The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose

Jason S. Gilchrist and Emily Otali

Abstract: The effects of food availability and distribution on population dynamics have been the subject of numerous experimental studies, but no study has quantified the effects of a concentrated supplementary food supply on groups of a social carnivore. We investigated the effects of refuse-feeding at garbage dumps on banded mongoose (*Mungos mungo*) groups. Garbage dumps represent a reliable, concentrated source of food. Data were collected from three refuse and seven nonrefuse-feeding groups in Queen Elizabeth National Park, Uganda. Groups were located using radiotelemetry, and home-range size and use, group size and population density, and intergroup encounter rate were analysed. Although refuse-feeding groups had home ranges similar in size to those of nonrefuse-feeding groups, their home-range use was more concentrated and their core areas always included the available predictable garbage dumps. Two of the three refuse-feeding groups were larger and denser than other groups. The two groups that shared the same garbage dump had significantly higher intergroup encounter rates than all other groups and their encounters occurred at the shared dump.

Résumé : Le effets de la disponibilité et de la répartition de la nourriture sur la dynamique des populations ont fait l'objet de nombreuses études expérimentales, mais personne n'a tenté de quantifier les effets de surplus de nourriture concentrée sur les groupes de carnivores sociaux. Nous examinons ici les effets de l'alimentation dans des dépotoirs chez des groupes de mangoustes rayées (*Mungos mungo*). Les dépotoirs constituent une source concentrée et fiable de nourriture. Des données ont été recueillies chez trois groupes alimentés en dépotoir et chez sept groupes alimentés ailleurs dans le Parc national Queen Elisabeth, en Ouganda. Les groupes ont été repérés par radio-télémétrie; la taille et l'utilisation des domaines, la taille des groupes, la densité des populations et les interactions entre les groupes ont été analysées. Bien que les domaines aient été de même taille chez les deux groupes, les mangoustes nourries de déchets utilisaient leurs domaines de façon plus concentrée et, comme on pouvait le prévoir, le coeur de leurs domaines contenait toujours les dépotoirs locaux. Deux des trois groupes nourris aux dépotoirs étaient plus nombreux que les autres groupes et leur densité était plus élevée. Les deux groupes qui fréquentaient le même dépotoir avaient des taux de rencontre plus élevés que tous les autres groupes et leurs rencontres avaient lieu au dépotoir.

[Traduit par la Rédaction]

Introduction

The distribution and abundance of animals often depend to a large extent on food availability and abundance (Lack 1954). This may be especially significant for group-living species, for which it has been suggested that food availability is a determinant of home-range size and group size (Macdonald 1983). If this is the case, groups given supplementary food would be expected to differ in home-range size and group size from groups in a similar environment without access to supplementary food.

Home-range size is generally the minimum necessary to provide the key resources (e.g., food, shelter, and mates) required by an individual or group. The availability of food is likely to be a primary determinant of home-range size (Mace et al. 1983). In a wide variety of animals, home-range size is inversely related to habitat productivity and food availability (e.g., Simon 1975; Tufto et al. 1996; Lee and Hauser 1998; Lurz et al. 2000; but see Arvidsson et al. 1997). If home-range area is determined by food availability, providing extra food should lead to a decrease in home-range size because an animal's or group's nutritional requirements are met by a smaller area (Akbar and Gorman 1993*b*; Simon 1975; Taitt 1981; Taitt and Krebs 1981).

An increased, reliable food source will support a larger or denser population unless the population is limited by other factors (Dobson and Kjelgaard 1985). Food can affect population size and density through its effects on demographic processes: natality, mortality, and dispersal. These processes are generally also regulated by predation, parasitism, disease, and intraspecific social interactions. In group-living species, similar processes govern group size and population density, but these will also be complicated by social relationships between groups, specifically intergroup interactions. As variation in density among populations has often been shown to be due to variation in the availability or quality of food (e.g., Kruuk and Parish 1982; Van Orsdol et al. 1985; Chapman

Received 4 January 2002. Accepted 26 June 2002. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 19 November 2002.

J.S. Gilchrist.[1] Department of Zoology, University of Cambridge, Downing Street, CB2 3EJ, Cambridge, U.K.
E. Otali. Makerere University Institute of Environment and Natural Resources, P.O. Box 7298, Kampala, Uganda.

[1] Corresponding author (e-mail: jsg24@cam.ac.uk).

DOI: 10.1139/Z02-113

and Chapman 1999), food supplementation should increase the carrying capacity of an area (see Akbar and Gorman 1993*a* and references therein).

Concentration of home-range use at concentrated sources of food may lead to an increased frequency of encounters between groups sharing access to these sources, and aggression could result. Attraction to a rich and reliable food source may therefore lead to competition between groups, and possibly be the motivation for persistent defence (Brown 1976; Robb and Grant 1998 and references therein). However, the extent to which an individual or group is territorial is based upon the defensibility of a resource, therefore the value of the resource will be offset against the costs of defence (Brown 1976). Home ranges could therefore overlap more extensively where resources are more abundant (see Boutin 1990), and where the net benefits of territory defence are reduced (e.g., Jonkel and McCowan 1971; Waser and Waser 1985). However, defence of a concentrated food source may be more feasible for group-living species, since a group can monopolise a resource more effectively than an individual. Communal resource defence may be especially easy for carnivores, which are generally more able to inflict injury on opponents than are herbivores.

