

Male mate guarding in a socially monogamous mammal, the round-eared sengi: on costs and trade-offs

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Abstract Mate guarding is predicted to be one of the driving forces for the evolution of monogamy, but supporting evidence in free-living mammals is rare. The goals of our study were three-pronged. First, we tested if mate guarding, measured as intrapair distance, occurs as a behavioral tactic in round-eared sengis (*Macrosclides proboscideus*), a socially monogamous species lacking paternal care and in which females breed asynchronously,

producing 2–3 litters during an 8-month long breeding season. Second, we determined if mate guarding involves costs which we identified as changes in male body mass. Third, we investigated whether variation in individual investment in mate guarding depended on the males' body mass and the number of neighboring males. Field data were collected in a semidesert in South Africa using radio-tracking, trapping, and direct observations during three successive breeding seasons. Mate guarding strongly depended on the females' reproductive state, and all males started to guard their mates prior to and during estrus, as exemplified by reduced intrapair distance. Mate guarding incurred costs: overall, males lost about 5% of body mass. Male body mass loss and initial body mass were negatively related to the intensity of precopulatory mate guarding. Furthermore, during estrus intrapair distance was inversely correlated with the number of neighboring males. The results show that mate guarding is the predominant male tactic in round-eared sengis. However, since mate guarding imposed costs, males may balance benefits and costs associated with guarding by varying their effort in relation to their physical capabilities and the competitive environment.

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Introduction

Male mate guarding is a common behavioral tactic to overcome sperm competition (Møller and Birkhead 1989, 1991). Mate guarding involves the close following of a receptive female, which may be accompanied by agonistic interactions with competing males and/or emitting vocal-

izations, such as mating calls (Manno et al. 2007; Manno and Dobson 2008). This tactic allows the male to monitor and court the female mate, as well as, to prevent access of male competitors to the female (Huck et al. 2004). The occurrence of male mate guarding is generally favored when females are only receptive for a short period (Parker 1974; Grafen and Ridley 1983) and when reproduction occurs asynchronously during a long breeding season (van Rhjin 1991; Stockley 1997; van Dongen 2008).

In some socially monogamous mammals, especially small ruminants, male mate guarding may be the driving force for the evolution of monogamy (reviewed in Brotherton and Komers 2003). In these species, a male actively maintains close spatial proximity to his female mate beyond her receptive period, resulting in a strong pair bond. Although mate guarding allows the males to monopolize their female mates, it seems to constrain males into monogamy because they are incapable of defending an extra female (Brotherton and Komers 2003). However, to our knowledge, no study has provided empirical evidence regarding the costs and trade-offs of mate guarding in socially monogamous mammals. This information is essential for understanding the role of male mate guarding from an evolutionary perspective, and the study of variation in mate guarding behavior at the individual level might provide insights into the evolution of male mating tactics in socially monogamous mammals.

Male mate guarding represents a time investment and is, therefore, traded-off against other activities critical for survival (Parker 1974). In polygynous mammals, the mate guarding tactic imposes costs, such as reduced foraging efficiency and decreased energy intake (bison, *Bison bison athabascae*, Komers et al. 1994; baboons, *Papio cynocephalus*, Alberts et al. 1996; and mandrills, *Mandrillus sphinx*, Setchell et al. 2005), which may lead to a reduction in male body mass and condition. Accordingly, males may adjust their guarding effort in response to their physical capabilities so that better quality males invest more heavily in mate guarding than lighter or smaller individuals, since better quality males are able to afford the higher energetic costs associated with mate guarding (Clinton and LeBoeuf 1993; Iribarne et al. 1995; Jivoff 2003).

Thus, the advantages of mate guarding will depend on the tactics adopted by other males in the population. If guarding is the predominant male tactic in a population with balanced adult sex ratios, the chances of finding an unguarded female are low. In this case, the benefits of prolonged guarding of one female are higher than searching for an additional single female (Parker 1974; Yamamura 1987). Furthermore, guarding intensity and duration may be sensitive to population characteristics, such as the local male density (Komdeur 2001), population density (Iribarne et al. 1995; Storey et al. 1995; Jirokul 1999; Currie and Valkama 2000), and adult sex ratios (Dick and Elwood

1996; Matthews 2002; Jivoff 2003), so that males invest more heavily in mate guarding with increasing pressure of the competitive environment, i.e., more rival males present.

