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ORIGINAL ARTICLE

Dynamics of direct inter-pack encounters in endangered African wild dogs

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Abstract

Aggressive encounters may have important life history consequences due to the potential for injury and death, disease transmission, dispersal opportunities or exclusion from key areas of the home range. Despite this, little is known of their detailed dynamics, mainly due to the difficulties of directly observing encounters in detail. Here, we describe detailed spatial dynamics of inter-pack encounters in African wild dogs (*Lycaon pictus*), using data from custom-built high-resolution GPS collars in 11 free-ranging packs. On average, each pack encountered another pack approximately every 7 weeks and met each neighbour twice each year. Surprisingly, intruders were more likely to win encounters (winning 78.6% of encounters by remaining closer to the site in the short term). However, intruders did tend to move farther than residents toward their own range core in the short-term (1 h) post-encounter, and if this were used to indicate losing an encounter, then the majority (73.3%) of encounters were won by residents. Surprisingly, relative pack size had little effect on encounter outcome, and injuries were rare (<15% of encounters). These results highlight the difficulty of remotely scoring encounters involving mobile participants away from static defendable food resources. Although inter-pack range overlap was reduced following an encounter, encounter outcome did not seem to drive this, as both packs shifted their ranges post-encounter. Our results indicate that inter-pack encounters may be lower risk than previously suggested and do not appear to influence long-term movement and ranging.

Significance statement

Direct aggressive encounters between competitors are an important and potentially dangerous aspect of territoriality. In spite of this, detailed data on movements in response to encounters are lacking, especially for large mammals. Collecting observational data on competitors leaving an encounter site in different directions is logistically challenging, and radiocollar technology has previously been ineffective in this regard due to low temporal resolution. We overcame these issues by using custom-built high-resolution GPS collars, showing that intruding African wild dog packs were more likely to win inter-pack encounters (residents initially moved further away from the encounter). Inter-pack encounters appeared to have only short-term impacts on movement, with their outcome having no discernible impact on the long-term ranging patterns of African wild dog packs.

Keywords Territoriality · Encounter · *Lycaon pictus* · Inter-pack · Aggression · Home range

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Introduction

Inter-group encounters may have important life history consequences, due to the potential for injury and death (e.g. grey wolf *Canis lupus*, Mech 1994; Cassidy et al. 2015; chimpanzee *Pan troglodytes*, Townsend et al. 2007; yellow baboon *Papio cynocephalus*, Shopland 1982); disease transmission (Craft et al. 2011); information exchange and dispersal opportunities (Sicotte 1993) or exclusion from important areas of their previous range (Ewing 1972). Although there may be considerable costs to direct inter-group encounters, relatively little is known of the detailed dynamics of these events.

Current knowledge of territorial encounters mainly comes from direct observations and suggests that several factors may affect their outcome. In particular, literature from social birds, primates and carnivores suggests that relative group size is important in determining encounter outcomes (e.g. green wood hoopoe, *Phoeniculus purpureus*, Radford and du Plessis 2004; chimpanzee, Wilson et al. 2001; black howler monkey, *Alouatta caraya*, Kitchen 2004; banded mongoose, *Mungos mungo*, Rood 1975; Furrer et al. 2011). As the benefits of winning a contest may vary according to where it occurs within the territory (e.g. Maynard-Smith 1982), location has also been shown to affect encounter outcome in some species (e.g. banded mongoose, Furrer et al. 2011, but see Rood 1975; chacma baboons, *Papio cynocephalus ursinus*, Kitchen et al. 2004; Verreaux's sifaka, *Propithecus verreauxi*, Koch et al. 2016) but not in others (e.g. chimpanzee, Wilson et al. 2001; black howler monkey, Kitchen 2004). In general, residents usually defeat intruders (e.g. white-headed capuchin, *Cebus capucinus*, Crofoot et al. 2008; white rhinoceros, *Ceratotherium simum*, Rachlow et al. 1998), and larger groups tend to defeat smaller ones (e.g. Ethiopian wolf, *Canis simensis*, Sillero-Zubiri and Macdonald 1998; grey wolf, Cassidy et al. 2015; banded mongoose, Furrer et al. 2011). In some species, however, group composition plays a more important role than group size per se in determining the outcome of encounters. For example, in chacma baboons (Hamilton et al. 1975, 1976; Cheney 1987), after controlling for location, the relative number of males in opposing groups appeared to play a role in determining the outcome of inter-group contests, with groups containing more males winning more often. Similar patterns have been reported for grey wolves, where packs with more males or older individuals than their rivals were more likely to triumph in encounters (Cassidy et al. 2015).

Recent developments in remote sensing, particularly in the form of GPS collars, may offer a new window into rare encounters by providing more data than has previously been collected by opportunistic direct observation. Additionally, the exhaustive GPS data provided by remote monitoring at short intervals captures all encounter instances, many of which may have been missed previously. This is a considerable improvement on direct observations, which tend to be conducted somewhat opportunistically and thus can provide only minimum estimates of encounter rates. Although some studies have begun to utilise collars for this purpose (e.g. Crofoot et al. 2008), inter-fix intervals have generally been too wide to allow detailed assessment of the spatial consequence of encounters, or even to allow remote detection of all encounters.

