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# Radiocollars do not affect the survival or foraging behaviour of wild meerkats

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## Abstract

The practice of radiocollaring is increasingly being used in the study of wild animal populations. However, methods of tracking and monitoring are known to affect some species negatively. On a wild population of habituated meerkats *Suricata suricatta*, we investigated the potential costs and consequences of carrying a radiocollar for small carnivores, focusing on detailed aspects of foraging behaviour and survival. Radiocollared individuals were no more likely to be predated than non-collared individuals in the same social group. We also found that collaring did not affect foraging efficiency, with collared individuals being equally efficient foragers (four measures) while wearing a collar compared with the pre-collaring period. To control for group-specific events, changes in foraging efficiency after collaring were compared with the behaviour of control individuals from the same group and no significant differences were found. In conclusion, we found no evidence to suggest radiocollars impact negatively on the bearer's welfare, survival or foraging ability.

## Introduction

Individuals of a diverse range of species are commonly fitted with radiotransmitters to facilitate ecological and conservation-based research (Withey, Bloxton & Marzluff, 2001). It is suggested that carrying a radiocollar may be costly to an individual in two ways. First, a collar may increase susceptibility to predation by providing an obvious visual target or by hindering the bearer's escape due to physical constraints or added weight. Indeed, studies of predation show that preference is often given to prey that are conspicuous from other conspecifics, by either visual or behavioural disparity (see Kruuk, 1972; Fitzgibbon & Fanshawe, 1988). Second, radiocollared individuals may suffer more subtle costs such as reduced foraging or hunting efficiency, again through physical constraints or increased conspicuousness. For example, collared individuals may be expected to prolong the time that they invest in feeding in order to compensate for lower efficiency and/or the potential additional energetic costs associated with carrying a collar. The welfare and behaviour of radiocollared animals is of importance not only in terms of wildlife ethics but also in the prevention of erroneous data collection (Amlaner & MacDonald, 1980).

Some of the potentially adverse effects that have been investigated previously in various species include survivorship (Daly *et al*., 1992), weight (Tuyttens, Macdonald & Raddam, 2002), condition (Jackson, Jackson & Seitz, 1985), various aspects of behaviour (Croll *et al*., 1996) and reproduction (Croll *et al*., 1996). Despite extensive investigation, results vary considerably between studies, with 47% of 96 studies in the latest review reporting a direct negative effect (Withey *et al*., 2001). There is also some evidence for indirect effects, such as in the water vole *Arvicola terrestris*, where offspring sex ratio was heavily skewed towards male-biased litters in radiotracked populations (Moorhouse & Macdonald, 2005). Furthermore, it is argued that there may be many subtle but important effects that are difficult to detect, such as weight loss and energetic costs in response to stress (Tuyttens, Macdonald & Raddam, 2003).

In the majority of previous studies, independent populations of collared and non-collared individuals were compared, meaning that environmental differences such as habitat, resource availability or predation pressure could not be taken into account. Such stochastic effects are hard to control for but are likely to have a huge impact on the results. The most accurate measures can be achieved by comparing individuals, one with the treatment and one without, from the same group, which are therefore exposed to as similar social and ecological environments as possible (Withey *et al*., 2001). This is, however, rarely possible and many previous studies attempt to buffer the effects of natural variation by increasing the sample size. Additionally, it is often impossible to collect behavioural data, and few studies examine more than one potential cost, in effect only uncovering a partial story. Finally, most previous studies examine only the short-term effects (mostly in the few days immediately post-collaring), and while these do, importantly, highlight any impact of the collaring procedure itself, they are usually unable to determine whether there is an acclimation period, as a few studies have indeed shown (e.g. Tuyttens *et al*., 2002). Such information is of great importance in relation to the validity of scientific data collected on individuals when collared periods are long.

Here, we use a long-term (established in 1993), intensively monitored study population of wild meerkats *Suricata suricatta* Schreber 1776. This population is habituated to regular close observation ($<1$ m), which enables accurate measures of individual survivorship, weight fluctuation, foraging success and time invested in foraging behaviour to be made. This also allows direct measurement and comparison between individuals in the same group, before and after a collaring event. The same-group non-collared controls provide a powerful control for the variation in resource availability and daily stochastic events, such as rain, group interactions and predator encounters, which often result in suspended foraging behaviour.

