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Fence management and time since pack formation influence African wild dog escapes from protected areas in South Africa

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ABSTRACT

In human-dominated and highly fragmented landscapes, keeping wildlife within reserve boundaries is vital for conservation success. In South Africa, fences are a widely employed conservation management tool for protected areas and are successful in mitigating human-wildlife conflict. However, fences are permeable, and predators are able to cross through reserve fences. African wild dogs (*Lycaon pictus*) often leave fenced boundaries, resulting in high capture and translocation costs. Moreover, when wild dog packs (up to 30 individuals) leave fenced reserves they enter human-dominated landscapes where they face strong persecution and livestock predation incurs high costs. The factors driving packs to leave managed reserves are poorly understood, thus, to effectively manage wild dogs in fenced systems, it is important to understand why they leave reserve boundaries. There are several hypotheses as to why wild dogs cross through reserve fences, including inter- and intra-specific competition, social behaviour, management, prey density and environmental variability. Using a long-term dataset comprising 32 resident packs across five reserves, we investigated the relative strength of these hypotheses on the probability of wild dogs exiting a fenced reserve. During the 14-year study period, we recorded 154 exit events. We found that the interaction of fence integrity and time since pack formation were the primary factors affecting the probability of a pack leaving a reserve. When fence integrity was poor, escape probability decreased with pack age likely due to the exploratory behaviour of new packs. When fence integrity was average, escape probability increased with pack age likely due to the fitness benefits of holding larger and more exclusive territories as packs age. When fence integrity was good, the probability of a pack escaping was very low (only 1% occurrence). The implications of this research suggest that the primary management consideration for reducing wild dog escapes from fenced reserves should be maintaining adequate reserve-wide fence integrity, rather than focusing on social structure or drivers of inter- and intra-specific competition.

1. Introduction

The expansion of human-dominated landscapes has led to an increase in the frequency of human-carnivore conflict, particularly in developing countries which hold high species richness but have low financial capital to support conservation. This highlights the need for better carnivore conservation strategies that effectively protect the remaining populations from being eliminated in regions where they are seldom tolerated (Treves & Karanth 2003). The fencing of protected areas (reserves) is a commonly employed management tool in South

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Africa for containing medium to large sized mammal species, demarcating boundaries, reducing illegal access by people and mitigating human-wildlife conflict where high human and livestock densities occur close to these reserves (Hayward & Somers 2012; Sapkota et al., 2014; Pekor et al., 2019). The use of electric fences can also be an effective measure for the exclusion of free-ranging predators from areas where agricultural attractants, such as livestock, are present (Acorn & Dorrance 1994; Cavalcanti et al., 2012; Otto & Roloff 2015). However, even high quality fences can be permeable and not 100% effective in keeping predators within reserve boundaries, where several factors influence fence permeability including rainfall and holes created by digging species (Cozzi et al., 2013; Kesch et al., 2015). Thus, in order to reduce human-wildlife conflict when predators leave reserve boundaries and enter human-dominated landscapes, it is vital for us to understand the factors driving predators to leave reserve boundaries for effective conservation management.

Once widely distributed across much of sub-Saharan Africa, populations of the African wild dog (*Lycaon pictus*) have declined dramatically over the past 30 years, and wild dogs now occupy just 14 of the 39 countries in which they formerly ranged (Woodroffe & Sillero-Zubiri 2012; Wolf & Ripple 2017). The only remaining viable population of wild dogs in South Africa is found in the Kruger National Park, with smaller sub-populations around the country managed as a metapopulation across a network of small (<1000 km^2) fenced reserves.

Multi-member, single-sexed dispersal groups of wild dogs leave packs in search of mating opportunities (McNutt 1996; Creel & Creel 2002; Davies-Mostert et al., 2012) and in the managed metapopulation, dispersal groups often cross reserve boundaries in search of mates (Whittington-Jones et al., 2014). These groups are captured and translocated in a human-mediated dispersal mimicking natural processes (Davies-Mostert et al., 2009). However, resident packs of wild dogs within the managed metapopulation also occasionally leave the boundaries of fenced reserves either temporarily or permanently, but the factors that contribute to established packs leaving fenced reserves are poorly understood (Davies-Mostert et al., 2009; KZN-WAG minutes 2004–2018; C. Kelly, personal observation). Drivers of wild dog movements beyond reserve boundaries may include lion (*Panthera leo*) density (van der Meer et al., 2011; Cozzi et al., 2013), or packs travelling longer distances in search of food in response to periods of low prey density (Frame et al., 1979). Cozzi et al., (2013) found that wild dogs in Botswana had a 31% likelihood of crossing a fence barrier. However, because there is currently no established corridor system in place to facilitate connectivity between South Africa's wild dog metapopulation (Whittington-Jones et al., 2014), wild dogs cross fences into a human-dominated landscape where they are subjected to a range of risks (e.g. snaring, vehicle collisions, conflict and persecution; Woodroffe & Ginsberg (1998)). Wild dogs are listed as Endangered on the IUCN Red List (Woodroffe & Sillero-Zubiri 2012); therefore, in human-dominated landscapes in South Africa it is vitally important for the species' future viability to identify the factors contributing to wild dogs escaping fenced reserves. This information will enable reserve managers to devise strategies and allocate the resources required to secure the current population.