Here, we use high-resolution GPS collar data from 11 free-ranging packs of African wild dogs (*Lycaon pictus*) in the Okavango delta region of Botswana to record and analyse the spatial dynamics of inter-pack encounters. African wild dogs are endangered (Woodroffe and Sillero-Zubiri 2012) pack-living canids (Mills and Gorman 1997), with large annual ranges (739 km^2 in northern Botswana; Pomilia et al. 2015) encompassing considerable areas of overlap with their neighbours (30–35%, Kruger NP, South Africa, Reich 1981; 62%, Selous GR, Tanzania, Creel and Creel 2002). Previous studies have indicated that direct encounters between packs are rare (Creel and Creel 2002; Woodroffe and Donnelly 2011), perhaps due to temporal partitioning of the use of overlapping areas (Mills and Gorman 1997), or perhaps simply because the size of their ranges and their low-population density make chance encounters unlikely. However, previous data were limited to near-simultaneous locations of neighbouring packs acquired by tracking the animals with a combination of VHF collars and direct observations (Mills and Gorman 1997; Creel and Creel 2002). This bias toward diurnal data on encounters continued into studies using early model GPS collars, collecting positional data at low resolution and restricted to daylight hours (e.g. Woodroffe and Donnelly 2011), both of which are likely to underestimate encounter rates.

In this study, we use data from high-resolution, custom-designed and built GPS radiocollars to investigate and describe the frequency, outcome and detailed spatial dynamics (at pack scale) of inter-pack encounters in African wild dogs over the complete 24-h cycle. These collars have been used previously to quantify African wild dog hunting dynamics (Hubel et al. 2016a) and energetic expenditure (Hubel et al. 2016b). Specifically, we (1) make the first direct measurement of the frequency of inter-pack encounters in this species continuously over the 24-h cycle; (2) assess which factors (residence status, pack size ratio) affect the outcome of encounters; and (3) describe the detailed spatial dynamics of direct encounters between competing packs at the time of encounters and over a range of time-scales following encounters. In line with previous literature described above, we predict that residents or larger intruding packs will be more likely to win encounters and will move least from the encounter site immediately following an encounter. We predict that losers will avoid the vicinity of encounter sites in the long term following an encounter, and may shift their range after an encounter to reduce overlap with the winning pack.

Methods

Study population and site

Data were collected between November 2011 and February 2015 from 11 packs of free-ranging African wild dogs in northern Botswana. The study area (ca. 2600 km^2; 19° 31′ S, 23° 37′ E; elevation ca. 950 m) was bordered on the west and northwest by permanent swamp of the Okavango delta and included the eastern section of the Moremi Game Reserve and neighbouring Wildlife Management Areas. Further details can be found in McNutt (1996). This sub-population of African wild dogs has been studied since 1989, and each individual was identified by its unique tricolour pelage pattern, distinctive ear notches and tail stripes. Pack size (all adults and yearlings >1 year) and the demographic composition of participating packs were extracted from the closest observation sessions either side of each encounter, when any observed injuries were also noted. It was not possible to record data blind because our study involved focal animals in the field.

Collars and collaring

This study used data produced by innovative Global Positioning System with Inertial Measurement Unit (GPS-IMU) animal collars (ca. 350 g; described in detail in Wilson et al. 2013). Key components of these collars comprised a GPS receiver (LEA-6T, uBlox AG) and a set of 3-axis Micro Electro-Mechanical Sensor (MEMS) accelerometer and gyroscope sensors, controlled by an MSP430 series microcontroller (Texas Instruments Inc.) running custom firmware written in the ‘C’ programming language. A 2G-B micro-SD flash card (Sandisk) provided data storage, and a 2.4-GHz radio link (Nanotron Technologies Gmbh) facilitated downloading of the collected data to a nearby vehicle. A conventional VHF tracking transmitter (Sirtrack) was integrated into the collar to facilitate airborne and ground-based tracking and physical location of the animal. To improve battery life, the collar was programmed to switch between different operating states depending on time of day and on the level of animal activity, as measured by the on-board accelerometer. If the animal was resting, GPS fixes were taken once per hour. When the animal was determined to be active, the GPS fix interval was reduced to 5 min, thus providing fixes with significantly improved temporal resolution during movement.

One individual in each pack was radiocollared following darting from a stationary vehicle within 15 m using TELINJECT darting equipment to deliver a mixture of xylazine (55 mg), 260 ketamine HCL (50 mg) and atropine (1.1–1.2 mg) and reversed after 45–60 min with yohimbine (4 mg) or atipamezole (5.5 mg) (further details in Osofsky et al. 1996). Most collars were removed and replaced when the dog was immobilised following collar expiry, but automatic drop-off units (Sirtrack, 70 g) were used to release two collars (total collar weight ca. 420 g) at the end of the study (see Fig. 1). During anaesthesia, we recorded the general health of each sedated animal, monitored vital signs, took body measurements and collected blood samples. All sedated individuals safely recovered from the anaesthesia and showed no injuries or signs of distress.

Data extraction and interpolation

To identify possible encounters between packs, the data were first reduced by exhaustive automated searches of all of the GPS locations from all GPS collars using custom-written code in programming languages Perl (www.perl.org) and R (R Core Team 2015). This produced summary files with all inter-pack encounters within 800 m and 12 h of each other. The summary files included KML maps showing locations, which allowed manual rejection of some false encounters based on erroneous spatial data. These errors were usually single points that were unrealistic distances from previous and subsequent points in a track; i.e. they would require the collar to move at unrealistic speeds (>19 ms^{-1}) in comparison to those measured previously (Hubel et al. 2016a, b). Overall, 1.7% of points were removed from our raw dataset on this basis.

GPS location data for each collar in an encounter were then extracted for 12 h before and after the time when the packs were closest together (centre point). Gaps between 5-min points were interpolated to 30-s intervals, with interpolated points equidistantly spaced between consecutive GPS fixes (i.e. we assumed that dogs moved directly and at constant velocity between GPS fixes). Interpolation compensated for different collars taking fixes at different times. Interpolated datasets were reprocessed through the automated search code,

Fig. 1 Injured subdominant resident adult male African wild dog following an inter-pack encounter. GPS radiocollar and drop-off unit also shown

and minimum distance center points (hereafter ‘estimated encounter locations’) were determined. All estimated encounter locations with close spatial-temporal overlap (inter-pack distance <800 m, within 5 min) in raw data were considered further.

