



## Life history patterns and biology of the slender mongoose (*Galerella sanguinea*) in the Kalahari Desert

BEKE GRAW\* AND MARTA MANSER

Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 180, Zurich 8057, Switzerland (BG, MM)

Kalahari Meerkat Project, Kuruman River Reserve, P.O. Box 64, Van Zylsrus, Northern Cape 8469, South Africa (BG, MM)

Mammal Research Institute, Department of Zoology and Entomology, Faculty of Natural and Agricultural Sciences, University of Pretoria, Private Bag x20, Hatfield 0028, Pretoria, South Africa (MM)

\* Correspondent: [bekgraw@gmail.com](mailto:bekgraw@gmail.com)

The mongoose family (Herpestidae) has provided a wealth of data on life history patterns and behavior of its more social species but little is known about the many solitary mongoose species. Here, we provide the 1st long-term data on life history patterns and the biology of the solitary slender mongoose (*Galerella sanguinea*) in the Kalahari Desert, South Africa. Slender mongooses are strictly diurnal, solitary foragers, opportunistically hunting vertebrates and invertebrates. Life history patterns, such as a prolonged period of offspring dependence, including age at 1st emergence, at 1st foraging, and at weaning, compared to social meerkats (*Suricata suricatta*), seem to be an adaptation to their mainly solitary life style.

Key words: diet, *Galerella sanguinea*, life history, mongoose, solitary

The mongoose family, Herpestidae, includes 33 species (Nyakatura and Bininda-Emonds 2012) whose members exhibit social systems that range from mostly solitary living to highly social and cooperative species. While group-living mongooses, such as meerkats (*Suricata suricatta*), banded mongooses (*Mungos mungo*), and dwarf mongooses (*Helogale parvula*), have received much attention from behavioral and ecological studies (e.g., Rasa 1973; Rood 1975, 1983, 1990; Doolan and Macdonald 1997a, 1997b, 1999; Cant et al. 2013), including studies of cooperative behaviors (e.g., Rasa 1977; Rood 1978, 1983; Clutton-Brock et al. 1998; Doolan and Macdonald 1999; Gilchrist et al. 2004; Clutton-Brock and Manser 2016) and communication (e.g., Rasa 1986; Beynon and Rasa 1989; Jansen 2013; Manser et al. 2014), little is known about the greater number of solitary living mongooses (Schneider and Kappeler 2014), many of whom are nocturnal. Here, we present long-term data on life history patterns and diet of the slender mongoose (*Galerella sanguinea*), collected in their natural habitat in the Kalahari Desert, South Africa. We compare our results to data from the literature on a population of slender mongooses in the Serengeti (Rood 1989) and to the 2 sympatric species of mongooses in the Kalahari, the meerkat and the yellow mongoose (*Cynictis penicillata*).

Slender mongooses are solitary, small mongooses (Taylor 1975; Rood 1989; Maddock and Perrin 1993) that are Pan-African, occurring throughout the continent south of the Sahara, with the possible exception of densely forested areas and extreme desert environments (Taylor 1975). Little is known about their biology and life history patterns. They have been described as mostly diurnal and as being more carnivorous than the more social mongooses (Taylor 1975; Vaughan 1976; Rood and Waser 1978). Their diet, requiring them to stalk vertebrate prey, has been hypothesized as the evolutionary force behind solitary foraging and living (Ewer 1973; Rood 1986).

### MATERIALS AND METHODS

*Study site.*—We studied slender mongooses in the southern Kalahari Desert at the Kuruman River Reserve (26°58'S; 21°49'E), South Africa, from May 2007 through May 2011. Slender mongooses occurred sympatrically with the obligately social meerkats and with the facultatively social yellow mongooses (Earlé 1981; Balmforth 2004; le Roux et al. 2008). The study area was a semiarid landscape of sparsely vegetated dunes and herbaceous flats divided by a dry riverbed lined with scattered *Acacia* and *Boscia* trees (see details in Clutton-Brock et al. 1999; Russell et al. 2002). The area had 2 distinct

seasons: a cold-dry winter from May to September and a hot-wet summer from October to April. Annual rainfall was around 250 mm and fell almost exclusively during the summer months (Clutton-Brock et al. 1999). During winter months, temperatures at night could drop below freezing.

