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 Turkménistan 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 km² 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
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 observa-
tions, 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 con-
ception, 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

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

<table>
<thead>
<tr>
<th>Age category</th>
<th>Overall description</th>
<th>Tooth wear</th>
</tr>
</thead>
<tbody>
<tr>
<td>Den cub 0–3 months</td>
<td>Not foraging with mother, remained in den, &lt; 30 cm long. Obtain black and white colouration at 1 month</td>
<td>‘Milk’ or deciduous teeth erupting</td>
</tr>
<tr>
<td>Foraging cub 3–16 months</td>
<td>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</td>
<td>Ranged from teeth still erupting to permanent teeth with no wear</td>
</tr>
<tr>
<td>Yearling Est. 1–3 years</td>
<td>Independent, few scars on body and in males no back scar and small testes</td>
<td>Slightly worn teeth, most noticeable on third incisor and canines</td>
</tr>
<tr>
<td>Adult Est. 3–8 years</td>
<td>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.</td>
<td>Moderate to extensive tooth wear, on all teeth. Third incisor no longer pointed. In older individuals teeth were frequently missing or rotten.</td>
</tr>
</tbody>
</table>

1Adult study animals followed for more than 2 years were seen to age considerably in this time, i.e. teeth wear, loss of condition.
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 the proportion of known adult honey badgers (50–70 days (female cub and vice versa). Gestation 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.

Cub development

Den cubs (0–3 months old) were never captured as they remained in the den whilst their mothers were 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 ± 0.9 months; n = 6) and female cubs (14.6 ± 1.2 months; n = 3) despite large differences in body size at independence (male mass at independence = 8.4 ± 0.17 kg; female mass at independence = 6.1 ± 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% ± 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 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 lutris* 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 (Offedal & 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 felines 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 indepth 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$^2$; males: 541 km$^2$; 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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