Meerkats are a non-endangered social-living mongoose from the Herpestidae family (Veron *et al*., 2004), and inhabit the semi-arid deserts of southern Africa (Skinner & Smithers, 1990). Groups consist of an unrelated dominant pair that act as the primary breeders, and subordinate (natal and immigrant) individuals that remain and assist with pup rearing and other forms of cooperation (Clutton-Brock *et al*., 1998*a*,*b*, 2001; Doolan & Macdonald, 1999). As part of a long-term study into the evolution of cooperative behaviour, some individuals are radiocollared to locate each study group. Meerkats are diurnal, foraging on an omnivorous (mainly insectivorous) diet, digging up to 20 cm below the ground to reach prey, and while doing so are unable to detect predators (Clutton-Brock *et al*., 1999*a*). Potential predators of adult meerkats at the study site include mammalian carnivores (African wild cat *Felis lybica*, Cape fox *Vulpes chama*, domestic dog *Canis familiaris*), reptiles (Cape cobra *Naja nivea*, puff adder *Bitis arietans*) and birds of prey (tawny eagle *Aquila rapax*, martial eagle *Polemaetus bellicosus*, giant eagle owl *Bubo lacteus*) later collectively referred to as 'raptors'. Vigilant individuals emit a variety of alarm calls to signal the presence of a predator (Manser, 2001), and refuge is sought in the closest bolthole, of which there are several thousand in each home range (Manser & Bell, 2004). The presence of a radiocollar may inhibit these natural behaviours, potentially hindering escape from predators by adding weight, acting as a physical constraint or target or possibly hindering foraging success through reduced prey capture rates, and therefore increasing the time that must be invested in foraging behaviours. Here, we investigate whether radiocollaring meerkats affects the likelihood of predation or imposes a discernable energetic cost.

# Materials and methods

## Study site

This study was conducted in the South African Kalahari desert, on ranch land near Van Zylsrus (26°58′S, 21°49′E). Detailed descriptions of habitat and climate are provided elsewhere (Clutton-Brock *et al*., 1999*b*; Russell *et al*., 2002). Data were collected continuously between 1998 and 2005, from 12 meerkat groups containing three to 49 individuals. All individuals were uniquely recognizable by a small hair dye patch applied to their fur while they stood warming their bodies (sunning) at the morning sleeping burrow.

## Radiocollaring and capture protocol

Target individuals were picked up by the tail-base while foraging and placed in a cloth bag, where they remained until fully anaesthetized to minimize stress. Here they were given a dose of either an intra-muscular or a gaseous anaesthetic. In most captures, a single intra-muscular injection of Ketamine hydrochloride and Medetomidine hydrochloride was given, and later reversed with Atipamezole (described in O'Riain *et al*., 2000). In later captures isoflurane was administered as described in Jordan, Cherry & Manser (2007). A Telonics® (Telonics Inc., Mesa, AZ, USA) (22–35 g) or Sirtrack® (Sirtrack, Havelock North, New Zealand) (17–22 g)-manufactured collar was fitted to the individual, with the transmitter hanging below the neck and a 15 cm whip antenna protruding over the shoulder. Collar units represented 3–6% body weight. This was mainly a factor of battery weight, as collars were designed to last for a period of 12 months to reduce recapture rates. Following collaring and reversal of the sedative, the individual was placed in a well-ventilated recovery box before being returned to the centre of the foraging group. The temperature and breathing rates of captured individuals were monitored throughout each procedure. No dominance change, dominance competition or change in reproductive status was effected as a result of these brief removals. Animal capture protocols were approved by the University of Cambridge ethical committee and the Northern Cape Conservation Service, South Africa.