The importance of food in affecting population dynamics has been assessed in numerous studies by experimentally increasing food availability (see Boutin 1990 and references therein). However, no study has quantified the effects of a concentrated supplementary food source on the population dynamics of a social carnivore. We tested the effect of food availability on home-range use and group size in a highly social, group-living carnivorous mammal by comparing refuse-feeding and nonrefuse-feeding groups of banded mongooses (*Mungos mungo* Gmelin, 1788) within Queen Elizabeth National Park, Uganda. For banded mongooses, which naturally forage on dispersed invertebrate prey (Rood 1975), food in garbage dumps represents a highly clumped resource. Our study therefore also contributes to the understanding of the effects of garbage dumps on the ecology of wild animals. This is especially relevant to the management of national parks, where human habitation and refuse sites often occur within or on the boundary of parks, and may affect the population dynamics of the species within them.

We compared home-range size and use, group size and population density, and intergroup encounter rate between refuse-feeding and nonrefuse-feeding groups. We predicted that, compared with nonrefuse-feeding groups, refuse-feeding groups would (*i*) have smaller home ranges and be more concentrated in their home-range use, with core areas located at garbage dumps; (*ii*) live in larger groups, at higher densities; and (*iii*) have a higher intergroup encounter rate where they share access to a garbage dump, and have encounters at the shared garbage dump.

Methods

Study species

The banded mongoose is a social, diurnal small carnivore classified in the family Herpestidae (Wozencraft 1982). Banded mongooses are widely distributed in woodlands, savannahs, and grasslands of eastern, central, and southern Africa (Kingdon 1997). They feed on termites, millipedes, dung beetles, beetle larvae, and occasionally small vertebrates (Rood 1975). They live in groups of 5–40 that typically consist of more than one breeding female and male (Cant 2000; Rood 1975). Groups can breed up to 4 times a year (Gilchrist 2001).

Study site

Fieldwork was carried out on and around Mweya peninsula, Queen Elizabeth National Park, southwestern Uganda (0°12′S and 27°54′E). The climate is equatorial, with little annual fluctuation in day length or temperature. The vegetation of the study site is predominantly short and medium fire climax grassland with numerous dense thickets dominated by *Capparis tomentosa* growing in association with *Azima tetracantha* and *Euphobia candelabrum* (Lock 1977; Spinage 1982). Mweya peninsula, which covers 4.95 km^2, houses the headquarters of the national park and a village. This contains a stable population of approximately 500–700 park and lodge staff, plus additional tourists, and hence numerous small garbage dumps where waste food is available. We monitored 401 banded mongooses from January 1998 to January 2000, in 10 groups, 3 of which had garbage dumps in their home range (see Table 1). Behavioural and demographic data were collected on all groups, including one group just outside the peninsula. We use the same group-identification numbers as Cant (2000) and De Luca and Ginsberg (2001).

We define garbage dumps as human refuse disposal sites. The foodstuffs available to mongooses at garbage dumps included meat, fish, fowl, gravy, rice, and a variety of local foods. Although we were unable to quantify the waste food available to mongooses at a site, a daily supply of food was available at predictable garbage dumps (the lodge kitchen bins, the main dump, and the canteen dump). Availability of food at the unpredictable small garbage dumps within the village depended upon villagers cooking meat or fish. Although food was often available within the village, it was scattered and less concentrated than at the predictable sites. Group 1*b* visited the lodge kitchen and village dumps, groups 1*d* and 2 visited the main dump, and group 2 also visited the canteen dump (see Fig. 2).

Locating and monitoring groups

One or two individuals in each group were fitted with a 150- to 152-MHz radio transmitter (model MMK7, Telonics Inc., Mesa, Arizona) attached to a collar and detectable at a range of 500–1000 m. Details of the trapping and immobilization procedure are described by Cant (2000; Cant et al. 2001). Groups were located using a receiver (model TR4, Telonics Inc.) fitted with antenna (Biotrack, Wareham, U.K.). Radio-collared individuals were located by homing in on the animal (White and Garrot 1990), following the transmitted signals as they increased in strength until the animal was seen, or to the nearest 5 × 5 m area if the group was in cover.

We usually visited each group once in the morning and once in the afternoon each day during their active period (between 07:00 and 19:30). On each visit to a group we recorded the location at which the animals were first found. Locations were recorded on a 1:5000 map of Mweya peninsula, drawn and fitted with a *x*–*y* grid of 100 × 100 m (1 ha) squares based upon an aerial photograph. We recorded the start and end times of each visit to a group. A group census

Table 1. Home-range use, group sizes, and intergroup interactions of banded mongoose (*Mungos mungo*) groups.

Group	Status[a]	No. of visits	MCP[b] (ha)	Kernel home range (ha)[c]	Kernel core area (ha)[d]	Group size[e]	No. of adults	No. of subadults	No. of infants	No. of pups	Observation time (h)	No. of intergroup encounters[f]
1*b*	R	534	141	66.4	2.4	24 ± 7.0	13	7	4	4	950	8
1*d*	R	131	100	56.7	2.5	9 ± 0.4	9	0	0	1	158	15
2	R	469	115	87.2	2.5	28 ± 3.7	21	5	2	3	531	27
1*c*	N	161	335	200.9	17.0	14 ± 2.4	10	2	2	2	205	1
1*h*	N	31	74	118.3	12.1	9 ± 0.0	9	0	0	1	42	0
4	N	116	107	76.5	6.7	10 ± 4.2	9	0	1	1	88	1
4*b*	N	395	96	61.1	3.8	12 ± 1.7	10	2	1	2	385	8
5	N	182	173	100.6	8.2	12 ± 2.4	7	4	1	1	167	6
7	N	223	90	76.2	5.7	14 ± 3.0	10	2	1	1	215	4
11	N	284	123	60.9	3.4	11 ± 1.6	9	1	1	1	255	4

[a] R, refuse-feeding group; N, non-refuse-feeding group.

