The Social System of
the Round-Eared Sengi
(Macroscelides proboscideus)

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I Summary and Conclusion

I.1 Deutsch

In dieser Studie wurde das Sozialsystem des Kurzohrrüsselspringers (*Macroscelides proboscideus*), einem kleinen nacht- und dämmerungsaktiven Säugetier, welches Wüsten und Halbwüsten im südlichen Afrika bewohnt, untersucht. Hauptziel dieser Arbeit war es vor allem, die Ursachen für die Evolution von Monogamie dieser Spezies zu ermitteln. An frei lebenden Tieren wurde, mit Hilfe von Telemetrie und Fangen, die soziale Organisation und die Partnerbewachung über eine Zeitspanne von 2,5 Jahren erforscht. Des Weiteren wurde in einer Laborstudie untersucht, inwieweit Annäherungsversuche an fremde verpaarte Weibchen aus Nachbargebieten in Kosten oder Nutzen für die Männchen resultieren. Hierfür wurde ihr Verhalten, sowie die Körpermassen und Glucocorticoidkonzentrationen in Urin und Kot bestimmt.

Die Freilandpopulation war durch ein ausgeglichenes adultes Geschlechterverhältnis und durch das Fehlen von Sexualdimorphismus in den Körpermassen charakterisiert. Die Tiere lebten in dauerhaften, territorialen und monogamen Paarbindungen. Allerdings nutzen die Männchen sehr viel größere Gebiete als die Weibchen. Die Territoriengrößen der Männchen verringerten sich jedoch mit zunehmender Populationsdichte, während die Anzahl der Nachbarmännchen fortwährend bei allen untersuchten Dichten konstant blieb. Dies weist darauf hin, dass die Gebietsnutzung der Männchen maßgeblich durch das Vorhandensein anderer benachbarter Männchen beeinflusst wird. Die Territoriengrößen der Weibchen waren unabhängig von der Populationsdichte. Einige verpaarte Männchen versuchten verwitwete Nachbarweibchen zu erobern. Die Männchen zogen sich jedoch in ihre ursprünglichen Gebiete zurück, wenn ein nicht verpaartes Männchen in die Witwengebiete einwanderte. Die Differenz der Körpermassen zwischen den verpaarten und nicht verpaarten Männchen war gering (ca. 10 %).

Kurzohrrüsselspringerweibchen reproduzierten 2-3 Würfe während einer langen Fortpflanzungsperiode. Die Geburten waren nicht synchron zwischen den Nachbarweibchen. Dies begünstigte eine Partnerbewachung durch den männlichen Partner kurz vor und während des post-partum Östrus. Männchen markierten über die Weibchenmarkierungen – möglicherweise um die reproduktive Verfassung der Weibchen zu verschleiern, die Paarbindung zu annoncieren und somit das Eindringen von Konkurrenten zu verhindern. Männchen verloren durchschnittlich 5 % ihrer Körpermasse während der Partnerbewachung, und der Verlust an Körpermasse war negativ korreliert mit der Distanz zum Weibchen kurz vor Beginn des Östrus. In dieser Zeit hielten sich zudem schwerere Männchen in engerer Nachbarschaft mit ihren Weibchen auf als leichtere Männchen. Des Weiteren wurde die Distanz zum Weibchen während des Östrus von der Anzahl der benachbarten Männchen, die an das Paarterritorium angrenzten, beeinflusst. Offensichtlich können Männchen ihren Aufwand bei der Partnerbewachung im Verhältnis zur eigenen körperlichen Verfassung und dem vorherrschenden Konkurrenzdruck anpassen.

In der Laborstudie zeigten beide Geschlechter promiskuitive Tendenzen. Weibliches Sexualverhalten mit Nachbarmännchen hing von der Dauer ab, die diese Männchen im Gebiet des Weibchens verbrachten, sowie von deren Markierverhalten. Die Eindringlinge wurden jedoch vom residenten Männchen attackiert. Aggression, die die eindringenden Männchen erfuhren, resultierte in einem Körpermasseverlust von circa 4 %; erstaunlicherweise korrelierte auch das Markierverhalten mit dem Körpermasseverlust. Stresshormone im Urin und im Kot korrelierten positiv mit dem Körpermasseverlust und ebenso mit dem Markierverhalten im Nachbargebiet.

Zusammenfassend zeigen Kurohrrüsselspringer eine monogame soziale Organisation. Aufgrund der vereinzelt lebende Weibchen, dem ausgeglichenem Geschlechtsverhältnis und der geringen Körpermassedifferenzen zwischen Rüsselspringermännchen, ist das Potential mehrere Weibchen zu monopolisieren gering. Dennoch zeigen beide Geschlechter promiskuitive Tendenzen. Asynchrone Reproduktion der Weibchen, die ihren Zyklus annoncieren, begünstigen zwei Verhaltenstaktiken der Männchen: Die Bewachung des eigenen Partners, um die Vaterschaft abzusichern, und Annäherungsversuche an benachbarte Weibchen, um den Reproduktionserfolg zu erhöhen. Da beide Verhaltenstaktiken energetische Kosten verursachen, können möglicherweise nur die Männchen ihren Reproduktionserfolg erhöhen, die sich durch eine bessere Qualität auszeichnen, was somit wiederum zu genetischen Vorteilen für die Weibchen führen könnte.

I.2 English

In the present study, I investigated the social system of the round-eared sengi (*Macroscelides proboscideus*), a small crepuscular mammal that lives in deserts and semi-deserts in Southern Africa. For studying the evolution of monogamy in this species, I determined the social organisation and male mate guarding in wild animals in the Goegap Nature Reserve, South Africa. Data were collected over three successive breeding seasons and one non-breeding season by radio-tracking and trapping over a period of 2.5 years. Additionally, extra-pair attempts of paired round-eared sengi males were studied under laboratory conditions using direct behavioural observations and morphological and physiological characteristics of males.

In the field, the population was characterised by balanced adult sex ratios and by a lack in sexual dimorphism in body mass. Round-eared sengis lived in perennial territorial male-female-pairs. However, males maintained much larger areas than females that were sensitive to population density and the presence of neighbouring males. At higher density males used smaller areas than at lower population density, but the number of neighbouring males was fairly constant throughout the whole study. Male space use appeared to be primarily limited by the presence of neighbouring males. In contrast, females maintained smaller-sized territories despite changes in population density. Some paired males attempted to take over widowed females, but shifted back to their original home range following the intrusion of an un-paired male, possibly because of a low variation (about 10 %) in body mass.

Female reproduced 2-3 litters during a long breeding season with an asynchronous birth interval between neighbouring females, favouring pre-copulatory and oestrus mate guarding. Males over-mark their females' scent while following, possibly for concealing the females' reproductive state and advertisement of the paired status, thereby decreasing the risk of intrusions by competitors. Mate guarding incurred costs, because, overall, males lost about

5 % of their body mass. On the individual level, male body mass loss was negatively related to the intensity of mate guarding during the pre-copulatory period. Furthermore, guarding was inversely correlated with male body mass in the pre-copulatory period and with the number of neighbouring males during oestrus, indicating that males vary their guarding effort in relation to their physical capabilities and the competitive environment.

In addition, both sexes demonstrated promiscuous tendencies in the experimental study. Female sexual behaviour with male neighbours was positively related to the time neighbouring males spent in the females' area and to male marking behaviour. Intruding males were attacked by resident males. Aggression experienced by intruding males was associated with body mass loss (about 4%) in these animals; the same was found for marking behaviour in the neighbouring area. Furthermore, glucocorticoid levels, determined from analyses of faeces and urine samples, positively correlated with male body mass loss and also with male marking behaviour of intruding males, indicating costs of this behaviour.

In conclusion, pair-living is the predominant social organisation in round-eared sengis. Males suffered from a limited opportunity to monopolise more than a single female that may have resulted from females living solitarily in small exclusive territories, balanced adult sex ratios and a low variation in body mass between males. However, both sexes have promiscuous tendencies. Female reproduced asynchronously and advertised their reproductive status, so that males pursued two behavioural tactics: Males engage in mate guarding for ensuring paternity and also in extra-pair attempts with neighbouring females, possibly for increasing their reproductive success. Since both male tactics were energetic costly they may serve as honest signals of quality providing only higher quality males with the opportunity to enhance their reproductive success, which in turn may be advantageous for females in terms of genetic benefits.

II Introduction

II.1 General Introduction

In mammals, a strong sexual asymmetry in costs of reproduction is caused by gestation and lactation leading to lower potential reproductive rates in females (Williams 1966). Consequently, female reproductive success is limited by access to resources, and resource distribution is considered to be the key factor in female spacing behaviour (Emlen & Oring 1977). On the contrary, food distribution plays a minor role in male spacing behaviour. Since male reproductive success primarily depends on the number of females they can fertilise, the distribution of male mammals is influenced by the spacing pattern of females, which ultimately determines the social organisation of a species (Emlen & Oring 1977). Accordingly, if females are dispersed, the potential for males to monopolise several females is reduced, and they may roam by searching widely for fertile females, or may be pair-living, i.e socially monogamous, by monopolising a single female and/or her territory (Reichard 2003). Since males generally enhance their fitness by fertilising multiple females, monogamy is rare in mammals occurring in less than five percent of species (Kleiman 1981).

Constructing a generalised framework for the evolution of monogamy has proven to be difficult, because apparently there is no single evolutionary pathway monogamy has taken in all species (Reichard 2003). Monogamy should only evolve when males are unable to realise any polygynous situation or when it entails greater fitness decrements, e.g. engaging in parental activities (Reichard 2003), such as in the California mouse (*Peromyscus californicus,* Ribble 2003) and in the Malagasy giant jumping rat (*Hypogeomys antimena,* Sommer 2003).

Although paternal care of monogamous males can evolve to enhance survival probabilities of the young (Woodroffe & Vincent 1994), and thereby also the fitness of parentally behaving males, monogamy evolved more often in the absence than in the presence of male care (Komers & Brotherton 1997).

Thus in the majority of monogamous mammalian species, other factors are likely to influence the occurrence of social monogamy. In some species, like the prairie vole (*Microtus ochrogaster*, Getz et al. 2003) and the Mentawai snub-nosed langur (*Simias concolor,* Watanabe 1981) low population density limits males to monopolise more than one female mate, resulting in pair-living. In other species, such as the Townsend's vole (*M. townsendii*, Lambin & Krebs 1991) and the oribi (*Ourebia ourebi*, Adamczak & Dunbar 2007) balanced adult sex ratios have been acknowledged to drive the occurrence of social monogamy.

In addition in some pair-living mammals, male mate guarding has been proposed to be a crucial factor contributing to the evolution of monogamy (reviewed in Brotherton & Komers 2003). This hypothesis has mainly been developed from studies of small ruminants, such as the klipspringer (*Oreotragus oreotragus,* Dunbar & Dunbar 1980; Tilson 1980), Kirk's dik-dik (*Madoqua kirkii,* Kranz 1991; reviewed in Brotherton & Komers 2003) and the blue duiker (*Philatomba monticola,* Dubost 1983). In these species males actively maintain spatial proximity to their female mate during breeding and non-breeding seasons, resulting in a strong pair bond. Both partners engage in the maintenance of the territory, but males are more vigilant and detect predators and competitors more easily than females (Tilson 1980; Kranz 1991; Dunbar & Dunbar 1990). Mate guarding allows the male to over-mark their female's scent and thereby advertising the paired status, which is believed to reduce the rate of intrusions from male competitors by advertisement of territory occupation (Brotherton et al. 1997) and concealing of the female's reproductive status (Brotherton 1994). The mate guarding strategy enables males to monopolise their female partner and breeding territory with reduced fighting costs, but it also constrains males into a monogamous relationship, because they are incapable of defending an extra female territory (Komers 1996; Brotherton et al 1997; Brotherton & Komers 2003).

II.2 Social Monogamy in Sengis

Sengis (or elephant-shrews, Macroscelidea) represent an ancient monophyletic clade with an early radiation from the Eutheria (Corbet & Hanks 1968), and comprises 17 species from 4 genera that are all endemic to the African continent. All sengi species are believed to be pair-living, but detailed information on the social organisation is available for only 6 species: the golden-rumped sengi (*Rhynchocyon chrysopygus*, Rathbun 1979; FitzGibbon 1995, 1997), the Rufous sengi (*Elefantulus rufescens*, Rathbun 1979), the rock sengi (*E. myurus*, Ribble & Perrin 2005), the Bushveld sengi (*E. intufi*, Rathbun & Rathbun 2006), the short-snouted sengi (*E. brachyrhynchus*, Leirs et al. 1995; Neal 1995) and the four-toed sengi (*Petrodromus tetradactylus*, FitzGibbon 1995, 1997). In sengis, male-female-pairs occupy largely overlapping ranges, which have little overlap to neighbouring individuals, and are maintained year-round by intra-sexual aggression (Rathbun 1979; FitzGibbon 1997; Ribble & Perrin 2005; Rathbun & Rathbun 2006). Although the social organisation has been confidently confirmed in these studies, the reason for social monogamy in sengis has not been addressed yet. Ribble & Perrin (2005) and Rathbun & Rathbun (2006) suggested that male sengis are constrained into social monogamy due to a male mate guarding strategy, but to date, detailed studies regarding environmental parameters related to the social organisation are absent. Furthermore, male mate guarding has not been demonstrated experimentally yet. Unlike ruminants, sengis live in dispersed pairs that are characterised by a weak bond, probably as a consequence of ecological pressures, such as predation and high inter-sexual competition for critical resources (Rathbun 1979; Kleiman 1981). Thus, the mate guarding model of ruminants, which are characterised by strong pair bonds, may not necessarily explain the evolution of social monogamy in sengis. Mate guarding may be important for paternity insurance, but it may have evolved secondarily after social monogamy was already in place.

In the present study, I investigated the social system of the round-eared sengi (*Macroscelides proboscideus*, Fig. 1), a small-bodied (35 g) omnivorous mammal (Sauer 1973; Kerley 1995), which is found in arid and semi-arid regions of South Africa, Namibia and Botswana (Skinner & Smithers 1990). The study was conducted in the Goegap Nature Reserve (29°37’S; 17°59’E), South Africa. The study site was about 37 ha large and characterised by dry riverbeds and sandy areas with patchily distributed shrubs consisting mainly of *Zygophyllum retrofractum*, *Lycium cinerum* and ephemeral wild flowers in spring. Data were collected by continuous trapping and radio-tracking during three successive breeding seasons and one non-breeding season over a 2.5 years period. In total 65 males and 62 females (young and adults combined) were trapped during the study. During radio-tracking periods, all adult individuals trapped at the study site were equipped with a radio-collar (27 males and 25 females).

Additionally, I investigated promiscuous tendencies of paired round-eared sengis (n = 16) by observing interactions between neighbours under laboratory conditions. Therefore I performed 6 observations lasting each 30 min. and documented morphological (body mass changes) and physiological characteristics (urine and faecal corticosterone levels) of males.

Fig. 1: Free-ranging round-eared sengi with ear tag. Picture by M. Schubert

III Synopsis

I investigated the social system of round-eared sengis in a semi-desert in the Northern Cape, South Africa. The population was characterised by a lack of sexual dimorphism in body mass: The mean body mass was 42.6 g (± 0.7 SE) for males and 43.3 g (± 0.6 SE) for females. Adult sex ratios were near parity; the population consisted of 47.5 % (± 0.7 SE) adult males and of 52.3 % (± 0.7 SE) adult females. Female round-eared sengis maintained areas that had little overlap (6.4 % ± 1.7 SE) with neighbouring females in breeding and non-breeding season. Males overlapped only with the home range of single females. Home ranges of the two pair mates overlapped 68.9 % (± 3.2 SE). Generally, inter- and intra-sexual overlap with neighbouring individuals was low, indicating territoriality and pair-living. Pairs were perennial and territories were maintained year-round. Body mass of male and female round-eared sengis did not predict home range sizes. However, males generally maintained significantly larger areas than females (1.4 ha (± 0.2 SE) versus 0.7 ha (± 0.1 SE)) and had significantly more neighbouring males and females compared to their female mate. There were 1.5 (± 0.2 SE) neighbouring males per male versus only 0.8 (± 0.2 SE) neighbouring males per female, and 0.9 (± 0.2 SE) neighbouring females per male versus 0.7 (± 0.1 SE) neighbouring females per female, respectively. The number of neighbouring males and females did not significantly differ during the study. Furthermore, male but not female territories were sensitive to population density. Males occupied areas that were 2.7 ha (± 0.6 SE) when population density was lowest (0.35 individuals/ha) and 1.0 ha (± 0.1 SE) when density was highest (1.59 individuals/ha) during the study. The average home range size for females was 0.9 ha (± 0.2 SE) when population density was lowest and 0.7 ha (± 0.1 SE) when density was highest. Generally inter- and intra-sexual overlap with neighbouring individuals did not differ between the sexes. However, for males the overlap with neighbouring males was significantly reduced in the breeding compared to the non-breeding season: 4.5 % (± 1.3 SE) in the breeding season and 20.3 % (± 6.8 SE) in the non-breeding season. There was no significant effect of season on home range overlap for female round-eared sengis (5.0 % ± 1.6 SE versus 12.8 % ± 5.3 SE).