## Predation

In order to determine whether collared individuals suffer a greater risk of predation than uncollared individuals, the number of predation events involving radiocollared dominant individuals and their non-collared dominant partners were compared. Death or dispersal can usually be ascertained for radiocollared individuals by tracking the collar, whereas the fate of non-collared individuals is less easily determined, as they are rarely found. For this reason, dominants were chosen as study subjects for the predation analyses, as they are much less likely to disperse than subordinates (Doolan & Macdonald, 1996*a*). Dominant individuals were readily recognized by their regular dominance assertion behaviours (Kutsukake & Clutton-Brock, 2006). Additionally, we only included stable dominant pairs where neither individual had ever been recorded to temporarily leave their group since obtaining dominance. When non-collared stable dominant individuals disappear from the population, we can be almost certain that they have been predated.

In this analysis, each paired sample of collared and non-collared individuals were the dominant pair of the same group, thus controlling for differences in predator density. This is necessary as different groups are known to suffer higher predation rates due to the location of their home range (K. A. Golabek, pers. obs.), which presumably incorporate the hunting range of predators. Our sample of 21 paired individuals only included pairs when both individuals remained dominant and either collared, or not, for a minimum of 365 days until either one of them died or a control condition changed (dominance loss or collar removal).

## Energetic costs

To determine whether radiocollaring adversely affected the foraging efficiency of the bearer, four measures of foraging efficiency were recorded for individuals both before they were fitted with a collar, and while wearing a collar. First, the percentage weight change (PWC) of individual meerkats during foraging sessions was recorded. Individuals were weighed on emergence from the overnight burrow in the morning before foraging had commenced, and later at 'lunch' each day (usually after 180 min, but at the least 90 min, of foraging). Weights were taken by coaxing individuals into a sand-filled tray on an electronic top-pan balance ($\pm 1$ g) using small rewards ($<0.5$ g) of hard-boiled egg (Clutton-Brock *et al.*, 1998*a*,*b*) or a few drops of water from a hamster bottle. PWC values were calculated by dividing the individual's weight change from 'morning' to 'lunch' weights by its weight at morning weights and then by the time spent foraging in between those measurements. In analyses involving PWC, data were collected up to 12 months before and 7 months after the collar was fitted and still worn by the bearer. Samples were taken opportunistically from days when both the collar and control individual were weighed at both morning and lunch. The minimum number of days sampled to calculate an individual's average PWC for each sample pair was three and the maximum was 31.

In addition to PWC, and as more sensitive indicators of any disturbance to actual foraging ability, focal observations were used to estimate three further measures of foraging efficiency. These measures were the proportion of focal spent foraging (Prop FO), mean foraging bout length (Mean FO) and foraging success (FO Success) per bout. Foraging bouts began when the individual started digging with the fore paws, with nose directed down, until the individual changed its behaviour for more than two seconds or moved away from that particular hole. Twenty-minute individual focal watches (Altmann, 1974) were conducted while walking within 2 m of the target animal, during which the exact behaviour, including the outcome of each foraging bout, was recorded on hand-held computers (Psion II, Psion Teklogix Ltd., Bourne End, UK) (Clutton-Brock *et al.*, 2001). All focal data were recorded in the 12 months before the collaring event and within 3 months of the collar being fitted.

To control for differences in food availability and other stochastic events between the pre-collared and collared periods, additional analyses comparing a collared and non-collared control were conducted. In these analyses, both individuals were the same sex, of a similar age and resided in the same group. Additionally, both members of the pair were present within the group, and the collared individual held the collar, for at least 3 months after their first collaring. All collared individuals and controls were adults ($>1$ year), which controlled for the potential effects of the development of foraging skills (Doolan & Macdonald, 1999; Brotherton *et al.*, 2001). We did not include data from pregnant or lactating individuals, or in most cases during periods when pups ($<10$ weeks) were foraging with the group, as some individuals increase their foraging effort in these periods (Brotherton *et al.*, 2001; Clutton-Brock *et al.*, 2001). However, the exception to this was when measuring individual foraging success (FO Success), as we assumed that the presence of pups does not affect an individual's foraging skills or ability. Data were only included when collected from collared and control individual on the same day, which allowed a unique control for differences in habitat quality and food availability, as well as removing bias introduced by stochastic events that may affect foraging behaviour, such as predator interactions or rain, under which circumstances foraging is suspended (Doolan & Macdonald, 1996*b*). Our sample was taken opportunistically from a database where both the collared and control individuals had been focaled on the same day/session. Our minimum sample to calculate an individual's average foraging efficiency per sample pair was three and the maximum was 21 focals.

