



## Movement-based analysis of interactions in African lions



Simon Benhamou<sup>a,\*</sup>, Marion Valeix<sup>b</sup>, Simon Chamailé-Jammes<sup>a</sup>, David W. Macdonald<sup>c</sup>,  
Andrew J. Loveridge<sup>c</sup>

<sup>a</sup> Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, Centre National de la Recherche Scientifique (CNRS), Montpellier, France

<sup>b</sup> Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, Centre National de la Recherche Scientifique (CNRS), Université Claude Bernard—Lyon 1, Villeurbanne, France

<sup>c</sup> Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Tubney, U.K.

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Spatial interactions can reveal the influence animals have on each other. In this context, ‘interaction’ refers to the joint occurrence in space (static interaction) or in both space and time (dynamic interaction). Most studies have focused on static interactions, estimated in terms of home range (HR) overlap. The few studies that have addressed dynamic interactions, corresponding to mutual attraction or avoidance within shared sections of animals’ HRs, used statistical tests that assume independent relocations. Thus, although serial correlation in relocations provides invaluable information on space use dynamics, it has often been considered a statistical impairment. We developed a permutation test that explicitly takes serial correlation into account to test adequately whether two animals tend to move independently of each other, or show mutual attraction or avoidance, when moving in shared HR sections. We applied this novel method to 55 GPS-collared free-ranging lions, *Panthera leo*, in Hwange National Park (Zimbabwe), for which we also investigated static interactions by computing activity-weighted (i.e. using utilization distribution) HR overlap. Overlapping HRs were not at all uncommon for lions from different social groups. Within shared HR sections, individuals that tended to move jointly were often related. We found only one case of avoidance, involving two males, suggesting that when male lions, even unrelated ones, moved within a shared HR section, they generally did so independently of each other. Potentially competing males usually appeared to show avoidance by establishing HRs sufficiently far apart to allow for only marginal overlap, with only males tolerant of each other sharing sections of their HRs. Our results show that the simultaneous study of static and dynamic interactions can provide a comprehensive view of how space/time sharing with conspecifics influences animal movements and space use.

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Evaluating how animals share space is of great interest in understanding a variety of ecoethological processes (e.g. sociality, territorial behaviour, mate searching, predator–prey relationships and disease transmission). Macdonald, Ball, and Hough (1980) first coined the terms static and dynamic interactions to draw attention to the fact that spatial interactions between animals could be analysed in terms of home range (HR) overlap or at finer spatial and temporal scales in terms of encounter rate. It is worth noting that, in this context where animals are infrequently directly observed, ‘interaction’ refers to the joint occurrence in space (static interaction) or in both space and time (dynamic interaction) of two

individuals, without prejudging of the nature of their behaviours. For the most part, questions of space sharing have been addressed in terms of static interaction. However, even the most sophisticated measures of HR overlap (reviewed in Millspaugh, Gitzen, Kernohan, Larson, & Clay, 2004), which take intensity of space use into account, only allow quantification of overall interaction between two individuals as a synthetic value of common space use. A step further is to focus on space–time sharing, that is, to study the co-occurrence of individuals within overlapping zones of their HRs (Minta, 1992). However, co-occurrence within shared areas does not necessarily involve direct interactions between individuals, as two individuals can co-occur on a large commonly used area while remaining beyond perceptual range of each other. The level of potential direct interactions between individuals would be better revealed by investigating whether two individuals tend to move jointly, independently or avoid each other when using a shared section of their HRs. This issue was first addressed by Macdonald

\* Correspondence: S. Benhamou, Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, Centre National de la Recherche Scientifique (CNRS), 1919 Route de Mende, 34293 Montpellier cedex 5, France.

E-mail address: [simon.benhamou@cefe.cnrs.fr](mailto:simon.benhamou@cefe.cnrs.fr) (S. Benhamou).

et al.'s (1980) pioneering work. However, in this and subsequent work (Doncaster, 1990), successive relocations of each individual were assumed to be independent from each other so as to enable classical statistical tests, whereas dynamic interaction should be better investigated from movement data sets, which are, by definition, composed of serially correlated relocations. Taking such a correlation into account obviously requires the design of dedicated statistical tests.

Large carnivores are highly mobile species whose spatio-behavioural strategies depend on not only targeting resource-rich areas (Mosser, Fryxell, Eberly, & Packer, 2009; Valeix, Loveridge, & Macdonald, 2012) but also complex social interactions. In African lions, *Panthera leo*, females form prides of several related adult females and their dependent offspring, and the females in a pride cooperate in hunting (Stander, 1992), defence of kills (Cooper, 1991), and protection of territory and young (Packer, Scheel, & Pusey, 1990). Male lions form cooperative coalitions which compete against other coalitions for exclusive access to female prides (Bygott, Bertram, & Hanby, 1979). Although females from a pride are always close relatives, male coalitions may be composed of either close kin or non-relatives where cooperation is based on mutualism (Grinnell, Packer, & Pusey, 1995; Packer & Pusey, 1982). Core areas are generally exclusive but relatively large HR overlaps between neighbouring lion groups can exist (Davidson, Valeix, Loveridge, Madzikanda, & Macdonald, 2011; Spong, 2002). Lion prides and coalitions defend their territories by scent marking and roaring (McComb, Packer, & Pusey, 1994; Schaller, 1972). Intergroup encounters may result in intense chases and fights that can lead to serious injury (West et al., 2006); hence, if neighbouring groups might sometimes come close for mutual defiance, spatial avoidance is expected between these groups to avoid aggressive encounters. However, the extent to which individuals from neighbouring groups avoid each other when using shared sections of their HRs is poorly understood.

The goal of our study was two-fold. We first developed a new conceptual framework to design a reliable null model of independent movements. Recent technological advances in animal-tracking tools such as GPS telemetry, which can provide accurate relocations with a relatively high and consistent frequency and over an extended duration, allow us to design movement-based analyses of interactions but challenge our capacity to elaborate statistically reliable null models that take locational serial correlations into account. In previous analyses of space–time sharing (Doncaster, 1990; Lühns & Kappeler, 2013; Macdonald et al., 1980; Miller, 2012; Minta, 1992), relocations for each individual were either assumed to be independent of each other or possibly subsampled to reach statistical independence. Second, we used this conceptual framework to investigate dynamic interactions between GPS-radiocollared African lions of both sexes from the same or different social groups in Hwange National Park, Zimbabwe. We hypothesized that individuals from the same group and of the same sex should tend to move in close proximity. We further hypothesized that, because of the cost of fighting, individuals from the same sex belonging to neighbouring groups should avoid each other, either by minimizing HR overlap and/or physically when moving through shared areas. Finally, for individuals of different sexes, we hypothesized that pride males should move jointly with females of the pride, whereas other males should move independently from these females.

## METHODS

### Study Area and GPS Tracking

The study area covered ca. 7000 km<sup>2</sup> in the northern region of Hwange National Park. This park covers ca. 15 000 km<sup>2</sup> of semiarid

dystrophic (low nutrient soil) savannah in northwestern Zimbabwe (19°00'S, 26°30'E). The vegetation is primarily woodland and bushland savannah, either monospecific stands of *Colophospermum mopane* or more heterogeneous landscape composed of *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* and *Terminalia sericea*. Rainfall averages ca. 600 mm but is highly variable, and it rains primarily between November and April. Lion density in the study area is estimated to be around 0.035 lions/km<sup>2</sup>.