In the present study, we investigated the mating behavior of the socially monogamous round-eared sengi (elephant-shrew, *Macroscelides proboscideus*), a member of the mammalian order Macroscelidea, which comprises 17 species from four genera that are all endemic to the African continent (Corbet and Hanks 1968). Although all sengi species are believed to be monogamous due to the occurrence of male mate guarding (Ribble and Perrin 2005), field studies on mating behavior are lacking. Unlike ruminants, sengis live in dispersed pairs that are characterized by a weak bond, probably, as a consequence of ecological pressures, such as predation and high intersexual competition for critical resources (Rathbun 1979; Kleiman 1981). Thus, the mate guarding model of ruminants, which are characterized by strong pair bonds, may not necessarily apply to sengis.

Round-eared sengis are a suitable model for studying male mate guarding because males and females show sexual behavior towards neighbors of the opposite sex (M.S. unpublished data). Furthermore, male home ranges are much larger compared to their female mate (1.5 ha vs 0.9 ha), possibly for monitoring neighboring females, as suggested for other sengi species (Rathbun 1979; FitzGibbon 1995, 1997; Ribble and Perrin 2005). In round-eared sengis, male body mass does not predict home range size. Instead, the use of space by males appears to be affected by population density and the presence of neighboring males, with males generally having only little overlap (<5%) with home ranges of paired neighboring females (Schubert et al. 2009).

Female reproductive behavior should favor a mate guarding tactic during her receptive period. Round-eared sengi females have a short postpartum estrus that lasts for about 1 day (Sauer and Sauer 1971), and reproduction occurs during a long breeding season from June to January, in which females produce 2–3 litters per breeding season, with a birth interval of about 11 days between neighboring females (Schubert et al. 2009). The precocial young, normally twins, are born after a gestation period of 61 days. Maternal care is characterized by an absentee system, i.e., care is restricted to short nursing bouts every 24 h. Pups are weaned at 4 weeks of age, and both sexes leave their natal territory (Sauer 1973). To date, there is no evidence that male round-eared sengi engage in direct parental care (Sauer and Sauer 1971; Sauer 1973). We predict that mate guarding occurs as a behavioral tactic in male round-eared sengis during female receptivity to ensure paternity. Furthermore, the chances for a male encountering an unpaired female are low, and asynchronous reproduction by females may increase male–male competition for copulations. Thus, males are also expected to engage in prolonged guarding prior to female receptivity. However,

guarding may impose costs for the males. In order to minimize these costs, males might balance their guarding effort not only in relation to demographic parameters but also to their individual abilities. Heavier males, i.e., males with a high body condition, might be expected to invest more intensely in mate guarding than lighter males, because they may be more capable of bearing mate guarding costs. Furthermore, the intensity of mate guarding behavior might depend on the intensity of male–male competition. Specifically, neighboring males often present the greatest threat to paternity assurance (Lifjeld et al. 1993; Currie and Valkama 2000; Komdeur 2001). Therefore, we predict that higher numbers of neighboring males would lead to greater levels of male mate guarding as a response to an increased risk of extrapair copulations during female fertility.

Methods

Study area

The study was conducted in the Goegap Nature Reserve, South Africa (29°37'S; 17°59'E) in December 2005, August to September 2006, and August to September 2007. The large 15,000-hectare nature reserve is situated in a semidesert in Namaqualand, South Africa. Vegetation is classified as succulent karoo (Cowling et al. 1999). Rainfall is low, averaging 160 mm per annum, and occurring predominantly in winter (Cowling et al. 1999). The study site, which was about 35 ha large, was characterized by a dry river bed and large sandy patches, interspersed shrubs consisting mainly of *Lycium cinerum* and *Zygophyllum retrofractum*, as well as, ephemeral wild flowers in spring time.

Study species

The round-eared sengi (Fig. 1) is one of the smallest sengi species and is found only in the southern regions of Africa (Skinner and Smithers 1990). This omnivorous mammal has a crepuscular to nocturnal activity pattern that is sensitive to ambient temperatures; activity decreases during cold nights and when food abundance is low (Sauer and Sauer 1971; Lovegrove et al. 1999).

