Animal Behaviour 140 (2018) 7–18

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

The role of middens in white rhino olfactory communication

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ARTICLE INFO

Article history:
Received 17 October 2017
Initial acceptance 1 December 2017
Final acceptance 6 March 2018

MS. number: 17-00830R

Keywords:
communal defecation
dung piles
intersexual communication
intrasexual communication
olfaction

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.

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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https://doi.org/10.1016/j.anbehav.2018.04.001
0003-3472/

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 km^2) that are part of larger, overlapping female home ranges (average 11.6 km^2; 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 km^2 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 km^2 (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