**Data collection.**—We captured 131 individual slender mongooses for DNA collection, radiotagging, and individual identification (for details, see Graw et al. 2016) throughout the study site. We marked all slender mongooses permanently with subcutaneous microchips (Identipet; Identipet Ltd., Johannesburg, South Africa), measured them, and determined sex and age. Measurements included body length (base of skull to tail base), tail length, head length (tip of nose to base of skull) and width (in broadest place), and neck circumference. We classified testes of males into 1 of 4 categories (not visible, small, medium, and big) and determined whether nipples on females were visible and showed signs of lactation. We weighed the mongooses and inspected them for general condition, parasites, and scars or wounds. We classified tooth wear, taking pictures of dentition when possible and noting which teeth showed wear or were missing.

Slender mongooses tolerated us at a distance of 2–30 m from their sleeping sites but did not tolerate us to follow them, allowing only observations of animals getting up in the morning and leaving to forage. We also could observe females returning to breeding and sleeping sites to provision dependent pups. We gathered over 2,000 sessions of behavioral observations.

All methods used for capturing, collaring, and handling slender mongooses followed guidelines for the use of wild mammals in research approved by the American Society of Mammalogists (Sikes et al. 2011). The study was conducted under permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (permit number: EC054-10).

**Age determination and classification.**—We allocated animals to 1 of 4 age classes, in coordination with age classes that have been applied to sympatric meerkats (Hollen and Manser 2006), based on tooth wear, size, body mass, and general condition. All 4 criteria were considered, as these can vary extensively between individuals and among habitats (Harris et al. 1992). As we had no slender mongoose teeth of known age, we described tooth wear in broad categories as none, slight, medium, or strong wear (Table 1). Our age classes were: pup

(0–3 months, dependent on mother), juvenile (3–6 months, leaving burrow with mother in the morning or already independent), subadult (6–12 months, independent), and adult (over 12 months of age). For males, based on body mass and testis size, we further distinguished between yearlings (1–2 years) and fully grown males (over 2 years of age; Table 1).

**Life history variables.**—We quantified life history variables as done in previous studies on carnivores by Gittleman (1986), Johnson et al. (2000), and Begg et al. (2005) and estimated them as follows:

1. Litter size: number of pups at emergence or seen being carried between burrows.
2. Gestation length: number of days between litter lost and birth of new litter.
3. Weaning age and lactation period in days: observation of nursing pups or signs of lactation in captured females.
4. Age of independence: age in days when first sleeping separate from mother.
5. Interbirth interval: days between births within 1 season.
6. Time to sexual maturity or 1st reproduction: months between birth and 1st litter.
7. Age at natal dispersal: age in months when last seen in natal range and consecutively found in different range.
8. Mortality and life expectancy:
  - Pup mortality: from birth to independence.
  - Adult mortality: mean annual mortality among known or followed adults.
  - Life expectancy: based on individuals of known age and age estimation.

**Diet and hunting behavior.**—Between February 2009 and September 2010, we collected 30 fecal samples of slender mongooses to analyze their contents. Samples were freshly collected as deposited by the animals and frozen within 2–4 h and kept at –20°C. We weighed each sample before soaking it in 5–10 ml of water for 5 min. We then rinsed the sample through a sieve with a 2-mm wire mesh. The washing water, with particles smaller than 2 mm, was collected and sieved again through a wire mesh of 1 mm. All gained particles were transferred to small plastic petri dishes and left to dry overnight. We sorted food particles, counted them, and identified them where possible down to animal class, with the help of a stereomicroscope. To compare the diet of slender mongooses with studies done on meerkats, we used the “frequency of occurrence” (FoO),

**Table 1.**—Description of age classes for slender mongooses (*Galerella sanguinea*) based on size, body mass, reproductive condition, and tooth wear. For tooth wear, I = incisor, P = premolar, M = molar; m = missing, g = growing, p = present with no wear; for adults, s = slight wear, mw = medium wear, st = strong wear.

