Neil R Jordan[1,2,3*], Christopher Buse[4], Alan M Wilson[4], Krystyna A Golabek[3,1], Peter J Apps[3], John C Lowe[4], Leanne K Van der Weyde[3] and J Weldon McNutt[3]

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

1. Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales (UNSW), NSW 2052, Australia
2. Taronga Conservation Society Australia, Taronga Western Plains Zoo, Applied Eco-Logic Group, Obley Road, Dubbo, NSW 2830, Australia
3. Botswana Predator Conservation Trust, Private Bag 13, Maun, Botswana
4. Structure and Motion Laboratory, Royal Veterinary College, University of London, London, United Kingdom

*Corresponding author: neil.jordan@unsw.edu.au; Phone: +61 (0) 2 6881 1452 (no fax)

Acknowledgments

We are grateful to the Office of the President of Botswana and the Department of Wildlife and National Parks for permission to conduct research in Botswana, and to various leaseholders for permission to work in the areas that they are responsible for, in particular the Sankuyo community. Pack composition data were collected in the field by some of the authors and Briana Abrahms, Arjun Dheer, Roman Furrer, Geoff Gilfillan, Dikatholo Kedikilwe, Kasim Rafiq, Drew Vanetsky, Jessica Vitale, Reena Hallelujah Walker and Ari Whiteman. The photograph in Fig. 1 was taken by Roman Furrer. We would also like to thank two anonymous reviewers and the editor for their constructive comments which improved the manuscript.

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

Introduction

Inter-group encounters may have important life-history consequences, due to the potential for injury and death (e.g. gray 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 woodhoopoe, *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; gray wolf, Cassidy et al. 2015; banded mongoose, Furrer et al. 2011). In some species however, pack composition plays a more important role than pack-size *per se* in determining the outcome of encounters. For example, in chacma baboons (Hamilton et al. 1975, 1976; Cheney 1987), after

84 controlling for location, the relative number of males in opposing groups appeared to play a role
85 in determining the outcome of inter-group contests, with groups containing more males winning
86 more often. Similar patterns have been reported for gray wolves, where packs with more males
87 or older individuals than their rivals were more likely to triumph in encounters (Cassidy et al.
88 2015).

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

99 Here we use high-resolution GPS collar data from 11 free-ranging packs of African wild
100 dogs (*Lycaon pictus*) in the Okavango delta region of Botswana to record and analyse the
101 spatial dynamics of inter-pack encounters. African wild dogs are endangered (Woodroffe and
102 Sillero-Zubiri 2012) pack-living canids (Mills and Gorman 1997), with large annual ranges (739
103 km^2 in northern Botswana; Pomilia et al. 2015) encompassing considerable areas of overlap
104 with their neighbours (30-35%, Kruger NP, South Africa, Reich 1981; 62%, Selous GR,
105 Tanzania, Creel and Creel 2002). Previous studies have indicated that direct encounters
106 between packs are rare (Creel and Creel 2002; Woodroffe and Donnelly 2011), perhaps due to
107 temporal partitioning of the use of overlapping areas (Mills and Gorman 1997), or perhaps
108 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 24h 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 24h 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

133 Data were collected between November 2011 and February 2015 from 11 packs of free-ranging
134 African wild dogs in northern Botswana. The study area (*ca.* 2600 km^2; 19°31'S, 23°37'E;
135 elevation *ca.* 950 m) was bordered on the west and northwest by permanent swamp of the
136 Okavango Delta and included the eastern section of the Moremi Game Reserve and
137 neighboring Wildlife Management Areas. Further details can be found in McNutt (1996). This
138 sub-population of African wild dogs has been studied since 1989, and each individual was
139 identified by its unique tricolour pelage pattern, distinctive ear notches and tail stripes. Pack size
140 (all adults and yearlings >1 year) and the demographic composition of participating packs were
141 extracted from the closest observation sessions either side of each encounter, when any
142 observed injuries were also noted. It was not possible to record data blind because our study
143 involved focal animals in the field.
144
145 *Collars and collaring*
146 This study used data produced by innovative GPS-IMU (Global Positioning System with Inertial
147 Measurement Unit) animal collars (ca. 350g; described in detail in Wilson et al. 2013). Key
148 components of these collars comprised a GPS receiver (LEA-6T, uBlox AG) and a set of 3-axis
149 MEMS (Micro Electro-Mechanical Sensor) accelerometer and gyroscope sensors, controlled by
150 an MSP430 series microcontroller (Texas Instruments Inc) running custom firmware written in
151 the 'C' programming language. A 2GB micro-SD flash card (Sandisk) provided data storage,
152 and a 2.4GHz radio link (Nanotron Technologies Gmbh) facilitated downloading of the collected
153 data to a nearby vehicle. A conventional VHF tracking transmitter (Sirtrack) was integrated into
154 the collar to facilitate airborne and ground-based tracking and physical location of the animal. To
155 improve battery life, the collar was programmed to switch between different operating states
156 depending on time of day and on the level of animal activity, as measured by the on-board
157 accelerometer. If the animal was resting, GPS fixes were taken once per hour. When the animal

158 was determined to be active, the GPS fix interval was reduced to 5 minutes, thus providing fixes
159 with significantly improved temporal resolution during movement.
160 One individual in each pack was radiocollared following darting from a stationary vehicle
161 within 15 m using TELINJECT darting equipment to deliver a mixture of xylazine (55 mg), 260
162 ketamine HCL (50 mg) and atropine (1.1– 1.2 mg) and reversed after 45 – 60 min with
163 yohimbine (4 mg) or atipamezole (5.5 mg) (further details in Osofsky et al. 1996). Most collars
164 were removed and replaced when the dog was immobilized following collar expiry, but
165 automatic drop-off units (Sirtrack, 70g) were used to release two collars (total collar weight ca.
166 420g) at the end of the study (see Fig. 1). During anaesthesia we recorded the general health of
167 each sedated animal, monitored vital signs, took body measurements and collected blood
168 samples. All sedated individuals safely recovered from the anaesthesia and showed no injuries
169 or signs of distress.
170
171 *Data extraction and interpolation*
172 To identify possible encounters between packs, the data were first reduced by exhaustive
173 automated searches of all of the GPS locations from all GPS-collars using custom-written code
174 in programming languages Perl (www.perl.org) and R (R Core Team 2016). This produced
175 summary files with all inter-pack encounters within 800m and 12h of each other. The summary
176 files included KML maps showing locations, which allowed manual rejection of some false
177 encounters based on erroneous spatial data. These errors were usually single points that were
178 unrealistic distances from previous and subsequent points in a track; i.e. they would require the
179 collar to move at unrealistic speeds (>19ms^{-1}) in comparison to those measured previously
180 (Hubel et al. 2016 a, b). Overall, 1.7% of points were removed from our raw dataset on this
181 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 (center point). Gaps between 5-minute points were interpolated to 30s 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, and minimum distance center points (hereafter 'estimated encounter locations') were determined. All estimated encounter locations with close spatial-temporal overlap (inter-pack distance <800m, within 5 min) in raw data were considered further.

Although 800m 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 150secs), during which packs could diverge considerably. In practice, 12/15 encounters had minimum inter-pack distances <310m (Table 1), and only Encounter 1 was >450m (614m). 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 30s), and closing speed between packs (negative values were converging, positive values diverging) every 30s 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 (<800m) 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 neighboring 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 neighbors. During the period that a given pack wore a collar, we summed the days that each of its neighbors 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.

Identifying neighbors and residence status

Packs with overlapping 95% kernel utility distributions [kud] during the study period were considered to be neighbors. 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 14634 ±16561 [$\dot{x}$ ± SD], range 215-77631, 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.

231 Following identification of encounter center points, packs were classified as 'resident' or
232 'intruder' based the distance of the encounter point to the boundary of the pre-encounter core
233 area estimate (50% kud and mcp respectively; hereby referred to as the pack's "core area"). In
234 all instances, the pack with the the shortest distance to their core area was deemed the
235 'resident', and the other pack was the 'intruder'. When one pack had a core area defined by
236 multiple discrete polygons, the distance to the closest core polygon was used. Thirteen
237 encounters were clearly in the exclusive pre-encounter area of one pack, while the other 2 were
238 in an area of inter-pack overlap (i.e. the area of range overlap in the 120 days preceding the
239 encounter). To avoid the risk of misclassification that might occur if ranging changed in
240 response to the encounter of interest, only data preceding the encounter were used to
241 determine residence status. Residence classification was consistent across the two range
242 estimate methods, except for encounter 5 where the encounter occurred approximately
243 equidistant from the core areas.
244
245 *Encounter outcome*
246 The winner of an inter-group encounter is usually defined as the group which stayed behind at
247 the encounter site following the encounter (e.g. capuchins; Crofoot et al. 2008). In keeping with
248 this, we defined the winner as the pack that remained closest to the encounter site 1 h following
249 the encounter (Table 1). Additionally we explored determining encounter outcome by defining
250 the winner as the pack that moved the least towards its own range core over the same 1 h
251 period. However this latter approach may be less reliable as residents began closer to home by
252 definition, and this may have skewed the results. Nevertheless we feel it is important to evaluate
253 whether moving toward home might be a relevant measure of winning a contest in this highly
254 vagile species, where remaining at the encounter site may not provide an accurate indication of
255 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 simple random selection script in R. Terms included in the models were pack-size ratio (the number of dogs, >1y, 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 AICc (Akaike's information criterion correction) 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

281 same-sex individuals in the opposing pack (opposite-sex adults in opposition pack / same-sex
282 adults in opposition pack). Increasing values represented increasing risk and opportunity
283 respectively, and we evaluated the effect of these on the outcome of encounters used paired t-
284 tests, as models did not run with these terms included due to our small sample.
285 We explored the immediate and longer-term behavioural responses to an encounter
286 using high-resolution GPS data from collars. All data were tested for normality using the Shapiro
287 test and all analyses were carried out in R (R Development Core Team 2016) using paired t-
288 tests where data were normally distributed and Wilcoxon paired test when not. Data were
289 recorded 'blind' using GPS collars, and parameters were extracted automatically, thereby
290 removing observer bias. The following measures were compared before and after the encounter
291 for residents and intruders.
292
293 *i) Short-term responses*
294 *Distance moved.* To determine whether the actual distance travelled by packs changed after an
295 encounter, we summed the distances of 30s steps for an hour either side of encounters. To
296 control for any intrinsic pack-specific differences in movement that may influence our results, we
297 subtracted the pre-encounter distances from post-encounter distances. Inter-pack distances
298 (the straight-line distance between encountering packs) and each pack's distance to the
299 encounter site and the closest edge of their estimated core area (50% kud and mcp, separately)
300 were also extracted and compared. Additionally, we investigated whether packs increased their
301 movement post-encounter by comparing their distance moved in the hour post-encounter, to the
302 distance moved during the same time period the previous day.
303 *Speed of movement.* To determine whether the speed at which packs moved changed following
304 an encounter, we extracted and compared the maximum recorded speed and the average
305 (median) speed in the hour before and after each encounter respectively. The speeds of each

306 pack post-encounter were subtracted from those pre-encounter so that positive values indicated
307 increased speed following the encounter.
308
309 *ii) Medium-term responses*
310 To explore changes in movement behavior we compared the straight-line distance between
311 each pack and the encounter site 12 h before and after the encounter. Post-encounter distances
312 were subtracted from pre-encounter distances for each pack and compared between packs and
313 within the pack.
314
315 *iii) Long-term responses*
316 To test whether ranging or range overlaps were affected by encounters, we also estimated
317 ranges over the same period beginning two days post encounter. As some collars were put out
318 <120 days before the encounter or expired <120 days following the encounter, we standardised
319 the compared pre- and post-encounter period length by reducing both to the shortest period.
320 Overlapping areas were calculated using 95% kuds and mcps and then compared pre- and
321 post-encounter using paired t-tests to test the hypothesis that range overlap would be
322 significantly reduced after an encounter.
323 *Return to proximity of encounter sites.* We compared changes in rates of visitation to the vicinity
324 (<800m) of encounter sites before and after encounters. These close passes were extracted
325 using the estimated encounter locations as points of interest and extracting locations from the
326 collars that fell within 800m. A rate of close passes was then calculated for each period (with
327 each day scored as having or not having at least one location <800m) and pre-encounter rates
328 were subtracted from post-encounter rates so that negative values indicated reduced visitation
329 post-encounter.
330

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, 2 occurred in the exclusive periphery of the resident pack (95% kud), and 2 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 [ẋ ± 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 [ẋ ± 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 [ẋ ± SD] (range 0-532) days of dyadic overlap. In this population, packs usually have four neighbors, so each pack would be expected to interact directly with one of its neighbors approximately every 47 days. The continual collection of data allowed us to describe the timing of encounters throughout the 24hr cycle.

Surprisingly, only 20% (3/15) of encounters occurred in full daylight. Of the remaining 12, 7 occurred within the period 2.5 hours before sunset or prior to sunrise. Of the 5 truly nocturnal encounters which occurred outside these times, all occurred on brightly moonlit nights (when illumination levels were >80% of full moon levels at lunar noon; https://www.timeanddate.com/moon/botswana/maun).

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 (Table 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 (Table 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).

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 five hours 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 visits 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.

