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Female territoriality and the function of scent-marking in a monogamous antelope (*Oreotragus oreotragus*)

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Abstract In monogamous species, females often choose between males according to the quality of the territories they defend, but the extent to which females themselves contribute to territory defence is frequently underestimated. Here we test for differences in male and female roles during paired scent-marking bouts, a key component of territorial defence, in a monogamous antelope. In two populations (Kenya, Zimbabwe) of klipspringer, *Oreotragus oreotragus*, both males and females usually scent-marked at the same site, but there were significant differences between sexes in terms of investment within bouts. Females initiated most bouts, thus dictating the marking strategy of the pair. Males initiated relatively few bouts, but deposited more scent marks per bout than females and were usually the last to scent-mark before leaving the site; they marked on the same branches as the female and thus overmarked her scent. Both sexes deposited more marks during paired than solo visits. Immediately preceding and following scent-marking bouts, males approached females and females left males more often than expected. Female scent-marking rates were higher when they were receptive than at other times, and this increase was matched by elevated marking rates of males. Females may increase marking rates when they are receptive in order to test the quality of their mate or to incite male competition. However, these ideas are unlikely to explain female scent-marking behaviour outside the mating season, which appears to be related primarily to territorial defence. We suggest that these differences in investment in scent-marking bouts are consistent with

predictions that females may be autonomously territorial and that overmarking of female scent by males is a form of mate-guarding.

Key words Olfaction · Klipspringer · Territoriality · Status signal · Monogamy

Introduction

In comparison to intrasexual competition between males, female competition over resources and mates has until recently received relatively little attention (Ahnesjö et al. 1993; Berglund et al. 1993). Nonetheless, the spatial and temporal distribution of females, one outcome of such competition, is acknowledged as being instrumental in determining reproductive strategies of males (Dunbar 1988; Clutton-Brock 1989; Davies 1991). The reason for this is that limits to male fitness depend on the number of females inseminated, while females are restricted by time and costs of rearing progeny to maturity, which in turn are related to the dispersion and availability of food resources. Where resources are limited or dispersed, or where competition between females is intense, female distribution may contribute to the evolution of monogamy (Wittenberger and Tilson 1980). For example, a recent study across mammals (Komers and Brotherton 1997) has shown that monogamy most commonly evolves where females are solitary and occupy small and exclusive ranges.

In several small African antelopes, like the klipspringer (*Oreotragus oreotragus*) and dikdik (*Madoqua kirkii*), monogamous pairs occupy exclusive, resource-based territories throughout the year (Dunbar and Dunbar 1974, 1980; Hendrichs 1975). It has been traditionally argued that, as in birds (Emlen and Oring 1977), males defend these territories from other males in order to provide their mates with access to a long-term and predictable food source (Owen-Smith 1977; Spinage 1986). However, the role of females in territory maintenance has been less clearly defined, ranging between passive occupation of

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male territories and autonomous territoriality. For example, Spinage (1986, p. 135) saw males as the territorial sex and female hornlessness as an indicator that females "cannot contribute to real territorial defence except in female to female situations", while Norton (1980, p. 99) suggested that role differentiation occurs within pairs whereby "the male defends the territory while the female conserves energy for reproduction and the rearing of offspring". In contrast, others suggest that pairs occupy joint territories which are defended co-operatively (e.g. Hendrichs 1975; Dunbar and Dunbar 1980) or that females defend their own sex-specific territories, which may be overlapped by that of the male (Jarman 1974).

These points raise the following questions concerning the social evolution of small antelopes. First, to what extent are females, rather than males, ultimately territorial in terms of area or resource defence? Second, if females are territorial in order to defend access to an exclusive food supply, why do males also play a part in defence? Evidence that females may be independently territorial arises from the fact that aggression during encounters is predominantly intrasexual in both the klipspringer (Dunbar and Dunbar 1980; Roberts 1994) and dikdik (Brotherton and Rhodes 1996), and that horns in females of one population of klipspringer appear to be expressed in response to relatively high rates of female competition (Roberts 1996). In relation to male defence, sex-specific territorial aggression suggests that males do not engage in encounters primarily to defend resources for their mates (Brotherton and Rhodes 1996). Instead, males appear to mate-guard females, by maintaining constantly close spatial proximity to mates, being aggressive towards rival males and by overmarking female scent marks (Dunbar and Dunbar 1980; Roberts 1994; Brotherton and Rhodes 1996; Brotherton et al. 1997).

