



## Chemical signals of age, sex and identity in black rhinoceros

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Olfactory communication may be particularly important to black rhinoceros, *Diceros bicornis*, because they are solitary living and have comparatively poor eyesight but their populations are structured by inter- and intrasexual relationships. Understanding olfactory functions and processes might achieve better conservation management but their study in rhinoceros remains anecdotal or descriptive. Experimental approaches are required but rarely possible as rhinoceros are difficult to observe and manipulate. We measured the olfactory investigation behaviour (duration and frequency of sniffing) of black rhinoceros in four experiments designed to determine the function of chemosignals in dung and urine. A habituation–dishabituation trial demonstrated that black rhinoceros discriminated individually distinctive odours from faecal signals (experiment 1). When adults (>6 years old) were presented with dung from conspecifics of different sex and age classes (adult, and subadult from 2 to 4 years old), male dung was investigated more by both sexes, and females investigated subadult dung more (experiment 2). Both dung and urine from the same adult donors were investigated by both sexes, but male dung was investigated more than female dung and female urine more than male urine, although differences were statistically weak (experiment 3). Lastly, fresh faecal samples and those aged 1, 2, 4, 16 and 32 days were similarly investigated, indicating that they still function as olfactory signals. Together the results indicate that dung or urine signalled age, sex and identity to conspecifics and signals may persist as dung decays. Chemosignals are likely to be important to the social and spatial organization of black rhinoceros.

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The ability of chemical signals to persist long after the signal is deposited by an animal at a chosen location allows for information exchange among conspecifics who may not encounter one another (Alberts 1992; Wyatt 2003). Olfactory communication, therefore, is a particularly important process for solitary-living species. Physiological constraints, such as diet and endocrine state, help ensure that chemical signals remain relatively honest because the physiological by-products of these biological processes are not easily bluffed, especially in urine and dung. These waste products become rich sources of information for conspecifics, perhaps leading to the evolutionary ritualization of defecation and urination for communication (Muller-Schwarze 2006).

For communication to be efficient and effective, receivers must be able to distinguish between chemical signals. These signals govern reproductive processes in many mammalian species, facilitating mate location and selection (Bronson 1989; Wyatt 2003),

especially in solitary-living species (Fisher et al. 2003a; Swaisgood et al. 2004). Fundamental to these functions is also the ability to determine the sex and age class (i.e. adult or subadult) of the signaller from olfactory cues (Brown 1979; Mossman & Drickamer 1996), so that potential mates and competitors can be identified. For example, female mice, *Mus musculus*, covered with male urine are attacked by males and male mice covered with female urine are mounted by males, demonstrating the importance of these chemosignals for sex recognition (Dixson & Mackintosh 1971; Connor 1972). Sex-specific odours are also important for activating sexual motivation in both sexes (Wyatt 2003). Unlike other signals, scent can remain in the environment long after the signaller deposited them, making it important to determine when a chemical signal was deposited. Scent freshness might predict signaller proximity, indicating the level of threat of a competitor or the profitability of pursuing a fertile mate. The chemical constituents of olfactory signals degrade with time, providing cues that receivers can use to determine signal age (Regnier & Goodwin 1977; Roberts 1998).

One of the most fundamental and important functions of signals is to convey individual identity (Barnard & Burk 1979; Halpin 1986; Sherman et al. 1997; Tibbetts & Dale 2007). Individual recognition is a prerequisite for many social functions when there are repeated

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social interactions with the same individual such as territoriality, dominance hierarchies, kinship and mate choice. In relatively solitary and aggressive species, individual recognition could be important for identifying rivals whose competitive ability varies, providing 'cheat-proof' signals based on past history of interaction or successful territory or female defence evidenced by the spatial and temporal pattern of olfactory marks (Gosling & Roberts 2001). In 'true' individual recognition, the receiver distinguishes individually discernible cues produced by the signaller and uses them to identify the signaller in future encounters. Individual recognition lies on a continuum with other forms of social recognition that may be less precise, such as recognizing familiar versus unfamiliar, or friend versus rival. Disentangling these possibilities can be methodologically challenging, but a prerequisite to all of these functions is the ability to discriminate individually distinctive 'signatures' afforded by olfactory signals (Halpin 1986).