Our objective was to examine the relative contribution of a range of variables to understand the drivers of wild dog pack escapes from managed, fenced reserves in South Africa. We hypothesised 3 causes that could increase the probability of wild dogs exiting a fenced reserve: (1) high levels of inter- or intra-specific competition and/or low prey density would lead to increased ranging behaviours in search of food; (2) newly formed packs that are naïve to their new landscapes engage in exploratory excursions which increase the likelihood of contact with perimeter fencing; (3) management constraints, such as insufficient resources allocated to maintaining perimeter fences, may result in permeable barriers that do not deter exits.

2. Methods

2.1. Study area

We included 5 reserves forming part of the wild dog metapopulation system in this study, all of which were located within the KwaZulu-Natal province of South Africa (Fig. 1). (A) 960 km^2 government-run Hluhluwe-iMfolozi Park (HiP) (B) uMkhuze Game Reserve is a government-run 400 km^2 park and forms the western section of the iSimangaliso Wetland Park. (C) Manyoni Private Game Reserve is a 230 km^2 privately owned reserve situated 30 km north of HiP. (D) Somkhanda Game Reserve is a 120 km^2 community owned reserve located approximately 50 km south of the Swaziland border. (E) Tembe Elephant Park is a government-run 300 km^2 reserve in the Maputaland coastal plain, bordering Mozambique to the north. KwaZulu-Natal falls within the Savanna biome, the primary vegetation types of which includes savanna woodlands, grasslands, forest and bush thickets (Fairbanks & Benn 2000; Mucina & Rutherford 2006). The climate in the region is subtropical, characterised by high temperatures and high summer rainfall ranging from 900 to 1200 mm annually (Fairbanks & Benn 2000).

2.2. Wild dog observations

Observations of wild dogs between 2003 and 2017 were provided by the Priority Species Monitoring Project for each of the 5 reserves. At least 1 animal from each monitored pack was lured to a bait, immobilised with a tranquiliser gun (DanInject; Texas, USA), and fitted with either a Very High Frequency (VHF) or GPS tracking collar (range of makes and models). Monitors attempted to locate each pack daily at dawn and dusk using a VHF antenna (Telonics; Arizona, USA) and portable receiver (Communications Specialists Inc; California, USA). However, this was restricted by weather conditions, personnel availability, collar malfunction and wild dogs occupying inaccessible areas. Once packs were sighted, coordinates were recorded on a handheld GPS (Garmin eTrex 10). The coordinates of packs fitted with GPS collars were recorded daily by remote download. To reduce the effect of both temporal and spatial autocorrelation in the analysis, and due to management priorities of extended battery life, we restricted data points to 2 per day (those closest to 0600 and 1800), aligning with the crepuscular activity cycle of wild dogs (Mills & Gorman 1997; Whittington-Jones et al., 2014; Jenkins, et al., 2015).

We classified an exit event as a pack location outside the reserve boundary fence (maps of pack exit locations on each reserve are available online in Supporting Information). We classified non-exits (i.e. when packs had the opportunity to escape but did not) as a pack location within 50 m of the boundary fence. The 50 m threshold was based on previous research on wild dog viewsheds (Kruger et al., 1999) – i.e. within 50 m the animals can see the fence and decide whether or not to travel through. We used ArcMap 10.5 (Environmental Systems Research Institute, California, USA) to identify all locations when a pack was within a buffer of 50 m from the boundary fence. Where the exact point of exit on the boundary fence was unknown ($n = 118$), we determined the most probable point of exit by calculating the distance from the location of the pack outside the reserve boundary to the nearest point on the fence.