[b] Minimum convex polygon (100%).

[c] Area within 95% volume contour from fixed kernel analysis.

[d] Area within 25% volume contour from fixed kernel analysis.

[e] Average (± standard error) of all adults, subadults, and infants counted on the first visit of each month.

[f] Number of intergroup encounters occurring during the observation time.

was conducted at the beginning of each visit. If the focal group had an encounter with another group during observations, the identity of the second group and the location of the encounter were recorded.

Home-range use

Home-range analyses were conducted using the fixed-kernel method (Seaman and Powell 1996; Silverman 1986; Worton 1989; Worton 1995). Analysis used the Home Ranger (version 1.5) software package (http://nhsbig.inhs.uiuc.edu/www/home_range.html), with a 70 × 70 grid and least-squares cross-validation smoothing, following standardization of the data to multivariate normal scores. Home-range size for each group was defined as the area within the 95% volume contour. The core area of use for each group was defined as the area within the 25% volume contour. In Table 1 we include home-range estimates calculated by means of the minimum convex polygon (MCP) method (calculated using the Antelope version 1.3 software package: http://nhsbig.inhs.uiuc.edu/www/home_range.html). Although MCP is generally regarded as a less efficient method of home-range estimation, it is repeatable across different software analysis programs and therefore the results are comparable with those of other studies (Harris et al. 1990; Larkin and Halkin 1994; Lawson and Rodgers 1997). We measured the overlap in home-range areas between each group and another using Map Maker Basic 3.0 (http://www.mapmaker.com).

During "babysitting" periods (Cant 2002), when there were pups in the den, groups moved less (paired *t* test, $t_{10} = -4.85$, $P = 0.001$) (home-range size: babysitting periods: 40.0 ± 10.7 ha (mean ± SE); non-babysitting periods: 90.5 ± 13.7 ha). Analysis was therefore restricted to visits when groups were not babysitting. Points may be considered biologically independent if an animal has time to cross its home range between relocations even though it might not do so (see Harrison 1997 and references therein). Banded mongooses are highly mobile, and the minimum relocation interval (92 min) was long enough for groups to cross their home range (J.S.G., unpublished data).

Group size and population density

Individuals were categorized by age as follows: adult, older than 365 days; subadult 183–364 days; infant, 91–182 days; pup, 0–90 days. For each group the numbers of individuals in each age category on the first visit of all months were averaged over the study period. Group size was defined as the average number of adults, subadults, and infants. Pups were counted only after emergence, usually 20–30 days after birth, and were excluded from the calculation of group size because of their dependence on adults. For each group, population density was calculated as group size / home-range size.

Encounter rate

For analysing intergroup encounters, we calculated the encounter rate per group as the total number of encounters (for the focal group) / total observation time. To test whether groups that shared access to a garbage dump had more encounters at the shared garbage dump than in other areas, we compared the encounter rate per group at the shared garbage dump grid square and all other grid squares with the encounter rate that would be expected on the basis of the relative proportions of grid squares in their home range. The expected frequency of intergroup encounters at the shared dump or all other grid squares was calculated as (number of garbage dump or other grid squares / total number of home-range grid squares) × total number of encounters. The goodness-of-fit test (*G* test; Sokal and Rohlf 1995) was used to test whether the frequency of observed encounters at the shared garbage dump grid square and other grid squares was equal to the expected frequency of encounters.

Statistical analysis

Statistical analyses were performed using MINITAB 12 (Minitab Inc. 1998) and Genstat 5.4 (Lawes Agricultural Trust, Rothamsted, U.K., 1998). We used the Mann–Whitney *U* test to compare values between refuse-feeding and nonrefuse-feeding groups in all analyses except home-range overlap. For home-range overlap we analysed the overlap (square root transformed) between each group and every other group with which it overlapped using restricted-estimate maximum likelihood (REML), with group identity as a random term. For comparisons of observed and expected frequencies we used the *G* test. All tests were two-tailed with the significance level $P \leq 0.05$.

Results

Home-range use

There was no significant difference between the home-range sizes of refuse-feeding and nonrefuse-feeding groups (Mann–Whitney *U* test, $U = 12.0$, $N_r = 3$, $N_n = 7$, $P = 0.362$; Fig. 1*a*). Group size and home-range size were not correlated (Spearman's rank correlation (r_S), = 0.304, $N = 10$, $P = 0.394$, for all groups; $r_S = -0.079$, $N = 7$, $P = 0.866$, for nonrefuse-feeding groups; Table 1).