Some pair-living males (30 %) intruded into the areas of widowed females. Whereas only one male was able to achieve polygyny, because his female mate also intruded into the widow's area, the majority of paired males shifted back to their original area and female mate, following the intrusion of another unpaired male into the widows' areas at the same time. Paired males that intruded into the widows' areas were the heaviest male neighbour. The variance between male body masses was 11.7 % (± 5.1 SE), and new unpaired males were lighter (42.9 g ± 1.7 SE) than the heaviest neighbouring male (48.2 g ± 1.8 SE).

Reproduction was seasonal, because pregnant females and young individuals (below 26 g) were only observed from July to January. Female round-eared sengis reproduced 2-3 litters per breeding season with a birth interval between neighbouring females of 11.6 d (± 1.3 SE), indicating that reproduction was asynchronously. All males (n = 10) started to guard their mates prior to and during oestrus as exemplified by reduced intra-pair distance. Pair mates increased their proximity shortly before and during oestrus, resulting in a decrease in inter-pair distance between mates. The intra-pair distance was 54.0 m (± 9.0 SE) 4-2 days before parturition, 37.3 m (± 7.1 SE) one day before birth until the day of birth (= pre-copulatory period), 27.3 m (± 5.6 SE) during female post-partum oestrus, i.e. the day after parturition and 88.4 m (± 11.4 SE) during post-oestrus (2-3 days after parturition). During mate guarding both sexes were observed to mark in their home range by rubbing their ano-genital region on the ground. While following their mate, males always over-marked the females' scent.

Mate guarding incurred costs for male round-eared sengis, because, overall, animals lost 4.6 % (± 1.1 SE) of their body mass. On the individual level, male body mass loss and initial male body mass were significantly positively related to the intensity of mate guarding during the pre-copulatory period. Furthermore, intra-pair distance was inversely correlated with the number of neighbouring males during female oestrus.

In a laboratory study, both sexes demonstrated promiscuous tendencies. Males and females intruded into the neighbouring area and initiated sexual behaviour with the neighbours of the opposite sex. Males significantly initiated more sexual behaviour, which was defined as sniffing, following and mounting, with neighbouring females than with their pair mates (2.1 interactions/h ± 0.4 SE versus 1.1 interactions/h ± 0.8 SE). Females displayed a similar frequency of sexual behaviours (sniffing, following) towards their own mate (0.9 interactions/h ± 0.4 SE) and towards the neighbouring male (1.3 interactions/h ± 0.5 SE). Sexual behaviour initiated by females with the neighbouring males was significantly positively related to the time males spent in the females' area and their marking behaviour in the neighbouring area. Males spent on average 56.7 % (± 9.3 SE) of observation and marked 0.7 times/h (± 0.3 SE) in the neighbouring area. Intruding males were attacked by resident males (2.6 times/h ± 1.0 SE), and aggression was significantly positively correlated with the time spent in the neighbouring area, indicating that aggression did not habituate over time. Aggression experienced by intruding males was associated with body mass loss (3.8 % ± 0.5 SE) in these males; the same was found for marking behaviour in the neighbouring area. Furthermore, male urine and faecal glucocorticoid levels were positively correlated. Corticosterone concentrations were 30.01 ng/ml (± 4.9 SE) in the urine and 2708.69 ng/g (± 705.16 SE) in the faeces. Urine and Faecal corticosterone levels were significantly positively correlated with body mass loss and also with marking behaviour of intruding males.

Little is known on the social system in sengis. Previous studies suggested that male mate guarding is the key determinant for the evolution of monogamy in sengis (Ribble & Perrin 2005; Rathbun & Rathbun 2006). However, the results of this study indicate that the social system of the round-eared sengi cannot be attributed to a single factor: Although costly mate guarding occurred shortly before and during oestrus, males also faced a limited opportunity to monopolise more than a single female due to solitary ranging females maintaining small exclusive ranges, the lack of sexual dimorphism associated with a low variance in body mass between males and balanced adult sex ratios co-evolving with social systems. Males lived in perennial pairs with year-round territoriality, as suggested by little overlap with neighbouring individuals of both sexes, which is generally seen as a good indicator for territorial behaviour (Powell 2000).

However, both sexes had promiscuous tendencies. Males maintained much larger territories than females, which may permit them to monitor the reproductive status of neighbouring females and the presence of neighbouring males. In the field study some pair-living males intruded into the areas of widowed females. Whereas only one male was able to achieve polygyny, because his female mate also intruded into the widow’s area, the majority of paired males shifted back to their original area and female mate, following the intrusion of an unpaired male into the widow’s area at the same time. Paired males that intruded into the widow’s area were the heaviest male neighbour. Although new unpaired males were lighter than the heaviest neighbouring male, the difference between male body mass was generally low (10 %) compared to species where one male is able to defend more than one solitary ranging female (e.g. cavies, *Cavia aperea* Asher et al. 2008). The reason that a single male cannot defend more than one female territory permanently might be due to a small variation in the resource-holding potential (RHP) between males. The RHP describes the fighting ability of an individual, enabling it to monopolise important resources such as females and is closely correlated with body mass (Schradin 2004; Asher 2008; but see Rödel & von Holst 2009). Generally, small asymmetries in the RHP of contestants results in long and intense fights that may cause high energetic costs, a decrease in time available for foraging, a high risk of injuries or even death (Neat et al. 1998). Thus a low variance in body mass between round-eared sengi males may reduce the benefits of defending more than one female territory permanently, because temporarily polygynous males suffer substantial costs, such as increased activity and a decrease in body mass as observed in the golden-rumped sengi (FitzGibbon 1997).

Although male sengis may not be able to spatially monopolise 2 female territories permanently, males may gain benefits in terms of extra-pair copulations with neighbouring females. In the laboratory study, both sexes demonstrated promiscuous tendencies, because males and females initiated sexual interactions with neighbours of the opposite sex. Males were even observed to mount neighbouring females, indicating the potential occurrence of extra-pair copulations.

Round-eared sengis males were only observed to scent-mark in the beginning of the pairing phase with the pair female and during the encounter experiment with a neighbouring pair, indicating that scent-marking may have been used as a modifiable behavioural tactic for increasing male mating success. This is because sexual behaviour initiated by female round-eared sengis with male neighbours was positively correlated with the time males spent and marked in the neighbouring area. Thus scent marks and marking frequency may therefore convey information about the male’s identity and quality, such as male condition (house mouse, Meikle et al. 1995), male competitive ability (pygmy slow lori *Nycticebus pygmaeus*, Fisher et al. 2003), and may also be linked to the MHC and immunocompetence (reviewed in Gosling & Roberts 2001, Johansson & Jones 2007).

However, intruding and marking in the neighbouring area was associated with higher levels of aggression from the resident male neighbour. Furthermore, aggression experienced and marking in the neighbour’s area was associated with male body mass loss and elevated hormonal stress levels in faeces and urine, indicating costs of this behaviour. Investment in costly behaviours can impact on the life-history, and hence on future reproductive success (Stearns 1992). Costly behaviours, such as sexual displays and/or increased activity may lead to a reduced body condition and male immune functions resulting in lower survival probabilities (reviewed in Zera & Harshman 2001). Thus, although intruding and marking in the neighbouring area may increase the chance of extra-pair copulations with neighbouring females, it may also decrease future reproduction for male round-eared sengis, because males may suffer reduced survivorship due to reduced body condition and elevated stress levels (von Holst 1998; Zera & Harshman 2001). Hence, the effort of paired round-eared sengi males engaging in sexual behaviour with neighbouring females could reflect honest signals of the male's quality, because the costliness of signals may be only paid by individuals of good condition (Zahavi 1975; Grafen 1990), and may therefore provide these males with the opportunity to engage in sexual behaviour with neighbouring females increasing their reproductive success.

In addition, male territory sizes were sensitive to population density and the presence of neighbouring males. At higher densities, males may adjust their ranges by either permitting increased overlap (microtine rodents, Ims 1987; root vole *Microtus oeconomus*, Gliwicz 1997) or by confining their movements to smaller areas (*Peromyscus leucopus* white-footed mouse, Wolff & Cicirello 1990; Townsend's vole, Lambin & Krebs 1991). Round-eared sengi males used smaller areas at higher densities; correspondently the number of neighbouring males was fairly constant during the whole study period despite changes in population density. Thus, male space use seems to be limited by the presence of adjacent males, and male-male competition may play an important role in shaping the social organisation of the round-eared sengi. Consequently, by adjusting range sizes in response to density, male round-eared sengis may reduce the level of male-male competition. Furthermore, overlap between neighbouring males was significantly reduced in the breeding compared to the non-breeding season. Neighbouring males often present the greatest risk to paternity (Komdeur 2001). Since female round-eared sengis reproduced asynchronously during a long breeding season, males may seek copulations with neighbouring females, thereby enhancing their reproductive success. Thus male territoriality may function to protect the females from intruding competitors into the pair's territory (Munshi-South 2007).

Besides territorial behaviour, male round-eared sengis also engaged in mate guarding shortly before and during female receptivity. Pre-copulatory guarding is advantageous when males have a limited opportunity to search for additional females (Parker 1974). Since the opportunity for males to monopolise additional females is limited due to environmental constrains, prolonged guarding may allow males to secure matings with their pair females when they come in oestrus. Female mammals often advertise their reproductive condition shortly before sexual receptivity, e.g. by scent-marks (Dixson 1983). Male round-eared sengis were observed to always over-mark their mate's scent shortly before and during oestrus. Thus persistent guarding may allow males to conceal the reproductive state of the females and to advertise the paired status, thereby decreasing the risk of intrusions by competitors, and possibly preventing cuckoldry by neighbouring males (Gowaty & Plissner 1987). Indeed, partners were spatially closely associated when they were surrounded by more adjacent (paired) males during female receptivity. Thus closer association between pair mates may lead to a greater within-pair paternity assurance.

However, mate guarding imposes costs for males, which became apparent by a body mass decrease of about 5 %. Body mass loss was associated with intra-pair distance during the pre-copulatory period, in which heavier males have guarded their female mates more closely than lighter males. Thus, mate guarding intensity and duration may depend on individual condition and the costs an individual is able or willing to afford. 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. Since paired round-eared sengi males do not only invest in mate guarding, but also in year-round territorial behaviour, individuals may employ different mating tactics depending on their individual qualities, with lighter individuals investing more in territorial behaviour, 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 defence, a decrease in defence while guarding may also be more critical for lighter than for heavier males in terms of territory take-over attempts of other males. This is because heavier (and older) males may be more experienced in territorial defence, increasing the possibility to invest more in courtship displays (Festa-Bianchet et al. 1996; Schwartz et al. 2007).

In conclusion, monogamy in round-eared sengis may have evolved, because males are not able to defend more than one female permanently due to environmental constraints, such as independently ranging females occupying small exclusive areas, and morphological constraints resulting from the lack of sexual dimorphism, and hence a low variation in body mass between males. However, both sexes may increase their fitness by promiscuous behaviour. Female round-eared sengis reproduced asynchronously and advertised their reproductive state, which may have created the circumstances for males to pursue two tactics: Ensuring their interest in mating with the pair female and engaging in extra-pair copulations with neighbouring females. Since both tactics were energetic costly only better quality males may be able to bear the costs of those behaviours leading to a higher reproductive success in these males, and possibly also in the females they were involved with, in terms of genetic benefits.

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V Manuscripts for Publication with Description of Own Contributions

Schubert, M., Pillay, N., Ribble, D. O. & Schradin, C. 2009. The Round-Eared Sengi and the Evolution of Social Monogamy: Factors that Constrain Males to Live with a Single Female.

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Data collection (2005-2007)

M. Schubert, 2 field assistants in March/April 2006 (B. Schmidt-Eisenlohr: 4 weeks, E. Jirka: 8 weeks)

Writing of the manuscript and statistical analyses

M. Schubert

Comments on the manuscript

N. Pillay, C. Schradin

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M. Schubert

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Data collection

M. Schubert

Analyses of urine and faecal samples

I. Zerenner-Fritzsche, M. Schubert

Writing of the manuscript and statistical analyses

M. Schubert

Comments on the manuscript

H. G. Rödel, N. Pillay, D. von Holst

VI List of Publications

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Schubert, M., Pillay, N. & Schradin, C. 2009: Paternal and Allo-parental Care in a Polygynous Mammal. *Journal of Mammalogy* **90**, 724—731.

Schradin, C., Krackow, S., **Schubert, M.**, Keller, C., Schradin, B. & Pillay, N. 2007: Regulation of Activity in Desert-Living Striped Mice: The Importance of Basking. *Ethology* **113**, 606—614.

Schradin, C., **Schubert, M.** & Pillay, N. 2006: Winter Huddling Groups in the Striped Mouse. *Canadian Journal of Zoology* **84**, 693—698.

Schradin, C., Schmohl, G., Rödel, H.G., Schoepf, I., Treffler, S.M., Brenner, J., Bleeker, M., **Schubert, M.**, König, B. & Pillay, N. Female home range size is regulated by resource distribution and intraspecific competition: a long term field study on African striped mice. Accepted for publication in *Animal Behaviour*

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VII Declaration

Hiermit versichere ich, die vorliegende Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

Ferner versichere ich, dass ich nicht anderweitig mit oder ohne Erfolg versucht habe, diese Dissertation einzureichen. Diese oder eine gleichartige Doktorprüfung wurde von mir an keiner anderen Hochschule endgültig nicht bestanden.

Bayreuth, 01.07.2009

(Melanie Schubert)

VIII Manuscripts

VIII.1 The Round-Eared Sengi and the Evolution of Social Monogamy: Factors that Constrain Males to Live with a Single Female

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Abstract

Animal dispersion in space and time results from environmental pressures, and affects the outcome of a species' social organisation. When females are solitary, males may either roam or be pair-living. We studied possible environmental influences affecting the social organisation of the round-eared sengi (*Macroscelides proboscideus*) in a semi-desert in South Africa, using trapping and radio-tracking across 2.5 years. Adult sex ratios did not deviate from 1:1 and we found no indication of sexual dimorphism in body mass. Females maintained exclusive areas, which had little overlap (< 4 %) with neighbouring females, and males overlapped predominately only with the home range of single females. Generally, inter- and intra-sexual overlap with neighbouring individuals was low (3-6 %) for both sexes, indicating territoriality and pair-living. Pairs were perennial and territories were maintained year-round. However, males generally maintained much larger areas than females, which were sensitive to population density. Male space use appeared to be primarily limited by the presence of neighbouring males. Female home ranges were smaller-sized despite changes in population density, possibly for energetic efficiency. Some paired males attempted to take over widowed females, but shifted back to their original home range following the intrusion of an un-paired male. We conclude that social monogamy is the predominant social organisation in round-eared sengis in a semi-desert that may have resulted from females living solitarily in small exclusive territories, balanced sex ratios, and from a low variation of body mass between males.

