



# Scent marking in a territorial African antelope: I. The maintenance of borders between male oribi

JUSTIN S. BRASHARES & PETER ARCESE

Department of Wildlife Ecology, University of Wisconsin-Madison

(Received 3 October 1997; initial acceptance 27 March 1998;  
final acceptance 4 May 1998; MS. number: A8033)

Scent marking is ubiquitous among the dwarf antelope and gazelles of Africa, but its function has been the subject of debate. This study examined preorbital gland scent marking in the oribi, *Ourebia ourebi*, a territorial African antelope. Several hypotheses for the function of scent marking by territorial antelope were tested with observational data. Of these, the hypotheses that scent marking is driven by intrasexual competition between neighbouring males, and that marks serve as an honest advertisement of a male's ability to defend his territory from rivals, were supported best. Thirty-three territorial male oribi on 23 territories marked most at borders shared with other territorial males, and territorial males marked more often at borders shared with multimale groups than at borders shared with a single male. This suggests that males perceived neighbouring male groups as a greater threat to territory ownership than neighbouring males that defended their territories without the aid of adult subordinates. Marking rate was unrelated to territory size or the number of females on adjacent territories, but males with many male neighbours marked at higher rates than those with fewer male neighbours. These results suggest that the presence of male neighbours has a greater effect on the scent marking behaviour of territorial antelope than has been considered previously.

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Scent marking is a widespread but poorly understood form of communication in mammals (Johnson 1973; Stoddart 1980; Brown & Macdonald 1985), reptiles (Alberts 1992; Alberts & Werner 1993; Carpenter & Duvall 1995), and amphibians (Jaeger & Gergits 1979; Ovaska & Davis 1992; Simons et al. 1994). Scent marking has been linked to a wide range of behaviours and contexts, including kin recognition and social learning (Aldhous 1990; Laland & Plotkin 1991; Ramsay & Giller 1996), the advertisement of reproductive condition (Walls et al. 1989; Palanza et al. 1994; Converse et al. 1995), interactions between predators and prey (Lewis & Murray 1993; Viitala et al. 1995), dispersal and dispersion (Gorman & Stone 1990; Hurst et al. 1993; Lenti Boero 1995), foraging (Henry 1977), reproductive suppression (Rylands 1985; Abbot et al. 1990; Snowdon et al. 1993) and to the maintenance of dominance hierarchies (Benson 1980; Gosling & Wright 1994; Gosling et al. 1996). However, scent marking is perhaps most often related to activities associated with the occupation of a territory or home range (Gorman 1984; Randall 1987; Clapperton et al. 1988; Gosling 1990; Simons et al. 1994;

Lenti Boero 1995). In this paper, we present the results of a study of preorbital gland scent marking in the oribi, *Ourebia ourebi*: Neotraginae, in Serengeti National Park, Tanzania. Our aim was to test several hypotheses related to the function of scent marking by territorial antelope.

Scent marking is ubiquitous among the dwarf antelope and gazelles of Africa (Neotraginae and Antilopinae: Estes 1991), but its function has been the subject of disagreement (e.g. Ralls 1971; Walther 1978; Gosling 1982, 1985). Studies of scent marking in antelope typically have focused on the behaviour of a single animal (Walther 1978; Gosling 1981, 1987) or of captive animals (Ralls 1974; Barrette 1977; Somers et al. 1990). Small sample sizes and variation in approach may have contributed to the large number of hypotheses proposed for the function of marking. By studying scent marking in the wild, with a sufficient number of study animals we hoped to determine which hypotheses best explain the scent marking behaviour of oribi.

Oribi in Serengeti National Park, Tanzania, are ideal subjects for behavioural study. From one to four adult males reside on territories with as many as eight females and, consequently, the population provides much variation for comparative analyses. Adult male oribi defend territories year-round either as a single male, referred to hereafter as a singleton, or as a dominant male with one

Correspondence: J. Brashares, Department of Wildlife Ecology, 1630 Linden Drive, University of Wisconsin, Madison, WI 53706, U.S.A. (email: jsbrasha@students.wisc.edu).

**Table 1.** Hypotheses, assumptions and predictions related to the function of scent marking on territories

Hypothesis	Assumption/prediction	References
Orientation	(1) Males mark in areas frequented most (2) Males seek out their own marks	Lyall-Watson 1964; Walther 1978 Ono et al. 1988
Dominance/threat	(1) Dominants mark more than subordinates (2) Dominants mark most around subordinates (3) Males mark prior to attacking other males, when 'motivated to aggression'	Ralls 1971 Barrette 1977 Moehlman 1985
Scent matching	(1) Males mark where intruders are most likely to encounter marks (2) Males mark themselves (3) Males make themselves available for scent matching by intruders (4) Dominant males remove or replace marks of others	Gosling 1982, 1985, 1986; Gorman 1984 Rylands 1990
Border maintenance	(1) Males mark where neighbours are most likely to encounter marks (2) Males mark preferentially along borders adjacent to the most threatening rivals	Gosling 1986; Smith et al. 1989 Johansson & Liberg 1996

