THE EFFECTS OF REFUSE FEEDING ON BODY CONDITION, REPRODUCTION, AND SURVIVAL OF BANDED MONGOOSES

EMILY OTALI* AND JASON S. GILCHRIST

Makerere University Institute of Environment and Natural Resources, P.O. BOX 7298, Kampala, Uganda (EO)
Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom (JSG)

We investigated the effect of refuse feeding on body condition, reproductive success, and survival in banded mongooses (*Mungos mungo*). Data were collected from 231 mongooses in 3 refuse-feeding groups and 311 mongooses in 8 non–refuse-feeding groups within Queen Elizabeth National Park, Uganda. Refuse-feeding adults were heavier and in better physical condition than non–refuse-feeding adults. Refuse-feeding females carried more fetuses than non–refuse-feeding females, but no difference was found in conception rate, number of emerging young, or number of independent young per female between refuse-feeding and non–refuse-feeding females. Male young in refuse-feeding groups had higher mortality than all other young. These findings show that for this social carnivore, access to garbage dumps had significant but contrasting effects on components of fitness but no overall effect on evolutionary fitness.

Key words: banded mongoose, body condition, garbage dumps, mortality, *Mungos mungo*, predation, refuse-feeding, reproduction, Uganda

Food availability plays a major role in animal population dynamics. Body condition, breeding success, and survival of animals often depend to a large extent on food abundance (Boutin 1990; Dobson and Kjelgaard 1985). This may be particularly true in cooperatively breeding species, where ecological constraints on breeding resulting from lack of food have been suggested to play a significant role (Emlen 1990; Reyer 1990).

Many experimental studies have manipulated food availability to evaluate its effects on population dynamics, but the majority of these studies have concentrated on temperate-zone herbivores (Boutin 1990). Carnivores often use human refuse as a source of food; examples include bears (Knight and Eberhardt 1985; Lunn and Stirling 1985), foxes (Harrison 1997; Kapel 1999; White et al. 1996), European wolves (*Canis lupus*—Ciucci et al. 1997), and golden jackals (*Canis aureus*—Macdonald 1979), but the effect of refuse feeding on the demography of carnivores has been poorly studied.

Understanding the effects of garbage dumps on the ecology of wild animals is especially relevant to the management of national parks because human habitation and refuse sites often occur within parks or on park boundaries. Such refuse sites

may therefore affect the population dynamics of species within protected areas. Garbage dumps can increase populations, including some of conservation value, (e.g., grizzly bear—Craighead et al. 1995; Knight and Eberhardt 1985; and European wolf—Ciucci et al. 1997); however, garbage dumps also can increase animal–human conflict (Blanchard and Knight 1995; Brennan et al. 1985; Vermeer 1992).

Generally, individual animals in good body condition have higher evolutionary fitness than those in poor body condition, through higher reproductive success per event (Dobson and Michener 1995; Festa-Bianchet 1998; Festa-Bianchet et al. 1998) or longer reproductive lifetimes (Cote and Festa-Bianchet 2001; Festa-Bianchet et al. 1997). Because food intake is often a correlate of body condition, individuals with access to experimentally supplemented food usually have greater body mass (Boutin 1990). Similarly, refuse-feeding individuals are usually heavier than their natural-feeding counterparts (Blanchard 1987; Lunn and Stirling 1985; Pons and Migot 1995). Therefore, supplementary-fed individuals may be expected to have a higher evolutionary fitness than unsupplemented individuals.

Reproduction is an energetically demanding activity, from mating where males may have to defend females, through gestation and lactation, to raising young (Clutton-Brock 1991). Therefore, individuals must be in good condition to go through these stages. Females generally increase their food intake during pregnancy and lactation (Muruthi et al. 1991), and in many species the timing of reproduction coincides with periods

---

* Correspondent: megr_paotal@hotmail.com

of increased food availability, or individuals only breed when in sufficiently good body condition (Festa-Bianchet 1988). Therefore, the quantity and quality of food are important factors that determine reproductive success, and individuals with access to supplementary food may be expected to have increased reproductive success (Arcese and Smith 1988; Pons and Migot 1995).

In a wild habitat, starvation, predation, and disease are the main threats to survival. If food is a limited resource, a reliable food supply may decrease mortality by reducing risk of starvation. However, because a concentrated food source may attract and concentrate feeding individuals (in time or space), it also may concentrate numbers of predators, or time spent by predators at the food source (the "pantry effect"—Batzli 1983). Consequently, increased mortality of the prey species may result.

