

Sex difference in the communicatory significance of localized defecation sites in Arabian gazelles (*Gazella arabica*)

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Abstract Mammalian scent marking in localized defecation sites (latrines) has often been interpreted in the context of (male) territory defense. However, latrines could have different functions in males and females, especially where territorial males monopolize groups of females with stable social alliances and pronounced home range overlap. We investigated the communicatory significance of latrines in wild Arabian gazelles (*Gazella arabica*) and assessed the spatial distribution of latrines within home ranges. Latrine density and utilization was highest in the center of female group home ranges, and less frequent in peripheral home range sections, pointing towards communication within groups rather than towards territoriality. When considering male home ranges, latrine densities and utilization were higher in non-overlap zones, contradicting a territorial function. This pattern appears to be caused by more

females than territorial males per given area establishing latrines. A subsequent survey of latrine utilization, based on camera trapping, suggests that males use latrines for territory defense: males visited latrines in overlap zones disproportionately more often than females, and successions of two males prevailed. Our study thus highlights that male territorial marking can be masked when males and females use the same marking system for different purposes.

Keywords Communication networks · Scent marking · Latrine · Over-marking · Camera trapping

Introduction

Olfactory signals play a central role in mammalian communication, and a widespread form of scent marking is localized defecation and urination in latrines (Kruuk 1995; Stewart et al. 2001; Ralls and Smith 2004; Wronski et al. 2006). Establishment of latrines and other forms of scent marking are considered to enable individuals (especially males) to signal territorial occupancy and their competitive ability towards neighboring territory holders, or intruding non-territorial males (Gosling 1982, 1985; Gosling and Roberts 2001a; Lewis 2005; Rosell and Thomsen 2006). To increase the likelihood of detection by other males, latrines are often established along territory boundaries—a pattern called peripheral marking that can be seen, e.g., in European badger (*Meles meles*: Kruuk 1978), oribi (*Ourebia ourebi*; Brashares and Arcese 1999a, b), Guenther's dikdik (*Madoqua guentheri*: Ono et al. 1988), or bushbuck (*Tragelaphus scriptus*: Wronski et al. 2006). Depending on the social system, additional functions of scent marking are possible, and the same kind of marking system can have more than one function (e.g., Lewis 2006). Jannett (1986),

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for instance, demonstrated that scent marking in male voles (*Microtus* sp.) not only serves intra-sexual information transfer but at the same time attracts females.

Mammalian females can use scent marking for inter-sexual information transfer where females inform males about their receptivity (pygmy marmosets, *Cebuella pygmaea*: Converse et al. 1995; mustached tamarins, *Saguinus mystax*: Heymann 1998; ring-tailed lemurs, *Lemur catta*: Kappeler 1998; bushbuck: Wronski et al. 2006). Scent marking in females can serve mate attraction and at the same time facilitate intra-sexual communication; e.g., females can signal their claim to monopolize opportunities for reproduction within a female group (house mouse, *Mus domesticus*: Hurst 1990a; mustached tamarins: Heymann 1998). In other species, females simultaneously scent mark to advertise their presence and to restrain other female group members from the marked resource (Sifaka, *Propithecus verreauxi*: Lewis 2005). Finally, just like males, females can also scent mark to defend their territories; this behavior is often seen in species forming monogamous pair-bonds like klipspringer (*Oreotragus oreotragus*: Dunbar and Dunbar 1980; Roberts and Dunbar 2000), Kirk's dikdik (*Madoqua kirkii*; Hendrichs 1975) and European beaver (*Castor fiber*: Rosell and Thomsen 2006).

Another form of latrine distribution besides peripheral marking is the marking of central parts of the home range (home site or core marking), which has been reported from a number of mammals such as klipspringer (Norton 1980), Guenther's dikdik (*Madoqua guentheri*: Ono et al. 1988), brown hyena (*Hyaena brunnea*: Mills et al. 1980) and meerkats (*Suricata suricatta*: Jordan et al. 2007). Communal marking of central home range sections is often related to home sites, such as dens or nests, or to key resources within the territory (brown hyena: Gorman and Mills 1984; spotted hyena, *Crocutta crocutta*: Mills and Gorman 1987; see also Electronic Supplementary Material, ESM). Functional explanations for core marking often consider a potential role for enhancing social bonds through information exchange between group members, e.g., in European rabbits (*Oryctolagus cuniculus*: Mykytowycz and Gambale 1969; Mykytowycz et al. 1976). Indeed, this form of latrine placement should be particularly suited for communication within groups, especially in species where female group members develop stable social alliances and show pronounced home range overlap. An open question in this context is whether males and females could use the same marking system (i.e., latrines) for different purposes, namely for territory defense in the male sex and for intra-group communication in females, which would lead to a sex difference in the spatial allocation of latrines, with more latrines being formed along territory margins by males, but more latrines being formed in core regions by females.

We investigated potential sex differences in the communicatory function(s) of latrines in the Arabian gazelle (*Gazella arabica*), which until recently was thought to be synonymous with its ecologically and behaviorally very similar sister species, the mountain gazelle (*G. gazella*) occurring on the Levant (Wronski et al. 2010; Lerp et al. 2012). In both species, males defend territories to monopolize groups of females (up to 16 individuals), while the members of female social groups (including their young up to 6 months of age) show pronounced home range overlap (Dunham 1998; Mendelssohn et al. 1995). A previous study from the Ibx Reserve in Saudi Arabia provided first insights into the distribution pattern of latrines in female group home ranges and found evidence for core marking (Wronski and Plath 2010), pointing towards a crucial function of latrines for communication among female group members. Detailed investigations of both male and female marking behavior, however, are still lacking, especially in large, natural populations (Thouless et al. 1991; Magin and Greth 1994; Mallon and Kingswood 2001).

