Comparative behaviour and ecology of two sympatric mongoose species (*Cynictis penicillata* and *Galerella pulverulenta*)

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The activity, movements, home range size, habitat selection, social structure, density, pattern of faeces deposition, anti-predator behaviour, diet, and availability and distribution of the main food sources of two mongoose species [the yellow mongoose *Cynictis penicillata* and the Cape grey mongoose *Galerella pulverulenta (= Herpestes pulverulentus*) in a coastal area of South Africa are compared. Both species were diurnal. *Galerella* did not use dens, whereas *Cynictis* never rested outside a den. Total distance moved, home range size and density did not differ between the two species. *Galerella* frequented bush, whereas *Cynictis* frequented open fields. The yellow mongoose was more social than the grey mongoose, but the basic social structure was similar. Faeces of *Cynictis* were found in large clumps close to the dens, while those of *Galerella* were more scattered. This parallels the greater constancy of use of the sleeping sites by *Cynictis*. Rodents (> 90% of Cape grey mongoose diet) were much more abundant in the bush, while availability of insects (main food source for the yellow mongoose) was higher in the open fields. Habitat selection, through its effects on anti-predator and feeding strategies, might have been the leading factor in the evolution of sociality in herpestids.

Die aktiwiteitsritmes, bewegings, tuisgebiedgrootte, habitatseleksie, sosiale struktuur, digtheid, patroon van misverspreiding, teen-roofdier gedrag, dieet en die beskikbaarheid en verspreiding van die hoof voedselbronne van twee muishondspesies [die geelmeerkat *Cynictis penicillata* en die klein grysmuishond *Galerella pulverulenta* (= *Herpestes pulverulentus*)] in 'n kusgebied in Suid-Afrika word vergelyk. Albei spesies was daglewend. *Galerella* het nooit van gate gebruik gemaak nie, terwyl *Cynictis* weer nooit buite sulke gate gerus het nie. Die totale afstand beweeg, tuisgebiedgrootte en digtheid van die twee spesies het ooreengestem. Die geelmeerkat was meer sosiaal as die klein grymuishond maar hul sosiale struktuur was dieselfde. *Galerella* het die bebosde dele en *Cynictis* die ou landerye verkies. Die mis van *Cynictis* het in groot hope naby gate voorgekom, terwyl dié van *Galerella* meer verspreid was. Dit stem ooreen met die gereelde gebruik van gate deur *Cynictis*. Knaagdiere (> 90% van die klein grymuishond se dieet) was baie meer talryk in die bebosde dele, terwyl insekte (die hoof voedselbron van *Cynictis*) weer meer volop was in die ou landerye. Habitatseleksie se uitwerking op teen-roofdier- en voedingstrategieë kon die aanleidende faktor gewees het in die evolusie van sosialiteit in die Herpestidae.

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The social behaviour of the 36 mongoose species (Herpestidae) ranges from solitariness to highly integrated groups (Rood 1986). The first attempts at analysing comparatively the evolution of sociality in herpestids have been partly frustrated by: (i) the lack of data on most species of this family (Rood 1986); (ii) the ecological and behavioural flexibility that carnivores often show as a response to different patterns of resource distribution (Macdonald 1983). Further data on most species are clearly needed (Maddock & Perrin 1993; Rood 1986).

From comparative studies, it is clear that the combination of small size, diurnal activity rhythms, and insectivorous diet is a necessary (although not sufficient) condition for group living in herpestids (Gorman 1979; Rood 1986). It has been hypothesized that insectivory allows group formation, while predation causes it (Rood 1986). Predation pressure is very difficult to measure in the field, and has been evaluated in only two species (*Helogale parvula* and *Mungos mungo*; Rasa 1986; Rood 1983). However, it is not necessary to postulate increased predation as a cause for sociality, because different habitat structure and predator assemblages lead to different anti-predator strategies, one of which may be communal defence and vigilance (Lima 1992).

The invasion of open grasslands is a recent phenomenon for herpestids (Lynch 1981; Taylor & Meester 1993b). The facts that (i) no grassland species is primarily a vertebrate feeder; (ii) while several species living in grassland (*Paracynictis, Ichneumia, Rhynchogale*), and some diurnal species (*Herpestes*) are solitary, all the diurnal species living in open grassland are social; (iii) only some bush- or forest-living species rest above ground, while all grassland species use a den (Baker 1992; Goldman 1987; Rood 1986; Taylor 1972, 1975, 1987), imply that life in grassland requires unique adaptations, particularly for diurnal animals. A five-species herpestid/viverrid assemblage showed minimum spatial overlap for diurnal animals; avoidance of interspecific interactions may play a role in this context (Maddock & Perrin 1993). This is consistent with current resource partitioning theory, which predicts that coexisting species segregate more often by habitat differences than by food preferences (Schoener 1974).

