



Top marks from top dogs: tandem marking and pair bond advertisement in African wild dogs



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Tandem marking occurs when both members of a pair scent-mark the same location in quick succession. This widespread behaviour, common in canids and monogamous antelopes, is generally believed to be involved in pair bond formation and advertisement. Despite their potential utility in determining tandem mark function, observations of individual contributions to tandem marking within pairs are rare. To this end, we made detailed observations of free-ranging dominant African wild dogs, *Lycaon pictus*, uncovering differences in the tandem-marking behaviour of pairs depending on their relatedness. In all packs, dominants were more likely to overmark their partner's scent mark than their own, but dominant-initiated scent marks were more likely to become tandem marks in related (full-sibling) pairs than in unrelated pairs. Despite this, females were more frequently on top at the end of marking bouts in related pairs than in unrelated pairs, because females in related pairs were more likely to overmark initial scent marks left by males, and less likely to have their scent marks subsequently overmarked by males. Scent-marking bout length was also significantly longer in related pairs. These differences suggest that advertising the presence of a mated dominant pair may be the main function of tandem marking in African wild dogs, but when mating opportunities are absent within the pack, contributions to tandem marking are altered, with individual advertisement perhaps becoming more important.

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Scent marking is often associated with dominance (Ralls, 1971); being performed almost exclusively (e.g. grey wolf, *Canis lupus*, Asa, Mech, Seal, & Plotka, 1990) or at higher rates (e.g. meerkat, *Suricata suricatta*, Jordan, 2007) by dominants than by subdominants. Scent marking commonly peaks at or immediately preceding the breeding period (e.g. leopard, *Panthera pardus*, Bothma & Coertze, 2004), suggesting a potential role in mate acquisition and defence, and generally males scent-mark at higher rates than females (Ralls, 1971) often with sex-specific scents (e.g. banded mongoose, *Mungos mungo*, Jordan, Manser, et al., 2011). In many pair-bonded canids however, males and females contribute similarly to scent marking (e.g. coyote, *Canis latrans*, Gese & Ruff, 1997), and although comparisons have been made between individuals of different dominance status (e.g. Peters & Mech, 1975), detailed observations of the marking behaviour within a dominant pair are less frequently described, and may provide important information on the function(s) of scent marking generally.

Tandem marking (Rothman & Mech, 1979), where both members of a pair scent-mark the same spot (overmarking sensu Johnston, Chaing, & Tung, 1994), is common in pair-bonded canids (e.g. coyote, Gese & Ruff, 1997; domestic dog, *Canis familiaris*, Lisberg & Snowdon, 2011; grey wolf, Peters & Mech, 1975) and antelopes (e.g. Kirk's dikdik, *Madoqua kirkii*, Brotherton, Pemberton, Komers, & Malarkey, 1997; klipspringer, *Oreotragus oreotragus*, Roberts & Dunbar, 2000). The two most prominent, although not mutually exclusive, functions proposed to explain this widespread behaviour are (1) pair bond formation and (2) advertising the presence of a mated pair. Captive wolves provide some support for the pair bond formation hypothesis, because newly formed pairs scent-marked at the highest rates, and eventually decreased their rates to those of established packs (Rothman & Mech, 1979). Indeed, tandem marking forms part of the courtship behaviour of many canids (coyote, Bekoff & Diamond, 1976; domestic dog, Fox & Bekoff, 1975; red fox, *Vulpes vulpes*, Macdonald, 1979; bush dog, *Speothos venaticus*, Porton, 1983). In African wild dogs and golden jackals, *Canis aureus*, tandem marking occurs almost immediately after the pair first meet (Frame & Frame, 1976; Golani & Keller, 1975), while in newly formed wolf pairs it occurs within 5 days (Rothman & Mech, 1979). Together, these patterns suggest that tandem marking plays a role in pair formation.

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However, the persistence of tandem marking beyond initial pair bonding in some species (e.g. coyote, Gese & Ruff, 1997; grey wolf, Peters & Mech, 1975) suggests that tandem marking may also contribute to long-term pair bond maintenance and advertisement. In both of these hypotheses the mated pair are the focus, but it may be more informative to consider the individuals that make up these pairs, individuals that would be expected to behave selfishly to an extent that depends on social circumstances.

In evaluating the potential function(s) of tandem marking, the order in which scent marks are deposited is important. Scent marks placed on top of previous marks are most important in affecting subsequent responses at those sites (e.g. banded mongoose, Jordan, Manser, et al., 2011; African wild dog, Jordan, Golabek, Apps, Gilfillan, & McNutt, 2013), perhaps because recipients attach greater significance to the top marks at such sites than lower marks (e.g. Johnston, Sorokin, & Ferkin, 1997). It is important therefore to consider individual contributions to tandem marking, particularly scent-marking order and which individual/sex has its scent mark on top at the end of a scent-marking bout. Although some of the most detailed work on tandem marking in canids was conducted remotely by snow tracking wolves (Peters & Mech, 1975), circumstances that made it impossible to determine the order of deposition within the pair, some ungulate studies provide additional resolution. For example, plains zebra stallions, *Equus burchelli*, overmarked mares (Klingel, 1974) and female klipspringers initiated most tandem-marking bouts, but males marked more during these bouts and usually left the final mark at a site (Roberts & Dunbar, 2000). Such patterns of marking, with males generally emerging on top, suggest a role in mate guarding, but as only high-quality mates may be able to afford the costs of repeatedly overmarking their mate (Gosling & Roberts, 2001; Rich & Hurst, 1998) tandem marking may also be a means of testing the competitiveness or 'quality' of a mate.