Trapping

Sengis were trapped using locally produced metal traps (26×9×9 cm, similar to Sherman traps), which were baited with a mixture of oats, peanut butter, marmite, and sunflower oil (Schubert et al. 2009). During cold weather, all traps were provided with cotton wool to avoid trap deaths. Trapping was performed in the morning between 4:00 a.m. and 8:00 a.m., depending on outside temperatures



Fig. 1 Free-ranging round-eared sengi with ear tag. Photograph was taken by M. Schubert

(between 4:00 a.m. and 6:00 a.m. when temperatures were high and between 6:00 a.m. and 8:00 a.m. when temperatures were lower). Traps were checked after 2 h. In order to identify the reproductive status of females and to accurately determine the exact day of parturition, trapping was performed daily. Females that had lost about 20 g of their body mass were considered to have given birth (details provided in Schubert et al. 2009). All individuals were marked using hair dye (Inecto Rapid, Rapido, Pinetown, South Africa) and ear tags (National Band and Tag Co., Kentucky, USA).

Radio-tracking

Males and females of ten pairs were equipped with a MD-2C radio-collar (Holohil Systems Ltd., Ontario, Canada) for approximately 1 month. Identification of pairs was known from trapping and confirmed by radio-tracking (space use of individuals; Schubert et al. 2009). Before attaching the radio-collar around the neck, individuals were briefly anesthetized with ether to reduce stress during the handling procedure. The average duration from setting the traps until capturing the individuals was 2 h; anesthetizing and attaching the collar took less than 2 min. Maximum duration from recovery until releasing the individuals took 30 min. Individuals were always released at the same site where they were captured. Radio-collars weighed 2.5 g, which was less than 10% of the adult body mass of males and females weighing 42.6 g (± 4.1 standard deviation (SD)) and 43.3 g (± 3.3 SD), respectively (Schubert et al. 2009). Radio-tracking was conducted with a Telonics TR-4 receiver (Telonics Inc., Arizona, USA) and H-antenna. Individual location was recorded using a GPS (eTrex venture, Garmin, USA), which had an accuracy of ± 5 m.

Data were collected using the homing-in method; sengis were approached until they were seen or known to be hidden in a particular shelter, like shrubs or burrows. To

determine the social distance between pair mates, individual locations were recorded every 10 min for 1.5 h. Since only one person performed the radio-tracking, data could not be collected simultaneously. Thus, first the location of one partner was recorded and then, immediately thereafter, the location of the pair mate. The chronological order in which an individual was radio-tracked (i.e., first or second) was maintained during the entire radio-tracking session. Radio-tracking was performed from 7:00 to 10:00 and from 18:00 to 22:00. For each pair, an average of seven (range 4–17) radio-tracking sessions was conducted.

Data analyses

Intrapair distance was determined as the distance between the points of individual locations of pair mates every 10 min, using the program MapSource. For each radio-tracking season, a median of the intrapair distances was calculated for data analyses.

Female reproductive state was classified into four categories: (1) precopulatory 2 (PC 2), defined as the time (2–4 days) prior to birth of the pups; (2) precopulatory 1 (PC 1), which lasted from the day before birth until the day of birth; (3) estrus was defined to be on the day after parturition, because female round-eared sengis have a postpartum estrus that lasts for 1 day (Sauer and Sauer 1971); and (4) postestrus of females occurred 2–3 days after parturition. Sufficient data for eight pairs were collected during PC 2, nine pairs during PC 1, nine pairs in estrus, and ten pairs in postestrus.

Data are presented as mean \pm SD. All statistical analyses were done with R version 2.8.1 (R Development Core Team 2008). Mixed-effects models were fitted with the package lme4 with the Laplace approximation of the likelihood function (Bates 2005). The p values were calculated by likelihood-ratio tests based on changes in deviance (using maximum likelihood estimates) when each term was dropped from the full (main effects) model. Interactions were tested by considering the changes, when these were added to the model (Faraway 2006). Alpha was set at 0.05.

We compared intrapair distance concerning the four different female reproductive states with a linear mixed model, which also included year and pair identity as random factors.

Body mass loss is commonly used as a measure of stress (von Holst 1998). We investigated whether mate guarding is costly by comparing male body mass before and after mate guarding using a paired t test. Mean body mass of males was calculated for the period starting 45–15 days before parturition (initial male body mass) and after termination of male mate guarding (2–4 days after birth). Since the population was monitored by continuously trapping, we also included two males that were not equipped with a radio-collar. Body mass data of one radio-tracked male could not

be collected for the postestrus period due to predation, resulting in body mass data being available for 12 males. In addition, we determined the effects of intrapair distances on body mass loss with a linear mixed model (LMM), including year as a random factor. Influence of mate guarding on body mass loss was investigated for the estrus, PC 2, and PC 1, but not for the postestrus because male mate guarding was already terminated by then (see results). Precopulatory 2 was included in the analyses to account for the fact that some males may have already started to guard their females prior to fertility.

