

# Life-history variables of an atypical mustelid, the honey badger *Mellivora capensis*

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## Abstract

The honey badger, or ratel, *Mellivora capensis* has not been well studied and data on life-history variables have previously been incomplete and contradictory. Here we present data on life-history variables that were collected from visual observations as part of the first intensive study of free-living honey badgers (25 radio-marked individuals) and we make comparisons with other similarly sized mustelids (5–25 kg). The honey badger is a non-social species and only the mother rears the young. The data do not support delayed implantation as gestation was a maximum of 50–70 days with the unusually small litter size of one cub. The long time to independence of both male and female cubs (12–16 months) resulted in birth intervals longer than 12 months with no distinct breeding season. Overall the honey badger appears to have a more K-selected life history compared to other species within the Mustelidae.

**Key words:** ratel, mustelid, gestation, litter size, life history

## INTRODUCTION

The honey badger, or ratel, *Mellivora capensis* is a relatively large mustelid (6–14 kg) that has an extensive distribution across the greater part of Africa south of the Sahara and extending through Arabia, Iran and western Asia to Turkmenistan and the Indian peninsula (Harrison & Bates, 1991; Neal & Cheeseman, 1996). With the exception of a 6-week study on its foraging habits in the southern Kalahari (Kruuk & Mills, 1983) there have been no previous field studies of the species. Consequently, little is known of its reproductive biology or social organization and the data on standard life-history variables for the honey badger are incomplete and contradictory (Gittleman, 1986; Johnson, Macdonald & Dickman, 2000). The present position of the honey badger, as the only extant species, within its own genus *Mellivora* and subfamily Mellivorinae and the uncertainty of its relationship to other mustelids invites behavioural comparisons with other similarly sized mustelids, i.e. otters, other badgers and the wolverine *Gulo gulo*.

This paper forms part of a broader study (Begg *et al.*, 2003a,b; 2004), which has shown that at least in the southern Kalahari, the honey badger is a solitary forager with a broad, largely carnivorous diet. It does not show the typical mustelid pattern of intrasexual territoriality

(Powell, 1979), instead males have large home-ranges that overlap extensively with other males and encompass the smaller home-ranges of up to 13 females with a polygynous or promiscuous mating system. Here we present novel life-history information as a contribution to understanding the social organization and breeding biology of the honey badger, which in turn is important for its conservation as these data are vital for use in population viability analysis models. In addition, comparative analyses incorporating information from this atypical mustelid may increase our understanding of the factors shaping life-history patterns in mustelids in general (as per Bekoff, Daniels & Gittleman, 1984; Gittleman, 1986; Johnson *et al.*, 2000).

## METHODS

### Study area

The study was initiated in July 1996 and continued until December 1999 (42 months) in the Kgalagadi Transfrontier Park (KTP), which encompasses an area of 36 200 km<sup>2</sup> with the Kalahari Gemsbok National Park, South Africa, and neighbouring Gemsbok National Park, Botswana. The study area has been described in detail previously (Begg *et al.*, 2003a). For the purposes of this paper, 3 seasons are distinguished: the hot, wet season (HW) from January to April when the mean monthly

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**Table 1.** Descriptions of age categories used to assess honey badgers *Mellivora capensis* in the southern Kalahari

Age category	Overall description	Tooth wear
Den cub 0–3 months	Not foraging with mother, remained in den, < 30 cm long. Obtain black and white colouration at 1 month	'Milk' or deciduous teeth erupting
Foraging cub 3–16 months	Weaned but still dependent on mother for food, initially smaller than mother but reaches adult dimensions at about 8 months. May be larger than adult female if cub is male. Bright white mantle	Ranged from teeth still erupting to permanent teeth with no wear
Yearling Est. 1–3 years	Independent, few scars on body and in males no back scar and small testes	Slightly worn teeth, most noticeable on third incisor and canines
Adult <sup>1</sup> Est. 3–8 years	Presence of scars on face and body, in adult males, large testes, and in older males a prominent back scar. White mantle appears to darken with age.	Moderate to extensive tooth wear, on all teeth. Third incisor no longer pointed. In older individuals teeth were frequently missing or rotten.

