

# Temporal patterns of den use suggest polygamous mating patterns in an obligate monogamous mammal

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Mating systems in animal societies contain both social and genetic components. Deviations between these components may have important ramifications for our understanding of the evolution of animal reproductive strategies and their ecological correlates. However, although there is ample evidence for discrepancies between genetically assigned paternities and social associations in birds, relatively few studies have documented such differences in mammals. Moreover, few studies have addressed how deviations between social mating associations and actual mating activities influence patterns of resource utilisation in males and females. The aardwolf is a socially monogamous hyaenid that exhibits polygamous mating behaviour. Suitable den sites for resting and rearing offspring is an important resource for terrestrial mammals, and dens are vital to aardwolves as thermal refugia for protection of offspring. We show that temporal patterns in aardwolf den use relates to predictions from polygamous mating rather than social monogamy. Male aardwolves used more dens, changed dens more frequently and stayed in dens for shorter periods of time than females during both wet and dry seasons. We suggest that lower male den fidelity is either caused by males trying to maximize female encounters and to monitor female activity, or that it had evolved as a non-adaptive behaviour related to elevated androgen levels. Our data did not point to territorial defence or space use optimization as cause for the observed sex differences, since we did not find any sex or seasonal differences in the spatial patterns of utilized dens. We suggest that aardwolves may have been ecologically constrained to exhibit social monogamy but that polymagous mating is maintained through extra pair copulations. We recommend that the evolutionary stability of these two conflicting strategies of male fitness maximization must be further investigated.

**Keywords:** aardwolf, dens, *Proteles cristatus*, sexual selection, space use, resource utilization

Mating systems are broad categorizations of individual strategies for maximizing reproductive success (Emlen & Oring 1977; Clutton-Brock 1989). In mammals, because of the inherent sex bias in parental investment caused by gestation and lactation, female fitness is generally regulated by the availability of resources whereas male fitness is regulated by the number of successful mating opportunities (Trivers 1972). These differences in fitness regulation between males and females have led to a major dominance of polygynous mating systems, with only approximately 5% of mammals exhibiting social monogamy (Clutton-Brock 1989). However, mating systems contain two separate components, one describing social associations related to mating and one describing the genetic outcome of actual mating activities (Kappeler & Van Schaik 2002). Such discrepancies between the social and genetic aspects of mating systems have been exemplified by a large body of research on extra pair copulations in socially monogamous birds (Griffith et al. 2002), where strict sexual fidelity to social partners may be the exception rather than a rule (Birkhead & Møller 1992). Less is known of discrepancies between social and genetic components of mating systems in mammals (Reichard 2003). However, although the frequency of extra-pair paternity is considered low (Lukas & Clutton-Brock 2012), it has been found in phylogenetically diverse mammalian groups such as carnivores, primates, and rodents (Clutton-Brock & Isvaran 2006; Cohas & Allaine 2009).

Discrepancies between social and genetic aspects of mating systems pose strong effects on the distribution of individual fitness (Westneat & Stewart 2003), the strength of sexual selection (Møller & Ninni 1998; Sheldon & Ellegren 1999) and the evolution of life-history traits (Møller & Cuervo 2000; Arnold & Owens 2002; Avise et al. 2002). For instance, monogamy has recently been linked to the evolution of cooperative breeding in mammals, but such a link depends on how much the genetic mating patterns deviate from social monogamy (Lukas & Clutton-Brock 2012). Subsequently, some studies have challenged the traditional view of mammalian mating systems (e.g. Kappeler 1997; de Bruyn et al. 2011;), and there is an emerging view that studies that quantify variations within classical mating system definitions can have important ramifications for our understanding of the evolution of animal reproductive strategies and their ecological correlates (Avise et al. 2002; Uller & Olsson 2008).

Numerous factors have been suggested to cause variation in mammalian mating systems, but the abundance and distribution of critical resources have repeatedly been put forward as both ultimate and proximate drivers (Emlen & Oring 1977; Greenwood 1980). Although comparative analyses indicate that monogamy in mammals most commonly have evolved because the spatial distribution of females limits the ability of males to monopolize multiple mates (Komers & Brotherton 1997), ecological constraints such as the necessity for paternal care may also influence social mating associations (Wright 2006; see also Kleiman 1977). In the latter case, it is predicted that extra-pair copulations will be negatively related to resource abundance during the period of parental care, because paternity assurance is predicted to be positively related to paternal care (Wright 1998). This prediction has been supported by empirical observations in the arctic fox (*Alopex lagopus*) (Cameron et al. 2011). However, to what extent deviations between social mating associations and actual mating activities influence patterns of resource utilisation in males and females has so far rarely been studied.