This paper addresses these questions by investigating the contribution made by each sex to territorial scent-marking in monogamous klipspringer pairs. We studied scent-marking because it is a key component of territorial defence and occurs much more frequently than overtly aggressive encounters between groups (Norton 1980; Roberts 1994, 1998; Roberts and Lowen 1997). In addition, while not yet quantified in detail, overmarking of female scent by males has been proposed to be an important component of possible mate-guarding behaviour in monogamous antelopes (Brotherton et al. 1997). Using data from two klipspringer populations, each located towards opposite ends of the species' range (Kenya and Zimbabwe), we test the predictions that patterns of scent-marking by females are consistent with autonomous territory defence, while male scent-marking is more consistent with mate defence than resource-defence territoriality.

Methods

Study areas

Klipspringers were observed at two study sites within their natural range. In the first, at the Eburru Cliffs, near Gilgil in Kenya (0°35'

S, 36°15' E), observations were carried out during January–June 1981 and January–April 1982. The second study was carried out between September 1991 and February 1993 around Siezi Spring on Sentinel Ranch in southern Zimbabwe (22°09' S, 29°27' E). Mean annual rainfall was 690 mm (divided between two wet seasons) at the Kenyan site and 332 mm (falling almost exclusively between November and February) at the Zimbabwe site.

Focal sampling

Behaviour was recorded by focal sampling (Altmann 1974) at intervals throughout the study period. Klipspringer pairs could be recognised on the basis of individual differences (horn size, ear notches) and presence of juvenile offspring. Seven pairs were followed in Kenya, with observations being made from a vehicle at the base of the cliffs, with binoculars and a field telescope. In Zimbabwe, five pairs were observed either on foot or from a natural viewing point just below the skyline of a ridge face. In both cases, data were recorded using a dictaphone and stopwatch and were transcribed the same evening.

Adult klipspringers scent-mark using preorbital glands, which they rub against twig termini to leave behind a small, visible deposit of secretion. Juveniles accompanying the adult pair do not scent-mark. During marking bouts, klipspringers may scent-mark once or several times each on a number of very closely positioned twigs, which they can often access without moving their forefeet (a scent-marking site; Roberts 1997). In three territories mapped in Zimbabwe (Roberts 1997), up to 22 discrete deposits were found to occur within a single site, although about half of almost 2,000 sites contained either one or two deposits. It was possible to judge precisely the arrival of subjects at a scent-marking site (and hence the beginning of a scent-marking bout): with practice, observers can recognise scent-marking sites from a range of local physical characteristics (Roberts 1997) and most sites were already known to the observer when these data were recorded. Because of the position of the preorbital gland, the act of scent-marking requires a characteristic inclination of the head, which can be easily recognised as a discrete action and may be repeated several times during a single site visit. Scent-marking bouts were therefore defined as scent-marking events in which one or more marks were deposited at a specific site. They were judged to begin when the first member of the pair arrived at a marking site and to be completed when animals moved one body length (about 1 m) or more from the site.

During each scent-marking bout, the following data were recorded: the first individual to scent-mark, the number of scent marks deposited by each sex and the last individual to scent-mark at the site. Cases in which both male and female of a pair scent-marked at the same site within an observation period were termed paired bouts, while solo bouts involved either the male or the female only. In Kenya, 313 scent-marking bouts by the seven pairs were observed, ranging between 10 and 61 bouts per pair, while 217 bouts (range 19–92 per pair) were recorded in Zimbabwe.

