



Original Investigation

Behavioural and endocrine correlates to the aardwolf mating system

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ABSTRACT

It is now widely recognized that mating systems contain both social and genetic components, where social components describe patterns of social associations while genetic components reflect patterns of mating activities. In many species these two components do not coincide. If the level of sexual asymmetry differs between these two components, for instance in monogamous pairs with high levels of infidelity, each component may impose different selection pressures on behavioural and physiological characteristics. However, we have limited knowledge of how social and genetic components influence behaviour and physiology. The aardwolf (*Proteles cristata*) is a small insectivorous hyaenid, which has been described as socially monogamous but sexually promiscuous. In this study, we evaluated if aardwolf space use, scent marking, foraging behaviour and endocrine fluctuations relate to predictions from social monogamy or polygamous mating. Our results did not show sex differences in behaviour or physiology that would be consistent with predictions from polygamous mating, and we suggest that social mate associations may regulate the observed endocrine and behavioural parameters more than actual mating patterns in this species. Such an interpretation would suggest that the fitness effect of promiscuous mating may be low, since it appears to impose little selection pressure on mating related behaviour. We stress that it is then unclear how promiscuous mating is maintained in this socially monogamous species.

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Introduction

Mating systems are often categorized as four main classes; monogamy, polygyny, polyandry, and promiscuity (Clutton-Brock, 1989; Davies, 1991). The degree of sex differences in mating competition and mate fidelity typically lead to a gradient in sex differences in behaviours, where a greater inter-sexual asymmetry in behaviour is expected as sex differences in mating competition increase (e.g., Clutton-Brock et al., 1982). At one extreme of this gradient, socially monogamous pairs are characterized by inter-sexual symmetry in behaviour, whereas the other extreme is formed by mating systems with substantial mating competition in one sex, such as highly polygynous harem systems in mammals (e.g., Le Boef and Reiter, 1988).

Behavioural traits related to mating activities are proximately regulated by the individual's hormonal environment. For example, experimental administration of exogenous androgens during both the mating and non-mating seasons in monogamous male birds caused males to shift from monogamous to polygynous mating (Hegner and Wingfield, 1987; Silverin, 1980; Wingfield, 1984). However, different mating strategies may also result in contrasting hormone fluctuations, where particularly social rank may be associated with different levels of stress-related steroid hormones (Creel et al., 1996). As with behaviour, sex differences in hormonal fluctuations are expected to be related to mating competition. In particular, we would expect that lower individual variation within sexes is associated with low levels of competition, and subsequently that the difference in mating competition between males and females are related to within sex variation between individuals.

Mating activity is not necessarily constrained to long-term social relationships (Griffith et al., 2002). It is now widely recognized that mating systems have two components; a social component which describes how individuals socially relate to mating partners, and a genetic component which describes the genetic effects of actual mating events (Kappeler and van Schaik, 2002).

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Discrepancies between these two components in terms of the associations of males and females appear to be a rule rather than sporadic deviations (Birkhead and Møller, 1992). However, it is not yet clear to what extent the social vs. the genetic components of mating systems influence behaviour and their hormonal characteristics.

The aardwolf (*Proteles cristata*) is an extreme resource specialist belonging to the family Hyenidae (De Vries et al., 2011; Koehler and Richardson, 1990; Matsebula et al., 2009). Aardwolves have been described as obligately monogamous socially (Koehler and Richardson, 1990; Richardson, 1985), as a result of the necessity for a high level of paternal care caused by the increased need for females to forage away from offspring during lactation (Richardson and Coetzee, 1988). However, aardwolves have been observed to engage in a high frequency of extra-pair copulations (Richardson, 1987; Sliwa, 1996), and Kotze et al. (2012) suggested that the temporal utilization of dens corresponded more closely with predictions from polygamous mating than from social monogamy. Therefore, the aardwolf is an appealing candidate for evaluating how social vs. genetic mating systems associate with sex differences in behaviour and endocrine fluctuations in a mammal.

The aim of this study was to test if sex-specific seasonal variation in behaviours and endocrine parameters relate to predictions from social monogamy in a population of wild aardwolves. In general, if social monogamy dictates behaviour and associated endocrine fluctuations, we would expect (i) symmetry between males and females in terms of their space use and behaviour due to similarities expected for a pair living, behaviourally monogamous species, (ii) symmetry between males and females in inter-individual variation in reproductive and stress-related adrenocortical hormone concentrations, and (iii) that neither males nor females will exhibit increased adrenocortical hormone concentrations during the mating season.