to three adult male subordinates. Unlike other polygynous territorial antelope, male oribi do not form bachelor groups. Instead, young males either assimilate into their existing social group as a subordinate, assimilate into a new social group as a subordinate, take over an adjacent territory from a resident male, or establish territories in previously undefended areas (Arcese et al. 1995). Breeding occurs throughout the year and, although dominant males guard mates, subordinates occasionally mount females. Females choose territories and mates, but typically they remain with one male or on one territory for a year or more. Details of these behaviours and other aspects of the study population are provided elsewhere (Jongejan et al. 1991; Arcese et al. 1995; Arcese 1999).

In addition to their unique social organization, male oribi display one of the highest documented rates of scent marking in mammals (up to 45 times per hour for adult males; this study). While females mark only rarely, males spend a large portion of each day marking their territories. Territories are scent-marked by all resident adult males with preorbital gland secretions and faecal pellets deposited on dung middens. Preorbital marks are black tar-like secretions deposited on grass and shrub stems inserted into the preorbital gland (Gosling 1972). Dung middens are accumulations of three or more distinct piles of freshly deposited (moist) faeces distributed 20–200 m apart along territory boundaries (Brashares & Arcese 1999).

Here, we describe: (1) the placement of scent marks by 33 adult male oribi on 23 contiguous territories; (2) relationships between the placement of marks and the number of males and females on neighbouring territories; (3) relationships between the placement of marks and the status of the marking male and the number of females on the marking male's territory; (4) the time of day, typical group size and composition, and behavioural context in which scent marking most frequently occurs; and (5) relationships between marking rates and male status, territory size, the number of females on the territory, and

the number of males and females on neighbouring territories. Finally, we compare our results with previous studies of scent marking in antelope.

### Hypotheses about Scent Marking on Territories

The hypotheses and predictions addressed in this study are outlined in Table 1 and reviewed briefly here. Few studies of scent marking have formulated or tested a rigid set of predictions, and thus, many hypotheses proposed so far have been difficult to test thoroughly (see Johnson 1973; Brown 1979; Gorman 1984; Gosling 1990). Of the hypotheses that apply to oribi (Table 1), Gosling's (1982) scent matching hypothesis provides the clearest set of predictions. The scent matching hypothesis posits that scent marks provide an olfactory link between a resident male and his territory, and that this enables intruding males to recognize the territory holder when encountered, thus reducing the chance of escalated conflicts (Gosling 1982, 1985). The scent matching hypothesis has been supported by studies of scent marking in antelope and other mammals (Clapperton et al. 1988; Somers et al. 1990; Wenhold & Rasa 1994).

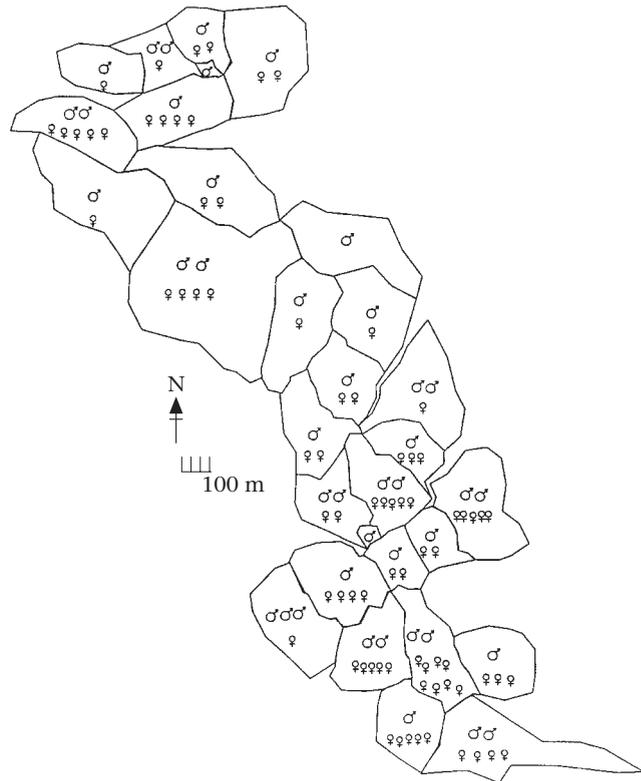
Ralls (1971) hypothesized that scent marks signal a male's dominance and intolerance of other males, and, thus, serve as a threat that he will soon attack. The orientation hypothesis suggests that marks help orient a male within his territory (Lyall-Watson 1964; Kleiman 1966). The dominance/threat and orientation hypotheses have received support from more recent studies of scent marking in antelope (Barrette 1977; Walther 1978; Ono et al. 1988), although both of these hypotheses have been accepted most often as default hypotheses after others were rejected. Lastly, scent marks placed along territory borders may serve to form a 'property line' between neighbours, thereby preventing frequent and potentially costly disputes between high-quality males ('border maintenance hypothesis': Gosling 1986; Smith et al. 1989; Johansson & Liberg 1996).