We hypothesized that the primary function of latrines for males is territory demarcation, and that males could show peripheral marking as proposed for mountain gazelles (Grau and Walther 1976) and for related ungulates such as Thomson's gazelle (*Eudorcas thomsonii*: Walther 1978) and gerenuk (*Litocranius walleri*: Gosling 1981, 1982). Nevertheless, the higher number of females in Arabian gazelle male territories would have a stronger impact on latrine distribution patterns than the one male territory holder, and if females indeed use latrines for intra-group communication, most latrines would still be established in core areas. To unravel those two interwoven aspects of olfactory communication, we investigated latrine establishment by males and females in a large, natural population on Farasan Islands, while combining an analysis of spatial distribution patterns with behavioral observations of latrine utilization. We tested for sex-specific differences in frequencies of latrine visits and predicted that males visit latrines in territory overlap zones disproportionately more often than females; also, over-marking (Johnston et al. 1994; Ferkin 1999a, b) or counter-marking (Hurst 1987; Johnston et al. 1995) of scent marks should become apparent in overlap zones of two male territories.

Materials and methods

Study area and study species

The Farasan Archipelago is an assemblage of islands located in the Red Sea (16°20'–17°20'N, 41°30'–42°30'E). The climate is arid, with annual rainfall being highly

variable, ranging between 50 and 100 mm (Child and Grainger 1990). Large parts of the islands are weathered flat gravel plains incised by—often well-vegetated—wadis and other broken terrain (Flamand et al. 1988; Habibi and Thouless 1997). Our study was carried out on the main island, Farasan Kebir, between the Pleistocene coast line and the main road (Fig. 1). The study area (roughly 3 × 5 km) is situated west of Al Qisar and Miharraq Village, and comprises former gardens, open gravel plains, bare coral rock, and an extensive *Acacia* thicket (Wadi Matr; Fig. 1). Mountain and Arabian gazelles inhabit a wide range of habitats but prefer rocky, hilly, vegetated terrain (Baharav 1981, 1983) while avoiding open sand plains and dense forests (Mendelssohn et al. 1995).

In total, the population on Farasan Kebir nowadays numbers about 800–1,000 animals (Cunningham and

Wronski 2011a); the southern part of Farasan Kebir, in which our study area is situated, harbors around 70–164 gazelles (the study area itself has fewer gazelles), equaling approximately 1.4–3.2 animals per km² (extrapolated from ground surveys carried out between June 2009 and May 2011 using a strip width of 300 m on each side of the transect line; Cunningham and Wronski 2009, 2011a; Wronski and Alageel 2010a, b). Mountain and Arabian gazelles are territorial with high site-fidelity (Dunham 1999; Geffen et al. 1999), and male territories usually encompass the home ranges of several females whose home ranges show extensive overlap (Walther et al. 1983; Wronski and Plath 2010). Male and female Arabian gazelles were distinguished by their horn size (Wronski and Sandouka 2008). Farasan gazelles are characterized by a complete reduction or strong deformation of horns in the female sex.

