



The role of middens in white rhino olfactory communication

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White rhinos, *Ceratotherium simum*, use dung odours to transmit information about their sex, age, territorial status (males) and oestrous state. Moreover, as white rhinos defecate in communal middens (i.e. dung heaps, or latrines) it has been suggested that these middens may act as information centres. However, it is uncertain which individuals primarily transmit information via middens, or for whom this information is intended. Using video-recording camera traps, we investigated the behaviour of white rhinos at middens. We hypothesized that territorial adult males would visit, defecate and sniff other dung more than other adults. In line with this, we found that they visited and defecated more than other individuals. Moreover, territorial males and potential male challengers were the main individuals to investigate dung piles. These olfactory investigations focused primarily on territorial male and adult female dung (male–male and female–male communication). Although investigating less often, investigation by adult females and subordinate males was also focused on territorial male and female dung, suggesting male–female and female–female communication. In addition to olfactory signals, there was a spatial aspect to midden use, where territorial males defecated only in the centre of a midden, while other individuals defecated primarily around the periphery. Yet, subordinate males also tended to defecate in the centre, suggesting an indication of residency. Lastly, territorial males defecated more frequently than any other adult, and were able to do so by regulating their dung output (i.e. producing smaller volumes per deposit). Our results indicate that middens act as information centres, where the primary function seems to be for territorial males to transmit and obtain information. However, non-territorial males may also assess female reproductive state, while females may be assessing the quality of all males, and the number of other females using a midden. Ultimately, our results highlight the importance of middens in white rhino communication.

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Many mammals use olfactory cues to communicate information including kin recognition (Stoffel et al., 2015), reproductive status (Archunan & Rajagopal, 2013) and territory ownership (Barja, de Miguel, & Bárcena, 2005). This information can be transmitted via scent glands (Cross, Zedrosser, Nevin, & Rosell, 2014; Vaglio et al., 2016), urine (Archunan & Rajagopal, 2013; Kimura, 2001) and/or dung (Karthikeyan, Muniasamy, SankarGanesh, Achiraman, & Archunan, 2013; Marneweck, Jürgens, & Shrader, 2017a). As many mammals defecate in communal middens (i.e. dung heaps, or latrines), it has been suggested that these middens may act as information centres (Eppley, Ganzhorn, & Donati, 2016; Rodgers, Giacalone, Heske, Pawlikowski, & Schooley, 2015). Middens can

be found in the centre of a territory or home range (e.g. swift fox, *Vulpes velox*; Darden, Steffensen, & Dabelsteen, 2008) or along the boundary (e.g. oribi, *Ourebia ourebi*; Brachares & Arcese, 1999). Further, the location of a midden has implications for its function. For instance, middens at the edge of a territory are probably used more for territorial marking, whereas middens in the centre may be used for social group communication (Dröscher & Kappeler, 2014; Jordan, Cherry, & Manser, 2007).

Middens of several ungulate species are utilized by both sexes: for example, dik-diks, *Madoqua kirkii* (Hendrichs & Hendrichs, 1971), klipspringers, *Oreotragus oreotragus* (Dunbar & Dunbar, 1974), bushbucks, *Tragelaphus scriptus* (Wronski, Apio, & Plath, 2006) and Arabian gazelles, *Gazella arabica* (Wronski, Apio, Plath, & Ziege, 2013). Although these species utilize middens, their mating strategies differ. Specifically, dik-diks and klipspringers are facultatively monogamous (Brotherton & Manser, 1997; Roberts & Dunbar, 2000), whereas bushbucks and Arabian gazelles are

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polygynous (Wronski, 2005; Wronski et al., 2013). However, even when species share a mating strategy, the ways in which they utilize middens can differ. For example, polygynous bushbucks use middens for intersexual communication (i.e. male–female communication; Wronski et al., 2006), while polygynous Arabian gazelle middens have a dual function of both male territorial defence (i.e. male–male communication) and within-female group communication (i.e. female–female communication; Wronski et al., 2013).

White rhinos, *Ceratotherium simum*, employ a polygynous mating strategy where adult males defend a territory and monopolize mating opportunities with multiple females (White, Swaisgood, & Czekala, 2007). They do this by defending small territories (average 1.65 km²) that are part of larger, overlapping female home ranges (average 11.6 km²; Owen-Smith, 1973, 1975). Thus, one female home range incorporates a number of male territories. Within their territories, white rhino males can have more than 30 middens (Owen-Smith, 1973) distributed across the landscape (Kretzschmar, Ganslosser, Goldschmid, & Aberham, 2001). However, these middens tend to be concentrated around frequented paths, water holes and territory boundaries (Owen-Smith, 1975), as in black rhinos, *Diceros bicornis* (Schenkel & Schenkel-Hulliger, 1969) and Indian rhinos, *Rhinoceros unicornis* (Laurie, 1982). Their placement tends to suggest that a key function of middens is territorial marking, and thus they are probably primarily utilized by territorial males. However, individuals of both sexes of white rhinos defecate in middens (Owen-Smith, 1973). Moreover, as white rhinos transmit information about their sex, age, male territorial status and female oestrous state in the odour of their dung (Marneweck et al., 2017a), it is likely that these middens act as information centres. It is unclear, however, whether these middens are utilized equally by the different sex and age classes (e.g. males, females, territorial males, subordinate males), or whether the information is only utilized by specific individuals (e.g. territorial males).

The key information transmitted by white rhinos in their dung odours (i.e. territory ownership and oestrous state; Marneweck et al., 2017a) is related to breeding opportunities. Therefore, it is likely that adults are the key utilizers of middens. Territorial males should use middens to both advertise territory ownership and search for mates (Brachares & Arcese, 1999; Wronski et al., 2006). Although it was originally thought that territorial male white rhinos monopolized mating, sneaky copulations by nonterritorial males can occur (Guerier, Bishop, Crawford, Schmidt-Kuntzel, & Stratford, 2012), suggesting that these males could also use middens as a way to search for mates. Nonterritorial males can be divided into two categories: those living within a territory but not challenging the territorial male for ownership (i.e. subordinate), and those that are passing through a territory gathering information with the potential of challenging a territorial male for territory ownership (Dunham, Warner, & Lawson, 1995; Owen-Smith, 1973). Based on their different priorities, these nonterritorial males are likely to behave differently at middens. For example, subordinate males may investigate female dung looking for sneaky mating opportunities, whereas visiting males may investigate the territorial male's dung to assess his condition. In addition to males, females probably also obtain information as well as deposit it within middens. In contrast to males, females do not maintain exclusive home ranges (Rachlow, Kie, & Berger, 1999), or compete for mates with other females (Owen-Smith, 1973). However, they may use middens to assess male quality, especially if mating occurs outside of territory ownership.

Although white rhino middens appear to be a simple collection of dung, there seems to be some degree of order with regard to the placement of dung within these middens (Owen-Smith, 1973).