Although 800 m is greater than the expected visibility in most habitats across the study site, this distance was chosen to allow for temporal off-sets in GPS fixes (up to 150 s), during which packs could diverge considerably. In practice, 12/15 encounters had minimum inter-pack distances <310 m (Table 1), and only encounter 1 was >450 m (614 m). In all cases, there was also clear evidence that the packs encountered one other, in that at least one of the packs orchestrated a clear change in direction. This suggests that the packs had come closer to one another during an inter-fix interval ‘blackspot’ in the raw data. As each pack’s location was estimated using a single collar, other individuals present at each encounter (12.07 ± 4.64 uncollared individuals [$\dot{x}$ ± SD], range 5–21), were likely to have been closer to inter-pack individuals than these distances suggest.

From interpolated data, we extracted each collar’s location, inter-fix speed (averaged over 30 s), and closing speed between packs (negative values were converging, positive values diverging) every 30 s for 12 h either side of each encounter. To evaluate whether packs avoided the general vicinity of encounter sites following encounters, estimated encounter locations were fed back into the data set as points of interest. GPS location data were subjected to the first level of automatic searching described above to extract all instances of close passes (<800 m) to these sites. Data from the packs involved in encounters at the specific sites were extracted to give pre- and post-encounter rates of close passes to these sites in both the preceding and following 120 days (excluding the day of the encounter).

Encounter frequency

An encounter could be detected only when both neighbouring packs had an individual wearing a radiocollar at the same time. Because collars were fitted at different times, we had to account for each pack’s potential to be detected encountering its neighbours. During the period that a given pack wore a collar, we summed the days that each of its neighbours also wore a collar, and pooled these. The number of encounters a pack experienced was then divided by this value to give the encounter rate of the focal pack.

Table 1 Summary of 15 inter-pack encounters in African wild dogs

					Pack identity		Distance to own 50% kud (km)[c]			Pack size[d]	
Encounter	Winner[a]	Related?	Date	Time[b]	Resident pack	Intruder pack	Resident	Intruder	Inter-pack distance at encounter (m)	Resident	Intruder
1	Intruder	Y	23 February 2012	1641 hours	MT	NM	0.61	24.0	614.0	14	3
2	Intruder	Y	30 April 2012	1939 hours	HW	SA	0	12.0	288.8	5	3
3	Resident	Y	03 May 2012	2325 hours	MT	HW	2.43	2.9	56.2	7	5
4	Resident	N	07 May 2012	0523 hours	MT	KB	1.96	9.1	23.8	7	6
5	Intruder	N	07 May 2012	2111 hours	MK	SA	1.3	1.8	442.3	4	3
6	Intruder	N	14 May 2012	0422 hours	KB	MT	0	2.2	36.0	6	7
7	Intruder	Y	25 May 2012	1622 hours	SA	MT	0.1	3.3	401.7	3	7
8	Intruder	N	10 October 2012	0522 hours	KB	MT	0.4	3.3	288.3	4	6
9	Intruder	N	21 August 2013	0344 hours	MB	KB	0.7	1.7	146.8	6	9
10	Resident	N	15 August 2014	1857 hours	MB	DB	0	17.2	66.8	11	12
11	Resident	N	21 August 2014	0432 hours	MB	HT	0	4.4	295.4	10	10
12	Intruder	Y	11 August 2014	2345 hours	ZU	AP	0	2.3	270.7	9	12
13	Intruder	N	08 May 2012	0528 hours	KB	MT	0	2.4	309.1	6	7
14	Intruder	N	17 August 2013	2140 hours	MB	KB	0	4.4	65.5	6	9
15	Intruder	Y	30 January 2014	1618 hours	HT	AP	0	0.7	141.9	4	10

[a] Losers were pack displaced furthest from encounter location 1-h post-encounter

[b] Coordinated Universal Time (UTC)

[c] Closest edge of 50% kud if outside, otherwise set to 0

[d] Adults and yearlings over 1 year old

Identifying neighbours and residence status

Packs with overlapping 95% kernel utility distributions (kud) during the study period were considered to be neighbours. Kud estimates were derived using the kernelUD function in the adehabitat package in R (Calenge 2006), with a bivariate normal kernel, where the smoothing factor (h) = 2400, grid = 400 and grid extent = 3. Pack kuds were estimated based on all location data from up to 120 days preceding the encounter (90 ± 38.10 [$\dot{x}$ ± SD], range 8–120, days per kud, and based on 14,634 ± 16,561 [$\dot{x}$ ± SD], range 215–77,631, locations per kud, N = 30). Given the potential for the home range estimation method and the choice of parameters to influence the shape and extent of the estimated range (e.g. Pomilia et al. 2015), ranges were also drawn as minimum convex polygons (mcp) using the mcp function in the adehabitat package. Results are provided for both methods and are qualitatively similar (see Table 2). All presented plots are based on kud estimates.

Following identification of encounter centre points, packs were classified as ‘resident’ or ‘intruder’ based on the distance of the encounter point to the boundary of the pre-encounter core area estimate (50% kud and mcp, respectively; hereby referred to as the pack’s ‘core area’). In all instances, the pack with the shortest distance to their core area was deemed the resident, and the other pack was the intruder. When one pack had a core area defined by multiple discrete polygons, the distance to the closest core polygon was used. Thirteen encounters were clearly in the pre-encounter exclusive area of one pack, while the other two were in an area of inter-pack overlap (i.e. the area of range overlap in the 120 days preceding the encounter). To avoid the risk of misclassification that might occur if ranging changed in response to the encounter of interest, only data preceding the encounter were used to determine residence status. Residence classification was consistent across the two range estimate methods, except for encounter five where the encounter occurred approximately equidistant from the core areas.