We tested for the effects of female reproductive state, male home range size, initial male body mass, and the number of neighboring males (all covariates) on the intrapair distances using a LMM. Individual identity and year were included as random factors. Data collection and analyses concerning home range sizes and number of neighboring males are described in Schubert et al. (2009). Male home range size was included in the model as a predictor variable because shorter intrapair distances might be due to smaller home ranges and not necessarily due to male mate guarding. Male home range size and the number of neighboring males were known for all males ($N=10$).

Results

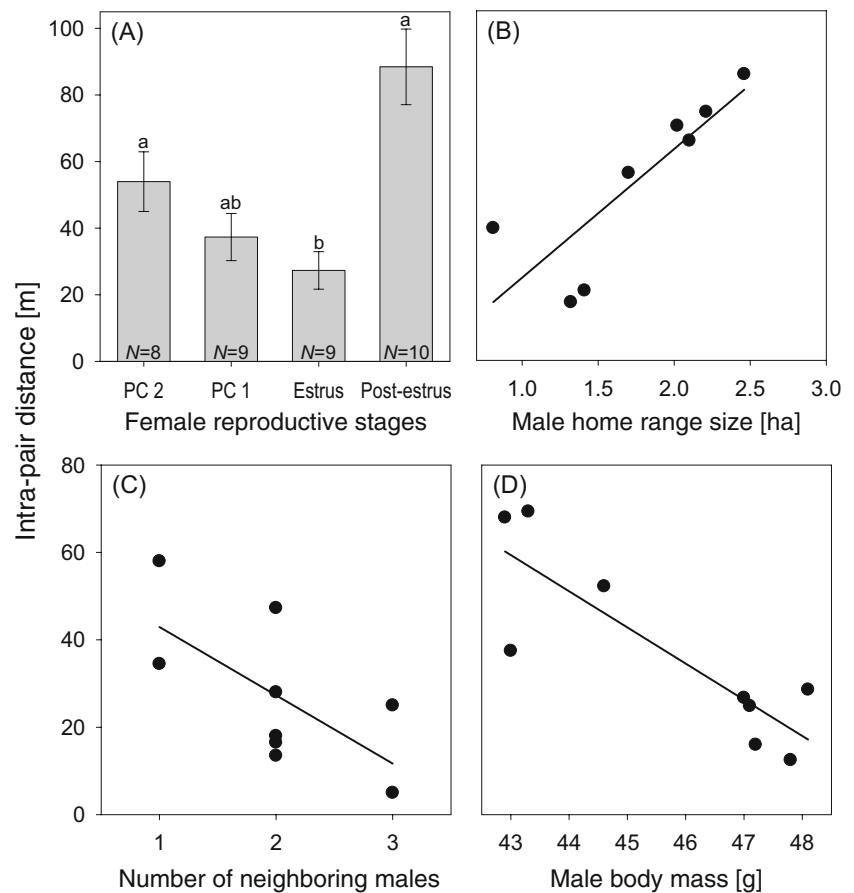
Description of behavior during mate guarding

All males ($N=10$) approached and followed their female partner prior to fertility. In response, females ran away predominately or fended males off by snapping at them with their mouth. Occasionally, males attempted to initiate body contact ($N=3$). In three cases, females approached their male mates in the precopulatory period, allowing males to sniff their ano-genital region. Both sexes were observed to mark in their home range by rubbing their ano-genital region on the ground. While following their mates, males always overmarked the females' scent ($N=2$ pairs). In addition, both sexes chased away conspecifics which intruded into the pairs' territory ($N_{\delta}=2$, $N_{\text{♀}}=1$). Since individuals chased with high speed, and chasing events were of short duration, the identity of the intruder could not be determined. After chasing, the male immediately returned to his female.

Intrapair distance during different female reproductive states

Distance between the male and the female of a pair differed significantly among the four female reproductive states. Intrapair distance was significantly reduced during PC 1 and the estrus states compared to the postestrus and PC 2 states ($\chi^2=27.65$, $df=3$, $p<0.001$, Fig. 2a).