Introduction

Animal dispersion in space and time results from environmental pressures and affects the outcome of a species' social organisation (Brown & Orians 1970). In species lacking paternal care, dispersed living females present an important prerequisite for the evolution of social monogamy, i.e. pair-living, because for males, the chances to encounter other potential mating partners are reduced (Komers & Brotherton 1997; Brotherton & Komers 2003). However, social systems are rarely attributable to a single factor (Sandell & Liberg 1992), and female dispersion *per se* is insufficient to account for the evolution of monogamy, since males could opt for other tactics, such as roaming (Kraus et al. 2003; Eberle & Kappeler 2004; Martin & Martin 2007). Thus, other factors may constrain males into socially monogamous relationships. Low population densities have been emphasised in some species, like prairie voles (*Microtus ochrogaster*, Getz et al. 2003) or Mentawai snub-nosed langurs (*Simias concolor*, Watanabe 1981), and balanced adult sex ratios have been acknowledged to drive the occurrence of social monogamy in other mammalian species, such as Townsend's voles (*M. townsendii*, Lambin & Krebs 1991) and oribis (*Ourebia ourebi*, Adamczak & Dunbar 2007).

Social monogamy is rare in mammals (Kleiman 1977), but is believed to occur in all species of a unique order, the sengis (Macroscelidea, Ribble & Perrin 2005; Rathbun & Rathbun 2006). Sengis (or elephant-shrews) represent an ancient monophyletic clade with an early radiation from the Eutheria (Corbet & Hanks 1968), and comprise 17 species from 4 genera that are all endemic to the African continent. The assumption that all sengi species are monogamous is based on field studies of 6 sengis species (Rathbun 1979; FitzGibbon 1995, 1997; Leirs et al. 1995; Neal 1995; Ribble & Perrin 2005; Rathbun & Rathbun 2006). The social organisation of sengis in these studies has been determined by investigating space use predominately, but to date, detailed studies regarding environmental parameters related to the social organisation are absent.

In the present study, we investigated potential ecological and physical parameters affecting the social system in the round-eared sengi (*Macroscelides proboscideus*), a small-bodied (35 g) omnivorous mammal (Sauer 1973; Kerley 1995), which is found in the more arid regions of South Africa, Namibia and Botswana (Skinner & Smithers 1990). In contrast to other sengi species, individual round-eared sengis occupy undefended home ranges, reaching over 100 ha and resulting in a solitary life style with non-territorial females and roaming males (Sauer & Sauer 1971, 1972; Sauer 1973). In Sauer's studies, the habitat was characterised by low food abundance and few shelter sites for individuals, and associated with an extremely low population density of 1 individual per 100 ha and an irregular dispersion of round-eared sengis, resulting in small isolated populations.

Generally, population density of round-eared sengis is positively correlated with cover (Joubert & Ryan 1999) and food availability (van Deventer & Nel 2006). Since Sauer's study was conducted in a desert and the present study in a semi-desert, demographical differences between the two study sites, which reflect the differential availability of key resources, may promote different social organisations (Lott 1984; Schradin & Pillay 2005a). Thus the aim of the current study was to determine the social organisation of the round-eared sengi in a semi-desert, by testing for ecological and physical correlates of social organisation. The following predictions were made:

Firstly, we investigated space use of female round-eared sengis. Environmental factors that influence female space use ultimately influence the social organisation of a population, because male space use is affected by female distribution in space and time (Emlen & Oring 1977). We predicted that females live independently of each other, thereby decreasing male monopolisation potential for several females. If males employ a roaming strategy, we suggest that they will maintain much larger home ranges than females in order to search widely for fertile females in breeding season (Michener & McLean 1996), and that male home ranges will be characterised by large overlap with male competitors (Sandell 1989; Gliwicz 1997).

Alternatively, males may monopolise single females resulting in pair-living. In this situation, male space is predicted to be similar to that of females, i.e. pairs use similar-sized areas that have little intra- and inter-sexual overlap with neighbouring individuals of both sexes (Komers & Brotheron 1997).

Secondly, given that males may roam, we expected that round-eared sengis lack sexual dimorphism, because male body mass is not necessarily related to the roaming ability for female mates (Schwagmeyer & Woonter 1986). Alternatively, the lack of sexual dimorphism may also be a characteristic of pair-living (Kleiman 1977).

Thirdly, we studied the male searching efficiency for female mates by documenting adult sex ratios in round-eared sengis. Since sex ratios co-evolve with social systems, we assume that sex ratios will be more female biased promoting a male roaming tactic, because of a high searching efficiency for female mates (Sandell & Liberg 1992; but see Eberle & Kappeler 2004). In contrast, low searching efficiency caused by balanced adult sex ratios may favour the monopolisation of single females (Sandell & Liberg 1992).

Fourthly, we determined the length of breeding season and synchronisation of female receptivity. Generally, if females reproduce asynchronously it is more likely that males will adopt a roaming strategy, since this provides the opportunity to obtain matings with multiple females (Ims 1987; Ostfeld 1990). Asynchronous breeding may also intensify male-male competition because it increases the costs of territorial defence and decreases the monopolisability of potential mates (Emlen & Oring 1977).

Methods

Study area

This study was conducted in the Goegap Nature Reserve (29°37’S; 17°59’E), South Africa from August 2005 to October 2007. This nature reserve is approximately 15 000 ha and is situated about 15 km south-east of the town of Springbok in the Northern Cape Province. In this semi-desert area, the vegetation consists mainly of *Zygophyllum retrofractum* and *Lycium cinerum* shrubs, and is classified as succulent karoo (Cowling et al. 1999; Mucina & Rutherford 2006). The average annual rainfall is 160 mm/yr (Rösch 2001) and occurs mostly during winter (June/July). Maximum plant growth occurs in spring, consisting of annuals and perennials. Spring is followed by a long dry summer with decreasing plant abundance (Schradin & Pillay 2005b). The study site was characterised by dry riverbeds and sandy areas with soft sand parts, as well as parts with coarse sand surface with patchily distributed shrubs interspersed. The size of the study area varied during the study from 11.93 to 36.70 ha, because of a decline in population density of sengis (see results).

Study animal

The round-eared sengi is crepuscular to nocturnal, with activity peaks at dusk, dawn and through the night. Activity is affected by ambient temperatures and food availability, with a decrease in activity during cold nights (Sauer & Sauer 1971). Furthermore, under unfavourable environmental conditions associated with cold temperatures and low food abundance, it employs torpor to overcome long-term energetic shortfalls (Lovegrove et al. 1999).

Reproduction occurs throughout the year, but there is a decline in pregnancies during early winter in March-May (Bernard et al. 1996). Females have a post-partum oestrus, which is reported to be one day (Sauer & Sauer 1971). The precocial pups, normally twins, are born after a gestation period of 61 d (Olbricht et al. 2006). Maternal care is characterised by an absentee system, i.e. maternal care is restricted to short nursing bouts every 24 h (Sauer 1973). Additionally, dependent pups are fed solid food via mouth-to-mouth feeding by the mother (Sauer 1973). To date, there is no evidence that male round-eared sengis engage in direct parental care (Sauer & Sauer 1971; Sauer 1973). Young sengis are weaned at about 4 weeks of age, and both sexes leave the natal territory thereafter (Sauer 1973). Females become sexually mature at 4-9 months, whereas males reach maturity at 3 months (Olbricht et al. 2006).

Trapping

Systematic capture-recapture was carried out continuously from September 2005-April 2006, July 2006-April 2007 and July 2007-October 2007, 4-7 times a week. Round-eared sengis were trapped using locally produced metal traps (26 × 9 × 9 cm, similar to Sherman traps), which were baited with a mixture of peanut butter, oats, marmite and sunflower oil. Trapping was performed between 18:00-22:00 and 04:00-07:00. Traps were checked every 1.5-2 h. In winter, traps were provided with cotton wool to avoid trap deaths. Individuals were weighed by placing them in a plastic box, which was situated on top of a kitchen scale (capacity 500 g, accuracy 0.1 g). Sexes could be easily distinguished because males have an abdominal penis. However, we could not assess breeding status of young sengis, because males have intra-abdominal testes (Woodall 1995) and females have no true vagina (van der Horst 1946). Late-stage pregnant females could be confidently identified because of a body mass increase during pregnancy of approximately 20 g. The average female body mass was 48.0 g (± 4.1 SD) 1 day after birth, 64.3 g (± 5.5 SD) 1 week before birth, 59.0 g (± 5.1 SD) 2 weeks before birth and 52.8 g (± 3.4 SD) 3 weeks before parturition (n = 11). All individuals were marked using hair dye (Inecto Rapid, South Africa) and ear tags (National Band and Tag Co., USA). The total number of round-eared sengis trapped during the 2.5 years project comprised of 65 males and 62 females (young and adults combined). During radio-tracking periods (see below), all adult individuals trapped at the study site were equipped with a radio-collar.

Radio-tracking

A total of 47 different adult individuals (24 females and 23 males) were used for radio-tracking studies. A total of 6 males and 8 females were radio-tracked in September/October (= breeding season (BS), see results) 2005, 11 males and 10 females in March/April (= non-breeding season (NBS), see results) 2006, 7 males and 6 females in the 2006 breeding season, and 5 males and 5 females in the 2007 breeding season. 11 (5 females and 6 males) individuals were radio-tracked twice: 1 time in the non-breeding season and 1 time in the subsequent or the previous breeding season. Of these animals, 9 individuals were radio-tracked in the same location and 2 in a neighbouring area (see results). In the 2007 non-breeding season, no individuals were radio-tracked due to low population density resulting from high mortality rates, which may have been caused by increased predation rates as a result of the radio-collars and radio-tracking (Webster and Brooks 1980).

Sengis were equipped with a MD-2C radio-collar (Holohil Systems Ltd., Canada) for a continuous period of approximately 2 months. Before attaching the radio-collar around the neck, individuals were briefly anaesthetised with ether. The duration of the whole procedure from capturing, anaesthetising the individuals, attaching the collar, and finally releasing them at the point of capture was 2-3 h. Radio-collars weighed 2.5 g, which was less than 10 % of the adult body mass. Radio-tracking was performed using a Telonics TR-4 receiver (Telonics Inc.) and an H-antenna.

Data were collected using the homing method: sengis were approached until they were seen or known to be hidden in a particular hiding spot, like shrubs or burrows. Locations were recorded with a GPS receiver (eTrex venture, Garmin, USA), which had an accuracy of ± 5 m. To determine space use, individual locations were determined every 2 h five times a day.

Two hours was chosen to avoid inter-fix autocorrelations and provide enough time for the individual to travel within the area. Radio-tracking was performed from 16:00-0:00 for 5 d in the 2005, 2006 and 2007 breeding seasons and in the 2006 non-breeding season. A mean of 24.6 (± 1.5 SD) fixes were obtained for each individual. After termination of home range data collection, individuals were radio-tracked once every day to check their location and status for another 6 weeks.

Data analyses

Population density was estimated using the capture-recapture method as "minimum number known to be alive" (MNA, Krebs 1966). Young sengis were excluded from density calculations because both sexes disperse before sexual maturity. The adult sex ratio was determined from the MNA and calculated as the proportion of adult males and females in the population. A binominal test was used to determine whether the number of males versus the number of females deviated from a 1:1 ratio.

A reproductive synchrony index (SI) was determined after Kempenaers (1993):

$$SI=\frac{1}{F}\sum_{p=1}^{F} f_{i,p}\left[\frac{\sum_{i=t} f_{i,p}}{t_p\,(F-1)}\right]_{t_p} \bullet\ 100$$

where F = the total number of breeding females in the population

$f_{i,p}$ = the number of fertile female individuals in the population on day i, excluding female p

t_p = the number fertility days for female p

Data collection on male mate guarding during female post-partum oestrus (M. S. unpublished data) revealed that females are probably fertile for approximately 24 h, which is in accordance with the results of Sauer & Sauer (1971). The reproductive synchrony index was determined for 2006 and 2007. At the start of this study in 2005, we were not able to identify all the females which prevented us from calculating a reproductive index for 2005.

To determine sexual dimorphism, only body mass data from individuals in the non-breeding season were included in the analysis. This was done to avoid bias of the increase in body mass during pregnancy.

Space use was estimated using the minimum convex polygon (MCP) analysis. This method describes the area boundary containing all positional fixes of an individual (Mohr 1947). For the determination of kernel home ranges, we used 95 % MCP to exclude fixes outside of the activity centre. The software RANGES 6 (Kenward et al. 2002) was used to analyse spatial areas. For the home range analyses, data were available for 45 individuals; 2 round-eared sengis (1 male, 1 female) were predated upon shortly after starting with the collection of home range data. To determine the amount of overlap between neighbouring home ranges, we included all fixes (100 %) in the analyses. Data were available for 41 individuals; in 2 cases data for neighbouring individuals could not be collected, and two round-eared sengis had only a widowed male neighbour, whose female had disappeared 2 d after starting to collect radio-tracking data.

Statistical analyses

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). 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).

In all tests, possible interactions between the main effects were tested, but interactions are only reported when significant results were obtained. Residuals were tested for normality visually by checking normal probability plots and with the Shapiro-Wilk test. Data are reported as mean ± SD, except for home range overlap data, which are presented as median (1^{rst} and 3^{rd} interquartile ranges).

We included year as a three-level fixed factor and also tested for all two-way interactions with the other predictor variables. There were no significant effects of year or interactions with year ($p > 0.10$); therefore year was removed from the models and p-values of the other predictor variables were recalculated.

Home range size. Home range size was determined for the breeding and the non-breeding seasons. Home range data were log transformed before testing. We calculated a linear mixed-effects model (LMM) with home range size as the response variable and included sex (male or female) as two-level factors, and body mass as a covariate. Population density was also added as a covariate for home range sizes in the breeding season. Pair identity was entered as a random factor in the model for the non-breeding and the breeding season. Individual identity was entered in the model when comparing home range sizes between the 2006 breeding and the 2006 non-breeding seasons.

Number of neighbouring individuals. The number of neighbours was determined in the breeding and the non-breeding seasons. The relationship between the number of neighbouring males (response variable) and sex was analysed using a LMM. By adding the covariates of population density (only for breeding season), home range size and the random factor of pair identity into the model, different possible effects were determined with regard to the number of neighbouring males. Individual identity was included in the model when comparing the number of neighbouring males between the 2006 breeding and the 2006 non-breeding seasons. The same procedure was used for the number of neighbouring females.

Home range overlap. To determine home range overlap with neighbouring individuals, one mean for adjacent males and neighbouring females was calculated for each individual. Home range overlap data were transformed with [$x^{0.4}$]. Firstly, the overlap of an individual with its “pair mate” was compared with the amount of overlap with neighbouring animals of both sexes in the breeding and non-breeding seasons, using repeated measurements ANOVA. Secondly, to determine the effects of different variables on the amount of overlap in breeding season with the mate, neighbouring females and neighbouring males (response variables), a LMM was used, which included sex (two-level factor), home range size and population density (covariates), and pair identity (random factor). A similar model was used for testing for effects on overlap with individuals in the non-breeding season, but population density (covariate) was excluded from the analysis.

Results

Population demography

Population density varied during the study period, with a peak at the beginning of data collection in 2005 (Table 1). During the course of the study, population density declined from 1.59 individuals/ha to 0.35 individuals/ha.

Pregnant females and young individuals (below 26 g) were only observed from July to January, indicating that reproduction was seasonal. Young were trapped between August and January; pregnant females were caught from July to December.

Females had an inter-litter interval of 61 d (n = 2). Reproduction was not highly synchronised, with a reproductive synchrony index of 0.0 % in 2006 and 2007, indicating no overlap in the fertile periods of females. The inter-birth interval between neighbouring females was 11.0 d (± 3.0 SD) in 2006 and 11.9 d (± 4.3 SD) in 2007.

Table 1: Size of the study area, and the proportion of males and females in round-eared sengis during three breeding seasons (BS) and one non-breeding season (NBS).

Season and year	*Study site [ha]*	*Sengis/ha*	*Males [%]*	*Females [%]*	p
BS 2005	11.93	1.59	45	55	0.597
BS 2006	26.80	0.63	51	49	0.999
BS 2007	36.70	0.35	41	59	0.523
NBS 2006	31.29	0.89	53	47	0.567

Adult sex ratio

The adult population sex ratio did not deviate from the expected 1:1 ratio during the entire study period (Table 1). On average, the population consisted of 47.5 % (± 5.5 SD) adult males and of 52.3 % (± 5.9 SD) adult females.

Sexual dimorphism in body mass

The mean body mass during the non-breeding season was 42.6 g (± 4.1 SD) for males and 43.3 g (± 3.3 SD) for females. There was no evidence of sexual dimorphism of body mass in male and female sengis (t-test for independent samples: $n_{males} = 33$, $n_{females} = 28$, df = 59, t = -0.770, p = 0.440).