Encounter outcome

The winner of an inter-group encounter is usually defined as the group which stayed behind at the encounter site following the encounter (e.g. capuchins; Crofoot et al. 2008). In keeping with this, we defined the winner as the pack that remained closest to the encounter site 1 h following the encounter (Table 1). Additionally, we explored determining encounter outcome by defining the winner as the pack that moved the least toward its own range core over the same 1-h period. However, this latter approach may be less reliable as residents began closer to home by definition, and this may have skewed the results. Nevertheless, we feel it is important to evaluate whether moving toward home might be a relevant measure of winning a contest in this highly vagile species, where remaining at the encounter site may not provide an accurate indication of encounter outcome.

We used a series of generalised linear mixed models (GLMMs), carried out in the lme4 package (Bates et al. 2015) in R, with a binomial error distribution to explore the potential factors affecting encounter outcome (win = 1 or lose = 0). To ensure independence, we followed the approach of Cassidy et al. (2015) and Crofoot et al. (2008) in selecting a single focal pack from each encounter, and did so using a simple random selection script in R. Terms included in the models were pack size ratio (the

Table 2 Comparison of the proportion of inter-pack range overlap in pre- versus post-encounter periods and changes in distances of packs to their own range core 1 h after versus 1 h before encounters, for 15 African wild dog inter-pack encounters. The overlap between each packs pre- and post-encounter range were also estimated to investigate the source of any shifts in inter-pack overlap. Ranges were estimated using minimum convex polygon (mcp) and kernel utility distribution estimates (kud) to buffer against biases in home range estimation

Proportion of inter-pack range overlap in pre- versus post-encounter periods									
		KDE method				MCP method			
Overlap	Period	Mean		SD	Paired t test result	Mean		SD	Paired t test result
Inter-pack	Pre-encounter	0.35	±	0.20		0.31	±	0.26	
	Post-encounter	0.22	±	0.15	$t_{14} = 2.61, P = 0.021$	0.15	±	0.19	$t_{14} = 2.13, P = 0.051$
Intra-pack	Pre-post (intruder)	0.68	±	0.20		0.65	±	0.25	
	Pre-post (resident)	0.67	±	0.23	$t_{14} = 0.27, P = 0.790$	0.65	±	0.27	$t_{14} = 0.07, P = 0.945$
Intra-pack	Pre-post (winner)	0.68	±	0.26		0.68	±	0.33	
	Pre-post (loser)	0.66	±	0.15	$t_{14} = 0.37, P = 0.719$	0.62	±	0.17	$t_{14} = 0.72, P = 0.482$
Changes in distances of packs to their own range core 1 h after versus 1 h before encounters									
		KDE method				MCP method			
Status	Calculation	Mean		SD	Paired t-test result	Mean		SD	Paired t-test result
Resident	Pre-post	0.09	±	1.66 km		−0.21	±	2.32 km	
Intruder	Pre-post	−1.07	±	2.71 km	$t_{14} = 1.53, P = 0.149$	−0.32	±	3.16 km	$t_{14} = 0.11, P = 0.911$

number of dogs, >1 year, in the focal pack divided by the number of dogs in the encountered pack); residence status (resident or intruder) at the point of encounter and their two-way interaction. A full model set was generated using the function 'dredge' in the MuMIn package (Barton 2016) on the global model. We then conducted model averaging (MuMIn package; Barton 2016) to identify those models whose cumulative Akaike's information criterion correction (AICc) weights were >0.95, and construct model-averaged estimates of the parameters (Grueber et al. 2011), and display all models where the AICc delta is less than the null model.

In keeping with the literature, we predicted that pack residence status and pack size ratio would affect encounter outcome; specifically, we expected intruders and smaller packs to move further away from the encounter site following the encounter, and to avoid its general vicinity, and therefore the risk of further encounters, in the longer term. Additionally, individuals may be expected to behave differently in encounters according to the costs and benefits of participating (see Kitchen and Beehner 2007). As we evaluated only one collar from each pack in an encounter, it is possible that their movements are not representative of the pack as a whole, and so we estimated the 'risk' and 'opportunity' for each collared dog involved in an inter-pack encounter. As aggression during African wild dog encounters is generally directed at same-sex opponents (Creel and Creel 2002), we defined 'risk' as the ratio of same-sex adults in the two packs (same-sex adults in opposition pack/same-sex adults in focal pack). Similarly, 'opportunity' for mating or dispersal was defined as the ratio of opposite-sex individuals to same-sex individuals in the opposing pack (opposite-sex adults in opposition pack/same-sex adults in opposition pack). Increasing values represented increasing risk and opportunity, and we evaluated the effect of these on the outcome of encounters using paired *t* tests, as models did not run with these terms included due to our small sample.

We explored the immediate and longer-term behavioural responses to an encounter using high-resolution GPS data from collars. All data were tested for normality using the Shapiro test and all analyses were carried out in R (R Core Team 2015) using paired t-tests where data were normally distributed and Wilcoxon paired test when not. Data were recorded 'blind' using GPS collars, and parameters were extracted automatically, thereby removing observer bias. The following measures were compared before and after the encounter for residents and intruders.

(i) Short-term responses

Distance moved. To determine whether the actual distance travelled by packs changed after an encounter, we summed the distances of 30-s steps for an hour either side of encounters. To control for any intrinsic pack-specific differences in movement that may influence our results, we subtracted the pre-encounter distances from post-encounter distances. Inter-pack distances (the straight-line distance between encountering packs) and each pack's distance to the encounter site and the closest edge of their estimated core area (50% kud and mcp, separately) were also extracted and compared. Additionally, we investigated whether packs increased their movement post-encounter by comparing their distance moved in the hour post-encounter, to the distance moved during the same time period the previous day.