A survey of national parks around coastal Natal (including South Africa, Zimbabwe, and Natal) suggests that banded mongooses (*Mungos mungo*) commonly have access to garbage dumps (M. A. Cant, pers. comm.), and this is probably also the case for other mongoose species (Earle 1981; Wenhold 1990). For banded mongooses, which naturally forage on dispersed invertebrate prey (Rood 1975), food in garbage dumps represents a concentrated, supplemental resource. We have previously shown that access to refuse affects the dynamics of banded mongoose groups and have suggested that refuse feeding can increase population density by increasing group size (Gilchrist and Otali 2002). Changes in population size are consequences of changes in reproductive output, survival, or migration of individuals (e.g., in Columbian ground squirrels [*Spermophilus columbianus*]—Dobson and Oli 2001). In this study, we examine the effects of supplemental food (at garbage dumps) on a range of demographic and ecological variables in a social carnivore by comparing refuse-feeding and non–refuse-feeding individuals of the cooperative-breeding banded mongoose. We test the following hypotheses: refuse-feeding individuals are in better condition and have higher reproductive success than non–refuse-feeding individuals, and refuse-feeding individuals have higher rates of mortality due to higher densities of predators at garbage dumps.

Materials and Methods

Study species.—The banded mongoose is a social, diurnal, small carnivore in the family Herpestidae (Honacki et al. 1982). Banded mongooses feed on termites, millipedes, dung beetles, beetle larvae, and occasionally small vertebrates (Rood 1975). They live in groups of 5–40, typically consisting of multiple breeding females and males (Cant 2000; Rood 1975). Females give birth after a 2-month gestation, and mating usually occurs 1–2 weeks after parturition (Cant 2000; Rood 1975).

Study site and population.—Fieldwork was carried out on and around Mweya peninsula, Queen Elizabeth National Park, southwestern Uganda (0°12′S, 27°54′E). The climate is equatorial with little annual fluctuation in day length or temperature. The vegetation of the study site was predominantly short and medium fire-climax grassland with numerous dense thickets dominated by *Capparis tomentosa* growing in association with *Azima tetracantha* and *Euphorbia candelabrum* (Lock 1977; Spinage 1982). Mweya peninsula (4.95

km²) houses the park headquarters and is populated by 500–700 park and lodge staff, plus additional tourists. Hence, it contains numerous small garbage dumps.

We monitored 542 mongooses from January 1998 to January 2000, in 11 groups, 3 of which had garbage dumps in their home range. Of the 11 groups, behavioral and demographic data were collected on 9 groups that were habituated to observers' presence, including 1 group just outside the peninsula. The 2 unhabituated groups farther off the peninsula were only used in analysis of trapping data. Mean group size (excluding pups) was 14 ± 2.0 *SE* and mean home range size was 90.5 ± 30.7 ha (Gilchrist and Otali 2002).

We defined garbage dumps as sites of human refuse disposal. 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 amount of waste food available to mongooses at a site, 3 groups had access to predictable garbage dumps (lodge kitchen bins, main dump, and canteen dump) with a daily supply of food available, and 1 group additionally had access to unpredictable, small garbage dumps within the staff housing area (Gilchrist and Otali 2002).

Locating and monitoring groups.—Our procedures followed American Society of Mammalogists guidelines (http://www.mammalogy.org/committees/index.asp). We usually visited each group once or twice a day, between 0700 h and 1930 h. One or 2 individuals in each group were fitted with a radiotransmitter (Telonics, Mesa, Arizona). For identification purposes, remaining individuals were uniquely marked with either a handmade color-coded plastic collar or a small patch of shaved fur.

Details of the trapping and immobilization procedure are given by Cant (Cant 2000; Cant et al. 2001). While immobilized, individuals were weighed (± 0.5 g), and head width (breadth of zygomatic arch; ± 0.1 mm) was measured. Head width was used as an index of body size because it was more highly correlated with age (in days) than body length.

Pregnancy and number of fetuses were detected by palpation of trapped females from 2 to 4 weeks after estrus. For females that were not trapped, pregnancy was evident as a visibly swollen abdomen after about the 4th week of the 8-week gestation. Parturition or abortion was detected when the abdomen size returned to normal.

Within a group, females generally give birth synchronously in a communal den (Cant 2000). A litter was defined as the total number of young born to all females in the group. Groups that were babysitting young in the den (Cant 2003; Rood 1974) were visited daily until young emerged, about 30 days after birth (Gilchrist 2001). The number of emergent young in a litter was determined by observation 1–5 days after 1st emergence. Young were usually independent about 90 days after birth (Gilchrist 2001). Therefore, the number of independent young was defined as the number surviving at 90 days. Age categories were defined as pups, 0–90 days; infants, 91–182 days; subadults, 183–364 days; and adults, >364 days.

Statistical analyses.—Statistical analyses were performed by using MINITAB 12 software (Minitab Inc., State College, Pennsylvania) and Genstat 5.4 software (Lawes Agricultural Trust, Rothamsted, United Kingdom). Normally distributed data (confirmed by Kolmogorov–Smirnov normality tests) were analyzed by using general linear models. Binomial data were analyzed by using generalized linear models or iterated reweighted restricted maximum likelihood models with logit link function fitted to the data. Where appropriate, comparisons of means were made with Student's *t*-tests. For analyses of body condition and reproductive success, we confirmed the absence of a group effect by repeating each analysis with group identity as the random term in a restricted estimate maximum likelihood model. For

comparisons of observed and expected frequencies, we used the *G*-test for goodness of fit (Sokal and Rohlf 1995). All tests were 2-tailed with a significance level of $P < 0.05$. All means are expressed $\pm$ *SE*.