Age class	Sex	Subclass	Size (cm)		Body mass (g)	Condition			Tooth wear		
			Body	Head		Nipples	Testes	Scars	I	P	M
Pup			10–20	5.8–6.5	≤ 300	No	Not visible-tiny	No	g	m or g	m or g
Juvenile			18–23	6.1–7.1	≤ 390	No	Very small	No	p	g	p
Subadult	M		21–24	6.6–7.0	400–490	No	Small	No/rare	p	p	p
	F		18–27	6.5–7.2	390–420						
Adult	M	Yearling	22–27	6.3–7.4	≤ 560		Medium-large	Present	s	s	s
	M	Grown	22–27	7.0–7.8	≥ 560 (avg.: 650)		Large	Present	s, mw, st	mw, st	s, mw, st
	F		20–28	6.7–7.5	≥ 420 (avg.: 490)	Yes		Present	s, mw, st	s, mw, st	s, mw, st

the proportion of samples that included a certain dietary item divided by the total number of samples, and the description of “bulk,” the estimated volume of each dietary item in the total volume of the sample (Doolan and Macdonald 1996). We compared diets between summer (October–March) and winter (April–September). Data for meerkat diets were taken from a study on a close-by population in a comparable habitat (Kgalagadi National Park) about 300 km away from our study site (Doolan and Macdonald 1996).

## RESULTS

**Reproduction.**—Females gave birth to 1–3 pups per litter (mean  $\pm$  SD:  $1.89 \pm 0.46$ ,  $n = 21$  litters) and produced 1–2 litters ( $1.28 \pm 0.46$ ,  $n = 21$  litters) per season. Pups were exclusively born during the wet summer months between October and March. We estimated gestation, based on 3 females that had lost the previous litter, as  $60 \pm 2$  days (range: 57–61 days). Interbirth interval in seasons when females gave birth to 2 litters was  $129 \pm 11$  days (range: 116–137,  $n = 3$ ). We made no behavioral observations indicating estrus, nor did we observe matings.

**Pup development.**—Pups were born into hollow trees where they remained for the first  $18 \pm 9$  days (mean  $\pm$  SD; range: 4–36 days,  $n = 13$ ) of their life, after which the mother moved them to another tree. Pups emerged for the 1st time after  $38 \pm 4$  days (range: 31–45 days,  $n = 11$ ) and started foraging with their mother at the age of  $49 \pm 8$  days (range: 37–63 days,  $n = 7$ ). Males were not involved in pup rearing. During the first days of foraging, pups remained at the burrow in the morning while the mother went off to forage on her own, after which (45–120 min later) she returned to pick up her pups and leave with them. Pups started leaving directly with their mother 3 weeks after starting to forage with her, at the age of  $73 \pm 13$  days (range: 48–89 days,  $n = 7$ ). The onset of directly leaving with the mother possibly coincides with the weaning of pups. In 2 instances, litters were observed suckling at 53 days and 73–77 days of age. We caught 1 female with pups that had stopped lactating 64–74 days after giving birth. Juveniles

became independent, sleeping for the 1st time away from their mother, at the age of  $115 \pm 19$  days (range: 81–148,  $n = 20$ ).

Age at 1st reproduction remained unclear. The youngest female of known age with pups was 2 years. Female slender mongooses all dispersed before reaching 10 months of age (Graw et al. 2016), potentially indicating that they became sexually mature as subadults. For males, based on their smaller body size and also testes size of yearlings, we assume that reproduction did not happen until their 2nd year.

**Mortality and lifespan.**—Of 23 observed litters, 4 (17%) were lost before emergence due to predation by yellow mongooses (2), infanticide (1), or unknown cause (1). Pup mortality rate before emergence is unknown, as in most cases we could only observe pups after emergence. We know of 1 case where 2 pups were seen prior to emergence (during the 1st burrow move), and later on only 1 emerged. After emergence, 3 (9%) out of 33 emerged pups disappeared and were presumed dead before independence (at 6 months). In 5 cases, pups were not seen with certainty up to independence and might have died, in which case mortality rate after emergence would be 24% (Table 2). We estimated a pup mortality rate in the Kalahari between 28% and 40% from birth to independence based on the above calculated litter size of 1.89 pups per litter and 12–17 dead pups out of a total of 43 pups born.

Mean annual mortality rate of adults was 22% based on the known adult individuals that died each year over the study period (Table 2). Between years, mortality varied between 14% and 33% ( $n = 4$ ). Known causes of death were predation by raptors (5) and a snake (1), disease (tuberculosis: 2; scabies: 2), and cars (2).

The oldest individual with known birthdate was 2.5 years of age at the end of our study. The adult monitored the longest was estimated to be around 2 years of age when first caught and was still present 5 years later, at around 7 years of age. We estimated 3 individuals in the study population to be between 8 and 10 years of age, based on tooth wear and physical deterioration (Table 3).