Speed of movement. To determine whether the speed at which packs moved changed following an encounter, we extracted and compared the maximum recorded speed and the average (median) speed in the hour before and after each encounter. The speeds of each pack post-encounter were subtracted from those pre-encounter so that positive values indicated increased speed following the encounter.

(ii) Medium-term responses

To explore changes in movement behaviour, we compared the straight-line distance between each pack and the encounter site 12 h before and after the encounter. Post-encounter distances were subtracted from pre-encounter distances for each pack and compared between packs and within the pack.

(iii) Long-term responses

To test whether ranging or range overlaps were affected by encounters, we also estimated ranges over the same period beginning 2 days post-encounter. As some collars were put out <120 days before the encounter or expired <120 days following the encounter, we standardised the compared pre- and post-encounter period length by reducing both to the shortest period. Overlapping areas were calculated using 95% kuds and mcps and then compared pre- and post-encounter using paired *t* tests to test the hypothesis that range overlap would be significantly reduced after an encounter.

Return to proximity of encounter sites. We compared changes in rates of visitation to the vicinity (<800 m) of encounter sites before and after encounters. These close passes were extracted using the estimated encounter locations as points of interest and extracting locations from the collars that fell within 800 m. A rate of close passes was then calculated for each period (with each day scored as having or not having at least one location <800 m) and pre-encounter rates were subtracted from post-encounter rates so that negative values indicated reduced visitation post-encounter.

Table 3 Generalised Linear Mixed Effects Models (GLMM) investigating the factors affecting the outcome (win or lose) of an inter-pack encounter ($N = 15$ encounters). Focal pack was included as a random term in all models. Δi = AICci − AICcmin, wi = Akaike weights. + indicates that the term was included in the model

	Included parameters							
Model	Intercept	Residence status	Pack size ratio	df	logLik	AICc	Δi	wi
(Null)	+			2	−6.30	17.61	2.57	0.15
1	+	+		3	−3.43	15.04	0.00	0.54
2	+		+	3	−4.00	16.17	1.13	0.31

Results

Encounter summary

We identified 15 inter-pack encounters involving 11 packs in 11 unique pack dyads. Table 1 is a summary of each inter-pack encounter and the demographics of participating packs. Eleven encounters occurred inside the estimated core (50% kud) of one pack, two occurred in the exclusive periphery of the resident pack (95% kud), and two encounters occurred in a peripheral area of inter-pack overlap (outside the 50% kud and inside 95% kud of both packs). In all cases, it was possible to classify residents and intruders based on their proximity to their own core at the point of encounter (Table 1). Encounters occurred between 0 and 2.43 km from the resident's core (0.50 ± 0.79 km [$\dot{x}$ ± SD]) and 0.71–23.95 km (6.11 ± 6.69) from the core areas of intruding packs. Within encounters, the difference between packs in the distance home (50% kud) ranged from 0.50 to 23.95 km (5.61 ± 6.75 [$\dot{x}$ ± SD]) at the point of encounter.

Detailed dynamics of each encounter are displayed as supplementary material (Online Resource 1). This includes plots over time on either side of the encounter showing (a) a map of the movement of each pack relative to (i) the other pack, (ii) their core home range and (iii) the encounter site; (b) the distance between each pack and the encounter site, and between packs; (c) distances to each pack's own home range core and (d) inter-pack closing speed and the speed of each pack individually. Ranges were estimated using the kud method unless stated.

Encounter frequency

Each dyad had an encounter once every 188.90 ± 47.22 [$\dot{x}$ ± SD] (range 0–532) days of dyadic overlap. In this population, packs usually have four neighbours, so each pack would be expected to interact directly with one of its neighbours approximately every 47 days. The continual collection of data allowed us to describe the timing of encounters throughout the 24-h cycle. Surprisingly, after converting to local time (UTC+2), only 33% (5/15) of encounters occurred in daylight hours. Of the remaining 10, 4 occurred within the 1 h after sunset or prior to sunrise. All six truly nocturnal encounters occurred on nights when illumination levels were >53% of full moon levels at lunar noon (https://www.timeanddate.com/moon/botswana/maun), and four of these occurred on brightly moonlit nights (>75% illumination).

Encounter outcome

Surprisingly, 11 of 15 (73.3%) encounters were 'won' by intruders, with residents travelling further from the encounter point 1 h following the encounter than did intruders. Using this post-encounter proximity to the estimated encounter location as a measure of success, GLMMs suggest that pack status (resident or intruder) is the best predictor of the outcome of an encounter (Tables 3, 4), with intruders more likely to emerge as winners. Pack size ratio was weighted as having less effect on encounter outcomes, with larger packs more likely to emerge as winners (Tables 3, 4). Interestingly, residents tended to be further away from the encounter site 1 h after the encounter than they were 1 h before the encounter (difference between pre- and post-encounter distances, −1.27 ± 3.08 km), while intruders were closer post-encounter than pre-encounter (1.52 ± 3.16 km). This difference in relative proximity (post- minus pre-encounter) was significant between residents and intruders (paired *t* test: $t_{14} = -2.45$, $P = 0.028$).