From 2002 to 2012, detailed lion pride/coalition histories were recorded and lions were closely monitored in the study area; 32 females and 42 males were fitted with GPS collars (manufacturers: Televilt/Followit Positioning, AB, Lindesberg, Sweden, or African Wildlife Tracking, Pretoria, South Africa, or Sirtrack Ltd., Havelock North, New Zealand). Lions were captured and collared under permits from the Zimbabwe Parks and Wildlife Management Authority (23(1) (c) (ii) 01/2002–2012), and animal capture and collaring followed the ASAB/ABS guidelines for the Use of Animals in Research. Lions were darted using a CO<sub>2</sub> propelled plastic 1.5 ml dart syringe (Daninject) administered by intramuscular injection (shoulder or rump). The drugs used were dissociative anaesthetic (Zoletil; dosage: 0.83 ± 0.32 (range 0.53–1.38) mg/kg; manufacturer: Virbac RSA, Halfway house, South Africa) and sedative (Medetomidine (Zalopine/Domitor); dosage = 0.05 ± 0.01 (range 0.04–0.06); manufacturer: Novartis, Isando, South Africa or Orion Pharma, Turku, Finland), which were then reversed with Atipamezole (dosage = 0.18 ± 0.07 (range 0.01–0.28) mg/kg; manufacturer: Farnos, Orion Corp., Finland or Novartis, Isando, South Africa). Doses were calculated for African lions and all animals were monitored until full recovery was achieved. Drugs were administered by trained project personnel who attended and successfully passed the Zimbabwe wildlife capture and handling course, and who held a dangerous drug licence (renewed annually through the Wildlife Veterinary Association and administered by Medicines Control Authority, Zimbabwe). No short-term or long-term adverse effect has been recorded since lion immobilization began in 1999 and no adverse effect has been reported in the literature. Animals were under complete chemical immobilization/anaesthesia during the marking and handling. Eyes were covered with a blind fold and ear plugs were used to reduce stimuli/stress during handling. Light leg restraint was used as a safety precaution in case of unexpected arousal of the immobilized animal. The GPS collars fitted weighed between 600 and 900 g, which represent 0.6 and 0.9%, respectively, of the smallest individual captured (100 kg). Collars were removed when batteries were flat or when they malfunctioned, and were usually replaced for long-term monitoring of the Hwange lion population. If not removed, collars would eventually fall off owing to deterioration of the collar material. Most lions collared were fully mature, and when subadults were collared, sufficient space was allowed to ensure that the collar did not become tight as the neck grew. All study animals were monitored regularly to ensure correct fitment of collars. Late stage pregnant females were not captured. Early stage pregnancy cannot be determined visually but the immobilization drugs used have no known effect on unborn fetuses, are extremely safe and widely used on wild and captive felids.

Because lions are mainly active by night, GPS locations were acquired only from 1800 to 0700 hours (to conserve batteries), on an hourly basis. As lions may also rest by night, locations resulting in apparent movements smaller than 50 m (which could be due to noise in GPS locations) were filtered out in all subsequent analyses, because our goal was to focus on movement interaction. We checked that relocating a lion every hour was enough to obtain reliable representations of its movements at the HR scale (rather than a scattered set of independent locations) by computing the serial correlation in location as  $1 - 0.5E(D_s^2)/E(D_c^2)$ , where  $E(D_s^2)$  is

the mean squared distance between any two relocations separated by a movement time (i.e. global time minus time involved in immobility phases) equal to 1 h, and  $E(D_C^2)$  is the mean squared distance between these relocations and their barycentre (see Appendix).

Of the 74 GPS-tracked lions, 55 had an established home range, not all of which overlapped temporally during the study period (another 19 were dispersing individuals not considered in this study). To investigate HR overlap and movement interactions, we focused on the 404 dyads composed of any two individuals that had a temporal overlap in tracking lasting at least 2 months.

#### Overlap in Utilization Distribution

Measuring the extent to which two animals use shared HR areas provides valuable insights into the potential level of interactions between them. Furthermore, considering movement data collected at times when at least one animal of a given dyad is moving through an area that is never used by the other would weaken subsequent statistical tests by including locations for which direct interaction could not feasibly occur. We therefore elected to use a hierarchical approach starting with the computation of HR overlap for each dyad, so as to assess the overall tendency of the two individuals to share space in a static way, before computing movement interaction to assess their tendency to move independently of each other, jointly (i.e. in the vicinity of each other), or to avoid each other when they simultaneously use shared HR sections.

We computed lions' activity utilization distributions (UDs with resting locations filtered out) using the biased random bridge/movement-based kernel density estimation method (Benhamou, 2011; Benhamou & Cornélie, 2010) on a virtual grid made of  $50 \times 50$  m quadrats, and HRs were defined as the areas encompassed within 0.95 UD isopleths (so as to ignore UD tails, which are poorly estimated). Because HRs are not used evenly, shared use of space is best measured as overlap in terms of activity rather than in terms of area (Fieberg & Kochanny, 2005; Millspaugh et al., 2004). A sensible way to compute the overlap  $O_{AB}$  between HRs of animals A and B is provided by Bhattacharyya's (1943) coefficient of their respective UD:  $O_{AB} = \int [u_A(\mathbf{z}) \cdot u_B(\mathbf{z})]^{0.5} d\mathbf{z}$ , where  $u_a(\mathbf{z})$  is the utilization density at location  $\mathbf{z} = (x, y)$  for any animal  $a$ . The coefficient value ranges between 0 (fully disjoint UD) and 1 (identical UD). For any dyad of lions A and B that were tracked simultaneously for at least 2 months, we therefore measured the UD overlap as:

$$O_{AB} \approx \sum_Q [U_A(Q) \cdot U_B(Q)]^{0.5}$$

where  $U_a(Q)$  is the HR-normalized fraction of activity of animal  $a$  in quadrat  $Q$  (whose centre is  $\mathbf{z}_Q$  and area is  $2500 \text{ m}^2$ ), computed as  $U_a(Q) = 2500u_a(\mathbf{z}_Q)/0.95$  if  $u_a(\mathbf{z}_Q)$  is larger than the 0.95 isopleth threshold (i.e. if  $\mathbf{z}_Q$  belongs to the HR) or  $U_a(Q) = 0$  otherwise. In this way, the poorly estimated UD tails (beyond the 0.95 isopleth) are ignored but the sum of  $U_a(Q)$  over all quadrats  $Q$  remains equal to 1. Note that any index based on the simple product sum  $\int u_A(\mathbf{z}) \cdot u_B(\mathbf{z}) d\mathbf{z}$  (Fieberg & Kochanny, 2005) cannot reliably measure the degree of overlapping because its maximum value depends on the UD shapes, but the volume of intersection ( $\int \text{minimum}[u_A(\mathbf{z}), u_B(\mathbf{z})] d\mathbf{z} = 1 - 0.5 \int |u_A(\mathbf{z}) - u_B(\mathbf{z})| d\mathbf{z}$ ; Schmid & Schmidt, 2006) may be used as well. We chose to use the Bhattacharyya's coefficient rather than the volume of intersection to have consistent static and dynamic interaction (see below) approaches. Shared HR sections were determined as the set of quadrats  $Q$  for which  $U_A(Q) > 0$  and  $U_B(Q) > 0$ . We also evaluated the proportions of activity of A and B in their shared HR sections (Fieberg & Kochanny, 2005; Smith & Dobson, 1994) as:

$$P_{A|B} = \sum_Q (U_A(Q) | U_B(Q) > 0) \text{ and } P_{B|A} = \sum_Q (U_B(Q) | U_A(Q) > 0)$$