Relevant aspects of 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

406 different 1 h either side of the encounter (pre-encounter, 3.97 +/- 2.69 km; post-encounter, 4.64
407 +/- 3.12 km; t_{14}=-0.59, P=0.562), suggesting inter-pack avoidance may only occur in the very
408 immediate aftermath of an encounter.
409 Packs moved further in the hour following an encounter (4.50 ± 2.46 km) than during the
410 same hour the previous day (2.62 ± 2.69 km; paired t-test: t_{29} = 2.82, P = 0.007). Importantly,
411 although winners generally moved less (1.22 ± 2.01 km) than losers (2.53 ± 4.71 km) on
412 encounter days compared to preceding days, this difference was not statistically significant
413 (paired t-test: t_{14} = 0.99, P = 0.333).
414 To assess whether intruders or residents were more or less likely to return towards their
415 core area following an encounter, we compared the change in each pack's distance to their own
416 core area before and after encounters (Fig. 3). Each pack's distance to its own core area 1 h
417 post-encounter was subtracted from that 1 h pre-encounter so that a positive value indicated a
418 'retreat' homeward. Although in the 1 h post-encounter intruders tended to move further ($\dot{x}$ ± SD:
419 -1.07 ± 2.71 km) toward their own core area than did residents (0.086 ± 1.66 km), this difference
420 was not significant (paired t-test: t_{14}=1.53, P=0.149).
421
422 *Speed of movement.* There was no significant difference in change in median speed either side
423 of the encounter according to pack residence status (Wilcoxon paired test: N=15, V=45,
424 P=0.421). There was also no difference between packs in the change in the maximum speed
425 they attained before and after the encounter (paired t-test; t_{14}=-0.77, P=0.455).
426
427 *ii) Medium-term responses*
428 Following short-term (1 h) differences described above, we found that changes in the distance
429 to encounter sites no longer differed between residents and intruders 12 h either side of
430 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 it (Table 2). This suggests broad-scale spatial avoidance post-encounter, but interestingly this reduced overlap was not the result of the intruder shifting their range away from residents; comparing each pack's pre-encounter range to its own post-encounter range showed similar degrees of overlap regardless of their 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 six-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 respectively. 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 20:00 and 06:00, 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, 1/3 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.

505 Alternatively, when we classified winners as the pack that moved least towards its own core
506 area, the result was reversed with residents emerging as winners more frequently. Although
507 intruders moved less far from the encounter than residents, the direction of their movements
508 were more likely to be towards home. We also found no evidence of one pack actively pursuing
509 another, except for an exceptional case (encounter 7) where the intruders appeared to actively
510 seek out the residents over more than 15 km and then pursue them briefly post-encounter. It is
511 important to reiterate here that our data is limited to tracking the movement of collared
512 individuals, and the responses of all individuals in encountering packs was not known, although
513 pack members tend to stick together.

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

528 Surprisingly, in contrast to previous studies which describe the risk and danger of
529 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 Figure 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 it 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 physically-damaging contact that may ensue. For example, the incidence of inter-pack prospecting by male meerkats 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 lower 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 and 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 behavioral change post-encounter, we observed only infrequent injury and no long-term shifts in ranging behavior 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 more short-lived than previously assumed. Perhaps the potential costs of meeting the neighbors 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.

Ethical statement

Funding This research was supported by grants from the Engineering and Physical Sciences Research Council (EP/H013016/1), the European Research Council (323041), the Paul G. Allen Family Foundation, Wild Entrust International and additional private donors.

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

Ethical approval This work was approved by the Royal Veterinary College Ethics & 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 analyzed 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.

References

603 Alexander KA, Kat PW, Munson LA, Kalake A, Appel MJ (1996) Canine distemper-related
604 mortality among wild dogs (*Lycaon pictus*) in Chobe National Park, Botswana. J Zoo Wildl Med
605 27:426-427
606
607 ASAB/ABS (2012) Guidelines for the Use of Animals. Anim Behav 83:301–309
608
609 Barton K (2016) MuMIn: Multi-Model Inference. R package version 1.15.6, https://CRAN.R-
610 project.org/package=MuMIn
611
612 Bates D, Maechler M, Bolker B, Walker S (2015). Fitting linear mixed-effects models using
613 lme4. J Stat Softw 67:1-48
614
615 Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space
616 and habitat use by animals. Ecol Modell 197:516-519
617
618 Cant M, Otali E, Mwanguhya F (2002) Fighting and mating between groups in a cooperatively
619 breeding mammal, the banded mongoose. Ethology 108:541–555
620
621 Cassidy KA, MacNulty DR, Stahler DR, Smith DW, Mech LD (2015) Group composition effects
622 on aggressive interpack interactions of gray wolves in Yellowstone National Park. Behav Ecol
623 26:1352-1360
624
625 Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL,
626 Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University
627 of Chicago Press, Chicago, pp 267-281

628

629 Craft ME, Volz E, Packer C, Meyers LA (2011) Disease transmission in territorial populations:
630 the small-world network of Serengeti lions. J R Soc Interface 8:776-786

631

632 Creel S, Creel NM (2002) The African wild dog: behavior, ecology, and conservation. Princeton
633 University Press, Princeton

634

635 Creel S, Creel NM, Mills MG, Monfort SL (1997) Rank and reproduction in cooperatively
636 breeding African wild dogs: behavioral and endocrine correlates. Behav Ecol 8:298-306

637

638 Crofoot MC, Gilby IC, Wikelski MC, Kays RW (2008) Interaction location outweighs the
639 competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. P Natl
640 Acad Sci USA105:577-581

641

642 Drewe JA (2010) Who infects whom? Social networks and tuberculosis transmission in wild
643 meerkats. Proc R Soc Lond B 277:633–642

644

645 Ewing LS (1972) Hierarchy and its relation to territory in the cockroach *Nauphoeta cinerea.*
646 Behaviour 42:152-174

647

648 Furrer RD, Kyabulima S, Willems EP, Cant MA, Manser MB (2011) Location and group size
649 influence decisions in simulated intergroup encounters in banded mongooses. Behav Ecol
650 22:493-500

651

652 Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and
653 evolution: challenges and solutions. J Evol Biol 24:699-711
654
655 Hamilton WJ, Buskirk RE, Buskirk WH (1975) Chacma baboon tactics during intertroop
656 encounters. J Mammal 56:857-870
657
658 Hamilton WJ, Buskirk RE, Buskirk WH (1976) Defense of space and resources by chacma
659 (*Papio ursinus*) baboon troops in an African desert and swamp. Ecology 57:1264-1272
660
661 Hubel TY, Myatt JP, Jordan NR, Dewhirst OP, McNutt JW, Wilson AM (2016a) Additive
662 opportunistic capture explains group hunting benefits in African wild dogs. Nat Commun
663 7:11033
664
665 Hubel TY, Myatt JP, Jordan NR, Dewhirst OP, McNutt JW, Wilson AM (2016b) Energy cost and
666 return for hunting in African wild dogs and cheetahs. Nat Commun 7:11034
667
668 Kat PW, Alexander KA, Smith JS, Munson L (1995) Rabies and African wild dogs in Kenya.
669 Proc R Soc Lond B 262:229-233
670
671 Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric
672 odds, male companion behaviour and reproductive investment. Anim Behav 67:125-139
673
674 Kitchen DM, Beehner JC (2007) Factors affecting individual participation in group-level
675 aggression among non-human primates. Behaviour 144:1551-1581
676

677 Kitchen DM, Cheney DL, Seyfarth RM (2004) Factors mediating inter-group encounters in
678 savannah baboons (*Papio cynocephalus ursinus*). Behaviour 141:197-218
679
680 Koch F, Signer J, Kappeler PM, Fichtel C (2016) The role of the residence-effect on the
681 outcome of intergroup encounters in Verreaux's sifakas. Sci Rep 6:28457
682
683 Markham AC, Alberts SC, Altmann J (2012) Intergroup conflict: ecological predictors of winning
684 and consequences of defeat in a wild primate population. Anim Behav 8:399-403
685
686 Smith JM (1982) Evolution and the Theory of Games. Cambridge University Press, Cambridge
687
688 McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between
689 groups of female lions, *Panthera leo*. Anim Behav 47:379–387
690
691 McNutt JW (1996) Sex-biased dispersal in African wild dogs, *Lycaon pictus*. Anim Behav
692 52:1067-1077
693
694 Mech LD (1994) Buffer zones of territories of gray wolves as regions of intraspecific strife. J
695 Mammal 75:199–202
696
697 Mills MG, Gorman ML (1997) Factors affecting the density and distribution of wild dogs in the
698 Kruger National Park. Conserv Biol 11:1397-1406
699
700 Mosser A, Packer C (2009) Group territoriality and the benefits of sociality in the African lion,
701 *Panthera leo.* Anim Behav 78:359–370

Osofsky SA, McNutt JW, Hirsch KJ (1996) Immobilization of free-ranging African wild dogs (*Lycaon pictus*) using a ketamine/xylazine/atropine combination. J Zoo Wildl Med 27:528-532

Pomilia MA, McNutt JW, Jordan NR (2015) Ecological predictors of African wild dog ranging patterns in northern Botswana. J Mammal 96:1214-1223

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria, http://www.Rproject.org

Rachlow JL, Berkeley EV, Berger J (1998) Correlates of male mating strategies in white rhinos (*Ceratotherium simum*). J Mammal 79:1317–1324

Radford AN, du Plessis MA (2004) Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. Anim Behav 68:803-810

Reich A (1981) The behavior and ecology of the African wild dog (*Lycaon pictus*) in the Kruger National Park. PhD thesis, Yale University

Rood JP (1975) Population dynamics and food habits of the banded mongoose. Afr J Ecol 13:89-111

Shopland JM (1982) An inter-group encounter with fatal consequences in yellow baboons, *Papio cynocephalus.* Am J Primatol 3:263–266

727 Sicotte P (1993) Inter-group encounters and female transfer in mountain gorillas: Influence of
728 group composition on male behavior. Am J Primatol 30:21-36
729
730 Sillero-Zubiri C, Macdonald DW (1998) Scent-marking and territorial behaviour of Ethiopian
731 wolves *Canis simensis.* J Zool 245:351-361
732
733 Townsend SW, Slocombe KE, Thompson ME, Zuberbühler K (2007) Female-led infanticide in
734 wild chimpanzees. Curr Biol 17:R355–R356
735
736 Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend
737 on numerical assessment, range location, or rank for wild chimpanzees? Anim Behav 61:1203-
738 1216
739
740 Wilson AM, Lowe JC, Roskilly K, Hudson PE, Golabek KA, McNutt JW (2013) Locomotion
741 dynamics of hunting in wild cheetahs. Nature 498:185-189
742
743 Woodroffe R (2011) Demography of a recovering African wild dog (*Lycaon pictus*) population. J
744 Mammal 92:305–315
745
746 Woodroffe R, Donnelly CA (2011) Risk of contact between endangered African wild dogs
747 *Lycaon pictus* and domestic dogs: opportunities for pathogen transmission. J Appl Ecol
748 48:1345-1354
749
750 Woodroffe R, Sillero-Zubiri C (2012) *Lycaon pictus*. The IUCN Red List of Threatened Species
751 2012: e.T12436A16711116,

http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T12436A16711116.en. Downloaded on 12 June 2017.

Tables

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

					Pack identity		Distance to own 50% kud (km)[b]			Pack size[c]	
Encounter	Winner[a]	Related?	Date	Time	Resident pack	Intruder pack	Resident	Intruder	Inter-pack distance at encounter (m)	Resident	Intruder
1	Intruder	Y	23/02/2012	16:41	MT	NM	0.61	23.95	614	14	3
2	Intruder	Y	30/04/2012	19:39	HW	SA	0	12.04	288.8	5	3
3	Resident	Y	03/05/2012	23:25	MT	HW	2.43	2.93	56.2	7	5
4	Resident	N	07/05/2012	05:23	MT	KB	1.96	9.05	23.8	7	6
5	Intruder	N	07/05/2012	21:11	MK	SA	1.29	1.79	442.3	4	3
6	Intruder	N	14/05/2012	04:22	KB	MT	0	2.19	36	6	7
7	Intruder	Y	25/05/2012	16:22	SA	MT	0.10	3.31	401.7	3	7
8	Intruder	N	10/10/2012	05:22	KB	MT	0.35	3.26	288.3	4	6
9	Intruder	N	21/08/2013	03:44	MB	KB	0.74	1.73	146.8	6	9
10	Resident	N	15/08/2014	18:57	MB	DB	0	17.17	66.8	11	12
11	Resident	N	21/08/2014	04:32	MB	HT	0	4.42	295.4	10	10
12	Intruder	Y	11/08/2014	23:45	ZU	AP	0	2.28	270.7	9	12
13	Intruder	N	08/05/2012	05:28	KB	MT	0	2.43	309.1	6	7
14	Intruder	N	17/08/2013	21:40	MB	KB	0	4.43	65.5	6	9
15	Intruder	Y	30/01/2014	16:18	HT	AP	0	0.71	141.9	4	10

[a]Losers were pack displaced furthest from encounter location 1-hr post-encounter; [b]closest edge of 50% kud if outside, otherwise set to 0; [c]adults and yearlings over 1 year old; [d] the winner of this encounter was the resident when using the mcp method of home range estimation, all others were unchanged

Table 2 Comparison of a) the proportion of inter-pack range overlap in pre- versus post-encounter periods and b) changes in distances of packs to their own range core 1h after versus 1h 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

a)

		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

b)

		KDE method			MCP method		
Status	**Calculation**	**Mean**	**SD**	**paired t-test result**	**Mean**	**SD**	**paired t-test result**
Resident	Pre-post	0.086 ±	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

Table 3 Generalized 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. ∆i = AICci - AICcmin, wi=Akaike weights

	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

774 **Table 4** Average effects of parameters in models from Table 1 (cumulative AIC weights were
775 >0.95) the factors affecting the outcome (win or lose) of an inter-pack encounter (N=15
776 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

777

778 **Figure captions**

779

780 **Fig. 1** Injured subdominant resident adult male African wild dog following an inter-pack

781 encounter. GPS radiocollar and drop-off unit also shown

782

783 **Fig. 2** Median distances (m), between packs (▬), and between the encounter site and intruder

784 (▬) and resident (▬) packs over (a) 12 h and (b) 1.5 h periods either side of the encounter.