Table 4 Average effects of parameters in models from Table 1 (cumulative AIC weights were >0.95) on the outcome (win or lose) of an inter-pack encounter ($N = 15$ encounters)

			Confidence interval			
Parameter	Est.	SE	2.50%	97.50%	*P*	Relative importance
(Intercept)	18.33	14.24	−11.14	47.79	0.22	
Residence status (Res)[a]	−15.84	9.03	−35.51	3.82	0.11	0.54
Pack size ratio	24.67	8.78	5.53	43.81	0.01	0.31

Initial post-encounter observations of packs were made 6.9 ± 7.8 [$\dot{x}$ ± SD] (range 0–32) days following an encounter (N = 30 interacting packs). Pack compositions were unchanged following all encounters, with no individuals dispersing or killed (despite fatalities from encounters having been observed previously [BPCT unpublished data]). Indeed, on only two occasions did we record injuries in the post-encounter observation session, whereas none were recorded in the observation session prior to encounters. A subdominant adult male from the resident pack suffered what were recorded in the field notes as 'bad wounds' on the head and neck, and both ears were collapsed when first seen 5 h following encounter 8 (Fig. 1). After encounter 6, a yearling male from the intruding pack was seen limping slightly at the next direct observation session 5 days later. While it is unknown whether these injuries were a direct result of the encounters, both are consistent with possible inter-pack fighting injuries. Both encounters that appear to have resulted in injuries involved unrelated packs, but the proportion of encounters that resulted in injury were not significantly different between encounters involving related (0) and unrelated (0.22) packs (binomial test of proportions with continuity correction: $\chi^2_{(1)}$ = 0.22, P = 0.642). As only 43% of initial post-encounter observations occurred within 3 days of the encounter, and one pack was not found until 32 days post-encounter, it is possible that minor or fast-healing injuries may have been slightly underestimated in this study.

Pack composition did not seem to affect encounter outcomes, as collared dogs within winning and losing packs did not differ in the risks they took (paired t test: t_{14} = 0.28, P = 0.784) or opportunities (t_{14} = 1.69, P = 0.113) they were exposed to by engaging in encounters.

(i) Short-term responses

Distance moved. Packs travelled similar distances in the hour following an encounter (4.22 ± 2.86 km) as the hour preceding it (4.01 ± 2.14 km; paired t test, t_{29} = −0.31, P = 0.756), but as described above, residents were further from the encounter site 1 h after the encounter than were intruders (Fig. 2). However, the total distance packs moved in the hour following an encounter was unrelated to their residence status (t_{14} = −0.31, P = 0.758) or whether or not they won the encounter (t_{14} = −0.61, P = 0.550). These results held when the distance they moved before the encounter was controlled for by comparing distances moved 1 h after the encounter with distances moved 1 h before (*winner* vs. *loser*, t_{14} = −0.34, P = 0.737; *resident* vs. *intruder*, t_{14} = −0.65, P = 0.524). Inter-pack distances, a potential sign of avoidance, were not significantly different 1 h either side of the encounter (pre-encounter, 3.97 ± 2.69 km; post-encounter, 4.64 ± 3.12 km; t_{14} = −0.59, P = 0.562), suggesting inter-pack avoidance may only occur in the immediate aftermath of an encounter.

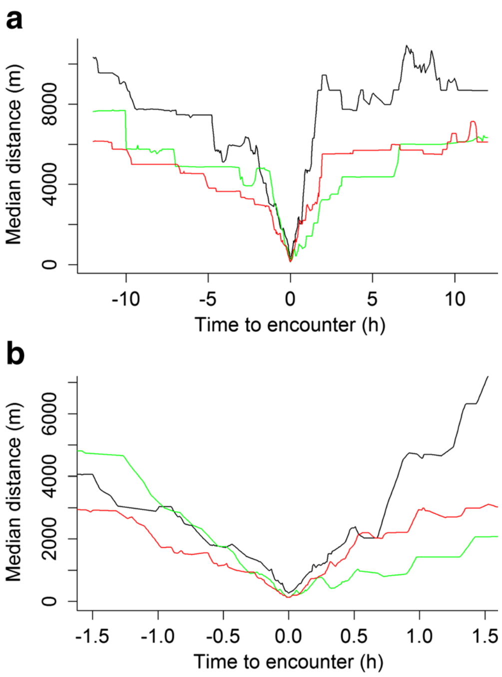

Fig. 2 Median distances (m), between packs (*black line*), and between the encounter site and intruder (*red line*) and resident (*green line*) packs over **a** 12-h and **b** 1.5-h periods either side of the encounter. N = 15 encounters

Packs moved further in the hour following an encounter (4.50 ± 2.46 km) than during the same hour the previous day (2.62 ± 2.69 km; paired t test: t_{29} = 2.82, P = 0.007). Importantly, although winners generally moved less (1.22 ± 2.01 km) than losers (2.53 ± 4.71 km) on encounter days compared to preceding days, this difference was not statistically significant (paired t test: t_{14} = 0.99, P = 0.333).

To assess whether intruders or residents were more or less likely to return toward their core area following an encounter, we compared the change in each pack's distance to their own core area before and after encounters (Fig. 3). Each pack's distance to its own core area 1 h post-encounter was subtracted from that 1 h pre-encounter so that a positive value indicated a 'retreat' homeward. Although in the 1 h post-encounter intruders tended to move further ($\dot{x}$ ± SD: −1.07 ± 2.71 km) toward their own core area than did residents (0.086 ± 1.66 km), this difference was not significant (paired t test: t_{14} = 1.53, P = 0.149).

Speed of movement. There was no significant difference in change in median speed either side of the encounter according to pack residence status (Wilcoxon paired test: N = 15, V = 45, P = 0.421). There was also no significant difference between packs in the change in the maximum speed they attained before and after the encounter (paired t test; t_{14} = −0.77, P = 0.455).