<sup>1</sup>Adult study animals followed for more than 2 years were seen to age considerably in this time, i.e. teeth wear, loss of condition.

temperature is approximately 20 °C or higher and when 70% of the rain falls; the cold, dry season (CD) from May to August when the mean monthly temperature is below 20 °C and rainfall is rare; the hot, dry season (HD) from September to December when the monthly temperature is approximately 20 °C and usually not more than 20% of the rain falls (Mills & Retief, 1984).

### Data collection

Details of capture and radio-marking techniques have been detailed previously (Begg *et al.*, 2003a,b) and will only be outlined here. Whilst sedated, 25 individuals (13 females and 12 males) were fitted with Telonics radio collars. All collars were removed from the honey badgers before the end of the battery life or at the end of the study period. A wildlife veterinarian subsequently implanted 10 of the radio-marked adults (5 females and 5 males) and 3 large cubs (1 male, 2 females) with intraperitoneal radio implants.

Over 2000 h were spent habituating 9 radio-marked adult honey badgers (5 females and 4 males) to the vehicle until they could be followed without any obvious influence on their foraging behaviour. Over the course of the study, 5461 h were spent with habituated honey badgers (females: 2881 h; males: 2580 h). During all observations honey badgers were observed from the roof of a vehicle from 10–30 m away depending on visibility and grass height.

### Age determination and classification

No information on ageing in honey badgers is available. For this reason the age classes used in the KTP study are presented in detail. While counting cementum annuli in teeth is known to be an accurate method of age determination in other carnivores (Kruuk, 1995), the absence of material from known age individuals for comparison and the problems with using cementum annuli in an animal living in a non-seasonal environment (Harris, Cresswell & Cheeseman, 1992) precluded using this

method in this study. Since tooth wear alone is known to show large differences both between individuals and in different habitats (Harris *et al.*, 1992), information on behaviour, size and condition were also assessed. To minimize error, honey badgers were simply allocated to 1 of 4 broad categories, den cub (0–3 months), foraging cub (3 months to independence, still with mother), young adult (1–3 years, independent from mother), and adult (older than 3 years; Table 1).

Cubs younger than 3 months were never captured as they remained in the den. From opportunistic observations, cubs were categorized primarily by their behaviour and estimated length in relation to the adult female. In adults, tooth wear was most noticeable on the third incisor on the upper jaw, which in young adults is different to other incisors and resembles a canine but is quickly worn down to resemble the other incisors in older badgers. It is likely that teeth of Kalahari honey badgers wear down more rapidly than teeth of badgers from other areas due to the abrasive action of the sand, as has been suggested for the brown hyaena *Hyaena brunnea* (Mills, 1990) in the same habitat.

### Life-history variables

The life-history variables described in this study are based on those used by Gittleman (1986) and Johnson *et al.* (2000) and were estimated as:

- (1) Litter size: average number of offspring at birth, estimated from the number of young carried to new den after 2–5 days.
- (2) Gestation length in days: average time from conception, estimated from time of oestrus or mating activity, to birth, estimated from when a female reused a burrow for > 2 days and a cub was later seen.
- (3) Weaning age and lactation period in days: length of time from birth to independence from maternal milk, estimated as time from birth to when females were observed taking prey items back to the den.
- (4) Age of independence: age when cub is independent of parental care (i.e. foraging independence; Bekoff *et al.*, 1984) estimated as the time from birth to when

a cub was observed away from its mother for more than 2-days and was foraging independently.

- (5) Inter-birth interval: period between successive births (months) for individual females.
- (6) Time to sexual maturity in months: estimated as the age at which individuals were observed to mate.

The following dichotomous or ordinal variables were also assessed as per Johnson *et al.* (2000): seasonal breeding (yes/no), social class (solitary, pairs, variable groups or groups) and the presence or absence of delayed implantation (yes/no). The presence or absence of delayed implantation was assessed by determining whether the actual gestation length observed was longer than expected when compared to closely related, similarly sized mustelids that are known to show no delayed implantation (Hancox, 1993). Annual adult mortality was estimated as the proportion of known adult honey badgers that died during each particular year of study (1997–99). It was assumed that the sample of marked animals was representative of the whole population and that the mortalities recorded were not a result of capture and marking techniques. This is justified since individual honey badgers were originally located through tracks, which is unlikely to bias capture towards any one particular group. There was no evidence that any animal died or was injured as a result of either radio-collars or radio-implants.