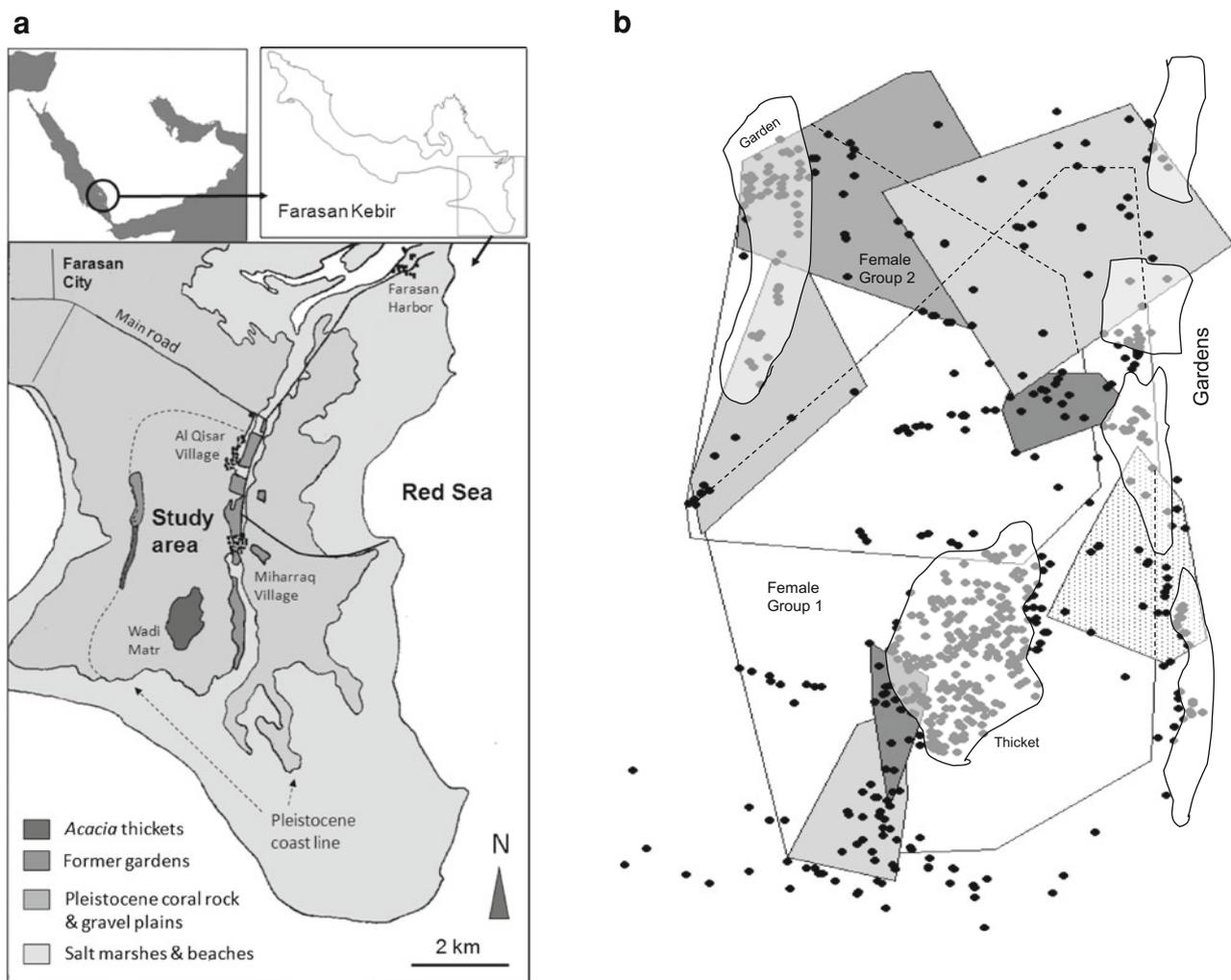


Fig. 1 a The Farasan Archipelago in the Red Sea and the study area within the southern part of Farasan Kebir. b Latrine distribution within two female group home ranges and seven male territories

(shaded areas). White, semitransparent areas indicate thickets and gardens. Depicted are 100 % MCP home range sections

Distribution patterns of latrines

Mapping latrines

Latrines were mapped between 26 March and 21 April 2009 by traversing the total study area on foot (in total 117.5 km). Open gravel plains were sampled systematically by the same two persons walking 54 transects (i.e. 2×27) approximately 25 m apart; densely vegetated areas were intensely searched by two persons while including as many trees, shrubs, and rocks as possible. Prior to the actual latrine survey, a test survey was carried out, and the perpendicular distances from a transect line to each latrine were determined. Distances were then tallied for belts of increasing distance from the count line, i.e. 5-m intervals (0–5, 5–10, 10–15 m, etc.). Thereafter, the number of latrines in each belt was inspected and the ‘fall-off’ point determined as 80 % of all sightings, resulting in a fixed strip width of 25 m on each side of the transect. GPS coordinates were recorded for 577 latrines using a Garmin 12 GPS, and positional data were later processed as UTM coordinates using a geographic information system (Arcview 3.2a in combination with Animal Movements; Hooge 1998).

To estimate how frequently individual latrines were used by gazelles, we determined their diameter as well as the numbers of fresh fecal pellet groups. We also noted the presence of urine or tracks, as well as obvious signs of male marking activity, i.e. scratches (Walther et al. 1983). To investigate the communicatory function of latrines in female and male Arabian gazelles, we concentrated on potential effects of their position in different home range sections and zones of overlap (or non-overlap) between home ranges (see “[Home range size and overlap](#)” below). As various ecological variables are known to affect latrine positions and utilization frequency (Attum et al. 2006; Attum 2007; Wronski and Plath 2010), we also determined the following ecological predictor variables for each latrine: We first carried out a rough habitat assessment in the vicinity (approx. 20 m) of each latrine including (1) habitat type/landscape unit (*Acacia* thicket, gravel plain, bare coral rock, salt marsh, drainage line or former garden; Habibi 1989) and (2) substrate type (sand, gravel, clay, grass, humus, rock) on which the latrine was established; we determined the following parameters for the closest tree: (3) its height, (4) distance to and (5) direction from the next latrine, as well as (6) percent canopy cover above the latrine; and, furthermore, we noted (7) distance to the next food plant (including all woody and non-woody plants) and (8) its height.

Home range size and overlap

In order to assign latrine positions to (9) female or male home range sections (see below) and (10) areas of home

range overlap, positional data of 28 individually known gazelles were taken. In total, the study area harbored about 53–139 females, organized in two social groups (Cunningham and Wronski 2009; Wronski and Alageel 2010a, b), of which 51 could be individually distinguished. A sufficient number of locations to calculate home ranges could be recorded for 21 females (15 females in group one: 6–19 sample points per individual for positional data; 6 females in group two: 7–23 sample points per individual) and 7 territorial males (16–26 sample points per individual). Contrary to gazelles in areas where densities are lower due to human pursuit (Walther et al. 1983; Wronski and Plath 2010), female groups on Farasan Islands were larger compared to those on the Arabian mainland (Cunningham and Wronski 2011b) and probably not based on relatedness, but rather on the use of communal resting sites such as Wadi Matr (Fig. 1). These large associations are probably not stable, contrary to the smaller family units (2–6 females) which are based on relatedness (Wronski and Plath 2010).

To obtain individual locations, daily patrols (between 0500 and 1100 hours and occasionally between 1700 and 1900 hours) throughout the study area were conducted from 26 March to 22 April, 3 June to 2 July, 7 to 18 October 2009 and from 10 to 19 February, 7 to 16 May and 14 to 20 June 2010 (in total 93 days). Gazelles were haphazardly encountered during these patrols and positional data recorded using a Garmin III GPS. Individuals were identified by external bodily characteristics such as horn length and shape, blood vessel patterns inside the ears, fur color, or other bodily characteristics such as scars or ear cuts, compiled in a file card system (after Walther et al. 1983).

From individual positional data, we generated minimum convex polygons outlining home range contours of males and females (Powell 2000). Outliers were removed with the aid of the harmonic mean method (Dixon and Chapman 1980). We assumed females to belong to the same group if overlap of their innermost home range section (i.e., the 30 % MCP home ranges) was evident (Wronski and Apio 2006). Group home ranges for the two female groups in our study area were then calculated using the total of all locations of all members of that group. Based on our home range data, we assigned latrine locations to female groups or solitary males and defined their locations as being within the <30, 31–70, 71–90, 91–100, and >100 % home range sections (Seaman and Powell 1996). Where home ranges overlapped between two neighboring female groups or solitary males, we scored the latrine as being in an overlap area and assigned it to one group or individual (for statistical purposes only), according to the innermost section that the latrine was inside, since that individual or group would be more likely to encounter that particular latrine (Darden

et al. 2008); such a case occurred only once though. If the latrine was in an overlap area with equal contours, the latrine was assigned to both female groups (55 cases) and to both male groups (13 cases).