## Statistical analyses

To test whether predation was equally likely between pairs of collared and non-collared meerkats, a McNemar test was used, null hypothesis: $P$ (collared predated: non-collared alive) = $P$(non-collared alive: collared predated). After 365 days, and/or until a change in one of the conditions (either dominance or collared status), one of four possible outcomes for each pair was recorded, alive:alive (both alive); alive:dead; dead:alive; dead:dead, and a $2 \times 2$ table of outcomes was constructed.

To test for any effect of collaring on the four measures of foraging efficiency, paired $T$-tests, before and after ($<3$ months) treatment, were performed. In addition, to control for ecological variability (e.g. changes in food abundance), we integrated the foraging efficiency of non-collared same-group controls into a second $T$-test, in which case the $T$-test statistics used are as follows: for PWC data; $T=(w_1-v_1)-(w_2-v_2)$, where '$w$' is the average PWC for the collared individual and '$v$' is the average PWC for the control individual. 1 denotes before the collaring event and 2 during collaring. Owing to the larger numerical scale of the focal data, the three latter measures were analysed by the ratio between individuals. Here, the $T$-test statistic used is $T=(x_1/y_1)-(x_2/y_2)$. Similarly, $x$ denotes a collared individual, and $y$ a non-collared individual. Parametric paired-sample $T$-tests were used throughout, as data did not differ significantly from the normal, as determined by the Anderson Darling test. All tests were carried out in Minitab® (Minitab Inc., State College, PA, USA) Release 14.20.

## Results

### Predation

Radiocollared individuals are no more likely to be predated than non-collared individuals from the same group (McNemar; $n = 21$, $P = 1.000$), suggesting that radiocollaring does not influence the likelihood of predation, either by added weight, reduced manoeuvrability or acting as a conspicuous target. Of 21 paired samples, 13 individuals were predated before any of the control conditions (dominance or collar status) changed within a minimum of 365 days. Of these, seven were radiocollared and six were non-collared controls. For four of the radiocollared individuals, predation was the clear cause of death as mauled bodies or chewed radiocollars were recovered. In one case, the individual died within the burrow, another simply disappeared and the third was killed by a car. We included this latter case in the predation analysis as reduced manoeuvrability could hinder escape from a vehicle equally to that of a predator.

### Energetic costs

No evidence was found to suggest that individuals suffered an energetic cost to wearing a collar. Neither the PWC, foraging success, proportion of time spent foraging nor the mean foraging bout length were significantly altered by the addition of a radiocollar (Table 1a). Additionally, when controlling for group-specific stochastic events the difference in PWC between collared and control individuals was not significantly different during the collaring period compared with the pre-collaring period (Table 1b).

Furthermore, the ratio between foraging ability between collared and non-collared individuals in prey acquisition (FO Success), overall time invested in foraging (Prop FO) and average foraging bout (Mean FO) was also not markedly different after the collaring event (Table 1b).

**Table 1** Paired $T$-tests on the effects of collaring on four estimates of foraging efficiency. (a) Shows before and after tests on the collared individual alone, and (b) incorporates a same-group control where the differences between collared and control individuals are compared before and after the collaring event

| Factor | $T$ statistic | d.f. | $P$ |
|---|---|---|---|
| (a) Pre-collared versus collared | | | |
| Percentage weight change (PWC) | −0.28 | 12 | 0.783 |
| Proportion time foraging (Prop FO) | −0.39 | 5 | 0.715 |
| Mean foraging bout (Mean FO) | −0.33 | 5 | 0.752 |
| Prey capture success (FO Success) | −0.13 | 8 | 0.899 |
| (b) Pre-collared versus collared (incorporated control) | | | |
| Percentage weight change (PWC) | −0.13 | 12 | 0.898 |
| Proportion time foraging (Prop FO) | 0.27 | 5 | 0.789 |
| Mean foraging bout (Mean FO) | −0.46 | 5 | 0.205 |
| Prey capture success (FO Success) | 0.47 | 8 | 0.652 |

The pre-collared period is up to 12 months before collaring, and the collared period is up to 7 months for the PWC data and 3 months for the others.