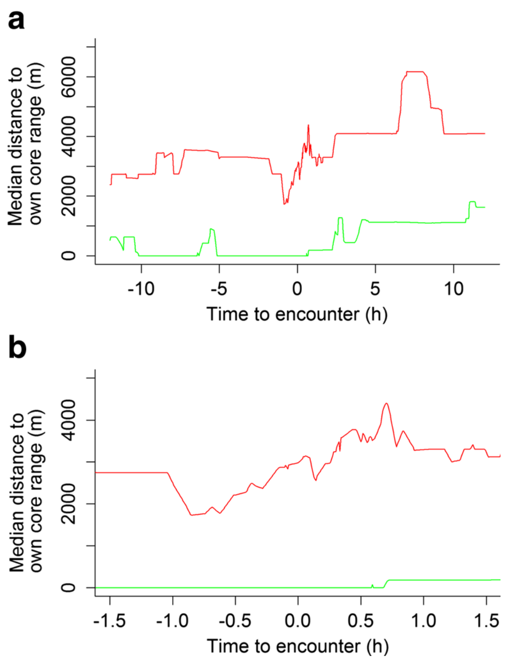

Fig. 3 Median distances (m) to own home range core for intruder (*red line*) and resident (*green line*) packs over **a** 12-h and **b** 1.5-h periods either side of the encounter. (Ranges estimated using the kernel density estimate method). $N = 15$ encounters

(ii) Medium-term responses

Despite short-term (1 h) differences described above, we found that changes in the distance to encounter sites no longer differed between residents and intruders 12 h either side of encounters ($t_{14} = -0.42$, $P = 0.678$). In common with the short-term results described above, inter-pack distances were also not significantly different 12 h either side of encounters (pre-encounter, 10.57 ± 5.63 km; post-encounter, 10.15 ± 5.57 km; $t_{14} = 0.20$, $P = 0.841$). Median distances between packs and between intruders, residents and encounter sites are shown in Fig. 1.

(iii) Long-term responses

The areas of inter-pack overlap were significantly lower following an encounter than before (Table 2). This suggests broad-scale spatial avoidance post-encounter, but interestingly, this reduced overlap was not the result of the intruding pack shifting its range away from the resident pack; comparing each pack's pre-encounter range to its own post-encounter range showed similar degrees of overlap regardless of residence status. Similarly, the percentage that a pack's pre-encounter range overlapped its own post-encounter range did not differ according to whether it was classified as the winner or loser. This indicates that reduced inter-pack overlap following an encounter is the result of either mutual avoidance or range shifts over time that are unrelated to encounters.

Return to proximity of encounter sites. There was no difference between residents ($\dot{x}$ ± SD, −0.0005 ± 0.115) and intruders (0.0028 ± 0.061) in the change in visitation rate to the vicinity of the site following an encounter (visits to <800 m/day; Wilcoxon paired test: $N = 13$, $W = 122$, $P = 0.706$). All packs (pooled) made close passes of the encounter site at similar rates before and after encounters (Wilcoxon paired test: $N = 13$, $W = 114$, $P = 0.967$).

Discussion

We described the detailed spatial dynamics of 15 African wild dog inter-pack encounters. On average, neighbouring packs had an encounter once every 6 months of dyadic overlap and most encounters were won by intruders, as measured by their tendency to stay closer to an encounter site than did residents shortly (1 h) after the encounter. Although some injuries were recorded and may have resulted from encounters, no dogs were killed during these encounters. In the short term, the distances travelled by packs after encounters and the speed at which they travelled were not significantly different to those from the same period before an encounter, nor between residents and intruders and winners and losers. In the longer term, although the area of inter-pack range overlap was significantly reduced following an encounter, these shifts did not appear to result from one pack shifting its range relative to the other, but rather from both packs shifting slightly, which may be due to mutual avoidance or natural home range drifts over time (see Pomilia et al. 2015) that are independent of encounters. There was no evidence of post-encounter avoidance of encounter sites by either residents or intruders, nor winner or losers.

As each African wild dog pack had approximately four neighbours, our measured dyadic inter-pack encounter rate (an encounter every 6 months), suggests that each pack would be expected to meet one of their neighbours every 47 days on average. This is similar to inter-pack encounter rates estimated from two other sites including the Selous Game Reserve in Tanzania, where wild dog packs were estimated to meet approximately every 40 days (Creel and Creel 2002), and to three districts in Kenya where inter-pack contact was estimated to occur approximately every 40.4 days (Woodroffe and Donnelly 2011). On the surface, the agreement between these values is striking and broadly suggests that our method of using remote data to identify encounters yielded accurate results. However, the parity of our encounter frequency results with those of other studies (e.g. Mills and Gorman 1997; Creel and Creel 2002; Woodroffe and Donnelly 2011) is actually surprising, as these previous studies were likely constrained to some degree by the need to conduct observations predominantly during daylight hours. Unlike Woodroffe and Donnelly's (2011) remote data collection, which was paused between 2000 hours and 0600 hours, our remote data imposed no such constraints and we found that the majority of encounters (10/15) in our study occurred during this nocturnal period. Indeed, even allowing that some direct observations in previous studies may have been conducted in the few hours before sunrise and following sunset, one third of our encounters still occurred outside of these observation times, hinting that actual inter-pack encounter rates in our study population are considerably lower overall than in other populations. The explanation for this potential disparity is currently unknown, particularly since one potential explanation, a possible difference in pack densities, does not seem to increase inter-pack encounter rates in this species (Woodroffe 2011).

Encounter outcome

In many species, the winner of an encounter can be clearly identified, as contests tend to occur in the vicinity of valuable resources such as fruiting trees, where winners tend to remain feeding post-encounter (e.g. capuchins; Crofoot et al. 2008). Identifying the victor is more challenging for highly mobile species such as African wild dogs, particularly as they are not usually competing over a specific resource such as a kill at the point of encounter. In the current study, there was no evidence from the GPS data that any of the encounters described here occurred at a kill site, which would have provided motivation for either pack to remain in the vicinity of an encounter. Kill sites can be identified by visual inspection of GPS and activity data (e.g. Hubel et al. 2016a), and inspection of data around encounter points suggested that none of our encounters occurred at kill sites, though we cannot completely rule out this possibility from our remote data. When we defined the winner as the pack that remained closest to the site 1 h post-encounter, most encounters were won by intruders which contrasted with our expectation. Alternatively, when we classified winners as the pack that moved least toward its own core area, the result was reversed with residents emerging as winners more frequently. Although intruders moved less far from the encounter than residents, the direction of their movements were more likely to be toward home. We also found no evidence of one pack actively pursuing another, except for an exceptional case (encounter 7) where the intruders appeared to actively seek out the residents over more than 15 km and then pursue them briefly post-encounter. It is important to reiterate here that our data is limited to tracking the movement of collared individuals, and the responses of other individuals in encountering packs was not known, although pack members tend to stick together.