2.3. Explanatory covariates

We included relevant ecological variables to quantify the potential effect of a range of predictors on the probability of a fence escape (Table 1). The preferred prey species of wild dogs in KwaZulu-Natal are impala (*Aepyceros melampus*) and nyala (*Tragelaphus angasii*) (Kruger et al., 1999; Somers et al., 2017; Vogel et al., 2019). From individual reserve surveys, we converted impala and nyala total abundance to impalas/nyalas per 100 km^2 for comparison across reserves. Each reserve consistently used the same census technique for the duration of

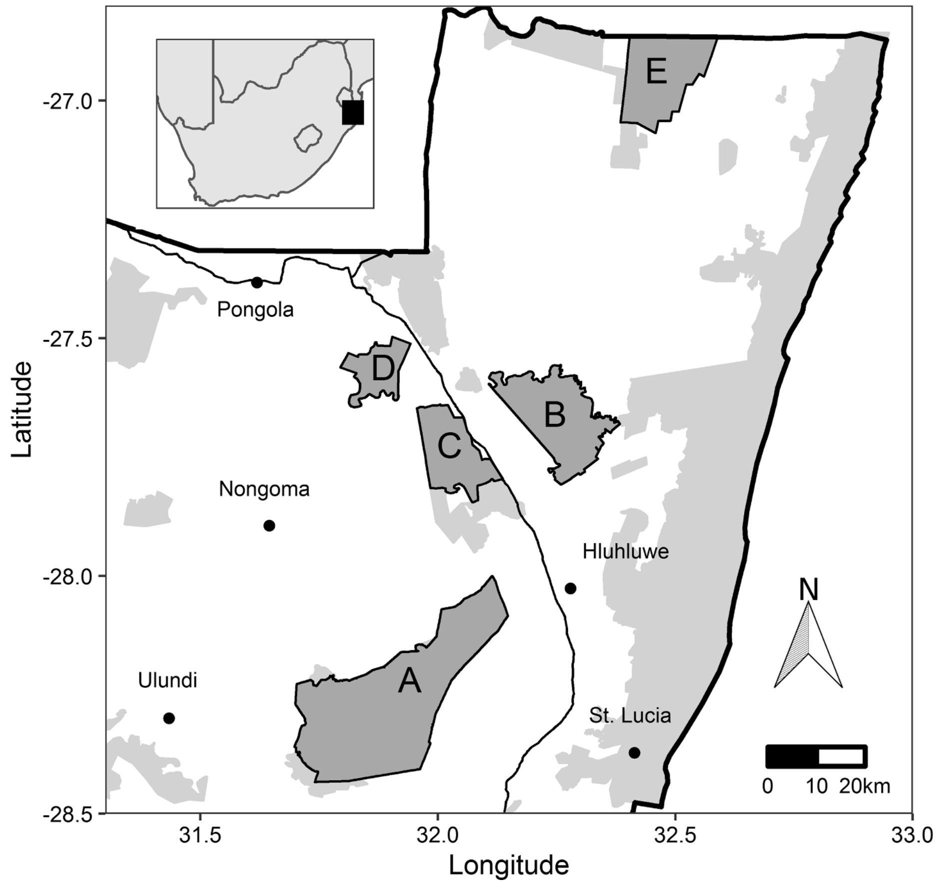

Fig. 1. The 5 reserves in KwaZulu-Natal, South Africa where we included data from 154 fence escapes by resident packs of African wild dogs between 2003 and 2017.

the study. Wild dog pack size (number of individuals per pack) and wild dog/lion densities (calculated as individuals per 100 km^2 for comparison across reserves of different sizes) were derived from information collected through the intensive Priority Species Monitoring Project for each reserve. Rainfall determines the quantity and quality of forage available to herbivores (Hopcraft et al., 2010), which could affect the distribution of prey and, consequently, the spatial decisions of wild dogs, therefore we used monthly rainfall records collected by each reserve. To account for the larger size of HiP and the North-South rainfall gradient across the reserve, we used monthly rainfall records from both the Hluhluwe and iMfolozi sections of the park corresponding to each location. The probability of a pack escaping from a fenced reserve could increase as a result of naïve animals exploring a novel environment; to investigate this, we included the time since pack formation (in months), calculated from Priority Species Monitoring Reports.