For analyses of body mass and condition, we used the mean mass and condition of each individual (based on 4.9 ± 0.26 captures/individual). Only adults were considered because they generally maintained a stable body mass (Cant 1998). Pregnant females were excluded. We used a residual index to measure body condition (Jakob et al. 1996). Log body mass was regressed on log head width and the equations for the line of best fit were used to calculate predicted body mass for each capture. Body condition index was calculated as observed body mass $\div$ predicted body mass, which has a mean of 1. Body mass and condition were contrasted between refuse-feeding and non–refuse-feeding individuals by using general linear models.

Measures of reproductive success included the number of times a female conceived per year, mean number of fetuses per female, number of emerging pups per female, and number of pups surviving to independence per female. These were contrasted between refuse-feeding and non–refuse-feeding females by using general linear models.

Conception rate per female was calculated as ([number of conceptions during the study period $-$ 1] $\div$ number of days between 1st and last conceptions) $\times$ 365. Mean number of fetuses per female was calculated as sum of fetuses in all conceptions $\div$ number of conceptions. Females that aborted were included in the analysis for conception rate, but were excluded from calculations of emerging and independent pups per female.

Number of emerging pups per female was calculated as total number of emerging pups in a litter $\div$ total number of pregnant females during the gestation period preceding parturition of the same litter. The number of pups reaching independence per female was calculated (excluding litters that died before emergence) as total number of pups in a litter 90 days after birth $\div$ total number of pregnant females during the gestation period preceding parturition of the same litter.

Mortality was inferred when single animals disappeared from the demographic record. The cause could not be confirmed in the majority of cases, but in most cases individuals had been healthy on the previous visit. It is unlikely that these mongooses emigrated, because confirmed cases of migration only involved single-sex subgroups (Cant et al. 2001; Gilchrist 2001). Individuals known to have emigrated (observed evicted or dispersing from the group—Cant et al. 2001) were not included in mortality calculations.

To test whether mortality was greater in refuse-feeding than non–refuse-feeding groups, we recorded the number of deaths within each age category and within each cohort born during the study period. The number of deaths was fitted to a binomial distribution, with the number of individuals alive when each cohort entered each age category as the denominator. Fifty litters emerged during the study. Mortality for adults was evaluated over the first 6 months of adulthood. Separate models were run for each age category (pups, infants, subadults, and adults). For adults, a 2nd model was fitted for individuals that were adults (estimated from biometric measurement or approximate dates of birth) when our study began. For each group we divided the study period into 6-month periods and analyzed the number of deaths as for the cohort analysis. Data analysis used an iterated reweighted restricted maximum likelihood model for pups because litter identity was a marginally nonsignificant random term ($t = 1.92$, *d.f.* $= 38$, $P < 0.1$). Neither group nor litter identity was significant for any other age category, and we used generalized linear models for such analyses. Calculations were initially made separately for each sex; however, where the sex $\times$ refuse interaction and sex term were nonsignificant (the case for all age categories except pups), we
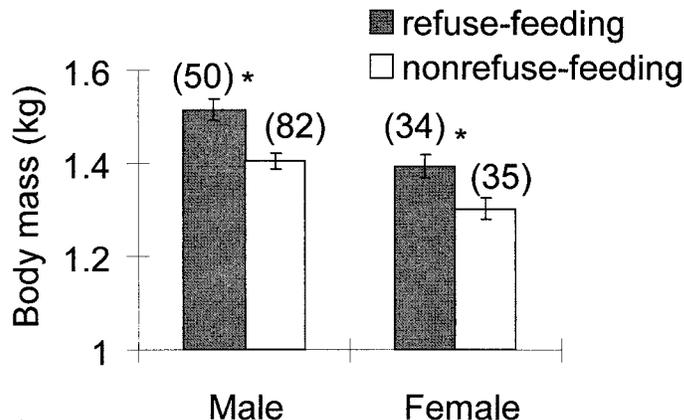

Fig. 1.—Body mass (mean $\pm$ *SE*) of refuse-feeding and non–refuse-feeding adult *Mungos mungo* at Queen Elizabeth National Park, Uganda. Asterisk denotes statistical significance ($P \leq 0.05$) between feeding categories within each sex. Sample sizes are in parentheses.

pooled data for the sexes to provide 1 value per cohort and fitted refuse as the fixed term.

We define predation as any event where a mongoose was killed by another species. Predation and predation attempts were recorded opportunistically. The species involved in these events were identified as potential predators. The location, number, and species of potential predators were scored by counting all individual predators within 100 m of the mongooses every 5 min during observations. We conducted 288 and 1,957 predator scans in 2 refuse-feeding groups and 69–419 scans in 4 non–refuse-feeding groups (total scan time > 259 h). The proportion of scans with ≥ 1 potential predator per scan was calculated for each group each day as the number of predator scans with ≥ 1 predator $\div$ total number of predator scans. Daily values were averaged to provide 1 value for each group. We used a general linear model to contrast the proportion of scans with a predator between refuse-feeding and non–refuse-feeding groups.