The aardwolf (*Proteles cristata*) is a small hyaenid that inhabits semi-arid grasslands in eastern and southern Africa (Koehler & Richardson 1990). The diet of the aardwolf almost exclusively consists of termites of the genus *Trinervitermes* (Kruuk & Sands 1972; Richardson 1987b; Matsebula et al. 2009; De Vries et al. 2011), causing it to have one of the most specialized diets among mammals. Although mostly a solitary forager, aardwolves have been reported as socially monogamous (Koehler & Richardson 1990). The high reliance on

very small and energetically unprofitable prey has been hypothesized to have caused aardwolves to exhibit social monogamy, since it necessitates a high level of paternal care caused by an increased need for the females to forage during lactation (Richardson & Coetzee 1988). Aardwolves should therefore exhibit limited sexual dimorphism both behaviourally and morphologically, but only the latter has been demonstrated (van Jaarsveld et al. 1995). Despite being described as obligately monogamous (*sensu* Kleiman 1977), extra pair copulations have been recorded (Richardson 1987a), and males have been observed to traverse rivals' territories, presumably to gain access to neighbouring females while at the same time defend their territories from intruders by frequent scent markings (Richardson & Coetzee 1988; Sliwa & Richardson 1997). The aardwolf is therefore an interesting species for studying how discrepancies between social mating associations and mating activities relate to resource utilization strategies.

Suitable den sites can constitute an important resource for terrestrial mammals, and the spatial and temporal variation in den utilization has frequently been linked to social organization, territoriality and the evolution of cooperative behaviour (Lovari et al. 1996; Dell'arte & Leonardi 2007; White & Cameron 2009). For instance, mountain brushtail possums (*Richosurus cunninghami*) increased their level of territoriality when their number of dens declined due to habitat destruction (Banks et al. 2011), and the availability and distribution of suitable den sites have been suggested to limit group size in Eurasian badgers (*Meles meles*) (Doncaster & Woodroffe 1993). Aardwolves are primarily nocturnal and dens are important as thermal refugia during periods of inactivity, particularly during the cold dry season when thermal and nutritional stresses are high (Williams et al. 1997). Dens are also vital for the rearing of cubs and as protection from black-backed jackals (*Canis mesomelas*) and other predators (Anderson & Richardson 2005). The aim of this study was to test if the spatial and temporal characteristics of aardwolf den use relates to predictions from social monogamy or from sexual polygamy. Given the symmetry between males and females that characterize monogamy (Clutton-Brock 1989), we predicted that males and females would have similar spatial and temporal characteristics in terms of number of dens used, frequency of den changes as well as spatial distribution of utilized dens within the home range. Any deviations from similar den utilization between males and females would imply that it is under sex-differential selection, which would suggest that the utilization of an important resource, dens, in this species is related more closely to polygamous mating patterns rather than their described social monogamy.

## **MATERIALS AND METHODS**

### *Study Site*

We conducted the study on Benfontein Game Reserve, approximately 10 km south east of Kimberley (28°50'S; 24°50'E). The reserve covers an area of approximately 11 400 ha and lies half within the Northern Cape Province and half within the Free State. The reserve has been used in previous studies of aardwolves (Richardson 1985; Anderson 1994; Sliwa 1996). The climate of this area is semi-arid, with the dry season comprising March to August and the wet season September to February (South African Weather Bureau).