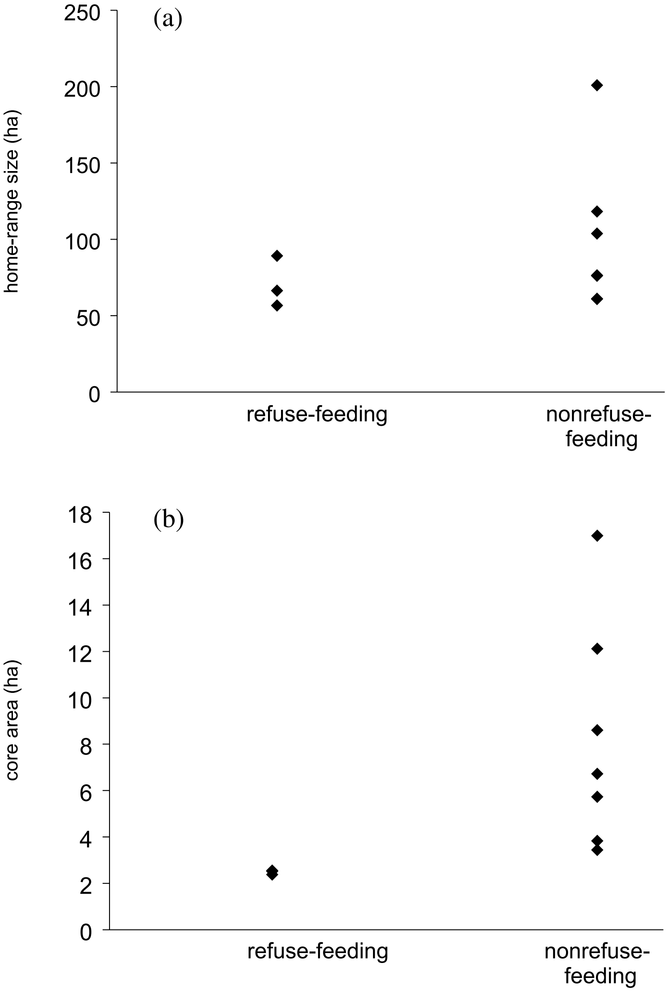
However, refuse-feeding groups concentrated their home-range use more than nonrefuse-feeding groups did. The core area used by refuse-feeding groups (both the actual core area and the proportion of the home range constituted by the core area) was smaller than that used by nonrefuse-feeding groups (Mann–Whitney *U* test, $U = 6.0$, $N_r = 3$, $N_n = 7$, $P = 0.023$; Fig. 1*b*). All refuse-feeding groups included the predictable garbage dumps (within their home range) in their core area (Fig. 2).

There was no significant difference in the area of home-range overlap (with each overlapping group) between refuse-feeding and nonrefuse-feeding groups (REML, $\chi^2 = 0.32$, df = 1, $P = 0.57$).

Group size and population density

There was no significant difference in group size (mean number of individuals, excluding pups) between refuse-feeding and nonrefuse-feeding groups (Mann–Whitney *U* test, $U = 20.0$, $N_r = 3$, $N_n = 7$, $P = 0.493$; Fig. 3) or in any age category (Mann–Whitney *U* test, adults: $U = 21.5$, $N_r = 3$, $N_n = 7$, $P = 0.304$; subadults: $U = 20.5$, $N_r = 3$, $N_n = 7$, $P = 0.424$; infants: $U = 20.5$, $N_r = 3$, $N_n = 7$, $P = 0.424$; pups: $U = 20.0$, $N_r = 3$, $N_n = 7$, $P = 0.494$; Table 1). Similarly, there was no significant difference in population density between refuse-feeding and nonrefuse-feeding groups (Mann–Whitney *U* test, $U = 24.0$, $N_r = 3$, $N_n = 7$, $P = 0.111$; Table 1). However, it is clear that one refuse-feeding group (1*d*) was substantially smaller than the other two refuse-feeding groups, which were themselves substantially larger, and denser (more individuals per hectare), than the nonrefuse-feeding groups (Fig. 3, Table 1).

Fig. 1. Utilization-distribution estimates for refuse-feeding and nonrefuse-feeding groups of banded mongooses (*Mungos mungo*). (*a*) Home-range sizes (area within the 95% volume contour fixed kernel estimated utilization distribution). (*b*) Core areas (area within the 25% volume contour fixed kernel estimated utilization distribution).