To understand the effect of management investment in deterring wild dog exits, we categorised fence integrity at both exit and non-exit locations as a categorical variable with a 3-level standard; 'good' (Fig. 2A), 'average' (Fig. 2B), and 'poor' (Fig. 2C), compiled from reserve reports, discussions with the KwaZulu-Natal Wild Dog Advisory Group and reserve staff. We defined a 'good' fence as one with a standard Bonnox/Veldspan game fence (1.8 m minimum height), bottom electric strands running low to the ground (~20 cm), electrics regularly maintained, and all holes fixed weekly. We defined an 'average' fence as one with small sections not maintained regularly resulting in missing electric strands, small holes, or gaps in the fence line. We defined a 'poor' fence as one with large sections not maintained, absent electrics and large gaps or holes in the fence line.

2.4. *Statistical analyses*

We created 18 *a-priori* candidate generalized linear mixed effects models with binomial distribution (1 = exit, 0 = non-exit) to investigate the factors affecting the probability of a pack exit. We tested various combinations of fixed effect explanatory covariates such as wild dog density, pack size, time since pack formation, lion density, prey density, rainfall and fence integrity with relevant interactions (Table 1). We included pack identity nested within individual reserve identity as nested random effects in all candidate models to account for multiple samples from the same packs in the same reserves and for reserve-specific differences (e.g., area size). We assessed collinearity between predictor variables prior to analysis using variance inflation factors (VIF) and Spearman rank correlation tests. Where high levels of correlation were found between variables (Spearman's rho > 0.6), one was discarded from the analysis, ensuring that all variables had VIF values $<$ 2 in the final statistical models (Zuur et al. 2007). We then used model selection based on Akaike Information Criterion (AIC*c*) to identify the best model(s) (Burnham & Anderson 1998). Models used in the model averaging procedure were those with a cumulative Akaike weight $\leq$ 0.95 and top models were selected where $\Delta AICc \leq 2$ following Burnham and Anderson (1998). We performed all statistical analyses and created all figures in RStudio v.1.1.383 (R Core Team, 2017) for Windows, using functions in the packages "car" (Fox & Weisberg, 2019), "ggeffects" (Lüdecke, 2018), "ggplot2" (Wickham, 2016), "lme4" (Bates et al., 2015), "MuMIn" (Barton, 2018) and "plotrix" (Lemon, 2006).

3. Results

In total, we recorded 1,687 wild dog pack locations within 50 m of a

Table 1
An *a priori* summary of the variables and interactions expected to affect the probability of resident packs of African wild dogs escaping from fenced reserves in KwaZulu-Natal, South Africa, 2003–2017. Upward arrows within the hypothesis column denote an increase in a variable and the response, while downward arrows denote a decrease in a variable and the response. Measures and units per variable are in parentheses.

Variables and interactions	Hypothesis	References
Wild dog density (individuals per 100 km^2)	↑ density = ↑ exits	Creel & Creel 2002, Parker 2010
Wild dog pack size (number of individuals per pack)	↓ pack size = ↑ exits	Creel & Creel 1996, Pomilia et al. 2015
Time since pack formation (months: observation date – pack formation date)	↓ time since formation = ↑ exits	Berger-Tal & Saltz 2014, Jenkins et al. 2015
Lion density (individuals per 100 km^2)	↑ lion = ↑ exits	Mills & Gorman 1997, Creel et al. 2001
Preferred prey density (impala/nyala per 100 km^2)	↓ prey = ↑ exits	Frame et al. 1979, Vogel et al. 2019
Rainfall (mm per month)	↑ rain = ↑ exits	Slotow 2012
	↑ rain = ↓ exits	Hopcraft et al. 2010
Fence integrity (poor/average/good)	↓ fence integrity = ↑ exits	Gusset et al. 2008, Davies-Mostert et al. 2009
Distance to river crossing (+/- 100 m)	↓ distance to river = ↑ exits	Somers et al. 2012, Whittington-Jones et al. 2014
Wild dog pack size × Fence integrity	↓ pack size + ↓ fence integrity = ↑ exits	Creel & Creel 1996, Gusset et al. 2008; Davies-Mostert et al. 2009, Pomilia et al. 2015
Lion density × Fence integrity	↑ lion + ↓ fence integrity = ↑ exits	Mills & Gorman 1997, Creel et al. 2001, Gusset et al. 2008, Davies-Mostert et al. 2009
Preferred prey density × Fence integrity	↓ prey + ↓ fence integrity = ↑ exits	Frame et al. 1979, Gusset et al. 2008, Davies-Mostert et al. 2009, Vogel et al. 2019
Time since pack formation × Fence integrity	↓ time since formation + ↓ fence integrity = ↑ exits	Gusset et al. 2008, Davies-Mostert et al. 2009, Berger-Tal & Saltz 2014, Jenkins et al. 2015
Time since pack formation × Wild dog pack size	↑ time since formation + ↑ pack size = ↑ exits	Creel & Creel 1996, Berger-Tal & Saltz 2014, Jenkins et al. 2015, Pomilia et al. 2015
Rainfall × Fence integrity	↑ rain + ↓ fence integrity = ↑ exits	Gusset et al. 2008, Davies-Mostert et al. 2009; Slotow 2012
Wild dog pack size × Lion density	↓ pack size + ↑ lion = ↑ exits	Creel & Creel 1996, Mills & Gorman 1997, Creel et al. 2001, Pomilia et al. 2015
Wild dog pack size × Preferred prey density	↓ pack size + ↓ prey = ↑ exits	Frame et al. 1979, Creel & Creel 1996, Pomilia et al. 2015, Vogel et al 2019
Lion density × Preferred prey density	↑ lion + ↓ prey = ↑ exits	Frame et al. 1979, Mills & Gorman 1997, Creel et al. 2001, Vogel et al. 2019
Distance to river crossing × Fence integrity	↓ distance to river + ↓ fence integrity = ↑ exits	Gusset et al. 2008, Davies-Mostert et al. 2009, Somers et al. 2012, Whittington-Jones et al. 2014
Distance to river crossing × Rainfall	↓ distance to river + ↑ rainfall = ↑ exits	Slotow 2012, Somers et al. 2012, Whittington-Jones et al. 2014