### *Animal captures and instrumentation*

Five male and five female aardwolves were fitted with VHF radio collars (Sirtrack Ltd, Havelock North, New Zealand: weight 68.25g ± 8g, mean ± 1sd). The mass of all collars corresponded to less than 1% of animal body mass, ensuring that they had minimal impact on energetics and locomotor ability in the animals. All animals were adult at the time of the study. Animals habituated quickly to be followed by a vehicle and spotlight without showing signs of distress. Animals were followed from 8 min to 4 h before darted from distances of

11-16 meters using a CO<sub>2</sub> powered remote injection rifle (Dan-Inject JM standard, Skellerup, Denmark, or Telinject G.U.T, Römerberg, Germany). Each animal was anaesthetized with a fixed dose of 36mg ketamine hydrochloride and 0.6mg medetomidine hydrochloride. The medetomidine was subsequently reversed with 3mg atipamezole hydrochloride. Animals were kept under anaesthesia for 33 to 75 min (average 48 min). All animals were fully mobile 10 min after administration of atipamezole, but were followed for up to 2 h to ensure full recovery. We opted to use remote injection as a capture technique since it previously has been shown to be successful for the species (Anderson & Richardson 1992), and since we regarded it to be more humane than trapping animals in either cage traps or foothold traps. Two of the study animals died of natural causes during the study and we lost contact with an additional four, either because of transmitter failure, mortality or because the animals left the study area. For the remaining four animals, the collars were removed at the end of the study. Animal captures were carried out by experienced personnel following approval from the South African Veterinary Council (AR11/11368), the Medicines Control Council (POS 139/2011/2012), the Northern Cape Province Department of Environment and Nature Conservation (FAUNA 255/2008, FAUNA 256/2009, FAUNA 846/2009, FAUNA 011/2010) and from the Animal Use and Care Committee of the University of Pretoria (EC031-07).

#### *Data Collection*

Daily den utilization data were recorded by tracking each individual to a particular den, and recording the coordinates of the den site with a handheld GPS together with the time of observation. We collected data on active space use by taking GPS locations either when a study animal was located outside a den opportunistically, or on the commencement of following the animals for behavioural observations. We collected data on aardwolf den and space use from July 2008 to July 2011.

#### *Data analysis*

We counted the number of dens used within each month for each individual. Each den was only counted once for each month, irrespective of how many times it was used. We determined the frequency of den change by counting the number of times that aardwolves moved between different dens, and also counted the number of days each aardwolf stayed in a particular den. However, it was not possible to maintain a continuous data collection throughout the study period. We therefore calculated two estimates of duration of den occupancy. As a most conservative estimate (MC), days where den locations were missing were assumed to be days that an aardwolf was not in the previously recorded den. Therefore, if two consecutive entries indicated that an aardwolf was in the same den, and a day was missing in between, the entries were taken as two separated den durations of one day each. As a least conservative estimate (LC), however, if an aardwolf was found in the same den for two consecutive observations separated by a maximum of three days, we conversely assumed that the aardwolf had remained in that den for the whole period of time. We also recorded the number of observations for each animal each month to enable us to control for unequal sampling efforts. All data were summarized on a monthly basis and each month classified as either wet (September to February) or dry (March to August) season based on rainfall patterns (De Vries et al. 2011). We only used den locations recorded in the mornings or early afternoons (before 16h00). We excluded den locations in the late afternoons or evenings since these might be dens used by the aardwolves to hide from the vehicle, since not all the animals were completely habituated to being followed during daylight, and aardwolves sometimes become active before sunset, particularly in during the dry season.