785 N=15 encounters

786

787 **Fig. 3** Median distances (m) to own home range core for intruder (▬) and resident (▬) packs

788 over (a) 12 h and (b) 1.5 h periods either side of the encounter. (Ranges estimated using the

789 kernel density estimate method). N=15 encounters

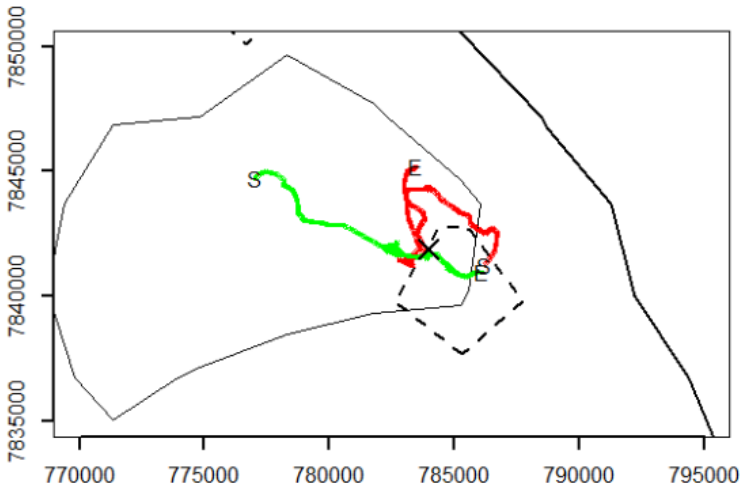
Encounter 1

Date: 23 February 2012
Time (LMT): 18:41

	Resident	Intruder
Pack ID:	MT	NM
Pack size[1]:	14	3
Outcome[2]:	Lose	Win

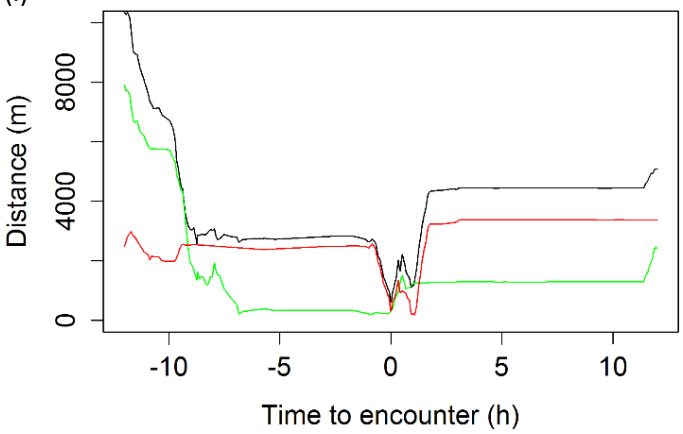
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

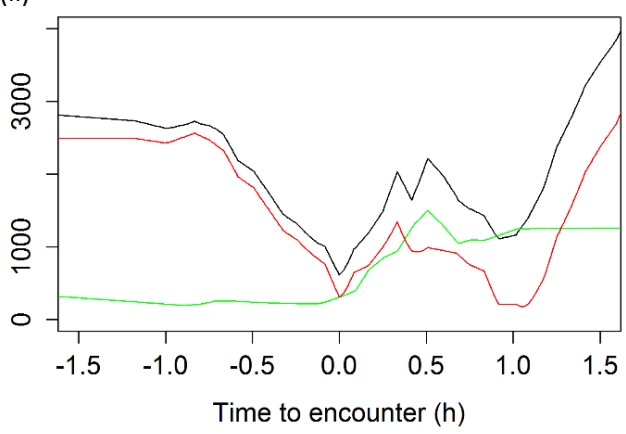


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, and intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

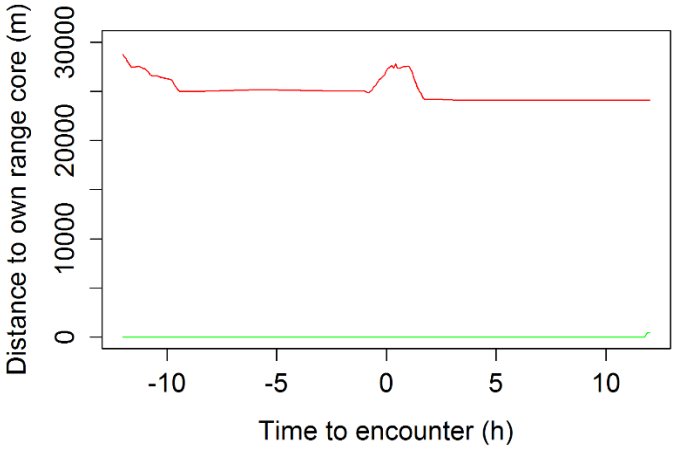
(i)



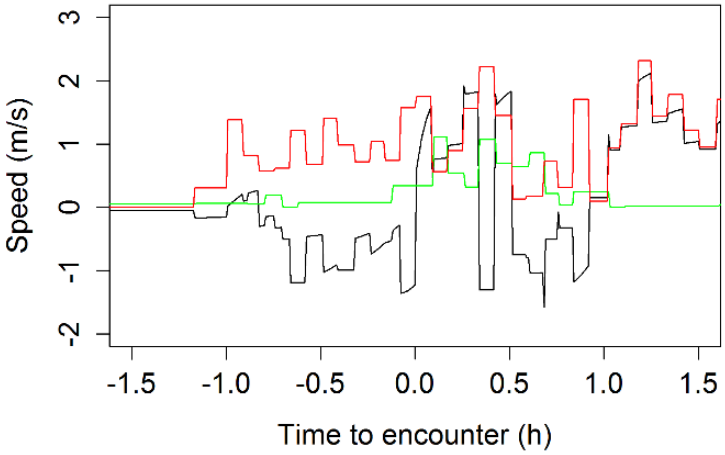
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.

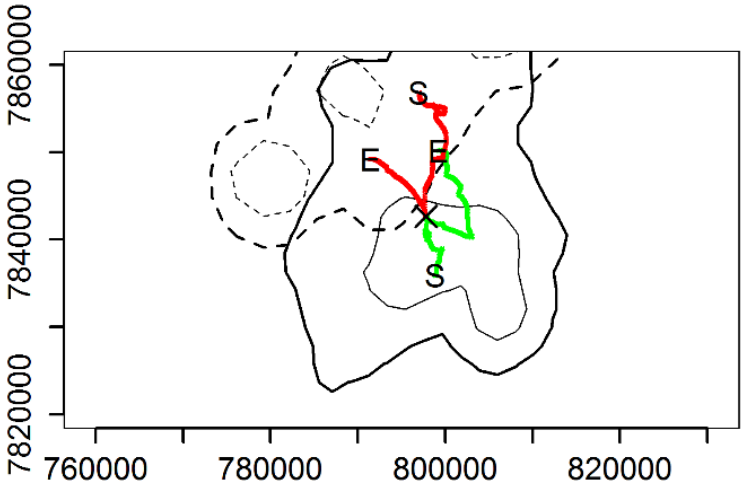


Encounter 2

Date:	30 April 2012	
Time (LMT):	21:39	
	Resident	Intruder
Pack ID:	HW	SA
Pack size[1]:	5	3
Outcome[2]:	Lose	Win

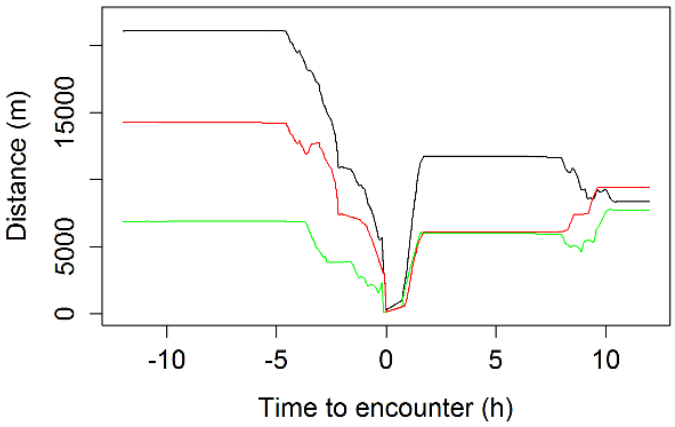
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

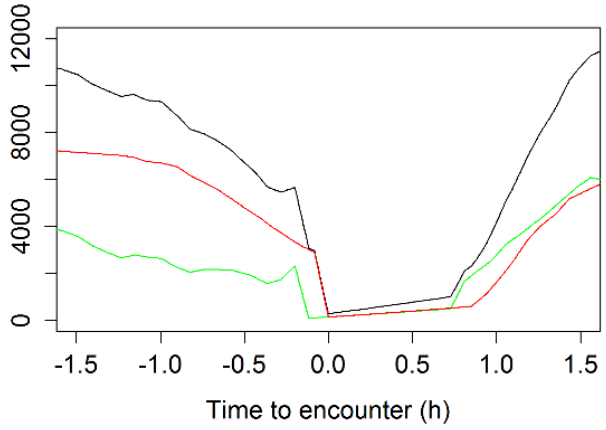


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

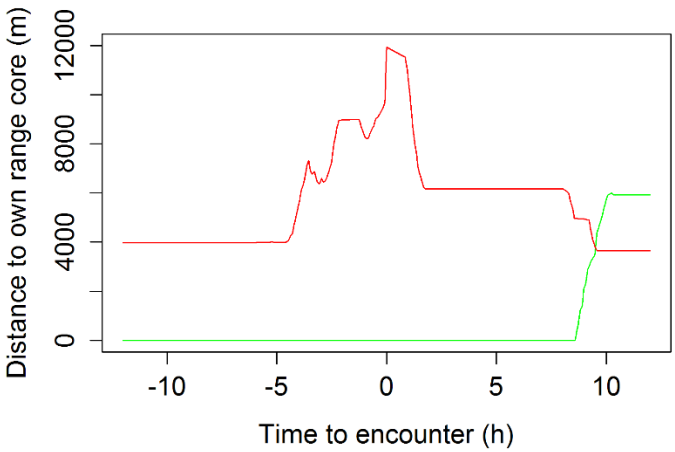
(i)



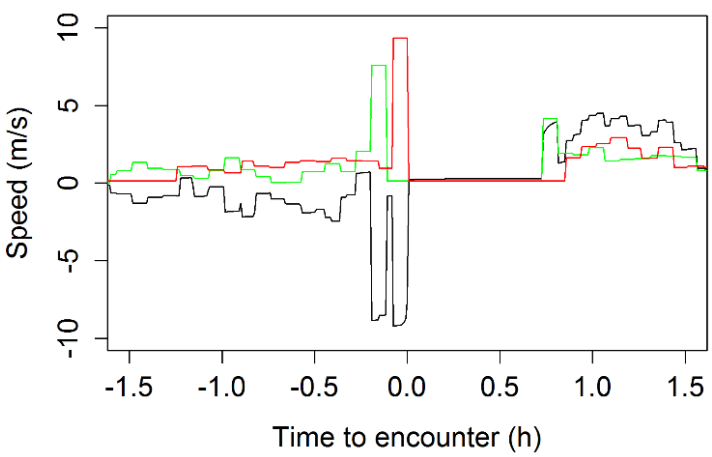
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.

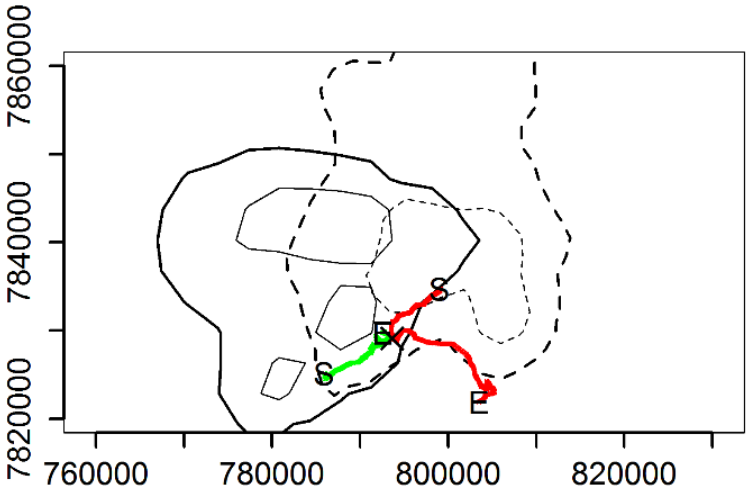


Encounter 3

Date:	4 May 2012	
Time (LMT):	01:25	
	Resident	Intruder
Pack ID:	MT	HW
Pack size[1]:	7	5
Outcome[2]:	Win	Lose

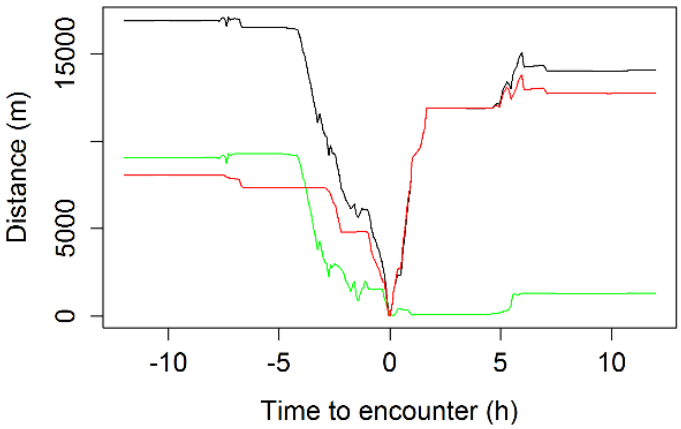
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