**Activity patterns.**—Slender mongooses in the Kalahari Desert were strictly diurnal. Activity patterns shifted in relation to outside temperatures and sunrise–sunset patterns ( $P < 0.001$ ,

**Table 2.**—Comparison of life history patterns among 3 sympatric mongoose species (slender mongoose, *Galerella sanguinea*; meerkat, *Suricata suricatta*; yellow mongoose, *Cynictis penicillata*) in the Kalahari Desert, South Africa.

	Slender mongoose	Meerkat	Yellow mongoose
Group size	1 (temporarily up to 6)	Up to 50	1 (temporarily up to 6?)
Litter size	1–3	3–7	2–3
Litters/year	1–2	1–3	1–2 (avg.: 1)
Gestation length (days)	60	70	
Weaning age (days)	$\approx 70$	$\approx 42$	
Age at independence (days)	115	120	
Interbirth interval (days)	116–137	73–149	
Sexual maturity, 1st reproduction	During 2nd year	During 1st year	
Age at natal dispersal	< 10 months	2–3 years?	9–12 months
Mortality (emerged pup, adult)	9–24/22–26	31/32	15–16/49–50
Lifespan in years (estimated)	8–10	13	
Activity period	Diurnal	Diurnal	Diurnal
Diet	Invertebrates and vertebrates	Mostly invertebrates	
Microhabitat	More covered	Open	More covered

**Table 3.**—Comparison between slender mongoose (*Galerella sanguinea*) populations in the Kalahari Desert, South Africa, and the Serengeti. Data for slender mongooses in the Serengeti taken from Rood (1989), Rood and Waser (1978), and Waser et al. (1994, 1995). Asterisk: based on the oldest known-aged animal. “?” indicates that no data was available or that the number has been inferred from the literature but has not been specifically stated by the authors.

	Kalahari	Serengeti
Group size	1 (temporarily up to 6)	1 (temporarily up to 5?)
Litter size	1–3	1–3
Birth seasonality	Highly seasonal (October–March)	Less seasonal
Gestation length (days)	60	?
Weaning age (days)	≈ 70	?
Age at independence (days)	115	≈ 65?
Interbirth interval (days)	116–137	90–180
Sexual maturity, 1st reproduction	During 2nd year	During 2nd year
Age at natal dispersal	< 10 months	< 6 months
Mortality % (emerged pup, adult)	9–24/22–26	37/19
Lifespan in years (estimated)	8–10	At least 8*
Activity period	Diurnal	Diurnal
Diet	Invertebrates and vertebrates	Mostly vertebrates
Microhabitat	More covered	More covered

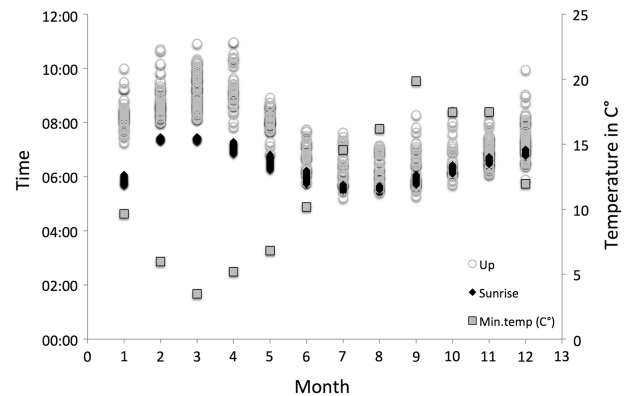
$R^2 = 0.669$ ; Fig. 1). During warm summer months (October–March), mongooses emerged on average 18 min (March,  $n = 32$ ) to 49 min (October,  $n = 33$ ) after sunrise. During winter (April–September), emergence shifted to 35 min (April,  $n = 59$ ) to 137 min (August,  $n = 30$ ) after sunrise. Females generally rose earlier than males (3–49 minutes,  $P = 0.006$ ,  $Z = -2.746$ ). During anecdotal observations in summer, female slender mongooses returned to their sleeping sites 64 min before to 25 min past sunset (average: 8 min before sunset,  $n = 13$ ).

**Diet and hunting behavior.**—Slender mongooses in the Kalahari Desert were omnivorous. Invertebrates were found in all samples, making up 79% of the volume. In 73% of all analyzed fecal samples ( $n = 30$ ), vertebrate remains were found, though this only made up a bulk percentage of 8%. Plant seeds from fruits eaten were found in 20% of all fecal samples, 13% of the volume. Diet shifted slightly between seasons, during summer months 83% of all samples ( $n = 12$ ) had vertebrate remains in them, making up a bulk of 12%, whereas in winter this was only the case in 67% of the samples ( $n = 15$ ) with a volume of 4%. Invertebrates on the other hand made up a bulk of 38% during summer but contributed 81% of volume in winter (Table 4).