Of the many hypotheses proposed for the function of scent marking in territories, several are not considered here because they do not apply to oribi, lack clear or testable predictions, or cannot be tested in the field. These include the hypotheses that marks facilitate foraging efficiency (Henry 1977), attract mates and enhance pair bonds (Rothman & Mech 1979; Porton 1983; Miquelle 1991), or serve as 'railway signals' to facilitate spatiotemporal separation of mutually intolerant individuals (Leyhausen & Wolff 1959; Clapperton et al. 1988). We also do not consider the related hypotheses that scent marking intimidates intruders (Geist 1965; Mykytowycz 1965) or provides the marker with 'self-assurance' (von Richter 1972) and 'a sense of ownership' (Joubert 1972; Mykytowycz 1975). Support for each of the latter hypotheses is reported in observations of territorial males that consistently repel intruders, but this is a common observation also in territorial species that do not scent mark and perhaps is explained better by conflict theory (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Petrie 1984; see also Gosling 1986).

## METHODS

### Study Population

The study was conducted in the northwest corner of the Serengeti National Park, Tanzania (01°38'S, 32°55'W). The main study area was located on a section (8 × 2 km) of Kogatende Ridge. This area is characterized by a series of parallel grassland ridges separated by narrow riverine forests. Oribi occur on ridge-tops and hillsides along Kogatende Ridge at densities of 8–9.3 animals per km<sup>2</sup> (Arcese et al. 1995; Mduma 1995). Since 1987, 23–29 oribi territories have been studied on this site (Jongejan et al. 1991; Arcese 1994; Arcese et al. 1995). Territories range from 0.2–1.1 km<sup>2</sup> in size and are held for up to 7 years by adult males (Arcese et al. 1995; this study). The size and shape of territories on the study site have changed relatively little despite changes in the resident males (unpublished data). Oribi in the study area were habituated to our vehicles and observed at distances of 20–60 m with × 10 binoculars and a × 40 spotting scope. We identified oribi individually using 14 naturally varying characteristics including horn length and shape, coat and tail colour, facial markings, the shape and size of the subauricular gland in relation to the eye, the pattern of marks in the ears, and natural scars (Jongejan et al. 1991). Early work on 29 artificially marked oribi confirmed the use of natural marks as reliable. We identified 60–95 individual oribi and followed them each year from 1987 to 1991, and during this study from September to December 1995. To allow a comparison of males by social status, we divided oribi on the study site into three male status classes: singleton, dominant and subordinate. We determined the status of males on multimale territories by observing social interactions among the resident males (Arcese 1999). Dominant males were those that displayed offensive threats towards cohabiting males and consistently elicited submissive behaviour from these



**Figure 1.** Arrangement of territories and composition of oribi groups in the study area. Territories were mapped by plotting the location of dung middens, conflicts between neighbours and daily sightings for all males (see Methods). Symbols indicate adult males and females resident on territories.

males (for a summary of offensive and submissive behaviour see Estes 1991, page 20). Dominance relationships on multimale territories were stable throughout the period of this study. We defined juvenile males as those approximately the size of adults, but with no or minimal visible horn growth (see Jongejan et al. 1991 for ageing criteria).

We mapped territory borders using the position of 11–34 dung middens surrounding each territory (Arcese 1994; Komers 1996; Fig. 1). Defecation at middens and preorbital scent marking are functionally independent behaviours because males frequently marked with the preorbital gland away from middens and not just prior to or following an act of defecation. Many males also defecated without associated bouts of preorbital marking (unpublished data). We assessed the accuracy of mapped borders by plotting oribi sightings collected throughout the study period on each territory and by plotting the site of conflicts between neighbouring males. Borders mapped using the location of dung middens averaged 3–5% larger in size than those mapped using only the sightings of males and conflicts between neighbours, but in every case concordance was greater than 90% between maps created using the different measures (unpublished data). Territory mapping and the plotting of data points were conducted using ArcView 3.0 geographical information systems software (ESRI 1996).

## Time Budgets

We conducted a 1-h watch biweekly for each of the 33 males, totalling 5 h for each male and 165 h in total. During watches, we recorded the behaviour of males at 5-min intervals as one of the following: sitting (head-up or down), walking, feeding (browsing or grazing), standing, grooming (standing or sitting), urinating or defecating, horning (grass or bush), preorbital marking (grass bitten first or not), courting/mating, or antagonism towards other oribi (butting, chasing or threatening). For each male, we alternated focal periods between morning (0700–1000 hours), midday (1000–1300 hours) and afternoon (1300–1600 hours) sessions. We recorded all scent marking opportunistically during these periods. A scent mark was recorded each time a male tilted its head and inserted the distal portion of a stem into the preorbital glands.