Specifically, Owen-Smith (1973) suggested that territorial males tended to defecate in the centre of middens, while adult females and subadults defecated around the periphery. As white rhino middens are large (up to 30 m diameter; average diameter at largest length 7 ± 0.29 m, $N = 149$; Marneweck, Jürgens, & Shrader, 2015), spatial distribution of this kind is possible. If this is the case, then perhaps there is not only an olfactory component to dung-mediated communication, but also a spatial component of dung placement within middens that further facilitates information transfer. At a larger spatial scale, there can be more than 30 middens within a male's territory, and these males defecate in a number of these middens daily (Owen-Smith, 1973). As dung is a limited resource, a question that then arises is how they achieve this. It is possible that, to maximize the distribution of dung, males regulate their dung output, relative to nonterritorial males and adult females. This behaviour has been reported for male oribi antelope (Brachares & Arcese, 1999). If so, then by limiting dung output per defecation, territorial male white rhinos would be able to increase the number of marking events, and thus mark a greater total area.

With the above points in mind, we hypothesized that: (1) territorial males would visit and defecate in middens more frequently than other adults (i.e. nonterritorial males or adult females); (2) as territorial males obtain a majority of the breeding opportunities, they should spend more time investigating (i.e. sniffing) dung within middens compared to other adults (i.e. nonterritorial males or females), and focus this investigation on the dung from adult females; (3) territorial males would regulate their dung output, relative to nonterritorial males and adult females, to increase marking events, despite their larger body size (2300 kg compared to 1600 kg for adult females; Owen-Smith, 1988) and thus greater potential dung output; (4) only territorial males would defecate in the centre of the middens.

METHODS

Behavioural Data Collection

We conducted this study in the 896 km² Hluhluwe-iMfolozi Park (HiP), KwaZulu-Natal, South Africa (−28.219853 S, 31.951865 E; Fig. 1), from November 2014 to August 2015. This resulted in approximately 5 months of wet season data (November 2014 to March 2015) and 5 months of dry season data (April 2015 to August 2015) for each midden. The average territory size of a white rhino in HiP is 1.65 km² (Owen-Smith, 1975). Therefore, to help ensure separation, we selected focal middens that were separated by at least 2 km. Video footage of the territorial males utilizing these middens indicated that the middens were in fact in separate territories. To record midden visits and use, we set up motion-triggered video-recording camera traps at 10 middens, each with a different resident territorial male (identified via differences in horn shape and size). We used infrared camera traps (either Cuddeback Black Flash E3 or Cuddeback Attack Black Flash 1194, Cuddeback, Green Bay, WI, U.S.A.) placed approximately 3 m from the edge of the midden to allow a sufficient field of view. These cameras do not emit visible light or have a flash, creating minimal disturbance at the midden and therefore allowing us to capture natural behaviour. We programmed the cameras to record 30 s videos at each trigger with a 1 s delay before becoming active again.

We recorded data on all the individuals that visited the middens. From 2403 data videos, we created an ID profile for each white rhino ($N = 233$ individuals), so that we could record individual visits, defecation and olfactory investigation. When individuals sniffed specific dung piles, we determined the age and sex of the white rhino that deposited the dung by reviewing previous

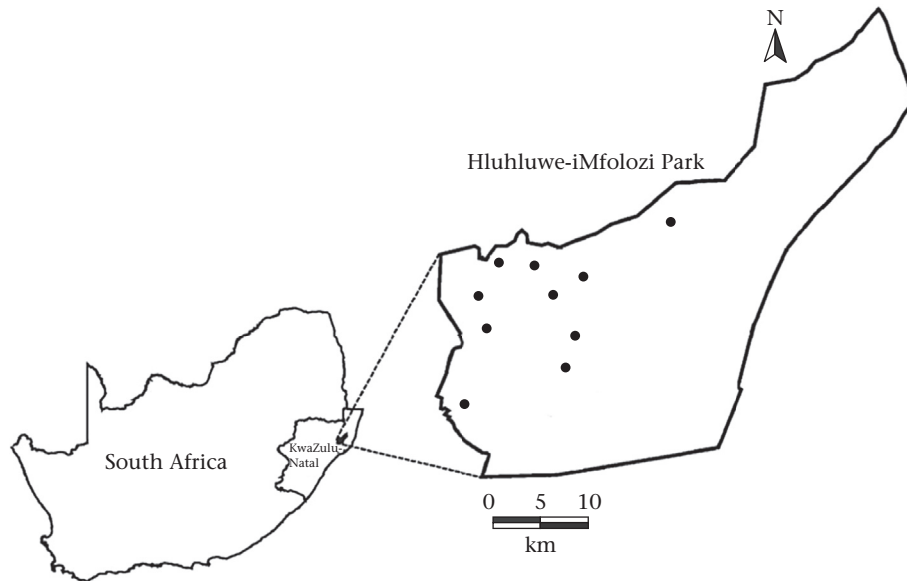


Figure 1. Location of Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa. Dots represent focal midden sites ($N = 10$).

video footage. Adults were identified as individuals >7 years old, subadults as 2–7 years old, and calves as <2 years old, based on body size and horn development (Hillman-Smith, Owen-Smith, Anderson, Hall-Martin, & Selaladi, 1986). Territorial males were identified as adult males performing territorial behaviours (i.e. dung kicking, spray urinating) at the middens, and nonterritorial males as adult males not performing these behaviours (Owen-Smith, 1973; Pienaar, Bothma, & Theron, 1993, 1971; Rachlow et al., 1999).

Living within a white rhino territory, there are often one or two subordinate adult males whom the territorial male tolerates (Owen-Smith, 1973). These males do not help defend the territory, nor do they try and challenge the territorial male for territory ownership (Owen-Smith, 1973). Challenges for territory ownership tend to come from lone adult males entering the territory (Dunham et al., 1995; Owen-Smith, 1973). Yet, these visits are infrequent (Owen-Smith, 1973, 1975). To distinguish these two types of non-territorial males, we identified subordinate males as lone, non-territorial adult males that were relatively frequent visitors to the middens (i.e. visiting on $>5\%$ of camera-active days) but did not perform territorial behaviours (e.g. dung kicking). Potential challengers were identified as lone, nonterritorial adult males that infrequently visited middens (i.e. visiting on $<5\%$ of camera-active days) and occasionally performed territorial behaviours. We generated the 5% cutoff based on the visit data. In our study, we found a clear divide in the midden visits by nonterritorial males, with ‘frequently’ seen individuals visiting on average for $9 \pm 1.3\%$ of the observation period (average 222 days) and ‘infrequent’ visitors visiting only for $1 \pm 0.1\%$ of the observation period. In contrast, territorial males visited the middens for $20 \pm 3.8\%$ of the observation period.

The oestrous state of adult female white rhinos can be determined by the behaviour of territorial males. Specifically, when a female is in oestrus, a territorial male moves with her and tries to prevent her from leaving his territory (Owen-Smith, 1973; Pienaar et al., 1993). Moreover, the territorial male will attempt to rest his chin on her flank and eventually mount her (Owen-Smith, 1973). Unfortunately, despite observing territorial males following oestrous females (C. Marneweck, personal observation), we did not record these sorts of behaviours at the middens with the camera

traps. As a result, we could not determine oestrous state, and thus grouped all adult females together for analysis.

Statistical Analysis

For all linear mixed-effects models, we tested that the assumptions of a linear model were met using the diagnostics normal QQ plot, residual-fitted plot and histogram for model residuals. For all models, we also tested for collinearity between the fixed factors of age and sex, of which there was none ($VIF = 1.1$). However, as the third fixed factor (state) utilizes a subset of the data (adults only), model selection and comparison via AIC values was not possible. Thus, for all following analyses, we created two models: one for age and sex, and a second for state using a subset of the data.