## RESULTS

### Reproduction

Adults did not co-operate in cub rearing, foraging, or territory defence and adult males were not involved in parental care. In all cases, only a single cub was observed with an adult female ( $n = 18$ ; six females, eight males, four unknown sex). While it is possible that a second cub was born but died before emergence from the burrow, this is considered unlikely as females were observed to carry the cub to a new den within a few days of birth and on no occasion were females observed to move more than one cub. For four females the sex of successive cubs was known and in all cases the sex alternated, i.e. a male cub reared to independence was followed by a female cub and vice versa. Gestation was estimated as 50–70 days ( $n = 4$ ). Cubs were born throughout the year ( $n = 17$ ) and female reproduction is therefore considered asynchronous, although there were slightly more births in the hot, wet season (47%,  $n = 8$ ) and hot, dry season (33%,  $n = 5$ ) than the cold, dry season (18%,  $n = 3$ ). This trend is supported by the timing of mating interactions with the majority observed in the hot, dry season (66%,  $n = 8$ ), with the cold, dry season intermediate (25%,  $n = 3$ ) and only a single observation of mating in the hot, wet season. The length of the oestrous cycle is not known, but behavioural indications of oestrous (latrine visits by females (Begg *et al.*, 2003b) and interactions with males) suggest that females are in oestrous or attractive to males for a minimum of 2 weeks.

### Cub development

Den cubs (0–3 months old) were never captured as they remained in the den whilst their mothers went foraging, but they were observed being carried from one den to another in the mother's mouth (not on the back as suggested by Ranjitsinh, 1982). In the early stages of development cubs were almost hairless and only attained the characteristic black and white pelage at 3–5 weeks old ( $n = 3$ ). Suckling is assumed to occur in the den as it was only seen above ground on one occasion when the female was moving to a new den. The suckling position was unusual as the mother lay on her back, placed the cub on her belly with his tail near her head, and clasped her forearms around him. At 2–3 months of age the cubs ( $n = 5$ ) accompanied their mothers when foraging, and females reverted to the typical pattern of sleeping in a different hole each night. Females carried prey items back to the den from 2 months onwards and weaning is thus assumed to occur between 2 and 3 months. Cub development was slow, and juveniles remained with their mothers for at least 12–16 months ( $n = 7$ ; range = 12–22 months) before independence. For the first 10–12 months they were entirely dependent on their mothers for food, with a gradual increase in hunting, climbing and digging proficiency until just prior to independence when they were able to catch prey items on their own.

Age of sexual maturity in males remains unknown, but the increase in testes size and mass after independence (Begg *et al.*, 2003a), the late dispersal of male cubs (Begg *et al.*, 2004) and the non-aggressive behaviour of older males towards young males suggests that young males were not sexually mature on independence and only reached maturity at 2–3 years old. Age of sexual maturity in females is also unknown, but unlike males they dispersed immediately on independence (Begg *et al.*, 2004) and reached adult weight before independence (6 kg; Begg *et al.*, 2003a). In many carnivores, including European badgers *Meles meles*, dispersal occurs in sexually mature animals (Cheeseman *et al.*, 1988) suggesting that female honey badgers might be sexually mature on independence at 12–16 months.

The trigger for independence remains unclear but appears to be either the presence of males during mating ( $n = 2$ ) or the birth of the next cub ( $n = 2$ ). While sample sizes were small there was no difference in the mean age to independence in male ( $14.2 \pm 0.9$  months;  $n = 6$ ) and female cubs ( $14.6 \pm 1.2$  months;  $n = 3$ ) despite large differences in body size at independence (male mass at independence =  $8.4 \pm 0.17$  kg; female mass at independence =  $6.1 \pm 0.27$  kg). As a result of the long time to independence, birth intervals were longer than 12 months and females did not breed every year.

### Mortality and lifespan

Of the 19 cubs identified, seven died before independence, eight reached independence and four were still dependent on their mothers at the end of the study. The mortality

of known outcome cubs (i.e. excluding the four cubs still dependent) between birth and independence was therefore 47%. The causes of cub mortality include starvation ( $n = 1$  den cub), infanticide ( $n = 2$  den cubs), predation ( $n = 3$ ; one den cub, two foraging cubs) and one death of unknown causes (den cub). On two occasions mother and the cub were killed at the same time, the indications of spoor and teeth marks on radio implants being that large predators were involved.