Do individuals live in pairs?

Throughout the entire study, females maintained exclusive areas with only little overlap between neighbouring females. Individuals overlapped significantly more with one sengi of the opposite sex in comparison to intra- and inter-sexual overlap with other neighbouring individuals in the breeding (*BS*) and non-breeding seasons (*NBS*) (*BS* - repeated measurements ANOVA: n = 32, F = 179.65, df = 2, $p < 0.001$, Fig.1a, *NBS* - repeated measurements ANOVA: n = 20, F = 7.46, df = 2, p = 0.006, Fig.1b). Individuals that shared a common home range, i.e. their home ranges largely overlapped, are defined as mates hereafter. Paired males and females were spatially faithful, because when individuals were radio-tracked again after 4-5 months, they maintained home ranges that overlapped 62.5 - 87.0 % (min, max) with their “old” home range (n = 9).

All pairs were stable, with a duration that could exceed two breeding seasons. Pairs only terminated when one of the pair mates disappeared or died. Death and disappearance most likely resulted from predation. During the entire study period, no pairs or single members of the pair were evicted by intruding conspecifics and no paired individual dispersed and left its mate.

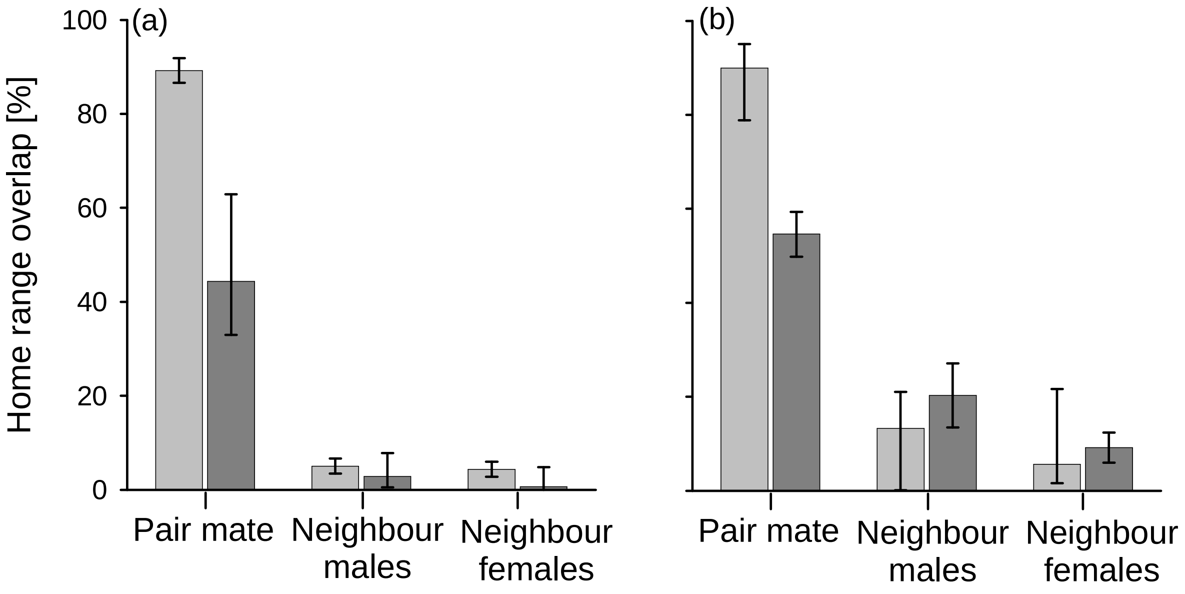

Fig. 1: Overlap of home ranges of male and female round-eared sengis with the pair mate, neighbouring males and neighbouring females in the (a) breeding and (b) non-breeding seasons. Overlap data are reported as mean (± SE), and are presented in light grey for females and in dark grey for males.

Widowed females: Ten females lost their mate, probably due to predation, and became widows. In one case, a neighbouring male-female pair intruded into the widowed female’s home range, resulting in a polygynous situation, which lasted for 5-6 weeks until one of the females died. The second widow shifted her home range into a neighbouring area to partner with a single male and became socially monogamous again. The other 8 widows formed pairs in their original home range with previously unpaired males. 5 of these males originated from neighbouring home ranges, which they abandoned. In the remaining 3 cases, the new males immigrated from outside the study area. The duration until a new male entered the area of the widowed female was 2.0 d (± 0.7 SD).

In 3 cases, already paired neighbouring males expanded their home ranges to encompass a widowed female’s home range along with that of their original female mate. At the same time, a new unpaired male intruded into the widow’s area. However all paired males returned to their original home range configuration and female mate after 2-3 days.

The average body mass was 45.1 g (± 2.4 SD) for former residents, i.e. males that disappeared, 42.9 g (± 4.8 SD) for new resident males and 48.2 g (± 5.1 SD) for the heaviest neighbouring male. There was a significant difference regarding the body mass for the 3 different male categories (LMM: n = 8, df = 2, χ^2 = 7.91, p = 0.019): new residents were lighter than the heaviest male neighbour, although not statistically significant after Bonferroni adjustment (t = -2.41, df = 7, p = 0.047). There was no difference regarding the body mass between former and new residents (t = 1.39, df = 7, p = 0.209) and former residents compared to the heaviest neighbouring male (t = -1.36, df = 7, p = 0.216). In the 3 observed cases, in which already paired neighbouring males intruded into the area at the same time as the new un-paired males, all neighbours were assigned to be the heaviest neighbouring male of the widowed female.

Male widowers: Six males lost their mate, probably due to predation, and became widowers. Four of these males left their home ranges to take over a single female in a neighbouring area and thus became pair-living again. Widowed males did not immediately leave their home ranges; instead they waited 8.5 weeks (± 5.2 SD) and then abandoned their original home ranges to take-over a widowed neighbouring female. Of the remaining 2 widowers, one remained solitary in his home range for about 4 months, after which he wandered around and then took over a new female about 0.5 km away from his original home range. The 6th widower did not leave his home range, but a female emigrated from outside the study area into his home range and he became socially monogamous again.

Space use of male and female round-eared sengis

Home range

During breeding season, the average home range size was 1.7 ha (± 1.1 SD) for males and 0.8 ha (± 0.3 SD) for female round-eared sengis, and home range sizes differed significantly between the sexes (Table 2). However, there was also a significant interaction between sex and population density with regard to home range sizes in the breeding season (Table 2). When considering the two sexes separately, male home range size was significantly affected by population density (post hoc: LM: $F = 12.40$, $df = 1$, $p = 0.004$, Fig. 2). With increasing population density, the differences between home range sizes of male and female round-eared sengis declined. In contrast, no relationship between home range size and population density was found for females (post hoc: LM: $F = 0.72$, $df = 1$, $p = 0.412$, Fig. 2). During the breeding season, individual body mass did not significantly influence sengi home range sizes (Table 2).

Home range size did not differ between the 2006 breeding season and the 2006 non-breeding season (LMM: $n = 30$, $\chi^2 = 0.38$, $df = 1$, $p = 0.542$). During the 2006 breeding season, the average home range size was 1.4 ha (± 0.4 SD) for males and 0.8 ha (± 0.3 SD) for females. Home range size was 1.0 ha (± 0.3 SD) for males and 0.7 ha (± 0.2 SD) for females in the non-breeding season. Male round-eared sengis maintained significantly larger home ranges in the non-breeding season compared to the home ranges used by their female mates (Table 2). Body mass did not affect home range sizes in the non-breeding season (Table 2).

Table 2: Linear mixed models testing for the effects of sex, population density and individual body mass of the home range owner in the breeding season (n = 32) and non-breeding season (n = 20). The random factor in both models was pair identity; the covariate, density, was not included in the analysis for home ranges in non-breeding season. Significant effects are given in bold.

	Breeding season			*Non-breeding season*		
Parameter	χ^2	df	p	χ^2	df	p
Sex *S*	11.90	1	**< 0.001**	19.70	1	**< 0.001**
Density *D*	7.81	1	0.005			
Body mass *BM*	1.24	1	0.264	0.27	1	0.606
$S \times D$	7.65	1	**0.006**			

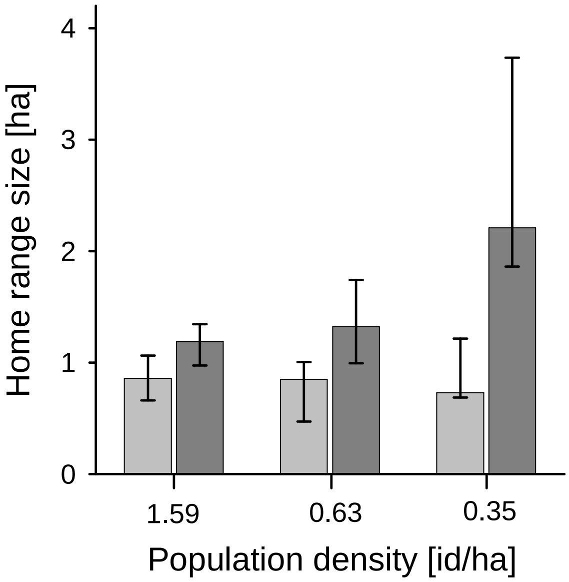

Fig. 2: Effect of population density on home range size of male and female round-eared sengis in the breeding season. Mean values ± SD are reported for females in light grey and for males in dark grey.

Neighbouring individuals

During the breeding season, male home ranges bordered with significantly more neighbouring males and females than home ranges of their female mate (Table 3). There were 1.5 (± 0.7 SD) neighbouring males per male versus only 0.8 (± 0.6 SD) neighbouring males per female, and 0.9 (± 0.7 SD) neighbouring females per male versus 0.7 (± 0.6 SD) neighbouring females per female. Population density and home range size did not significantly affect the number of adjacent males and females for round-eared sengis (Table 3). The number of neighbouring males did not differ between the 2006 breeding season and the 2006 non-breeding season (LMM: n = 30, χ^2 = 0.09, df = 1, p = 0.775). The same was found for the number of neighbouring females (LMM: n = 28, χ^2 = 0.22, df = 1, p = 0.639). In the non-breeding season, the number of neighbouring males (*NM*) and females (*NF*) was not affected by sex (*NM* - LMM: n = 20, χ^2 = 0.73, df = 1, p = 0.392, *NF* - LMM: n = 18, χ^2 = 0.01, df = 1, p = 0.925) and home range size (*NM* - LMM: n = 20, χ^2 = 0.19, df = 1, p = 0.666, *NF* - LMM: n = 18, χ^2 = 0.33, df = 1, p = 0.567). On average, 1.4 (± 1.0 SD) neighbouring males and 1.1 (± 0.9 SD) neighbouring females bordered with male home ranges in the non-breeding season. Female home ranges bordered with 1.2 (± 1.2 SD) neighbouring males and 1.0 (± 0.7) neighbouring females.

Table 3: Linear mixed models testing for effects of sex and breeding season, and the covariates density and home range size on the number of adjacent males and females in round-eared sengis in the breeding season (n = 32). Pair identity was included as a random factor. Significant effects and p-values just outside significance are presented in bold.

	Number of neighbouring males			*Number of neighbouring females*		
Parameter	χ^2	df	p	χ^2	df	p
Sex	6.69	1	**0.010**	3.65	1	**0.056**
Density	1.80	1	0.180	2.11	1	0.146
Home range size	0.09	1	0.760	2.51	1	0.114

Overlap with partner

Sex influenced the overlap with the mate in the breeding season, and there was also an interaction between sex and density (Table 4). When considering the two sexes separately, male overlap was significantly positively affected by population density (post hoc - LM: F = 9.84, df = 1, p = 0.008, Fig. 3). In contrast, female overlap with her mate was negatively influenced by population density (post hoc - LM: F = 7.30, df = 1, p = 0.018, Fig. 3). Home range size affected the overlap with the partner for both sexes (Table 4).

The overlap with the mate did not differ in the 2006 breeding season compared to the 2006 non-breeding season (LMM: n = 30, χ^2 = 0.04, df = 1, p = 0.844). In the 2006 non-breeding season, overlap with the pair mate was affected by sex (LMM: n = 20, χ^2 = 11.29, df = 1, p < 0.001, Fig. 1b) and slightly by home range size (LMM: n = 20, χ^2 = 3.72, df = 1, p = 0.053).

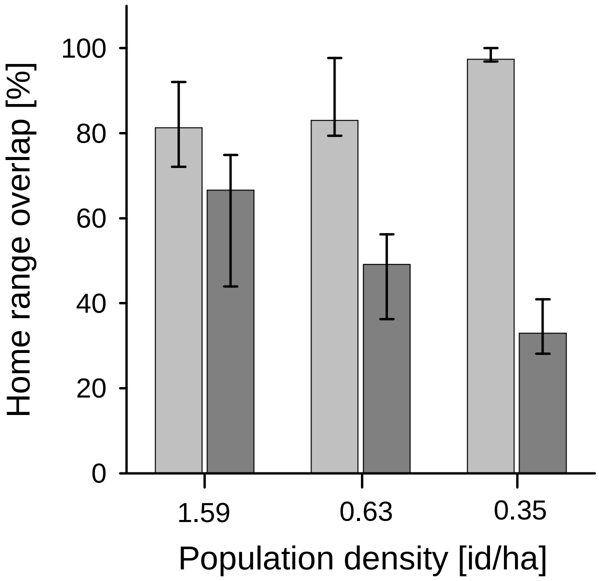

Fig. 3: Effect of population density on home range overlap with the pair mate of male and female round-eared sengis in the breeding season. Mean values ± SD are reported for females in light grey and for males in dark grey

Table 4: Linear mixed models testing for the effects of sex and the covariates population density and individual home range size concerning the amount of intra- and inter-sexual overlap with adjacent individuals in round-eared sengis (n = 32). Pair identity was included as random factor. Significant effects are given in bold.

	Mate			*Neighbouring males*			*Neighbouring females*		
Parameter	χ^2	df	p	χ^2	df	p	χ^2	df	p
Sex *S*	27.58	1	< **0.001**	0.36	1	0.551	0.03	1	0.855
Density	0.25	1	0.616	<0.01	1	0.953	<0.01	1	0.988
Home range size	9.82	1	**0.002**	0.43	1	0.513	0.04	1	0.842
$S \times D$	11.09	1	**0.001**						

Overlap with neighbouring individuals

In the breeding season, male and female sengis showed overlap with neighbouring individuals of both sexes (Fig. 1a). The degree of overlap with neighbouring males and females was not significantly affected by sex and population density (Table 4).

There was no significant difference regarding the degree of home range overlap with neighbouring individuals of both sexes in the 2006 breeding season compared to the 2006 non-breeding season (*NF* - LMM: n = 26, $\chi^2 = 0.08$, df = 1, p = 0.784, *NM* - LMM: n = 28, $\chi^2 = 2.64$, df = 1, p = 0.102), but there was an interaction between overlap with neighbouring males and the sex of the home range owner, just outside a statistical significance (LMM: n = 28, $\chi^2 = 3.25$, df = 1, p = 0.070). For males, the degree of overlap with neighbouring males was higher in the non-breeding than in the breeding season (post hoc - LM: F = 4.88, df= 1, p = 0.049, 15.4 % (11.2, 18.6, 1st and 3rd interquartile ranges) versus 1.2 % (0.4, 3.3)). This was not found for female sengis (post hoc - LM: F = 1.69, df= 1, p = 0.221, 14.0 % (1.7, 24.4) versus 5.1 % (6.5, 7.7)). In the non-breeding season, the overlap with male neighbours was affected by the sex of the home range owner (LMM: n = 20, $\chi^2 = 5.02$, df = 1, p = 0.025) and by home range size (LMM: n = 20, $\chi^2 = 4.47$, df = 1, p = 0.035). The degree of overlap with female neighbours in the non-breeding season was not significantly affected by sex (LMM: n = 18, $\chi^2 = 0.02$, df = 1, p = 0.894) and home range size (LMM: n = 18, $\chi^2 = 0.57$, df = 1, p = 0.450).

Discussion

We investigated potential ecological and physical parameters affecting the social organisation of the round-eared sengis in a semi-desert. Our study population was characterised by a lack of sexual dimorphism in body mass, a population density ranging from 0.35-1.59 individuals/ha, and balanced adult sex ratios. Females maintained exclusive home ranges and reproduced asynchronously during a long breeding season. Round-eared sengis lived in perennial pairs and were territorial, as suggested by little overlap with neighbouring individuals of both sexes, which is generally seen as good indicator for territorial behaviour (Powell 2000).