Visit and defecation frequency

We calculated individual visit and defecation frequency by dividing the number of visits or defecations by the number of days the camera was active (range 172–282 days). To assess differences in midden visit and defecation frequency for each age and sex, we ran a linear mixed-effects model using the R package nlme (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2015). We set visit or defecation frequency as the response variable, age and sex, plus their interaction, as fixed factors; and rhino ID as a random factor. We then repeated this with adult state as the fixed factor (i.e. territorial male, subordinate male, potential challenging male, or female).

Information acquisition

For analysis of information acquisition, we recorded each midden visit ($N = 1675$) with a yes or no regarding olfactory investigation (i.e. acquiring information). We defined olfactory investigation as standing still and sniffing a dung pile (nose <20 cm from ground with nostril flares). To investigate which age and sex deposited or acquired information most often during their visits, we ran a generalized linear mixed-effects model with a binomial distribution using the R package lme4 (Bates, Maechler, Bolker, & Walker, 2015). We set the number of visits containing investigation as the response variable, age and sex, plus their interaction, as fixed factors; and rhino ID as a random factor. As above, we then

repeated this with adult state as the fixed factor (i.e. territorial male, subordinate male, potential challenging male, or female).

After each olfactory investigation event, we looked back into the video log to identify the depositor of the dung pile. By doing this, we were able to identify the depositor of 593 of 772 (77%) of the sniffed dung piles, and thus limited our analysis to these 593 data points. To assess which adult dung piles were investigated by each adult state (i.e. territorial male, subordinate male, potential challenging male, or female), we ran a generalized linear mixed-effects model with a binomial distribution. We set state of the investigator as the response variable, sex of the dung depositor as the fixed factor, and rhino ID as a random factor. We then repeated this same analysis but used state of the dung depositor as a fixed factor. Further, to assess the difference in the proportions of adult dung piles that were investigated by each adult state, we conducted a chi-square test with post hoc comparisons.

Dung weight

To compare the weights of the dung piles deposited, we collected 40 whole dung samples from different adult white rhinos (territorial males $N = 12$, nonterritorial males $N = 10$, oestrous females $N = 4$, nonoestrous females $N = 14$) between January and May 2015. We followed individuals on foot (two people: one researcher and one armed guard) until defecation occurred so we were able to record territorial and oestrous state from observed behaviour (Pienaar et al., 1993; Rachlow et al., 1999). However, we were unable to classify nonterritorial males as either subordinate or potential challengers and thus grouped them together for analysis.

Territorial males spread their dung by kicking after defecation (Owen-Smith, 1973). As a result, it is not as easy to collect as the dung deposited by females and nonterritorial males. However, as the dung was fresh (<5 min from defecation), the temperature, colour and moisture of the dung made it easily distinguishable from older dung in the midden. We spread and dried each dung pile in direct sunlight for 72 h and then weighed the contents to determine dry weight. As data were not normally distributed, we performed a Kruskal–Wallis with post hoc Dunn's test to explore any differences in dry weight.

Defecation location

Finally, from 433 observed defecations, we recorded the locations of dung piles according to each midden's dimensions and categorized them as centre, midrange, edge or outside the midden. Middens are often ellipses, and the average diameter of the widest part was 7.7 m (range 5–10 m) and that of the narrowest part 5.5 m (range 3–8 m). The average area of the middens was 34.1 m² (range 15.7–50.3 m²). They are located on flat ground with the centre indicated by a depression created by the kicking of territorial males while they defecate (Owen-Smith, 1973). We divided each midden into zones of approximate thirds. For small middens (<30 m²), we classified the centre as a 1.5 m radius around the centre point, the midrange as a 1.5–3 m radius from the centre point, and the edge as a 3–4.5 m radius from the centre point. Anything further than 1 m from the edge of the midden was considered outside. For medium-sized middens (30–40 m²), we classified the centre as a 2.5 m radius around the centre point, the midrange as a 2.5–5 m radius from the centre point, the edge as 5–7.5 m from the centre point, and anything over 1 m from the edge as outside the midden. For large middens (>40 m²), we classified the centre as a 3 m radius around the centre point, midrange as 3–6 m from the centre point, the edge as 6–9 m from the centre point and, as in the other middens, anything over 1 m from the edge as outside.

To assess the effect of age and sex on chosen defecation location, we ran a linear mixed-effects model. We set location of defecation as the response variable, age and sex, plus their interaction, as fixed

factors, and rhino ID as a random factor. We then repeated this for the fixed factor of adult state. All statistical analyses and figures were created using R Studio version 0.99.903 for Windows (R Core Team, 2016).

Ethical Note

To minimize disturbance, we never approached a midden when a white rhino was present. Further, the cameras we used emitted no visible flash or audio, and we placed them 3 m from the edge of a midden, attached to a nearby tree. Additionally, we utilized our resources in such a way that batteries and memory cards were changed only once per month to further minimize any potential disturbance at the sites. Cameras were present to record behaviour at the sites, and we conducted no potentially harmful manipulations. We recorded no distress or behavioural manipulation as a result of the camera placement.

RESULTS

In total, we recorded behaviour from 115 adult white rhinos across the 10 middens (Table 1). We observed little variation in midden use between subadults and calves; thus, we only present data associated with adults. All results referring to age can be found in the Appendix.

Visit and Defecation Frequency

State significantly affected the visit frequency of adults, where territorial males visited significantly more often than nonterritorial males and females (Table 2, Fig. 2). Within nonterritorial males, subordinates visited 85% more often than potential challengers, and 60% more often than adult females (Table 2, Fig. 2). Potential challengers visited middens with the same frequency as adult females (Table 2, Fig. 2). State also significantly affected the defecation frequency of adults, where territorial males defecated more often than nonterritorial males and females (Table 2, Fig. 3). Finally, nonterritorial males (both subordinate and potential challengers) defecated with the same frequency as females (Table 2, Fig. 3).

Information Acquisition

State affected information acquisition, where territorial males investigated more often than subordinate males and females, but with the same proportion of visits involving investigation as for potential challengers (Table 3, Fig. 4). However, there was no statistically significant difference in the investigation of potential challengers and subordinate males. Additionally, females investigated less often than potential challengers but with the same frequency as subordinate males (difference not significant at $P < 0.05$; Table 3, Fig. 4). There was no difference in the sex of the depositor of dung sniffed by adults, with males' and females' dung sniffed equally by males and females (Table 4, Fig. 5a). Further, all adults, regardless of state, investigated the same dung piles (Table 5, Fig. 5b), where territorial males' dung was sniffed most often.