The period just after independence is probably a critical period for cubs. A male cub weighing 8.8 kg on independence was captured a month later and found to weigh only 6.5 kg. Two months later he was found dead. Three of five radio-marked young males (60%) died before reaching adult status. One was thought to have died of starvation, one became blind in one eye and was later found dead and the remains of a third were found in a hyaena den. In adults, mean annual mortality (estimated as the mean proportion of known adults that died each year during 3 years) was  $34\% \pm 6\%$  (SE).

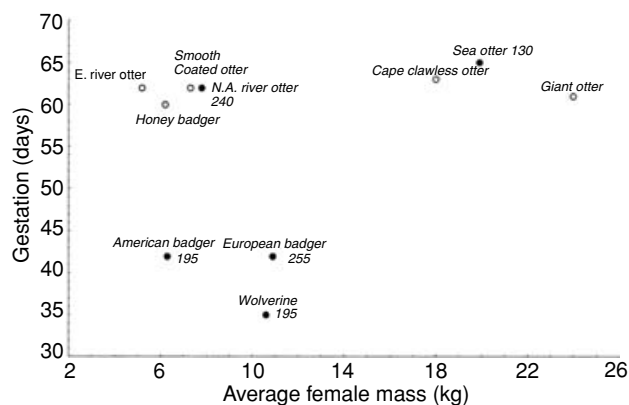
On the basis of tooth wear and physical deterioration of individuals during the study, it is predicted that life expectancy for honey badgers in the southern Kalahari is less than 7 years, possibly even less. However, honey badgers are known to live up to 28 years in captivity (Tel-Aviv Ramat Gan Zoological Centre, Israel; ISIS Sheets).

## DISCUSSION

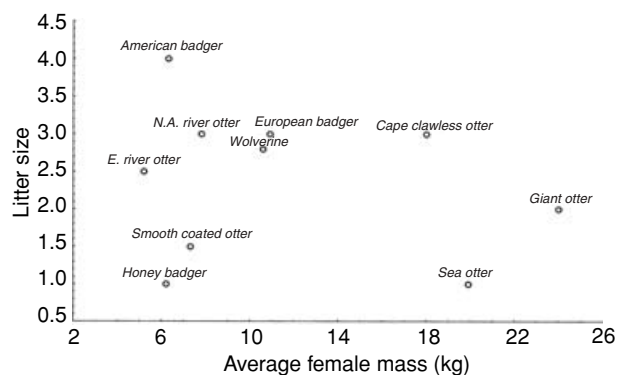
According to the criteria defined by Creel & Macdonald (1995) the honey badger is considered to be a non-social species as there are uni-parental breeding groups and the male does not play any part in parental care. The honey badger is widely reported to show delayed implantation in common with a variety of other mustelids including the American badger *Taxidea taxus* and European badger *Meles meles* (Estes, 1992; Hancox, 1993; Johnson *et al.*, 2000). This assertion appears to be based solely on a record of two gestation periods of 153 and 162 days for two captive honey badgers in Howletts Zoo, England (Johnstone-Scott, 1981). The data from the KTP do not support delayed implantation as gestation was a maximum of 50–70 days, similar to the 62–72 days gestation recorded for captive honey badgers in Israel (Mendelsohn & Yom-Tov, 1999). The long gestation times reported for honey badgers in captivity in England remain unexplained.

Size (primarily body weight) is an important variable in analysing life-history variation. As most life-history traits correlate with the rate of physiological activity and consequently with size (Gittleman, 1986) it is useful to compare the honey badger with other similar sized mustelids (female mass = 5–25 kg; Fig. 1; Johnson *et al.*, 2000). The data show that honey badger gestation is comparable in length to the gestation of 10 other similar sized mustelids (excluding the cases of delayed implantation).

This study also provides no evidence for the reported litter sizes of 1–4 cubs (mean = 2.5; Neal & Cheeseman, 1996; Johnson *et al.*, 2000) as in all cases only a



**Fig. 1.** A comparison of the average length of gestation in 10 medium to large sized mustelids (5–25 kg) with the closed circles representing those species that show delayed implantation. The length of the delay (in days) is represented by the number next to name. All data except for the honey badger *Mellivora capensis*, which are from this study, are from Johnson *et al.* (2000).