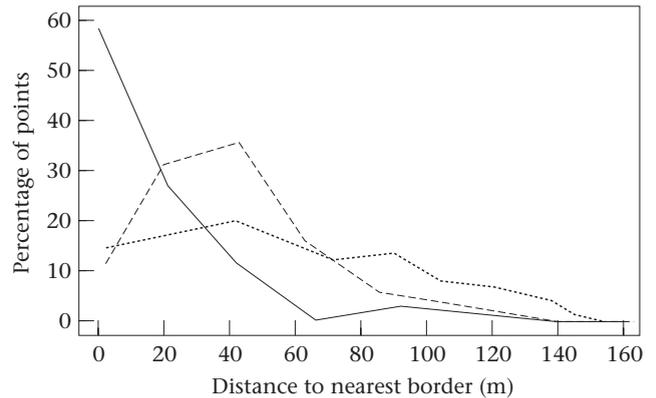
## Animal Locations

For each scent mark observed during focal male watches, we recorded the location of the mark, the identity of group members present (within 100 m of the focal animal), and we noted if marks occurred coincident with aggressive interactions between males, courting by males of resident females, urination and defecation by males or females, or feeding. Conflicts between males involved physical encounters between neighbouring males, males sharing a multimale territory, and territorial males and transient trespassing males. In addition, we also recorded one observation of the location and behaviour of each focal male in the study area each day. This required that we searched each focal territory until the resident male or males were located and their position recorded. Observations collected in this manner are referred to as 'sightings'. We also recorded opportunistically conflicts between males throughout the study period.

All locations were measured using a global positioning system receiver. The global positioning system (GPS) is a space-based triangulation system that uses satellites and computers to provide instantaneous estimates of latitude, longitude and altitude (Ackroyd & Lorimer 1994). To account for GPS error, we adjusted coordinates recorded for each observation using data provided by an additional fixed-point GPS receiver located on the study site following Gann 1993 (see also Ackroyd & Lorimer 1994; Bierman 1995). After adjustment, coordinates are considered accurate to within  $\pm 5$  m (Bierman 1995).

## Analysis of Mark Placement and Context of Marking

For each territory, we tested for pattern in the placement of marks in two ways. First, we compared the distribution of distances to the nearest border of observed scent marks with the mean distribution of five randomly generated sets of points. Second, we compared the distribution of observed marks with a set of points reflecting daily male sightings (Fig. 2). We tested for patterns in marking associated with the composition of neighbouring territories by comparing the observed number of marks along



**Figure 2.** Example frequency of the distribution of scent marks (—,  $N=57$ ), daily sightings of males (---,  $N=68$ ) and randomly generated points ( $\cdot\cdot\cdot$ ,  $N=72$ ) for one singleton male. All distributions differed significantly from each other (Kolmogorov–Smirnov tests:  $P<0.01$ ).

each border to an expected concentration of marks for each border based on its length. Lastly, to determine whether males were more likely to scent-mark in the presence of females, juvenile males or other adult males, we calculated the expected number of marks for each male based on the average amount of time a male spent in the company of these other group members. We then compared this expected value to the observed number of marks during which females, juvenile males and other adult males were within 5 m of the marking male.

## Statistical Analyses

We used Minitab release 10 (Minitab 1994) and SAS 6.11 (SAS Institute 1990) for statistical analyses. Parametric tests were employed when their assumptions were met. We used a Mann–Whitney  $U$  test to compare the means of data not distributed normally, and a Kolmogorov–Smirnov test to compare distributions (Sokal & Rohlf 1981). We also used a Kruskal–Wallis test and rank sum difference tests (Kanji 1993) for multiple comparisons to test for significant differences, and a Spearman rank correlation for data not distributed normally. We used  $G$  tests for data representing counts and revised the level of significance using the Bonferroni adjustment for planned comparisons (SAS Institute 1990). For each analysis we aggregated data by subject. We did not pool data because intrasubject variance was frequently smaller than between-subject variance and sample sizes among individuals were seldom equal (for a review of pooling and aggregating see Leger & Didrichsons 1994).