To test whether refuse-feeding groups encountered more predators in refuse areas, we compared the number of predator scans with and without ≥ 1 predator in refuse areas to the number that would be expected based upon predator occurrence in nonrefuse areas. Refuse areas were defined (from a grid map of the study area divided into 1-ha squares) as the squares containing a garbage dump and the adjacent squares; nonrefuse areas applied to all other squares. The expected number of scans with predators in refuse areas was calculated as (number of predator scans with ≥ 1 predator in nonrefuse areas $\div$ total number of scans in nonrefuse areas) $\times$ (total number of scans in refuse areas). The expected number of scans with no predators was calculated as above, but with the numerator = number of predator scans with no predators in nonrefuse areas. We used the *G*-test to test whether predator occurrence was equivalent for refuse and nonrefuse grids.

RESULTS

Refuse-feeding males were significantly heavier ($1,515.9$ g $\pm$ 23.97 *SE*, $n = 50$) than non–refuse-feeding males ($1,405.4 \pm 18.72$ g, $n = 82$; $F = 13.20$, *d.f.* $= 1$, 130, $P < 0.001$; Fig. 1). Similarly, refuse-feeding females were significantly heavier ($1,393.6 \pm 25.26$ g, $n = 34$) than non–refuse-feeding females ($1,303.4 \pm 24.90$ g, $n = 35$; $F = 6.47$, *d.f.* $= 1$, 67, $P = 0.013$; Fig. 1). Refuse-feeding males had significantly higher index values for body condition (1.025 ± 0.009 *SE*) than non–refuse-
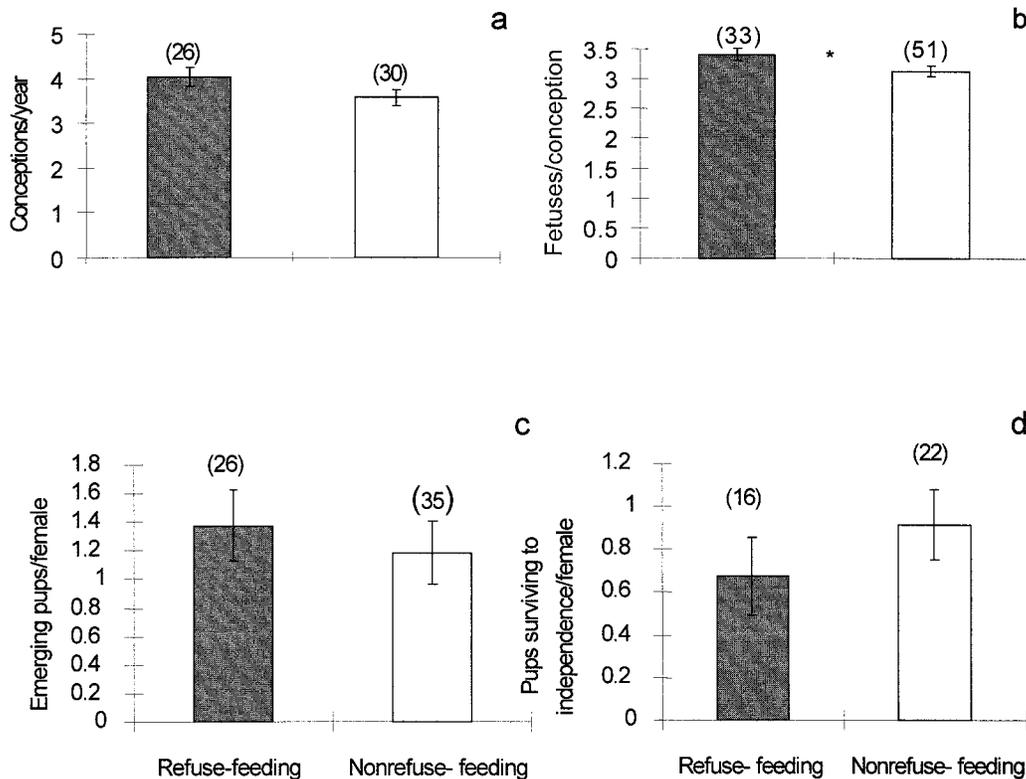
FIG. 2.—Reproductive parameters (mean ± *SE*) for refuse-feeding and non–refuse-feeding adult female *Mungos mungo* at Queen Elizabeth National Park, Uganda: a) number of conceptions/year; b) number of fetuses/conception; c) number of emergent pups/female; and d) number of pups surviving to independence/female. Asterisk denotes statistical significance ($P \leq 0.05$) between feeding categories. Sample sizes are in parentheses (for c and d, n = number of litters).

feeding males (0.982 ± 0.007; $F = 15.34$, *d.f.* = 1, 128, $P < 0.001$). Similarly, body condition index values for refuse-feeding females (1.053 ± 0.016) were significantly higher than those of non–refuse-feeding females (0.979 ± 0.012; $F = 13.70$, *d.f.* = 1, 43, $P = 0.001$).