fence across 14 years, 154 of which resulted in a pack exiting a reserve (see Table 2 for pack-specific exit data). Thus, only 9.1% of times wild dogs were close to a fence did they escape from the reserve. We found that fence integrity, time since pack formation, and an interaction between fence integrity and time since pack formation were the most important predictors of wild dogs escaping from a fenced reserve (Fig. 3; Table 3) (all models are summarised in Table S1, available online in Supporting Information). When fence integrity was poor, 12% of fence encounters resulted in a pack leaving the reserve, and the probability of exiting decreased with pack age (Fig. 3). When the fence integrity was average, 17% of fence encounters resulted in a pack escaping, and the probability of exiting increased with pack age (Fig. 3). When the fence was good, only 1% of fence encounters resulted in a pack leaving the reserve, and the probability of an exit increased with pack age. However, due to the low number of observations (n = 4 exits) of old packs encountering good fences (Fig. 3), there are large confidence intervals, and this result must be interpreted with caution. Lion density, prey density, wild dog density, pack size, rainfall, and distance to river crossing were not significant predictors of a pack leaving a fenced reserve (Table S1).

4. Discussion

Our results support the hypotheses that the condition of the fence, rather than competition with other predators or the availability of prey, is the most important determinant in keeping wild dogs within reserves, particularly for newly formed packs. The high perimeter-to-area ratio of small reserves increases the likelihood of packs contacting the perimeter fence (Davies-Mostert et al., 2013). Therefore, when coupled with the large territories held by wild dogs, this highlights the challenges faced by managers to contain wild dogs in small areas and underscores the importance of maintaining high-quality fences for reserves in South Africa. Breaching the fence may be further exacerbated when introducing new packs to a reserve as they often engage in an initial exploratory phase of the unfamiliar area before switching to more knowledge-based localized movement patterns with contracted territories (Berger-Tal & Saltz 2014; Jenkins et al., 2015).

'Predator-proof' fences are not 100% effective in preventing wild dogs from exiting reserves (Gusset et al., 2008; Davies-Mostert et al., 2009), and our study suggests that the probability of a fence breach is higher in established packs when the condition of the fence was either average or good. Ultimately, fences are porous to wild dogs when in either poor or average condition compared to good condition where they are almost impermeable. Wild dog fitness is linked to territory size and exclusivity; established packs occupy larger territories than new packs and have minimal overlap with neighbours (Marneweck 2020). Therefore, if old packs are under selective pressure to maintain large, exclusive territories due to the associated fitness benefits, then it is likely that these established packs are more likely to expand their territories beyond the fenced reserve boundaries. When residing within small, fenced reserves, this means that fence encounters are likely more frequent and passing beyond fence boundaries thus more common for these packs.