**Fig. 2.** A comparison of the litter sizes of 10 medium to large mustelid species (adult female mass is 5–25 kg) showing the unusually smaller litter sizes of the honey badger *Mellivora capensis*, smooth coated otter *Lutrogale perspicillata* and sea otter *Enhydra lutris*. All data except for the honey badger, which are from this study, are from Johnson *et al.* (2000).

single cub emerged from the burrow in the KTP. In captivity a litter of two was recorded on one occasion at Howletts Zoo, England (17%;  $n = 6$  litters), but both died within a few days (Johnstone-Scott, 1981), and the same was observed once in Israel (20%;  $n = 5$  litters; Y. Yom-Tov, pers. comm.). The small litter size of the honey badger is unusual amongst other similarly sized mustelids, with the sea otter *Enhydra lutra* and the Indian smooth-coated otter *Lutrogale perspicillata* the only other mustelids recorded to have an average litter size of one (Fig. 2; Johnson *et al.*, 2000). A wide variety of studies has shown the effects of food resources on reproductive success and litter size (Gittleman, 1986) and it has been suggested that individuals living in areas with low food availability have smaller litters than those in more productive environments (Carr & Macdonald, 1986; Boutin, 1990; Geffen *et al.*, 1996). For example, litter sizes of the similarly sized Eurasian otter *Lutra*

*lutra* may reach four but the mean number of cubs per litter is usually less and is smaller in coastal areas (1.55–1.95) than in inland areas (2.3–2.8; Kruuk, 1995). Inter-annual variations in food availability within its range may also affect the Eurasian otter's reproductive cycle and breeding success (Ruiz-Olmo *et al.*, 2002). Given that the KTP is a semi-arid habitat, it is therefore possible that litter sizes of two may be more common in free-living honey badgers in more productive habitats and further studies will elucidate this further. However, current anecdotal evidence does not support this as single cubs are most commonly seen in all habitats with only two confirmed records of two cubs. The small litter size of the honey badger in the semi-arid Kalahari was also associated with an extended period of dependence (12–16 months) compared to most other small carnivores (Bekoff *et al.*, 1984; Kruuk, 1995) and may be a response to difficulties in provisioning more than one cub for this extended period (Ofstedal & Gittleman, 1989).

The estimated duration of lactation (60–90 days) falls within the range of 63–126 days reported for other similarly sized mustelids (Johnson *et al.*, 2000), but the extended time of provisioning after weaning appears unusual for a small carnivore (Bekoff *et al.*, 1984; Kruuk, 1995). Bekoff *et al.* (1984) suggested that the relatively slow progress toward independence in the large carnivores, particularly in the large canids and felids is related to the need to 'teach' the young to hunt large prey items, while in the mustelids and viverrids prey items are small and are caught through rushing or ambushing prey rather than through elaborate stalking procedures. However, similarly long periods of dependence (8–12 months) have been observed in the medium sized Eurasian otter (Kruuk, 1995) and now in the honey badger. Kruuk (1995) suggested that the unusual amount of skill required when hunting fish is likely to be the reason for the long dependence of otter cubs on provisioning by the mother. Honey badgers also require some skill to catch diverse prey, including their staple diet of gerbils (with its numerous escape holes), and both poisonous and non-poisonous snakes, particularly since honey badgers appear to have compromised their speed for strength and digging power (Begg *et al.*, 2003a). The long time to independence of honey badger cubs is therefore likely to be the result of a gradual development of the necessary hunting, digging and climbing skills.

Since the hot, dry and hot, and wet seasons are the times of food abundance for both male and female honey badgers in the KTP, with increased consumption rates and decreased foraging time compared to the cold, dry season (Begg *et al.*, 2003a), it was predicted that honey badgers would show synchronous breeding to take advantage of this seasonality in resources. However, in common with the Eurasian otter in Britain (Kruuk, 1995) the reproduction of the honey badger in the KTP appears asynchronous with no distinct breeding season. This finding is supported by preliminary data from the Kruger National Park, South Africa, where breeding has been recorded in February, March, June and December (Fairall, 1968). Other sources have suggested that breeding is seasonal in other parts of its range with spring births

and autumn matings in Turkemenia, and births timed to coincide with the maximum availability of honey in Central Africa and Nigeria (Kingdon, 1989; Hancox, 1992), but given the lack of in-depth studies on the honey badger in these and other areas this could not be confirmed.