Using displacement from the encounter site to classify winners, surprisingly, adult pack size ratio had little effect on encounter outcome. Most previous studies on other species have shown that relative group size is important (e.g. banded mongoose, Cant et al. 2002; African lion, *Panthera leo*, Mosser and Packer 2009; McComb et al. 1994); however, other work has suggested that pack size ratio was less important in grey wolf encounters than was the specific composition of packs (Cassidy et al. 2015). This was possibly because packs with additional adult males or older wolves were more likely to win encounters (Cassidy et al. 2015); but in this study, we found no evidence that potentially pertinent details of African wild dog pack composition affected the outcome of encounters. Encounter outcome appeared to be unaffected by either the risk (inter-pack ratio of same-sex individuals) or opportunity (the sex ratio in the opposing pack) that encounters presented to the collared individuals. It is possible that remaining together as a pack during and in the aftermath of encounters may be more important to African wild dogs than opportunistic inter-pack matings, particularly as successful breeding is almost monopolised by the alpha pair (Creel et al. 1997).

Surprisingly, in contrast to previous studies which describe the risk and danger of inter-pack encounters in African wild dogs (e.g. Creel and Creel 2002) and other species (e.g. chimpanzees, Townsend et al. 2007), no wild dogs were killed in the encounters we recorded in this study. We also found that only around 15% of encounters resulted in injury (less than half of that described in observed encounters in the Selous, Tanzania; Creel and Creel 2002), but Fig. 1 clearly suggests that encounters are not all amicable affairs, and there is clearly potential for serious injury and disease transmission. Though it may be interesting to note that both encounters that likely resulted in injuries involved unrelated packs, the proportion of encounters that resulted in injury were not significantly different between encounters involving related and unrelated packs, leading us to conclude that relatedness was unimportant in this context. The apparently low incidence of injuries resulting from inter-pack encounters is also important because, as previous authors have pointed out (e.g. Woodroffe and Donnelly 2011), packs infected with potentially fatal viral pathogens (e.g. canine distemper, Alexander et al. 1996; rabies, Kat et al. 1995) can transmit them to other packs. These infections can have serious consequences for endangered populations as they are major causes of mortality (Kat et al. 1995; Alexander et al. 1996). Inter-pack encounters may be particularly suited to pathogen transmission, due to the direct and damaging contact that may ensue. For example, the incidence of inter-pack prospecting by male meerkats (*Suricata suricatta*) was correlated with those individuals subsequently testing tuberculosis-positive, suggesting a possible route for transmission of infection between social groups (Drewe 2010). While our study population currently appears disease-free, inter-pack encounters remain a possible route of transmission in general, but in common with previous authors, our results suggest that infrequent inter-pack encounters may result in infrequent transmission of virulent pathogens (Woodroffe and Donnelly 2011).

Interestingly, no immediate dispersal resulted from opposite-sex individuals meeting during these interactions, though it is expected that information on future dispersal opportunities may be gleaned during such encounters.

In terms of long-term effects of encounters, packs might be expected to avoid areas where encounters have previously taken place, as has been shown in yellow baboons (Markham et al. 2012). We found little measurable impact, however, on long-term movement and space use following encounters. Indeed, although we found that the area of inter-pack range overlap was significantly smaller in the period following an encounter than preceding it, this overlap was not the result of only one of the interacting packs shifting its range relative to the other. Rather, both packs shifted their ranges after an encounter, but we are currently unable to distinguish whether this was a form of mutual avoidance, or whether it may be explained by shifts in ranging that are unrelated to the encounter itself. Although wild dog packs inhabit reasonably consistent ranges over a number of years, home ranges estimated over shorter weekly or monthly scales show a degree of variability (Pomilia et al. 2015). We also found no evidence that losers avoid winners, but cannot rule out that natural shifts in short-term ranges, rather than mutual avoidance post-encounter, may explain the reduced inter-pack range overlap following encounters.

Conclusion

Overall, our results show low but not infrequent rates of inter-pack encounters between neighbouring wild dog packs that are broadly consistent with previous findings from direct observation in other locations. The outcome of encounters was an immediate movement away from the encounter site by both packs, but this was slightly more pronounced in residents than intruders. Although our findings suggest that encounters evoke some immediate behavioural change post-encounter, we observed only infrequent injury and no long-term shifts in ranging behaviour after losing an encounter or any avoidance of the encounter site by either participating pack. This suggests that the effects of inter-pack encounters in wild dogs may be much shorter-lived than previously assumed. Perhaps the potential costs of meeting neighbours are outweighed by either the benefits of the information acquired during such an encounter or the avoided potential costs of preventing an encounter in such a highly vagile species.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no competing interests.

Ethical approval This work was approved by the Royal Veterinary College Ethics and Welfare Committee, and adhered to the ASAB/ABS Guidelines for the Use of Animals in Research (ASAB/ABS 2012). This work was undertaken under research permits from the Botswana Ministry of Environment Wildlife and Tourism, Department of Wildlife and National Parks held by JWM and AMW.

Informed consent This article does not contain any studies with human participants performed by any of the authors.

Data availability statement The datasets generated during and/or analysed during the current study are not publicly available as they contain potentially sensitive information on the den site locations of an endangered species. Data are available from the corresponding author on reasonable request.

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