The level of investigation of dung deposited by adult white rhinos of different states varied with state of the investigator: for territorial male investigators: territorial male > female > nonterritorial challenger = nonterritorial subordinate (Table 6, Fig. 5b); for nonterritorial subordinate male investigators: territorial male = female > nonterritorial subordinate = nonterritorial challenger (Table 6, Fig. 5b); for nonterritorial challenger male investigators: territorial male = female > nonterritorial subordinate = nonterritorial challenger (Table 6, Fig. 5b); and for female

Table 1
Total number of individual adults visiting each midden during the study

Midden ID	Number of adult individuals visiting over sample period				Total
	Territorial males	Nonterritorial males		Females	
		Subordinate	Potential challenger		
M0006	1	1	2	8	12
M0079	1	1	0	4	6
M0113	1	2	0	5	8
M0127	1	1	1	10	13
M0128	1	0	3	7	11
M0129	1	0	4	11	16
M0131	1	1	2	11	15
M0132	1	2	1	5	9
M0136	1	3	0	11	15
M0142	1	2	0	7	10
Total	10	13	13	79	115

Table 2
Linear mixed-effects model for visit and defecation frequency of adult white rhinos

Adult state	Estimate	SE	df	t	P
Visit frequency					
Nonterritorial subordinate * Female	-0.056	0.012	103	-4.460	<0.001
Nonterritorial challenger * Female	0.017	0.011	103	1.529	0.424
Territorial * Female	-0.167	0.014	103	-11.596	<0.001
Nonterritorial challenger * nonterritorial subordinate	0.072	0.015	103	4.726	<0.001
Territorial * nonterritorial subordinate	-0.111	0.018	103	-6.189	<0.001
Territorial * nonterritorial challenger	-0.183	0.017	103	-10.854	<0.001
Defecation frequency					
Nonterritorial subordinate * Female	-10.253	6.366	103	-1.611	0.377
Nonterritorial challenger * Female	2.184	5.580	103	0.391	0.980
Territorial * Female	-89.616	7.330	103	-12.226	<0.001
Nonterritorial challenger * Nonterritorial subordinate	12.436	7.813	103	1.592	0.388
Territorial * Nonterritorial subordinate	-79.364	9.146	103	-8.678	<0.001
Territorial * Nonterritorial challenger	-91.800	8.617	103	-10.653	<0.001

Bold indicates factors significant at $P < 0.05$.

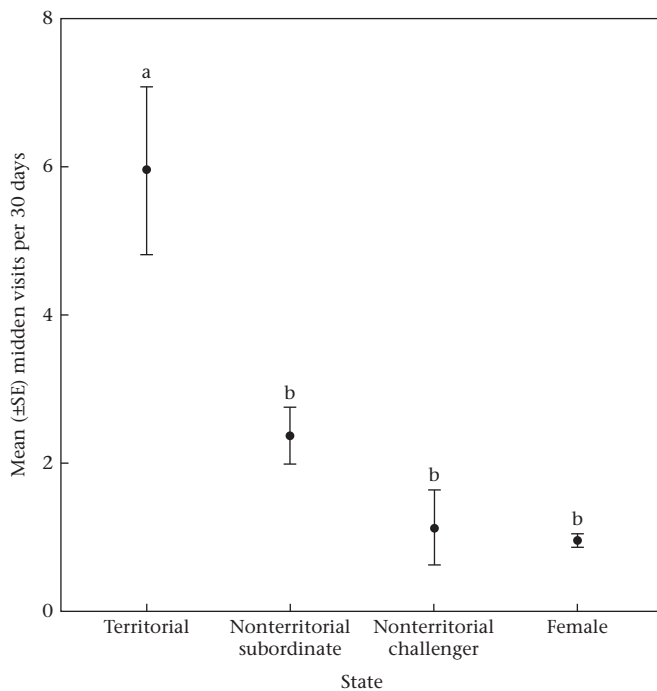


Figure 2. Midden visits by white rhinos of each adult state. Letters indicate significance between groups ($P < 0.05$).

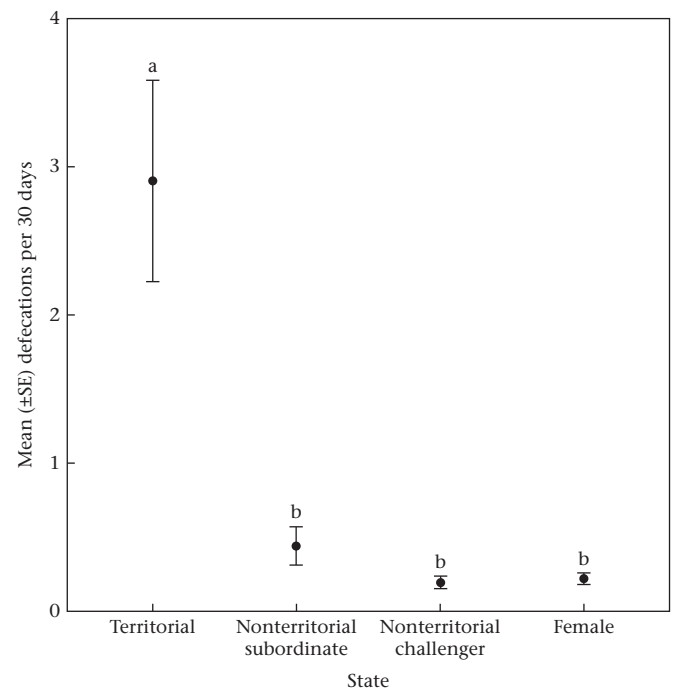


Figure 3. Midden defecations by white rhinos of each adult state. Letters indicate significance between groups ($P < 0.05$).

Table 3
Generalized linear mixed-effects model for information acquisition of adult white rhinos

Adult state	Estimate	SE	Z	P
Nonterritorial subordinate * Female	0.552	0.226	2.444	0.066
Nonterritorial challenger * Female	1.312	0.339	3.871	<0.001
Territorial * Female	1.377	0.251	5.483	<0.001
Nonterritorial challenger * Nonterritorial subordinate	0.760	0.370	2.054	0.161
Territorial * Nonterritorial subordinate	0.826	0.292	2.831	0.023
Territorial * Nonterritorial challenger	0.066	0.385	0.170	0.998

Bold indicates factors significant at $P < 0.05$.

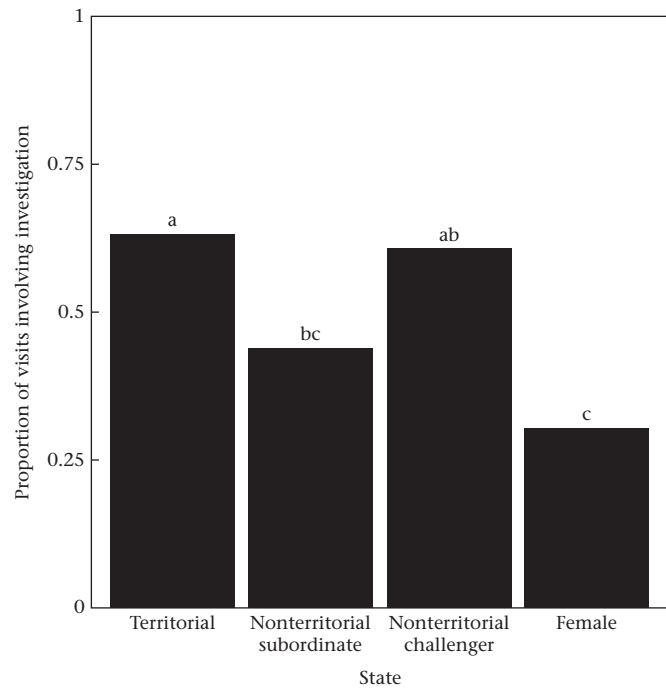


Figure 4. Proportion of midden visits involving investigation by white rhinos of each adult state. Letters indicate significance between groups ($P < 0.05$).

investigators: territorial males = females > nonterritorial subordinate = nonterritorial challenger (Table 6, Fig. 5b).