We hypothesize that: (i) two similar-sized, small (< 1 kg; Smithers 1983) mongooses [the yellow mongoose *Cynictis penicillata* and the Cape grey mongoose *Galerella pulverulenta* (or *Herpestes pulverulentus*)] would differ more widely by habitat selection than by food habits: the species living in the more open habitat would (ii) be more social, (iii) rest in dens, (iv) eat more insects, (v) show different anti-predator adaptations. To control for ecological flexibility, the two species were studied in the same area, so they were exposed to essentially the same array of ecological variables (e.g. weather, food and predators).

Study area, material and methods

Data for the present analysis were taken from the results (published and unpublished) of all studies conducted on the carnivores in the Postberg Nature Reserve (33°5'S, 18°E; 2700 ha), a section of the West Coast National Park, Cape Province, South Africa. The climate is Mediterranean. Average monthly temperatures (max.; min.) range from 14,6°C; 8,7°C in July to 21°C; 13,2°C in February. Annual rainfall averages 253 mm, almost all in winter (Boucher & Jarman 1977). Dominant veld type is West Coast Strandveld (Acocks 1975). Over 80% of the area is covered by a complex mosaic of scrubby associations (hereafter 'bush'), especially of the communities *Atriplex-Zygophyllum* and *Ehrharta-Maurocenia*. The rest of the area (20%), cultivated until 1969, is covered by short (≤ 10 cm) grass (Boucher & Jarman 1977). The following studies were reviewed: on the diet and dietary overlap of the small carnivores of the reserve (Macdonald & Nel 1986); on the summer ranging behaviour and feeding ecology of the Cape grey mongoose (Cavallini & Nel 1990a; Cavallini & Nel 1990b); on the autumn ranging behaviour and activity budget of the yellow mongoose (Cavallini 1993a; Cavallini 1993b); on the diet of the yellow mongoose (Avenant & Nel 1992); two unpublished student's projects: (i) on the winter ranging behaviour of the Cape grey mongoose (Wolff 1989); (ii) on the insect availability (Smit 1989); and unpublished data. Mongooses were trapped and equipped with radio-collars, and methodologies for data collection were similar across the studies.

The following data were analysed:

- beginning and end of activity was recorded by means of fluctuation in the intensity of radio signals and (whenever possible) by direct observation
- movements were evaluated by the linear distance between successive locations recorded every 15 min
- home range size was measured by minimum convex polygon (Hayne 1949) and harmonic mean (Dixon & Chapman 1980; 95% contour) methods; the first, being widely used, allows a comparison with other studies, whereas the second reduces the importance of excursions outside the usual range and allows the determination of the core area
- habitat selection was recorded by visually classifying the habitat at each location (as determined by radio-telemetry)
- social structure and density (by an analysis of range overlap, captures and direct observation)
- patterns of faeces deposition (by direct counts along transects on foot)
- diet was examined by faecal analysis; identification of scats was confirmed by the presence of *Cynictis* or *Galerella* hair.

The diet composition was evaluated with the estimated volume method (Kruuk & Parish 1981). To estimate percentage volume, the total number of each kind of prey were counted or estimated for each sample; the number of items was multiplied by the bulk of each prey before ingestion, and the proportion of total bulk for each food category was estimated; the average proportion across samples is therefore an estimate of the volume of ingested food

- availability and distribution of the main food sources (by live trapping and mark–recapture for small mammals, by direct counts along transects on foot and sticky traps for insects)
- anti-predator response (by observing the reactions to the approach of a man walking slowly towards the mongoose).

Results are given as means ± *S.D.* Standard nonparametric tests (Siegel & Castellan 1988) were used: Mann-Whitney's *U* (hereafter M), Wilcoxon matched-pairs signed-ranks test (hereafter W), Spearman rank correlation (hereafter S). All probability values were two-tailed.