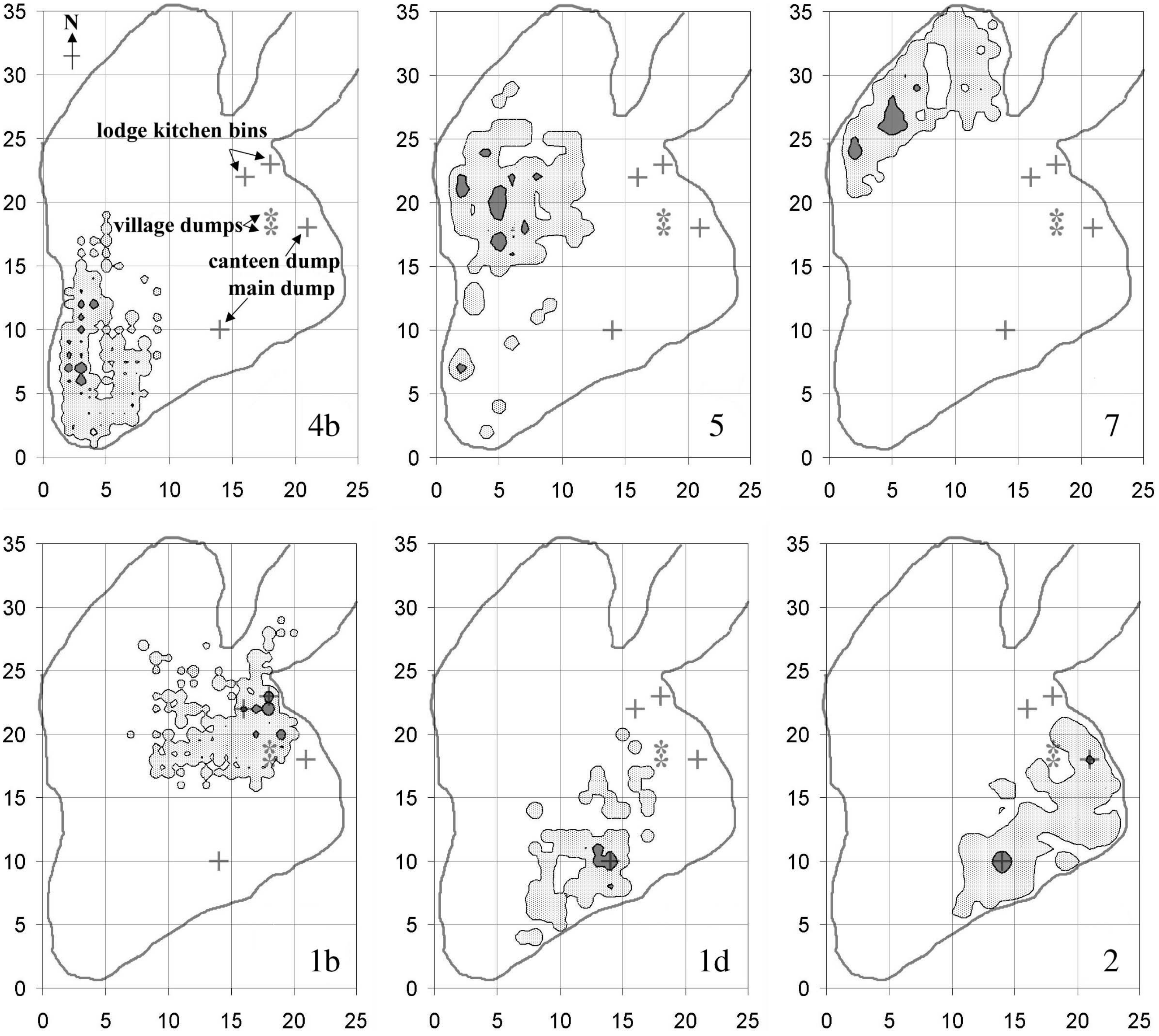
Encounter rate

The two refuse-feeding groups that shared access to a garbage dump (groups 2 and 1*d* at the main dump), and therefore had the opportunity to compete for access to refuse, had a significantly higher intergroup encounter rate than all other groups (Mann–Whitney *U* test, $U = 19.0$, $N_{2 \text{ or } 1d} = 2$, $N_{\text{others}} = 8$, $P = 0.050$; Fig. 4)[2]. The groups that shared the same refuse area had a higher intergroup encounter rate in the shared

---

[2] There was no significant difference in intergroup encounter rates between refuse-feeding and nonrefuse-feeding groups (Mann–Whitney *U* test, $U = 22.0$, $N_r = 3$, $N_n = 7$, $P = 0.255$; Table 1).

Fig. 2. Maps showing the home ranges of banded mongoose groups on Mweya peninsula. The top three maps show selected nonrefuse-feeding groups and the bottom three maps show the three refuse-feeding groups. The number in the lower right corner of each map is the group identification number. The first map (group 4*b*) also identifies the various garbage dumps. The scale is 1 unit = 100 m. Light shading indicates the home range (95% fixed kernel estimate); dark shading indicates the core area (25% fixed kernel estimate); +, predictable garbage dump; *, unpredictable garbage dump (see the text).



garbage dump grid square than in all other grid squares (*G* test, group 2: $G = 118.19$, df = 1, $P < 0.001$; group 1*d*: $G = 60.50$, df = 1, $P < 0.001$). There was no difference in intergroup encounter rates between refuse-feeding and nonrefuse-feeding grid squares for group 1*b*, which had sole access to the garbage dumps within its home range (*G* test, $G = 0.70$, df = 1, $P = 0.476$).

Discussion

Our results demonstrate that garbage dumps, as a concentrated source of food, affect the home-range use and population dynamics of a social carnivore, the banded mongoose. Refuse-feeding groups used smaller core areas within their home ranges than nonrefuse-feeding groups, and their core areas coincided with predictable garbage dumps. Two of the three refuse-feeding groups were larger and denser than the other groups. The two groups that shared the same garbage dump had significantly higher intergroup encounter rates than any other group, and had such encounters at the shared garbage dump.

Garbage dumps provided a reliable and concentrated food source, but groups with garbage dumps in their home range did not have smaller home ranges than groups without. This result contrasts with those from the majority of food-addition experiments on other species, where home-range size decreases (Boutin 1990). Either some other resource determines home-range size (see Brown 1976), perhaps availability of den sites,

Fig. 3. Mean sizes (number of individuals) of refuse-feeding and nonrefuse-feeding groups.