Dung Weight

Dung piles from territorial males were significantly lighter than dung piles from nonterritorial males ($H_3 = 5.804$, $P = 0.027$; Fig. 6), oestrous females ($H_3 = 5.804$, $P = 0.028$; Fig. 6) and nonoestrous females ($H_3 = 5.804$, $P = 0.047$; Fig. 6). The dung piles from nonterritorial males, oestrous females and nonoestrous females, however, were similar (nonterritorial versus oestrous: $H_3 = 5.804$, $P = 0.319$; nonterritorial versus nonoestrous: $H_3 = 5.804$, $P = 0.345$; oestrous versus nonoestrous: $H_3 = 5.804$, $P = 0.217$; Fig. 6).

Table 4
Generalized linear mixed-effects model for the investigation of dung from male and female depositors

State of investigating rhino	Estimate	SE	Z	P
Nonterritorial subordinate * Female	-0.418	0.337	-1.241	0.594
Nonterritorial challenger * Female	0.305	0.481	0.634	0.919
Territorial * Female	0.108	0.383	0.281	0.992
Nonterritorial challenger * Nonterritorial subordinate	0.723	0.503	1.437	0.469
Territorial * Nonterritorial subordinate	0.526	0.409	1.286	0.565
Territorial * Nonterritorial challenger	-0.197	0.536	-0.368	0.982

Defecation Location

Territorial and subordinate males primarily defecated in the centre of the midden (100% and 65%, respectively; Table 7, Fig. 7), whereas females and potential challenging males primarily defecated towards the edge or outside of the midden (females: 52% edge, 22% outside; potential challenging males: 63% edge, 6% outside; Table 7, Fig. 7). However, there was no statistical difference between subordinate and potential challenging males (Table 7, Fig. 7).

DISCUSSION

Olfactory communication could be one of the least reliable forms of communication, as the direction and duration of information transfer, and thus the probability of being detected by a desired target, is greatly influenced by wind, heat and other factors (Alberts, 1992; Bossert, 1968; Nimmermark & Gustafsson, 2005). However, some mammals increase the detection of their olfactory signals by utilizing communal marking sites (Darden et al., 2008; Eppley et al., 2016; Rodgers et al., 2015). White rhinos defecate in communal middens, but it is unclear why or how frequently individuals use these sites. As information on sex, age, territorial and oestrous state are identifiable via dung odours (Marneweck et al., 2017a), it is likely that middens act as information centres for white rhinos. Upon exploring this, we found that, of the different adult states, territorial males visited and utilized middens most of all. Moreover, these males focused their olfactory investigation primarily on their own dung, followed by deposits from adult females, and, lastly, from nonterritorial males. We found a similar pattern of olfactory investigation for nonterritorial males and females. Within middens, we found that there was a spatial order to where the rhinos defecated. Specifically, territorial males defecated exclusively in the centre, subordinate males defecated both within the centre and around the periphery, while potential challengers and females defecated primarily around the midden periphery.

Visit and Defecation Frequency

The extensive visiting and use of middens by territorial males suggests that middens are important sources of information for these individuals. This is in line with a polygynous mating system, where males deposit information for territorial defence and acquire

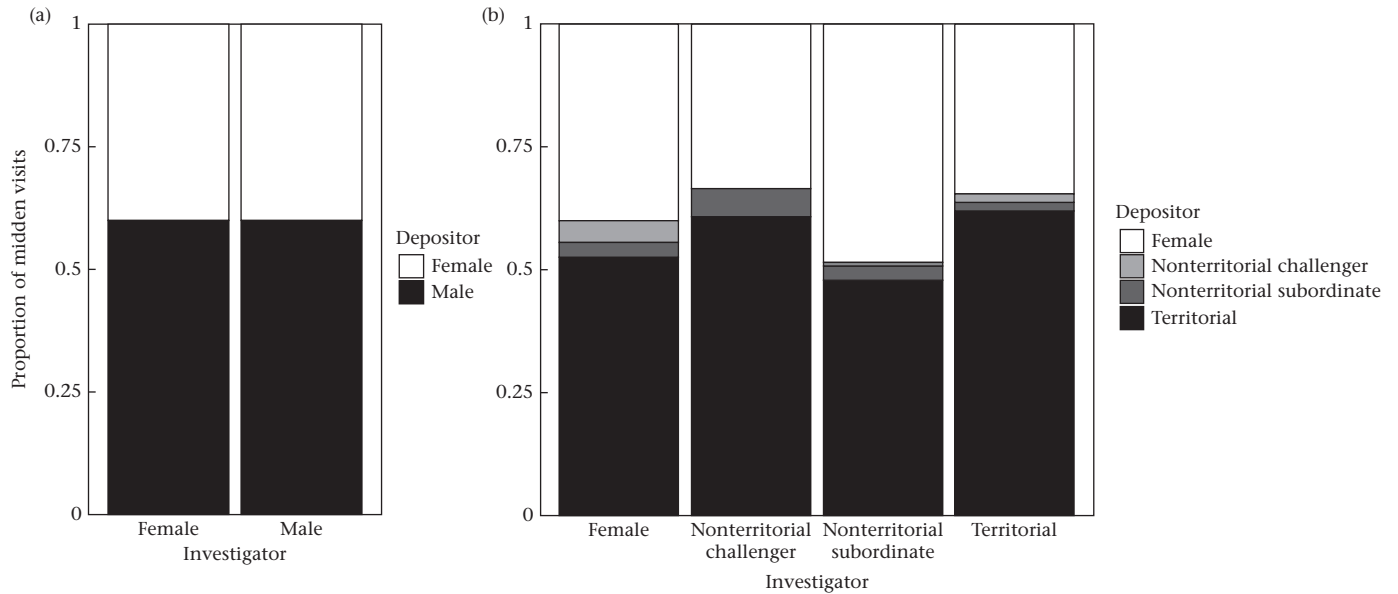


Figure 5. Dung piles identified by (a) sex and (b) adult state that were investigated by adults. Letters indicate significance between groups ($P < 0.05$).