## RESULTS

### Territory Types

We observed 33 adult male oribi on 23 contiguous territories from September to December 1995 (Fig. 1). This included 14 singletons, nine dominants and 10 subordinates. Twenty of 23 territories had both 'unshared' borders that were natural boundaries made by riparian

**Table 2.** Location of marks with respect to different types of neighbours and borders

Neighbour/Border comparison	Males examined	$\Sigma$ marks				
		1 versus 2	$G_T$	$df$	$P$	
Shared versus unshared	All males	1796	71	716.4	29	<0.001
	Singletons	721	36	256.6	12	<0.001
	Dominants	497	15	238.6	8	<0.001
	Subordinates	578	20	221.2	9	<0.001
Multimale versus unimale	All males	854	448	105.9	20	<0.001
	Singletons	408	199	52.6	9	<0.001
	Dominants	236	118	20.3	5	0.001
	Subordinates	210	131	20.2	6	0.003
Unimale versus unimale	All males	949	762	30.3	27	0.30
	Singletons	422	378	7.9	12	0.79
	Dominants	253	214	11.4	8	0.18
	Subordinates	254	170	11.0	7	0.14
Multimale versus multimale	All males	504	420	9.7	15	0.84
	Singletons	332	354	6.9	11	0.80
	Dominants	80	35	0.5	2	0.77
	Subordinates	92	31	2.2	2	0.33
0–3 Females versus 4–8 females	All males	515	663	22.6	19	0.31
	Singletons	264	298	8.7	9	0.46
	Dominants	140	169	3.6	5	0.61
	Subordinates	111	196	10.3	5	0.07

$G_T$  is the sum of  $G$  values for all males. We tested for heterogeneity in male marking patterns by subtracting the  $G_p$  (for all marks pooled) from  $G_T$  to obtain  $G$  heterogeneity ( $G_H$ ; Sokal & Rohlf 1981) to test for heterogeneity among males or categories.  $G_H$  was not significant ( $P > 0.05$ ) for comparisons presented here. Female number was divided into the two categories based on a median-split for territories in the study area.

thickets or woodlands, and ‘shared’ borders maintained by resident males on adjacent territories. Three territories were bordered on all sides by occupied territories. Both unimale and multimale territories bordered 16 territories, only unimale territories bordered six territories, and only multimale territories bordered one territory. Nineteen territories were bordered by territories with zero to three females and four to eight females (Fig. 1).

## Spatial Context of Marks

### Location in territories

We recorded a total of 1953 preorbital gland scent marks during the study period. Seventy-five to 90% of marks were placed in the periphery (outer 10%) of each of the territories studied. Males marked closer to territory borders than would be expected if marks were placed at random on territories, or if marks were clumped where males resided most often in their territories (Kolmogorov–Smirnov tests:  $N=33$ ,  $P < 0.01$  for all males regardless of status; Table 2). The placement of marks also differed significantly from areas used most often by females (Kolmogorov–Smirnov tests:  $N=31$ ,  $P < 0.01$  for all males regardless of status). Patterns of territory use were similar for male and female oribi (Kolmogorov–Smirnov tests:  $N=31$ , NS for all males).

### Effect of neighbour/border type

Males on territories with shared and unshared borders marked more often near shared borders than near unshared borders (Table 2). Males also marked near borders shared with multimale groups more often than they marked near

borders shared with singletons (Table 2). Where territories were bordered by more than one territory defended by a singleton, males marked each about equally (Table 2). Males also marked about equally along borders shared by two or more different multimale groups (Table 2).

### Effect of male status and female number

Singleton and dominant males showed similar patterns in marking. Unlike singleton and dominant males, subordinate males marked borders adjacent to multiple-female territories marginally more than expected if marks were placed randomly with regard to females (Table 2). Furthermore, while the placement of marks along a territory’s periphery was similar for singleton and dominant males (rank-sums test:  $df=1$ , NS), singleton and dominant males each marked slightly closer to borders than did subordinates (Kruskal–Wallis test:  $H_2=5.28$ ,  $P=0.07$ ). Males in each status class showed about equal tendencies to mark within the outer 10% of their territories, and near borders adjacent to multimale groups (Kruskal–Wallis test:  $H_2 < 3.1$ , NS for all classes), despite large differences in territory size and shape (see Fig. 1). The number of females on a neighbouring territory had no apparent effect on the placement of marks by dominant and singleton male oribi (Table 2), nor did the number of females living with the marking male (Spearman rank correlation:  $r_s=0.07$ ,  $N=33$ , NS).