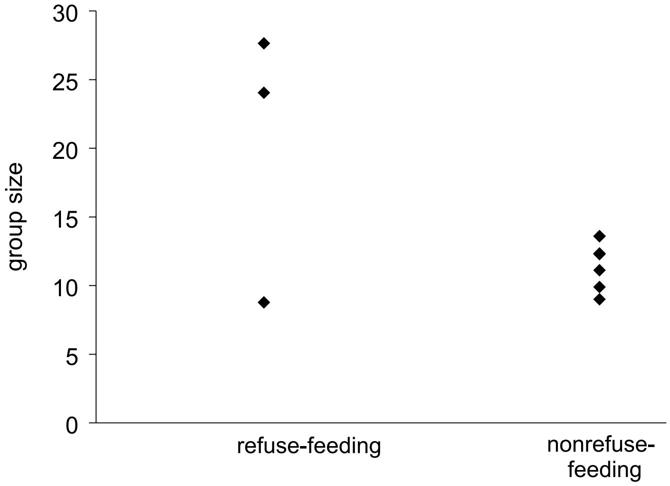
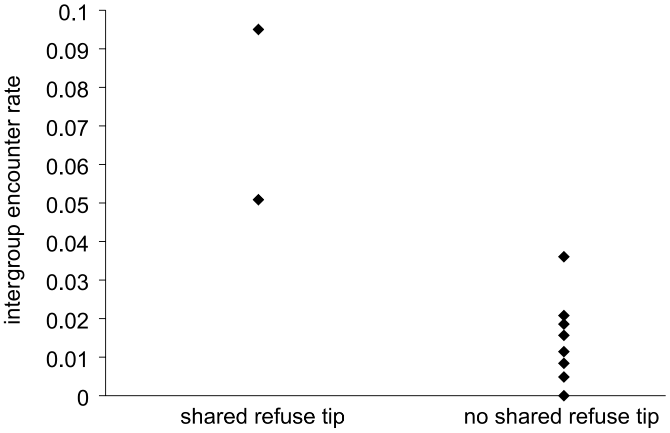


Fig. 4. Intergroup encounter rates (number of encounters per hour) for groups that shared access to a garbage dump and those that did not share access to a garbage dump.



or the food provided by garbage dumps was insufficient (in terms of quality or quantity) to reduce the refuse-feeding groups' natural food requirements. It may be that garbage is indeed "supplementary", and that mongoose groups maintain a home range (or territory) large enough to supply them with an adequate amount of their natural food: invertebrates.

Refuse-feeding groups had smaller core areas than nonrefuse-feeding groups, and their core areas included garbage dumps. Groups will often concentrate their home-range use at sites with concentrated food (e.g., Di Bitetti 2001), and similar clumping of carnivores at garbage dumps has been documented in other carnivore species (see Macdonald 1983). Together with the increased body mass and body condition of individuals in refuse-feeding groups (Otali and Gilchrist 2002), this implies that garbage dumps did offer a reliable and abundant food source. Alternatively, garbage dumps may simply have offered "easier" (rather than more) food than natural areas, as animals tend to prefer "easily" available food (e.g., Mitchell et al. 1981). We did not manipulate the availability of food to groups, but one group experienced a change in status (from refuse-feeding to nonrefuse-feeding) during the study, and the increase in its core area supported the prediction: following a female take-over (where the resident female was displaced by six new females), group 1*d* (subsequently identified as group 11) stopped using the main garbage dump, and the percentage of its home range represented by the core area increased from 4.4 to 5.6% (Table 1).

Group size is commonly correlated with food availability in group-living species (e.g., Kruuk and Parish 1982; Macdonald 1983; Van Orsdol et al. 1985), but there was no difference in the mean numbers of banded mongooses (in any age category) between refuse-feeding and nonrefuse-feeding groups. This suggests that food abundance and reliability do not affect group size or structure. However, two of the refuse-feeding groups were substantially larger and had more individuals in each age category than all other groups. The refuse-feeding group (group 1*d*) with fewer individuals in each age class, and 3 times smaller than the other two refuse-feeding groups, was the only group during the entire study to have only one reproductive female. The reproductive output and success of group 1*d* were therefore low: few pups emerged and none survived to independence (J.S.G., unpublished data). This may explain why this group was substantially smaller than the other refuse-feeding groups.

In contrast to other studies (e.g., Steenbeek and van Schaik 2001), there was no positive correlation between group size and home-range size in this study. Larger groups did not necessarily require a larger home range in order to meet their resource requirements (see Macdonald 1983). However, the two largest groups were refuse-feeding groups (Table 1). Access to refuse may have enabled (*i*) those large groups to reduce their home-range size, or (*ii*) those groups to increase in size without having to increase home-range size. The rapid rate of renewal of the mongooses' natural prey could also explain the lack of correlation between group size and home-range size (Waser and Waser 1985). Despite the low variation in average group size among the nonrefuse-feeding groups, there was substantial variation in home-range size. This could reflect differences in habitat quality (or prey dispersion; Macdonald 1983) between groups.

There was no difference in population density between refuse-feeding and nonrefuse-feeding groups. However, the density (number of individuals per hectare) of group 1*d* was half that of the other two refuse-feeding groups (see above). These other refuse-feeding groups were the largest groups in the study, and had substantially higher densities than all other groups. Therefore, by supporting an increase in group size without an increase in home-range size, garbage dumps may increase population density. Rood (1986) similarly observed that where food is sparsely distributed, mongoose densities are lower. In most studies where supplementary food has been provided to populations, their density has increased (Boutin 1990). Additionally, garbage dumps may support or increase populations (e.g., various gull species, Harris 1970; Patton 1988; Pons and Migot 1995), including some of conservation value (e.g., the grizzly bear (Knight and Eberhardt 1985; Craighead et al. 1995) and European wolf (Ciucci et al. 1997)). Further work is needed to clarify whether garbage dumps do indeed increase population density in social carnivores.