To investigate the function of tandem marking, we investigated its occurrence within dominant pairs of free-ranging African wild dogs in northern Botswana. African wild dogs live in packs in which a single pair typically monopolizes breeding and parents are assisted in pup rearing by mature offspring that have delayed dispersal (Girman, Mills, Geffen, & Wayne, 1997). African wild dogs scent-mark using urine (Frame & Frame, 1976), with the majority of scent marks in a pack being deposited by the dominant pair (Jordan et al., 2013; Parker, 2009). We investigated factors that potentially affect overmarking within the dominant pair. Despite earlier reports to the contrary (Frame & Frame, 1976), both sexes of wild dog disperse (McNutt, 1996), and therefore both male and female breeders are vulnerable to being usurped by same-sex immigrants. As a result, if the pair bond maintenance hypothesis applies in this species, both sexes might be expected to contribute similarly to tandem marking and dominant males and females might be expected to initiate and finish a similar number of marking bouts. We also investigated whether the details of tandem marking depended on relatedness within the dominant pair. In some study packs, the social role of a dominant that died was taken over by an opposite-sex sibling of the surviving dominant. In such circumstances neither social dominant has (out)breeding opportunities within the pack; both of them would benefit from an opposite-sex immigrant as a mate, and therefore, as in unrelated pairs, both of them are vulnerable to displacement by a same-sex immigrant. If tandem marking is involved in maintaining the pair bond, we might expect that closely related socially dominant pairs would show lower rates of tandem marking or perhaps a cessation of tandem marking altogether as each sex shifts to self-advertisement to attract an immigrant of the opposite sex. Alternatively, within related pairs the need to avoid having a same-sex immigrant attracted by the opposite-sex

dominant's marks might lead to greater competition to leave the top mark, and thus an increase in tandem marking.

METHODS

Study Population and Site

The research was undertaken under permit from the Botswana Department of Wildlife and National Parks and adhered to the ASAB/ABS Guidelines for the Use of Animals in Research. Data were collected between May 2011 and September 2012 from 13 packs of free-ranging African wild dogs in northern Botswana. The study area (ca. 2600 km²; 19°31'S, 23°37'E; elevation ca. 950 m) is bordered by the Okavango Delta and includes the Moremi Game Reserve and Wildlife Management Areas. Further details can be found in McNutt (1996). This subpopulation of African wild dogs has been studied since 1989, and 95.5% of all ($N = 112$) individuals observed in the current study were of known age and origin. Each individual was identified by its unique tricolour pelage pattern, distinctive ear notches and tail stripes, all of which were drawn and photographed (usually in the few weeks following emergence from the den or immigration). Immigrant dogs first photographed as adults were assumed to be unrelated to the residents. In this study, a pack is defined as a group containing at least one adult male and female. The dominant pair could be easily identified within established packs from behaviours in addition to their stereotyped tandem marking (Jordan et al., 2013). Only the dominant female bred in each of our study packs, and was closely guarded by the dominant male, who licked her vulva and lifted her with his shoulders during her brief receptive period in April/May. Outside the breeding period, the dominant pair also typically rested together, and were often the focus of social activity during rallies, when many individuals greeted and submitted to them prior to pack movement. Apart from young pups and the individual(s) that made the kill, the dominant pair also fed first at kill sites, and repelled others while doing so.

We determined relatedness by assuming that the male that was dominant during oestrus fathered the entire litter that year, although extrapair paternity is known in this species (Spiering, Somers, Maldonado, Wildt, & Gunther, 2010) and so mixed paternity is possible. Study packs were divided according to the relatedness of the dominant pair, which were either full siblings ('related', $N = 2$ packs) or were less closely related ('unrelated', $N = 11$). It was not possible to determine relatedness to any greater degree of accuracy, owing to both small sample sizes and the long-distance dispersal in this species meaning that relatedness between different coalitions of previously unknown immigrants was impossible to determine.

Behavioural Observations

One to four individuals were radiocollared in each pack using Vectronic (Vectronic Aerospace GmbH, Berlin, Germany; <320 g) or Sirtrack (Sirtrack, Havelock West, New Zealand; <180 g) transmitters mounted on collars which allowed them to be located by radiotracking from the air and from a vehicle. To allow radiocollars to be fitted, wild dogs were darted from a vehicle from <15 m using Telinject (Telinject U.S.A., Inc., Agua Dulce, CA, U.S.A.) darting equipment with a mixture of ketamine HCl with xylazine and atropine (Osofsky, McNutt, & Hirsch, 1996), with an intramuscular reversal of anaesthesia with yohimbine. Drug dosages were based on weights given in Smithers (1983) and were adjusted based on visual estimates of relative size, as dogs were not weighed during immobilizations. Based on weights given in Smithers (1983), fitted collars represented 0.64–1.14% of body weight. Immobilized

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