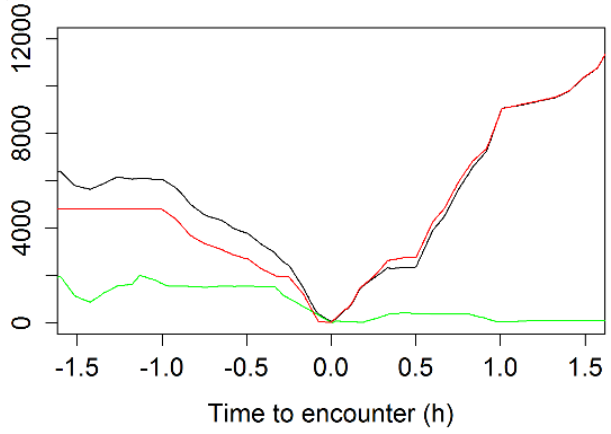


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

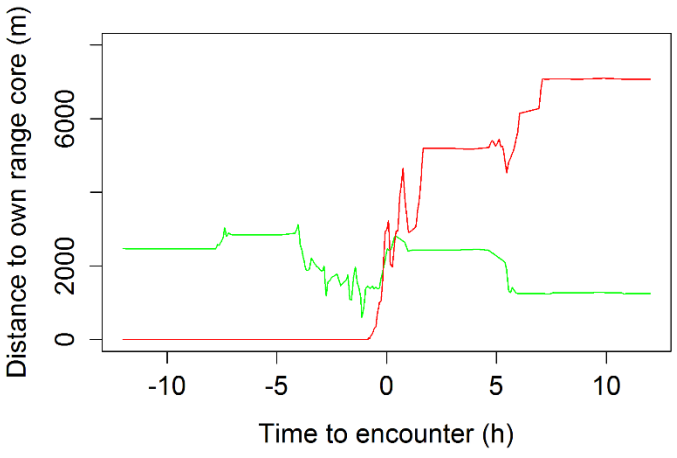
(i)



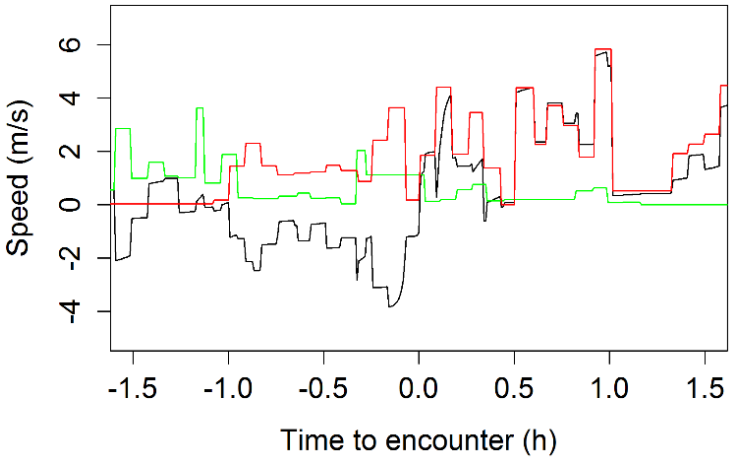
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



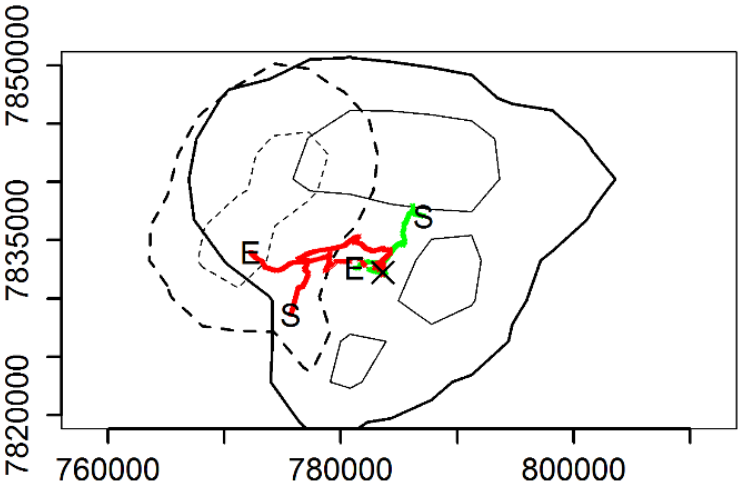
Encounter 4

Date:	7 May 2012
Time (LMT):	07:23

	Resident	Intruder
Pack ID:	MT	KB
Pack size[1]:	7	6
Outcome[2]:	Win	Lose

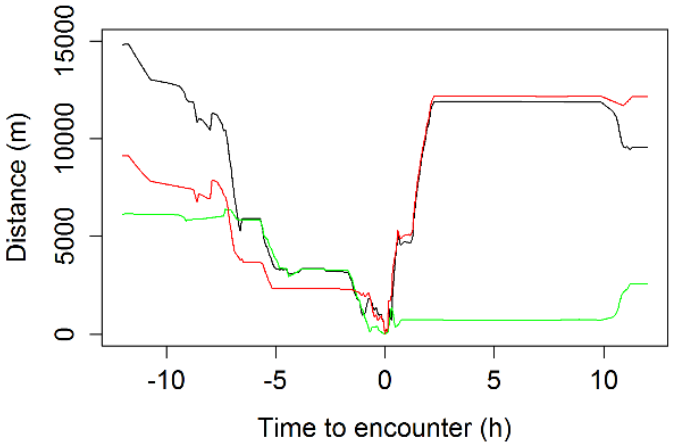
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

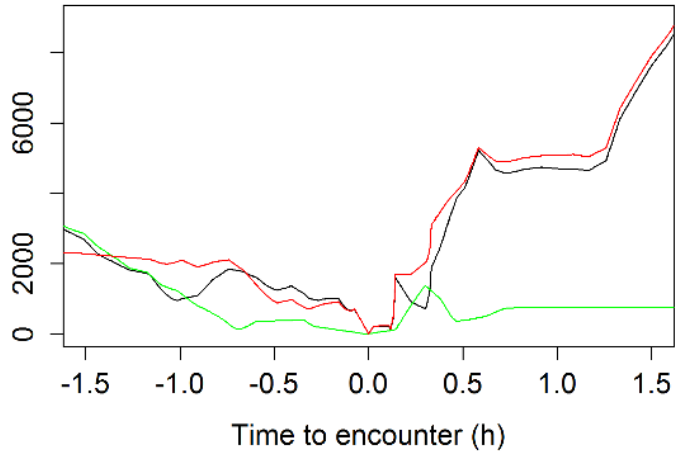


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

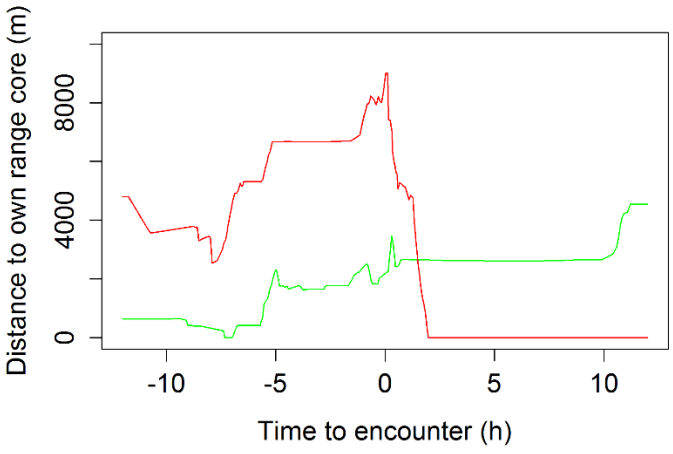
(i)



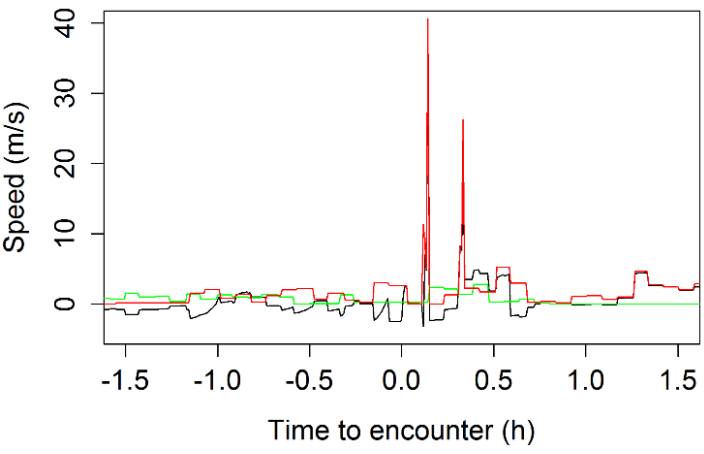
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



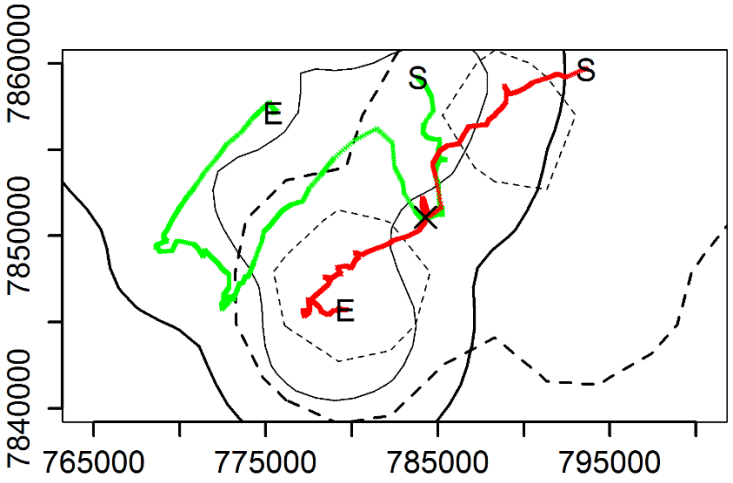
Encounter 5

Date:	07 May 2012
Time (LMT):	23:11

	Resident	Intruder
Pack ID:	MK	SA
Pack size[1]:	4	3
Outcome[2]:	Lose	Win

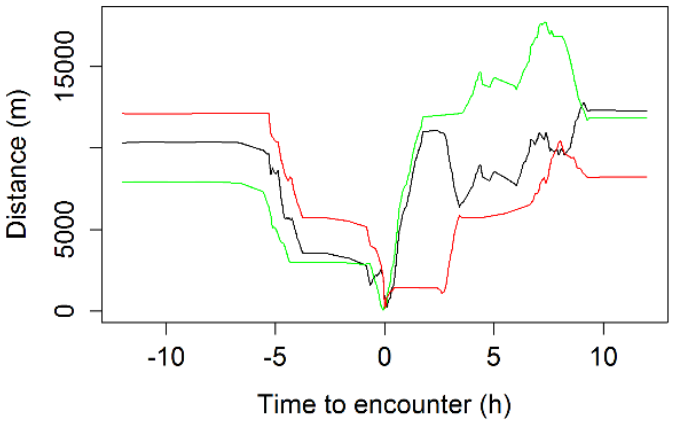
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

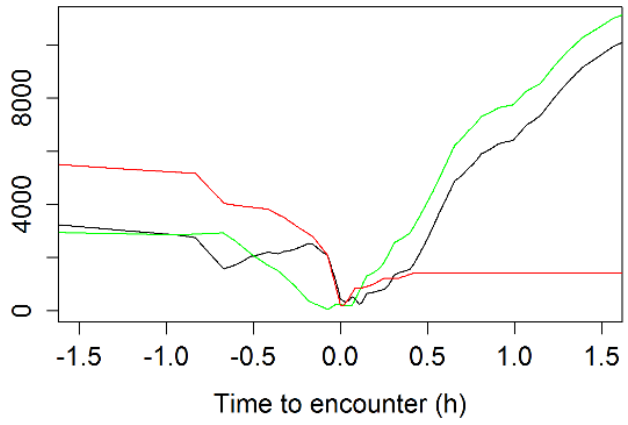


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

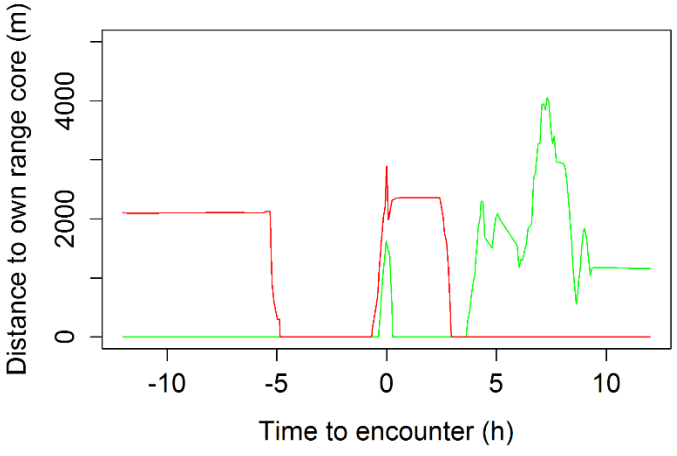
(i)



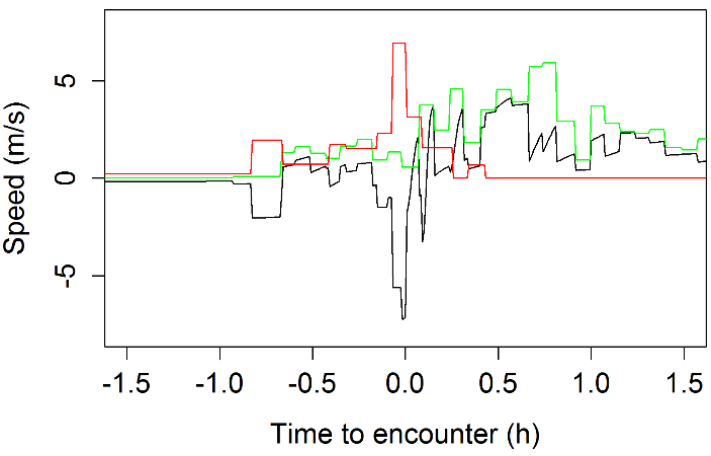
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