#### Movement Interaction

To determine whether two individuals tended to move independently of each other, jointly or avoid each other, we considered all locations that were synchronized (recorded within 2 min of each other) in both animals when they moved simultaneously through shared HR sections (i.e. areas within the 0.95 UD isopleths of both animals). Call  $\mathbf{Z}_A(t)$  and  $\mathbf{Z}_B(t)$  the locations of animals A and B at a given time  $t$ , involving a distance  $D_{AB}(t) = \|\mathbf{Z}_A(t) - \mathbf{Z}_B(t)\|$  between them. It can be assumed that the level of potential direct interaction at time  $t$  depends on a reverse (i.e. decreasing) sigmoidal function of the distance  $D_{AB}(t)$ . Indeed, when the two animals are close to, or far away from, each other, the level of potential direct interaction should not be subject to a noticeable change and hence remain high or low, respectively, if the distance is doubled or halved. In contrast, at intermediate, critical distances, small variations in distance should involve large changes in the level of potential direct interaction. We propose to define this level between the animals A and B at time  $t$  as:

$$I_{AB}(t) = \exp\left[-0.5(D_{AB}(t)/\Delta)^2\right]$$

where  $\Delta$  is the critical distance at which the function shows its maximum slope. This index ranges between 0 and 1 ( $>0.88$  for  $D_{AB}(t) < \Delta/2$ ,  $0.61$  for  $D_{AB}(t) = \Delta$ , and  $<0.14$  for  $D_{AB}(t) > 2\Delta$ ). We chose this particular expression for  $I_{AB}(t)$  because it corresponds to the Bhattacharyya coefficient between the 'potential influence domains' of animals A and B,  $I_A(\mathbf{z}, t)$  and  $I_B(\mathbf{z}, t)$ , modelled as circular bivariate Gaussian probability density functions centred on the current animal's location with standard deviation  $\sigma = \Delta/2$ :  $I_{AB}(t) = \int [I_A(\mathbf{z}, t) \cdot I_B(\mathbf{z}, t)]^{0.5} d\mathbf{z}$ , with  $I_a(\mathbf{z}, t) = (2\pi)^{-1} \sigma^{-2} \exp[-0.5(\|\mathbf{z} - \mathbf{Z}_a(t)\|/\sigma)^2]$  for any animal  $a$ . In the present study, we set  $\Delta$  to 200 m. Lions from the same group were often observed within this distance, suggesting that they have to be less than 200 m from each other to maintain social cohesion. We further analysed the data with  $\Delta$  set to 100 and 1000 m so as to check that the results are not too sensitive to the choice of this parameter (see Appendix Table A1).

The null hypothesis that the two animals moved independently of each other can then be tested by considering  $I_{AB}(t)$  for each of the  $n$  synchronized (i.e. recorded at similar times  $t_i$  for  $i = 1$  to  $n$ ) locations lying on any shared HR section. Because of the short delay between relocations (1 h in the present study), classical tests assuming locational independence cannot be used. We designed a test satisfying the constraints imposed by serially correlated relocations. It rests on the computation of all the putative values of the level of potential direct interaction expected for a temporal shift  $k$  ranging between 0 and  $n-1$  (modulo  $n$ , involving a wrapping of the time series) between the two movements:  $J_{AB}(t_i)_k = \exp[-0.5(\|\mathbf{Z}_A(t_i) - \mathbf{Z}_B(t_i+k)\|/\Delta)^2]$  with  $j = i-k$  for  $i > k$  and  $j = n + i - k$  otherwise, for  $i = 1$  to  $i = n$  and for  $k = 0$  to  $k = n-1$ . The actual movement interaction between animals A and B can be defined as the mean value of actual (i.e.  $k = 0$ ) levels,  $M_{AB}(0) = \sum J_{AB}(t_i)_0 / n = \sum J_{AB}(t_i) / n$ , and can be compared to the  $n$  mean values obtained with a shift  $k$ ,  $M_{AB}(k) = \sum J_{AB}(t_i)_k / n$ , for  $k = 0$  to  $k = n-1$ . Randomization is here restricted to movement shifts instead of full mixing to preserve the movement structure. The  $n$  values of  $M_{AB}(k)$  obtained in this way are therefore not independent of each other, but their whole distribution obtained with all possible values of  $k$  corresponds to the distribution expected under the null hypothesis of independent movements with the constraint of preserving the

intramovement serial correlation in relocation for both animals. Under this null hypothesis,  $M_{AB}(k)$  should not depend on  $k$ , and the actual movement interaction  $M_{AB}(0)$  should therefore lie anywhere in the  $M_{AB}(k)$  distribution. In contrast, when the two animals tend to move jointly or to avoid each other, the actual movement interaction  $M_{AB}(0)$  should lie in the left or right tail of the  $M_{AB}(k)$  distribution, respectively. As in any permutation test, the movement interaction test consists in computing the probability  $P = (n_e + 1)/n$  of getting a value equal to or more extreme than the observed value  $M_{AB}(0)$ , where  $n_e$  is the number of these most extreme values. It is worth noting that this method can theoretically deal with time-lagged spatiotemporal coincidences to test whether an animal tended to follow another one with some time lag  $T$  by looking at the  $T$ -lagged synchronized relocations of both individuals and then build up the expected distribution for movement independence using multiple shifts as explained above.

## RESULTS

Mean  $\pm$  SD HR size was  $374 \pm 191 \text{ km}^2$  ( $N = 29$ ) for females and  $524 \pm 357 \text{ km}^2$  ( $N = 26$ ) for males. The median of beeline distances between hourly relocations (after exclusion of distances less than 50 m, assumed to correspond to resting) was  $675 \pm 71 \text{ m}$  in females and  $849 \pm 137 \text{ m}$  in males, and 95% of these distances were less than about 2 km (females) or 3 km (males). Consequently, the movement-based serial correlation in location (i.e. the serial correlation computed from relocations that are at least 50 m away from the previous one so as to filter out periods during which the animal was not moving; see Appendix for details) was very high ( $>0.95$ ) for any individual. This indicates that relocating lions on an hourly basis provided a very reliable representation of their movements at the HR scale and that tests assuming relocation independence cannot be used.