No significant difference was found in mean conception rate between refuse-feeding females (4.037 conceptions/year ± 0.208 *SE*, $n = 26$) and non–refuse-feeding females (3.573 ± 0.194 conceptions/year, $n = 30$; $F = 2.65$, *d.f.* = 1, 54, $P = 0.109$; Fig. 2a). However, refuse-feeding females had a significantly higher mean number of fetuses (3.412 fetuses/female ± 0.107 *SE*, $n = 33$) than non–refuse-feeding females (3.136 ± 0.086 fetuses/female, $n = 51$; $F = 4.02$, *d.f.* 1, 82, $P = 0.048$; Fig. 2b). No difference was found in the mean number of pups emerging per female that gave birth between refuse-feeding and non–refuse-feeding groups (refuse-feeding = 1.378 ± 0.251 *SE*, $n = 26$ litters; non–refuse-feeding = 1.187 ± 0.216, $n = 35$ litters; $F = 0.33$, *d.f.* = 1, 59, $P = 0.566$; Fig. 2c). Also, no difference was found in the mean number of independent pups per female between refuse-feeding and nonrefuse-feeding groups (refuse-feeding = 0.676 ± 0.184 *SE*, $n = 16$ litters; non–refuse-feeding = 0.917 ± 0.157, $n = 22$ litters; $F = 1.00$, *d.f.* = 1, 36, $P = 0.325$; Fig. 2d).

There were 236 deaths among the 449 individuals monitored (annual mortality rates: pups = 0.701 ± 0.045 *SE*; infants = 0.345 ± 0.067; subadults = 0.216 ± 0.080; adults = 0.143 ± 0.109). The proportion of pups dying varied dependent on sex

and access to refuse (sex × refuse interaction: $\chi^2 = 4.51$, *d.f.* = 1, $P = 0.034$; Fig. 3). Male pups had a higher mortality rate than did female pups in refuse-feeding groups ($t = 2.16$, *d.f.* = 34, $P < 0.05$). Their mortality rate also was higher than that of male pups in non–refuse-feeding groups ($t = 2.30$, *d.f.* = 34, $P < 0.05$). No difference was found between mortality rates of female and male pups in non–refuse-feeding groups ($t = 0.96$, *d.f.* = 34, $P < 0.4$) or between female pups in refuse-feeding and non–refuse-feeding groups ($t = 0.38$, *d.f.* = 34, $P < 0.8$). Within infants, subadults, and adults, no differences were found in mortality between the sexes, and no differences were found between refuse-feeding and non–refuse-feeding groups (access to refuse: infants, $\chi^2 = 1.10$, *d.f.* = 1, $P = 0.353$; subadults, $\chi^2 = 0.64$, *d.f.* = 1, $P = 0.425$; adults, $\chi^2 = 0.80$, *d.f.* = 1, $P = 0.370$; adults [noncohort analysis], $\chi^2 = 0.37$, *d.f.* = 1, $P = 0.574$).

In only 17 of the 33 deaths with known cause did the individual look ill or weak before disappearance. The other 16 individuals were seen killed or being eaten. Of these, 10 were pups, of which 8 were killed by marabou storks (*Leptoptilos crumeniferus*), 1 was killed by a monitor lizard (*Varanus niloticus*), and 1 was killed by a warthog (*Phacochoerus africanus*). We also observed 1 adult mongoose killed and eaten by a warthog, and 2 adults died of human-inflicted burns. All of these encounters occurred within refuse areas. Additionally, within refuse areas, we observed marabou storks and monitor lizards attempting to catch pups, warthogs tossing
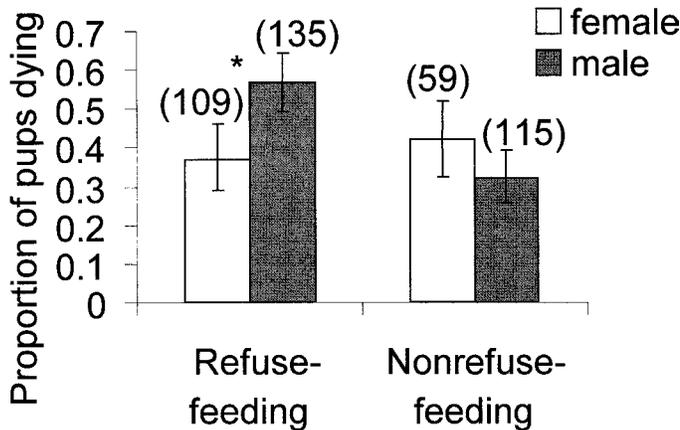
FIG. 3.—Proportion (mean $\pm$ SE) of refuse-feeding and non–refuse-feeding pups of *Mungos mungo* dying before independence at Queen Elizabeth National Park, Uganda. Asterisk denotes statistical significance ($P \leq 0.05$) between sexes within feeding groups. A significant difference also was found between male pups in refuse-feeding and non–refuse-feeding groups. Sample sizes are in parentheses.