Camera trapping

In another approach, we established numbers of latrine visits for males and females to test for a potential sex-bias in latrine use. Camera traps (Trailmaster, TM 1550) connected to Olympus cameras (Stylus 80) were used to record visits of gazelles at 15 latrines between June 2009 and May 2011 for a total of 285 days (i.e., approximately 6,840 continuous camera trapping hours); altogether, we recorded 320 latrine visits. For our analysis, we further distinguished between latrines in the overlap zone of the two female group home ranges (5 latrines, 62 days) and in the overlap zone of neighboring male home ranges (3 latrines, 50 days). The remaining 7 camera traps were located in neither overlap zone. Different habitat types were not considered when placing camera traps. The date and time of each visit were recorded by the camera.

Statistical analysis

Distribution patterns of latrines

Nearest neighbor data and count data were log-transformed to approximate normal distributions. Mean distance to the next two latrines (a correlate of latrine density), latrine size, and numbers of fresh fecal pellet groups per latrine (potential estimates of utilization frequency) were used as dependent (response) variables for step-wise backwards selection multiple regressions based on likelihood ratios; predictor variables [ecological variables (1–8), position in different home range sections (9), and home range overlap (10)] were excluded if $P > 0.10$. Likewise, the presence or absence of urine markings, tracks and scrapes were analyzed using comparable step-wise backwards selection logistic regression models. In order to establish the communicatory function of latrines in both sexes, the regression models were calculated separately for latrines located in male home ranges and those located in female group home ranges. Our main article reports on effects of the latrine position in different home range sections and home range overlap; significant effects of other (ecological) predictor variables are presented in the Electronic Supplementary Material (ESM).

Camera trapping

We tested for differences between observed and expected numbers of male and female latrine visits using a χ^2 test.

Expected values were calculated on the basis of the average sex ratio of our study population that was established during three counts throughout the entire study area (southern sector of Farasan Kebir; Cunningham and Wronski 2009; Wronski and Alageel 2010a, b).

In an attempt to record putative communication transfer through latrine use, we established four categories of presumed information exchange (Wronski et al. 2006). Categories were defined as successions of two different individuals (of the same or opposite sex) using the same latrine, partly representing cases of over-marking (Johnston et al. 1994, 1995; Ferkin 1999a, b): FF latrine use by a female entailing the ‘response’ of another female, MF latrine use by a male entailing a female to reply, FM vice versa, and MM latrine use by a male provoking another male to respond. While gazelles on the camera trapping images were not always individually recognizable (as described for home range analysis), we could unambiguously discern whether a latrine was successively used by the same or two different individuals by comparing scars, scratches, horn shape, ear cuts, and other marks. The mean (\pm SD) trapping interval was 13 h and 10 min \pm 20 h and 49 min. Observed numbers were tested against expected numbers of successions using a χ^2 test; the latter values were established on the basis of the overall sex ratio of gazelles photographed during the camera trapping survey. The proportions of males (and females) were squared to obtain expected, relative values for MM (and FF, respectively) while expected values for FM and MF were calculated by multiplying the proportion of males and females.

Results

Distribution patterns of latrines

Female group home ranges

We first considered distances between latrines as an estimate of latrine densities and found latrine density to be affected by the position of latrines within female group home ranges (i.e. home range sections; Table 1). Distances were largest in the outermost home range section [mean (\pm SE) distance, $>90\%$: 77.9 \pm 4.18 m, $n = 306$] but distinctly smaller in the inner sections ($<30\%$: 47.34 \pm 5.32 m, $n = 29$; 31–70%: 41.85 \pm 2.0 m, $n = 152$; 71–90%: 41.92 \pm 3.05 m, $n = 90$; Fig. 2); in other words, latrine densities were highest in the core sections of female group home ranges.

In a second step, we analyzed latrine size as a potential estimate for the age of a latrine (i.e., duration of utilization) and/or utilization frequency. Overlap between neighboring

Table 1 Results from step-wise backwards selection multiple regressions and logistic regressions for patterns of latrine distribution within female group home ranges

Multiple regressions	<i>B</i>	SE	<i>t</i>	<i>P</i>
(a) Distance to the next two latrines				
Habitat	20.634	1.712	12.053	≤0.001
Substrate	4.191	1.635	2.563	0.011
Distance to the next food plant	2.436	0.275	3.042	0.002
Home range section	5.337	1.755	3.042	0.002
(b) Latrine size				
Habitat	0.731	0.190	3.844	≤0.001
Substrate	0.686	0.126	5.529	≤0.001
Direction from the next tree	0.330	0.190	3.844	≤0.001
Distance to the next tree	−0.03	0.014	−2.118	0.035
Home range overlap	1.495	0.693	2.156	0.032
(c) Number of fresh fecal pellet groups				
Habitat	0.152	0.033	4.639	≤0.001
Direction from the next tree	0.076	0.016	4.717	≤0.001
Logistic regressions				
	<i>B</i>	SE	Wald	<i>P</i>
(d) Urine marks at latrine sites				
Substrate	0.143	0.063	5.214	0.022
Direction from the next tree	0.069	0.035	3.829	0.050
Home range section	−0.300	0.077	15.354	≤0.001
Home range overlap	−1.097	0.422	6.770	0.009
(e) Presence of tracks				
Substrate	0.547	0.093	34.729	≤0.001
Direction from the next tree	0.127	0.046	7.687	0.006
Canopy cover	−0.088	0.038	5.311	0.021
(f) Presence of scrapes				
Substrate	0.291	0.074	15.540	≤0.001

(a) Distance to the next latrine ($R^2 = 0.376$, all excluded variables: $P \geq 0.152$), (b) latrine size ($R^2 = 0.117$, excluded variables: $P \geq 0.380$), and (c) numbers of fresh fecal pellets ($R^2 = 0.077$, excluded variables: $P \geq 0.162$) were used as dependent variables