Asynchronous breeding in the honey badgers in the KTP may simply be a consequence of the long cub dependency, which results in a birth interval longer than 12 months (Kruuk, 1995). From the age of 8 months, cubs equal or exceed their mother's body mass, yet they are still completely dependent on provisioning by their mother and are fed an average of 45% of the food biomass caught by a female during a foraging period (Begg *et al.*, 2003a). While no data are available on the body mass or condition of females with and without cubs, cubs are likely to be a significant drain on a female's resources. Oestrous could therefore be triggered by an increase in female condition once a cub begins to catch its own food just prior to or at independence.

In 1973, Trivers and Willard hypothesized that females should adjust their litter sex ratio in response to available resources in order to optimize their fitness. Increasing evidence shows that in polygynous species with large variation in male reproductive success, females in better condition may maximize their fitness by producing more sons than daughters (Clout, Elliott & Robertson, 2002). Honey badgers show marked sexual size dimorphism and as a result sons grow larger and faster than daughters (Begg *et al.*, 2003a). A female with a dependent son has to provide for a cub almost 2 kg larger than herself in the last 4–8 months of dependence. The preliminary observation that the sex of honey badger cubs in successive female litters tended to alternate may therefore be related to female body condition and the differing maternal costs of raising sons or daughters. Females might only invest in 'expensive' males when they can 'afford' it (Clutton-Brock, Albon & Guinness, 1985) and as a result females in poor condition after raising a male cub to independence may produce a female cub in the next litter.

In the honey badger asynchronous breeding and the long birth interval results in a skewed operational sex ratio (Emlen & Oring, 1977), with fewer receptive females than males at any time. These factors directly affect male spacing and movement patterns and therefore social behaviour (Begg *et al.*, 2004). Overall, the honey badger appears to be comparatively *K*-selected among mustelids, with small litter size, an extended period of cub dependence, and increased maternal investment. The short life span observed in our study population may be due to the particularly harsh conditions in the semi-arid KTP. The combination of only a single cub, late sexual maturity and long birth interval has consequences for the conservation of the honey badger, as they are likely to result in a low reproductive output and slow population turnover. This, together with relatively high adult and cub mortality rates and large range requirements (females: 126 km<sup>2</sup>; males: 541 km<sup>2</sup>; Begg *et al.*, 2004) may reduce population resilience and make local extinctions more likely (Woodroffe, 2001). This is of particular concern since the honey badger is actively persecuted throughout

its range and is also frequently inadvertently killed by the non-selective use of poisons and gin traps set for other similarly sized carnivores (Begg & Begg, 2002). This study provides the first information on life-history variables of the honey badger in a semi-arid environment. The drawback has been the lack of information in other more productive habitats to allow for comparison.