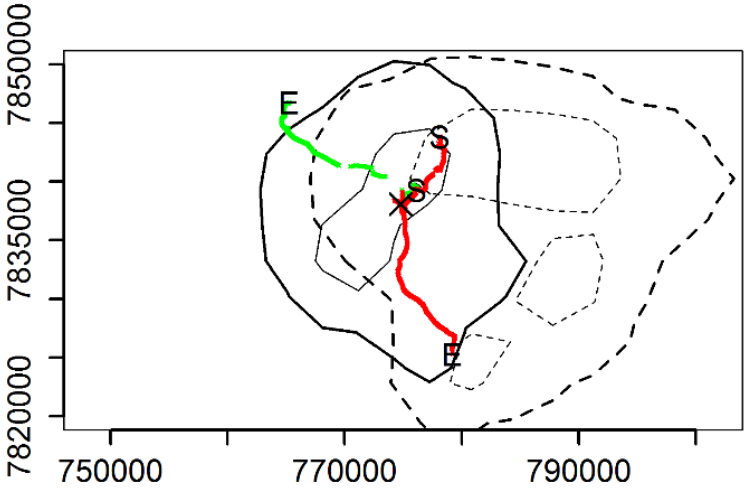
Encounter 6

Date: 14 May 2012
Time (LMT): 06:22

	Resident	Intruder
Pack ID:	KB	MT
Pack size[1]:	6	7
Outcome[2]:	Lose	Win

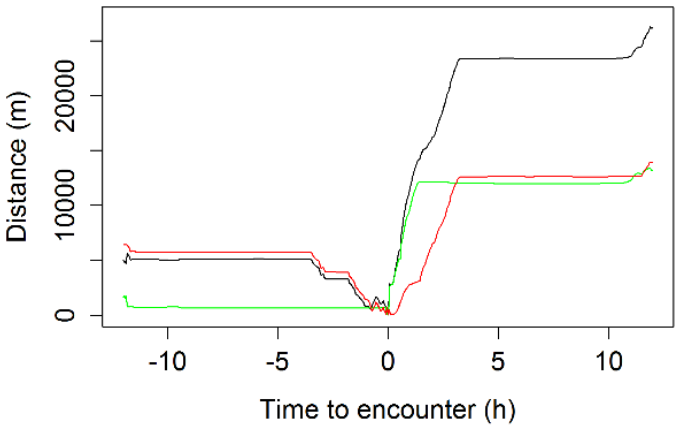
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

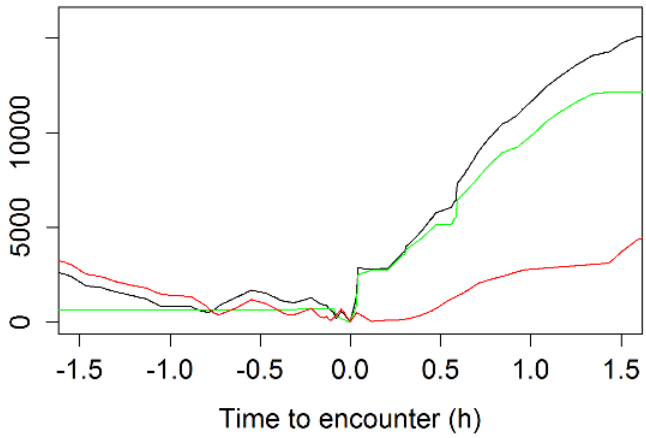


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

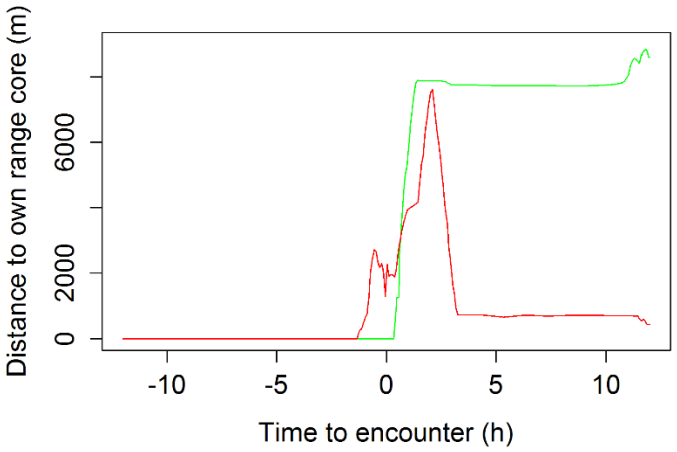
(i)



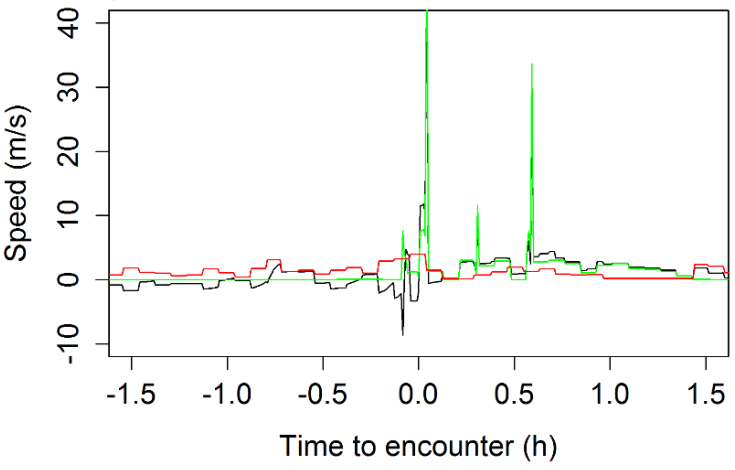
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



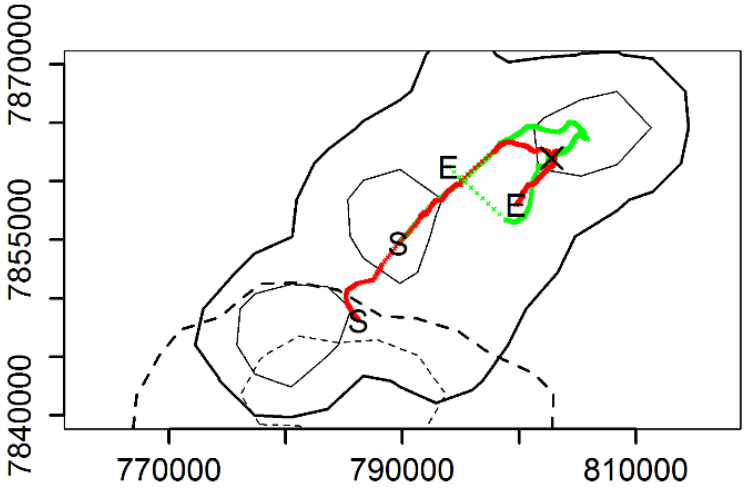
Encounter 7

Date:	25 May 2012
Time (LMT):	18:22

	Resident	Intruder
Pack ID:	SA	MT
Pack size[1]:	3	7
Outcome[2]:	Lose	Win

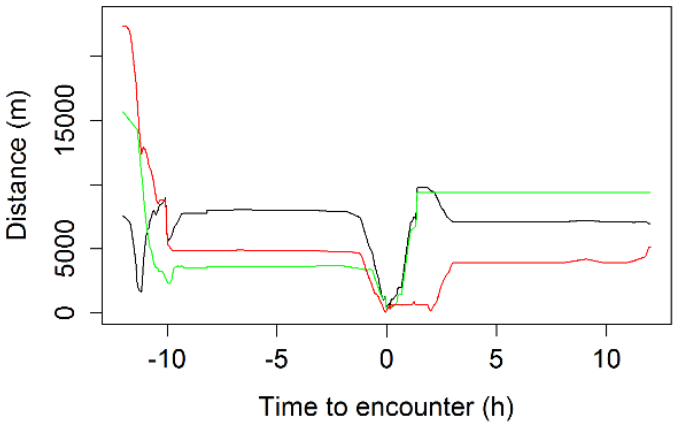
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

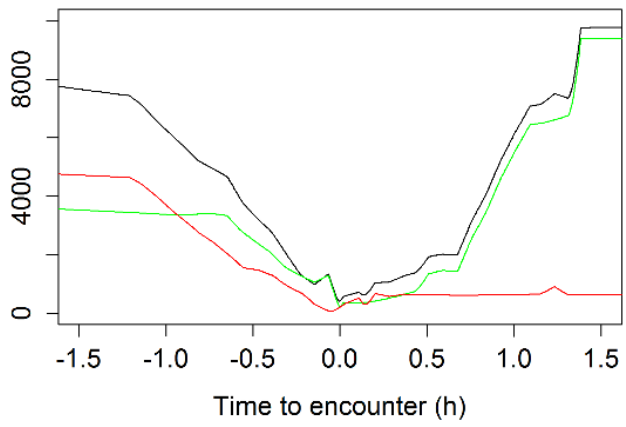


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

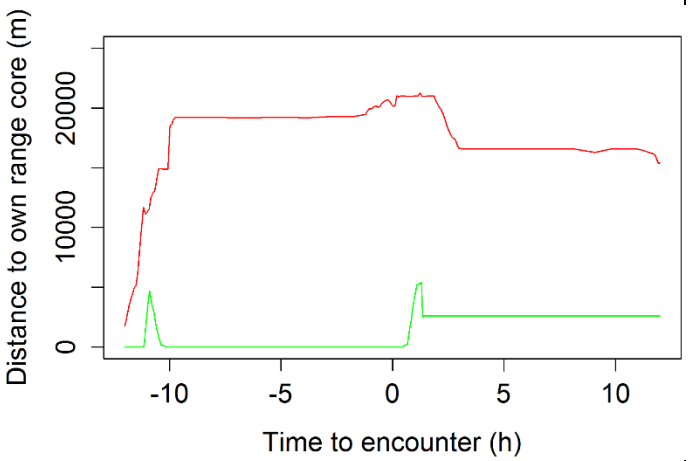
(i)



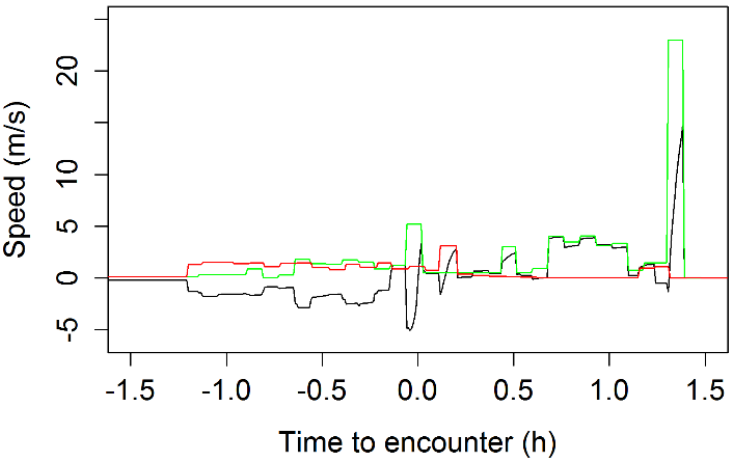
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



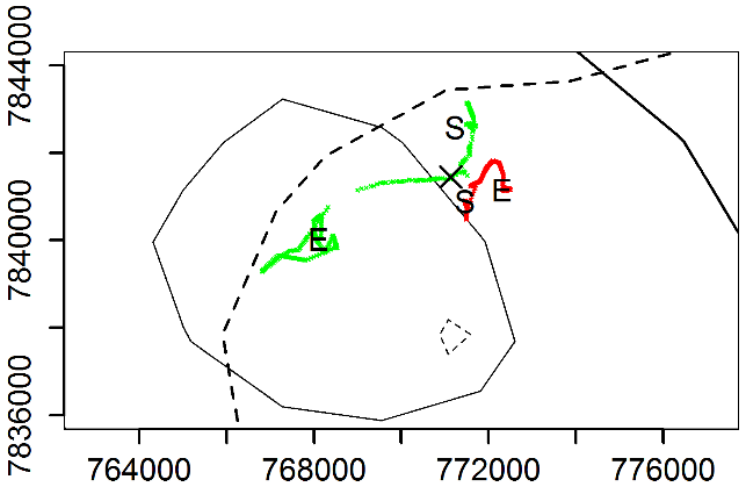
Encounter 8

Date:	10 Oct 2012
Time (LMT):	07:22

	Resident	Intruder
Pack ID:	KB	MT
Pack size[1]:	4	6
Outcome[2]:	Lose	Win

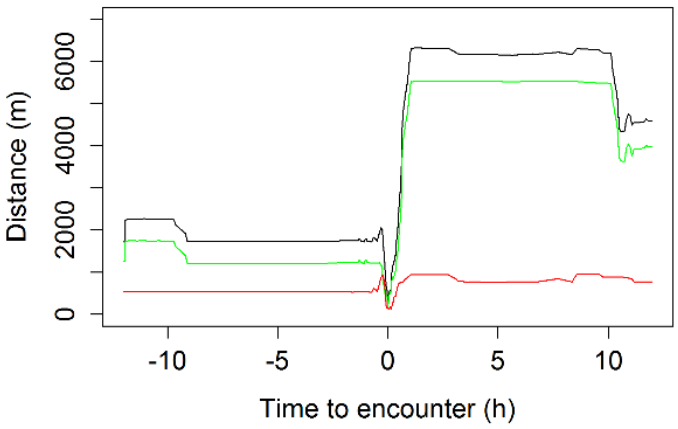
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