Results

Trapped mongooses of the two species had very similar masses (0,86 ± 0,10 kg for *Cynictis* and 0,86 ± 0,09 kg for *Galerella;* M, $p > 0{,}8$; $n_1 = 11$, $n_2 = 5$). Both species were diurnal, usually starting activity shortly after sunrise and stopping around sunset (Table 1). From March–May (autumn), yellow mongooses started and stopped at approximately the same time as the Cape grey mongooses in April–July (M, start: $p > 0{,}4$; stop: $p > 0{,}9$; $n_1 = 65$, $n_2 = 7$), but started significantly later and stopped significantly earlier than Cape grey mongooses in November–February (summer; M, $p < 0{,}001$; $n_1 = 65$, $n_2 = 31$). The same results were obtained for the differences in time between the sunrise and the start of activity times, and those between the sunset and the stop of activity times. Both species occasionally rested around midday for variable lengths of time. While Cape grey mongooses did not use dens (at least in November–February, outside the breed-

Table 1 Activity, movements, home range size, habitat selection, social structure, density, pattern of faeces deposition, diet, and availability and distribution of the main food sources of the yellow mongoose *Cynictis penicillata* and the Cape grey mongoose *Galerella pulverulenta* in a coastal area of South Africa. Data given as means ± *S.D.* NS = no significant difference ($p > 0{,}05$)

Variable	*Cynictis*	*Galerella*
Body mass	0,86 ± 0,10 kg, *n* = 11	0,86 ± 0,09 kg, *n* = 5, (NS)
Activity	Diurnal	Diurnal
Movements	3230 ± 1135 m/day	4060 ± 960 m/day (NS)
Home range size (harmonic mean)	84 ± 31 ha	53 ± 9,5 ha (NS)
Home range size (minimum convex polygon)	102 ± 32 ha	68 ± 21 ha (NS)
Habitat selection	Open fields (99%)	Bush (100%)
Social structure	Loose sociality	Mostly solitary
Density	6–7,1 individuals/100 ha	< 10 individuals/100 ha
Pattern of faeces deposition	Clumped, close to dens	Small groups, distribution similar to sleeping places
Diet	Insects (65%), small mammals (27,5%)	Small mammals (> 90%), insects (< 5%)
Distribution of food	Insects more abundant in open fields	Small mamals more abundant in bush

ing season), yellow mongooses never rested outside a den.

Average distance moved per day was 3230 ± 1135 m for yellow mongooses and 4060 ± 960 m for Cape grey mongooses, and the average movements per hour did not differ between male *Cynictis* and male *Galerella* (W, $p > 0,5$; $n = 17$; Table 1). The same analysis was not performed for females, since only one adult female *Galerella* was radio-tracked. The activity rhythms (metres moved per hour) of the two species did not follow the same pattern (i.e. they were not correlated; S, $p > 0,1$; $n = 17$). Male yellow mongooses moved an average of 292 ± 140 m per hour during daytime (range: 81–490 m), females 228 ± 89 m (range: 71–332 m); male Cape grey mongooses moved 224 ± 84 m per hour (range: 32–347 m), and females 283 ± 86 m per hour (range: 140–410 m). Male home range sizes did not differ significantly between the species, either according to the minimum convex polygon (Hayne 1949; *Cynictis* = 102 ± 32 ha; *Galerella* = 68 ± 21 ha; M, $p = 0,127$; $n_1 = 3$, $n_2 = 3$) or according to the 95% harmonic mean (Dixon & Chapman 1980; *Cynictis* = 84 ± 31 ha; *Galerella* = 53 ± 9,5 ha; M, $p = 0,127$; $n_1 = 3$, $n_2 = 3$). Core areas (50% harmonic mean) of *Galerella* were smaller than those of *Cynictis* (7,5 ± 2 ha *vs.* 20 ± 12 ha; M, $p = 0,050$; $n_1 = 3$, $n_2 = 3$). The size of the home range of the only adult female Cape grey mongoose tracked (minimum convex polygon, 30,6 ha) was similar to that of female yellow mongooses (10,5–49,3 ha; $n = 4$). Habitat selection differed strikingly between the two species: while *Galerella* were never located outside the bush (although it was seen once at its margins), over 99% of *Cynictis* locations were in the short-grass plains.

Social structure of the Cape grey mongoose is characterized by a large range overlap among males, and loose associations between some of the males. Territoriality among females cannot be ruled out. The yellow mongoose is much more social, males and females denning together, synchronizing their activity and occasionally foraging close to each other. Also in *Cynictis*, however, overlap among males was substantial, while the ranges of female groups showed almost no overlap. Density of the two species is similar, being estimated at 6–7,1 individuals/100 ha for *Cynictis*, and less than 10 individuals/100 ha for *Galerella*. Cape grey mongoose faeces were located singly or in small and medium groups (mostly under 10 scats), often close to the sleeping sites. On the other hand, yellow mongoose faeces have been found only in large (> 50 scats) clumps close to the dens.