## Temporal and Social Context of Marking

Scent marking was unrelated to the time of day for all males (Kruskal–Wallis test:  $H_2=1.64$ ,  $P=0.44$ ), and for

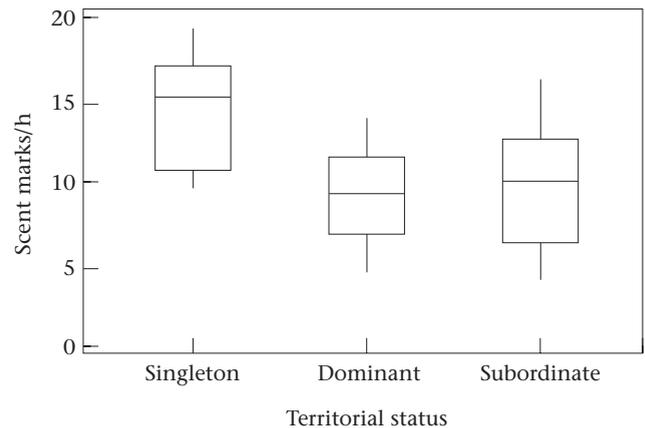
each male status class ( $H_2 < 2.98$ , NS for all classes). Males were about equally likely to mark in the presence of females as in their absence ( $G$  test:  $G_{30} = 36.94$ , NS; and for each male status class, NS, for all classes). Dominant males were slightly more likely to mark in the absence of their subordinates than in their presence ( $G_8 = 14.93$ ,  $P = 0.06$ ), but the reverse was the case for subordinate males ( $G_9 = 16.05$ ,  $P = 0.07$ ). Dominant and subordinate males frequently walked and marked along borders together with no apparent aggression between them.

To test the predictions of the scent matching and dominance/threat hypotheses, we compared the marking rates of resident males following encounters with trespassing neighbours and trespassing transients. In about 740 h of informal observation and 165 h of focal male sampling, we recorded the marking rates of males during 25 5-min periods following agonistic encounters between resident males and trespassing neighbours and transients. Resident males marked an average of 1.0 marks/min following 14 encounters with trespassing neighbours, but only 0.1/min following 11 encounters with transient intruders. The baseline rate of marking for males during focal watches was 0.2/min. Thus, the marking rate of resident males was significantly higher following encounters with trespassing neighbours than transient intruders (Mann–Whitney  $U$  test:  $U = 35$ ,  $N_1 = 11$ ,  $N_2 = 14$ ,  $P < 0.02$ ), and it was also higher than the baseline marking rate ( $U = 76$ ,  $N_1 = 14$ ,  $N_2 = 33$ ,  $P < 0.01$ ). The marking rate of resident males following encounters with transient intruders was similar to the baseline marking rate ( $U = 140.5$ ,  $N_1 = 11$ ,  $N_2 = 33$ , NS).

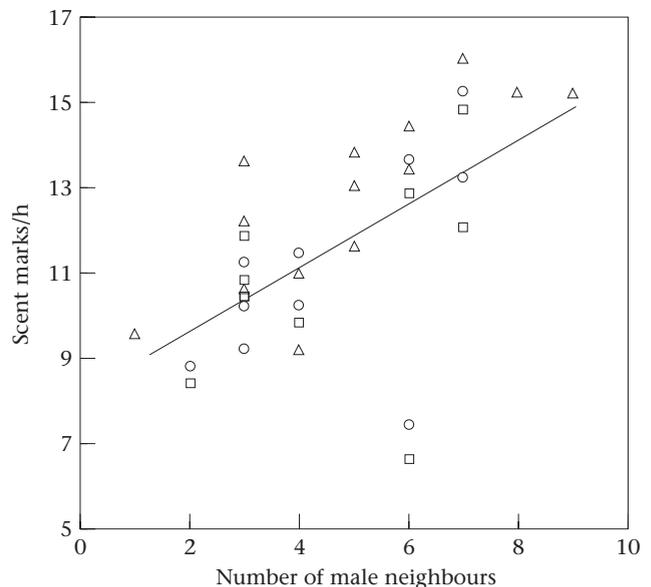
Fourteen of 25 encounters began when a resident male approached a trespassing neighbour by running from a considerable distance ( $> 80$  m) to immediately evict the trespasser. In 11 encounters between a resident male and a transient intruder, intruders entered the territory across an unshared border, after which resident males ran at the intruder from initial distances of 100–180 m to evict it. All of these encounters lasted under 30 s, and in no case did territorial males pause to allow trespassers to sample the odour of the resident male as expected by the scent matching hypothesis (Table 1; Gosling 1982). In contrast, on 81 occasions, we observed dominant and subordinate male group members separated by 80–150 m but within full view of one another, and in no case, did the dominant attempt to chase the subordinate. Thus, dominant males appeared to differentiate between resident and intruding males.

### Marking Rate

Marking rates differed significantly between individuals of each status class (Kruskal–Wallis test:  $H_{13} = 25.1$ ,  $P = 0.02$ ;  $H_8 = 16.34$ ,  $P = 0.04$ ;  $H_9 = 17.46$ ,  $P = 0.04$ ; singleton, dominant and subordinate males, respectively). Singleton males marked more often than dominant males (Mann–Whitney  $U$  test:  $U = 29$ ,  $N_1 = 9$ ,  $N_2 = 14$ ,  $P = 0.03$ ) and subordinate males ( $U = 36$ ,  $N_1 = 10$ ,  $N_2 = 14$ ,  $P = 0.04$ ; see Fig. 3). However, the sum of all marks by dominant and subordinate males on multimale territories exceeded that on



**Figure 3.** Median marking rates of males by class. Box-plots show the median (horizontal line), interquartile range (box), and range of the data (whiskers). Singleton males marked at higher rates than dominant and subordinate males (Kruskal–Wallis test:  $H_2 = 6.54$ ,  $P = 0.04$ ). Marking rates for dominant and subordinate males were similar (rank-sum difference test:  $df = 1$ , NS).