Our results in a semi-desert population contradict the findings of Sauer in the Namib Desert, where round-eared sengis were considered to live solitarily in undefended home ranges (Sauer & Sauer 1971, 1972; Sauer 1973). Female reproductive success is generally limited by access to resources, and resource distribution is considered to be the key factor in female spacing behaviour (Emlen & Oring 1977). Round-eared sengis in our study used a different life history strategy than the sengis from Sauer`s studies, even though both populations were characterised by balanced adult sex ratios. In the Namib, the study site was flat and open with scantily distributed shrubs. Food availability was generally low, especially in dry season when round-eared sengis left their home range in order to find a more favourable habitat or changed the size of their home ranges to converge around areas with more favourable food supply; some individuals even died of starvation. Home ranges were maintained by mutual avoidance. Thus the low and uneven distribution of key resources in space and time may have reduced the economic value of establishing a territory in the Namib Desert. Since females maintained very large undefended and overlapping areas that centred on resource “hot spots” with other individuals, males might have had the opportunity to encounter several females, favouring a roaming tactic for male round-eared sengis in the Namib Desert.

In contrast, our study site in the succulent karoo semi-desert was characterised by relatively denser vegetation, which was distributed along dry riverbeds and rocky outcrops. Population density was much higher than in the Namib Desert (1.59-0.35 individuals per ha versus 1 individual per 100 ha), and females maintained exclusive areas that were characterised by little overlap with neighbouring females, thereby probably minimising feeding competition with other females (Wrangham 1980). Furthermore, females maintained smaller-sized territories throughout the entire study period, i.e. in the breeding and non-breeding seasons, despite changes in population density**.** Thus territories of female round-eared sengis may have been minimised for energetic efficiency, because home ranges may allow them to forage sufficiently on the one hand and to reduce predation risk and energy expended on the other hand (Sandell 1989). Although the availability of resources may have been reduced in the dry season (Schradin & Pillay 2005b) leading to a cessation in reproductive activity in round-eared sengis, the abundance of resources may have been still high enough to allow individuals to maintain their territories. Thus a more even distribution of resources in space and time may have favoured year-round territoriality in round-eared sengis from a semi-desert, creating the opportunity for males to become territorial and pair-living.

Female round-eared sengis reproduced asynchronously during a long breeding season, so that males could have adopted a roaming strategy, since it would have provided the opportunity to obtain matings with multiple females (Ims 1987; Ostfeld 1990). However, social systems are rarely attributable to a single factor, and pair-living with one female may still offer higher reproductive benefits than searching widely for female mates (Sandell & Liberg 1992). Roaming may entail high costs such as an increase in predation due to the high mobility of males (Magnhagen 1991). Roaming males may also require adequate information about a female’s reproductive state and the area she lives in, and must also encounter other competitors, which can cause injuries and may demand a greater time and energy investment (Schwagmeyer 1988; Michener & McLean 1996), which may increase male mortality rates (Kraus et al. 2008). Unfortunately, there are no data regarding survival probabilities of roaming male round-eared sengis in the Namib Desert. In our study, the oldest male was reported to be over 2.5 years (Schubert unpublished data), which may indicate that pair-living in the semi-desert may serve as risk-adverse strategy (Brotherton & Komers 2003). However, future research investigating benefits and trade-offs of different male strategies in the desert and semi-desert is needed for direct comparison.

Although round-eared sengis were pair-living in the semi-desert, our results also indicate that males had polygynous tendencies, because they maintained much larger areas than females. These larger home ranges may permit males to monitor the reproductive status of neighbouring females and the presence of neighbouring males, as suggested for other sengi species (Rathbun 1979; FitzGibbon 1995, 1997; Ribble & Perrin 2005). In the golden-rumped sengi (*Rhynchocyon chrysopygus*), heavier males maintain larger home ranges (FitzGibbon 1997), which may enhance male reproductive success by searching for extra-pair matings with neighbouring females, as observed in pair-living red foxes, *Vulpes vulpes* (Iossa et al. 2008). In our study, we did not find a correlation between male body mass and territory size. Instead male territory sizes were sensitive to population density and the presence of neighbouring males, and the largest male areas were observed when population density was lowest. At higher densities, males may adjust their ranges by either permitting increased overlap (Ims 1987; Gliwicz 1997) or by confining their movements to smaller areas (Wolff & Cicirello 1990; Lambin & Krebs 1991). Round-eared sengi males used smaller areas at higher densities, but the number of neighbouring males was fairly constant during the whole study period despite changes in population density. Thus, male space use seems to be limited by the presence of adjacent males, and male-male competition may play an important role in shaping the social organisation of the round-eared sengi. Consequently, by adjusting range sizes in response to density, male round-eared sengis may reduce the level of male-male competition. Furthermore, overlap between neighbouring males was significantly reduced in the breeding compared to the non-breeding season. Neighbouring males often present the greatest risk to paternity (Currie & Valkama 2000; Komdeur 2001). Since female round-eared sengis reproduced asynchronously during a long breeding season, males may seek copulations with neighbouring females, thereby enhancing their reproductive success. Thus territorial defence by males may function as a form of mate guarding, preventing competitors from gaining access to females (Emlen & Oring 1977). In addition, higher investment in territorial maintenance during the breeding season may also present a form of indirect paternal investment, because males defend resources for dependent young (Rutberg 1983).

Pair-living males intruded into the areas of widowed females. Whereas only one male was able to achieve polygyny, because his female mate also intruded into the widow’s area, the majority of paired males shifted back to their original area and female mate, following the intrusion of another unpaired male into the widow’s area at the same time. Paired males that intruded into the widow’s area were the heaviest male neighbour. Although new unpaired males were lighter than the heaviest neighbouring male, the difference between male body mass was generally low (10 %) compared to species where one male is able to defend more than one solitary ranging female (e.g. wild cavies, *Cavia aperea* Asher et al. 2008). The reason that a single male cannot defend more than one female territory permanently might be due to a small variation in the resource-holding potential (RHP) between males. The RHP describes the fighting ability of an individual, enabling it to monopolise important resources such as females and is closely correlated with body mass (Schradin 2004; Asher 2008; but see Rödel & von Holst 2009). Generally, when asymmetries in the RHP of contestants are small, fights should be long and intense, which may cause high energetic costs, a decrease in time available for foraging, a high risk of injuries or even death (Neat et al. 1998). Thus a low variance in body mass between round-eared sengi males may reduce the benefits of defending more than one female territory permanently, because temporarily polygynous males suffer substantial costs, such as increased activity and a decrease in body mass as observed in the golden-rumped sengi (FitzGibbon 1997).

Although male sengis may not be able to spatially monopolise 2 female territories permanently, they may employ a mixed reproductive strategy, i.e. maintaining a pair bond with one female, while seeking extra-pair copulations with neighbouring females (Trivers 1972), as observed in many other socially monogamous mammals, such as the aardwolf (*Proteles cristatus*, Richardson 1987), the alpine marmot (*Marmota marmota*, Goossens et al. 1998), the fat-tailed dwarf lemur (*Cheirogaleus medius*, Fietz et al. 2000) and the red fox (Iossa et al. 2008).

In conclusion, the results from our study and Sauer's study indicate that round-eared sengi populations may be characterised by social flexibility caused by environmental variability, with pair-living occurring in a semi-desert and non-territoriality occurring in the Namib Desert. Whether to defend a single female or to search widely for additional mates will be determined by the trade-off between costs and benefits. In our study, female round-eared sengis maintained exclusive areas, possibly because of female-female competition for critical resources. Although, asynchronous breeding may have provided the opportunity for round-eared sengi males to search for multiple fertile females, males were territorial and lived in perennial pairs, suggesting that pair-living offered higher reproductive benefits for males than roaming. Nevertheless, our results revealed that males have polygynous tendencies, as indicated by the large home ranges used and intrusions into areas of widowed females. While a low variance in male body mass and balanced adult sex ratios may have limited the opportunity for males to monopolise additional females, male round-eared sengis in the semi-desert may maximise their reproductive success by maintaining a pair bond with a single female, while seeking copulations with neighbouring females.

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VIII.2 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 thought to be one of the driving forces for the evolution of monogamy, but supporting evidence in free-living mammals is rare. The first goal of our study was to test if mate guarding, measured as intra-pair distance, occurs as a behavioural tactic in round-eared sengis (*Macroscelides proboscideus*), a socially monogamous species lacking paternal care. 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 neighbouring males. Field data were collected in a semi-desert in South Africa using radio-tracking, trapping and direct observations during 3 successive breeding seasons. Mate guarding strongly depended on the females' reproductive state, and all males started to guard their mates prior to and during oestrus as exemplified by the reduced intra-pair distance. Mate guarding incurred costs, because, overall, males lost about 5 % of their body mass. On the individual level, male body mass loss was negatively related to the intensity of mate guarding during the pre-copulatory period. Furthermore, intra-pair distance was inversely correlated with male body mass during the pre-copulatory period and with the number of neighbouring males during oestrus, indicating that males vary their guarding effort in relation to their physical capabilities and the competitive environment. We conclude that, since mate guarding imposed costs for males, it may only be performed for a limited time and constrain males to guard only a single female, thereby reducing the potential for polygyny.

Introduction

Male mate guarding is a common behavioural tactic to overcome sperm competition (Møller & Birkhead 1989, 1991). Mate guarding involves the close following of a receptive female, which allows the male to monitor and court the female mate, as well as to prevent access of male competitors to the female. The occurrence of male mate guarding is generally favoured when females are only fertile for a short period (Parker 1974; Grafen & 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 has been suggested to be the driving force for the evolution of monogamy (reviewed in Brotherton & Komers 2003). In these species, a male actively maintains close spatial proximity to his female mate beyond her fertile period, resulting in a strong pair bond. Although mate guarding allows the males to monopolise their female mates, it seems to constrain males into monogamy, because they are incapable of defending an extra female (Brotherton & 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 behaviour 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; 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 with better quality males investing 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 & LeBoeuf 1993; Iribarne et al. 1995).

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; Jirokul 1999; Currie & Valkama 2000) and adult sex ratios (Dick & Elwood 1996; Matthews 2002), with males investing more heavily in mate guarding with increasing pressure of the competitive environment, i.e. more rival males.

In the present study, we investigated the mating behaviour of the socially monogamous round-eared sengi (*Macroscelides proboscideus*), a member of the mammalian order Macroscelidea, which comprises 17 species from 4 genera. Although all sengi species are believed to be monogamous due to male mate guarding (Ribble & Perrin 2005), field studies on mating behaviour are lacking. Social monogamy in round-eared sengis can be attributed to several factors, such as independently ranging females, balanced adult sex ratios and probably a low resource holding potential of males (Schubert et al. 2009). Individuals live in dispersed pairs that are characterised by a weak bond, probably as a consequence of ecological pressures, such as predation risk and high inter-sexual competition for critical resources (Rathbun 1979; Kleiman 1981).

In round-eared sengis, female reproductive behaviour, such as asynchrony of breeding and short oestrus period (Schubert et al. 2009), should favour a male guarding tactic during her receptive period. Therefore, we predict that male round-eared sengis would guard their mate during oestrus to ensure paternity. Males are also expected to engage in prolonged guarding prior to female receptivity, because the chances for a male encountering an unpaired female are low and asynchronous reproduction by females may increase male-male competition for copulations. However, guarding may impose costs for the males. In order to minimise these costs, males might balance their guarding effort 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 behaviour might depend on the intensity of male-male competition. Specifically, neighbouring males often present the greatest threat in paternity risks (Lifjeld et al. 1993; Currie & Valkama 2000; Komdeur 2001). Therefore, we predict that higher numbers of neighbouring males would lead to greater levels of male mate guarding as a response to an increased risk of extra-pair 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-September 2006 and August-September 2007. The 15 000 ha large nature reserve is situated in a semi-desert in Namaqualand. The vegetation is classified as succulent karoo (Cowling et al. 1999). Rain falls predominately in winter and is highly predictable with 160 mm rain per annum (Cowling et al. 1999). The study site, which was about 35 ha large, was characterised by dry a 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

Sengis (or elephant-shrews) represent an ancient monophyletic clade that belongs to the superorder Afrotheria, and is endemic to the African continent (Corbet & Hanks 1968). The round-eared sengi is one of the smallest sengi species and is found only in the southern regions of Africa (Skinner & Smithers 1990). This omnivorous mammal has a crepuscular to nocturnal activity pattern that is sensitive to ambient temperatures with a decrease in activity during cold nights and when food abundance is low (Sauer & Sauer 1971; Lovegrove et al. 1999). Reproduction occurs during a long breeding season from June-December, in which females reproduce asynchronously (Schubert et al. 2009). Females have a short postpartum oestrus that lasts for about one day (Sauer & Sauer 1971). 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 hours (Sauer 1973). To date, there is no evidence that male round-eared sengis engage in direct parental care (Sauer & Sauer 1971; Sauer 1973). Pups are weaned at 4 weeks of age and both sexes leave their natal territory. Sexual maturity is reached at about 3-9 months with males becoming mature earlier than females (Olbricht et al. 2006).

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. During cold weather, all traps were provided with cotton wool to avoid trap deaths. Trapping was performed in the morning between 04:00-08:00, depending on outside temperatures (04:00-6:00 when temperatures were high and 06:00-8:00 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 (see Schubert et al. 2009 for detailed description). All individuals were marked using hair dye (Inecto Rapid, South Africa) and ear tags (National Band and Tag Co., USA).

Radio-tracking

The males and the females of 10 pairs were equipped with a MD-2C radio-collar (Holohil Systems Ltd., Canada) for approximately 1 month. The 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 anaesthetised with ether to reduce stress during the handling procedure. The average duration from setting the traps until capturing the individuals was 2 h; for anesthetising and attaching the collar less than 2 min. were needed. The maximum duration from recovery until releasing the individuals was 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 (males: 42.6 g (± 4.1 SD), females: 43.3 g (± 3.3 SD), Schubert et al. 2009). Radio-tracking was conducted with a Telonics TR-4 receiver (Telonics Inc.) and an 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 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 radio-tracking was only performed by one person, data could not be collected simultaneously. Thus, first the location of one partner was recorded and then immediately the location of the pair mate. The chronological order, which individual was radio-tracked first or second, was maintained during the radio-tracking session. Radio-tracking was performed from 07:00-10:00 and from 18:00-22:00. For each pair, an average of 7 (range 4-17) radio-tracking sessions was conducted.

Data analyses

Intra-pair distance was determined as the distance between the points of individual locations of pair mates every 10 minutes using the program MapSource. For each radio-tracking season, a median of the intra-pair distances was calculated for data analysis.

The female reproductive state was classified in four categories: (1) Pre-copulatory period 2, defined as the time (4-2 days) prior to birth; (2) Pre-copulatory period 1, which lasted from the day before birth until the day of birth; (3) Oestrus was defined to be on the day after parturition, since female round-eared sengis have a post-partum oestrus that lasts for one day (Sauer & Sauer 1971); (4) Post-oestrus of females occurred 2-3 days after parturition. Sufficient data for 8 pairs were collected during the pre-copulatory period 2, 9 pairs during the pre-copulatory period 1, 9 pairs in oestrus, and 10 pairs in the post-oestrus period.

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). 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).

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

We investigated whether mate guarding is costly by comparing male body mass before and after mate guarding using a paired t-test. The body mass of males was calculated as a mean for the period starting 45-15 days before parturition (= initial male body mass), and after the termination of male mate guarding (2-4 days after birth). Since the population was monitored by continuously trapping, we also included 2 males that were not equipped with a radio-collar. Body mass data of one radio-tracked male could not be collected for the post-oestrus period due to predation, resulting in body mass data being available for 12 males. In addition, we determined the effects of intra-pair distances on body mass loss with a LMM, including year as a random factor. The influence of mate guarding on body mass loss was investigated for the oestrus, pre-copulatory period 2 and 1, but not for the post-oestrus, because male mate guarding was already terminated by then (see results). The pre-copulatory period 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 neighbouring males (all covariates) on the intra-pair distances using a LMM. Individual identity and year were included as random factors. Data collection and analysis concerning home range size and number of neighbouring males are described in Schubert et al. (2009). Male home range size was included in the model as a predictor variable, because shorter intra-pair distances might be due to smaller home ranges and not necessarily due to male mate guarding. Male home range size and the number of neighbouring males were known for all males (n = 10).