The effectiveness of any fence is largely determined by the degree to which it is maintained. There are various factors that contribute to the deterioration of fence integrity, which may exacerbate the potential for escapes to occur, both in newly formed and resident packs. In some areas, wild dogs have adopted fence-hunting strategies (i.e. pushing prey to the fence thereby blocking their escape path) that can compromise fence integrity, potentially increasing the likelihood of wild dogs leaving reserves (Rhodes & Rhodes 2004; Davies-Mostert et al., 2013). Poor and average quality reserve fences often have large holes below or gaps in the fence line where electric strands are absent, which likely facilitates an easy exit for wild dogs out of the reserve boundaries. This can result from the activity of hole-digging specialists such as aardvarks (*Orycteropus afer*) and warthogs (*Phacochoerus africanus*) (Somers et al., 2012; Kesch et al., 2014) or megaherbivores such as elephants (*Loxodonta africana*) inflicting structural damage to fences, resulting in entire

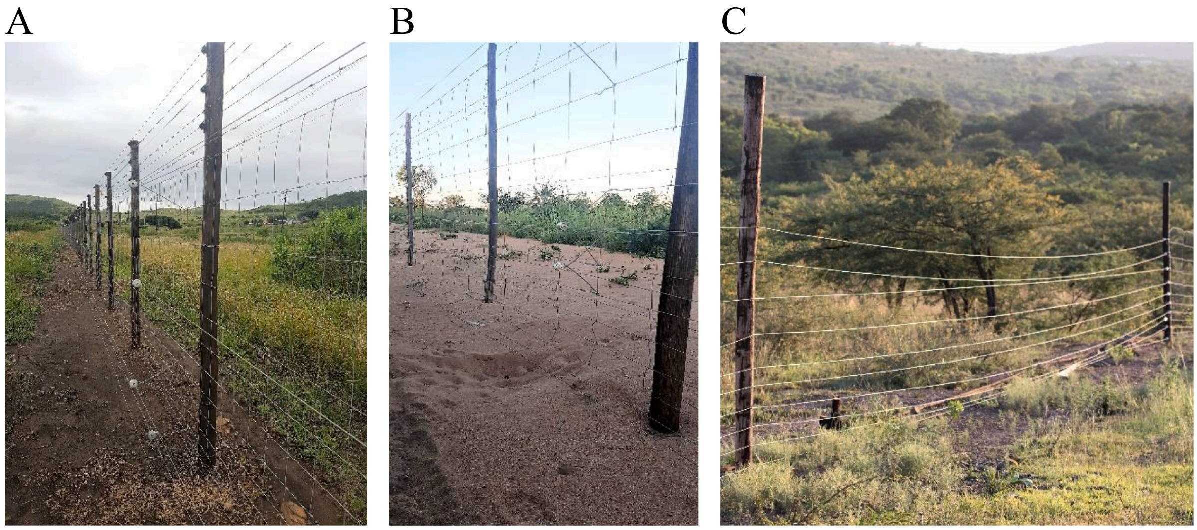

Fig. 2. (A) Good quality, (B) Average quality and (C) Poor quality fence categories recorded across 5 reserves in KwaZulu-Natal, South Africa, 2003–2017.

Table 2
The 32 resident African wild dog packs included in our study of exits from fenced metapopulation reserves in KwaZulu-Natal, South Africa, 2003–2017.

Pack	Reserve	Pack age at start (months)	Time active (years)	Pack size (range)	Total locations ≤ 50 m fence (VHF | GPS)	Number exits	Number non-exits	Proportion of exits
Albie	Tembe	0	5	3–15	97 (17 | 80)	4	93	0.04
Alfies	HiP	20	4	7–13	55 (0 | 55)	3	52	0.05
Bhejie	HiP	10	<1	11–24	19 (0 | 19)	1	18	0.05
Boomerang	HiP	1	1	3	1 (1 | 0)	1	0	1
Brodies	HiP	1	1	6	1 (0 | 1)	0	1	0
Cagents	HiP	4	6	4	1 (1 | 0)	0	1	0
Crocodile	HiP	8	5	6–25	11 (11 | 0)	3	8	0.27
Crossroads	HiP	20	3	11–20	24 (0 | 24)	1	23	0.04
Dela & Zeus	HiP	7	3	2–5	13 (0 | 13)	3	10	0.23
Dojo	HiP	24	11	11	1 (1 | 0)	1	0	1
Hluhluwe	HiP	53	4	11–17	10 (10 | 0)	3	7	0.3
Juma 3	HiP	35	2	13	1 (1 | 0)	1	0	1
Madlozi	HiP	5	5	6–9	73 (0 | 73)	11	62	0.15
Main	Tembe	10	7	3–16	304 (179 | 125)	24	280	0.08
Manyoni	Manyoni	5	6	3–15	562 (224 | 338)	0	562	0
Mhlanganweni	HiP	8	2	12	1 (1 | 0)	0	1	0
Mtonjeneni	Tembe	0	<1	4	1 (1 | 0)	0	1	0
New iMfolozi	HiP	26	5	16–26	11 (11 | 0)	1	10	0.09
Shiyane	HiP	10	5	7–25	16 (2 | 14)	14	2	0.88
Sokhwezela	HiP	16	6	13–20	43 (0 | 43)	1	42	0.02
Somkhanda	Somkhanda	17	4	7–11	164 (74 | 90)	1	163	0.01
Thobothi	HiP	1	1	5	4 (4 | 0)	4	0	1
Tshokolwane	HiP	20	4	9–25	122 (0 | 122)	14	108	0.11
Tulele	HiP	2	2	6	1 (1 | 0)	0	1	0
Ume	HiP	11	6	12–23	5 (5 | 0)	5	0	1
Veggie	HiP	1	3	5–16	7 (7 | 0)	0	7	0
WD	uMkhuze	26	4	2–10	59 (59 | 0)	30	29	0.51
WD1	uMkhuze	11	1	5	2 (2 | 0)	0	2	0
WD2	uMkhuze	5	7	9–28	72 (61 | 11)	27	45	0.38
WD3	uMkhuze	13	1	4	3 (1 | 2)	0	3	0
WD6	uMkhuze	3	<1	4	1 (0 | 1)	0	1	0
WD7	uMkhuze	3	<1	8	2 (2 | 0)	1	1	0.5