### Overlap in Utilization Distribution

The existence of UD overlap largely depended on the distance between HRs. When the distance between the UD-weighted HR barycentres was above 40 km, most overlaps were very low or null, whereas for distances less than 40 km, only 26% of the female–female dyads ( $N = 58$ ), 11% of the male–male dyads ( $N = 38$ ) and 19% of the female–male dyads ( $N = 107$ ) showed strictly no UD overlap. Within 40 km, the overlap tended to decrease linearly with the interbarycentre distance  $IB$  (female–female dyads  $O_{FF} = 0.5 - 0.0171IB$ ,  $r^2 = 0.70$ ; male–male dyads  $O_{MM} = 0.67 - 0.0181IB$ ,  $r^2 = 0.75$ ; female–male dyads  $O_{FM} = 0.62 - 0.0181IB$ ,  $r^2 = 0.69$ ). For interbarycentre distances lower than 15 km, the overlap was always larger than 0.1, and was higher than 0.5 in 43% of the cases. For distances ranging between 15 and 20 km, UD overlap ranged from 0 to 0.6, and nine of 32 dyads had an overlap lower than 0.1. It seems therefore that neighbouring lions in Hwange National Park should establish their HR centres at least 15–20 km apart to be able to avoid overlap but also that considerable overlap can exist in this range of distances.

### Movement Interactions

For most of the 404 dyads on which we initially focused, there was no or only a marginal UD overlap. We filtered out the dyads for which the UD overlap was smaller than 0.2 and for which there was less than about 100 synchronized relocations within the zone of overlap. Hence, we ultimately tested movement interaction on 52 dyads, including 10 female–female dyads, 10 male–male dyads and 32 male–female dyads (Table 1). For individuals from the same sex, we distinguished dyads of individuals from the same group and dyads of individuals from different groups. For male–female dyads,

we contrasted dyads including the pride male, from dyads including a male occasionally mating with the female, and dyads including an independent male.

Expected values of movement interactions under the null hypothesis of independent movement ( $\sum_k M_{AB}(k)/n$ ) were very low ( $<0.03$  in all cases). This suggests that lions meet very rarely when moving independently of each other in a shared HR section. In this context, actual movement interaction ( $M_{AB}(0)$ ) in the range 0.05–0.1 could lead to rejection of the null hypothesis in favour of a tendency of moving jointly that is statistically but not biologically significant, as it would involve the two animals moving jointly occasionally and independently of each other most of the time. In contrast, animals tending to avoid each other were necessarily characterized by extremely low values of movement interaction. Thus, dyads characterized by a statistically significant rejection of the null hypothesis were considered as composed of animals avoiding each other if the actual movement interaction was statistically lower than the corresponding expected value, but as moving jointly only if the actual movement interaction was larger than 0.1.

### Female–female interactions

For the eight dyads of females from different prides whose UDs showed an overlap larger than 0.2 (Table 1), a member of the dyad spent an activity fraction of  $0.56 \pm 0.19$  (mean  $\pm$  SD) in shared HR sections. No avoidance was detected in the movements of the two females of any dyad of females from different prides (even with  $\Delta = 1000 \text{ m}$ ; Appendix Table A1). The results indicate that, when moving in shared HR sections, the two individuals moved either completely independently or jointly only very occasionally (low movement interaction yet statistically larger than the expected value for independence). For the two dyads of females from the same pride, the UD overlap was larger than 0.7, one member of the dyad spent about 90% of her activity in shared HR sections, and the females moved jointly. These two dyads were composed of related females, either sisters (GUVF1 \* GUVF2; Fig. 1) or mother and daughter (GUVF1 \* GUVbF4). No results were obtained for GUVF2 \* GUVbF4, as there was no temporal overlap in the tracking data for these two females.

### Male–male interactions

Similarly to females, for the seven dyads of males from different coalitions whose UDs showed an overlap larger than 0.2, individuals spent an activity fraction of  $0.55 \pm 0.22$  in shared HR sections (Table 1). In six dyads, males moved independently of each other, and in one dyad (BULM2 \* GUVbM2; Fig. 1), the two males significantly avoided each other while moving in shared HR sections. These two males were from two coalitions that differed greatly in size: BULM2 lived as a single male at that time and stayed consistently 15 km away from the larger coalition of four males of which GUVbM2 was then a member. The former spent only 14% of his activity in shared HR sections, whereas the latter spent 51% there (Table 1). No other male–male dyad corresponded to individuals avoiding each other (even with  $\Delta = 1000 \text{ m}$ ; Appendix Table A1). In the three dyads of males from the same coalition, the males showed a significant tendency to move jointly. Two of these three dyads were composed of related animals, either brothers (MPOM1 \* MPOM4) or a father and son (MPOM3 \* GUVbM2). The third dyad comprised one male (BULM2) formerly in a coalition with his brother before the latter was killed, and who then joined another single unrelated male (BALcM2).