Mating was observed once in Kenya and on three occasions in Zimbabwe, in three different pairs. In Zimbabwe at least, breeding seemed to be highly seasonal. All observed copulations occurred between 25 and 31 July 1992, while one other instance of courtship behaviour was recorded for a different pair on 15 July. Neither courtship nor copulations were observed at any other time of the year. The appearance of young in monitored groups between March and April (Roberts 1994) lends further evidence for reproductive synchrony: the klipspringer has a 5-month gestation period and lambs remain concealed for 3 months before beginning to accompany the adult pair around the territory (Norton 1980). To compare marking rates (number of bouts per hour) when females are receptive with rates during the rest of the year, bout rate data recorded between 15 and 31 July are compared with rates from the same pair outside this period. For the Kenyan pair in which mating was observed, data are divided into those collected within 1 week either side of the observation (oestrus lasts up to 7 days; Cuneo 1965) and the rest of the year. All observations of scent-marking were obtained during focal watches of undisturbed pairs,

rather than of known scent-marking sites, resulting in an accurate reflection of the frequency of marking in relation to female receptivity.

Data analysis

Data were analysed using non-parametric tests throughout. Comparisons between males and females, and between the same individuals when females were either receptive or not receptive, were made using pair-wise Wilcoxon signed-rank tests (Sokal and Rohlf 1995). Spearman rank correlations between the number of scent-marks deposited by each sex during paired bouts were carried out for each pair. As the significance of the correlations of two Zimbabwean pairs fell outside the 95% confidence level, we used a one-sample Wilcoxon test to check that the 12 Spearman correlation coefficients deviated significantly from 0 (where significance values were less than 0.001, the value 0.001 was used as an approximate P in this test). Analyses were carried out using SPSS for Windows and all tests are non-directional.

Using data from the Zimbabwe study, we investigated how spatial proximity was maintained during scent-marking bouts by recording the frequency with which individual pair members either approached to within 1 m or moved more than 1 m away from their mates. We then used binomial tests to compare the frequency of approaches and departures by each sex with the expected frequency for each. Observed frequencies were determined by calculating the proportion of scent-marking bouts in which either an approach or departure was the behaviour recorded immediately before or after the bout (with no other behaviour inbetween), in relation to the total number of events immediately before or after marking bouts (other behavioural events recorded included feeding, defecation and urination, and courtship). Expected frequencies were calculated as the proportion of approaches and departures between individuals in relation to the total number of behavioural events recorded outside scent-marking bouts. For this analysis, data from the five Zimbabwean pairs were pooled, amounting to 898 male and 845 female behavioural events. A similar method has been used to investigate context of scent-marking in woodchucks and red squirrels (Ouellet and Ferron 1988; Ferron and Ouellet 1989).

Results

Involvement in scent-marking bouts

Marking sites were usually visited by both members of the pair (Fig. 1) with the proportions for each pair ranging from 57 to 70% and 69 to 100% in Kenya and Zimbabwe, respectively. Paired bouts were more common than solo ones for both males (Wilcoxon signed-ranks test, $T=0$, $n=12$ pairs, $P<0.001$) and females ($T=0$, $n=12$ pairs, $P<0.001$). There was no difference in the frequency of solo marking bouts between males and females ($T=12$, $n=11$ pairs, $P>0.1$).

Females initiated the majority of paired bouts (Fig. 2; $T=5$, $n=12$ pairs, $P<0.01$), marking first in 63% of bouts in Kenya (range 28–100%) and 90% in Zimbabwe (range 83–95%). In contrast, males were usually last to mark at each site ($T=0$, $n=12$ pairs, $P<0.001$), terminating 82% of bouts in Kenya (range 58–96%) and 93% (range 78–100%) in Zimbabwe. Probably because of these patterns, and because several bouts often occurred consecutively at different sites (also in dikdik; Tilson and Tilson 1986), females consistently left males more often and approached them less often than expected