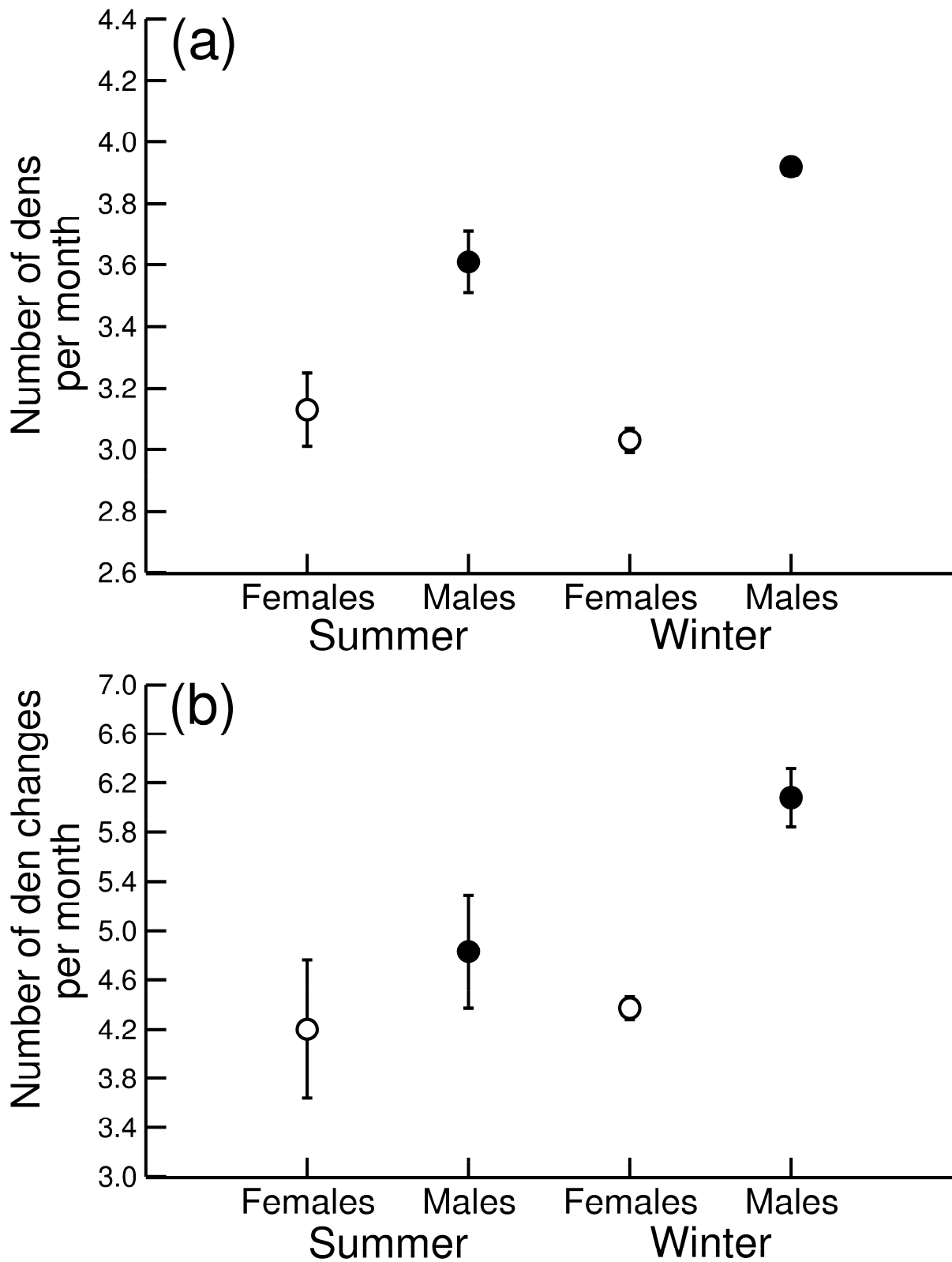
To delineate home ranges, we calculated 95% minimum convex polygons (MCP) from active location data. Bootstrap simulations suggested that there was only sufficient amount of relocations for accurate home range estimation for three males and three females, and only these six animals were included in home range related analyses. For each den used by these six animals, we calculated the distance to the nearest home range borders as determined from the 95% MCP's. To evaluate if the spatial distribution of dens differed from a random spatial distribution, we conducted a k-nearest neighbour analysis for dens used by each individual within each season (Clark & Evans 1954).

We used generalized linear mixed models (GLMM) with a Poisson error distribution and a log link to evaluate effects of season and sex on the number of dens used, the frequency of den change and on the duration of den use for both most and least conservative estimates. We weighted monthly values by the number of observation events for each individual that particular month. To account for non-independence within individuals as well as temporal pseudo-replication we added sample month nested within each individual as a random effect structure. Due to an unbalanced number of observation months on different individuals, the reported means and standard errors were weighted by the number of observation months for each individual and season. Weighted standard errors were estimated according to Cochran (1977) following Gatz & Smith (1995). We used linear mixed models (LMM) to evaluate effects of sex and season on distance to nearest home range border and the spatial clustering of dens. In these models, we used the distance to home range border and seasonal clustering indices for each individual as response variables. Similarly to previously described models, we added sex, season, and the interaction between sex and season as fixed effects. For the model evaluating distance to home range border, we added animal identity and den nested within month as random effects, whereas we only included individual as a random effect for the model on spatial clustering. For all models we tested the significance of fixed effects using sequential likelihood ratio tests (Crawley 2007). All spatial analyses were carried out in ArcView 3.3 using the Animal Movement Extension 2.0 and ArcMap 9.3.1 (ESRI, Redlands, CA, USA) and all statistical analyses were carried out using R version 2.12.0 (<http://www.r-project.org>).