(d) Presence or absence of urine markings ($-2 \log\text{-likelihood} = 690.884$, Nagelkerke $R^2 = 0.089$), (e) presence or absence of male tracks ($-2 \log\text{-likelihood} = 697.464$, Nagelkerke $R^2 = 0.107$, excluded variables: $P \geq 0.118$), (f) presence or absence of male scrapes ($-2 \log\text{-likelihood} = 755.523$, Nagelkerke $R^2 = 0.073$, excluded variables: $P \geq 0.094$) were used as dependent variables

Factors were excluded if $P > 0.1$. Effects discussed in the main article are in bold; for descriptive statistics on the other effects shown here, see the ESM

female group home ranges had a statistically significant effect (Table 1), and latrines were distinctly larger in overlap areas [mean (\pm SE) size: $3.56 \pm 0.49 \text{ m}^2$, $n = 57$] than in areas with no overlap ($2.35 \pm 0.23 \text{ m}^2$, $n = 520$; Fig. 3).

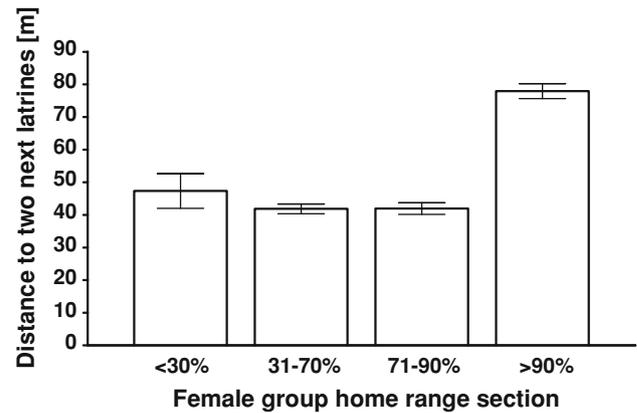


Fig. 2 The mean (\pm SE) distance (m) to the two nearest latrines (as an estimate for latrine densities) in the <30 % ($n = 29$), 31–70 % ($n = 152$), 71–90 % ($n = 90$), and >90 % ($n = 306$) sections of female group home ranges

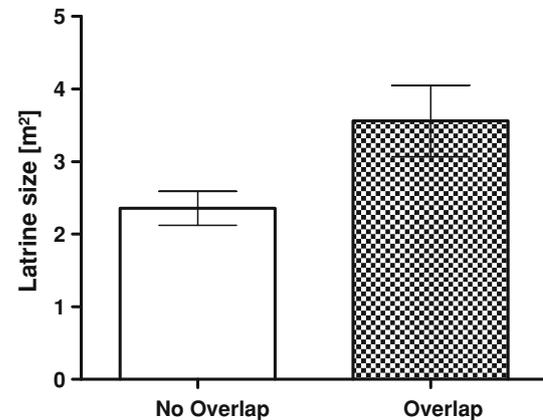
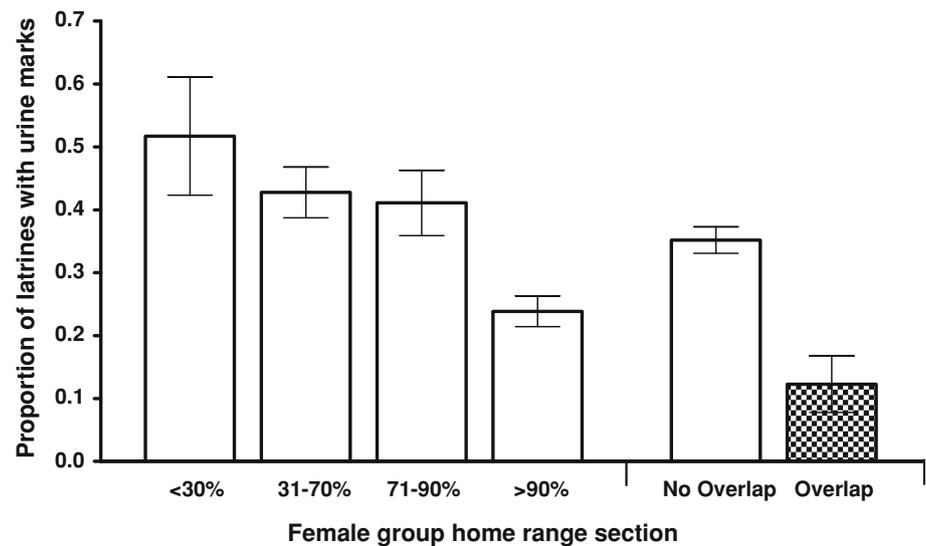


Fig. 3 Mean latrine size (\pm SE) for areas of overlap ($n = 57$) between female group home ranges and for areas where group home ranges do not overlap ($n = 520$)

As an estimate of the frequency of recent latrine use, we analyzed numbers of fresh fecal pellet groups in each latrine. No effects of the position of latrines relative to female group home range sections or overlap with neighboring groups was uncovered (Table 1). The presence of urine marks in latrines is another clear indication of recent use. Significant effects of (1) the position in different female group home range sections and (2) overlap between neighboring female group home ranges were uncovered (Table 1). The percentage of latrines with urination marks was highest in the inner home range section (<30 %: 0.52 ± 0.10 , $n = 29$), followed by the 31–70 % (0.43 ± 0.04 , $n = 152$) and 71–90 % sections (0.41 ± 0.05 , $n = 90$) and was lowest in the peripheral areas (>90 %: 0.24 ± 0.02 , $n = 306$; Fig. 4). Moreover, the mean (\pm SE) proportion of latrines that were recently used for urination was higher in non-overlap zones (0.35 ± 0.02 , $n = 520$) than in areas of home range overlap (0.12 ± 0.05 , $n = 57$; Fig. 4).