sections being broken or compromised and open to transgression (Slotow 2012; Kesch et al., 2015).

While our findings provide important information for wild dog conservation and management, they also highlight several avenues for further research. For example, we were unable to include the possible impact of other competitors on the probability of wild dogs leaving reserves (e.g., spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*)). We were also unable to include the distribution of prey as a possible contributing factor as these historical data were unavailable. Territory size could also be a contributing factor as our results suggest that older packs may be looking to extend territory, but exploring this was also beyond the scope of our study. Thus, future studies should focus on examining the factors influencing the probability of wild dogs exiting fenced reserves in much finer-scale detail than we were able, i.e., intraguild pressure, prey distribution, territory sizes.

Conservation management goals are often constrained by limited funding and a lack of available resources (James et al., 1999; Creel et al., 2013; Packer et al., 2013). Therefore, it is important to be able to identify the most cost-effective solutions through which management goals can be achieved effectively. This is of particular relevance to the field of conservation fencing whereby the potential costs of a fence breach may far outweigh the definite cost of ensuring sufficient fence

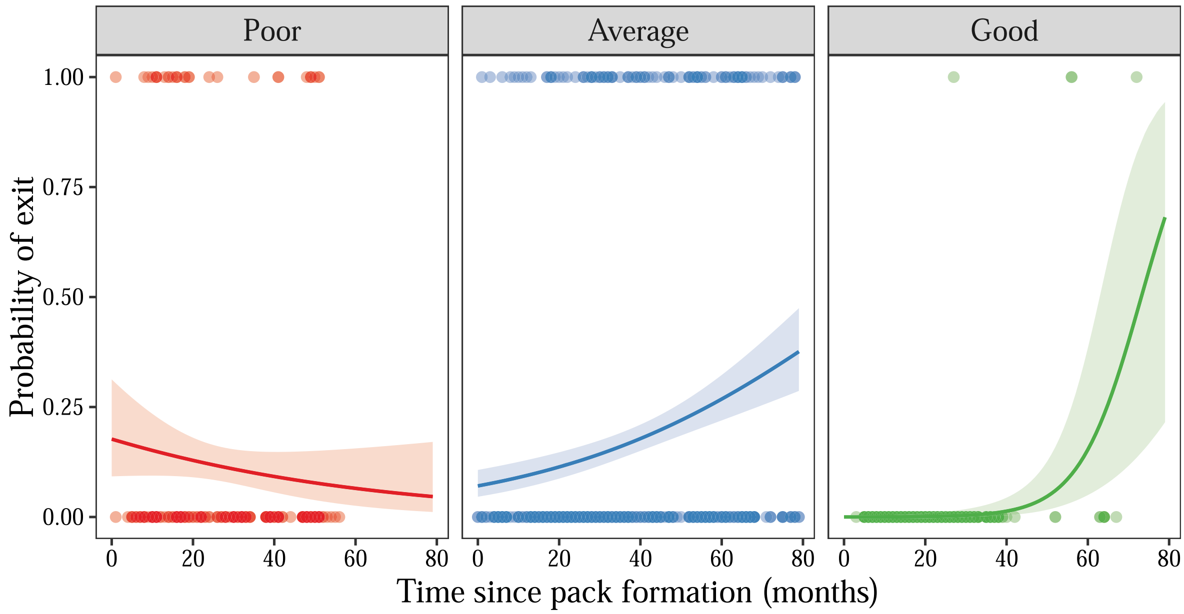

Fig. 3. Probability of resident African wild dog packs exiting fenced reserves in KwaZulu-Natal, South Africa, 2003–2017, in response to poor, average, and good fence integrity interacting with time since pack formation. 95% confidence intervals are represented by the shaded regions.