## Discussion

### Predation

Radiocollared meerkats were no more likely to be predated than their non-collared same-group controls. In this study, we were able to control for ecological differences in home range and movements, by pairing collared individuals with same-group controls. Although this slightly reduced our sample size, it greatly improved the study's precision, enabling differential predator pressure in different home ranges to be incorporated into the predation assessment. For example, a raptor's hunting range may include one meerkat group's home range and not another, thus biasing the likelihood of predation for any one individual in the population. Additionally, our study period was also relatively long (>1 year), which should compensate for the relatively low predator density in the area (Clutton-Brock *et al.*, 1999*b*). Where predation pressure is normally low, a study encompassing only a week or a few months would probably not be sufficient to expose any true difference that may occur between collared and non-collared individuals in relation to predation rates.

### Energetic costs

We found no evidence that meerkats incurred any energetic costs when carrying a radiocollar. Few previous studies directly compare the foraging efficiency of individuals foraging under the same conditions, instead generally comparing collared and non-collared individuals across a population. In meerkats, environmental factors such as rain (Doolan & Macdonald, 1996*b*), social factors like inter-group encounters, and predator encounters (Manser, 2001; Manser & Bell, 2004) are known to disrupt foraging behaviour and such events must be adequately controlled for when assessing foraging/feeding efficiency.

Owing to the high levels of habituation of our study population, we were able to follow individuals within 1 m without affecting their behaviour (Clutton-Brock *et al.*, 1999*c*) and directly assess the potential effects of collaring on individual foraging investment, and prey capture rates. As Tuyttens *et al.* (2003) highlighted, it is important to test for subtle changes such as energetic costs that may exist and have important effects. Unfortunately, in other species, where detailed observations of foraging behaviour or accurate measures of condition (e.g. weight) cannot be recorded directly, a less sensitive measure must be used. For example the overall foraging trip duration is often used in marine species or overall weight change when close observations are not possible. These indirect measures are probably not sensitive enough to detect changes in time spent hunting or hunting success. However, these measures are likely to be the best estimates possible when working under different ecological conditions. Our detailed measures allow us to suggest confidently that, in a Herpestid species living under similar environmental constraints, collared individuals incur no weight loss and do not need to compensate for extra weight or bulk by foraging for longer periods of the day. Additionally, the collar does not seem to hinder prey capture success or the time invested in each foraging bout in the short term.

Korpimaki, Koivunen & Hakkarainen (1996) found evidence that voles *Microtus agrestis* suffer increased predation rates only on the day after collaring. Additionally, collared female kangaroo rats show behavioural adaptations in the first few nights after collaring by reducing excursions from the burrow, whereas males did not and were therefore more likely to be predated as a consequence (Daly *et al*., 1992). Although in our study we did not test for any immediate effects of collaring, it was apparent that predation was no greater during the early collared period, as only one predation event occurred within 2 months of collaring. Unfortunately, any immediate effects of collaring on foraging efficiency were not effectively investigated, as data were only available to assess foraging within the first 3 months, and not the direct hours or days after the collaring event. Tuyttens *et al*. (2002) recorded lower condition scores of European badger *Meles meles,* within 100 days of collaring compared with afterwards, demonstrating evidence of a condition acclimation period. In order to fully confirm our conclusion that collaring has no effect on foraging behaviour in meerkats, further investigation into the immediate effects of collaring in meerkats should be carried out, requiring weight data and focal follows on the target individuals in the immediate hours and days after collaring.

