Notes and records

Long-distance transboundary dispersal of African wild dogs among protected areas in southern Africa

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Introduction

African wild dogs (Lycaon pictus), hereafter wild dogs, have exhibited severe declines in their distribution throughout Africa, disappearing from at least 25 countries during the past 50 years (Fanshawe et al., 1997). Wild dogs occur at low densities and even the largest protected areas typically support low populations. The species is highly susceptible to edge effects and problems associated with small population sizes. Throughout their range, wild dogs live mainly in protected areas in highly fragmented populations, and few areas hold more than 100 individuals (Fanshawe et al., 1997), although a number of large contiguous populations persist in parts of east and southern Africa. In South Africa, wild dogs historically occurred throughout the country (Skinner & Smithers, 1990), but owing to widespread persecution and prey loss, now occur naturally only in a single viable population in Kruger National Park and some adjacent farming areas (Fanshawe et al., 1997; Lindsey, Du Toit & Mills, 2004). Because there is no suitable large protected area to establish a second viable population of wild dogs in South Africa, conservation efforts focused on creating a managed metapopulation using a network of smaller reserves (Mills et al., 1998). Consequently, beginning in 1997, packs were reintroduced into small (85–1100 km²), isolated, fenced reserves with the goal of establishing a minimum of nine packs linked through active management by 2007 (Davies-Mostert, Mills & Macdonald, 2009; Gusset, 2010). Northern Botswana is an important stronghold for the species; however, very few resident packs occur in the south-east of the country bordering South Africa and Zimbabwe. In Zimbabwe, the largest population occurs in the Zambezi Valley, with secondary populations in Hwange National Park and associated conservation areas, as well as the lowveld region in the south (Rasmussen, 1997). Populations in southern Africa could feasibly be linked by dispersal if wild dogs were capable of navigating the intervening landscape.

This study describes eight long-distance (>80 km) dispersal events by wild dogs between isolated nature reserves, and in one case on private land. All these occurred between September 1992 and April 2011. Wild dog dispersal typically involves same-sex groups that leave their natal pack in search of mates (McNutt, 1996). Although dispersal distances of up to 250 and 195 km have been previously reported for males and females, respectively (Fuller et al., 1992), the dispersal events reported here are the longest recorded for wild dogs and show that isolated subpopulations could potentially be linked in a metapopulation via dispersing individuals.

Materials and methods

Study species

Wild dogs are medium-sized (~25 kg) social canids that live in packs of anywhere from 2 to 30 adults and yearlings (Woodroffe, McNutt & Mills, 2004). New packs typi-
cally form when small same-sex groups (usually siblings) disperse from their natal pack to locate and join opposite-sex groups from unrelated packs (McNutt, 1996).

Study areas

Data for this study were collected between 1992 and 2011 from three fenced reserves in South Africa that are part of the metapopulation programme for wild dogs, two reserves in Zimbabwe and one reserve in Botswana. Sites included Pilanesberg National Park (Pilanesberg; 500 km²), Marakele National Park (Marakele; 740 km²) and the De Beers Venetia Limpopo Nature Reserve (Venetia; 320 km²) in South Africa; Hwange National Park (Hwange; 14,650 km²) and Save Valley Conservancy (Save; 3450 km²) in Zimbabwe; and the Northern Tuli Game Reserve (Tuli; 720 km²) in Botswana (Fig. 1, Table 1). All sites supported populations of wild dogs at some point during the study period, either as naturally occurring or as reintroduced packs (Table 1). All reserves occur within the savannah biome that dominates this region.

Methods

Identification of wild dogs was based on pelage characteristics, as each wild dog has a unique coat pattern and can be readily identified using photographs (Maddock & Mills, 1994; Creel, Mills & McNutt, 2004). Within the fenced reserves in South Africa, and unfenced reserve in Botswana, wild dogs were monitored intensively by researchers and staff, and data were recorded when wild dogs broke out of reserves and went missing. Populations in Zimbabwe were monitored less frequently, and therefore, dispersal dates and intervals provided here are only an approximate estimation. When new wild dogs appeared in reserves, they were easily identified using photographs from the other reserves.

Wild dogs periodically break out of the fenced reserves in South Africa and are usually recaptured <80 km away, and returned (H.T. Davies-Mostert, pers. obs.; Gusset et al., 2008a). However, this study focused only on long-distance (>80 km) dispersal events that occurred during the study. Dispersal distances were calculated as the straight-line distance from the last confirmed sightings in the source reserve to where they were first re-sighted or recaptured. When these details were unknown, the shortest straight-line distance between reserve edges was used to obtain a minimum dispersal distance. Wild dogs were classified as adult (≥ 24 months old) or sub-adult (12–23 months old).