Table 5
Generalized linear mixed-effects model for the investigation of adult dung of each state

State of investigating rhino	Estimate	SE	Z	P
Nonterritorial subordinate * Female	0.134	1.028	0.131	0.999
Nonterritorial challenger * Female	-0.727	1.157	-0.628	0.922
Territorial * Female	0.385	1.212	0.317	0.989
Nonterritorial challenger * Nonterritorial subordinate	-0.861	1.266	-0.680	0.903
Territorial * Nonterritorial subordinate	0.250	1.315	0.190	0.998
Territorial * Nonterritorial challenger	1.111	1.419	0.783	0.860

Table 6
Chi-square results of dung investigation

Adult state	df	χ^2	P
Territorial males			
Territorial * Nonterritorial challenger	3	166.420	<0.001
Territorial * Nonterritorial subordinate	3	166.420	<0.001
Territorial * Female	3	166.420	<0.001
Nonterr challenger * Nonterritorial subordinate	3	166.420	1.000
Nonterritorial challenger * Female	3	166.420	<0.001
Nonterritorial subordinate * Female	3	166.420	<0.001
Nonterritorial subordinate males			
Territorial * Nonterritorial challenger	3	128.810	<0.001
Territorial * Nonterritorial subordinate	3	128.810	<0.001
Territorial * Female	3	128.810	0.933
Nonterritorial challenger * Nonterritorial subordinate	3	128.810	0.216
Nonterritorial challenger * Female	3	128.810	<0.001
Nonterritorial subordinate * Female	3	128.810	<0.001
Nonterritorial potential challenger males			
Territorial * Nonterritorial challenger	3	30.636	<0.001
Territorial * Nonterritorial subordinate	3	30.636	<0.001
Territorial * Female	3	30.636	0.127
Nonterr challenger * Nonterritorial subordinate	3	30.636	0.157
Nonterritorial challenger * Female	3	30.636	0.002
Nonterritorial subordinate * Female	3	30.636	0.019
Females			
Territorial * Nonterritorial challenger	3	102.300	<0.001
Territorial * Nonterritorial subordinate	3	102.300	<0.001
Territorial * Female	3	102.300	0.154
Nonterritorial challenger * Nonterritorial subordinate	3	102.300	0.527
Nonterritorial challenger * Female	3	102.300	<0.001
Nonterritorial subordinate * Female	3	102.300	<0.001

Bold indicates factors significant at $P < 0.05$.

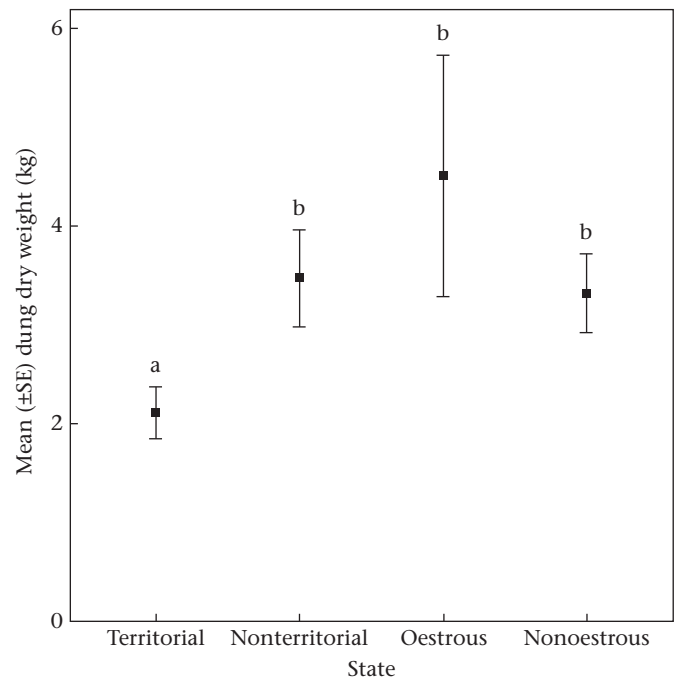


Figure 6. Mean dung dry weight from adult white rhinos of each adult state. Letters indicate significance between groups ($P < 0.05$).

Table 7
Linear mixed-effects model for defecation location by adult white rhinos of each state

Adult state	Estimate	SE	df	t	P
Nonterritorial subordinate * Female	1.119	0.235	72	4.772	<0.001
Nonterritorial challenger * Female	0.521	0.276	72	1.889	0.242
Territorial * Female	1.850	0.255	72	7.259	<0.001
Nonterritorial challenger * Nonterritorial subordinate	−0.599	0.325	72	−1.841	0.263
Territorial * Nonterritorial subordinate	0.730	0.308	72	2.371	0.092
Territorial * Nonterritorial challenger	1.329	0.340	72	3.907	0.001

Bold indicates factors significant at $P < 0.05$.

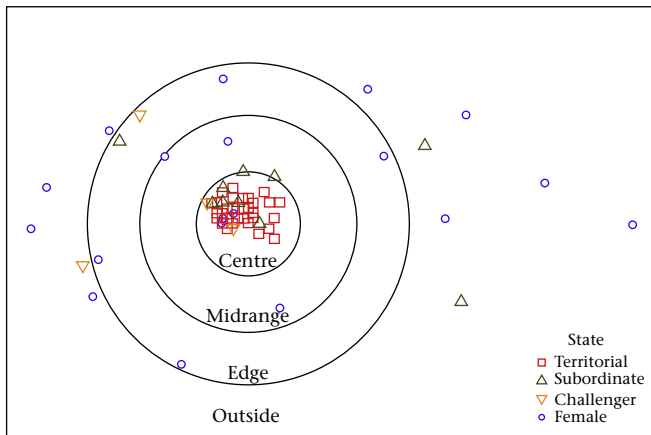


Figure 7. Example of defecation location by each adult white rhino class within a focal midden.

information on female reproductive state (Emlen & Oring, 1977). As territorial males defecate in middens along territory boundaries, and throughout the territory, it is likely that they use olfactory cues to indicate territory ownership (Owen-Smith, 1975). This can be directed at rival males (i.e. male–male communication), and/or towards adult females (potential mates) visiting the territory (i.e. male–female communication). Midden use by meerkats, *Suricata suricatta*, is also dominated by reproductive males (Jordan, 2007), where all individuals visit middens but males deposit scent marks more often. Additionally, territorial male oribi also mark with dung at a higher frequency than females and males without a harem (Brachares & Arcese, 1999). Moreover, the high frequency of visits to the middens, coupled with greater investigation (i.e. sniffing), suggests that territorial males are the individuals that are acquiring the most information. This would be important for territorial defence (e.g. detecting an intruding rival male), and for increasing their fitness (e.g. locating a visiting oestrous female).

Information Acquisition

Interestingly, all the territorial males extensively sniffed their own dung when visiting middens. This was unexpected, but it is possible that they did this to assess the strength of their own olfactory signals within the midden. As territorial males deposit small volumes of dung within middens, and spread it by kicking, it is likely that the greater surface area reduces odour persistence (Marneweck, Jürgens, & Shrader, 2017b). Thus, as these odours probably signal territorial ownership, it would be important for males to ensure that their dung odours are detectable. Group-living European badgers, *Meles meles*, mark territory boundaries with faeces (Kilshaw, Newman, Buesching, Bunyan, & Macdonald, 2009). During visits to these middens, badgers spend time investigating

their own faecal marks, as well as those from alien groups (Palphramand & White, 2007). Moreover, Palphramand and White (2007) noted that re-marking was rare in their study. Perhaps, like white rhinos, individuals were sniffing their own faeces to assess signal strength, and if it was still active, were restraining from re-marking in the midden.