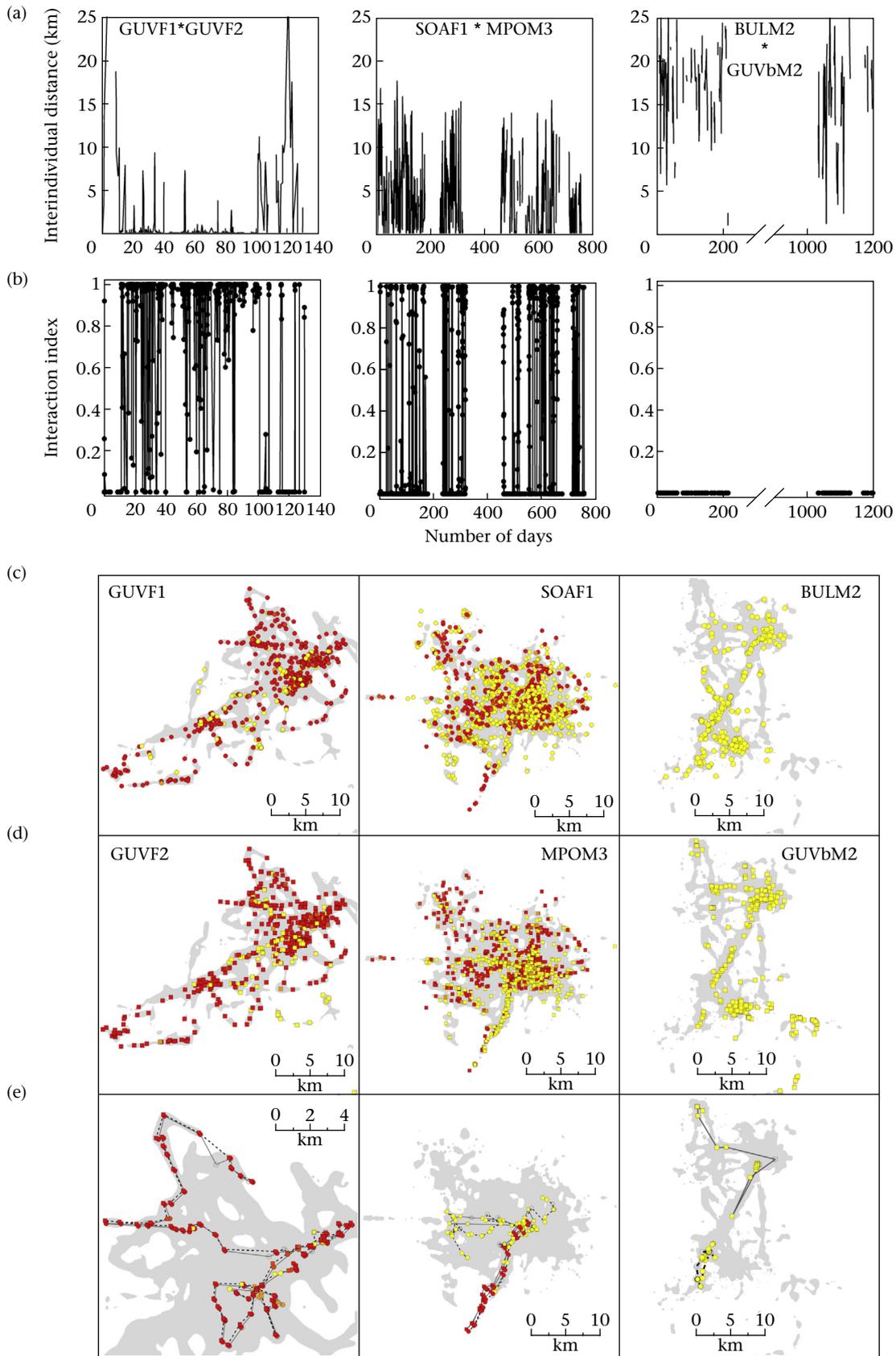
### Female–male interactions

For the 32 female–male dyads whose UDs showed an overlap larger than 0.2 (Table 1), females and males spent an activity

**Table 1**  
Interactions for lion dyads

Individuals 1*2	Home range overlap O	Activity of 1 or 2 in shared HR sections	Synchronized relocation number	Actual movement interaction	Expected movement interaction	$P_1$
<b>Female–female</b>						
From different prides						
NYMaF7*NYMF4	0.29	0.29/0.56	632	0.000	0.002	0.070
SHUF3*SHUF5	0.54	0.42/0.93	159	0.000	0.001	0.101
NYMF4*BALcF2	0.45	0.45/0.72	292	0.008	0.002	0.038
NYMaF7*GUVF1	0.50	0.66/0.51	802	0.008	0.002	0.002
GUVF1*GUVaF2	0.34	0.30/0.63	103	0.010	0.001	0.039
SCOF1*SPIF4	0.35	0.33/0.63	338	0.011	0.001	0.003
SCOF1*BACF2	0.57	0.69/0.73	1149	0.012	0.002	0.001
BACF2*NGAaF1	0.26	0.28/0.75	435	0.013	0.002	0.005
From the same pride						
GUVF1*GUVbF4	<b>0.72</b>	<b>0.69/0.87</b>	<b>98</b>	<b>0.504</b>	<b>0.010</b>	<b>0.010</b>
GUVF1*GUVF2	<b>0.70</b>	<b>0.61/0.93</b>	<b>578</b>	<b>0.773</b>	<b>0.005</b>	<b>0.002</b>
<b>Male–male</b>						
From different coalitions						
BULM2*GUVbM2	<b>0.22</b>	<b>0.14/0.51</b>	<b>294</b>	<b>0.000</b>	<b>0.003</b>	<b>0.037</b>
GUVbM2*BALcM2	0.43	0.51/0.49	206	0.000	0.002	0.228
MPOM3*BULM2	0.53	0.81/0.48	265	0.000	0.001	0.423
PAMM1*MANM2	0.56	0.59/0.75	151	0.000	0.000	0.172
BULM2*SPIaM6	0.26	0.23/0.55	320	0.001	0.001	0.359
BULM2*NEMM1	0.46	0.39/0.75	460	0.001	0.001	0.274
SPIaM6*CHKM1	0.67	0.60/0.93	113	0.001	0.003	0.416
From the same coalition						
BULM2*BALcM2	<b>0.60</b>	<b>0.52/0.92</b>	<b>817</b>	<b>0.666</b>	<b>0.004</b>	<b>0.001</b>
MPOM1*MPOM4	<b>0.70</b>	<b>0.68/0.90</b>	<b>572</b>	<b>0.698</b>	<b>0.004</b>	<b>0.002</b>
MPOM3*GUVbM2	<b>0.44</b>	<b>0.40/0.65</b>	<b>1831</b>	<b>0.717</b>	<b>0.003</b>	<b>0.001</b>
<b>Male–female</b>						
Independent male						
CATF1*BULM2	0.49	0.82/0.42	121	0.000	0.001	0.463
SCOF1*NGOM1	0.46	0.62/0.62	511	0.001	0.002	0.333
BACF2*SCObM1	0.32	0.58/0.40	152	0.013	0.002	0.007
SCOF1*NGOM3	0.48	0.64/0.61	816	0.023	0.002	0.001
SOAF1*GUVbM2	0.41	0.81/0.25	776	0.070	0.006	0.003
Occasional mating						
GUVaF4*SPIaM6	<b>0.40</b>	<b>0.65/0.37</b>	<b>525</b>	<b>0.107</b>	<b>0.002</b>	<b>0.002</b>
SPIF2*MANM2	<b>0.77</b>	<b>0.78/0.90</b>	<b>779</b>	<b>0.112</b>	<b>0.004</b>	<b>0.001</b>
CATF1*BALcM2	<b>0.47</b>	<b>0.65/0.46</b>	<b>734</b>	<b>0.383</b>	<b>0.004</b>	<b>0.001</b>
Pride male						
NYMF4*SPIaM6	0.60	0.86/0.52	528	0.006	0.002	0.025
NYMaF7*MPOM4	0.47	0.49/0.69	99	0.010	0.003	0.091
NYMaF7*MPOM1	0.64	0.73/0.78	300	0.010	0.001	0.003
BACF2*NGOM3	0.40	0.78/0.34	323	0.021	0.002	0.003
NYMF4*SPIaM5	0.60	0.73/0.69	487	0.038	0.004	0.002
SCOF1*SCObM1	0.46	0.67/0.48	138	0.042	0.002	0.007
NEHF1*GOOM1	0.77	0.76/0.93	686	0.049	0.003	0.001
SHUF5*SHAM1	0.59	0.95/0.51	230	0.095	0.003	0.004
SHUF3*SHAM1	<b>0.69</b>	<b>0.76/0.83</b>	<b>1562</b>	<b>0.103</b>	<b>0.002</b>	<b>0.001</b>
NYMaF7*MPOM3	<b>0.48</b>	<b>0.73/0.41</b>	<b>1556</b>	<b>0.134</b>	<b>0.003</b>	<b>0.001</b>
GUVbF4*NEMM1	<b>0.54</b>	<b>0.73/0.51</b>	<b>288</b>	<b>0.150</b>	<b>0.002</b>	<b>0.003</b>
NYMF3*MPOM1	<b>0.47</b>	<b>0.78/0.40</b>	<b>261</b>	<b>0.161</b>	<b>0.009</b>	<b>0.004</b>
BALcF2*SPIaM5	<b>0.67</b>	<b>0.78/0.69</b>	<b>389</b>	<b>0.161</b>	<b>0.011</b>	<b>0.003</b>
BALcF1*SPIaM6	<b>0.73</b>	<b>0.97/0.64</b>	<b>935</b>	<b>0.165</b>	<b>0.003</b>	<b>0.001</b>
GUVaF4*BULM2	<b>0.48</b>	<b>0.87/0.35</b>	<b>1159</b>	<b>0.211</b>	<b>0.002</b>	<b>0.001</b>
NKwAF1*PAMM1	<b>0.23</b>	<b>0.40/0.23</b>	<b>251</b>	<b>0.216</b>	<b>0.005</b>	<b>0.004</b>
SOAF1*MPOM3	<b>0.51</b>	<b>0.95/0.32</b>	<b>1498</b>	<b>0.311</b>	<b>0.005</b>	<b>0.001</b>
SPIF2*PAMM1	<b>0.57</b>	<b>0.68/0.57</b>	<b>1254</b>	<b>0.319</b>	<b>0.005</b>	<b>0.001</b>
LINF1*PAMM1	<b>0.26</b>	<b>0.53/0.23</b>	<b>227</b>	<b>0.326</b>	<b>0.017</b>	<b>0.004</b>
NYMF3*MPOM4	<b>0.51</b>	<b>0.73/0.47</b>	<b>168</b>	<b>0.391</b>	<b>0.013</b>	<b>0.006</b>
SPIbF4*MAGM1	<b>0.24</b>	<b>0.45/0.16</b>	<b>165</b>	<b>0.395</b>	<b>0.024</b>	<b>0.006</b>
GUVF1*MPOM3	<b>0.59</b>	<b>0.79/0.51</b>	<b>2260</b>	<b>0.411</b>	<b>0.002</b>	<b>0.000</b>
BACF2*MAGM1	<b>0.81</b>	<b>0.87/0.81</b>	<b>2112</b>	<b>0.543</b>	<b>0.005</b>	<b>0.000</b>
GUVF2*MPOM3	<b>0.54</b>	<b>0.89/0.40</b>	<b>457</b>	<b>0.733</b>	<b>0.007</b>	<b>0.002</b>