Results

Eight long-distance (>80 km) dispersal events were recorded. All involved movements to areas to which the individuals had not been previously exposed (Fig. 1). The details of these events, in order from shortest to longest, with dispersal and arrival dates in parentheses are as follows. (i) Five adult females dispersed 81 km from Marakele (1 November 2005) to Pilanesberg (16 December 2005). These females dispersed and arrived as a group and associated with a group of males in Pilanesberg. The females were captured and moved back to Marakele following concerns about potential inbreeding because of related founder stock at both sites. (ii) Two sub-adult males dispersed 169 km south-westwards from south-western Venetia (6 September 2003) to private farmland (20 September 2003). These males initially dispersed from Venetia with two sub-adult females, their litter-mates, but probably split into separate groups because the females were not with them 14 days later. The males were recaptured and returned to Venetia and later trans-located to Marakele, but the females were never found again. (iii) Two males dispersed 199 km from Hwange (18 February 1992 in the evening) to the 40 km peg near Bulawayo (15 March 1992). These males were later observed with females and pups on 3 September 1992, 172 km from their last fix and 44 km from their original dispersal site. (iv) Three adult males dispersed 255 km from Marakele (8 May 2005) to Venetia (19 June 2005). These males initially dispersed as a group of five, but two males subsequently split from the group and dispersed elsewhere (see case v). After arriving on Venetia, the three males associated with a group of four females, and then all seven dispersed soon thereafter. One animal from this group was killed by a vehicle 40 km east of Venetia (12 August 2005), a total straight-line distance of 304 km from the natal range. The others were never found again. (v) Two adult males dispersed 262 km from Marakele (8 May 2005) to NTGR (19 October 2005). These males initially dispersed from Marakele with the three males from above, but subsequently split from them. They were never seen with females and their fate remains unknown. (vi) One adult male dispersed 296 km from Tuli (photographed last on 20 August 2006) to
Marakele (15 November 2006). This male was seen prior to dispersal within a group of three other males and one female, but it is not known whether he dispersed alone or with the group, as the group was not seen again on Tuli. In Marakele, he associated with a lone female before they both disappeared. (vii) Two sub-adult males dispersed 447 km from Save (last seen in 29 April 2009) to Tuli (photographed on 19 April 2011). These males

joined up and sired pups with the resident alpha female. (viii) Three adult males dispersed 476 km from Tuli (6 April 2008) to Hwange (20 October 2008) where they were observed with an adult female. These males dispersed from their natal pack in Tuli 24 h after the pack was released from a holding boma following translocation from Marakele.

**Discussion**

Five of eight dispersal events we documented covered 255–476 km and are longer than any previously reported for wild dogs. The previous record for dispersal distance was 250 km for two males in Kruger National Park, South Africa (Fuller et al., 1992). Maximum dispersal distances of wild dogs from other large continuous populations are 77 km for four females in Selous Game Reserve, Tanzania (Creel & Creel, 2002), 169 km for males in northern Botswana (McNutt, 1996), 195 km for four females in and near Masai Mara National Reserve, Kenya (Fuller et al., 1992), and 150 km from Hluhluwe-iMfolozi Park, South Africa (Somers et al., 2008). Wild dogs can exhibit sex-biased dispersal, but with different sexes dominating the dispersal cohort in different populations: females in northern Tanzania (Frame & Frame, 1976), males in northern Botswana (McNutt, 1996) and neither sex dominating in northern KwaZulu-Natal, South Africa (Somers et al., 2008). Our results indicate that both sexes are capable of long-distance dispersal, with both dispersing >80 km in our study. That said, most of the events we describe involved males, which dispersed farther than females, thus reinforcing earlier findings that males are the less philopatric sex.

The long dispersal distances in our study are probably due to the isolation of subpopulations and distance between reserves. Among wolves (*Canis lupus*), the greatest straight-line dispersal distances (1092 km) occurred in low-density populations with disjunct pack distributions (Boyd et al., 1995; Wabakken et al., 2007). Wabakken et al. (2007) concluded that the excessive dispersal distances of wolves occur across areas containing suitable habitat and food resources, so the ultimate factor for long-distance dispersals was finding a mate. The same is true for wild dogs, particularly those in isolated or low-density populations (Somers et al., 2008; Gusset et al., 2009a). For example, private lands between fenced reserves in South Africa often had similar habitat to fenced reserves, and similar if not higher prey numbers (H.T. Davies-Mostert, pers. obs.). Therefore, it seems the ultimate factor for the long-distance dispersal of wild dogs in our study was finding a mate. This might especially be true for subpopulations in isolated reserves, where wild dogs usually occurred in 1–2 packs of related individuals. Wild dogs tend not to mate with relatives, even if given frequent opportunities (McNutt, 1996); thus, one of the only options for nonalpha members to breed in isolated reserves was to emigrate and search for nonrelated mates. That several of the dispersing wild dogs found and associated with members of the opposite sex in other reserves supports this assertion. In contrast, in large continuous populations, the mean dispersal distance of wild dogs often was <50 km and the maximum dispersal was never >250 km (McNutt, 1996; Creel & Creel, 2002).