Similar to territorial males, we found that all other adults (subordinate males, potential challenging males and females) displayed a similar pattern of olfactory exploration by focusing their sniffing on territorial male and adult female dung. Sniffing the territorial male's dung would allow these individuals to determine territory ownership, and how recently the territorial male was in the area. Moreover, for potential challengers, sniffing the dung of the territorial male may provide insight into his body condition (Gosling & Roberts, 2001; Rajagopal, Archunan, Geraldine, & Balasundaram, 2010), and thus help assess whether he can be challenged for territory ownership. With regard to the sniffing of adult female dung, territorial males tend to monopolize mating opportunities within their territories (Owen-Smith, 1973). However, nonterritorial males can obtain sneaky copulations (Guerier et al., 2012). Thus, it makes sense that both subordinate males and potential challengers would be interested in the reproductive state of females in the area. In addition, potential challengers may get an idea of the number of females that move through the territorial male's territory, and thus gain insight into territory quality (i.e. number of potential mates). In separating nonterritorial males into subordinate residents and potential challengers, it is possible that we may have misclassified some individuals. However, as we were able to record a large sample of visits by these different males ($N = 282$) over the average 222 days that the cameras were operational, we are confident that the number of potential misclassifications is very small, and thus unlikely to affect our results.

For females, defecating in middens is a way to advertise oestrous state (i.e. female–male communication). However, females did not just deposit information, but also obtained information when visiting middens. They investigated the territorial male's dung and, less frequently, the dung from nonterritorial males (although this lower frequency of investigation may be due to nonterritorial male dung not always being present in the middens). By investigating the territorial male's dung, a female may be able to assess his quality (Charpentier, Boulet, & Drea, 2008; Johansson & Jones, 2007). This would then help her to decide whether to breed with him or not. As nonterritorial males sometimes breed (Guerier et al., 2012), it is possible that females may be assessing the quality of all the males that have defecated in the midden, and thus not limiting their options to breeding with the territory owners. Furthermore, it is possible that oestrous females may use middens to assess male quality, and hence avoid territories of suboptimal males when in oestrus (White et al., 2007). However, as the oestrous state of females in this study was unknown, this would require further investigation.

In addition to investigating the dung of adult males, females surprisingly also sniffed the dung of other adult females. In fact, they did this almost as often as they explored the dung of territorial males, suggesting female–female communication. The question is, however, what are they communicating and/or what information are they interested in obtaining? Adult females live in home ranges that extensively overlap with those of other females (Owen-Smith, 1975, 1973; Rachlow et al., 1999; White et al., 2007). Thus, it is highly unlikely that females use olfactory signals to demarcate home range boundaries. Moreover, as male white rhinos do not provide any parental care (Owen-Smith, 1973), females are unlikely to compete over mates. Jordan et al. (2011) highlight that scent marking in females is often overlooked and is poorly understood. Female intrasexual overmarking in banded mongooses, *Mungos mungo*, was not a result of food competition, reproductive suppression or mate competition (Jordan et al., 2011). We suggest that intrasexual investigation of dung in female white rhinos is a function of familiarity, keeping track of the other females whose home ranges overlap, and thus know who is close by. A by-product of this is that the presence of dung from a range of females within middens may transmit information on the local density of adult females, which dispersing individuals may use to determine where to settle (Shrader & Owen-Smith, 2002). Moreover, females may use information on the number of females moving through the territory as an indicator of territorial male quality (White et al., 2007).

Defecation Location

One factor that may increase signal detection and thus enhance detectability is the spatial arrangement of dung within middens. The location of a scent mark is important in several species. For example, giant pandas, *Ailuropoda melanoleuca*, spend more time investigating odours placed higher from the ground because that indicates greater body size and associated competitive ability (White, Swaisgood, & Zhang, 2002). In addition, female dwarf mongooses, *Helogale parvula*, spend more time investigating scent marks placed higher from the ground, even when they do not differ chemically (Sharpe, 2015). This suggests that the location of a scent mark is as important as the odour profile itself.

For white rhinos, many different individuals defecate in one midden (up to 16 individuals in this study; see Appendix). By defecating in specific areas, white rhinos add a spatial component to their olfactory signals, which may increase detectability and strengthen information on identity (Sharpe, 2015; White et al., 2002). By defecating extensively in the centre of middens, both territorial and subordinate males may indicate residency, whereas the kicking of dung in the centre of the midden may indicate territory ownership. Potential challenging males defecated primarily around the edge of the midden, possibly to communicate to the territorial male that they were there, indicating subordination (Owen-Smith, 1973) and thus avoiding confrontation with the territory owner. In contrast, it is possible that when these males defecated in the centre of the middens, they were issuing a challenge to the territorial male. Although we were unable to record any direct confrontations between individuals, we often observed that a territorial male would kick aggressively and overmark if he found a potential challenger's dung in the centre of the midden (as opposed to a subordinate male's dung). Further, the territorial male often returned the same day (up to three times) to investigate the midden with no further defecation. However, data were insufficient to draw any conclusions, and this requires further exploration. Finally, the peripheral locations of adult females' dung piles probably increase their detectability.

Dung Weight

Within adults, territorial males defecated more frequently in middens, probably to reaffirm territory ownership. As they have a number of middens both along boundaries and within their territory, it makes sense for these males to reduce the volume of dung per deposit and increase the frequency of defecation. Limiting dung volume per defecation event allows them to regulate their dung output, a strategy also utilized by several other communally defecating, territorial ungulates, such as oribi (Brachares & Arcese, 1999), common duikers, *Sylvicapra grimmia* (Lunt & Mhlanga, 2011), and Chinese water deer, *Hydropotes inermis* (Sun, Xiao, & Dai, 1994). Ultimately, dung is a limited resource, and therefore territorial males utilizing dung for olfactory communication across their territory must manage their dung output to ensure effective distribution. Owing to the nature of territorial dung kicking, it is possible that some part of each territorial male's defecation was not collected. This would mean that the weight of territorial male defecations was underestimated. However, because the dung was collected immediately after defecation (<5 min), and the ease of identifying fresh dung by its heat and colour, it is unlikely that portions of dung large enough to affect the results were omitted. Additionally, it is possible that the dung output of white rhinos could vary throughout the day, and thus spatially across the middens. However, we collected dung throughout the day (0610–1800 h). Thus, if there were temporal and spatial variations in dung weight we would have expected a wide variance in the dung weights we recorded from the different white rhino states, which we did not. As a result, we are confident that our data provide a reliable measure of white rhino dung weight.

Conclusion

The results of our study suggest that middens are in fact information centres for white rhinos. Territorial males seem to be the main users, probably transferring information on territorial ownership (male–male and male–female communication) and receiving information from visiting adult females (female–male communication) and nonterritorial males (male–male communication). Yet, as both nonterritorial males and adult females deposit and obtain information from middens as well, it is likely that middens are also key information sources for these individuals. Overall, our results indicate that middens are key components of white rhino communication. Yet, as a number of mammals defecate in communal middens (Dröscher & Kappeler, 2014; Jordan et al., 2007), the role of middens as a source of information transfer is probably not restricted to white rhinos alone.

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Appendix

Interaction of Age and Sex

The interaction between age and sex had a significant effect on visit and defecation frequency (Table A1) where, within adults, males visited and defecated more frequently than females (Figs A1 and A2). Similarly, this interaction significantly affected the proportion of visits involving information acquisition, where adult males investigated more often than adult females (Table A2, Fig. A3). Finally, the interaction between age and sex significantly affected defecation location, where there was no difference between the ages of females, but adult males defecated in different locations to subadults and calves (Table A3, Fig. A4). In all cases, the actions of territorial males are what led to the significantly higher values for adult males compared to the other age and sex classes.