Bold figures indicate dyads for which individuals significantly tended to move jointly at  $P_1 = 0.05$  (one-tailed test) with an actual movement interaction larger than 0.1. Bold italic figures indicate dyads of individuals for which avoidance was detected (i.e. actual movement interaction significantly lower than the expected value at  $P_1 = 0.05$ ; this concerns a single male–male dyad). Note that using  $P_1$  values requires being able to predict in advance that the rejection of the null hypothesis of movement independence should correspond to attraction or avoidance. Otherwise, a two-tailed test should be performed and the correct  $P$  values are  $P_2 = 2P_1$ .



**Figure 1.** Temporal series of interaction index and maps for three dyads of lions: female GUVF1 \* female GUVF2 showing routine joint movements (movement interaction index = 0.77) of two females from the same pride, female SOAF1 \* male MPOM3 showing occasional joint movements between a female and her pride male (movement interaction index = 0.31), and male BULM2 \* male GUVbM2 showing dynamic avoidance between two males from neighbouring coalitions sharing large sections of their home ranges (HR; movement interaction index < 0.0001). (a) Temporal series of the interindividual distance when the two individuals were recorded at synchronous times in shared HR sections. (b)

fraction of  $0.73 \pm 0.14$  and  $0.52 \pm 0.20$ , respectively, in shared HR sections, with no difference between the different types of dyads. When lions were moving in shared HR sections, no avoidance was detected. For dyads involving a female and a male that was not the pride male and was never seen mating with that female, the two individuals moved either completely independently or jointly only very occasionally (low movement interaction yet statistically larger than the expected value for independence). For dyads involving a female and a male that was not the pride male but was occasionally seen mating with that female, the two individuals moved jointly. For dyads involving a female and her pride male, the two individuals moved jointly in 16 of the 24 dyads (see example in Fig. 1).

## DISCUSSION

We developed a novel method to compute spatiotemporal coincidence between two animals based on movement data, referred to as movement interaction, and tested whether its level was significantly different to that expected from independent movements. Although this method may also be applied to time-lagged spatiotemporal occurrences (e.g. to test a specific hypothesis of an individual moving with a given delay along the route followed by another one), in this paper we considered only spatiotemporal coincidence because the specific hypotheses we tested cannot be formulated in terms of time-lagged movement interactions.

Its application to lion movement data allowed us to test several hypotheses related to how interactions may be influenced by sex and social bonds between individuals. Movement interactions between two individuals were computed only for animals that shared HR sections at times when both were moving through them, so as to restrict computations to situations where there was a non-null probability that they would meet. Consequently, movement interaction could reveal dynamic avoidance only when two animals that did not wish to meet were forced by circumstances to move through shared HR sections. In the absence of such a constraint, it is most likely that the two individuals would completely segregate their space use, resulting in nonoverlapping HRs. Our findings suggest that HR overlapping in lions is not at all uncommon, even for adult males from different coalitions that would be expected to be strictly territorial; hence there is a realistic need to understand dynamic interactions.

Females from the same pride and males from the same coalition tended to move jointly. In most cases (the two dyads of females and two of the three dyads of males), animals were related. Females from the same pride benefit from the association to maintain access to the highest-quality habitat (Mosser & Packer, 2009) and for advantage in intergroup contests for territory (McComb et al., 1994), to increase their hunting success (Stander, 1992), better defend their kills against kleptoparasitism by other predators (Cooper, 1991) and to defend cubs against predation and infanticidal males (Grinnell & McComb, 1996). Lionesses in other ecosystems are known to live in fission–fusion social units that allow pride members to form subgroups of differing sizes (Schaller, 1972). In Hwange National Park, pride size was small compared to that in some other ecosystems, and females from the same pride were seen together in 89% of sightings (unpublished data), which is consistent with the high level of movement interaction found between females from the same pride in this study. For males, larger

coalitions are more likely to gain residence in a pride, have longer tenure and gain access to more females than small coalitions (Bertram, 1975; Bygott et al., 1979). Hence, relatives usually disperse and stay together, and unrelated males also sometimes cooperate to secure access to female prides (Grinnell et al., 1995; Packer & Pusey, 1982). In our study, one dyad of males moving jointly comprised unrelated males, which had joined to form a coalition, and were frequently seen together.

Our study demonstrates that, in Hwange National Park, when lions from different social groups do share parts of their HRs, dynamic avoidance is rare. We found only one case of avoidance between two neighbouring males where there was a large asymmetry in the coalition sizes. One explanation may be that avoidance between lions may occur at a larger scale than the critical distance  $\Delta$  considered in this study ( $\Delta = 200$  m). However, even a five-fold increase in critical distance did not provide support for this suggestion (Appendix Table A1). Avoidance between territorial males may be achieved through nonaggressive territorial advertisement to define nonoverlapping HRs, facilitated by scent marking (Schaller, 1972) and roars carrying several kilometres (McComb, Pusey, Packer, & Grinnell, 1993; McComb et al., 1994). Individuals may also behave in the context of existing dominance hierarchies established in previous competitive interactions. Some males may be less hostile towards one another and move independently when in their shared HR area.