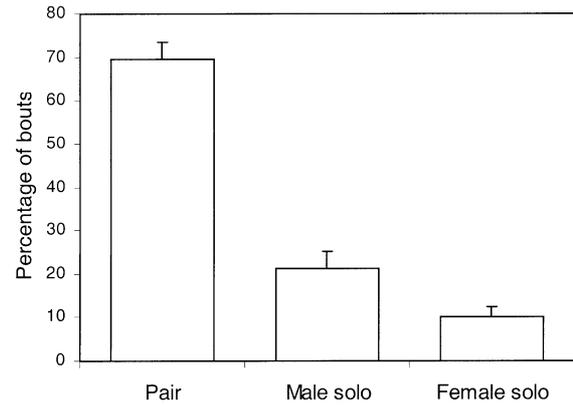


Fig. 1 Proportion of all scent-marking bouts attended by either or both members of the pair. Data are expressed as mean percentages (+SE) from 12 pairs in the two study sites

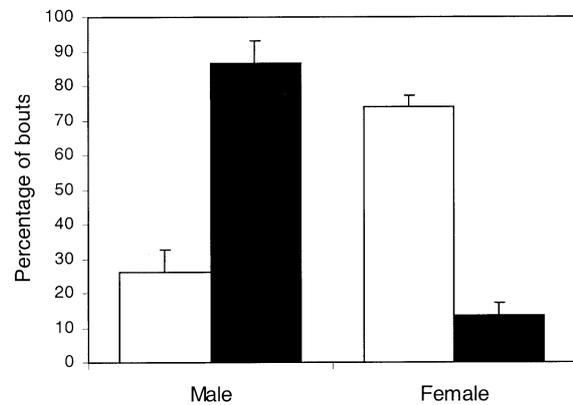


Fig. 2 Mean percentage (+SE) of scent-marking bouts by pairs that were initiated (open bars) or terminated (closed bars) by males or females. Initiation and termination refers to the identity of the first or last individual, respectively, to scent-mark during a bout

(given their frequencies during all observations), both preceding and following bouts (Table 1). Conversely, males approached the female more often before and after marking than predicted.

Number of marks deposited

The number of scent marks deposited during each bout ranged from 1 to 16 and 1 to 9 for Kenyan males and females, respectively, and in Zimbabwe, from 1 to 15 in males and 1 to 10 in females. In paired bouts in Kenya, the numbers of marks deposited by males and females were significantly correlated in every pair (Table 2). In Zimbabwe, significant correlations were recorded in three of five pairs, with a positive tendency ($P<0.1$) in another. A one-sample Wilcoxon test was used to test the deviation of the correlation coefficients from 0 and confirmed the significance of the relationship when all pairs were considered together. Despite this relationship between the number of male and female marks within

Table 1 Maintenance of proximity by males and females during scent-marking site bouts in Zimbabwe. The significance of differences between observed and expected frequencies of approaches and departures between mates (to within or beyond 1 m), either

Behaviour	Males				Females			
	Obs	Exp	<i>z</i>	<i>P</i>	Obs	Exp	<i>z</i>	<i>P</i>
Event immediately preceding scent-marking bout								
Leave	9.2	9.1	0.02	0.98	47.1	33.4	2.91	<0.01
Approach	43.6	31.2	2.69	<0.01	11.0	10.4	0.19	0.85
Event immediately following scent-marking bout								
Leave	11.3	9.1	0.75	0.45	50.3	33.4	3.59	<0.001
Approach	41.9	31.2	2.32	<0.05	6.7	10.4	-1.22	0.22

Table 2 Spearman's rank correlations between the number of marks deposited by males and females within paired scent-marking bouts. (*n*=number of bouts recorded for each pair)

Site	Pair	<i>r_s</i>	<i>n</i>	<i>P</i>
Kenya	F2	0.706	27	<0.001
	R2	0.680	31	<0.001
	RF	0.649	34	<0.001
	RT	0.884	7	0.008
	SE	0.699	32	<0.001
	SP	0.602	33	<0.001
	SS	0.753	25	<0.001
Zimbabwe	CA	0.324	92	0.002
	FH	0.555	45	<0.001
	EE	0.298	32	0.097
	TO	0.162	19	0.508
	SZ	0.502	29	0.005