**Figure 4.** Relationship between marking rate and number of male neighbours for 14 singleton ( $\Delta$ ), nine dominant ( $\square$ ), and 10 subordinate males ( $\circ$ ). Spearman rank correlation:  $r_s = 0.66$ ,  $N = 33$ ,  $P < 0.05$ .

territories defended by singletons ( $U = 9$ ,  $N_1 = 9$ ,  $N_2 = 14$ ,  $P < 0.01$ ). Marking rates of dominant and subordinate males were similar ( $U = 43$ ,  $N_1 = 9$ ,  $N_2 = 10$ ,  $P = 0.84$ ; see Fig. 3). Marking rates by males of each status class were positively correlated with the total number of male neighbours surrounding a territory (Spearman rank correlation:  $r_s = 0.78$ ,  $N = 14$ ,  $P < 0.001$ ;  $r_s = 0.64$ ,  $N = 9$ ,  $P < 0.05$ ;  $r_s = 0.58$ ,  $N = 10$ ,  $P < 0.05$ ; singleton, dominant and subordinate males, respectively; Fig. 4), but were unrelated to the total number of female neighbours resident on adjacent territories ( $r_s < 0.30$ , NS for each male status class). Male marking rate was also unrelated to territory size, measured as territory area ( $r_s < 0.20$ , NS for each male

status class) and total length of shared borders ( $r_s < 0.30$  for each, NS male status class), and to the number of females residing on the territory of the marking male ( $r_s < 0.10$ , NS for each male status class).

## DISCUSSION

Male oribi marked with preorbital gland secretions preferentially along borders shared with other territories and marks were rarely placed in areas not immediately adjacent to another territory. Males marked more often along borders shared with multimale groups than with singleton males, but the number of females on adjacent territories did not have a similar effect. Marking rate was unrelated to territory size, or to the number of females on the territory or on neighbouring territories, but males with many male neighbours marked more often than those with fewer males as neighbours. Marking also was unaffected by time of day or the proximity of females. Observations of encounters between rival males suggest that resident male oribi identified intruders at a distance and quickly chased them from the territory. Intrusions by neighbours were slightly more common than by transients and, unlike neighbours, transient males always entered a territory across an unshared border. We now consider these results in light of our four main hypotheses (Table 1).

### Scent Matching Hypothesis

The scent matching hypothesis assumes that by matching mark odour with body odour, intruders on territories gain an opportunity to assess whether other males encountered on the territory are owners or trespassers. However, on oribi territories defended by more than one adult male, subordinates marked about as often as dominants, and thus were about equally represented by marks within territories. Under the scent matching hypothesis, an intruding male would have had about a 50% chance of mistakenly determining that a dominant male was not a resident, or that the subordinate was the dominant owner. In either case, scent matching will not have served its assumed function under the scent matching hypothesis (Gosling 1982). This suggests that scent matching does not explain why oribi in Serengeti marked their territories as they did. Moreover, none of the predictions for the scent matching hypothesis in Table 1 were supported. Marks were not located where they were most likely to be encountered by trespassing males because males rarely marked in areas adjacent to undefended habitat. However, all transient oribi from outside the study area entered territories from these undefended areas. Males also did not mark themselves or present themselves to trespassing males for scent matching, nor did dominant males remove marks by subordinates or otherwise prevent them from marking. Scent matching might be more common in species where more than one intruding male often encounter one another inside large territories defended by males that cannot observe most or all of their territory at once.

### Dominance/Threat Hypothesis

We also failed to support the dominance/threat hypothesis (Ralls 1971; Table 1). Subordinate males marked as often as dominants, and dominant males were marginally more likely to mark in the absence of subordinates than in their presence. Singleton males marked most often, even though no adult subordinates were present (Fig. 4). Lastly, we never observed marking prior to or during encounters between resident and trespassing males, but we often did so afterwards. Moreover, 96% of all marks were placed without regard to conflicts underway.

### Orientation Hypothesis

The possibility that scent marks play a role in orientation cannot be dismissed entirely (Gosling 1985), but our study also does not support this hypothesis (Table 1; Lyall-Watson 1964). If orientation does affect mark placement by oribi, our results suggest that males require orientation aids primarily along borders with other males. However, because we often observed territorial males respond to trespassing neighbours or transient males immediately as they crossed borders at 80–150 m, we assume that owners can identify the location of borders visually. It is possible, however, that males use marks to aid navigation when cover is dense.