Overlapping males and females tended to move jointly in two-thirds of the dyads for which the male was the pride male, and in dyads where the male was occasionally seen mating with the female. Overlapping males and females moved independently of each other when the male was not observed to mate or otherwise consort with the female. No clear pattern based on pride or coalition size was detected to explain the two strategies in dyads involving a pride male, but territorial males can protect their cubs directly by accompanying the pride and fighting rivals, or indirectly by maintaining the security of a territory through patrolling, scent marking and roaring, thus discouraging rivals from entering their territory. These two differing strategies may exist in the study system and influence our results.

Some caveats should be borne in mind when interpreting these findings. First, our analysis tested for dynamic interaction in the overall data set for a given dyad, whereas the tendency to interact may vary with time and place. Our method is able to detect a very weak tendency to move jointly. Consequently a low value of movement interaction index that is nevertheless significantly higher than the value expected for independent movements will indicate a sporadic tendency to move jointly with poor biological significance, except if the times involving joint movements can be related to some covariate. It is therefore particularly useful to look at time series of local interaction values, even in cases of relatively high movement interaction, to understand better the biological significance of the results. For example, the global movement interaction for the mother–daughter dyad GUVF1 \* GUVbF4, which were tracked together for 9 weeks, was 0.50. The time series showed that in fact they usually moved far from each other for the first and the last 5 weeks, but were in close proximity for the second to the fourth week, the movement interaction index then reaching 0.85 for this limited period. As seasonality may influence patterns of associations between individuals (e.g. Stenhouse et al., 2005), an obvious next step would be to explore seasonality in interaction. Additionally, moving jointly

Local interaction index computed from these interindividual distances. (c) Map of the synchronous locations of one individual of the dyad in shared HR sections (grey areas). (d) Map of the synchronous locations of the other individual in shared HR sections. (e) Focus on a 10-day period of simultaneous movements (for the two dyads GUVF1 \* GUVF2 and SOAF1 \* MPOM3, one of the two paths was slightly shifted for visual clarity). Dots and squares are used to differentiate between the two individuals. In the maps, yellow, pale orange, dark orange and red colours indicate four classes of interaction indices: 0–0.25, 0.25–0.50, 0.50–0.75 and 0.75–1, respectively. Empty symbols are used in (e) when a location missed its synchronous counterpart (no local interaction was computed in this case).

in some locations does not necessarily mean mutual attraction. Indeed, locally high interaction values can be obtained when animals move in the vicinity of a common attractor, such as a waterhole, without interacting directly. In such cases, the movement interaction can be computed and tested specifically on a data set restricted to times when both individuals moved within the attractor area. Note, however, that at this finer scale, relocations must be much more frequent than at the HR scale to obtain a high serial correlation. Finally, only relocations when both animals had moved more than a given distance related to GPS noise (50 m in our study) are included in the calculation of the movement interaction index, so as to focus specifically on whether members of a dyad moved together. Consequently, times when they rested together (which have considerable, although potentially different, sociological significance) were filtered out. However, as resting places should not be serially correlated, co-occurrence of resting should easily be investigated using classical statistical tests.

The seminal approaches of Macdonald et al. (1980) and Doncaster (1990) did not take serial correlation in relocation into account. This issue remained unresolved by Shirabe (2006) and Long and Nelson (2013), who recently developed approaches based on comparing vectors of displacement. Additionally, these approaches do not account for the proximity of animals, and thus reflect movement coordination rather than interaction. Our method addresses more directly the issue of movement interaction by using successive distances between individuals when moving. An approach combining both distance between individuals and direction of movements is necessary to address questions of asymmetrical movement interactions (e.g. predators and prey). A purely descriptive approach of this type was made by Pays, Benhamou, Helder, and Gerard (2007) to study the dynamics of fusion–fission in roe deer, *Capreolus capreolus*, but a reliable inferential framework is still missing. As extensive GPS data sets are becoming widely available, the study of animal interaction in space could benefit from a stronger methodological framework, similar to that currently being developed in the study of habitat selection (Hooten, Hanks, Johnson, & Alldredge, 2013).

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## APPENDIX: SERIAL CORRELATION IN LOCATION

Consider a time series of locations on the plane  $\mathbf{z} = (x, y)$ . Call  $V_x$  the marginal variance on the  $x$  axis, and  $C_x$  the marginal covariance between successively recorded locations on this axis, and similarly

$V_y$  and  $C_y$  for the y axis. The serial correlations between successive locations are therefore expressed in terms of x and y coordinates, respectively, as  $r_x = C_x/V_x$  and  $r_y = C_y/V_y$ . The serial correlation in location can be expressed as  $r_z = (C_x + C_y)/(V_x + V_y)$ . Note that this expression of  $r_z$  corresponds to the mean of  $r_x$  and  $r_y$  weighted by their respective variances, so as to give more weight to the axis that accounts for the largest part of the total variance and to obtain a value of  $r_z$  that does not depend on the arbitrary orientations of x and y axes. Call  $V_{\Delta x} = 2(V_x - C_x)$  and  $V_{\Delta y} = 2(V_y - C_y)$  the variances of differences in coordinates x and y, respectively, between any two successive relocations. As the marginal variance sum  $V_x + V_y$  corresponds to the mean squared distance between locations  $\mathbf{z}$  and their barycentre,  $E(D_c^2)$ , and the difference variance sum  $V_{\Delta x} + V_{\Delta y}$  corresponds to the mean squared distance between successive

locations,  $E(D_s^2)$ , the serial correlation in location can be computed as:  $r_z = 1 - 0.5[V_{\Delta x} + V_{\Delta y}]/[V_x + V_y] = 1 - 0.5 E(D_s^2)/E(D_c^2)$ . The value of  $r_z$  should be close to 0 when relocations correspond to a set of points drawn independently from each other from the UD, and will tend to reach 1 when the distances travelled between successive relocations are negligible with respect to the HR size. When focusing on movement, it is preferable, before computing the serial correlation in this way, to filter out locations that are at less than  $L_{min}$  apart, a threshold distance set to 50 m in the present study, so as to obtain a movement-based serial correlation in location. Note that this correlation is necessarily lower than the global value which includes locations not involved in movement, as the shortest distances between successive relocations ( $D_s < L_{min}$ ), which are not involved in movement, have been removed.