FIG. 4.—Proportion (mean $\pm$ SE) of visual scans for predators (see text) with 1 or more predators present for refuse-feeding and non–refuse-feeding groups of *Mungos mungo* at Queen Elizabeth National Park, Uganda. Asterisk denotes statistical significance ($P \leq 0.05$) between feeding categories. Sample sizes are in parentheses.

individuals, and humans throwing objects at mongooses. Outside refuse areas, 1 adult mongoose wearing a radiocollar was tracked to a rock python (*Python sebae*), and the collar was defecated by the python some time later. We also observed a leopard (*Panthera pardus*) eating an adult mongoose and a lion (*Panthera leo*) "playing" with a dead mongoose. An adult mongoose was found freshly killed by an unknown predator on 3 occasions.

Of these potential predators, marabou storks, warthogs, and humans occurred often enough to permit the analysis of differences in occurrence between refuse-feeding and non–refuse-feeding groups. Refuse-feeding groups had a significantly higher proportion of scans with these species present than did non–refuse-feeding groups (marabou storks, refuse = 0.289 $\pm$ 0.021 *SE,* nonrefuse = 0.01 $\pm$ 0.014, F = 121.14, *d.f.* = 1, 5, $P < 0.001$; warthogs, refuse = 0.375 $\pm$ 0.051, nonrefuse = 0.062 $\pm$ 0.032, F = 26.60, *d.f.* = 1, 5, P = 0.004; humans, refuse = 0.416 $\pm$ 0.118, nonrefuse = 0.000 $\pm$ 0.000, F = 8.84, *d.f.* = 1, 5, P = 0.031; Fig. 4). The number of potential predators (per scan) experienced by refuse-feeding groups also was greater than that for non–refuse-feeding groups (marabou storks, refuse = 0–29, nonrefuse = 0–3; warthogs, refuse = 0–21, nonrefuse = 0–4; humans, refuse = 0–70, nonrefuse = 0).

Both refuse-feeding groups had significantly higher occurrence of predators in refuse than in nonrefuse areas (marabou storks: G = 1,142.584 and 62.197, *d.f.* = 1, $P < 0.001$; warthogs: G = 381.861 and 115.452, *d.f.* = 1, $P < 0.001$; humans: G = 2,174.962 and 21.294, *d.f.* = 1, $P < 0.001$).

DISCUSSION

Examination of our results shows that garbage dumps, as sources of concentrated food, had a significant effect on body condition, reproduction, and survival of banded mongooses. Refuse-feeding individuals were heavier and in better condition
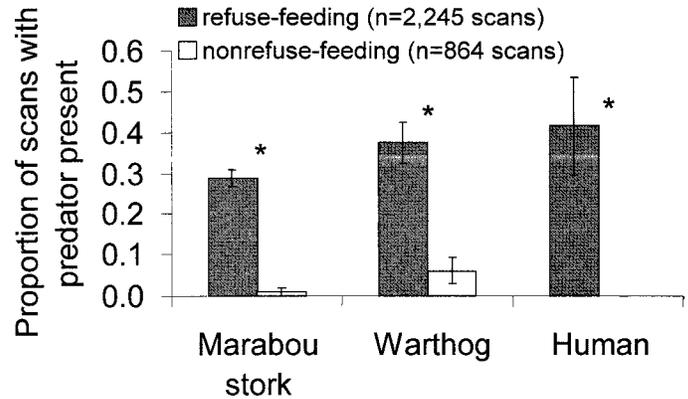
than non–refuse-feeding individuals of the same sex. This suggests that refuse-feeding mongooses had more food or better quality food than natural-feeding, non–refuse-feeding group members. Alternatively, because refuse-feeding mongooses concentrate their home range use at refuse areas (Gilchrist and Otali 2002), they may expend less energy foraging and therefore increase their body energy reserves.

Despite refuse-feeding females being in better condition, little evidence was found that they experienced increased reproductive fitness or that access to refuse affected reproductive skew (Gilchrist 2001). Experimental manipulation of food availability, for example, by preventing refuse-feeding groups from accessing food at the garbage dumps and by providing non–refuse-feeding groups with supplementary food, would provide a good test of these findings.

The lack of a difference in conception rate between refuse-feeding and non–refuse-feeding females is in contrast to studies of other species, which have shown that individuals in better body condition have higher reproductive rates (Brooker and Rowley 1995; Helle and Kauhala 1995; Wauters and Dhondt 1995) or that conception rate is positively correlated with food availability (Arcese and Smith 1988; Eden et al. 1989; van Noordwijk and van Schaik 1999).

However, females in better condition or with access to supplemental food may allocate more resources to production within litters by increasing litter or clutch size (Karels et al. 2000; Samson and Huot 1995; Schoech 1996).

Female mongooses with access to refuse gestated larger litters than non–refuse-feeding females. However, the number of emergent pups per female was not greater for refuse-feeding than non–refuse-feeding females.