Fig. 4 The proportion of latrines with fresh urine markings (mean \pm SE) as an estimate for the frequency of latrine use shown for the <30 % ($n = 29$), 31–70 % ($n = 152$), 71–90 % ($n = 90$) and >90 % ($n = 306$) home range sections of female group home ranges and for areas of female group home range overlap ($n = 57$) and no overlap ($n = 520$)



Neither the presence of tracks nor scrapes at latrines were affected by the position of latrines relative to the home range section within female group home ranges, nor overlap between neighboring female group home ranges (Table 1).

Male home ranges

In only two cases—when considering the latrine density and the presence of tracks—was a statistically significant effect of male home range overlap uncovered (Table 2): latrine densities were higher and more tracks were found in non-overlap areas (mean distance between latrines: 59.64 ± 2.45 m, $n = 559$; presence of tracks: 0.63 ± 0.02 , $n = 559$) than in areas where male home ranges overlapped (mean distance: 111.97 ± 16.97 m, $n = 18$; Fig. 5a; presence of tracks: 0.44 ± 0.12 , $n = 18$; Fig. 5b).

Camera trapping

Frequency of LDS use

We tested for a sex-bias in latrine use and asked whether there are differences in the frequency of latrine use in the overlap area of female groups or solitary male home ranges. Based on three census counts of Farasan gazelles the overall sex ratio (female:male, including non-territorial bachelor males that roam the area in search of an opportunity to take over a territory) was determined as about 1:0.44 in the southern part of Farasan Kebir (Cunningham and Wronski 2009, 2011b; Wronski and Alageel 2010a, b), which was taken as the expected sex ratio for latrine visits if no sex-bias in latrine use was apparent. The sex ratio observed at latrines during our camera trapping survey was slightly more biased (1:0.56; 179 female visits: 100 male

visits), but a χ^2 test revealed no statistically significant difference between expected and observed ratios ($\chi^2 = 3.807$, $df = 1$, $P = 0.051$; Fig. 6a, b).

When considering only the latrines located in areas where the 71–90 % home range sections of different female groups overlapped, the sex ratio was not significantly different from expected values (1:0.53; i.e., 32 female visits:17 male visits; $\chi^2 = 0.36$, $df = 1$, $P = 0.55$; Fig. 6a). When considering only those latrines that were located in areas where the 71–90 % home range sections of territorial males overlapped, however, the observed sex ratio was 1:8.5 (i.e., 2 female visits:17 male visits), and a χ^2 test revealed a statistically significant deviation from the expected ratio ($\chi^2 = 39.09$, $df = 1$, $P < 0.001$; Fig. 6a).

Information exchange through latrines

In total, 246 observations of putative information exchange (inferred from observed successions of two different individuals utilizing the same latrine, possibly evoking over-marking) were obtained from camera trapping sessions at 15 latrines. The expected number of such potential incidences of information exchange based on observed sex ratios at latrines was 12.9 % for a male entailing the response of another male (MM), 23 % for latrine use by a female causing a male to respond or vice versa (FM, MF), and 41.2 % for signals sent by a female provoking another female's response (FF). A χ^2 test showed a significant deviation between observed and expected values with the category MM being far more frequent than expected and the categories FM and MF being less frequent than expected [MM: 53 (21.5 %); FM: 44 (17.9 %); MF: 42 (17.1 %); FF: 107 (43.5 %); $\chi^2 = 21.36$, $P < 0.001$, $df = 3$; Fig. 6b]. These results indicate that signals sent by an individual mainly elicit a response of other individuals

Table 2 Results from step-wise backwards selection multiple regressions and logistic regressions for patterns of latrine distribution within male group home ranges

Multiple regressions	<i>B</i>	SE	<i>t</i>	<i>P</i>
(a) The next two latrines				
Habitat	9.414	1.357	6.937	≤0.001
Substrate	7.735	1.794	4.312	≤0.001
Distance to the next food plant	2.578	0.307	8.396	≤0.001
Canopy cover	1.830	0.900	2.033	0.042
Home range overlap	48.151	12.441	3.870	≤0.001
(b) Latrine size				
Habitat	0.279	0.133	2.104	0.036
Substrate	0.673	0.125	5.401	≤0.001
Direction from the next tree	0.352	0.081	4.351	≤0.001
Distance to the next food plant	0.060	0.029	2.052	0.041
(c) Number of fresh fecal pellet groups				
Habitat	0.156	0.032	4.825	≤0.001
Direction from the next tree	0.066	0.016	4.062	≤0.001
Logistic regressions				
(d) Urine marks at latrine sites				
Habitat	0.231	0.068	11.433	0.001
Substrate	0.175	0.064	7.411	0.006
Direction from the next tree	0.120	0.038	9.953	0.002
(e) Presence of tracks				
Habitat	0.206	0.086	5.802	0.016
Substrate	0.490	0.090	29.680	≤0.001
Direction from the next tree	0.118	0.043	7.386	0.007
Home range overlap	-1.354	0.519	6.808	0.009
(f) Presence of scrapes				
Substrate	0.289	0.081	12.691	≤0.001
Direction from the next tree	0.108	0.035	9.776	0.002

(a) Mean distance to the two next latrines ($R^2 = 0.232$, all excluded variables: $P \geq 0.203$); (b) latrine size ($R^2 = 0.097$, all excluded variables: $P \geq 0.236$); and (c) numbers of fresh fecal pellets ($R^2 = 0.074$, excluded variables: $P \geq 0.128$) were used as dependent variables

(d) Presence or absence of urine markings ($-2\log\text{-likelihood} = 700.514$, Nagelkerke $R^2 = 0.070$, excluded variables: $P \geq 0.213$); (e) presence or absence of male tracks ($-2\log\text{-likelihood} = 692.972$, Nagelkerke $R^2 = 0.152$, excluded variables: $P \geq 0.483$) and (f) presence or absence of male scrapes ($-2\log\text{-likelihood} = 752.509$, Nagelkerke $R^2 = 0.081$, excluded variables: $P \geq 0.113$) were used as dependent variables

Effects discussed in the main article are in bold; for descriptive statistics on the other effects shown here, see the ESM

of the same sex, pointing towards an important function of latrines for intra- rather than inter-sexual communication.