Results

Description of behaviour during mate guarding

All males (n = 10) approached and followed their female partner during the pre-copulatory period. As a response, females ran away predominately or were fended off males of by snapping at them with their mouth. Occasionally, males attempted to initiate body contact. In 3 cases, females approached their male mates in the pre-copulatory 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 mate, males always over-marked the females' scent. In addition, both sexes were noticed to chase away conspecifics which intruded into the pairs' territory. 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.

Intra-pair distance during different female reproductive states

The distance between the male and the female of a pair differed significantly among the four female reproductive states, and was significantly reduced during the pre-copulatory period 1 and the oestrus period compared to post-oestrus and the pre-copulatory 2 (LMER: $\chi^2 = 27.65$, df = 3, $p < 0.001$, Fig. 1).

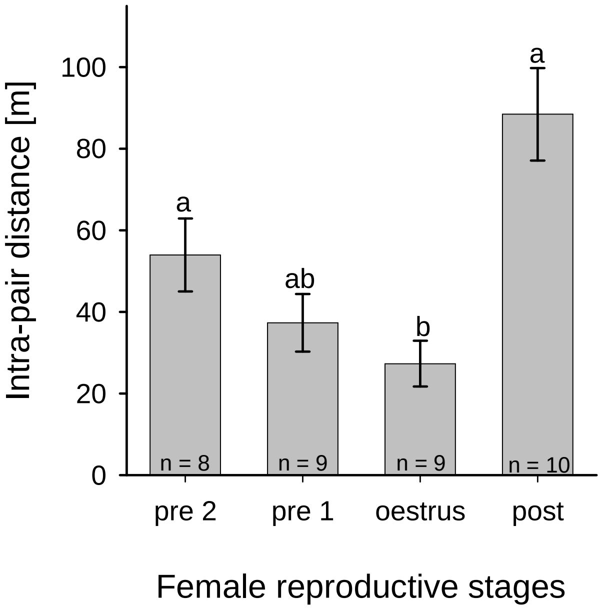

Fig. 1: Distance between pair mates in the different female reproductive states. Pre 2 and 1 describe the pre-copulatory periods 2 and 1; and post describes the post-oestrus period. Data are presented as mean (± SD) and were tested post hoc using a paired t-test with Bonferroni adjustment.

The effect of mate guarding on male body mass loss

Males significantly lost weight during mate guarding accounting 4.6 % (± 3.7 SD) of their initial body mass ($\chi^2 = 8.68$, df = 1, p = 0.003, Fig. 2a). Most importantly, the intra-pair distance during the pre-copulatory period 1, which was the period shortly before parturition, was correlated with male body mass loss ($\chi^2 = 8.68$, df = 1, p = 0.003, Fig. 2b): males that were at closer proximity with their female mate lost more body mass than males that maintained a greater intra-pair distance. Such a correlation was not found during the pre-copulatory period 2 and oestrus period ($p > 0.10$).

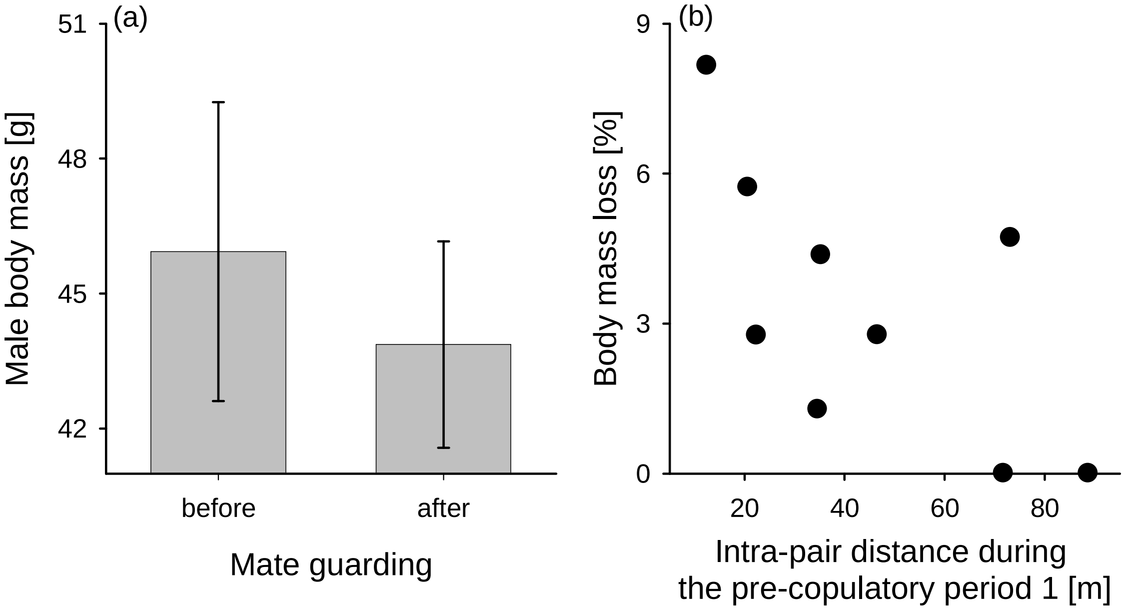

Fig. 2: (a) Comparison of male body mass before and after termination of mate guarding (n = 12), and (b) correlation between body mass loss and intra-pair distance during the pre-copulatory period 1.

Effects on intra-pair distance

We found a significant interaction between home range size (which was 2.0 ha (± 1.2 SD)) and female reproductive state (Table 1). Post hoc analyses suggests that male home range size only affected intra-pair distance during the pre-copulatory period 2, although only with a statistical tendency ($\chi^2 = 3.11$, $p = 0.078$, Fig. 3a), but not in the pre-copulatory period 1, the oestrus and the post-oestrus period ($p > 0.10$). During the pre-copulatory period 2, males that occupied smaller home ranges tended to be closer to their female mate than males that inhabited larger home ranges. In addition, there was a significant interaction between the number of neighbouring males (1.8 individuals ± 0.8 SD) and female reproductive state (Table 1). Males that were surrounded by more neighbouring males guarded their female mates more intensely during the oestrus period ($\chi^2 = 5.00$, $p = 0.025$, Fig. 3b). However, there were no effects of the number of neighbouring males on intra-pair distance during the pre-copulatory periods 1 and 2 and the post-oestrus ($p > 0.10$). There was a significant interaction between the initial male body mass and female reproductive state (Table 1). Initial male body mass negatively affected by intra-pair distance during the pre-copulatory period 1 ($\chi^2 = 9.02$, $p = 0.002$, Fig. 3c) and showed the same tendency during post-oestrus ($\chi^2 = 3.28$, $p = 0.070$). However, there was no effect of male body mass on the distance of pair mates during the pre-copulatory period 2 and the oestrus ($p > 0.10$).

Table 1: Effects of different predictor variables on intra-pair distance in round-eared sengis. Statistics was calculated with linear mixed models including individual identity and year as random factors. Significant effects are given in bold.

Predictor variables	χ^2	df	P
Female reproductive stage *R*	31.66	3	**< 0.001**
Male home range size *H*	7.86	1	**0.005**
N neighbouring males *N*	2.36	1	0.12
Male body mass *B*	0.49	1	0.48
$H \times R$	13.47	3	**0.004**
$N \times R$	11.78	3	**0.008**
$B \times R$	21.50	3	**< 0.001**

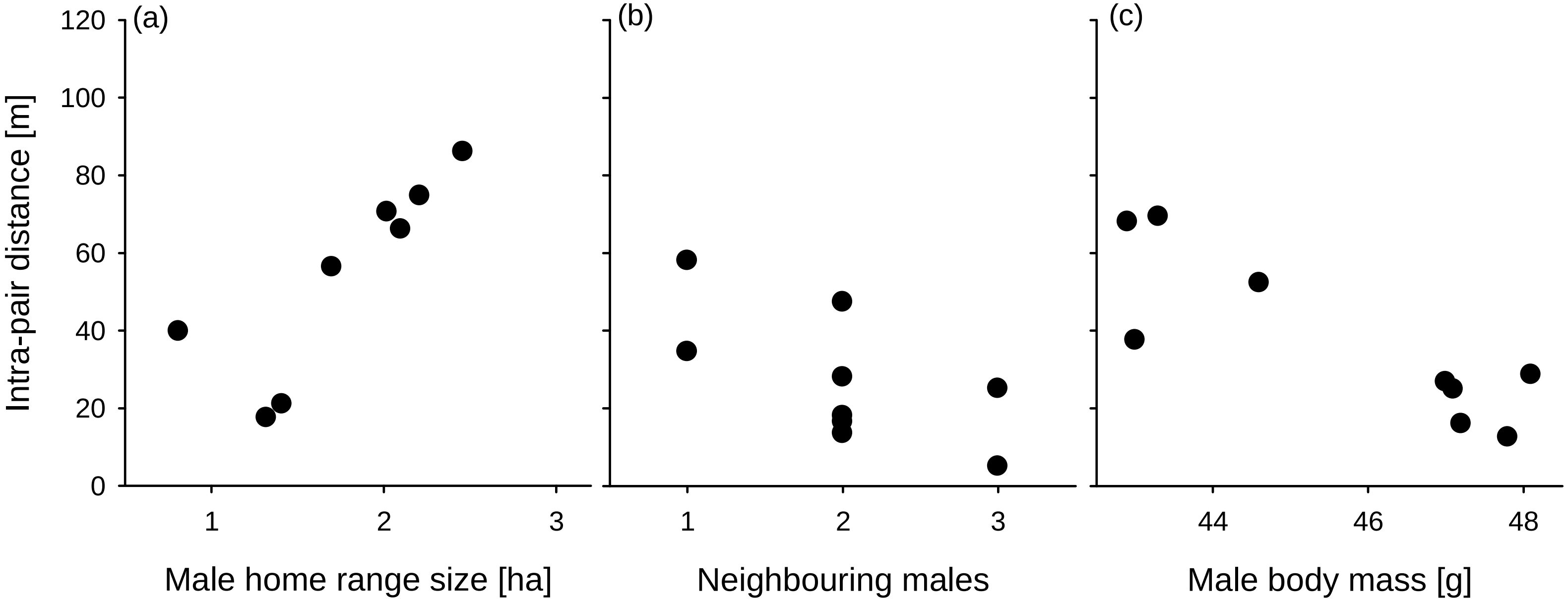

Fig. 3: Correlation between intra-pair distance and: (a) male home range size during the pre-copulatory period 2; (b) the number of neighbouring males during the oestrus period; (c) initial male body mass during the pre-copulatory period 1.

Discussion

In the present study we demonstrated that male round-eared sengis engaged in mate guarding prior 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 neighbouring males guarded their female mates more intensely.

Shorter distances might be due to smaller male home ranges and not necessarily due to male mate guarding. In our study, reduced intra-pair distance shortly before and during female receptivity did not correlate with male home range size, indicating that reduced intra-pair distance is a result of male guarding rather than male space use. Asynchronous reproduction in female round-eared sengis (Schubert et al. 2009) 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 extra-pair copulations (Trivers 1972). Thus, mate guarding may function as an anti-cuckoldry tactic by males to protect their mating interests with their pair female (Gowaty & Plissner 1987). Pre-copulatory guarding is advantageous when males have a limited opportunity to search for additional females (Parker 1974). Since male round-eared sengis are constrained into a socially monogamous relationship by a low opportunity to monopolise additional unpaired females (Schubert et al. 2009), prolonged guarding may allow males to secure matings with their female mates when they come in oestrus. Furthermore, female mammals often advertise their reproductive condition, which peaks shortly before sexual receptivity (Dixson 1983), but male sengis were observed to always over-mark their mate’s scent shortly before and during oestrus. Persistent guarding may allow males to conceal the reproductive state of the female and advertise the paired status, thereby decreasing the risk of intrusions by competitors.

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) and can impact on survival and investment in future mating attempts (Stearns 1992). Thus, mate guarding behaviour may be influenced by the ability to recover the body condition (Poole 1989). Female round-eared sengis are in oestrus 2-3 times per year with reproductive events spread throughout a long breeding season of about 9 months and an inter-litter interval of 61 days (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 intra-pair distance during the pre-copulatory period 1, it appears that the costs of mate guarding are associated with following the female. Males may have travelled shorter distances during mate guarding, since female round-eared sengis use much smaller territories in comparison to their male partner (0.9 ha versus 1.5 ha, Schubert et al. 2009). 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 afford. In our study, heavier males guarded their female mates more closely during the pre-copulatory period 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. Paired round-eared sengi males do not only invest in mate guarding, but also in year-round territory defence

(Schubert et al. 2009). Generally, male territorial defence may function as a form of mate guarding, as occurs in the large treeshrew (*Tupaia tana*, Munshi-South 2007). Male round-eared sengis may therefore employ different mating tactics depending on their individual qualities, with lighter individuals investing more in territorial defence, 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 defence, a decrease in defence while guarding may also be more critical for lighter than for heavier males in terms of territory take-over attempts of other males. This is because heavier (and older) males may be more experienced in territorial defense, increasing the possibility to invest more in courtship displays (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 neighbouring males rather than floaters are the primary threat in cuckoldry risks (Lifjeld et al. 1993; Currie & Valkama 2000; Komdeur 2001). Since sengi males are believed to maintain larger areas to monitor the reproductive state of neighbouring females (Ribble & Perrin 2005), closer association between pair mates may lead to a greater within-pair paternity assurance.

In conclusion, mate guarding may function 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 favoured prolonged mate guarding in round-eared sengis. However, males apparently modified their guarding effort in relation to prevailing physical and ecological parameters: lighter males invested less in direct mate guarding than heavier ones, and males decreased their guarding effort with a decrease in the competitive environment, thereby possibly minimising energy investment. However, since guarding imposed costs for all males, it may only be performed for a limited time period and generally constrain males to guard only a single female, reducing the potential for polygyny.

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VIII.3 Benefits and Costs of Extra-Pair Attempts in the Socially Monogamous Round-Eared Sengi (*Macroscelides proboscideus*): A Male’s Perspective

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Abstract

Although monogamy is interpreted as risk-adverse strategy by reducing intra-sexual conflicts, most pair-living males increase their reproductive success by engaging in extra-pair copulations. However, little is known on costs involved of such extra-pair attempts from the male’s perspective. We investigated promiscuous tendencies of paired male and female round-eared sengi (*Macroscelides proboscideus*), a pair-living small mammal occurring in Southern Africa. In particular, we measured potential costs of extra-pair attempts for the males. For this, we conducted laboratory experiments, involving interactions between neighbouring pairs. Data collection included direct behavioural observations and establishing the morphological and physiological characteristics of males. Both sexes intruded into the neighbouring area, and males initiated more sexual behaviour with neighbouring females than with their pair mates. Females also initiated sexual behaviour with male neighbours, and the frequency of this behaviour was positively related to the time neighbouring males spent in the females’ area and to male marking behaviour. Intruding males mounted neighbouring females, indicating the potential occurrence of extra-pair copulations. However, males were attacked by resident males. Aggression experienced and marking behaviour of intruding males was associated with body mass loss in these animals. Furthermore, glucocorticoid levels, determined from analyses of faeces and urine samples, positively correlated with male body mass loss and male marking behaviour of intruding males, indicating costs of this behaviour. In conclusion, male and female round-eared sengis have promiscuous tendencies. Although interactions with neighbouring females may offer benefits for males in terms of enhanced reproductive success, males also seem to pay substantial costs, as indicated by body mass loss and elevated stress hormone levels.

Introduction

Monogamy is commonly thought to be a risk-adverse strategy. By monopolising a single female, males enhance their individual fitness by reducing intra-sexual conflicts with other males in the population (Brotherton & Komers 2003). However, male mammals usually have higher reproductive rates than females, because they do not have to invest in costly gestation and lactation (Williams 1966). Thus the male-bias in potential reproductive rates enables most pair-living males to employ a mixed reproductive strategy, i.e. to be pair-living with one female while seeking extra-pair copulations with other females thereby improving their reproductive success (Trivers 1972), such as in the aardwolf (*Proteles cristatus*, Richardson 1987), the alpine marmot (*Marmota marmota*, Goossens et al. 1998), the fat-tailed dwarf lemur (*Cheirogaleus medius*, Fietz et al. 2000) and the red fox (*Vulpes vulpes*, Iossa et al. 2008). There are numerous studies investigating costs and benefits of extra-pair copulations in female mammals (reviewed in Jennions & Petrie 2000), but little attention has been paid to extra-pair attempts of males.