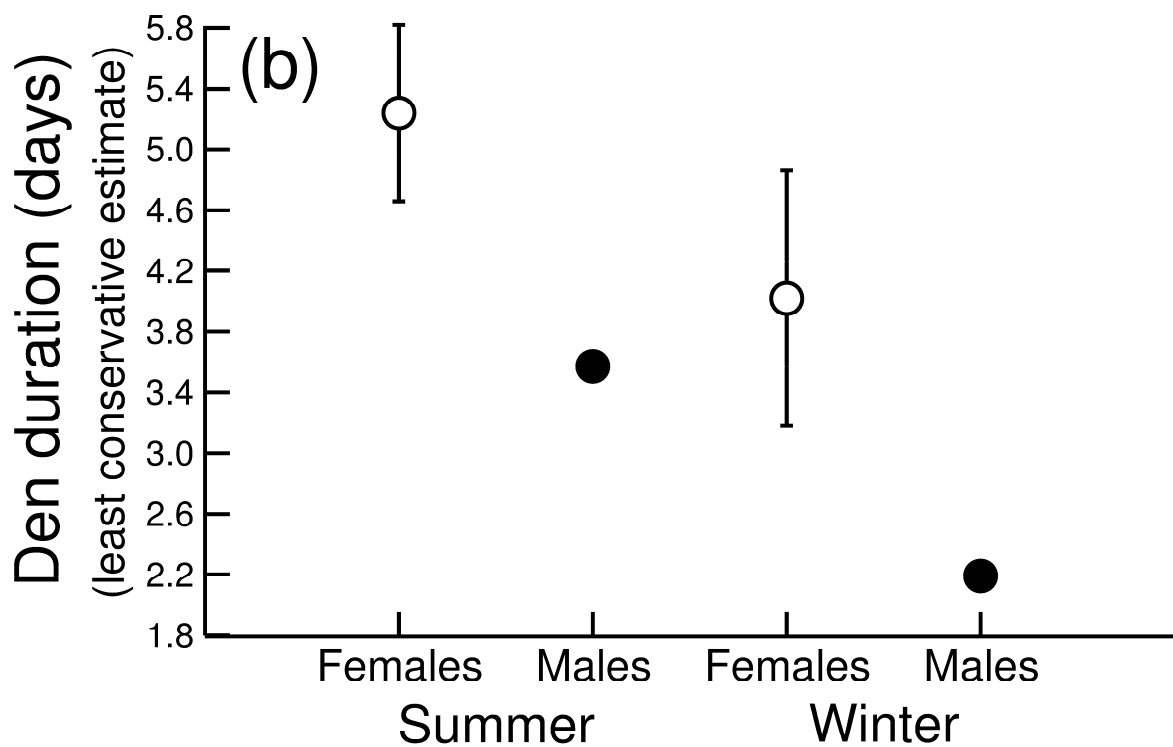
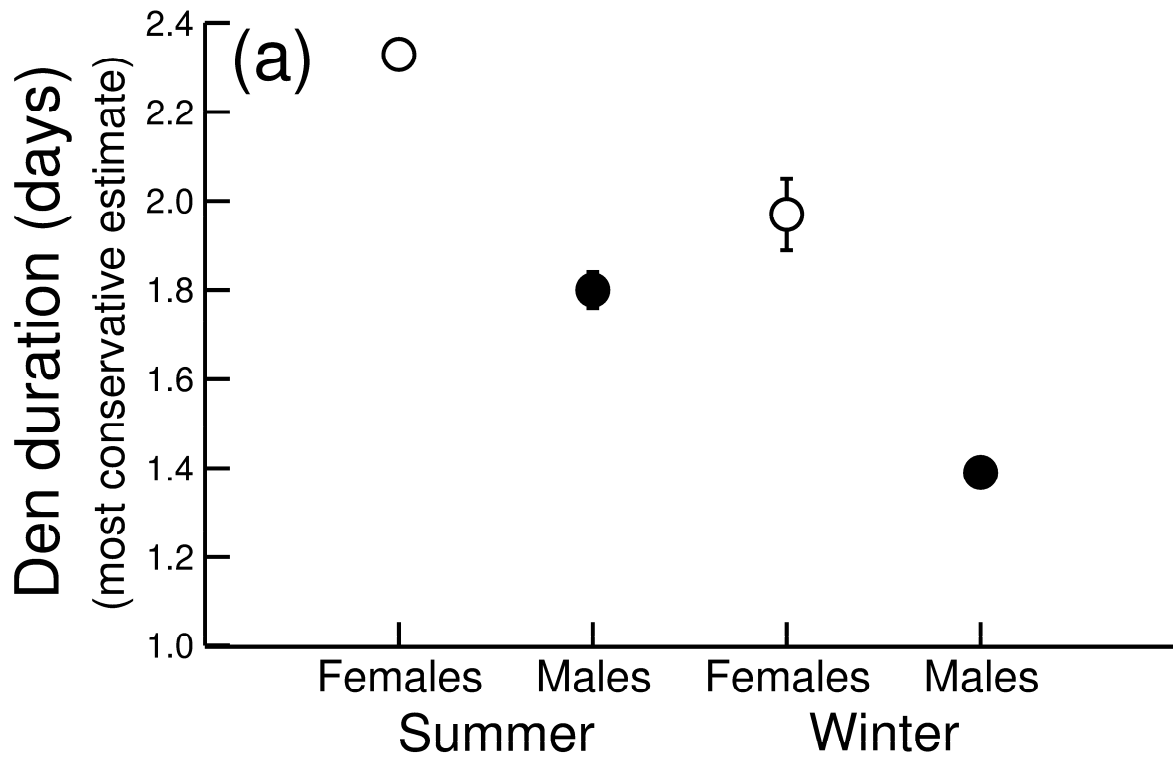
## RESULTS