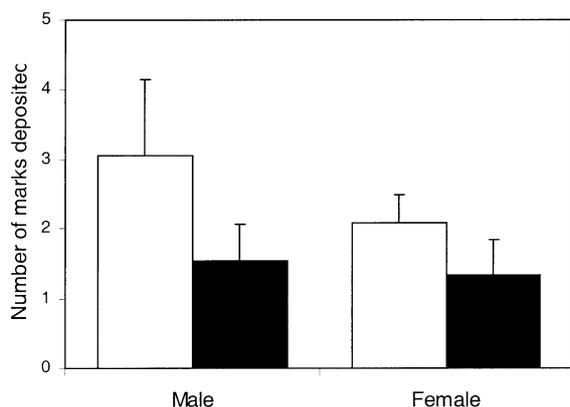


Fig. 3 Differences in the number of discrete scent marks (mean+SE) deposited by males and females during paired (*open bars*) or solo (*closed bars*) scent-marking bouts

bouts, males in Kenya (mean of 3.36 marks/bout, range 2.2–5.8) and Zimbabwe (2.65 marks/bout, range 2.2–3.5) deposited more scent marks during paired bouts (Fig. 3; $T=0$, $n=12$ pairs, $P<0.01$) than females (Kenya 2.11, range 1.4–3.0; Zimbabwe 2.07, range 1.6–2.8).

Comparing within sexes, males marked more often during paired bouts than solo ones (Fig. 3; $T=0$, $n=11$ pairs, $P<0.01$) in both Kenya (1.55/solo bout, range

immediately before or after scent-marking, are tested by binomial tests. Expected values are calculated from the frequencies of approaches and departures outside scent-marking bouts

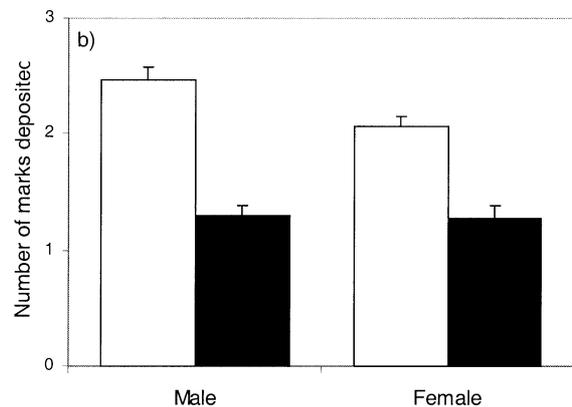
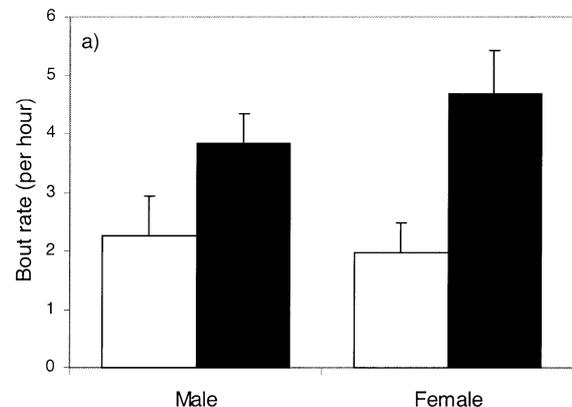


Fig. 4 Differences in rates of scent-marking bouts (**a**) and the number of marks deposited during each bout (**b**), when females were receptive (*closed bars*) and during the remainder of the year (*open bars*). Data are means (+SE) from six pairs

1.0–2.1) and Zimbabwe (1.51/solo bout, range 1.0–2.2) indicating that the female's presence was influential in determining male marking investment at scent-marking sites. Females also deposited more marks in paired than solo bouts (Kenya, 1.00 marks/bout, range 1.0–1.0; Zimbabwe, 1.85 marks/bout, range 1.5–2.3). There was no difference in the number of marks deposited during solo bouts of males and females ($T=18$, $n=10$ pairs, $P>0.1$).