Fig. 2 **A** Distance between pair mates in the different female reproductive states. Data are presented as mean \pm SD. Correlation between intrapair distance and **B** male home range size during PC 2; **C** the number of neighboring males during the estrus period; and **D** initial male body mass during PC 1. Different letters show significant differences between groups. See text for statistics



Effect of mate guarding on male body mass loss

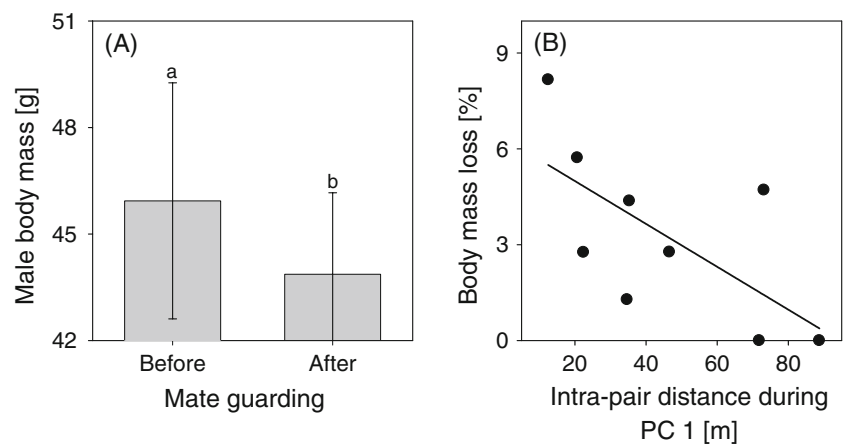
Males significantly lost weight during mate guarding, accounting for $4.6 \pm 3.7\%$ of their initial body mass ($\chi^2 = 8.68$, $df=1$, $p=0.003$, Fig. 3a). Most importantly, intrapair distance during PC 1, which was the time shortly before parturition, was related to male body mass loss ($\chi^2 = 8.68$, $df=1$, $p=0.003$, Fig. 3b). Males that were at closer proximity

with their female mates lost more body mass than males that maintained a greater intrapair distance. Such a significant relationship was not found during PC 2 and the estrus ($p > 0.10$).

Effects on intrapair distance

We found a significant interaction between home range size (which was 2.0 ± 1.2 ha) and female reproductive

Fig. 3 **A** Comparison of male body mass before and after termination of mate guarding, and **B** correlation between body mass loss and intrapair distance during PC 1. See text for statistics



(Table 1). Post hoc analyses suggest that male home range size only affected, though not significantly, intrapair distance during the PC 2 ($\chi^2=3.11$, $p=0.078$, Fig. 2b), but not during PC 1, estrus, and postestrus ($p>0.10$). During PC 2, males that occupied smaller home ranges were closer to their female mate than males that inhabited larger home ranges. In addition, there was a significant interaction between the number of neighboring males (1.8 ± 0.8 individuals) and female reproductive state (Table 1). Males that were surrounded by more neighboring males guarded their female mates more intensely during the estrus period ($\chi^2=5.00$, $p=0.025$, Fig. 2c). However, no significant effects of the number of neighboring males on intrapair distance were found for PC 1 and PC 2 and the postestrus period ($p>0.10$). There was also a significant interaction between initial male body mass and female reproductive state (Table 1). Initial male body mass negatively affected intrapair distance during PC 1 ($\chi^2=9.02$, $p=0.002$, Fig. 2d) and the postestrus, though not significantly ($\chi^2=3.28$, $p=0.070$). However, no significant effect of male body mass on distance of pair mates was found during PC 2 and estrus ($p>0.10$).

Discussion

We demonstrated that male round-eared sengis engaged in mate guarding prior to and during female receptivity. Mate guarding resulted in male body mass loss. Furthermore, round-eared sengi males in a better body condition and males that were surrounded by more neighboring males guarded their female mates more intensely.

Generally, shorter distances might be due to smaller male home ranges and not necessarily due to male mate guarding. However, reduced intrapair distance shortly before and during female fertility did not correlate with male home range size, indicating that reduced intrapair distance is a result of mate guarding rather than male space use. Asynchronous reproduction in female round-eared sengis (Schubert et al. 2009)

Table 1 Effects of different predictor variables on intrapair distance in round-eared sengi. Statistics were calculated with linear mixed models, including individual identity and year as random factors. Only significant interactions are presented; significant effects are given in bold