The two groups that shared the same garbage dump (1*d* and 2) had a significantly higher encounter rate than all other groups studied, and were more likely to have encounters at the shared resource than anywhere else in their home range. Sharing a resource is likely to increase competition, which can result in aggression or fights (Robb and Grant 1998). In a study of refuse-feeding herring gulls, Pons (1992) observed most aggressive encounters at the refuse site that offered most food. Fights between banded mongoose groups often resulted in injury, and sometimes death (Cant et al. 2001, 2002; J.S.G. and E.O., personal observations)[3]. Moreover, refuse-feeding groups did not tolerate a greater home-range overlap with other groups than nonrefuse-feeding groups. Clearly, access to a concentrated food source did not lead to a relaxation of territorial behaviour or to increased tolerance of neighbouring groups.

Our conclusions are limited by the number of refuse-feeding groups (three) that we were able to study. In the absence of additional refuse-feeding groups within a similar habitat, future work could consist of manipulating the availability of food to the groups studied, by, for example, denying refuse-feeding groups access to food at the garbage dumps, and providing nonrefuse-feeding groups with a concentrated food source within their home range.

In conclusion, the effects of access to refuse on group-living banded mongooses were apparently both beneficial and detrimental. Although garbage dumps did not decrease home-range size, in two of three groups they supported larger groups and therefore greater population density. This may be seen by wildlife managers as a positive by-product of poor waste disposal; however, competition for access to garbage dumps increased the frequency of intergroup encounters, which can result in injury and even death of individuals. Although garbage dumps are not necessarily bad for banded mongooses, they clearly affect their population dynamics and behaviour. This is unlikely to be desirable in national parks, where one of the usual aims is to conserve the natural balance of the ecosystem.

Acknowledgements

For financial support we thank the Biotechnology and Biological Sciences Research Council, the World Wildlife Fund Prince Bernhard Scholarship Fund, the British Ecological Society, and the Department of Zoology and King's College, University of Cambridge. We thank the Uganda Wildlife Authority and Chief Warden Latif for permission to conduct the study and for logistical support, and Francis Mwanguhya for assistance with data collection. We are grateful to Prof. T.H. Clutton-Brock, Andy Russell, and Peter Neuhaus for commenting on earlier drafts of this paper, and to Mike Cant for assistance in planning the research.

References

Akbar, Z., and Gorman, M.L. 1993*a*. The effect of supplementary feeding upon the demography of a population of woodmice *Apodemus sylvacitus*, living on a system of maritime sand-dunes. J. Zool. (Lond.), **230**: 609–617.

Akbar, Z., and Gorman, M.L. 1993*b*. The effect of supplementary feeding upon the sizes of the home ranges of woodmice *Apodemus sylvaticus* living on a system of maritime sand-dunes. J. Zool. (Lond.), **231**: 233–237.

Arvidsson, B., Askenmo, C., and Neergaard, R. 1997. Food supply for settling male rock pipits affects territory size. Anim. Behav. **54**: 67–72.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can. J. Zool. **68**: 203–220.

Brown, J.L. 1976. The evolution of diversity in avian territorial systems. Wilson Bull. No. 76. pp. 160–169.

Cant, M.A. 2000. Social control of reproduction in banded mongooses. Anim. Behav. **59**: 147–158.

Cant, M.A. 2002. Patterns of helping effort in cooperatively breeding banded mongooses *Mungos mungo*. J. Zool. (Lond.). In press.

Cant, M.A., Otali, E., and Mwanguhya, F. 2001. Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*). J. Zool. (Lond.), **254**: 155–162.

Cant, M.A., Otali, E., and Mwanguhya, F. 2002. Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. Ethology. In press.

Chapman, C.A., and Chapman, L.J. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates, **40**: 215–231.

Ciucci, P., Boitani, L., Francisci, F., and Andreoli, G. 1997. Home range, activity and movements of a wolf pack in central Italy. J. Zool. (Lond.), **243**: 803–819.

Craighead, J.J., Summer, J.S., and Mitchell, J.A. 1995. The grizzly bears of Yellowstone. Island Press, Washington, D.C.

De Luca, D.W., and Ginsberg, J.R. 2001. Dominance, reproduction and survival in banded mongooses: towards an egalitarian social system? Anim. Behav. **61**: 17–30.

Di Bitetti, M.S. 2001. Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. J. Zool. (Lond.), **253**: 33–45.

Dobson, F.S., and Kjelgaard, J.D. 1985. The influence of food resources on population dynamics in Columbian ground squirrels. Can. J. Zool. **63**: 2095–2104.

Gilchrist, J.S. 2001. Reproduction and pup care in the communal breeding banded mongoose. Ph.D. dissertation, University of Cambridge, Cambridge.

Harris, M.P. 1970. Rates and causes of increases of some British gull populations. Bird Study, **17**: 325–335.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T., and Wray, S. 1990. Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. Mammal Rev. **20**: 97–123.

Harrison, R.L. 1997. A comparison of gray fox ecology between residential and undeveloped rural landscapes. J. Wildl. Manag. **61**: 112–122.