Scent-marking and female receptivity

Rates of scent-marking bouts by both males and females were higher when females were receptive compared with the rest of the year (Fig. 4a; $T=0$, $n=6$ pairs, $P<0.05$; between 6 and 28 bouts per pair were recorded when females were receptive and 17 to 49 bouts per pair during the rest of the year). However, fewer marks were deposited per bout by each sex during receptive periods (Fig. 4b; $T=0$, $n=6$ pairs, $P<0.05$), probably because pairs were visiting a greater number of sites during this time.

Discussion

Are the observed patterns of scent-marking by females consistent with the hypothesis that females are territorial? The finding that females initiated the majority (up to 95%) of paired scent-marking bouts provides strong evidence that they are: females did not simply accompany males during territorial advertisement, nor did they appear to advertise ownership co-operatively with males. Instead, they took the leading role in it. By initiating marking bouts, females also appeared to be responsible for strategic decision-making about which scent-marking sites to visit, and in which order. Females also left males before and after scent-marking more often than during other activities, suggesting that they were then less concerned about maintaining spatial proximity with their mate than with territory advertisement.

These results also support the suggestion (Brotherton et al. 1997) that scent-marking by males is an important component of mate-guarding in small antelopes. Males were the last to scent-mark in the majority of bouts and marked more often than females, sometimes marking repeatedly over the female's scent. Although females had often left a marking site as, or before, males arrived, males were apparently capable of assessing the number and precise location of female marks, and of using this information to adjust their investment in the bout. Males scent-marked more often at the site during paired bouts, at which the female also scent-marked, than they did during solo ones, and consequently the number of marks deposited by males and females in each bout were positively correlated. Males always marked on precisely the same branches as females (see also Dunbar 1985). Frequently, where females had scent-marked only one of several closely positioned branches, each of which was within reach without moving and which contained older scent marks from previous visits, males marked the same branch as the female and ignored the others. Males therefore appear to scent-mark in such a way to ensure that almost every branch on which females have scent-marked is subsequently overmarked with their own scent.

There are two main mechanisms by which overmarking might contribute to mate-guarding. The first is that overmarking masks the female's reproductive condition and reduces the rate of challenges by competitors (oes-

trus concealment: Tyler 1972; Moodie and Byers 1989; Komers 1996; Brotherton and Manser 1997). Alternatively, overmarking may advertise the mated status of the female, as in equids, in which overmarking fails to reduce approaches by competitors which have investigated overmarked female urine (Klingel 1974). This suggestion fits well with general theory about scent-marking: scent marks are usually thought to be a form of status advertisement with a spatial reference (Gosling 1982) or simply as a conditional threat, signalling costs of competition if the threat is ignored (Gosling 1990). In monogamous antelopes, overmarking might ensure that the male's signal and threat of potential costs relates specifically to the female.

Determining which of these mechanisms is valid ultimately requires an experimental approach. However, in seasonally breeding populations (as in Zimbabwe), it would appear that concealment will be of benefit for only a small proportion of the year and cannot explain sustained levels of overmarking at other times. In addition, as receptivity will be highly predictable, the benefits gained from concealment may be minimal. Status advertisement, on the other hand, can explain these sustained levels: because of the benefits of owner advantage (Davies 1978; Wiltenmuth 1996; Alcock and Bailey 1997), it may pay males to maintain access to the female during the non-breeding season, particularly as there are no alternative mating opportunities at this time. We therefore suggest that scent-marking by males helps to reduce the number of attempted challenges by neighbouring males, by advertising the potential costs of competition over the female. When they encounter overmarked female scent marks, intruding males are forewarned that the female will be actively defended and less determined rivals will be deterred.

Scent-marking rates of both sexes increased when females were receptive. Elevated marking rates have also been recorded during the mating season for the klip-springer in Ethiopia (Dunbar and Dunbar 1974) as well as in grysbok (Novellie et al. 1984) and dikdik (Kranz 1991). In the Zimbabwe study at least, where the mating season appeared to be highly synchronous, this increase is unlikely to be related to changes in resource availability. Annual variation in scent-marking rates appears to be characterised by a roughly constant level of scent-marking across the year with the exception of two sharp peaks (approximately 170% higher than normal rates) in July and November–December (Roberts 1994). The second peak is coincident with a sudden increase in food availability due to the pre-rains leaf-flush (Roberts 1994), but the first peak is probably not related to resources as it occurs several months into the dry season when there is no comparably radical alteration in food abundance or quality.