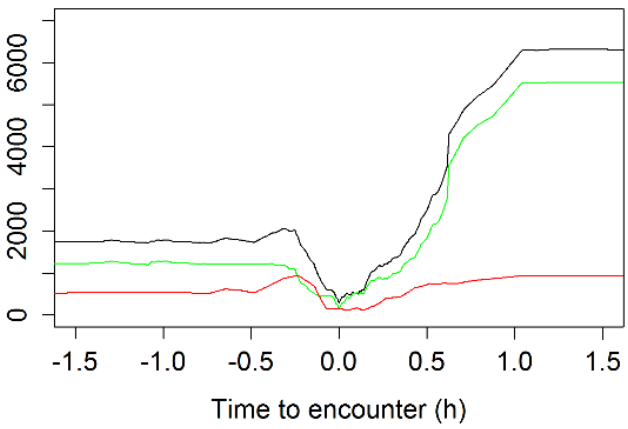


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

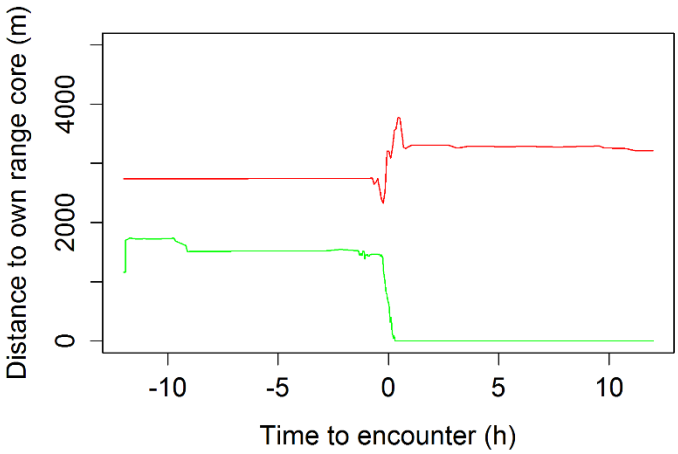
(i)



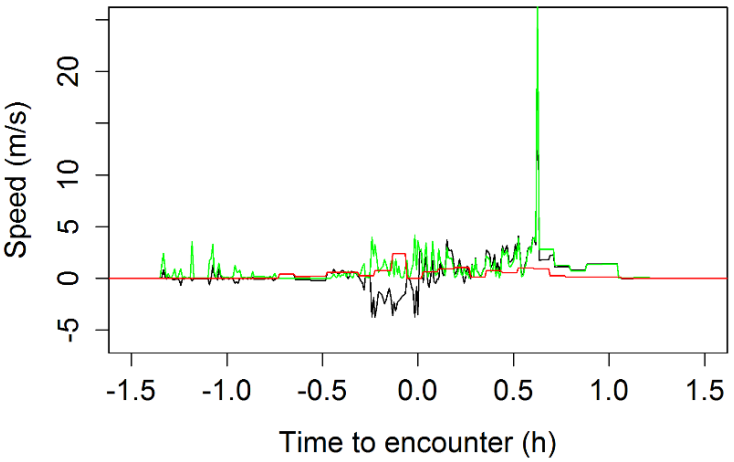
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



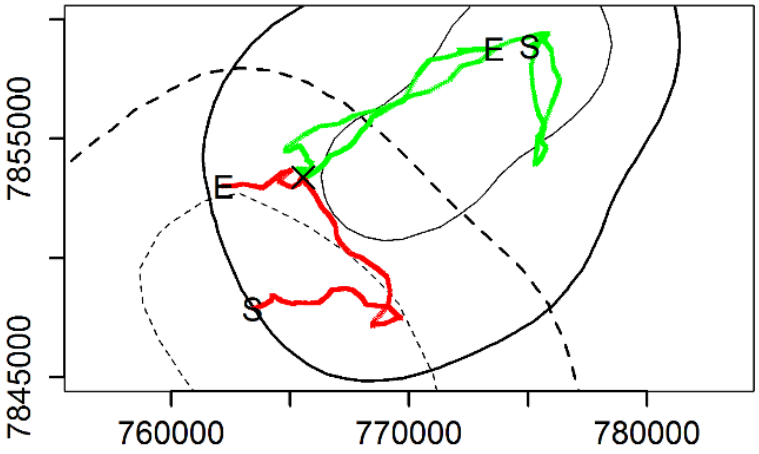
Encounter 9

Date:	21 Aug 2013
Time (LMT):	03:44

	Resident	Intruder
Pack ID:	MB	KB
Pack size[1]:	6	9
Outcome[2]:	Lose	Win

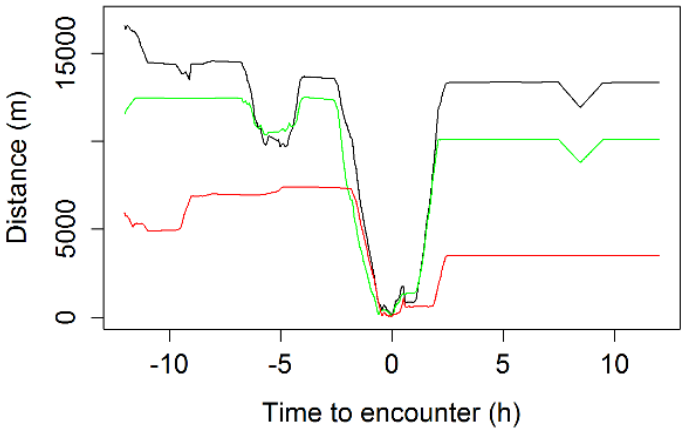
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

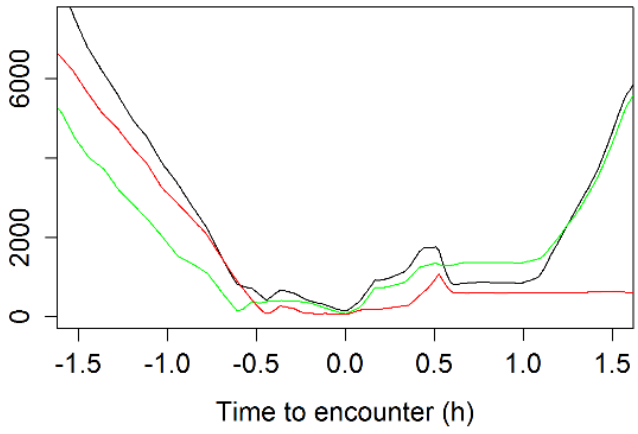


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

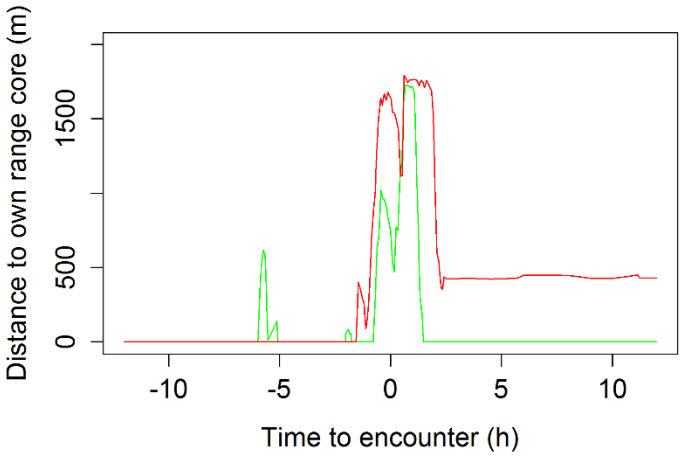
(i)



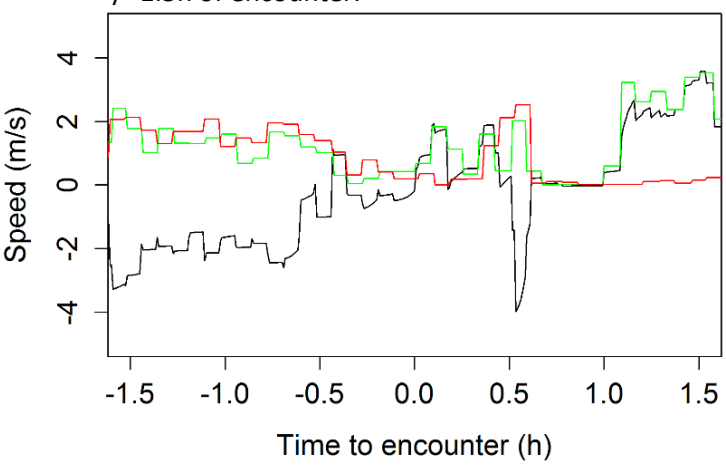
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



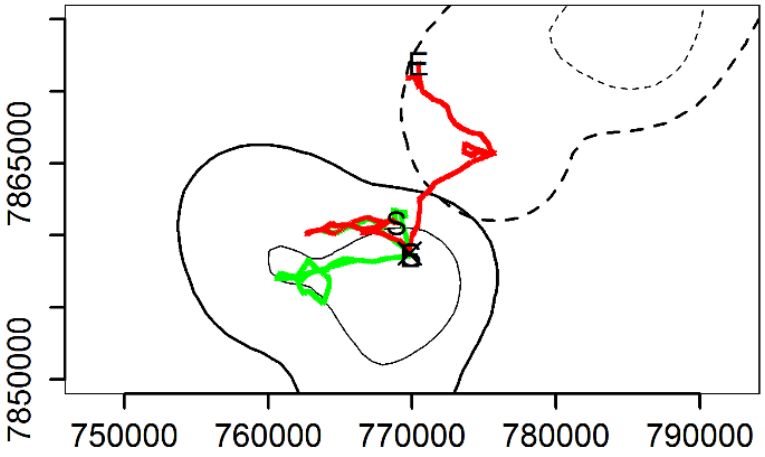
Encounter 10

Date: 15 Aug 2014
Time (LMT): 20:57

	Resident	Intruder
Pack ID:	MB	DB
Pack size[1]:	11	12
Outcome[2]:	Win	Lose

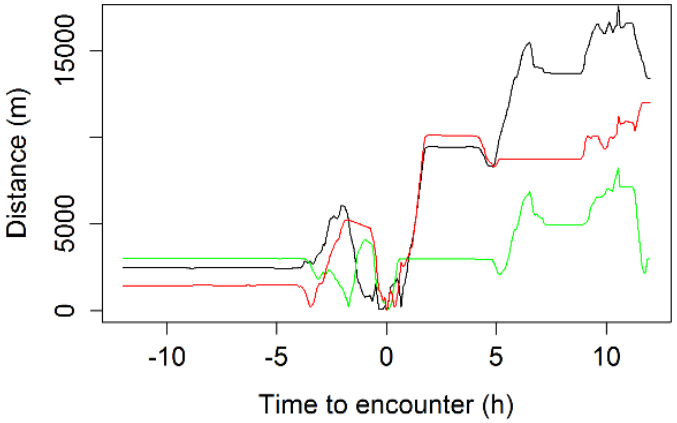
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

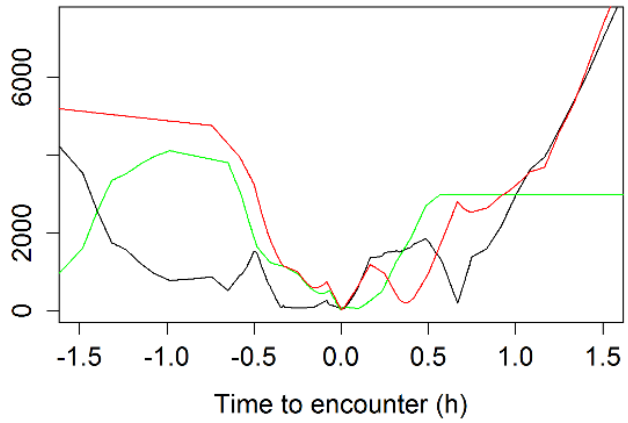


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

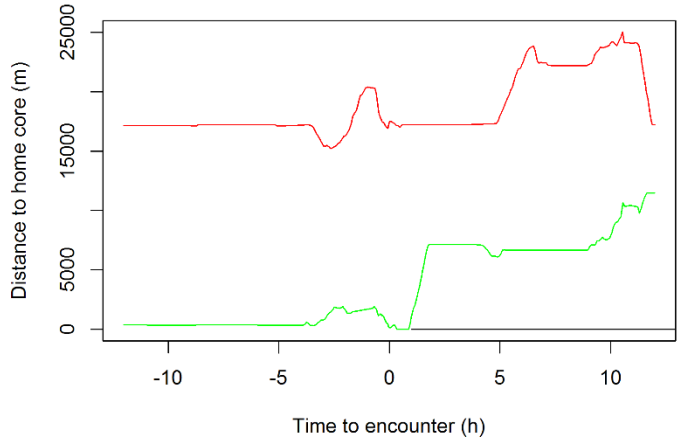
(i)



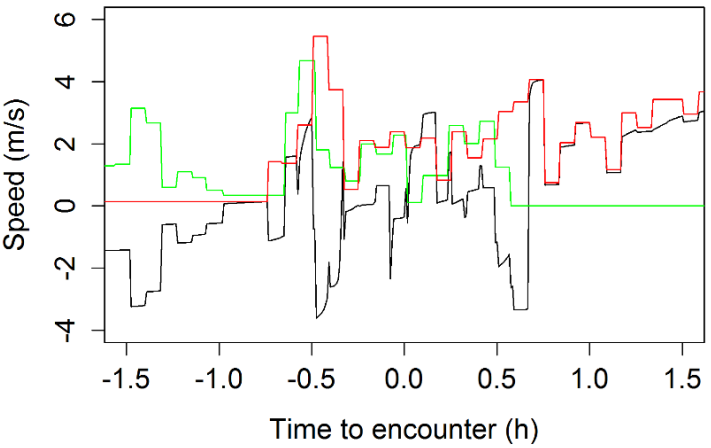
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.