Material and methods

Study area

We conducted the study on Benfontein Nature Reserve, approximately 10 km southeast of Kimberley, Northern Cape Province, South Africa (28.80°S, 24.77°E; Fig. A.1). Benfontein covers 11,400 ha of semiarid terrain and lies within a transitional zone between dry Karoo, grassland and Kalahari thornveld (Schulze and McGee, 1978). The study area has a semiarid climate, with a dry season comprising March to August and a wet season September to February (Kotze et al. 2012). The reserve has hosted the majority of previous studies on aardwolf (De Vries et al., 2011; Ganswindt et al., 2012; Kotze et al., 2012; Richardson, 1985; Sliwa, 1996; Sliwa and Richardson, 1998).

Study animals

We immobilized seven wild aardwolves (four males and three females; Table 1) and fitted them with very high frequency radio collars (VHF; Sirtrack Ltd, Havelock North, New Zealand: weight 68.25 g ± 8 g, mean ± 1sd). For this, we located aardwolves by driving around the reserve at night and scanning with a hand-held spotlight. Once an individual was located we followed it by a 4 × 4 vehicle from a distance of >100 m until the animal became habituated to our presence. We remote injected aardwolves with a standard dose of 36.0 mg ketamine hydrochloride and 0.6 mg medetomidine hydrochloride using a CO₂-powered remote injection system (Kotze et al. 2012). The darted animals took 5–10 min to become anaesthetized, and aardwolves were kept anaesthetized for 45–60 minutes. The medetomidine was subsequently reversed

with 3.0 mg of atipamezole hydrochloride. All individuals were fully mobile within 10 minutes after reversal, but we remained with the animals for approximately 30 minutes to ensure recovery. Animal handling procedures were approved by the Animal Use and Care Committee at University of Pretoria (EC031-07).

Spatial and behavioural data collection

Between March 2010 and July 2011 we relocated and observed radio-tagged aardwolves to record home range size and utilization as well as spatially explicit scent marking and foraging behaviour using a handheld PDA loaded with the software CyberTracker™ (<http://www.cybertracker.org>). We located each animal at its day time den, and once it had emerged we followed it for 84 ± 50 min (mean ± sd) to continuously record movements using a GPS unit. We recorded scent marking and foraging behaviours using a handheld PDA loaded with the software CyberTracker™ (<http://www.cybertracker.org>). In addition to record the coordinates of animal movements, we also stored a GPS coordinate for each logged behaviour. We defined scent marking as the action of an aardwolf straddling a grass stalk, rapidly squatting and wiping a smear of secretion onto the grass from the anal pouch (Richardson, 1985; Sliwa, 1996; Sliwa and Richardson, 1998). We defined foraging behaviour as the action of an aardwolf lowering its head to ground level and proceeding to lick travelling termites off the soil or mound surface into its mouth (Koehler and Richardson, 1990). In total, we recorded 269 spatial movement tracks and 157 behavioural sessions for the seven collared aardwolves (Table 1).

Quantification of sex specific space use and behaviour

We used 95% Minimum Convex Polygons (MCPs: Mohr 1947) to estimate seasonal home range sizes for each animal. We based the MCP's on all pooled relocation data, including both data recorded during spatial data collection and opportunistic sightings recorded while following other study animals or moving around the study area for logistic reasons. We used MCP's to characterize home range size because they are relatively robust to possible temporal autocorrelation among data (Swihart and Slade, 1985). We calculated home range sizes using Hawth's Tools (<http://www.spatial ecology.com/htools>).

We quantified home range utilization as densities of continuous movement tracks. We created line density isopleths which represent the density of linear features in the neighbourhood of a pre-determined raster cell, measured as the length of lines per unit of area. We used a 20 m X 20 m raster cell size as we typically were not more than 20 m from the animal being observed, and defined the search area as a circle around each raster cell. The radius of the search circle was calculated from the mean distance between 10,000 random points to the closest line segment within each aardwolf's annual home range, and ranged from 129.74 m to 496.28 m (mean ± sd = 236.28 ± 129.46).

We used a normalized Shannon spatial diversity index (H' , Payne et al., 2005) to estimate the evenness of home range use in aardwolves. The index was calculated on the cell values of line densities:

$$H' = \frac{\sum_{i=1}^K P_i \times \log(P_i)}{\log(R)}$$

where R is the number of pixels within each home range and P_i is the relative abundance of the linear features within a raster cell (i.e. the length of linear features within the cell divided by the total length of linear features in all cells). An index value of 0 indicates complete unevenness in space use while a value of 1 indicates

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