An increase in male marking rates when females are receptive is consistent with our mate-guarding explanation, but the elevated marking rates of females at this time might be due to several alternative explanations. Females might increase marking rates to advertise their re-

productive condition (Ralls 1971; Kappeler 1998), to test the quality of their mate (Hoi 1997; Slagsvold and Lifjeld 1997) or to solicit extra-pair copulations as they appear to do in some birds and other mammals (Richardson 1987; Ågren et al. 1989; Gray 1996). Alternatively, higher marking frequencies when females are receptive may reflect female competition over mates (Berglund et al. 1993). Females may compete over mates if, for example, the costs of doing so are less than the risk of postponing mating (perhaps because of mate desertion), or for reasons of sperm depletion resulting from extra-pair copulations (Barnard and Markus 1989). In this case, increased female scent-marking might effectively place limits on the male's ability to seek extra-pair matings elsewhere, in view of the potential costs to the male of missed overmarking of female scent while he is absent from the territory. Further work is required to select between these hypotheses but elevated levels of female marking during receptive periods certainly appear to be explained by reasons unrelated to simple territorial defence.

Such explanations for elevated marking levels when females are receptive are, however, unlikely to explain the prevalence of female-initiated marking throughout the year and may be secondary adaptations to provide subsidiary benefits to those gained by territoriality. Our data do not preclude the possibility, for example, that females continuously instigate male competition to test mates, or to provide a continuous record of their reproductive condition, but it seems unlikely that females would continue to do this in the months of early pregnancy. Perhaps a more plausible alternative to our suggestion that female scent-marking is related directly to territory defence is that it might help to ensure constant, year-round provision of anti-predator vigilance by the male, increasing the probability of survival for herself and her offspring. This is consistent with the general explanation for the evolution of monogamy in this species (that males provide parental care through a vigilance service to the female and offspring: Dunbar and Dunbar 1980) and could work through selection on males for overmarking female scent, as described above. Future studies might test between these ideas by recording context-dependent variations in female marking rates (see Kappeler 1998 for an example of this kind of approach), such as in the presence of paired and unpaired competitors of either sex, or in relation to variation in predation risk. However, the evidence presented here, together with high levels of intrasexual aggression (Dunbar and Dunbar 1980; Roberts 1994) and its relationship with scent-marking (Norton 1980; Roberts 1994), and against the background of an almost universally accepted link in territorial mammals between scent-marking and territorial defence (reviewed by Brown 1979; Gosling 1982, 1985, 1990; Gorman 1984, 1990; Brown and Macdonald 1985), we conclude that it is most likely that the primary function of female scent-marking is for territorial advertisement.

This study has presented evidence which suggests that, in two populations of a monogamous species, males

and females are independently territorial and that females in particular may defend resources required for reproduction. While it challenges the conventional view, in which females reside in territories defended by the male (Owen-Smith 1977; Norton 1980), this conclusion is consistent with Jarman's (1974) interpretation of the social ecology of the small antelopes, as well as recent work on monogamy in mammals in general (Komers and Brotherton 1997). Extreme spatial dispersion of females, resulting largely from intrasexual aggression and territoriality, may assist males to monopolise females, in large part by overmarking female scent marks. Similar sex-specific functions for apparently paired territorial signalling have been proposed for vocal duets of monogamous birds (Levin 1996) and mammals (gibbons; Cowlshaw 1992). While understanding the evolution of mammalian monogamy is made difficult by the fact that there is relatively little variation between males (Clutton-Brock 1989) and because females rarely move between territories (Bradbury and Vehrencamp 1977), the pattern of territorial signalling by males and females appears to provide a useful avenue for investigation. Further study should investigate the mechanisms by which male overmarking improves male reproductive success and the extent to which females of other monogamous species may, like female klipspringers, be territorial in their own right.

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