When considering only latrines located in the overlap zone of female group home ranges there was no statistically significant deviation from the expected frequency distribution [MM: 6 (18.2 %); FM: 9 (27.3 %); MF: 7 (21.2 %); FF: 11 (33.3 %); χ^2 test: $\chi^2 = 1.53$, $df = 3$,

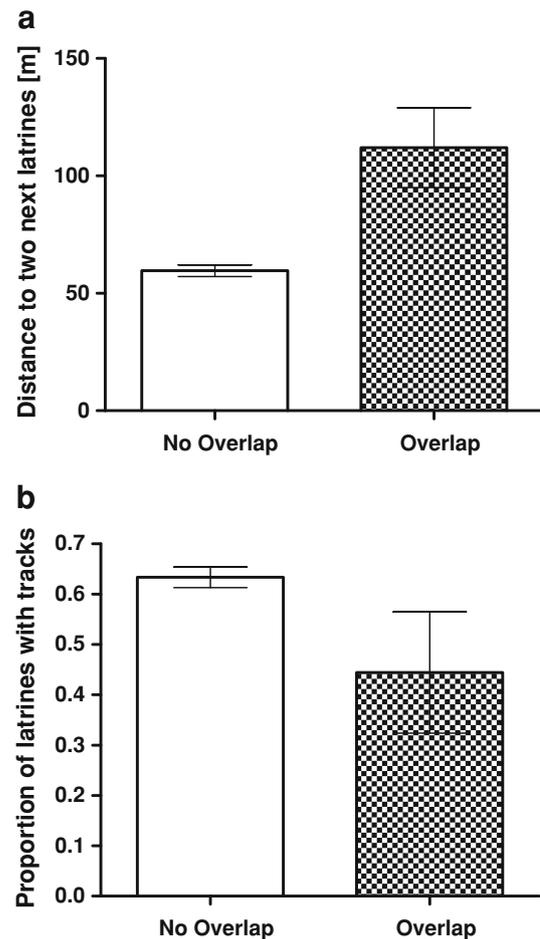


Fig. 5 **a** Mean distances (m) (\pm SE) to the two nearest latrines (as an estimate for latrine densities) in areas of male home range overlap ($n = 18$) and no overlap ($n = 559$). **b** The proportion of latrines with tracks (mean \pm SE) as an estimate for frequency of latrine use shown for areas of male home range overlap ($n = 18$) and no overlap ($n = 559$)

$P = 0.68$; Fig. 6b]. However, in the case of latrines situated in the overlap zone of male territories, a significant deviation was found, and the category MM was by far the most frequent succession [MM: 13 (86.7 %); FM: 1 (6.6 %); MF: 1 (6.6 %); FF: 0; $\chi^2 = 73.28$, $P < 0.001$, $df = 3$; Fig. 6b], corroborating the assumption that latrines play a role in the territorial marking behavior of males.

Discussion

As predicted, latrine densities were highest in the central portion of female group home ranges (i.e. areas where females spend most of their time), where markings are more likely to be detected by other female group members, rather than in the peripheral (or overlap) parts. Successions of two individuals of the same sex visiting the same latrine

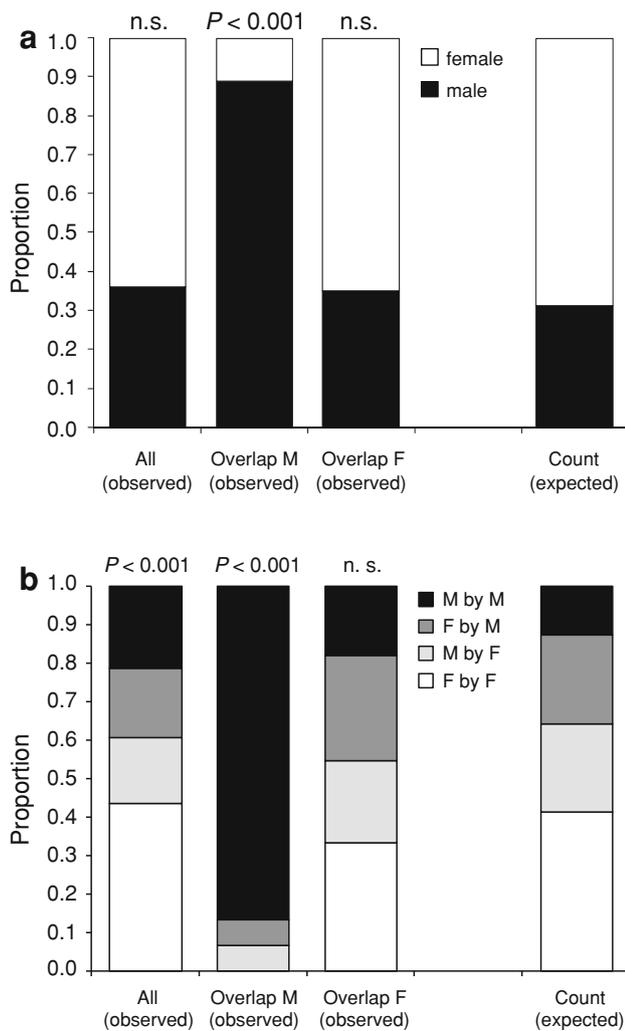


Fig. 6 a The frequency of latrine use by male and female Farasan gazelles averaged over all latrines, at latrines located in the overlap of female group home ranges, and at latrines located in the overlap of home ranges of territorial males. Also depicted is the expected sex ratio obtained from three gazelle counts in the study area. **b** Information exchange through latrines for signals sent by a female entailing the response of another female (*F by F*), signals sent by a male entailing a female to reply (*M by F*), signals sent by a female causing a male to respond (*F by M*), and for signals sent by a male provoking another male to respond (*M by M*). Proportions are shown for all latrines, latrines located in the overlap of female group home ranges, and for latrines located in the overlap of home ranges of territorial males. Also depicted are the expected proportions for the four categories of information exchange, calculated from the observed sex ratio

in home range overlap zones—possibly including over-marking (Somers et al. 1990; Johnston et al. 1994; Ferkin 1999a, b; Brashares and Arcese 1999a, b; Roberts and Dunbar 2000) or counter-marking (Hurst 1987, 1990b; Johnston et al. 1995)—occurred more frequently than expected by chance in the case of male, but not female home range overlap zones.