Predictor variables	χ^2	df	<i>p</i>
Female reproductive stage (<i>R</i>)	31.66	3	<0.001
Male home range size (<i>H</i>)	7.86	1	0.005
N neighboring males (<i>N</i>)	2.36	1	0.12
Male body mass (<i>B</i>)	0.49	1	0.48
<i>H</i> × <i>R</i>	13.47	3	0.004
<i>N</i> × <i>R</i>	11.78	3	0.008
<i>B</i> × <i>R</i>	21.50	3	<0.001

could have provided males with the opportunity to employ a mixed reproductive strategy, i.e., forming a pair bond with a single female while seeking extrapair copulations (Trivers 1972). Thus, mate guarding may function as an anticuckoldry tactic by males to protect their mating interests with their pair female (Gowaty and Plissner 1987). Precopulatory guarding is advantageous when males have a limited opportunity to search for additional females (Parker 1974). Since male round-eared sengi are constrained into a socially monogamous relationship by independently ranging females, balanced adult sex ratios, and hence, a low opportunity to encounter additional unpaired females (Schubert et al. 2009). Prolonged guarding may allow males to secure matings with their female mates when they become receptive. Furthermore, female mammals often advertise their reproductive condition, which peaks shortly before sexual receptivity (Dixson 1983), but male sengis were observed to always overmark their mate's scent shortly before and during estrus. Persistent guarding may allow a male to conceal the reproductive state of the female and advertise the paired status, thereby, decreasing the risk of intrusions by competitors, as suggested for the dik-dik (*Madoqua kirkii*; Brotherton and Komers 2003).

Our results indicate that mate guarding imposes costs for males, since they lost 5% of their body mass on average. The loss of body mass is a commonly used measure of stress (von Holst 1998; Monclús et al. 2005) and can impact on survival and investment in future mating attempts (Stearns 1992). Thus, mate guarding behavior may be influenced by the ability to recover body condition (Poole 1989). Female round-eared sengi are in estrus 2–3 times per year with reproductive events spread throughout a long breeding season of about 8 months (Schubert et al. 2009). Thus, periods of recovery between mate guarding episodes may allow the males to engage in costly mate guarding because they are able to fully recover their energy reserves. However, costs may be too high to guard several females, and may constrain males to mate guard only a single female during a limited period of time.

Since body mass loss was associated with intrapair distance during the precopulatory period 1, it appears that the costs of mate guarding are associated with following the female. Males may have traveled shorter distances during mate guarding, since female round-eared sengi use much smaller territories in comparison to their male partner. Thus, reduction in body mass may have arisen from the effort of following the female instead of increased mobility. There is increasing evidence that mate guarding comes at the price of decreased energy intake due to shorter and more interrupted feeding time (Komers et al. 1994; Alberts et al. 1996; Komdeur 2001; Setchell et al. 2005). Thus, mate guarding intensity and duration may depend on individual condition, and the costs an individual is able or willing to pay. Heavier round-eared

sengi males guarded their female mates more closely during the precopulatory period 1 and the postestrus than lighter males. Clearly, more intense guarding may have been costlier for lighter males, whereas, heavier individuals could afford to dedicate more energy and time in the mate guarding tactic. Round-eared sengis copulate multiple times with the pair mate during female receptivity (M. S. unpublished data). Since the pair bond is suggested to be weak (Rathbun 1979; Kleiman 1981), and both sexes engage in sexual behavior with neighbors of the opposite sex (M. S. unpublished data), prolonged guarding may allow heavier males to ensure their paternity because males may prevent other males to gain access to the pair female and/or restrain females from moving into neighboring areas (Jivoff 2003; Manno et al. 2007).

Paired round-eared sengi males do not only invest in mate guarding but also in year-round territory defense (Schubert et al. 2009). Generally, male territorial defense may function as a form of mate guarding, as occurring in the large treeshrew (*Tupaia tana*, Munshi-South 2007) and in the Columbian ground squirrel (*Spermophilus columbianus*, Manno and Dobson 2008). Male round-eared sengis may, therefore, employ different mating tactics depending on their individual qualities with lighter individuals investing more in territorial defense, which may be at lower costs, and better quality males intensely guarding their female mates shortly before female fertility. Since mate guarding would be traded-off against territorial defense, a decrease in defense while guarding may also be more critical for lighter than for heavier males in terms of territory takeover attempts of other males. This is because heavier (and older) males may be more experienced in territorial defense, increasing the possibility of investing more in courtship displays (age, Columbian ground squirrel Manno et al. 2007; Manno and Dobson 2008, body mass, bighorn sheep *Ovis canadensis*: Festa-Bianchet et al. 1996; collared lizards, *Crotaphytus collaris*: Schwartz et al. 2007).