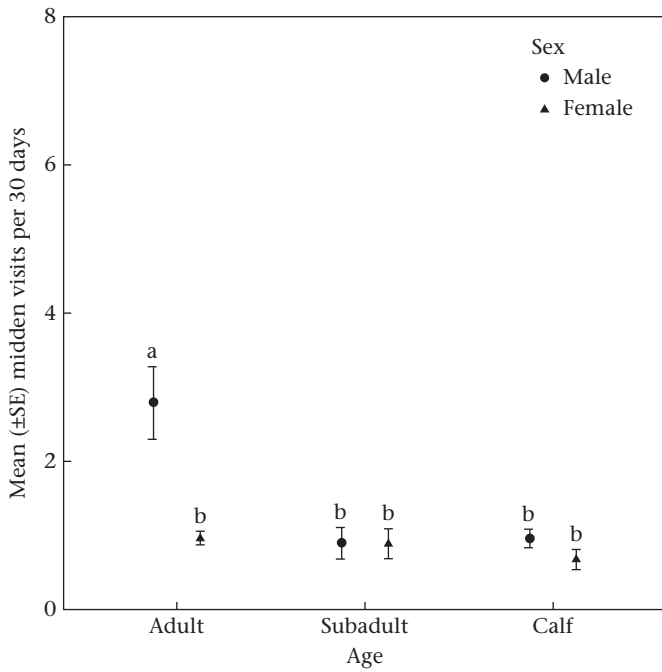


Fig. A1. Midden visits by white rhinos of each age class. Letters indicate significance between groups ($P < 0.05$).

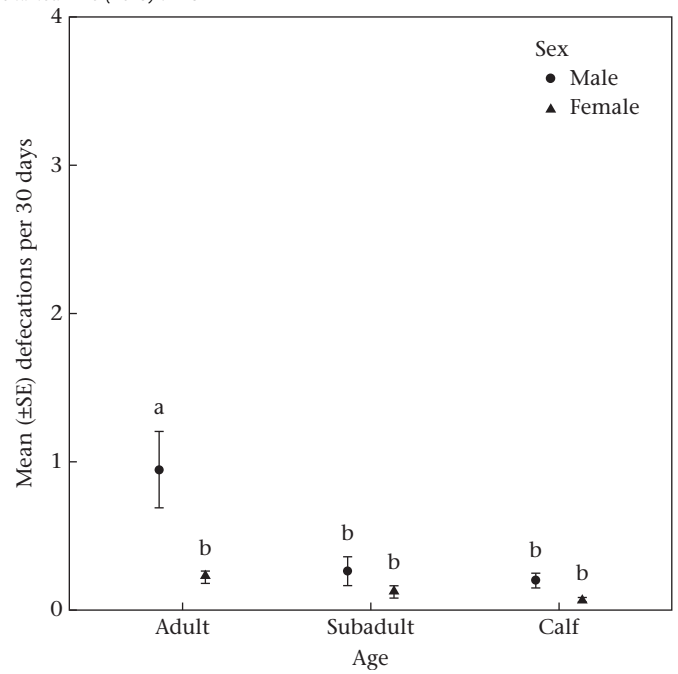


Fig. A2. Midden defecations by white rhinos of each age class. Letters indicate significance between groups ($P < 0.05$).

Table A1

Linear mixed-effects model for visit and defecation frequency of white rhinos

Factor	Estimate	SE	df	t	P
Visit frequency					
Age	-0.009	0.012	167	-0.797	0.426
Sex	0.059	0.010	167	6.096	<0.001
Age * Sex	-0.049	0.017	167	-2.973	0.003
Defecation frequency					
Age	-0.005	0.006	167	-0.894	0.372
Sex	0.023	0.005	167	4.850	<0.001
Age * Sex	-0.019	0.008	167	-2.29	0.023

Bold indicates factors significant at $P < 0.05$.

Table A2

Generalized linear mixed-effects model for information acquisition by white rhinos

Factor	Estimate	SE	Z	P
Age	-1.104	0.360	-3.063	0.002
Sex	1.002	0.209	4.807	<0.001
Age * Sex	-1.056	0.475	-2.223	0.026

Bold indicates factors significant at $P < 0.05$.

Table A3

Linear mixed-effects model for defecation location by white rhinos

Factor	Estimate	SE	df	t	P
Age	0.312	0.338	103	0.921	0.359
Sex	-1.195	0.185	103	-6.466	<0.001
Age * Sex	0.956	0.419	106	2.281	0.025

Bold indicates factors significant at $P < 0.05$.

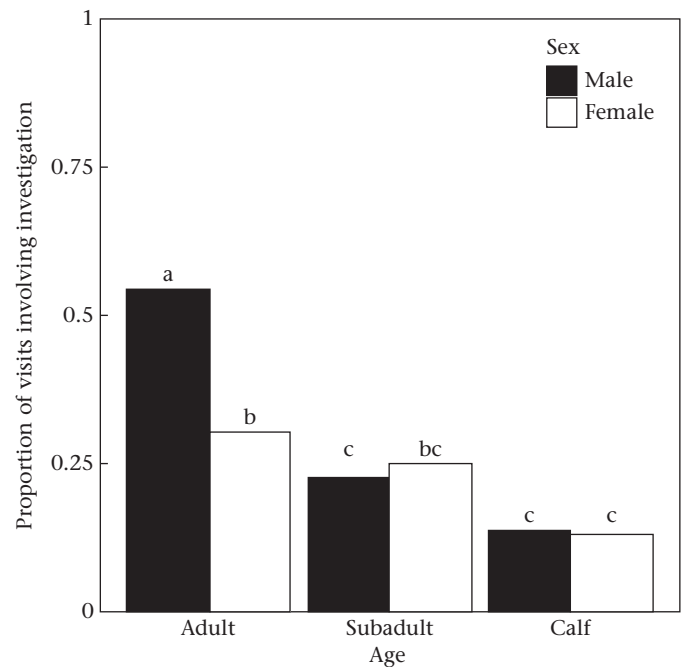


Fig. A3. Proportion of midden visits involving investigation by white rhinos of each age class and sex. Letters indicate significance between groups ($P < 0.05$).

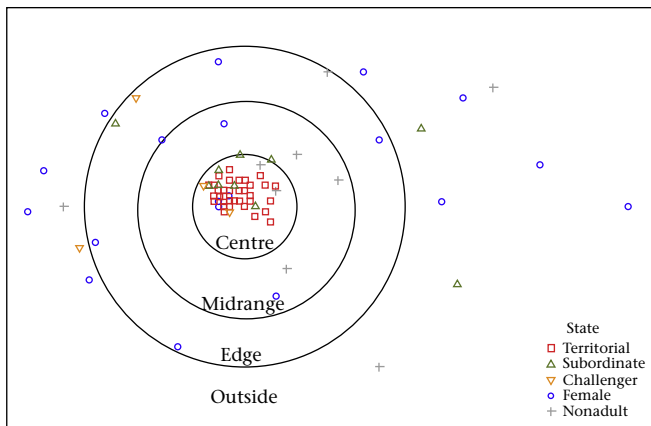


Fig. A4. Example of defecation location by each white rhino class within a focal midden.