In general, results from a broad range of studies investigating the potential costs that radio-tagged animals might incur vary considerably (see Withey *et al*., 2001). It is likely that this disparity results from the wide diversity in tagging techniques, in terms of both the procedures and devices used and, perhaps most importantly, the huge differences in behavioural ecology and morphology across these taxa. As Withey *et al*. (2001) suggest, it appears that the effects of tagging are taxon and technique specific. We therefore strongly recommend careful planning that takes into account results from previous studies on closely related, if not the same, species before the attachment of tagging devices is undertaken on a large scale in the field. Recommendations for planning can also be found in Withey *et al*. (2001) review, in supplement to White & Garrott's advice (1990). While acknowledging the limitations that exist in terms of different species and environments, we would suggest that researchers think creatively about their particular study animals and exploit behavioural characteristics to design an effective study under such constraints. Negative impacts of collaring could potentially not only invalidate the basic assumption that the behaviour and predation risk of tagged individuals is equal to that of untagged individuals (see Amlaner & Macdonald, 1980; Millspaugh & Marzluff, 2001), but may also impact negatively on the bearer's welfare.

In conclusion, radiocollared meerkats were no more likely to be predated than non-collared controls from the same group, of the same dominance status, and exposed to the same environmental and social conditions. Furthermore, collared individuals exhibit no greater energetic cost in the first 3 months after the collaring date, as their foraging efficiency when collared was not significantly different from either their own pre-collared levels or from same-group controls. We find no discernable costs to carrying a radio-collar in meerkats in either likelihood of predation or energetic costs, and suggest that this manipulation does not compromise the data evaluated from the study. However, we suggest further investigation to exclude the possibility of an immediate effect in the first few hours/days. Our study into the potential effects of radiocollaring on survival and foraging behaviour supports the continued use of radio-collars in small carnivore research, particularly herpestids under similar environmental conditions, but we suggest stringent research and planning before the use of such devices in other animal groups.

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## References

Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* **49**, 227–267.

Amlaner, C.J. & Macdonald, D.W. (1980). *A handbook on biometry and radio tracking*. Oxford, UK: Pergamon Press.

Brotherton, P.N.M., Clutton-Brock, T.H., O'Riain, M.J., Gaynor, D., Sharpe, L., Kansky, R. & McIlrath, G.M. (2001). Offspring food allocation by parents and helpers in a cooperative mammal. *Behav. Ecol*. **12**, 590–599.

Clutton-Brock, T.H., Brotherton, P.N.M., O'Riain, M.J., Griffin, A.S., Gaynor, D., Kansky, R., Sharpe, L. & McIlrath, G.M. (2001). Contributions to cooperative rearing in meerkats. *Anim. Behav*. **61**, 705–710.

Clutton-Brock, T.H., Brotherton, P.N.M., Smith, R., McIlrath, G., Kansky, R., Gaynor, D. & Skinner, J.D. (1998*b*).

Infanticide and expulsion of females in a cooperative mammal. *Proc. Roy. Soc. Lond. Ser. B* **265**, 2291–2295.

Clutton-Brock, T.H., Gaynor, D., Kansky, R., MacColl, A.D.C., McIlrath, G., Chadwick, P., Brotherton, P.N.M., O'Riain, J.M., Manser, M. & Skinner, J. (1998*a*). Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. Roy. Soc. Lond. Ser. B* **265**, 185–190.

Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., MacColl, A.D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D. & Brotherton, P.N.M. (1999*b*). Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J. Anim. Ecol.* **68**, 672–683.

Clutton-Brock, T.H., Maccoll, A., Chadwick, P., Gaynor, D., Kansky, R. & Skinner, J.D. (1999*c*). Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari. *Afr. J. Ecol.* **37**, 69–80.

Clutton-Brock, T.H., O'Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R., Griffin, A.S. & Manser, M. (1999*a*). Selfish sentinels in cooperative mammals. *Science* **284**, 1640–1644.

Croll, D.A., Jansen, J.K., Goebel, M.E., Boveng, P.L. & Bengtson, J.L. (1996). Foraging behavior and reproductive success in chinstrap penguins: the effects of transmitter attachment. *J. Field Ornithol.* **67**, 1–9.

Daly, M., Wilson, M.I., Behrends, P.R. & Jacobs, L.F. (1992). Sexually differentiated effects of radio transmitters on predation risk and behaviour in kangaroo rats (*Dipodomys merriami*). *Can. J. Zool.* **70**, 1851–1855.