Besides the physical condition of males, ecological parameters influenced male mate guarding in the round-eared sengi. Partners were spatially closely associated when they were surrounded by more adjacent (paired) males during female receptivity. Several studies have indicated that neighboring males rather than floaters are the primary threat in cuckoldry (Liffield et al. 1993; Currie and Valkama 2000; Komdeur 2001). Since sengi males are believed to maintain larger areas to monitor the reproductive state of neighboring females (Ribble and Perrin 2005), closer association between pair mates may lead to a greater within-pair paternity assurance.

Conclusions

Mate guarding may function not only to ensure paternity but also presents a time and energy investment tactic, which

is believed to evolve only when guarding results in greater fitness advantages than searching for additional mating opportunities (Parker 1974). A low encounter rate of unpaired females and asynchronous reproduction may have favored prolonged mate guarding in round-eared sengis. However, mate guarding imposed costs for males. To balance the benefits of mate guarding in terms of preventing cuckoldry and the costs, which became apparent by reduced body condition, males modified their guarding effort in relation to prevailing physical and ecological parameters. Thus, lighter males invested less in direct mate guarding than heavier ones, and males decreased their guarding effort in a less competitive environment.

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References

- Alberts SC, Altmann J, Wilson ML (1996) Mate guarding constrains foraging activity of male baboons. *Anim Behav* 51:1269–1277
- Bates D (2005) Fitting linear mixed models in R. *R News* 5:27–39
- Brotherton PNM, Komers PE (2003) Mate guarding and the evolution of social monogamy in mammals. In: Reichard UH, Boesch C (eds) *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge University Press, Cambridge, pp 42–58
- Clinton WL, LeBoeuf BJ (1993) Sexual selection's effects on male life history and the pattern of male mortality. *Ecology* 74:1884–1892
- Corbet GB, Hanks J (1968) A revision of the elephant-shrews, Family Macroscelididae. *Bull Br Mus (Nat Hist) Zool* 16:1–111
- Cowling RM, Esler KJ, Rundel PW (1999) Namaqualand, South Africa—an overview of a unique winter-rainfall desert ecosystem. *Plant Ecol* 142:3–21
- Currie D, Valkama J (2000) Population density and the intensity of paternity assurance behavior in a monogamous wader: the Curlew *Numenius arquata*. *Ibis* 142:372–381
- Dick JTA, Elwood RW (1996) Effects of natural variation in sex ratio and habitat structure on mate-guarding decisions in amphipods (Crustacea). *Behavior* 133:985–996
- Dixon AF (1983) The hormonal control of sexual behavior in primates. In: Finn CA (ed) *Reviews of reproductive biology*. Clarendon Press, Oxford, pp 131–219
- Faraway JJ (2006) Extending the linear model with R. *Generalized linear, mixed effects, and nonparametric regression models*. Chapman and Hall/CRC Press Company, New York
- Festa-Bianchet M, Jorgenson JT, King WJ, Smith KG, Wishart WD (1996) The development of sexual dimorphism, seasonal, and lifetime mass changes in bighorn sheep. *Can J Zool* 74:330–334