Table 3
Average effects of explanatory variables from the top models explaining the probability of resident African wild dog packs escaping from fenced reserves in KwaZulu-Natal, South Africa, 2003–2017, based on the model evaluation procedure. Reference level for the fence integrity variable was 'poor'. For a full list of model outputs, see Supporting Information Table S1.

Variable	$\hat{\beta}$	SE ($\hat{\beta}$)	CI	*n* models	Importance
Fence integrity (Average)	1.75	0.57	(0.63, 2.87)	7	1.00
Fence integrity (Good)	−2.05	1.60	(−5.20, 1.09)	7	1.00
Time since pack formation	0.64	0.46	(−0.26, 1.55)	2	1.00
Fence integrity (Average) × Time since pack formation	0.18	0.47	(−0.75, 1.11)	1	1.00
Fence integrity (Good) × Time since pack formation	1.30	0.91	(−0.49, 3.09)	1	1.00

integrity through regular maintenance (Bode & Wintle 2010). A recapture operation following animals exiting a reserve can be a difficult, expensive, and protracted undertaking that must factor in a variety of costs, which may include veterinarians, ground staff, helicopter support, temporary holding facilities, subsequent translocation, conflict with local communities and compensatory payments for livestock losses (English et al., 1993; Lindsey et al., 2005; Jackson et al., 2012, KZN-WAG minutes 2004–2018). Although costs vary depending on the nature of the situation, the average cost of recapturing wild dogs (including helicopter, veterinary bills, and professional time) is approximately US$10,000 per operation (EKZNW, unpubl. data; Wildlife ACT Fund, unpubl. data), while the cost of fence maintenance in South Africa is approximately US$32,000 per year per 100 km (Lindsey et al., 2012). Thus, multiple escapes per annum could exceed normal fence maintenance costs. Although fence maintenance represents a significant financial commitment, reserve management should weigh this against the potential costs of multiple recapture operations over the course of a year. Our results suggest that in many instances continual fence maintenance could significantly reduce escapes, which could reduce the cost of recapturing and increase the likelihood of meeting conservation goals.

5. Conclusions and management suggestions

Reserves with wild dogs must meet the specified government-legislated standards for a predator-proof fence in South Africa; however, it is essential that these standards be maintained for such reintroductions to be deemed successful in the long-term. This long-term success depends on reducing the probability of packs exiting reserves, preying on livestock, incurring both compensatory and rehoming expenses, and ultimately being persecuted. The rate of exits per pack ranged from 0 to 18 times per year, varying considerably across reserves, and this variation means that suggesting a regular interval for fence patrols is unhelpful. Rather, we recommend that intensive monitoring of newly formed packs be prioritised when resources for fence maintenance are low; this would allow implementation of fine-scaled mitigation measures to reduce the likelihood of new packs escaping. Once a pack reaches approximately 3.5 years old (i.e. 40 months old), we also recommend higher intensity monitoring in reserves with average and good fence integrity due to the higher probability of exit by packs of this age. In order to minimise escapes by both new packs and established packs, we suggest that management should aim at maintaining good reserve-wide fence integrity. Our finding that a well-maintained electric fence is essential for the effective containment of newly formed packs is not only a key component of wild dog management in South Africa but may have wide implications for the management of other species in protected areas surrounded by high-density human populations (such as the newly fenced protected area network in Malawi). We recommend further study on a per-reserve basis to determine the root cause of problems with fences and implement the necessary mitigation strategies to manage against these. Such mitigations may include the installation of remote-sensing alarm systems to monitor fence breaks and combining daily anti-poaching patrols with general fence maintenance checks for structural or electrical issues, including the filling of any gaps created by hole-digging species. Although these mitigation efforts are already implemented in some reserves, continual effort is needed regarding wild dogs, particularly because their natural long-distance movements places them in contact with perimeter fences more often than other species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

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