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### REFERENCES

- Begg, C. M. (2001). *Feeding ecology and social organization of honey badgers in the southern Kalahari*. Ph.D. thesis. University of Pretoria, South Africa.
- Begg, K. S. & Begg, C. M. (2002). The conflict between beekeepers and honey badgers in South Africa; a Western Cape perspective. *Open Country* **4**: 25–37.
- Begg, C. M., Begg, K. S., du Toit, J. T. & Mills, M. G. L. (2003a). Sexual and seasonal variation in the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger *Mellivora capensis*. *J. Zool. (Lond.)* **260**: 301–316.
- Begg, C. M., Begg, K. S., du Toit, J. T. & Mills, M. G. L. (2003b). Scent marking behaviour of the honey badger *Mellivora capensis* (Mustelidae) in the southern Kalahari. *Anim. Behav.* **66**: 917–929.
- Begg, C. M., Begg, K. S., du Toit, J. T. & Mills, M. G. L. (2004). Spatial organisation of the honey badger *Mellivora capensis* in the southern Kalahari: home range size and movement patterns. *J. Zool. (Lond.)* **265**: 27–39.
- Bekoff, M., Daniels, T. J. & Gittleman, J. L. (1984). Life history patterns and the comparative social ecology of carnivores. *Ann. Rev. Ecol. Syst.* **15**: 191–232.
- Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: pattern, problems and the future. *Can. J. Zool.* **68**: 203–220.
- Carr, G. M. & Macdonald, D. W. (1986). The sociality of solitary foragers: a model based on resource dispersion. *Anim. Behav.* **34**: 1540–1549.
- Cheeseman, C. L., Cresswell, W. J., Harris, S. & Mallinson, P. J. (1988). Comparison of dispersal and other movements in two badger (*Meles meles*) populations. *Mammal Rev.* **18**: 51–59.
- Clout, M. N., Elliott, G. P. & Robertson, B. C. (2002). Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. *Biol. Conserv.* **107**: 13–18.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. (1985). Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**: 131–133.
- Creel, S. & Macdonald, D. W. (1995). Sociality, group size and reproductive suppression among carnivores. *Adv. Stud. Behav.* **24**: 203–257.
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science* **197**: 215–223.
- Estes, R. D. (1992). Behaviour guide to African mammals. Los Angeles: University of California Press.
- Fairall, N. (1968). Reproductive seasons of some mammals in the Kruger National Park. *Zool. Afric* **3**: 189–210.
- Geffen, E., Gompper, M. E., Gittleman, J. L., Luh, H., Macdonald, D. W. & Wayne R. K. (1996). Size, life history traits and social organization in the Canidae: A re-evaluation. *Am. Nat.* **147**: 140–160.
- Gittleman, J. L. (1986). Carnivore life history patterns: allometric, phylogenetic and ecological associations. *Am. Nat.* **127**: 744–771.
- Hancox, M. (1992). Some aspects of the distribution and breeding biology of honey badger. *Small Carnivore Conservation IUCN/SSC* **6**: 19.
- Hancox, M. (1993). Delayed implantation in badgers and other mustelids: a review. *Small Carnivore Conservation IUCN/SSC* **8**: 14–15.
- Harris, S., Cresswell, W. J. & Cheeseman, C. L. (1992). Age determination of badgers (*Meles meles*) from tooth wear: the need for a pragmatic approach. *Comm. Mammal Soc.* **65**: 679–684.
- Harrison, D. L. & Bates, P. J. J. (1991). *The mammals of Arabia*. Harrison Zool. Mus. Publ. **1991**: 135–137.
- Johnson, D. S. P., Macdonald, D. W. & Dickman, A. J. (2000). An analysis and review of models of the sociobiology of the Mustelidae. *Mammal Rev.* **30**: 171–196.
- Johnstone-Scott, R. (1981). Notes on the management and breeding of the African ratel. *Proc. Symp. ABWAK/Ratel* **5**: 6–15.
- Kingdon, J. (1989). *East African mammals: Carnivores*, 3A: 87–103. Chicago: University of Chicago Press.
- Kruuk, H. (1995). *Wild otters: predation and populations*. New York: Oxford University Press.
- Kruuk, H. & Mills, M. G. L. (1983). Notes on the food and foraging of the honey badger (*Mellivora capensis*) in the Kalahari Gemsbok National Park. *Koedoe* **26**: 153–157.
- Mendelsohn, H. & Yom-Tov, Y. (1999). *Mammals of Israel*. Israel: Israeli Academy of Science.
- Mills, M. G. L. (1990). *Kalahari hyaenas: comparative behavioural ecology of two species*. London: Unwin Hyman.
- Mills, M. G. L. & Retief, P. F. (1984). The response of ungulates to rainfall along the riverbeds of the southern Kalahari, 1972–1982. *Koedoe* **1984**(Suppl): 129–142.
- Neal, E. & Cheeseman, C. (1996). *Badgers*. London: Poyser Natural History.
- Oftedal, O. T. & Gittleman, J. L. (1989). Patterns of energy output during reproduction in carnivores. In *Carnivore behaviour; ecology and evolution*: 355–378. Gittleman, J. L. (Ed). London: Chapman & Hall.
- Powell, R. A. (1979). Mustelid spacing patterns: variations on a theme by *Mustela*. *Z. Tierpsychol.* **50**: 153–165.
- Ranjitsinh, M. K. (1982). Transportation of young by ratel. *J. Bombay Nat. Hist. Soc.* **19**: 661–662.
- Ruiz-Olmo, J., Olmo-Vidal, J. M., Mañas, S. & Batet, A. (2002). The influence of resource seasonality on the breeding patterns of the Eurasian otter (*Lutra lutra*) in Mediterranean habitats. *Can. J. Zool.* **80**: 2178–2189.
- Trivers, R. L. & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**: 90–92.
- Woodroffe, R. (2001). Strategies for carnivore conservation: lessons from contemporary extinctions. In *Carnivore Conservation*: 61–92. Gittleman, J. L., Funk, S. M., Macdonald, D. & Wayne, R. (Eds). Cambridge: Cambridge University Press.