Doolan, S.P. & Macdonald, D.W. (1996*a*). Dispersal and extra-territorial prospecting by slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari. *J. Zool. (Lond.)* **240**, 59–73.

Doolan, S.P. & Macdonald, D.W. (1996*b*). Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *J. Zool. (Lond.)* **239**, 697–716.

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

Fitzgibbon, C. & Fanshawe, J. (1988). Stotting in Thomson Gazelles – an honest signal of condition. *Behav. Ecol. Sociobiol.* **23**, 69–74.

Jackson, D.H., Jackson, L.S. & Seitz, W.K. (1985). An expandable drop-off transmitter harness for young bobcats. *J. Wildl. Mgmt.* **49**, 46–49.

Jordan, N.R., Cherry, M.I. & Manser, M.B. (2007). Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Anim. Behav.* **73**, 613–622.

Korpimaki, E., Koivunen, V. & Hakkarainen, H. (1996). Do radio-collars increase the predation risk of small rodents? *Ethol. Ecol. Evol.* **8**, 377–386.

Kruuk, H. (1972). *The spotted hyena*. Chicago: The University of Chicago.

Kutsukake, N. & Clutton-Brock, T.H. (2006). Aggression and submission reflect reproductive conflict between females in cooperatively breeding meerkats. *Behav. Ecol. Sociobiol.* **59**, 541–548.

Manser, M. (2001). The acoustic structure of suricates' alarm calls varies with the predator type and the level of response urgency. *Proc. Roy. Soc. Lond. Ser. B* **268**, 2315–2324.

Manser, M.B. & Bell, M.B. (2004). Spatial representation of shelter locations in meerkats, *Suricata suricatta*. *Anim. Behav.* **68**, 151–157.

Millspaugh, J.J. & Marzluff, J.M. (2001). *Radio tracking and animal populations*. San Diego, CA: Academic Press.

Moorhouse, T.P. & Macdonald, D.W. (2005). Indirect negative impacts of radio-collaring: sex ratio variation in water voles. *J. Appl. Ecol.* **42**, 91–98.

O'Riain, M.J., Bennett, N.C., Brotherton, P.N.M., McIlrath, G.M. & Clutton-Brock, T.H. (2000). Reproductive suppression and inbreeding avoidance in wild populations of cooperatively breeding meerkats (*Suricata suricatta*). *Behav. Ecol. Sociobiol.* **48**, 471–477.

Russell, A.F., Clutton-Brock, T.H., Brotherton, P.N.M., Sharpe, L.L., McIlrath, G.M., Dalerum, F.D., Cameron, E.Z. & Barnard, J.A. (2002). Factors affecting pup growth and survival in cooperatively breeding meerkats *Suricata suricatta*. *J. Anim. Ecol.* **71**, 700–709.

Skinner, J.D. & Smithers, R.H.N. (1990). *The mammals of the southern African subregion*. Pretoria: University of Pretoria.

Tuyttens, F.A.M., Macdonald, D.W. & Raddam, A.W. (2002). Effects of radio-collars on European badgers (*Meles meles*). *J. Zool. (Lond.)* **257**, 37–42.

Tuyttens, F.A.M., Macdonald, D.W. & Raddam, A.W. (2003). Response to Delahay, Waldram, Mallinson, Spyvee, Handoll, de Leeuw and Cheeseman. *J. Zool. (Lond.)* **260**, 120–121.

Veron, G., Colyn, M., Dunham, A.E., Taylor, P. & Gaubert, P. (2004). Molecular systematics and origin of sociality in mongooses (Herpestidae, Carnivora). *Mol. Phylogenet. Evol.* **30**, 582–592.

White, G.C. & Garrott, R.A. (1990). *Analysis of wildlife radio-tracking data*. San Diego, New York: Academic Press Inc.

Withey, J.C., Bloxton, T.D. & Marzluff, J.M. (2001). Effects of tagging and location error in wildlife radiotelemetry studies. In *Radio tracking and animal populations*: 43–75. Millspaugh, J.J. & Marzluff, J.M. (Eds). San Diego, CA: Academic Press.