Although competition may be less pronounced in monogamous species compared to polygynous ones (Wiegmann & Nguyen 2006), pair-living males must also compete with other males to reduce potential threats. This has led to the evolution of energetically costly strategies such as mate guarding to prevent territory and female take-overs (Brotherton & Komers 2003). Such male tactics seem plausible for explaining the evolution of monogamy, but there is limited empirical data on the potential trade-off between benefits and costs for pair-living males with polygynous tendencies. Benefits of intruding into neighbouring areas can increase the reproductive fitness of the intruding male through extra-pair copulations with the neighbouring female. However, excursions into the neighbouring areas may also be associated with costs such as increased predation risk due to increased mobility (Magnhagen 1991). In addition, fights with male competitors (Marler & Moore 1988; Haller 1995; Briffa & Sneddon 2007), as well as the display of other specific behaviours such as marking

(Gosling & Roberts 2001), may involve great energetic demands and injury risks lowering male fitness.

In the present study, we investigated sexual and competitive interactions between neighbouring pairs of round-eared sengis (*Macroscelides proboscideus*), which are naturally socially monogamous and lack sexual dimorphism in body mass (Schubert et al. 2009). Round-eared sengis are a suitable model for studying extra-pair attempts and intra-sexual competition between males, for three reasons. Firstly, round-eared sengi males are more aggressive and have a greater level of marking behaviour than females (M. S. unpublished data), indicating that males are the competing sex. Secondly, our previous studies provide evidence that males employ strategies probably to achieve extra-pair matings, such as the maintenance of much larger home ranges than females and intrusions into neighbouring territories of single females (Schubert et al. 2009). Thirdly, males engage in costly mate guarding during their females' prior and during oestrus, and guarding intensity is associated with the competitive environment (i.e. the number of neighbouring males) and male physical capabilities (M. S. unpublished data).

The main aim of our study was to investigate whether round-eared sengis have promiscuous tendencies. Since round-eared sengis are smaller-sized mammals (35 g) with a predominately nocturnal activity pattern (Sauer & Sauer 1971), direct observations of animals are difficult to perform in the wild. For this reason, we performed laboratory experiments with wild-caught sengis. The experimental design involved documenting the interactions between neighbouring pairs, in which each male was paired with a single female in their own area. By doing so, we avoided imbalances in resource value between the male competitors, because such imbalances, e.g. the presence of female mate can substantially influence male-male competition (reviewed in Riechert 1998).

If male sengis have polygynous tendencies, we expected them to intrude into the neighbouring area and to initiate sexual behaviour with the neighbouring females.

Furthermore, monopolisation and engaging in contact with neighbouring females may require specific behaviours linked to male-male competition. This might include aggression towards the neighbouring male (direct competition) and/or male marking behaviour in the neighbouring area (indirect competition), which may also serve as information transmission about the male’s quality for females (reviewed in Gosling & Roberts 2001). In addition, we investigated whether extra-pair copulation attempts entail costs for the males. Such costs might be apparent by a loss in body mass and/or by elevated glucocorticoid levels (von Holst 1998). In particular, we expected positive relationships between male glucocorticoid levels and/or body mass loss and different behaviours associated with extra-pair attempts such as the intrusion into and marking in the neighbouring area or the initiation of sexual behaviour with neighbouring females.

Methods

The Study Species

Round-eared sengis belong to the ancient monophyletic mammalian clade of the Macroscelidea (elephant-shrews) that comprises 17 species from 4 genera, which are all endemic to the African continent (Corbet & Hanks 1968), and that is placed in the superorder Afrotheria (Springer et al. 2004). The round-eared sengi is a small-bodied (35 g) omnivorous mammal (Sauer 1973; Kerley 1995) that occurs in more arid regions of South Africa, Namibia and Botswana (Skinner & Smithers 1990). It has a crepuscular to nocturnal activity pattern, with activity peaks at dusk, dawn and through the night. Activity is influenced by ambient temperatures and food availability, with a decrease in activity under unfavourable environmental conditions, such as cold nights and low food abundance (Sauer & Sauer 1971; Lovegrove et al. 1999).

Trapping

Individuals were trapped in an approximately 60 ha large area at the farm “Klein Goegap” (29°37’S; 17°59’E), that bordered on the Goegap Nature Reserve, and is situated in a semi-desert in the Northern Cape Province, South Africa. Trapping was performed for 5 d in October 2007 (middle spring), after a 7 d pre-baiting period. Individuals were trapped with locally produced metal traps (26 × 9 × 9 cm, similar to Sherman traps), which were baited with a mixture of peanut butter, oats, marmite and sunflower oil. Traps were set at 04:00 a.m. and checked at 06:30 a.m. All trapped individuals were weighed and sexed, and only individuals with a body mass > 35 g (= adults, see Schubert et al. 2009) were used for the study; individuals < 35 g were immediately released from the traps. Sexes could be easily distinguished, because males have an abdominal penis (Woodall 1995). Round-eared sengi were individually marked with hair dye (Inecto Rapid, South Africa) and ear tags (National

Band and Tag Co., USA). After weighing and marking, study subjects were placed in the traps again and taken to an enclosure at the Goegap Nature Reserve. In total, we caught 8 males and 8 females suitable for the experiment.

Husbandry

During the first 7 days after capture, each individual was placed alone in a cage (500 mm × 500 mm × 400 mm, see Fig. 1 for time schedule). Tanks were made of metal and a plexiglass front; the inside of the cages was painted with a warm orange colour to simulate the natural environment. The habituation period allowed the sengis to become accustomed to conditions in captivity and to the presence of an observer, who was situated 2 m in front of the cages. After one week, test subjects were habituated to human presence and the use of a blind was not necessary.

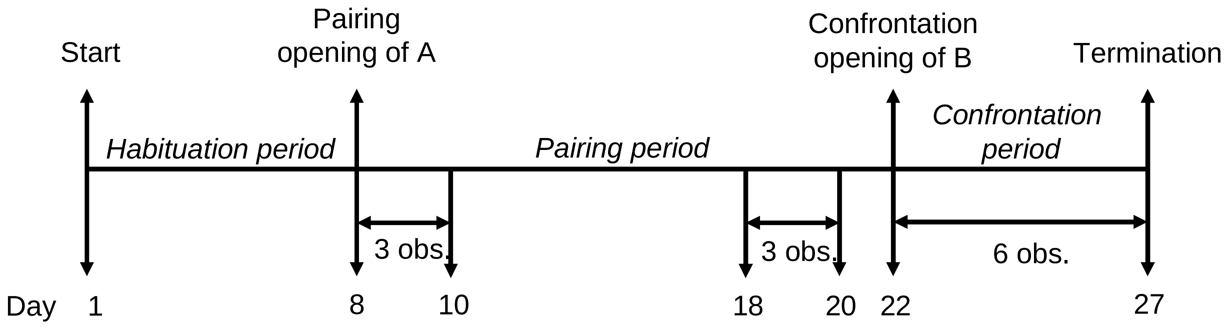

Fig. 1: Time table of the experiment.

All cages contained a layer of 5 cm sand, hiding spots, such as small pipes that were covered with black paper on the one side, dead branches and stones for environmental enrichment. Data collection was not hampered by tank enrichment. Lights were switched on from dawn to sundown (approximately from 06:30-19:30) to simulate the natural day and night cycle. At sunrise a heater was switched on to allow the sengis to warm up, which would have been achieved through sun basking in the wild. Cleaning of cages was done every 10th day: the top layer of sand, which contained faeces and urine, was removed and replaced with a new layer, which was mixed with the remaining sand.

Water and food were provided at sundown. Individuals received boiled butternut 2 times a week and a salad mix (different kinds of lettuce, carrots, baby leaf spinach) 5 times a week. Their diet was supplemented with peanuts, sunflower and canary seeds (Lopis, South Africa), cat food (chicken flavour, Purr-fect, Spar Brands, South Africa), a mixture of hard-boiled eggs-ProNutro (Bokomo Foods, South Africa) and mealworms.

For husbandry, we followed the guidelines of Tripp (1972), Woodall et al. (1989), Ehrlich (2003) and advice of J. Bitterwolf from the Cologne Zoo (Germany).

Pairing

For the experiment we established 8 male-female pairs. Each male was paired with an unfamiliar female, i.e. they were trapped more than 1 km apart from each other. Before pairing (habituation period), potential mates were singly placed in neighbouring cages that were connected by a PVC gutter pipe (35 cm length, 8 cm diameter), however, during the first 7 days after capture, this connection was blocked by a wire grid (see A1, A2 in Fig. 2). This allowed pairs to smell each other, thereby gaining information about one another and increasing familiarity. On the day of pairing, the wire grid was removed and the behaviour of the male and the female was observed. Each pair was observed 6 times during the pairing period; 3 times in the beginning and 3 times at the end of the pairing period, which lasted 14 d (see Fig. 1). Observations were performed for 15 min in the morning (06:00-08:00) and in the evening (17:00-19:30) using continuous recording (Martin & Bateson 1993).

Approaching, sniffing and body contact were pooled and are referred to as socio-positive behaviour. Individuals of both sexes initiated significantly more positive social interactions in the beginning than in the end of the pairing period ($\chi^2 = 21.87$, df = 3, $p < 0.001$), and males generally initiated significantly more social interactions than female round-eared sengis ($\chi^2 = 7.26$, df = 3, $p = 0.007$). The average level of socio-positive behaviour initiated by males was 10.8 interactions/h (± 3.5 SE) in the beginning and 2.8 interactions/h (± 1.0 SE) at the end of the pairing phase; the average for females was 5.1 interactions/h (± 1.8 SE) in the beginning and 3.7 interactions/h (± 1.3 SE) later on. Additionally, 2 males were observed to mark in the beginning of the pairing phase with 4.0 or 3.2 marks/h, respectively. Since no aggression was observed and both sexes initiated positive social interactions with their mate, pairing was regarded successful.

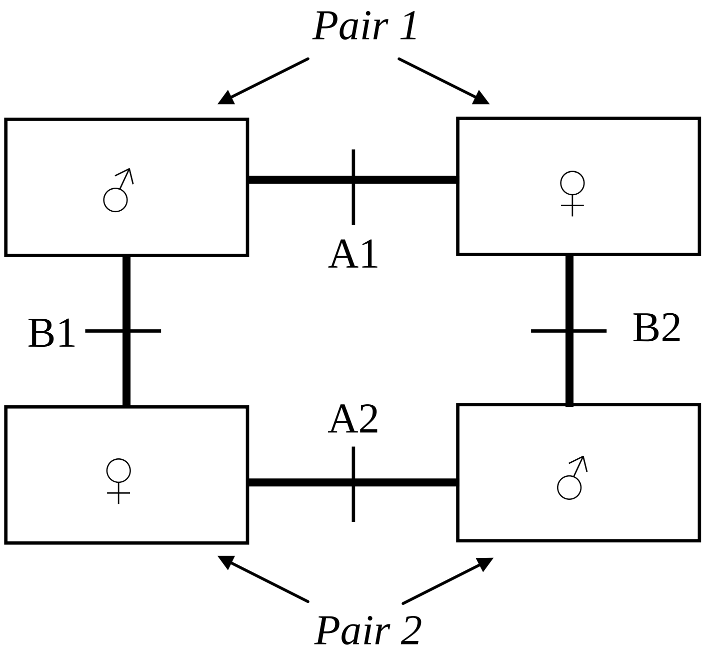

Fig. 2: Experimental set-up for testing social interactions between pairs of round-eared sengi, consisting of tanks (squares; 500 mm × 500 mm × 400 mm) and interconnecting plastic tubes (solid lines; 35 cm length, 8 cm diameter). A and B indicate the positions of wire grids that were removed during the experiments.

Encounter Experiment with Neighbours

Each pair was housed in two adjoining cages that were connected by a PVC pipe. For the experiments to test interactions between different pairs, each of the two cages of a pair was also connected by a PVC pipe with the cages of one neighbouring pair (Fig. 2), resulting in 4 experimental set-ups of the 8 pairs. Until the start of the experiment, the connections between the neighbouring cages were blocked with a wire grid (see B1, B2 in Fig. 2). Thus individuals could smell each other and thereby gain information about neighbouring animals. These grids were removed on D 22 when the experiment started (see Fig. 1). The encounters of neighbouring individuals were observed for 6 days. Six observations, each 30 min. were performed for each set of neighbouring pairs in the morning (06:00-08:00) and in the evening

(17:00-19:30) using continuous recording (Martin & Bateson 1993). We scored all observed behaviours. Sexual behaviour was defined as following and sniffing (naso-nasal and ano-genital) an individual of the opposite sex and mounting. Aggressive behaviour was classified as chasing, jumping on and wrestling with opponents. Marking behaviour included the rubbing of the ventral side on the ground in both sexes. All behaviours were calculated as frequency per hour for statistical analyses.

Collection of Body Mass Data

Generally, body mass data of females and males were collected every 10th day when clearing the cages for monitoring individual health status. For analyses, body mass data were collected on D 18 and on the morning after termination of the experiment (D 28). Individuals were removed from the cages and were weighed by placing them in a plastic box, which was situated on top of a kitchen scale (capacity 500 g, accuracy 0.1 g). The duration from catching round-eared sengis, weighing them and re-introducing them in the cage again was about 5-10 min.

Collection of Urine and Faecal Samples

Male urine and faecal samples were collected twice, once to ascertain baseline hormonal levels samples, which were collected 2 days (D 20) before the encounter experiment with a neighbouring pair, and again on the last day of the experiment (D 27). Because sengis are crepuscular with activity peaks during night time, samples were collected between 21:00-23:00. For sample collection, each male was removed from the tank and placed in a small cage that did not contain any bedding; each male received 10-15 mealworms. The average duration for catching males and placing them in an empty cage was 5-10 min; the maximum duration for keeping males alone in the cage was 1 h with cages being checked every 30 min. for urine and faecal samples. If males did not urinate and/or defecate after 1 h the data collection was terminated and the male was reintroduced into its tank. Samples were immediately deep-frozen at –30°C after collection. Of the 8 males, we could collect faecal samples and urine samples of 5 round-eared sengi males before and 6 faecal samples and 5 urine samples of 7 males were collected after termination of the experiment.

All individuals were released early in the morning (05:00-06:00) the day after termination of the confrontation experiment at the point of capture. Food (oats-peanut butter-marmite-oil-mix) was provided randomly in the trapping area for 5 days afterwards.

Analyses of Glucocorticoid Metabolites from Urine and Faeces

Concentrations of free corticosterone in the urine samples were measured using a radio immunoassay (see Fenske 1988 for detailed method description). Faecal corticosterone metabolites were determined using an enzyme immunoassay with labelled biotinylated steroids (for details see Touma et al. 2004, 2005; Monclús et al. 2006).

Data Analyses

Statistical analyses were done using the program R version 2.8.1 (R Development Core Team 2008). Linear mixed-effects models (LMM) were fitted with the package lme4 with the Laplace approximation of the likelihood function (Bates 2005). P-values were calculated using 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). Percentage values were arcsine-root transformed and male and female sexual behaviours and male marking behaviour were log (x+0.1) transformed prior to analyses. Due to moderate sample size (n = 8), we only included a maximum of 2 predictor variables into the models and did not consider interactions.

The male-male pair identity was included as a random factor, and we also included individual identity as a further random factor in cases where we compared the behaviour (paired data) of animals in their own and the neighbouring area.

Analyses of data on glucocorticoid values were done with Spearman rank correlation due to the low sample size (n = 5 to 6).

Results

Male Location: Own versus Neighbouring Area

All males (n = 8) were observed to intrude into the neighbour's tank, and there was no difference regarding time spent in the own (43.3 % ± 9.3 SE) versus the neighbour's tank (56.7 % ± 9.3 SE; LMM: $\chi^2 = 0.95$, df = 1, p = 0.330).

The time spent in the neighbour's tank by a male was not associated with his body mass ($\chi^2 = 0.03$, df = 1, p = 0.864), or with the location of the female mate ($\chi^2 = 0.43$, df = 1, p = 0.512).