Males used significantly more dens per month (GLMM:  $\chi^2_1 = 5.16$ ,  $P = 0.02$ ; Fig. 1a) and changed dens more frequency than females (GLMM:  $\chi^2_1 = 9.33$ ,  $P < 0.01$ ; Fig. 1b). Males also stayed in dens for shorter periods than females during both seasons (MC, GLMM:  $\chi^2_1 = 11.24$ ,  $P < 0.01$ ; LC, GLMM:  $\chi^2_1 = 5.76$ ,  $P = 0.02$ ; Fig. 2a,b). There was no significant interaction effect between sex and season on number of used dens (GLMM:  $\chi^2_1 = 0.64$ ,  $P = 0.42$ ), but there was a trend for a significant effect of season (GLMM:  $\chi^2_1 = 3.57$ ,  $P = 0.06$ ). There was similarly no significant interaction effect between sex and season on the frequency of den change (GLMM:  $\chi^2_1 = 1.69$ ,  $P = 0.19$ ), but a significant effect of season with more frequent den changes occurring during the dry (which contains the mating season) than during the wet season (GLMM:  $\chi^2_1 = 9.00$ ,  $P < 0.01$ ; Fig. 1b). The duration of den use also differed significantly between seasons (MC, GLMM:  $\chi^2_1 = 15.33$ ,  $P < 0.01$ ; LC, GLMM:  $\chi^2_1 = 52.69$ ,  $P < 0.01$ ), with both sexes staying in dens for shorter periods during the dry than during the wet season (Fig. 2a,b). However, there was no interaction effect between sex and season for duration on den use (MC, GLMM:  $\chi^2_1 = 0.08$ ,  $P = 0.78$ ; LC, GLMM:  $\chi^2_1 = 1.12$ ,  $P = 0.29$ ).