The diet of the Cape grey mongoose is dominated (> 90% by volume) by small mammals, minor items being insects (less than 5%), while the yellow mongoose ate mostly insects (65% by volume) and small mammals (27,5% by volume). The mean availability of insects was higher (M, $p < 0,01$) in the open fields (418,8 insects/m^2 of sticky traps) than in the bush (270 insects/m^2. The difference was even greater (M, $p < 0,001$) when considering only the daytime insect captures (235,4 *vs.* 125 insects/m^2). Furthermore, termites (*Microhodotermes viator*; the most heavily utilized insect species by *Cynictis*) were recorded only during transects in the open fields. The two main rodent prey species were abundant in the bush (*Rhabdomys pumilio*: 93,3 individuals/ha; *Otomys unisulcatus*: 61,5 individuals/ha), but very scarce (*Rhabdomys*: less than 10 individuals/ha) or absent (*Otomys*: no nests recorded) in the open fields, being present only at the edges of the fields.

No instance of attack by predators was observed, but when approached by a human observer, the Cape grey mongoose quickly took refuge in thick bush ($n = 3$), while the yellow mongoose ran for up to 150 m to a shallow hole or to one of the dens ($n = 7$). As the species names imply, the coat colour is very different between the two species, and matches well the dominant colour of the habitat frequented. As a result, the dark *Galerella* is especially visible in the open fields (pers. obs.).

Discussion

The average home range size of male yellow mongooses (minimum convex polygon: 102 ha) is closer to the value (113 ha) predicted from Harested & Bunnell's (1979) equation for carnivores (home range size = $0,011 \times \text{weight}^{1,36}$) than that of male grey mongooses. Ranges of females were all substantially smaller. According to Gittleman & Harvey (1982), home range of a carnivorous species should be larger than that of an insectivorous species of the same size. The influence of group size (which tends to increase home range size; see also Rood 1986) is difficult to quantify, given the loose group structure in both species. The home range size was not significantly larger in the insectivorous, more social species (*Cynictis*) than in the carnivorous, almost solitary one (*Galerella*). The two tendencies (larger home ranges for carnivores than insectivores, and for group-living than for solitary species) therefore balance each other in this case (with a possible prevalence of group size). Also, activity patterns and the extent of movements did not differ between the two species. Use of the home range was, however, different, *Galerella* concentrating activity in a smaller core area. The beginning and end of daily activity was related to season rather than to species. The pattern of scat deposition may be essentially the same in the two species, with larger clumps reflecting merely the more frequent use of the same sleeping site by *Cynictis*. Defecating close to resting sites might be a general phenomenon for herpestids (see also Palomares 1993).

All our predictions were confirmed by data: (i) whereas habitat selection was strikingly different between the two species, *Cynictis* selecting more open habitats (a result consistent with other studies: Stuart 1981, 1991), food habits showed some overlap; (ii) *Cynictis*, living in grassland, is more social than the bush-dwelling *Galerella*; (iii) only *Cynictis* used underground dens; (iv) insects were an important food resource for the grassland species (*Cynictis*), but not for *Galerella*; (v) anti-predator adaptations differed between the two species: coat colours matched the respective habitat, and escape behaviour was markedly different (a quick dash into the nearest bush for *Galerella*, a long run towards a den for *Cynictis*).

The more insectivorous diet of *Cynictis* may be a secondary adaptation to the higher insect availability in the open fields. In fact, the yellow mongoose retains the ability to hunt small rodents (Cavallini 1992b), presumably the usual prey of ancestral mongooses. Furthermore, both species have a dentition well adapted to kill small vertebrates, with slicing carnassials (Ewer 1973; Smithers 1983; Cavallini 1992a; Taylor & Meester 1993a), although the yellow mongoose shows some dental adaptation for crushing soft food (Taylor & Meester 1993a). Small mammals are still an important food source for *Cynictis*, in spite of their relative scarcity in the open fields. Dietary, behavioural, and morphological differences may therefore be secondary results of different habitat selection. This is consistent with the opportunistic feeding habits observed in other mongoose species (e.g. Cavallini & Serafini 1995). We predict that in their largely overlapping geographic ranges (Cavallini 1992a; Taylor & Meester 1993a): (i) the dietary overlap between the two species will be variable in space and time, according to the relative availability of small mammals and invertebrates in closed and open habitats; (ii) the habitat overlap will remain low, *Galerella* consistently selecting more bushy areas than *Cynictis*. Further observational and experimental studies throughout the overlapping ranges of the two species are needed to test these predictions.

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