Slender mongooses were seen hunting small birds such as white-browed sparrow weavers (*Plocepasser mahali*) in trees and shrubs ( $n = 2$ ). They were skilled climbers, regularly entering bird nests to eat eggs and presumably chicks. Birds, such as southern pied babblers (*Turdoides bicolor*), crimson-breasted shrikes (*Laniarius atrococcineus*), and glossy starlings (*Lamprotonis nitens*) commonly reacted with alarm and mobbing to slender mongooses, presumably because they were a danger to their eggs and chicks. One slender mongoose was observed feeding on a steenbok (*Raphicerus campestris*) carcass during winter time (M. Manser, pers. obs.).

**DISCUSSION**

Slender mongooses in the Kalahari Desert were strictly diurnal, opportunistic hunters of invertebrate and vertebrate prey, showing a birth seasonality and diet shifts adapted to the seasonality of



**Fig. 1.**—Time slender mongooses (*Galerella sanguinea*;  $n = 9$ ) emerged in the morning (up) over the course of a year (May 2009–May 2010) in the Kalahari Desert, South Africa, in relation to sunrise and minimum average temperature per month (minimum temperature in °C). Month 1 represents May 2009 and Month 12 is April 2010.

their habitat. Slender mongooses in the Serengeti show less seasonality, with births occurring throughout the year (Waser et al. 1995). In the Serengeti, pups become independent and both sexes disperse much earlier (Rood and Waser 1978; Waser et al. 1994), than in the Kalahari, where mainly the females dispersed. While these variations may result from differences in the definition of “independence,” they possibly reflect the harsher environmental conditions in the Kalahari Desert in terms of food availability and nighttime temperatures, especially during winter months.

Comparing the 3 sympatric mongoose species in the Kalahari, life history differences (Table 2) such as litter size and interbirth interval may be associated with adaptations to their differing social structures. Litter size and number of litters per year are greatest in the cooperatively breeding meerkat, and meerkats also have the shortest interbirth interval (Table 2). Gestation length correlates with body size, with the smallest-sized dwarf mongoose having the shortest period (Rood 1980), the largest-sized meerkats having the longest period (Clutton-Brock et al. 2002), and the medium-sized slender and yellow mongooses in between (Rasa et al. 1992). Benefits of group protection to pups

**Table 4.**—Diet of slender mongooses (*Galerella sanguinea*) in the Kalahari Desert, 2010–2011, based on frequency of occurrence (FoO) and volume percentage (Volume).

Prey category	Total (n = 30)			Summer (n = 12)			Winter (n = 15)		
	n	FoO (%)	Volume (%)	n	FoO (%)	Volume (%)	n	FoO (%)	Volume (%)
Vertebrata	22	73.33	8.19	10	83.33	12.19	10	66.67	4.25
Reptilia	20	66.67	6.84	9	75.00	12.90	9	60.00	4.12
Mammalia	4	13.33	1.44	1	8.33	1.43	3	20.00	1.54
Invertebrata	30	100.00	78.67	12	100.00	37.99	15	100.00	80.57
Insecta	30	100.00	75.07	12	100.00	34.41	15	100.00	77.22
Coleoptera	11	36.67	3.69	8	66.67	10.39	2	13.33	1.03
Isoptera	16	53.33	59.32	4	33.33	1.79	9	60.00	69.37
Orthoptera	17	56.67	5.40	7	58.33	9.68	7	46.67	3.09
Neuroptera	3	10.00	0.81	0	0.00	0.00	3	20.00	1.16
Arachnida	8	26.67	1.35	5	41.67	2.87	2	13.33	0.51
Araneae	7	23.33	1.08	5	41.67	2.87	2	13.33	0.51
Scorpiones	1	3.33	0.27	0	0.00	0.00	0	0.00	0.00
Myriapoda	1	3.33	0.18	0	0.00	0.00	1	6.67	0.26
Plantae	6	20.00	12.60	4	33.33	44.44	1	6.67	1.93
<i>Grewia flava</i>	4	13.33	9.36	4	33.33	37.28	0	0.00	0.00
Unidentified vegetation	17	56.67	1.53	8	66.67	2.87	6	40.00	0.77

in the more social species might be reflected in age at emergence and 1st foraging. Possibly because they have no babysitter at the burrow to protect them, slender mongoose pups need to be able to efficiently and quickly run back into shelter on their own, and stay hidden much longer. Meerkat pups start foraging with their group much earlier than slender mongoose pups (Clutton-Brock et al. 1999). Yellow mongoose pups are provisioned at the burrow and join adults on foraging trips (le Roux 2007) similarly late as slender mongooses, when they have probably outgrown their most vulnerable time period (see Rasa et al. 1992).