### Border Maintenance Hypothesis

Our results support strongly the idea that scent marking by oribi males is driven by competition among neighbours, and that it serves to maintain borders between competing males (see Dubost & Freer 1981; Gosling 1990; Lenti Boero 1995). We found that scent marks were placed primarily along shared borders, even though transient intruders entered territories across unshared borders. Males also marked preferentially along borders adjacent to territories defended by multimale groups, perhaps because males recognized multimale groups as more threatening potential rivals than singleton males. We also found that male marking rate was strongly related to the number of males on neighbouring territories, but not to territory size or the number of females on the same territory or adjacent territories. The border maintenance hypothesis suggests that neighbours present the greatest threat to territory owners (Gosling 1990), and for dik dik, *Madoqua kirkii* (Hendrichs 1975), waterbuck, *Kobus ellipsiprymnus* (Spinage 1982) and oribi, this idea is supported. Male oribi from neighbouring territories accounted for over 48% of evictions of territory owners on our study area from 1989 to 1992 (Arcese 1999).

Our results on the location of preorbital marks resemble those of studies that have examined faecal and preorbital marking by several other species of antelope (e.g. Hendrichs 1975; Walther 1978; Dubost & Freer 1981; Gosling 1987; Somers et al. 1990). But, in general, previous authors have reached different conclusions. For example, Walther (1978) concluded that marks helped

male Thomson's gazelle, *Gazella thomsoni*, to orient within its territory. Although the male studied by Walther marked most often along borders with other territories (Walther 1978, page 173), he suggested that because nonterritorial males frequently trespassed on the territory of the study animal, marking probably did not function in defence. In contrast, we suggest that marks by oribi were intended to deter intrusions by resident males on adjacent territories, and not by nonterritorial trespassers. For oribi or species in which individuals hold contiguous, semipermanent territories, scent marks may serve notice among neighbours that territories are occupied and actively defended. Marks also may facilitate tolerance between neighbours without physical contests which, in oribi, can result in severe wounding or death (Arcese 1999). Along these lines, Gosling (1987, page 622) has suggested that scent marking may place 'a spatial limit on the owner advantage' between neighbours.

Scent marks also may serve as an economical means of preventing neighbours from gradually expanding their territory if well-marked borders dissuade trespass. The loss of territory area to neighbours is a greater problem than outright eviction in many territorial species (mammals, Gosling 1986, 1990; reptiles, Stamps & Krishnan 1990, 1995; birds, Hunter 1987; Arcese 1989). Establishing borders by marking may also explain why territory borders remained largely unchanged on the study site despite changes in resident males (Arcese 1994). Males in this study marked at high rates along existing borders after a takeover, thus perpetuating the existing territory shape and size.

### Role of Subordinate Males

Territories defended by multimale groups were marked at higher rates than those of singletons primarily because subordinates contributed substantially to the number of marks. To the extent that dominant males reduce marking rates when subordinates are present, subordinates may reduce the time or energy that dominants expend in marking. Perhaps as a result of aid by subordinates in marking or other aspects of defence, dominant males were evicted less often from territories than singletons (Arcese 1999). Scent marking by subordinate males may constitute aid to dominant males if it reduces the rate of challenges by intruders. This might occur if marks appear at higher densities along borders defended by multimale groups as opposed to a single male, especially if marks provide information about the risk of intrusion to potential rivals. If scent marks are specific to individuals, marks from more than one male at a border also may suggest a queue for ownership to potential rivals, which might then choose to intrude on territories with fewer male defenders.

To test these hypotheses, future studies might reduce the number of marks along borders with the expectation of observing higher numbers of intrusions, higher marking rates by owners, or both. If scent marks serve as an honest signal of a male's intent to defend and maintain its territory, males that mark more often should suffer fewer challenges from rivals. In this case, we also might

expect to observe reduced marking by males coincident with increased age, deteriorating body condition, or the cumulative effects of injuries.

### Acknowledgments

The Directors General of the Serengeti Wildlife Research Institute and Tanzania National Parks kindly permitted us to work in Serengeti National Park. We thank C. Snowdon, N. E. Mathews, W. G. Holmes and two anonymous referees for comments on early drafts of the manuscript. M. Patterson, E. Patterson, J. Knocker, R. Knocker, S. Mduma and A. R. E. Sinclair provided much logistical support. Our work was supported by the College of Agriculture and Life Sciences at the University of Wisconsin, the Max McGraw Wildlife Foundation and by grants provided to P.A. by the USDA (Hatch grant no. N684), the Committee for Research and Exploration of the National Geographic Society (U.S.A.), and the National Science Foundation (IBN-9458122).

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