Pup mortality in the den could be due to pup–pup competition, starvation, infanticide, or predation. Young may compete for access to lactating females (which allosuckle—Neal 1970; Rood 1975). Because lactation is energetically costly (Clutton-Brock 1991), we might expect refuse-feeding females to lactate more because they were generally in better condition than non–refuse-feeding females. Therefore, it is doubtful that

young in refuse-feeding groups would be more likely to starve. If pup–pup competition occurs in the den, parents could increase their own fitness by killing the pups of others. There is circumstantial evidence for intragroup infanticide in refuse-feeding groups. However, there is little evidence that it is a common occurrence: in more than 6 years of observations, adult males have only twice been observed to kill preemergent young (Cant 2000), and bones of newborn pups have been found in feces from only 1 adult male and 3 adult females (Gilchrist 2001). We observed only 1 case of predation on preemergent young (an intergroup infanticide). Predation on preemergent young probably is rare because dens are accessible to only small predators, and a ''babysitter'' usually guards the den (Cant 2003; Rood 1974). However, the high predator density in refuse areas may make preemergent young more vulnerable to predation both in the den and during movement of pups between dens.

The fact that refuse feeding does not reduce mortality suggests that starvation is not an important cause of death. Refuse-feeding groups encountered potential predators more often than did non–refuse-feeding groups, specifically within refuse areas. The abundance of potential predators in refuse areas shows that other species also visited garbage dumps, either to feed on refuse or to prey on mongooses. Therefore, the increased mortality rate of pups in refuse-feeding groups probably was due to predation. However, why male refuse-feeding pups had higher mortality than female pups is not clear, because male and female pups were equally likely to associate with an escorting adult (Gilchrist, in press).

Refuse feeding had contrasting effects on some components of fitness of banded mongooses, but no overall effect on evolutionary fitness. Individuals with access to refuse showed improved body condition, but little evidence of increased reproductive success. Furthermore, rather than decreasing mortality by reducing starvation, access to refuse appeared to increase mortality by predation. Such effects are unlikely to be desirable within national parks, where usually one of the aims is to conserve the natural balance of the ecosystem. Because mongooses and other wild animals commonly have access to human refuse in African national parks, waste food disposal needs to be better managed and controlled.

ACKNOWLEDGMENTS

LITERATURE CITED

ARCESE, P., AND J. N. M. SMITH. 1988. Effects of population density and supplemental food on reproduction in song sparrows. Journal of Animal Ecology 57:119–136.

BATZLI, G. O. 1983. Responses of Arctic rodent populations to nutritional factors. Oikos 40:396–406.

BLANCHARD, B. M. 1987. Size and growth patterns of the Yellowstone grizzly bear. International Conference on Bear Research and Management 7:99–107.

BLANCHARD, B. M., AND R. R. KNIGHT. 1995. Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. Journal of Wildlife Management 59:560–565.

BOUTIN, S. 1990. Food supplementation experiments with terrestrial vertebrates—patterns, problems, and the future. Canadian Journal of Zoology 68:203–220.

BRENNAN, E. J., J. G. ELSE, AND J. ALTMANN. 1985. Ecology and behavior of a pest primate—vervet monkeys in a tourist lodge habitat. African Journal of Ecology 23:35–44.

BROOKER, M., AND I. ROWLEY. 1995. The significance of territory size and quality in the mating strategy of the splendid fairy wren. Journal of Animal Ecology 64:614–627.

CANT, M. A. 1998. Communal breeding in banded mongooses and the theory of reproductive skew. Ph.D. dissertation, University of Cambridge, Cambridge, United Kingdom.

CANT, M. A. 2000. Social control of reproduction in banded mongooses. Animal Behaviour 59:147–158.

CANT, M. A. 2003. Patterns of helping effort in co-operatively breeding banded mongooses (*Mungos mungo*). Journal of Zoology (London) 259:115–121.

CANT, M. A., E. OTALI, AND F. MWANGUHYA. 2001. Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*). Journal of Zoology (London) 254:155–162.

CIUCCI, P., L. BOITANI, F. FRANCISCI, AND G. ANDREOLI. 1997. Home range, activity and movements of a wolf pack in central Italy. Journal of Zoology (London) 243:803–819.

CLUTTON-BROCK, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey.

COTE, S. D., AND M. FESTA-BIANCHET. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127:230–238.

CRAIGHEAD, J. J., J. S. SUMMER, AND J. A. MITCHELL. 1995. The grizzly bears of Yellowstone. Island Press, Washington, D.C.

DOBSON, F. S., AND J. D. KJELGAARD. 1985. The influence of food resources on life-history in Columbian ground squirrels. Canadian Journal of Zoology 63:2105–2109.

DOBSON, F. S., AND G. R. MICHENER. 1995. Maternal traits and reproduction in Richardson's ground squirrels. Ecology 76:851–862.

DOBSON, F. S., AND M. K. OLI. 2001. The demographic basis of population regulation in Columbian ground squirrels. American Naturalist 158:236–247.

EARLE, R. A. 1981. Aspects of the social and feeding behaviour of the yellow mongoose *Cynictis penicillata* (G. Cuvier). Mammalia 45:143–152.