Male-Male Aggression

The frequency of aggression received by a male was not affected by his initial body mass ($\chi^2 = 2.17$, df = 1, p = 0.141), but was significantly and positively correlated with the time spent in the neighbouring area ($\chi^2 = 10.92$, df = 1, $p < 0.001$), with higher levels of aggression being associated with greater time spent in the neighbour's area (Fig. 3).

The frequency of aggression initiated by males was positively correlated with their body mass, although only with a statistical tendency ($\chi^2 = 3.41$, df = 1, p = 0.064). In addition, the frequency of aggression was significantly, but negatively related to the time they spent in the neighbour's area ($\chi^2 = 8.92$, df = 1, p = 0.003).

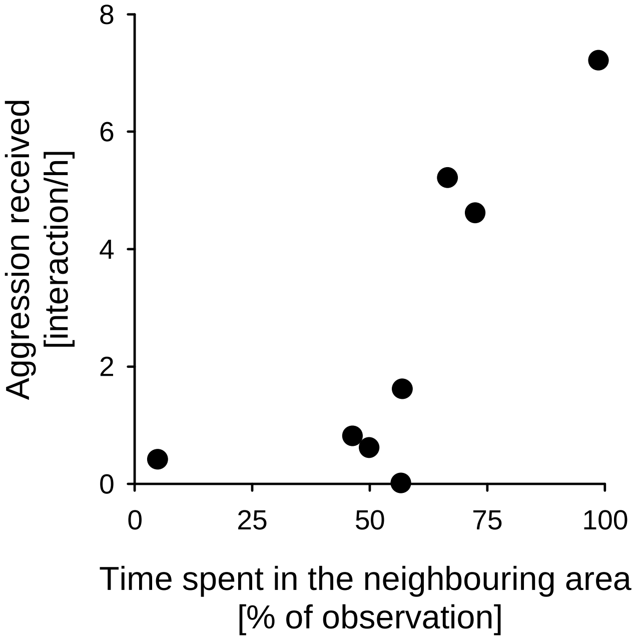

Fig. 3: Correlation between the aggression that male round-eared sengis received from the neighbouring male and the percentage time they spent in the neighbouring area (n = 8).

Marking Behaviour

There was no significant difference between male marking frequency in their own and the neighbour’s tank (χ^2 = 1.99, df = 1, p = 0.158); the marking frequency per hour was 1.8 (± 0.7 SE) in the own and 0.7 (± 0.3 SE) in the neighbouring area. Male marking behaviour in the neighbour’s tank was neither affected by body mass (χ^2 = 0.11, df = 1, p = 0.743) nor by the time they spent in this area (χ^2 = 1.76, df = 1, p = 0.185). There was also no effect of marking in the neighbour’s area on the frequency of aggression received by the resident male (χ^2 = 0.33, df = 1, p = 0.566).

Sexual Behaviour of Males

Males initiated more sexually motivated behaviours (sniffing, following, mounting) with their neighbouring female (2.1 interactions/h ± 0.4 SE) than with their own mate (1.1 interactions/h ± 0.8 SE; $\chi^2 = 5.08$, df = 1, p = 0.024). Also, we found no correlations between sexual behaviour initiated with neighbouring females and male body mass ($\chi^2 = 1.17$, df = 1, p = 0.279), or with the time they spent in the neighbour's area ($\chi^2 = 0.57$, df = 1, p = 0.451). Furthermore, the frequency of sexual behaviour with neighbouring females did not influence the frequency of aggression received by the resident male ($\chi^2 = 0.28$, df = 1, p = 0.596).

Sexual Behaviour of Females

Females displayed a similar frequency of sexually motivated behaviours (sniffing, following) towards their own mate (0.9 interactions/h ± 0.4 SE) and towards the neighbouring male (1.3 interactions/h ± 0.5 SE; $\chi^2 = 0.69$, df = 1, p = 0.405). The level of sexual behaviour initiated by females towards neighbouring males was positively correlated with male marking performance ($\chi^2 = 5.65$, df = 1, p = 0.017) and with the time the neighbouring males spent within the neighbour's area ($\chi^2 = 5.23$, df = 1, p = 0.022).

Changes in Body Mass

Body mass of round-eared sengis did not differ significantly between males and females (χ^2 = 1.75, df = 1, p = 0.186; 40.5 g (± 0.5 SE) versus 42.0 g (± 1.1 SE), but by time, i.e. before and after confrontation with a neighbouring pair (χ^2 = 3.26, df = 1, p = 0.071) with an interaction between time and sex (χ^2 = 6.83, df = 1, p = 0.009). When investigating the two sexes separately, only female body mass differed before and after the confrontation experiment (χ^2 = 8.22, df = 1, p = 0.004). Female body mass was on average 41.0 g (± 1.1 SE) before and 43.0 g (± 1.2 SE) after the confrontation experiment. In contrast, male body mass did not significantly differ before and after termination of the experiment (χ^2 = 0.15, df = 1, p = 0.701, 40.6 g ± 0.5 SE versus 40.4 g ± 0.6 SD).

Although there was no indication for a general loss in male body mass during the experiment, there was a huge variation among the different males: 4 of 8 males lost on average 3.7% of body mass, whereas 3 males gained body mass (4.0%); and one male maintained a rather constant body mass.

The level of aggressive interactions received from the neighbouring males significantly influenced the changes in body mass (χ^2 = 9.78, df = 1, p = 0.002, Fig. 4); the more aggressive interactions the males received from the neighbours, the greater was their body mass loss. In addition, there was a positive correlation between the frequency of marking in the neighbouring area and male body mass loss (χ^2 = 8.26, df = 1, p = 0.004).

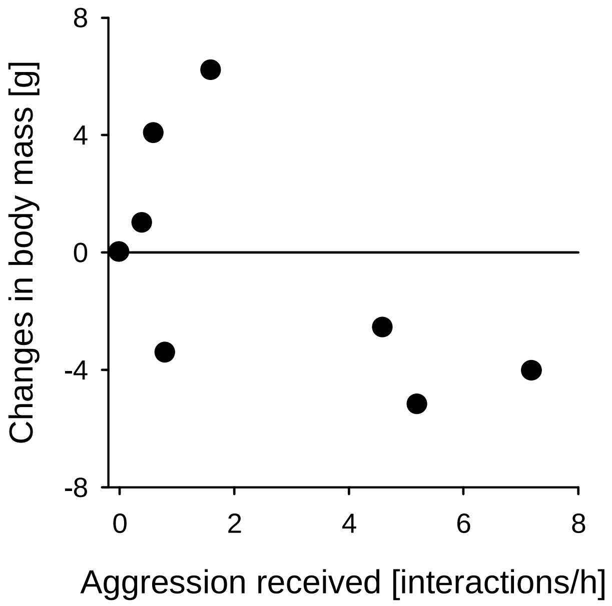

Fig. 4: Correlation between the aggression received by male round-eared and their changes in body mass during the experiment. Body mass gain is indicated by positive values and body mass loss by negative values.

Male Corticosterone Levels measured from Urine and Faeces

Urine and faecal corticosterone levels were positively correlated, just failing to reach statistical significance (Spearman rank correlation, $r_S = 0.67$, $n = 8$, $p = 0.071$). . Corticosterone concentrations were 30.01 ng/ml (± 4.9 SE) in the urine and 2708.69 ng/g (± 705.16 SE) in the faeces. Urine and faecal corticosterone levels were significantly correlated with the changes in male body mass loss (urine: $r_S = -0.83$, $n = 5$, $p = 0.042$, faeces: $r_S = -0.90$, $n = 6$, $p = 0.037$). Males with higher corticosterone levels experienced higher body mass loss, whereas males with lower stress hormonal levels gained body mass (Fig. 5a,b).

Both stress hormone measures were also correlated with male marking behaviour in the neighbour area (urine: $r_S = 0.85$, $p = 0.034$; faeces: $r_S = 0.87$, $p = 0.054$), but not with the level of aggression received (urine: $r_S = 0.31$, $p = 0.564$; faeces: $r_S = 0.70$, $p = 0.233$).

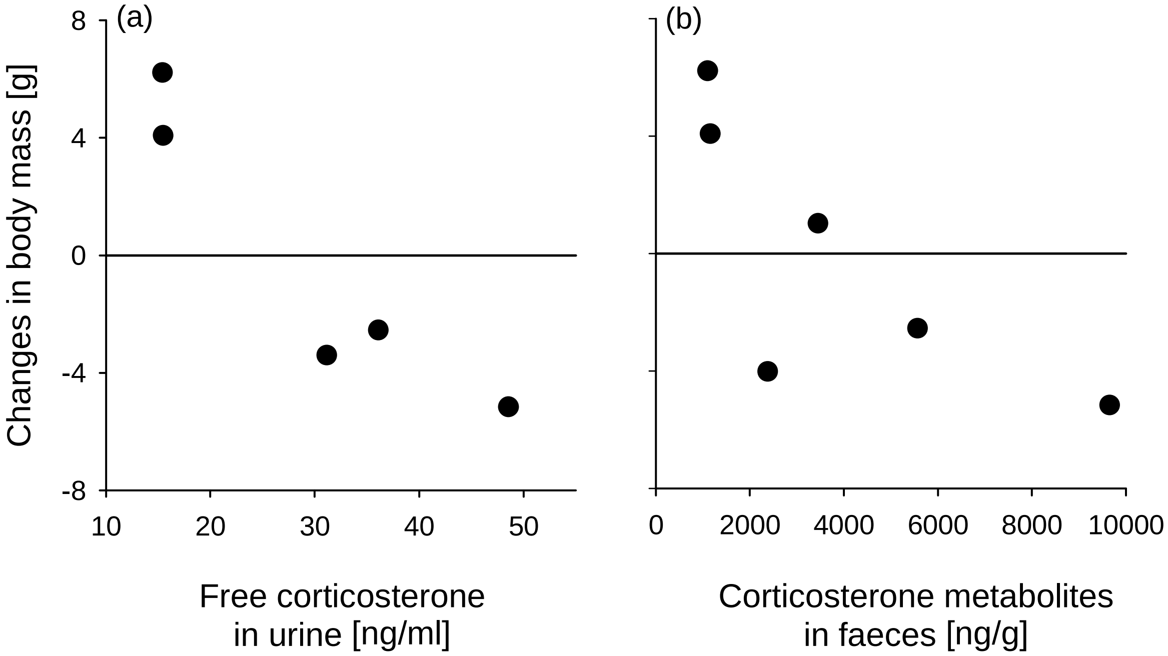

Fig. 5: Correlations between male body mass changes and (a) the concentrations of free corticosterone in urine (n = 5), and (b) corticosterone metabolites in faeces (n = 6) collected after the confrontation experiment, respectively. Body mass gain is indicated by positive values and body mass loss by negative values.

Discussion

In the present study, we demonstrated that pair-living male and female round-eared sengis have promiscuous tendencies. Males initiated more sexual behaviour with neighbouring females than with their pair mate, and were also observed to mount female neighbours, indicating the potential occurrence of extra-pair copulations. However, intruding and marking in the neighbour's tank were correlated with aggression from the neighbouring male, with concomitant body mass loss and elevated corticosterone levels.

In socially monogamous mammal species, males also have to compete with each other for females and territories. Selection favours traits that increase access to fertile females and large male body mass usually results in superiority in male-male contests (Clutton-Brock 1989; but see Rödel & von Holst 2009). In monogamous golden-rumped sengis (*Rhynchocyon chrysopygus*) and red foxes, larger males maintain larger home ranges (FitzGibbon 1997, Iossa 2008), and sire more extra-pair young (Iossa 2008). In free-ranging round-eared sengis, male body mass does not predict male home range sizes (Schubert et al. 2009). However, the heaviest male neighbours were observed to intrude into single female areas (Schubert et al. 2009) and male body mass influences mate guarding intensity during the female's oestrus (M. S. unpublished data). In the present study, male body mass did not significantly influence all tested predictor variables, such as being in the neighbour's tank, sexual and marking behaviour and aggression; although, we obtained a tendency between aggression initiated by a male and initial body mass. This may have been due to the low sample size used in this study. Furthermore, the variance in male body mass between neighbours (4.4%) was lesser than that in the field study (about 10%). Future research incorporating an experimental set-up that accounts for a greater variance in male body mass between neighbouring males may shed light on the influence of body mass on male mating tactics in round-eared sengis.

In addition, specific male behaviours may also be correlated with other male traits, such as age (Krebs 1971) and social experience (reviewed in Rutte et al. 2006), so that older males may be more experienced, e.g. in territorial defence or courtship displays (collared lizards *Crotaphytus collaris*: Schwartz et al. 2007) or may possess better qualities than younger males (see Brooks & Kemp 2001 for review), by showing age-related characteristics in the performance of male behaviours that increase extra-pair paternity (blue tits *Cyanistes caeruleus*: Poesel et al. 2006). Unfortunately, we do not have life history data for our male round-eared sengis, because all individuals were wild caught.

More male round-eared sengis were observed to scent mark than females (7 of 8 males versus 1 of 8 females). Males were only noticed to mark in the beginning of the pairing phase and during the encounter experiment with a neighbouring pair, indicating that marking may be used by male round-eared sengis as a behavioural tactic, which can be modified by males in response to social circumstances, such as for advertising for female mates or as a response to the presence of an opponent male. Scent marks and marking frequency may convey information about the male’s identity and quality, such as infection status (house mouse *Mus musculus*, Kavaliers & Colwell 1992), male condition (house mouse, Meikle et al. 1995), male competitive ability (pygmy slow lori *Nycticebus pygmaeus*, Fisher et al. 2003) and may also be linked to the MHC and immunocompetence (reviewed in Gosling & Roberts 2001, Johansson & Jones 2007). Since the time spent and marking in the neighbouring area was positively correlated with sexual behaviour initiated by female round-eared sengis with male neighbours, marking may be used as a behavioural tactic to increase male mating success in round-eared sengis. In collared lizards behavioural patterns associated with advertisement to female mates influences male mating success rather than morphological male characteristics and the initiation of aggressive interactions with competitors (Baird et al. 2007). In our study, intruding and marking in the neighbour’s tank was associated with higher levels of aggression from the resident male neighbour, indicating that aggression may serve as defence of the pair area and the female mate rather than to acquire extra-pair females. Thus, although male physical characteristics may generally confer advantages to male success in intra-sexual competitions over females (Clutton-Brock 1989), modifiable male behaviours may play a key role in male extra-pair attempts in round-eared sengis.

However, aggression experienced and marking in the neighbour’s tank was associated with male body mass loss and elevated hormonal stress levels in the faeces and urine, indicating costs. Investment in costly behaviours can impact on the life-history, and hence on future reproductive success (Stearns 1992). In the mountain spiny lizard (*Sceloporus jarrovi*) increased activity and aggression in males enhances their reproductive success, but is negatively correlated with feeding time and survival probabilities (Marler & Moore 1988; Marler et al. 1991). Furthermore, house mice males that highly invest in scent-marking suffer from reduced growth rate and body size (Gosling et al. 2000), and increased sexual displays have also been shown to reduce male immune functions associated with a reduced life span in birds (reviewed in Zera & Harshman 2001). Thus, although intruding and marking in the neighbouring area may increase extra-pair attempts with neighbouring females, it may also decrease future reproduction for male round-eared sengis, because males may suffer reduced survivorship due to reduced body condition and elevated stress levels (von Holst 1998; Zera & Harshman 2001).

In conclusion, monogamy is rare in mammals and may evolve when males are unable to realise any polygynous situation. In our study on a small pair-living mammal, we have shown that both sexes have promiscuous tendencies. However, males faced a trade-off between benefits arising from sexual behaviour with neighbouring females and costs associated with the excursions to the neighbouring area, which became apparent by aggression received from the resident male, body mass loss and by elevated stress hormonal levels. Costs were predominately correlated with intrusion and marking in the neighbouring area, rather than with defending the female mate and the pair area, suggesting that costs involved reduce the potential for round-eared sengi males to achieve permanently polygnous situations. However, costly extra-pair attempts may serve as honest signals of male quality

(Zahavi 1975, Grafen 1990), and may therefore provide higher quality males with the opportunity to engage in sexual behaviour with neighbouring females increasing their reproductive success.

Acknowledgements

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