Our results point towards an important function of latrines for communication amongst the members of female social groups. It has been demonstrated for other mammalian species that communication among female group members via feces can be related to resource defense (Roberts and Dunbar 2000) and/or the advertisement of social and reproductive status (Heymann 1998). Additionally, latrines can enhance confidence among group members by allowing individuals to familiarize within the shared group home range (Mykytowycz and Gambale 1969; Mykytowycz et al. 1976; Ikeda 1984). Individual olfactory cues associated with excreta play an important role in the discrimination between related and non-related individuals (kin-discrimination), e.g., in Columbian ground squirrel (*Urocitellus columbianus*: Raynaud and Dobson 2011), or Gidgee skink (*Egernia stokesii*: Bull et al. 2000). Especially the communal use of localized defecation sites in the center of group home ranges facilitates information exchange between all group members. By regularly visiting latrines, individuals can thus “update” their knowledge about group members, e.g., concerning their social or sexual status. Thus, latrine use may help to maintain dominance hierarchies and internal group-bonds and, therefore, can increase the social cohesion within a group. This has been shown for ring-tailed lemurs (*Lemur catta*: Ramsay and Giller 1996), coypus (*Myocastor coypus*: Gosling and Wright 1994) and mice (*Mus musculus*: Gosling et al. 1996).

How can this line of interpretation be reconciled with the observation of latrines being larger in overlap zones between different female group home ranges? One might be tempted to argue that communication between female groups also plays a role, leading to larger latrine dimensions over time. Other data from our present study, however, do not support this interpretation. Moreover, size as a presumed indicator of current latrine use needs to be carefully reevaluated. As discussed in the ESM, latrine dimensions are strongly influenced by several ecological predictor variables, and overlap zones coincide with less preferable habitat types (e.g., gravel plains). Here, only very few latrines are formed in selected areas, probably resulting in an increased accumulation rate and, thus, increased dimensions over time.

Theoretically, an alternative explanation for core marking in Arabian and mountain gazelles (Wronski and Plath 2010; this study) would be that females, just like males, attempt to demarcate territories, but territory dimensions could just be too large for efficient peripheral marking, so demarcation of the central portion of the home range—from an economic point of view—would be a more suitable solution (gerenuk: Gosling 1981; klippspringer: Roberts and Lowen 1997; meerkats: Jordan et al. 2007; general review: Gosling and Roberts 2001b). Individual

home ranges in mountain and Arabian gazelles, however, are rather small and measure between 0.22 and 2.46 km² (Baharav 1983; Walther et al. 1983; Dunham 1998; Wronski 2010), so home range dimensions certainly do not preclude peripheral marking. This interpretation receives support from the observation that males (unlike females) regularly patrolled latrines in overlap zones.

The spatial distribution pattern of latrines uncovered in this study at first sight seems to negate any information exchange between territorial males, as no accumulation of latrines at the periphery of male home ranges was uncovered. However, results obtained from camera trapping suggest that latrines located in overlap zones of male territories were almost exclusively visited by males (Fig. 6a) and the rate of marking (i.e., defecation, urinating, or scraping) was higher (24 % of all visits) than in overlap zones between female home ranges (13 % of all visits). In non-overlap zones the rate of marking was similar (25 % of all visits) to that observed in the overlap zone between male territories. Moreover, our analysis of presumed information exchange through latrines along borders of male territories revealed that signals sent by a male mostly provoked another male to respond (MM; Fig. 6b). We argue that large parts of male territory borders are located on gravel plains and, thus, in a non-preferable habitat type (see ESM), preventing males from establishing more peripheral latrines. Also, any bias towards establishment of more peripheral latrines by territorial males will be masked by more latrines being established in core areas by the much larger number of females. Likewise, the fact that numbers of fresh tracks were higher in non-overlap areas of male home ranges (Fig. 5b) can be attributed to the biased sex ratio in male home ranges, as females will use the same latrines as the territory holder. However, from our current data, we cannot draw conclusions on the role of bachelor males, i.e. non-territorial males, in this marking system. It remains unclear to what degree bachelor use latrines for communication and at what scale they interfere with the marking scheme of territorial males. Scent marking in non-territorial adult males could function as an alternative mating tactic informing potential mates and male territory holders about their presence and status. Eventually, such adult bachelor males thus challenge territory holders and attempt to take over territories (Apio et al. 2007).

In summary, both sexes of Arabian gazelles use latrines within the same area for communication purposes, but our results suggest different functions of latrine use for males and females: (1) a primarily non-territorial communicatory context for females, which appear to communicate primarily with other members of their social groups, and (2) a territorial context for males, which communicate with other territory holders (or non-territorial males that challenge territory holders) via latrines at the periphery of

territories. An olfactory association between the resident and the defended area may allow intruders to not only identify the resident but also assess its resource holding potential (e.g., by checking how readily the territory holder will counter-mark), and thus reduce the frequency of escalated agonistic encounters (scent-matching; Gosling 1982; Gosling and Roberts 2001a). Our study highlights how territorial marking can be masked when males and females use the same marking system for different purposes.

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Ethical standards Our experiments comply with the current laws of the Kingdom of Saudi Arabia and the ethical standards of the Zoological Society of London.

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