an adaptive process of smaller males to com-
pro mise for their lower access to females: 1) Males with a greater mate guarding beha-
viour will have a greater probability of assuring paternity; and 2) they could increase
their final reproductive success (offspring recruitment) by protecting female and off-
spring against predators and assisting the female in feeding offspring. This observation
which is compatible with this hypothesis was obtained when H007’s pregnant female
was favoured with male presence when an Iberian lynx, Felis pardinus, tried to chase
them (Palomares and Delibes 1993). H007 fought with the lynx, while the female esca-
ped. 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 coopera-
tive 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 advan-
tages, 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 adaptive 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.
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