According to our anecdotal observations, slender mongooses were suckled for an extended period of time, well beyond that of social meerkats (Table 2), reflecting again the benefit of a group providing for their young. Weaning by slender mongooses seemed to coincide with the pups starting to leave and forage directly with their mother in the morning. Independence, as we have defined it, sleeping away from the mother for the 1st time, occurred for both slender mongooses and meerkats at similar ages, but likely for different reasons. For slender mongooses, it probably does not reflect dietary independence, as they need to be efficient enough hunters to provide for themselves before leaving their mother, whereas for meerkats, it is the age when juveniles are capable of providing completely for themselves.

Compared to the diet of sympatric, obligate group-foraging meerkats, and controlling for the season in which samples were collected, the diet of slender mongooses consisted of more vertebrates, with a higher FoO and volume percentage (Doolan and MacDonald 1996; Table 5). A diet consisting of vertebrates that need to be stealthily hunted in addition to hunting for invertebrates has been associated with a solitary lifestyle (Rood 1986; Veron et al. 2004). In sympatric yellow mongooses, le Roux et al. (2009) showed that group foraging has a negative effect on foraging efficiency in this typically solitary forager. A diet like that of meerkats, mostly based on invertebrates that need to be dug up from the soil, not only makes foraging as a group possible but also might make it necessary in order to avoid predation.

**Table 5.**—Comparison of diets of slender mongooses (*Galerella sanguinea*) and meerkats (*Suricata suricatta*) in the Kalahari Desert, based on frequency of occurrence (FoO) and volume percentage (Volume). Data for meerkats taken from Doolan and Macdonald (1996).

Prey category	Slender mongoose (n = 17)		Meerkat	
	FoO (%)	Volume (%)	FoO (%)	Volume (%)
Vertebrata	70.6	6.7	9.2	3.3
Reptilia	58.8	4.8	9.2	3.3
Invertebrata	100	84.7	78.1	68.9
Insecta	100	82.0	75.1	
Coleoptera	29.4	2.3	27.5	
Orthoptera	64.7	5.2	1.6	3.3
Arachnida	29.4	1.2		
Scorpiones	0	0	1.9	4.5

In conclusion, the slender mongoose is a diurnal, opportunistic, solitary forager that can adapt its diet to its habitat and season. Diets of the 3 sympatric mongoose species seem to influence social structure, as has been suggested for mongooses (Ewer 1973; Rood 1986). Social organization goes along with life history patterns, such as extended nursing and later emergence in the slender mongoose, where mothers raise pups by themselves, in comparison to the 2 other sympatric species where at least the pair or the whole group contributes to raising offspring. Comparisons of different populations within the same species and between similar sympatric species allow identification of constraints on life history strategies. Future research on other animal families with variation in social structure and the ecological environment should confirm how specific life history traits are affected by these.

#### ACKNOWLEDGMENTS

We thank the Kalahari Research Trust and in particular T.H. Clutton-Brock for letting us work and use the facilities at the

Kalahari Meerkat Project research site. We are grateful to the families J. and S. Koetze, P. and M. Koetze, and F. and L. de Bruin for allowing us to work on their lands. Invaluable help during field work and data collection was provided by D. Jansen, K-L. Roelofse, M. Fenkes, T. Schellenberg, N. Milling, C. Young, N. Harrison, H. Stühlen, C. Sanderson, and C. Prussick. We are thankful to the managers of the meerkat project, T. Flower, R. Sutcliffe, D. Bell, M. Price, C. Borgeaud, J. Sampson, and N. Thavaraja for continued support during this study. A big thank you goes out to all the meerkat volunteers and researchers that reported slender sightings. L. Lüthi in Zurich washed and analyzed the fecal samples. The University of Zurich provided financial support for the study. The study was conducted with ethical clearance from the Ethical Committee of the University of Pretoria and under license from the Northern Cape Department of Nature Conservation. B. G. and M.B.M. were funded by the University of Zurich.