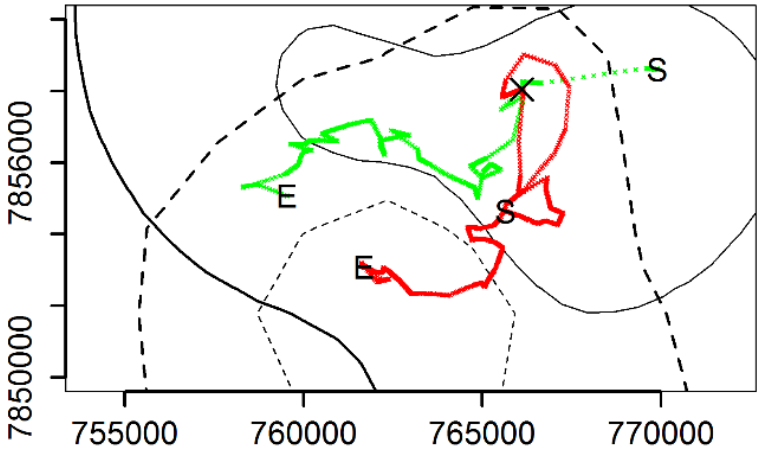


Encounter 11

Date:	21 Aug 2014	
Time (LMT):	06:32	
	Resident	Intruder
Pack ID:	MB	HT
Pack size[1]:	10	10
Outcome[2]:	Win	Lose

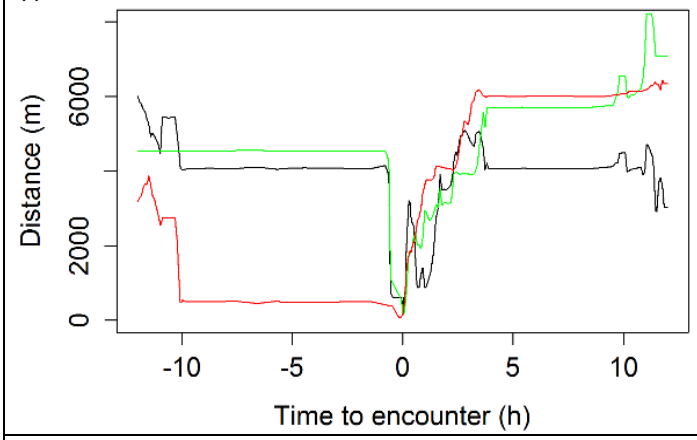
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

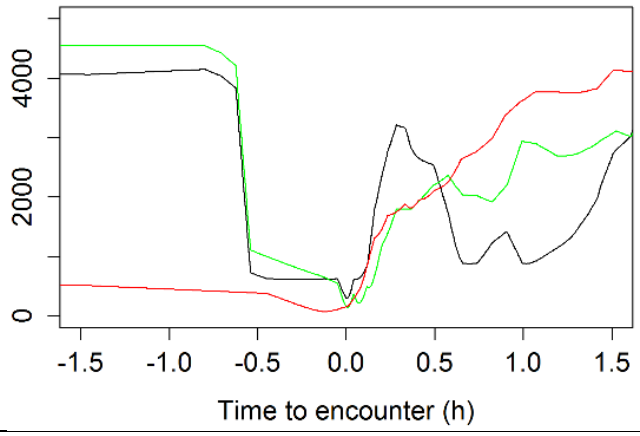


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

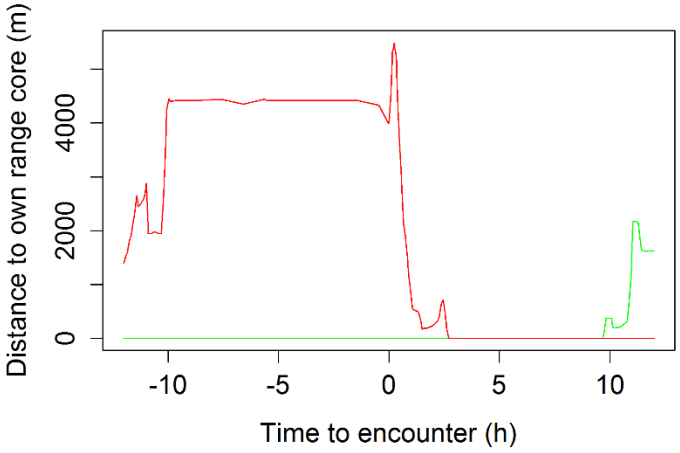
(i)



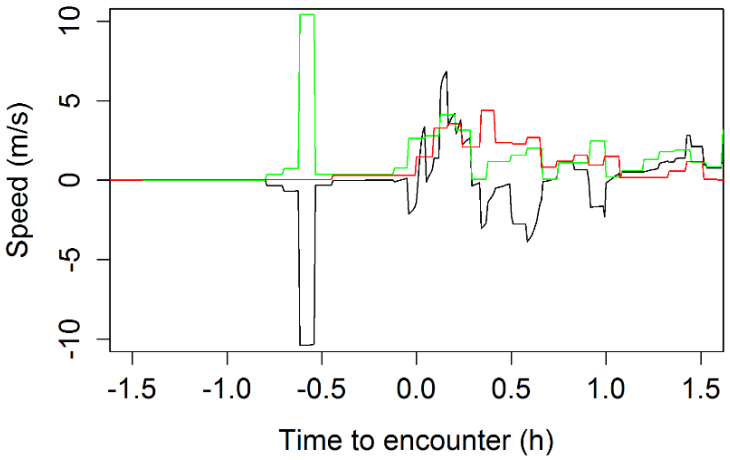
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



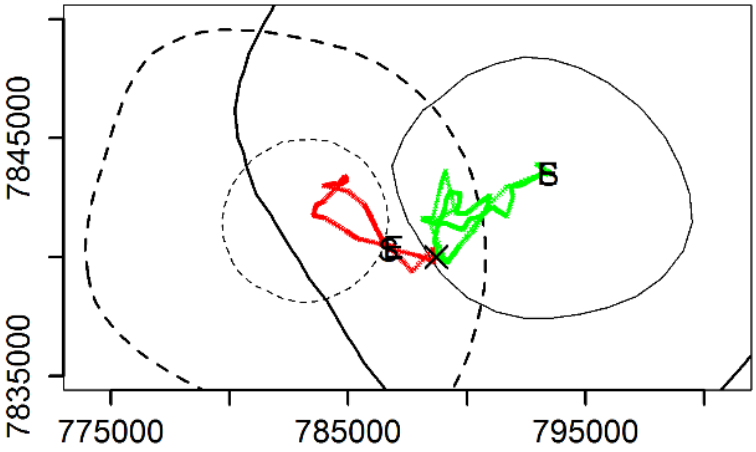
Encounter 12

Date:	12 Aug 2014
Time (LMT):	01:45

	Resident	Intruder
Pack ID:	ZU	AP
Pack size[1]:	9	12
Outcome[2]:	Lose	Win

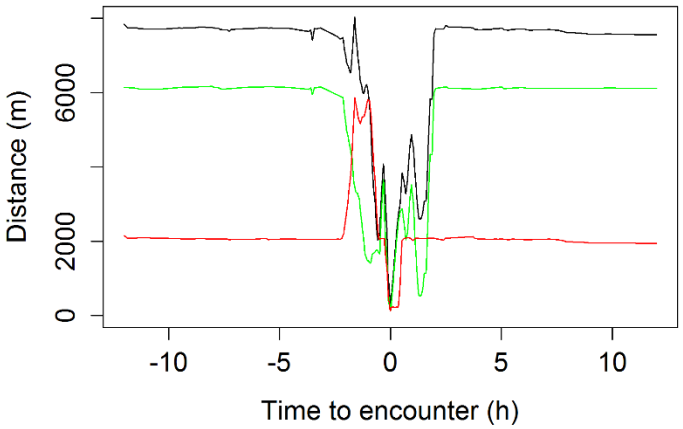
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

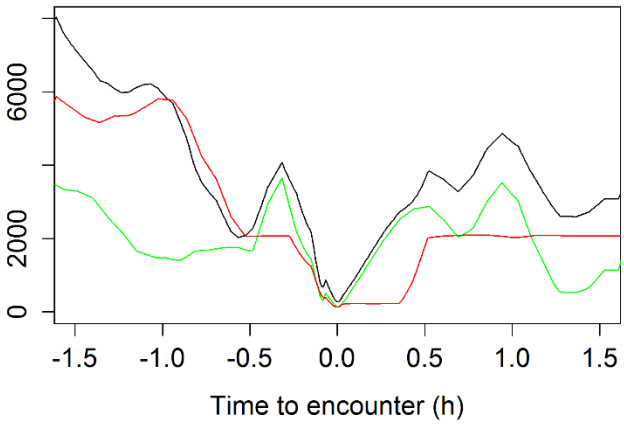


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

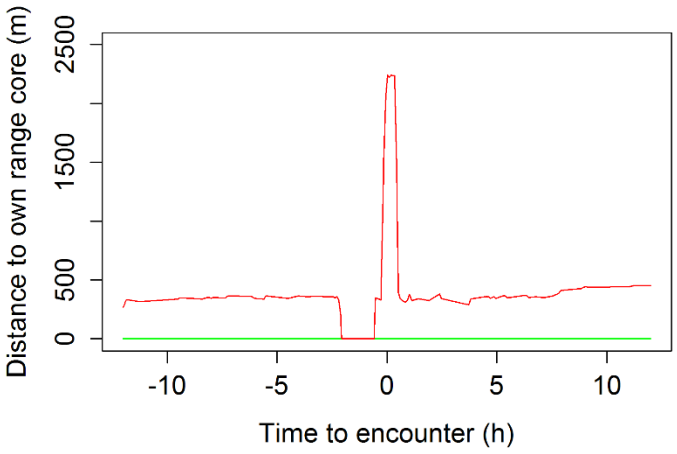
(i)



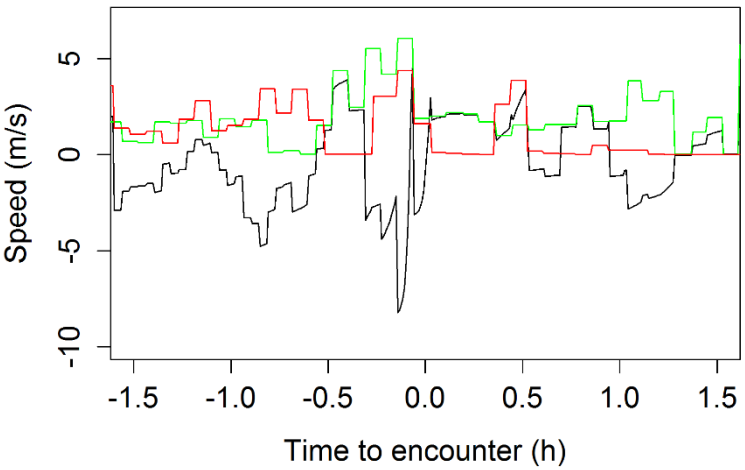
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



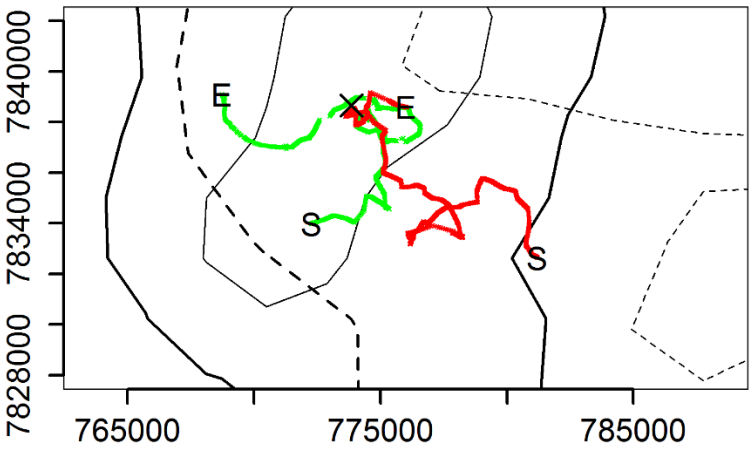
Encounter 13

Date:	08 May 2012
Time (LMT):	07:28

	Resident	Intruder
Pack ID:	KB	MT
Pack size[1]:	6	7
Outcome[2]:	Lose	Win

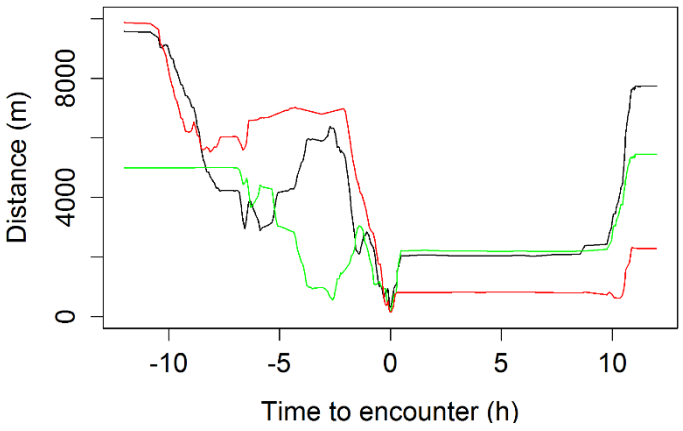
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