There was no significant interaction effect between sex and season on distance to the nearest home range border (LMM:  $\chi^2_1 = 0.82$ ,  $P = 0.37$ ), nor did these distances differ between dens used by males and females (LMM:  $\chi^2_1 = 1.15$ ,  $P = 0.28$ ) nor between seasons (LMM:  $\chi^2_1 = 1.84$ ,  $P = 0.17$ ; Table 1). Similarly, there was no difference between males and



**Figure 1.** Number of dens used per month (a) and number of observed den changes per month (b) in 5 female and 5 male aardwolves during the wet and the dry season (mean  $\pm$  SE weighted for number of observation months per individual).



**Figure 2.** Most conservative (a) and least conservative (b) estimates of the duration of den use for 5 female and 5 male aardwolves during the wet and the dry season (mean  $\pm$  SE weighted for number of observation months per individual). The most conservative estimates were calculated as absolute observed duration. For the least conservative estimates, if an aardwolf was found in the same den for two consecutive observations separated by a maximum of three days, we assumed that it had remained in that den for the whole period of time.

**Table 1.** Distance to home range border (delineated by 95% minimum convex polygons of active locations) for three female and three male aardwolves (mean  $\pm$  SE), seasonal spatial clustering index as well as test results from a nearest neighbour cluster analysis evaluating whether or not the location of the used dens deviated from a random spatial clustering pattern.

ID	Distance to home range border (m)	Observed nearest neighbour distance (m)	Expected nearest neighbour distance (m)	<i>R</i>	<i>Z</i>	<i>P</i>
Wet season						
F6	522.46 $\pm$ 55.06	159.81	171.83	0.93	-0.63	0.27
F7	212.32 $\pm$ 22.89	105.63	87.14	1.21	1.77	0.04
F9	421.93 $\pm$ 61.10	260.37	266.45	0.98	-0.16	0.44
M2	338.18 $\pm$ 51.15	177.15	237.77	0.75	-2.63	<0.01
M8	577.43 $\pm$ 51.62	178.99	208.42	0.86	-1.43	0.08
M14	410.94 $\pm$ 92.32	318.53	302.49	1.05	0.37	0.36
Dry season						
F6	423.92 $\pm$ 64.95	107.11	134.98	0.79	-1.81	0.04
F7	92.39 $\pm$ 22.23	260.44	204.97	1.27	1.46	0.07
F9	332.75 $\pm$ 58.89	153.60	284.04	0.54	-3.83	<0.01
M2	310.62 $\pm$ 38.19	103.88	158.39	0.66	-3.36	<0.01
M8	571.89 $\pm$ 53.49	246.96	204.11	1.21	1.88	0.03
M14	465.50 $\pm$ 92.83	579.62	411.21	1.41	2.82	<0.01

*R*: Spatial clustering index calculated following Clark & Evans (1954). An index value of one indicate that the spatial clustering follow prediction from a random spatial distribution, a value less than one suggest that locations are more clustered and a value higher than one suggest that locations are more dispersed than what could be predicted from a random spatial distribution.

*Z* and *P*: Two-tailed *Z* score and associated probability value (*P*) for testing whether or not the spatial clustering index significantly differed from expectations from a random spatial distribution.



females in the spatial clustering of dens (LMM:  $\chi^2_1 = 0.04$ ,  $P = 0.83$ ), nor a difference in spatial clustering of dens between the seasons (LMM:  $\chi^2_1 = 0.02$ ,  $P = 0.88$ ). However, there was a trend for an interaction effect between sex and season on clustering of dens (LMM:  $\chi^2_1 = 1.72$ ,  $P = 0.06$ ), where the dens of males were less clustered than females during the wet but more during the dry season (Table 1).

We did not observe males and females sharing dens during the day, but the same dens were used by males and females on separate occasions. However, one of the males was observed to share dens during the day with two other males, albeit one at a time, on five occasions.

## DISCUSSION

To our knowledge, this is the first study to show that resource utilization in mammals may relate more closely to mating strategies than to social mating associations. The temporal patterns of aardwolf den use did not agree with predictions from social monogamy. Instead, males used more dens, changed dens more frequently, and stayed in dens for shorter periods than females during both wet and dry seasons. These patterns are more resonant with polygamous mating, where we would predict a higher degree of male mobility, especially during the mating season in order to optimize mating opportunities (Sandell 1989). The observed seasonal variation in the duration of den use and in the frequency of den change, with dens being used for shorter periods during the wet than during the dry season, which is when mating occurs, may further corroborate such an interpretation.