LITERATURE CITED

BALMFORTH, Z. E. 2004. The demographics, spatial structure and behaviour of the yellow mongoose, *Cynictis penicillata*, with emphasis on cooperative breeding. Ph.D. dissertation, University of Sussex, Brighton, United Kingdom.

BEGG, C. M., K. S. BEGG, J. T. DU TOIT, AND M. G. L. MILLS. 2005. Life-history variables of an atypical mustelid, the honey badger *Mellivora capensis*. *Journal of Zoology (London)* 265:17–22.

BEYNON, P., AND O. A. E. RASA. 1989. Do dwarf mongooses have a language? Warning vocalizations transmit complex information. *South African Journal of Science* 85:447–450.

CANT, M. A., E. VITIKAINEN, AND H. NICHOLS. 2013. Demography and social evolution in banded mongooses. *Advances in the Study of Behaviour* 45:407–445.

CLUTTON-BROCK, T. H., ET AL. 1998. Costs of cooperative behavior in suricates, *Suricata suricatta*. *Proceedings of the Royal Society of London, Series B* 265:185–190.

CLUTTON-BROCK, T. H., ET AL. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology* 68:672–683.

CLUTTON-BROCK, T. H., AND M. B. MANSER. 2016. Meerkats: cooperative breeding in the Kalahari. Pp. 294–317 in *Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior* (W. D. Koenig and J. L. Dickinson, eds.). Cambridge University Press, Cambridge, United Kingdom.

CLUTTON-BROCK, T. H., A. F. RUSSELL, L. L. SHARPE, A. J. YOUNG, Z. BALMFORTH, AND G. M. MCILRATH. 2002. Evolution and development of sex differences in cooperative behavior in meerkats. *Science* 297:253–256.

DOOLAN, S. P., AND D. W. MACDONALD. 1996. Dispersal and extraterritorial prospecting by slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari. *Journal of Zoology* 240:59–73.

DOOLAN, S. P., AND D. W. MACDONALD. 1997a. Breeding and juvenile survival among slender-tailed meerkats (*Suricata suricatta*) in the southwestern Kalahari: ecological and social influences. *Journal of Zoology* 242:309–327.

DOOLAN, S. P., AND D. W. MACDONALD. 1997b. Band structure and failures of reproductive suppression in a cooperatively breeding carnivore, the slender tailed meerkat (*Suricata suricatta*). *Behaviour* 134:827–848.

DOOLAN, S. P., AND D. W. MACDONALD. 1999. Co-operative rearing by slender tailed meerkats (*Suricata suricatta*) in the southern Kalahari. *Ethology* 105:851–866.

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

EWER, R. F. 1973. *The carnivores*. Weidenfield and Nicholson, London, United Kingdom.

GILCHRIST, J. S., E. OTALI, AND F. MWANGUHYA. 2004. Why breed communally? Factors affecting fecundity in a communal breeding mammal: the banded mongoose (*Mungos mungo*). *Behavioral Ecology and Sociobiology* 57:119–131.

GITTLEMAN, J. L. 1986. Carnivore life history patterns: allometric, phylogenetic and ecological associations. *American Naturalist* 127:744–771.

GRAW, B., A. K. LINDHOLM, AND M. B. MANSER. 2016. Female-biased dispersal in the solitarily foraging slender mongoose, *Galerella sanguinea*, in the Kalahari. *Animal Behaviour* 111:69–78.

HARRIS, S., W. J. CRESSWELL, AND C. L. CHEESEMAN. 1992. Age determination of badgers (*Meles meles*) from tooth wear: the need for a pragmatic approach. *Journal of Zoology* 228:679–684.

HOLLEN, L. I., AND M. B. MANSER. 2006. Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the role of age, sex and nearby conspecifics. *Animal Behaviour* 72:1345–1353.

JANSEN, D. A. W. A. M. 2013. Vocal communication in banded mongooses (*Mungos mungo*). Ph.D. dissertation, University of Zurich, Zurich, Switzerland.

JOHNSON, D. S. P., D. W. MACDONALD, AND A. J. DICKMAN. 2000. An analysis and review of models of the sociobiology of the Mustelidae. *Mammalian Review* 30:171–196.

MADDOCK, A. H., AND M. R. PERRIN. 1993. Spatial and temporal ecology of an assemblage of viverrids in Natal, South Africa. *Journal of Zoology* 229:277–287.