**Table A1**  
Movement interactions for lion dyads

Individuals 1*2	$\Delta = 100$ m			$\Delta = 1000$ m		
	Actual movement interaction	Expected movement interaction	$P_1$	Actual movement interaction	Expected movement interaction	$P_1$
<b>Female–female</b>						
From different prides						
NYMaF7*NYMF4	0.000	0.001	0.074	0.019	0.022	0.392
SHUF3*SHUF5	0.000	0.000	0.088	0.016	0.024	0.365
NYMF4*BALcF2	0.001	0.001	0.288	0.062	0.034	0.007
NYMaF7*GUVF1	0.004	0.001	0.004	0.043	0.029	0.123
GUVF1*GUVaF2	0.007	0.001	0.029	0.045	0.023	0.136
SCOF1*SPIF4	0.007	0.000	0.003	0.045	0.020	0.003
SCOF1*BACF2	0.008	0.001	0.001	0.044	0.040	0.026
BACF2*NGAaF1	0.007	0.001	0.002	0.074	0.033	0.002
From the same pride						
GUVF1*GUVbF4	<b>0.453</b>	<b>0.006</b>	<b>0.010</b>	<b>0.572</b>	<b>0.033</b>	<b>0.010</b>
GUVF1*GUVF2	<b>0.700</b>	<b>0.003</b>	<b>0.002</b>	<b>0.852</b>	<b>0.049</b>	<b>0.002</b>
<b>Male–male</b>						
From different coalitions						
BULM2*GUVbM2	<b>0.000</b>	<b>0.001</b>	<b>0.037</b>	<b>0.006</b>	<b>0.045</b>	<b>0.034</b>
GUVbM2*BALcM2	0.000	0.000	0.233	0.006	0.017	0.141
MPOM3*BULM2	0.000	0.000	0.423	0.005	0.007	0.268
PAMM1*MANM2	0.000	0.000	0.166	0.021	0.006	0.013
BULM2*SPIaM6	0.000	0.000	0.322	0.019	0.012	0.013
BULM2*NEMM1	0.000	0.000	0.252	0.008	0.001	0.298
SPIaM6*CHKM1	0.000	0.001	0.398	0.035	0.035	0.496
From the same coalition						
BULM2*BALcM2	<b>0.590</b>	<b>0.002</b>	<b>0.001</b>	<b>0.795</b>	<b>0.035</b>	<b>0.001</b>
MPOM1*MPOM4	<b>0.611</b>	<b>0.002</b>	<b>0.002</b>	<b>0.817</b>	<b>0.022</b>	<b>0.002</b>
MPOM3*GUVbM2	<b>0.647</b>	<b>0.001</b>	<b>0.001</b>	<b>0.808</b>	<b>0.038</b>	<b>0.001</b>
<b>Male–female</b>						
Independent male						
CATF1*BULM2	0.000	0.000	0.463	0.012	0.021	0.036
SCOF1*NGOM1	0.000	0.001	0.350	0.020	0.022	0.456
BACF2*SCObM1	0.010	0.001	0.007	0.042	0.024	0.072
SCOF1*NGOM3	0.017	0.001	0.001	0.059	0.020	0.001
SOAF1*GUVbM2	0.045	0.002	0.001	<b>0.204</b>	<b>0.098</b>	<b>0.004</b>
Occasional mating						
GUVaF4*SPIaM6	0.099	0.001	0.002	<b>0.132</b>	<b>0.027</b>	<b>0.002</b>
SPIF2*MANM2	0.085	0.001	0.001	<b>0.211</b>	<b>0.049</b>	<b>0.001</b>
CATF1*BALcM2	<b>0.350</b>	<b>0.002</b>	<b>0.001</b>	<b>0.447</b>	<b>0.025</b>	<b>0.001</b>
Pride male						
NYMF4*SPIaM6	0.003	0.001	0.017	0.032	0.032	0.500
NYMaF7*MPOM4	0.003	0.001	0.091	0.023	0.040	0.222
NYMaF7*MPOM1	0.006	0.000	0.010	0.032	0.014	0.003
BACF2*NGOM3	0.014	0.001	0.003	0.066	0.026	0.009
NYMF4*SPIaM5	0.028	0.001	0.002	<b>0.118</b>	<b>0.050</b>	<b>0.004</b>
SCOF1*SCObM1	0.025	0.001	0.007	0.088	0.025	0.007
NEHF1*GOOM1	0.034	0.009	0.001	<b>0.120</b>	<b>0.029</b>	<b>0.001</b>
SHUF5*SHAM1	0.076	0.001	0.004	<b>0.177</b>	<b>0.029</b>	<b>0.004</b>
SHUF3*SHAM1	0.090	0.001	0.001	<b>0.144</b>	<b>0.020</b>	<b>0.001</b>
NYMaF7*MPOM3	<b>0.109</b>	<b>0.001</b>	<b>0.001</b>	<b>0.204</b>	<b>0.033</b>	<b>0.001</b>

(continued on next page)

**Table A1** (continued)

Individuals 1*2	$\Delta = 100$ m			$\Delta = 1000$ m		
	Actual movement interaction	Expected movement interaction	$P_1$	Actual movement interaction	Expected movement interaction	$P_1$
GUVbF4*NEMM1	<b>0.128</b>	<b>0.001</b>	<b>0.003</b>	<b>0.214</b>	<b>0.022</b>	<b>0.003</b>
NYMF3*MPOM1	<b>0.111</b>	<b>0.004</b>	<b>0.004</b>	<b>0.283</b>	<b>0.065</b>	<b>0.004</b>
BALcF2*SPIaM5	<b>0.127</b>	<b>0.004</b>	<b>0.003</b>	<b>0.322</b>	<b>0.082</b>	<b>0.003</b>
BALcF1*SPIaM6	<b>0.139</b>	<b>0.001</b>	<b>0.001</b>	<b>0.252</b>	<b>0.038</b>	<b>0.001</b>
GUVaF4*BULM2	<b>0.177</b>	<b>0.001</b>	<b>0.001</b>	<b>0.287</b>	<b>0.027</b>	<b>0.001</b>
NKWaF1*PAMM1	<b>0.175</b>	<b>0.003</b>	<b>0.004</b>	<b>0.309</b>	<b>0.039</b>	<b>0.004</b>
SOAF1*MPOM3	<b>0.259</b>	<b>0.002</b>	<b>0.001</b>	<b>0.423</b>	<b>0.077</b>	<b>0.001</b>
SPIF2*PAMM1	<b>0.247</b>	<b>0.002</b>	<b>0.001</b>	<b>0.465</b>	<b>0.052</b>	<b>0.001</b>
LINF1*PAMM1	<b>0.303</b>	<b>0.006</b>	<b>0.004</b>	<b>0.399</b>	<b>0.154</b>	<b>0.004</b>
NYMF3*MPOM4	<b>0.372</b>	<b>0.006</b>	<b>0.006</b>	<b>0.454</b>	<b>0.075</b>	<b>0.006</b>
SPIbF4*MAGM1	<b>0.359</b>	<b>0.009</b>	<b>0.006</b>	<b>0.495</b>	<b>0.152</b>	<b>0.006</b>
GUVF1*MPOM3	<b>0.357</b>	<b>0.001</b>	<b>0.000</b>	<b>0.495</b>	<b>0.026</b>	<b>0.000</b>
BACF2*MAGM1	<b>0.436</b>	<b>0.002</b>	<b>0.000</b>	<b>0.698</b>	<b>0.066</b>	<b>0.000</b>
GUVF2*MPOM3	<b>0.635</b>	<b>0.004</b>	<b>0.002</b>	<b>0.834</b>	<b>0.056</b>	<b>0.002</b>

Bold italic figures indicate dyads for which individuals significantly tended to move jointly at  $P = 0.05$  with an actual movement interaction larger than 0.1. Bold italic figures indicate dyads of individuals for which avoidance was detected (i.e. actual movement interaction significantly lower than the expected value at  $P_1 = 0.05$ ; concerns a single male–male dyad and only for a one-tailed test). Note that  $P_1$  values correspond to a one-tailed test. For a two-tailed test, the correct  $P$  values are  $P_2 = 2P_1$ .