In her seminal review, Kleiman (1977) identified two primary classes of monogamy in mammals. In facultative monogamous species, monogamy is thought to have evolved as a response to female over-dispersion, in which only one female is energetically defendable for a single male (see also Komers & Brotherton 1997). Obligate monogamy, on the other hand, is thought to have evolved in response to the necessity for paternal care. Although the generality of this latter hypothesis has been challenged (Komers & Brotherton 1997), it is a likely explanation for social monogamy in the aardwolf because its reliance on energetically sub-optimal prey requires females to forage more intensively during lactation, with a subsequent need for paternal care (Richardson 1987a; Richardson & Coetzee 1988). Therefore, one can predict that the willingness of females to engage in extra pair copulations would be low, since paternal care likely is related to paternity assurance (Griffith et al. 2002). This prediction was supported for the similarly insectivorous carnivore the bat eared fox (*Otocyon megalotis*) (Wright et al. 2010). However, our study supported a previously observed discrepancy between social monogamy and polygamous mating patterns in aardwolves (Richardson 1987a; Richardson & Coetzee 1988). We therefore suggest that aardwolves form a special case of obligate monogamy, in which males seem to maximize fitness by providing necessary care for resident offspring while at the same time attempt to maximize mating opportunities outside their pair bond. We recommend that the obvious conflict between these two male strategies of fitness maximization requires further investigation.

Androgens have well known effects on male behaviour (Ketterson & Nolan 1992), including dominance related aggression (Mazur & Booth 1998), activity (Denardo & Sinervo 1994), territoriality (Moore 1984) and home range size (Chandler et al. 1994). We therefore suggest that elevated androgen levels in males compared to females could be a proximate explanation to the observed sex differences in den utilization. On an ultimate scale, however, the lack of either seasonal or sex differences in the spatial distribution of utilized dens contradicts that the observed sex differences in temporal den utilization was related to territorial defence, since males then would have been predicted to utilize dens closer to their home range borders (Gorman & Mills 1984). We similarly note that it is unlikely that the

need for increased space use or mobility caused the observed differences in temporal den use, neither between sexes nor between seasons. Although Eurasian badgers have been shown to utilise more dens to minimise travelling costs between areas traversed in the night and resting sites (Davison et al. 2008), male aardwolves often traverse their whole home range multiple times during an activity period (Sliwa & Richardson 1998). However, although aardwolves mate above ground (Koehler & Richardson 1990), males may utilize dens as a way to increase the likelihood of encountering females, or to monitor activity and possibly also reproductive status of females within their home range. An additional, not mutually exclusive, explanation could be that the lower den fidelity in males is not an adaptive sex difference in behaviour, but rather a behaviour that is proximately regulated by androgen levels without having been under direct sex specific selection *per se* (e.g., Emlen et al. 1991).

In the Northern Cape province of South Africa, offspring are born from October through December, and only emerge from the dens about one month after birth (Richardson 1985). These observations are supported from our study, where two of the females only moved from their breeding dens about six weeks after giving birth. Although we found that females on average spent a longer time in each den during the wet season, we did not find that they use fewer dens. We suggest that these seemingly contradictory results are caused by anti-predatory behaviour. Once cubs are moved from the natal den, females may move them quite frequently in order to prevent attracting unwanted predators such as black-backed jackal (*Canis mesomelas*; Koehler & Richardson 1990). Similar behaviour has been observed in spotted-tail quolls (*Dasyurus maculatus*), which also rear offspring in dens (Belcher & Darrant 2004).

### **Conclusions**

We showed that the utilization of an important resource, dens for thermoregulation and protection, may relate more closely to polygamous mating strategies than to social mating associations in an obligate monogamous mammal. The observed differences in temporal den use did not appear to be caused by territorial defence by males. Instead, we suggest that lower den fidelity in males could have been caused by male behaviour related to maximizing female encounters, monitoring female activity or that it is a non-adaptive behaviour related to elevated androgen levels. We suggest that although aardwolves have been ecologically constrained to exhibit social monogamy, polygamous mating has been maintained through extra pair copulations resulting in cryptic alternative mating strategies. We recommend that the evolution and in particular, the evolutionary stability of these two conflicting strategies of male fitness maximization requires further investigation.

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