EDEN, S. F., A. G. HORN, AND M. L. LEONARD. 1989. Food provisioning lowers inter-clutch interval in moorhens *Gallinula chloropus*. Ibis 131:429–432.

EMLEN, S. T. 1990. White-fronted bee-eaters: helping in a colonially nesting species. Pp. 487–526 in Cooperative breeding in birds: long term studies of ecology and behaviour (P. B. Stacey and W.D. Koenig, eds.). Cambridge University Press, Cambridge, United Kingdom.

FESTA-BIANCHET, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). Journal of Zoology (London) 214:653–661.

FESTA-BIANCHET, M. 1998. Condition-dependent reproductive success in bighorn ewes. Ecology Letters 1:91–94.

FESTA-BIANCHET, M., J. M. GAILLARD, AND J. T. JORGENSON. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist 152:367–379.

FESTA-BIANCHET, M., J. T. JORGENSON, C. H. BERUBE, C. PORTIER, AND W. D. WISHART. 1997. Body mass and survival of bighorn sheep. Canadian Journal of Zoology 75:1372–1379.

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

GILCHRIST, J. S. In press. Pup escorting in the banded mongoose: behavior, benefits and maintenance. Behavioral Ecology.

GILCHRIST, J. S., AND E. OTALI. 2002. The effects of refuse feeding on home-range use, group size, and intergroup encounters in the banded mongoose. Canadian Journal of Zoology 80:1795–1802.

HARRISON, R. L. 1997. A comparison of gray fox ecology between residential and undeveloped rural landscapes. Journal of Wildlife Management 61:112–122.

HELLE, E., AND K. KAUHALA. 1995. Reproduction in the raccoon dog in Finland. Journal of Mammalogy 76:1036–1046.

HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPPL (EDS.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Lawrence, Kansas.

JAKOB, E. M., S. D. MARSHALL, AND G. W. UETZ. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

KAPEL, C. M. O. 1999. Diet of arctic foxes (Alopex lagopus) in Greenland. Arctic 52:289–293.

KARELS, T. J., A. E. BYROM, R. BOONSTRA, AND C. J. KREBS. 2000. The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels. Journal of Animal Ecology 69:235–247.

KNIGHT, R. R., AND L. L. EBERHARDT. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:323–334.

LOCK, J. M. 1977. The vegetation of Rwenzori National Park, Uganda. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 98:372–448.

LUNN, N. J., AND I. STIRLING. 1985. The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. Canadian Journal of Zoology 63:2291–2297.

MACDONALD, D. W. 1979. The flexible social system of the golden jackal, Canis aureus. Behavioral Ecology and Sociobiology 5:17–38.

MURUTHI, P., J. ALTMANN, AND S. ALTMANN. 1991. Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. Oecologia 87:467–472.

NEAL, E. 1970. The banded mongoose, Mungos mungo Gmelin. East African Wildlife Journal 8:63–71.

PONS, J. M., AND P. MIGOT. 1995. Life-history strategy of the herring gull—changes in survival and fecundity in a population subjected to various feeding conditions. Journal of Animal Ecology 64:592–599.

REYER, H. U. 1990. Pied kingfishers: ecological causes and reproductive consequences of cooperative breeding. Pp. 529–557 in Cooperative breeding in birds: long term studies of ecology and behaviour (P. B. Stacey and W. D. Koenig, eds.). Cambridge University Press, Cambridge, United Kingdom.

ROOD, J. P. 1974. Banded mongoose males guard young. Nature 248:176–177.

ROOD, J. P. 1975. Population dynamics and food habitats of the banded mongoose. East African Wildlife Journal 13:89–111.

SAMSON, C., AND J. HUOT. 1995. Reproductive biology of female black bears in relation to body-mass in early winter. Journal of Mammalogy 76:68–77.

SCHOECH, S. J. 1996. The effect of supplemental food on body condition and the timing of reproduction in a cooperative breeder, the Florida scrub jay. Condor 98:234–244.

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

SPINAGE, C. A. 1982. A territorial antelope: the Uganda waterbuck. Academic Press, London, United Kingdom.

VAN NOORDWIJK, M. A., AND C. P. VAN SCHAIK. 1999. The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, Macaca fascicularis. Primates 40:105–130.

VERMEER, K. 1992. Population growth of the glaucous-winged gull Larus glaucescens in the Strait of Georgia, British Columbia, Canada. Ardea 80:181–185.

WAUTERS, L. A., AND A. A. DHONDT. 1995. Lifetime reproductive success and its correlates in female Eurasian red squirrels. Oikos 72:402–410.

WENHOLD, B. A. 1990. The ethology, sociology and interspecific interactions of the yellow mongoose, Cynictis penicillata, in the Karoo. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

WHITE, P. C. L., G. SAUNDERS, AND S. HARRIS. 1996. Spatio-temporal patterns of home range use by foxes (Vulpes vulpes) in urban environments. Journal of Animal Ecology 65:121–125.