MANSER, M. B., ET AL. 2014. Vocal complexity in meerkats and other mongoose species. *Advances in the Study of Behavior* 46:281–310.

NYAKATURA, K., AND O. R. P. BININDA-EMONDS. 2012. Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biology* 10:12.

RASA, O. A. E. 1973. Prey capture, feeding techniques, and their ontogeny in the African dwarf mongoose, *Helogale undulata rufula*. *Zeitschrift für Tierpsychologie* 32:449–488.

RASA, O. A. E. 1977. The ethology and sociology of the dwarf mongoose. *Zeitschrift für Tierpsychologie* 43:337–406.

RASA, O. A. E. 1986. Coordinated vigilance in dwarf mongoose family groups: the ‘watchman’s song’ hypothesis and the costs of guarding. *Ethology* 71:340–344.

RASA, O. A. E., B. A. WENHOLD, P. HOWARD, A. MARAIS, AND J. PALLETT. 1992. Reproduction in the yellow mongoose revisited. *South African Journal of Zoology* 27:192–195.

ROOD, J. P. 1975. Population dynamics and food habits of the banded mongoose. *African Journal of Ecology* 13:89–111.

ROOD, J. P. 1978. Dwarf mongoose helpers at the den. *Journal of Comparative Ethology* 48:277–287.

ROOD, J. P. 1980. Mating relationships and breeding suppression in the dwarf mongoose. *Animal Behaviour* 28:143–150.

ROOD, J. P. 1983. The social system of the dwarf mongoose. *American Society of Mammalogists* 7:454–488.

ROOD, J. P. 1986. Ecology and social evolution in the mongooses. Pp. 131–152 in *Ecological aspects of social evolution*. Birds and

- mammals (D. I. Rubenstein and R. W. Wrangham, eds.). Princeton University Press, Princeton, New Jersey.
- ROOD, J. P. 1989. Male associations in a solitary mongoose. *Animal Behaviour* 38:725–727.
- ROOD, J. P. 1990. Group size, survival, reproduction and routes to breeding in dwarf mongooses. *Animal Behaviour* 39:566–572.
- ROOD, J. P., AND P. M. WASER. 1978. The slender mongoose, *Herpestes sanguineus*, in the Serengeti. *Carnivore* 1:54–58.
- LE ROUX, A. 2007. Communication in the yellow mongoose, *Cynictis penicillata*. Ph.D. dissertation, University of Stellenbosch, Stellenbosch, South Africa.
- LE ROUX, A., M. I. CHERRY, L. GYGAX, AND M. B. MANSER. 2009. Vigilance behavior and fitness consequences: comparing a solitary-foraging and an obligate group-foraging mammal. *Behavioral Ecology and Sociobiology* 63:1097–1107.
- LE ROUX, A., M. I. CHERRY, AND M. B. MANSER. 2008. The effects of population density and sociality on scent marking in the yellow mongoose. *Journal of Zoology* 275:33–40.
- RUSSELL, A. F., ET AL. 2002. Factors affecting pup growth and survival in cooperatively breeding meerkats *Suricata suricatta*. *Journal of Animal Ecology* 71:700–709.
- SCHNEIDER, T. C., AND P. M. KAPPELER. 2014. Social systems and life-history characteristics of mongooses. *Biological Reviews* 89:173–198.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- TAYLOR, M. E. 1975. *Herpestes sanguineus*. *Mammalian Species* 65:1–5.
- VAUGHAN, T. A. 1976. Feeding behavior of the slender mongoose. *Journal of Mammalogy* 57:390–391.
- VERON, G., M. COLYN, A. DUNHAM, P. TAYLOR, AND P. GAUBERT. 2004. Molecular systematics and origin of sociality in mongooses (Herpestidae, Carnivora). *Molecular Phylogenetics and Evolution* 30:582–598.
- WASER, P. M., L. F. ELLIOTT, N. M. CREEL, AND S. R. CREEL. 1995. Habitat variation and mongoose demography. Pp. 421–448 in *Serengeti II: dynamics, management and conservation of an ecosystem* (A. R. E. Sinclair and P. Arcese, eds.). University of Chicago Press, Chicago, Illinois.
- WASER, P. M., B. KEANE, S. R. CREEL, L. F. ELLIOTT, AND D. J. MINCHELLA. 1994. Possible male coalitions in a solitary mongoose. *Animal Behaviour* 47:289–294.

*Submitted 9 July 2015. Accepted 19 October 2016.*

*Associate Editor was Roger Powell.*