Jonkel, C.J., and McCowan, I.M. 1971. The black bear in the spruce pine forest. Wildl. Mongr. No. 27. pp. 5–57.

Kingdon, J. 1997. The Kingdon field guide to African mammals. Academic Press, London.

Knight, R.R., and Eberhardt, L.L. 1985. Population dynamics of Yellowstone grizzly bears. Ecology, **66**: 323–334.

Kruuk, H., and Parish, T. 1982. Factors affecting population-density, group-size and territory size of the European badger, *Meles meles*. J. Zool. (1965–1984), **196**: 31–39.

Lack, D. 1954. Natural regulation of animal numbers. Clarendon Press, Oxford.

---

[3] However, although mortality rates were relatively high, the rate was not significantly higher in refuse-feeding groups, except for male pups (Otali and Gilchrist 2002).

Larkin, R.P., and Halkin, D. 1994. A review of software packages for estimating animal home ranges. Wildl. Soc. Bull. **22**: 274–287.

Lawson, E.J., and Rodgers, A.R. 1997. Differences in home-range size computed in commonly used software programs. Wildl. Soc. Bull. **25**: 721–729.

Lee, P.C., and Hauser, M.D. 1998. Long-term consequences of changes in territory quality on feeding and reproductive strategies of vervet monkeys. J. Anim. Ecol. **67**: 347–358.

Lock, J.M. 1977. The vegetation of Rwenzori National Park, Uganda. Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr. **98**: 372–448.

Lurz, P.W.W., Garson, P.J., and Wauters, L.A. 2000. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris* L.). J. Zool. (Lond.), **251**: 167–178.

Macdonald, D.W. 1983. The ecology of carnivore social behaviour. Nature (Lond.), **301**: 379–384.

Mace, G.M., Harvey, P.H., and Clutton-Brock, T.H. 1983. Vertebrate home-range size and energetic requirements. *In* The ecology of animal movement. *Edited by* I.R. Swingland and P.J. Greenwood. Clarendon Press, Oxford. pp. 32–53.

Mitchell, D., Becnel, J.R., and Blue, T. 1981. The neophobia-optimality explanation of contrafreeloading in rats: a reassessment. Behav. Neural Biol. **32**: 454–462.

Otali, E., and Gilchrist, J.S. 2002. The effects of refuse feeding on body condition, reproduction and survival of banded mongooses. J. Mammal. In press.

Patton, S.R. 1988. Abundance of gulls at Tampa Bay landfills. Wilson Bull. No. 100. pp. 431–442.

Pons, J.M. 1992. Effects of changes in the availability of human refuse on breeding parameters in a herring gull *Larus argentatus* population in Brittany, France. Ardea, **80**: 143–150.

Pons, J.M., and Migot, P. 1995. Life-history strategy of the herring gull—changes in survival and fecundity in a population subjected to various feeding conditions. J. Anim. Ecol. **64**: 592–599.

Robb, S.E., and Grant, J.W.A. 1998. Interactions between the spatial and temporal clumping of food affect the intensity of aggression in Japanese medaka. Anim. Behav. **56**: 29–34.

Rood, J.P. 1975. Population dynamics and food habitats of the banded mongoose. East Afr. Wildl. J. **13**: 89–111.

Rood, J.P. 1986. Ecology and social evolution in the mongooses. *In* Ecological aspects of social evolution. *Edited by* D.I. Rubenstein and R.W. Wrangham. University Press, Princeton, N.J. pp. 131–152.

Seaman, D.E., and Powell, R.A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology, **77**: 2075–2085.

Silverman, B.W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London.

Simon, C.A. 1975. The influence of food abundance on the territory size in the iguanid lizard *Sceloporus jarrovi*. Ecology, **56**: 993–998.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research., 3rd. ed. W.H. Freeman and Co., New York.

Spinage, C.A. 1982. A territorial antelope: the Uganda waterbuck. Academic Press, London.

Steenbeek, R., and van Schaik, C.P. 2001. Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. Behav. Ecol. Sociobiol. **49**: 100–110.

Taitt, M.J. 1981. The effect of extra food on small rodent populations. 1. Deermice (*Peromyscus maniculatus*). J. Anim. Ecol. **50**: 111–124.

Taitt, M.J., and Krebs, C.J. 1981. The effect of extra food on small rodent populations. 2. Voles (*Microtus townsendii*). J. Anim. Ecol. **50**: 125–137.

Tufto, J., Andersen, R., and Linnell, J. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J. Anim. Ecol. **65**: 715–724.

Van Orsdol, K.G., Hanby, J.P., and Bygott, J.D. 1985. Ecological correlates of lion social organization (*Panthera leo*). J. Zool. Ser. A, **206**: 97–112.

Waser, P.M., and Waser, M.S. 1985. *Ichneumia albicauda* and the evolution of viverrid gregariousness. Z. Tierpsychol. **68**: 137–151.

White, G.C., and Garrott, R.A. 1990. Analysis of wildlife radio tracking data. Academic Press, London.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology, **70**: 164–168.

Worton, B.J. 1995. Using Monte-Carlo simulation to evaluate kernel-based home-range estimators. J. Wildl. Manag. **59**: 794–800.

Wozencraft, W.C. 1982. Reviewer for the family Herpestidae. *In* Mammal species of the world. *Edited by* J.H. Honacki, K.E. Kinman, and J.W. Koeppl. Allen Press, Lawrence, Kans. pp. 271–276.