Olfactory communication is thought to govern many aspects of rhinoceros social behaviour. All rhinoceros species display ritualized behaviours when distributing their faeces and urine and investigating the faeces and urine of conspecifics (e.g. Goddard 1967; Schenkel & Schenkel-Hulliger 1969; Joubert & Eloff 1971; Owen-Smith 1973; Borner 1979; Laurie 1982; van Strien 1986; Kiwia 1989), similarly to other terrestrial vertebrates (see review in Alberts 1992). Other than pedal and sweat glands in some species, rhinoceros lack the specialized scent glands present in many mammalian species. The coarse diet of black rhinoceros, *Diceros bicornis*, however, produces a large amount of faecal material and they defecate approximately four to five times daily (Owen-Smith 1988), providing ample quantities for frequent olfactory signalling. Black rhinoceros defecate in communal dung heaps (Schenkel & Schenkel-Hulliger 1969) that might serve as a kind of community information exchange, as seen in other mammals (Eisenberg & Kleinman 1972). While defecating, male black rhinoceros scrape at the ground and spread their dung, but females do not ritualize defecation, suggesting that it probably functions as a male signal to competitors or potential mates. Female black rhinoceros squirt small amounts of urine frequently when they come into oestrus and male black rhinoceros spray urine over bushes and elevated objects. Both behaviours probably maximize the odour field and its detection by conspecifics, suggesting a reproductive advertisement function of urine. However, our understanding of olfactory communication in black rhinoceros, and other rhinoceros species, remains largely descriptive and anecdotal. Previous published experimental investigations of olfactory communication in black rhinoceros are limited (Goddard 1967) and, to our knowledge, there have been no such studies on any other rhinoceros species. This dearth of information is perhaps unsurprising for such a rare, difficult-to-observe, large and dangerous animal, which together limit opportunities for detailed behavioural research, but the knowledge gained may assist with conservation management for wild or captive populations (Carlstead et al. 1999; Linklater 2003, 2004; Swaisgood 2007) and contribute to our understanding of mammalian communication systems.

Research on olfactory communication has promising applications in conservation (Swaisgood 2007; Swaisgood & Schulte 2010; Campbell-Palmer & Rosell 2011). For example, studies of chemical communication in another solitary mammal, the giant panda, *Ailuropoda melanoleuca*, were instrumental in helping to turn around its conservation breeding programme (Swaisgood et al. 2000, 2004) with potential application also to the conservation of wild populations (Swaisgood et al. 2004; Nie et al. 2012). Captive breeding programmes for black rhinoceros have not sustained the population (Foose & Wiese 2006) and may also benefit from the management of communication processes. Black rhinoceros conservation programmes in the wild are improving (Linklater et al.

2011), but could also benefit from a better understanding of the species' basic ecology and behaviour. For example, translocation is an important tool for the reintroduction or restocking of populations (Linklater et al. 2012). Preliminary evidence suggests that broadcasting dung around release sites may influence postrelease settlement in newly established reserves (Goddard 1967; Linklater et al. 2006). A better understanding of the meaning of chemical signals in dung and urine will help the development of olfactory management as a conservation tool in this species.

We report an experimental approach to understanding black rhinoceros chemical communication, providing a foundation for understanding communication processes in rhinoceros and other species sharing similar life history traits. In particular, we used controlled olfactory discrimination tests with temporarily captive black rhinoceros to ask the following questions. (1) In a habituation–dishabituation paradigm (Halpin 1986), do rhinoceros show evidence of discriminating individually distinctive odours in dung? Do rhinoceros discriminate (2) the sex and (3) age of scent donors based on odours in dung? (4) Do rhinoceros also use urine as a chemical signal, as determined by differential investigation of dung versus urine? (5) Do rhinoceros discriminate dung aged for various lengths of time? As the black rhinoceros is a relatively intractable and difficult-to-study species, addressing these questions will significantly advance understanding of the species' behaviour and conservation.

## METHODS

### *Scent Sample Collection and Presentation*

We conducted four scent presentation experiments on black rhinoceros, *D. b. var. minor*, captured by the Ezemvelo KwaZulu-Natal Wildlife veterinary and game-capture team from KwaZulu-Natal wildlife reserves, South Africa, and held temporarily in captivity at iMfolozi Game Reserve prior to their transport and release into other reserves during 2004–2006 (e.g. Linklater et al. 2006). Rhinoceros subjects were held individually in enclosures approximately 80 m<sup>2</sup> configured in two equal portions, one with an elevated roof as shade, and connected by a short corridor. Animals were fed lucerne hay, pelleted domestic ungulate food and freshly cut browse each morning and evening and water was available ad libitum from troughs (see also Linklater et al. 2010).

We collected dung and urine-soaked sand samples from donor rhinoceros whose sex and age were known because they were part of this or other capture–translocation–release efforts (Linklater et al. 2006; Linklater & Swaisgood 2008). Dung was much easier to locate and collect than urine and so most research focused on dung chemosignals. Control samples comprised river sand collected from the same location as the enclosures' substrate, matching any odour cues deriving from the sand in urine-soaked sand or clinging to dung samples. All samples, each of approximately 300 ml, were sealed in plastic bags and frozen the same day as collection.

For our experiments, each rhino received a maximum of one scent presentation every 2 days (with the exception of the individual discrimination experiment; see below). We conducted presentations in the early morning or evening (0500–0900, 1600–1900 hours) when rhino are most active and avoiding periods when routine husbandry activities (e.g. feeding and cleaning) might interfere with tests. Scent samples were thawed and allowed to reach ambient temperature before presentation. To begin a presentation, we dropped samples into the enclosure from a walkway above it, from which behavioural observations were also made. We recorded all occurrences of sniffing events (bouts separated by 5 s) and the duration of sniffing, where sniffing was operationally

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