Finding pack mates is contingent on a combination of well-timed dispersal (i.e. arriving when potential mates are available), choosing the correct search direction, and surviving the risks associated with traversing unprotected ranchland. Given the vast distances covered and possible directions that could have been followed, the likelihood of dispersing wild dogs locating other packs by chance in the sparsely populated landscape of northern South Africa was extremely low. Of six primary dispersal events recorded at Marakele between 2003 and 2006, three groups found members of the opposite sex (two cases are described above), one group was captured and translocated to a different population, and the outcome was unknown for the remaining two (H.T. Davies-Mostert, unpublished data). The frequency at which the dispersers found mates was suggestive of long-range communication, such as olfactory cues, which facilitates detection of other wild dogs. A better understanding of how this mechanism operates, and particularly its effective distance, would be useful for landscape-level conservation planning for the species.

All wild dogs that immigrated onto fenced reserves were identified; thus, no immigrants were from the large population in Kruger National Park (ca. 300 individuals; Woodroffe, McNutt & Mills, 2004), which was well within the dispersal ranges we recorded (Table 1, Fig. 1), or other resident packs in Limpopo Province (Lindsey, Du Toit & Mills, 2004), which may have been <50 km from Venetia. Thus, wild dogs at the edge of large continuous populations may disperse towards potential mates within the main population, rather than crossing large vacant
areas where potential mates are absent. However, this hypothesis needs to be tested.

Wild dogs dispersed through seemingly inhospitable landscape, managing to cross a matrix of numerous private lands (Fig. 2), many with high and electrical fencing for game ranching purposes, and where predators were not welcome (Lindsey, Du Toit & Mills, 2004). In fact, within the reserves themselves, wild dogs often broke through ‘predator-proof’ electrical fencing by digging under or slipping through the strands, suggesting that this type of fencing does not prevent wild dog movements. This is in contrast to other large carnivores, such as lions (*Panthera leo*), which can be effectively contained in small reserves by high electrical fencing (Davies-Mostert, Mills & Macdonald, 2009). Anthropogenic mortality of wild dogs is expected to be higher on private lands than on reserves (Woodroffe, McNutt & Mills, 2004), and we suspect that many of the dispersing wild dogs that were never seen again were killed by humans. Regardless, wild dogs successfully dispersed long dis-
tances to other reserves across a matrix of private lands, including well-fenced areas, indicating that wild dogs are capable of navigating across some of the most human-altered and fragmented landscapes in southern Africa. Indeed, recent research showed that wild dogs in an anthropogenic landscape altered their activity to use moonlight periods more and thus decrease encounters with humans (Rasmussen & Macdonald, 2011). Such behaviour, even though not necessarily optimal for hunting, may thus help to explain how wild dogs succeed to disperse across such human-dominated landscapes.

**Management implications**

The metapopulation conservation programme for wild dogs in South Africa actively manages gene flow among subpopulations, via transfer of wild dogs into subpopulations every few years (Davies-Mostert, Mills & Macdonald, 2009). However, without human assistance, wild dogs have contributed to this process themselves, by dispersing among isolated subpopulations and finding groups of the opposite sex; however, thereafter their fate is unknown. Although many of our dispersers were prevented from successfully reproducing (either because of the direct management interventions or because of the absence of suitable mates), our results cautiously suggest protected areas for wild dogs need not be contiguous, and widely spaced subpopulations can be connected via dispersing individuals or groups; thus, active management may not be necessary in all situations. Given the importance of dispersal in wild dog conservation, dispersal can be enhanced in innovative ways, if necessary (e.g. Graf et al., 2006; McNutt et al., 2008). We also caution managers of small reserves that traditional ‘predator-proof’ fencing may not be adequate to contain wild dogs, especially for those individuals attempting to disperse. Managers in other areas of Africa should consider our results, especially where wild dog populations are small and fragmented. Dispersers may be necessary to prevent inbreeding and/or local extinctions of wild dogs in small, isolated subpopulations (McNutt, 1996). Therefore, if increasing the size of protected areas is not an option, establishing a network of small subpopulations on isolated reserves may be adequate to maintain a metapopulation. However, it should be noted that when wild dog populations become very fragmented, such as those occurring in places like Senegal, long-distance dispersals may cause elevated mortality as wild dogs disperse from their natal home ranges with no hope of finding mates.

Future research should investigate what minimal distance is necessary between reserves to maintain gene flow among subpopulations, identify the success of these movements and determine the dispersal levels necessary to achieve metapopulation viability. Also, because wild dogs can navigate across vast expanses of fragmented and human-altered landscapes, several factors might increase their survivorship while dispersing, such as establishing corridors and improving human tolerance of transient wild dogs, which probably will be key to their survival. South Africa’s metapopulation project, for instance, has invested heavily in the conservation and management of wild dogs within reserves, but less so in the linkage between reserves. The nature of the dispersal events described here illustrates that future efforts may additionally aim to facilitate inter-population movement and, in this way, benefit population dynamics of the typically small populations.

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**References**

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