- FitzGibbon CD (1995) Comparative ecology of two elephant-shrew species in a Kenyan coastal forest. *Mamm Rev* 25:19–30
- FitzGibbon CD (1997) The adaptive significance of monogamy in the golden-rumped elephant-shrew. *J Zool Lond* 242:167–177
- Gowaty PA, Plissner JH (1987) Association of male and female American robins (*Turdus migratorius*) during the breeding season: paternity assurance by sexual access or mate-guarding. *Wilson Bull* 99:56–62
- Grafen A, Ridley M (1983) A model of mate guarding. *J Theor Biol* 102:549–567
- Huck MA, Lottker P, Heymann EW (2004) Proximate mechanisms of reproductive monopolization in male moustached tamarins (*Saguinus mystax*). *Am J Primatol* 64:39–56
- Iribarne O, Fernandez M, Armstrong D (1995) Precopulatory guarding time of the male amphipod *Eogammarus oclairi*: effects of population structure. *Mar Biol* 124:219–223
- Jirokul M (1999) Population density influences male-male competition in guppies. *Anim Behav* 58:1169–1175
- Jivoff P (2003) A review of male mate guarding success in the blue crab, *Callinectes sapidus*, in reference to the potential for fisheries-induced sperm limitation. *Bull Mar Sci* 72:273–286
- Kleiman DG (1981) Correlations among life history characteristics of mammalian species exhibiting two extreme forms of monogamy. In: Alexander RD, Tinkle DW (eds) Natural selection and social behavior. Chiron Press, New York, pp 332–344
- Komdeur J (2001) Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risks. *Proc R Soc Lond B Biol Sci* 266:2075–2081
- Komers PE, Messier F, Gates CC (1994) Plasticity of reproductive behavior in wood bison bulls: on risks and opportunities. *Ethol Ecol Evol* 6:485–495
- Lifjeld JT, Dunn PO, Robertson RJ, Boag PT (1993) Extra-pair paternity in monogamous tree swallows. *Anim Behav* 45:213–229
- Lovegrove BG, Laws MJ, Roxburgh L (1999) Confirmation of pleisiomorphic daily torpor in mammals: the round-eared elephant shrew, *Macroscelides proboscideus* (Macroscelidea). *J Comp Physiol* 169:453–460
- Manno TG, Dobson FS (2008) Why are male Columbian ground squirrels territorial? *Ethology* 114:1049–1060
- Manno TG, Nesterova AP, Debarbieri LM, Kennedy SE, Wright KS, Dobson FS (2007) Why do male Columbian ground squirrels give a mating call? *Anim Behav* 74:1319–1327
- Matthews LM (2002) Tests of the mate guarding hypothesis for social monogamy: does population density, sex ratio, or female synchrony affect behavior of male snapping shrimp (*Alpheus angulatus*)? *Behav Ecol Sociobiol* 51:426–432
- Møller AP, Birkhead TR (1989) Copulation behavior in mammals: evidence that sperm competition is widespread. *Biol J Linn Soc* 38:119–131
- Møller AP, Birkhead TR (1991) Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behavior* 118:170–186
- Monclús R, Rödel HG, von Holst D, de Miguel J (2005) Behavioural and physiological responses of naïve rabbits to predator odour. *Anim Behav* 70:753–761
- Munshi-South J (2007) Extra-pair paternity and the evolution of testis size in a behaviourally monogamous mammal, the large treeshrew (*Tupaia tana*). *Behav Ecol Sociobiol* 62:201–212
- Parker GA (1974) Courtship persistence and female-guarding as male investment strategy. *Behavior* 48:157–184
- Poole JH (1989) Announcing intent: the aggressive state of musth in African elephants. *Anim Behav* 37:140–152
- R Development Core Team (2008) A language and environment for statistical computing. R Foundation for Statistical Computing, Austria: Vienna, ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Rathbun GB (1979) The social structure and ecology of elephant-shrews. *Adv Ethol* 20:1–79
- Ribble DO, Perrin MR (2005) Social organization of the eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Belg J Zool* 135:167–173
- Sauer EGF (1973) Zum Sozialverhalten der kurzohrigen Elefantenspitzmaus, *Macroscelides proboscideus*. *Z Säugetierkd* 38:65–97
- Sauer EGF, Sauer EM (1971) Die kurzohrige Elefantenspitzmaus in der Namib. *Namib and Meer* 2:5–43
- Schubert M, Pillay N, Ribble DO, Schradin C (2009) The round-eared sengi and the evolution of social monogamy: environmental parameters constrain males to live with a single female. *Ethology* (in press)
- Schwartz AM, Baird TA, Timanus DK (2007) Influence of age and prior experience on territorial behavior and the costs of defense in male collared lizards. *Ethology* 113:9–17
- Setchell JM, Charpentier M, Wickings EJ (2005) Mate guarding and paternity in mandrills: factors influencing alpha male monopoly. *Anim Behav* 70:1105–1120
- Skinner JD, Smithers RHN (1990) The mammals of Southern Africa subregion, 2nd edn. University of Pretoria Press, Pretoria
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Stockley P (1997) Sexual conflict resulting from adaptations to sperm competition. *Trends Ecol Evol* 12:154–159
- Storey AE, French RJ, Payne R (1995) Sperm competition and mate guarding in meadow voles (*Microtus pennsylvanicus*). *Ethology* 101:265–279
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man. Aldine Press, Chicago, pp 136–179
- van Dongen WFD (2008) Mate guarding and territorial aggression vary with breeding synchrony in golden whistlers (*Pachycephala pectoralis*). *Naturwissenschaften* 95:537–545
- van Rhijn JG (1991) Mate guarding as a key factor in the evolution of parental care in birds. *Anim Behav* 41:963–970
- von Holst D (1998) The concept of stress and its relevance for animal behavior. *Adv Study Behav* 27:1–131
- Yamamura N (1987) A model on correlation between precopulatory guarding and short receptivity to copulation. *J Theor Biol* 127:171–180