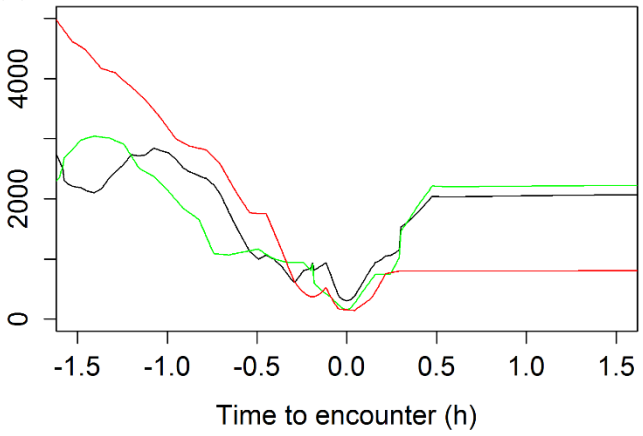


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

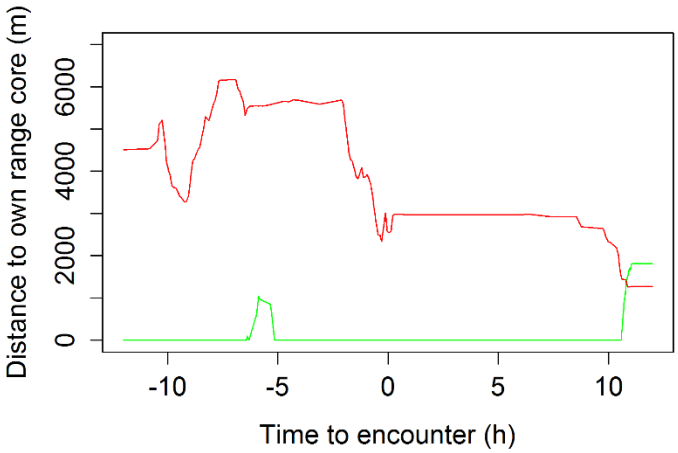
(i)



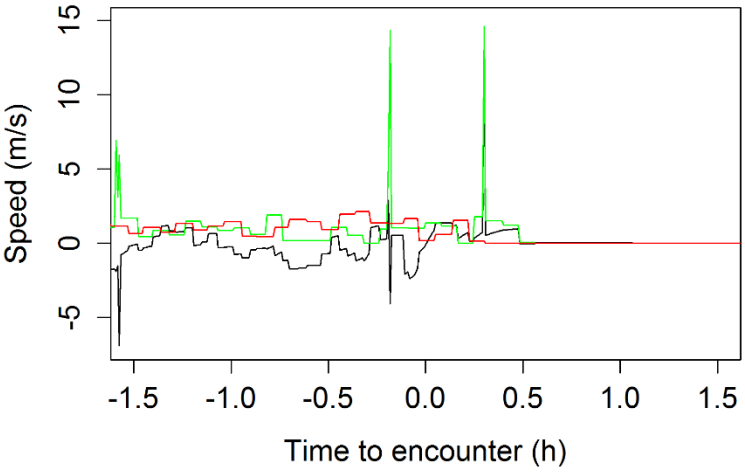
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.



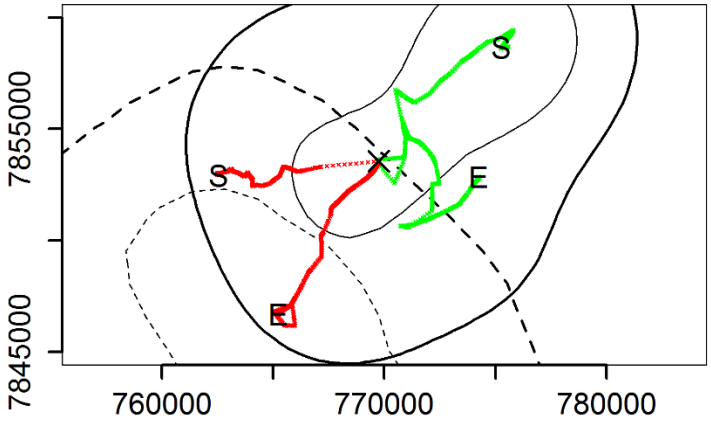
Encounter 14

Date:	17 Aug 2013
Time (LMT):	23:40

	Resident	Intruder
Pack ID:	MB	KB
Pack size[1]:	6	9
Outcome[2]:	Lose	Win

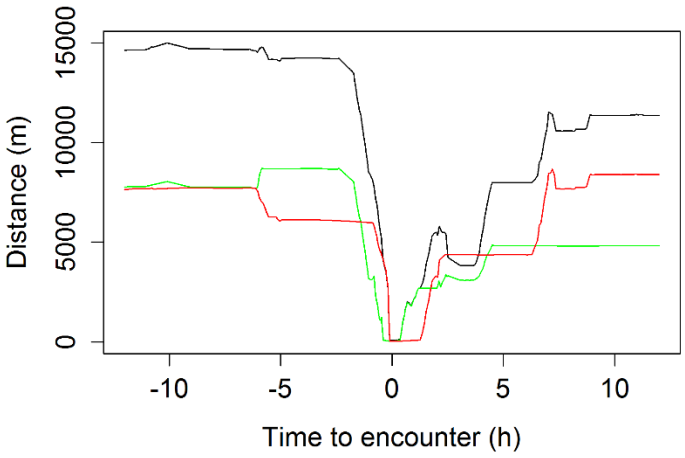
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

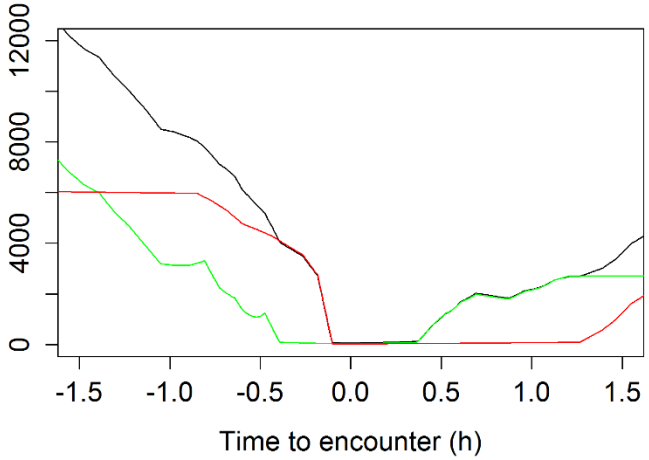


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

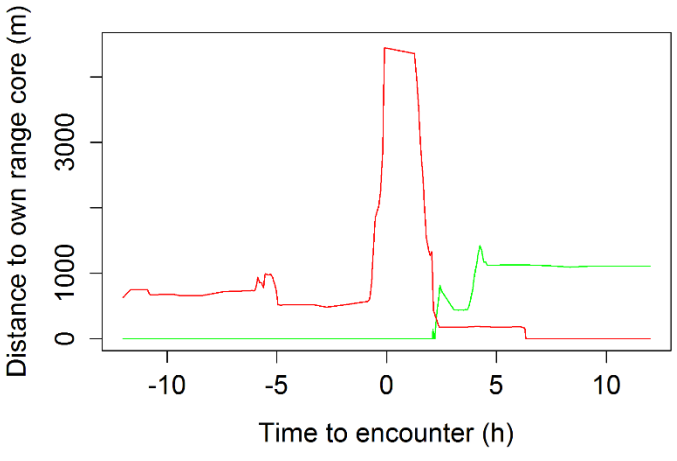
(i)



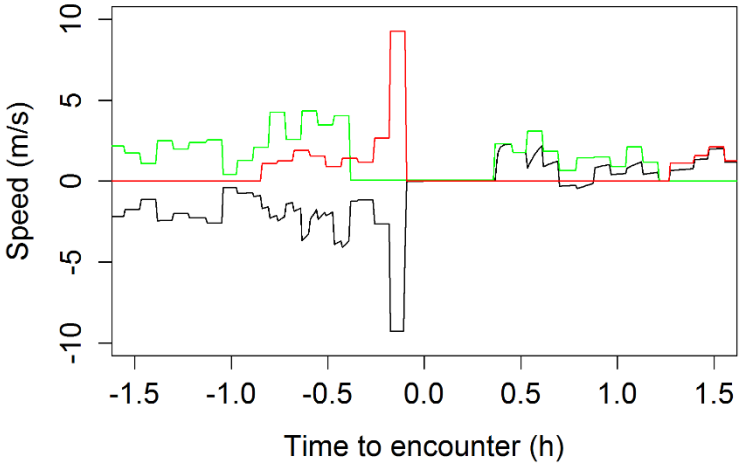
(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.

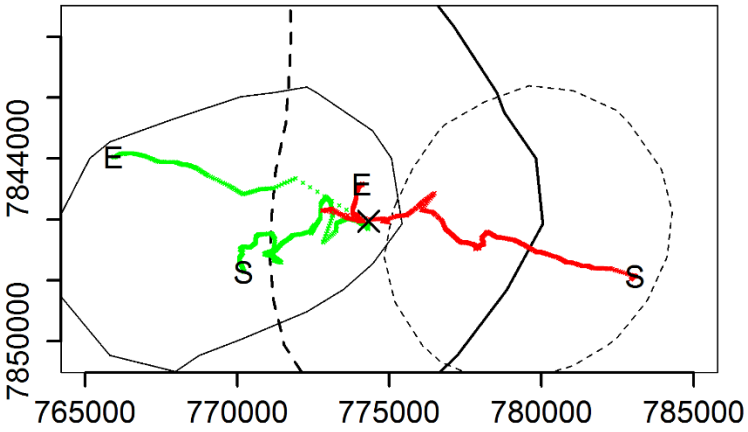


Encounter 15

Date:	30 Jan 2014	
Time (LMT):	18:18	
	Resident	Intruder
Pack ID:	HT	AP
Pack size[1]:	4	10
Outcome[2]:	Lose	Win

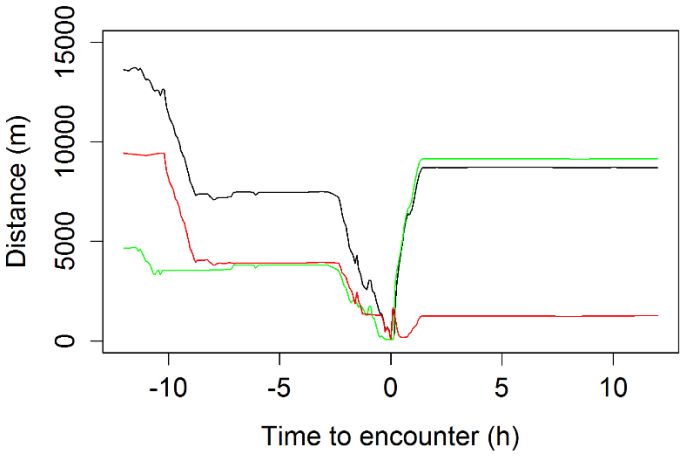
[1]Number of adults and yearlings (>12months); [2]'winner' was closest pack to encounter site 1h following encounter.

a) Interpolated movement of resident and intruder packs +/- 12h of encounter at X. resident range (95% UD) and core range (50% UD kernel), and ---- intruder range and ---- core range boundaries. S=start (-12h), E=end (12h).

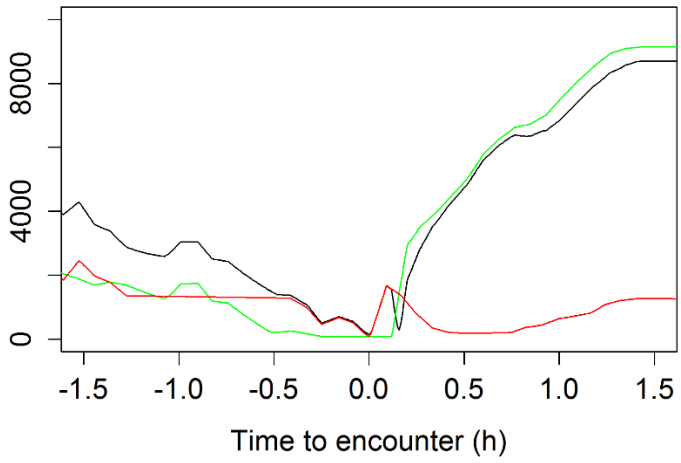


b) Interpolated distances (m) showing: Inter-pack, resident-encounter site, intruder-encounter site at: (i) +/- 12h; (ii) +/- 1.5h from the encounter.

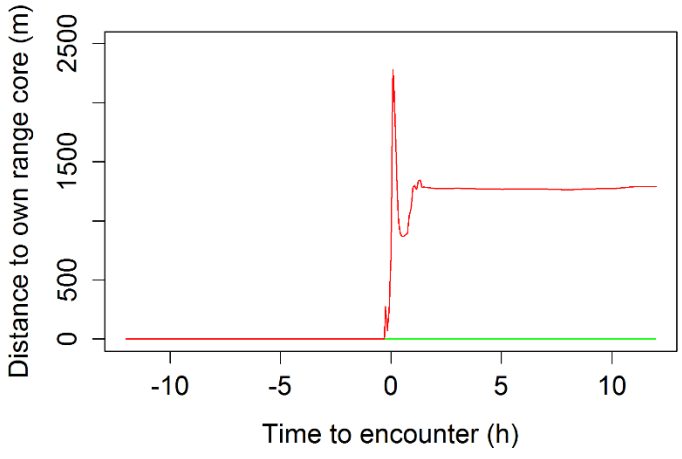
(i)



(ii)



c) Interpolated distances to own home range core (m) +/- 12h of encounter: resident; intruder.



d) Inter-pack closing speed (m/s) (+ve converge, -ve diverge) and speed of resident and intruder, +/- 1.5h of encounter.