RESEARCH ARTICLE

Exploring the utility of movement parameters to make inferences about dynamic interactions in moving objects

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Abstract

"Dynamic interactions" in animals are inter-individual interactions defined by proximity in both space and time and are important for understanding spatial behaviors such as mating, predation, and territoriality, as well as phenomena such as disease spread. Dynamic interactions are typically quantified by analyzing GPS locations as *points* or by examining the *paths* that are inferred as trajectories between subsequent points. Current path-based approaches measure movement similarity in terms of step length and azimuth, which is associated with a relatively narrow conceptualization of interaction (e.g., traveling together). This research explores how other, more complex movement parameters may differ with proximity to another individual; if proximity-related movement differences can be detected, this information can be used to generate new dynamic interaction metrics. This approach was first tested using simulated movement data with known interaction properties, then applied to 10 blackbacked jackal (*Canis mesomelus*) dyads in Etosha National Park, Namibia. In general, an individual's movement was often different when it was close to another individual, suggesting that dynamic interaction can potentially be inferred by analyzing movement parameters. Movement parameters that describe directional persistence, speed, and change performed better, but there was considerable variation across movement parameters, proximity, and individuals.

1 | INTRODUCTION

While moving objects that interact can range from micro-scale (e.g., gas particles) to macro-scale (e.g., weather systems), the two most frequently studied types of objects are related to human and animal movement (see Miller, Dodge, Miller, & Bohrer, 2019 for an overview). Understanding the nature, frequency, and duration of interactions between and among these types of moving objects is necessary to better understand spatial/social processes ranging from communication to mating to disease spread. The ability to quantify dynamic interactions based on location data has been the focus of recent attention on the importance of contact tracing in the context of contagious disease spread. Behaviors and processes related to interactions can occur across many different types of moving objects, scales, and contexts, but they are generally difficult to measure for reasons such as semantic uncertainty (what is an "interaction"?) and analytical tractability (how should interactions be quantified and subsequently interpreted?). In spite of the importance of studying interactions, they have not been a dominant research focus in the main sub-disciplines within which movement data are analysed: GIScience and movement ecology.

1.1 | Measuring dynamic interactions

Measuring interactions in animals has progressed from the use of "static" or purely spatial metrics (e.g., relative amount of overlapping home ranges) to "dynamic" interaction metrics that incorporate temporal information additionally (Doncaster, 1990). Dynamic interactions are more appropriate for studying interactions stemming from social behaviors related to attraction or avoidance. The basic unit for studying animal interactions is two individuals, or a dyad, although social network analysis may be more appropriate for studying animal species with strong group dynamics—such as primates (Krause, Lusseau, & James, 2009).

Dynamic interactions in animals can be defined as direct contact, sharing resources such as waterholes or food, stalking/chasing, or even mere awareness of each other. Most studies focused on analyzing dynamic interactions are primarily concerned with positive interaction (as in the examples previously described), and negative interaction such as avoidance may be more problematic to identify and subsequently quantify. While there have been impressive technological advancements in the ability to capture or record ancillary information on interactions, such as animal-borne video cameras (Kays, Crofoot, Jetz, & Wikelski, 2015; Krause et al., 2013), this equipment is not widely available or broadly applicable, therefore dynamic interactions are typically inferred by equating social association/interaction with spatiotemporal association (the "gambit of the group"; Whitehead & Dufault, 1999). In addition to the uncertainty introduced by this assumption, studies that compared dynamic interaction metrics have shown a disconcerting lack of congruence in the ability to detect and measure interactions (Long & Nelson, 2012, 2013; Long, Nelson, Webb, & Gee, 2014; Miller, 2012, 2015). Interactions are difficult and sometimes impossible to observe in reality, therefore simulated movement data with known interaction properties have been used to clarify some of the differences among dynamic interaction metrics (Joo, Etienne, Bez, & Mahévas, 2018; Long, 2015; Long et al., 2014; Long, Webb, Nelson, & Gee, 2015; Miller, 2015), but more applications comparing dynamic interactions in real animal movement data are needed.

1.2 | Point- and path-based dynamic interaction metrics

The two main approaches to measuring dynamic interactions between individuals in a dyad involve treating the locations as discrete points or focusing on the paths that are inferred as trajectories between consecutive points; each of these approaches has attendant strengths and weaknesses. For point-based metrics, interaction is defined either as a function of distance (e.g., the mean distance between individuals or the number of times a pair is within a distance threshold) or as the relative frequency with which two individuals are recorded in some shared area

(e.g., the overlapping portion of their home range) within a temporal threshold. Consequently, these metrics rely on subjective parameters such as home range estimation or a distance threshold. The former parameter has been the subject of extensive debate for decades (see Powell, 2012 for an overview of a recent special issue on home range estimation), while the latter parameter should be determined by the animal's movement properties and the type of interaction of interest (but in practice is also influenced by the spatial and temporal resolution of the location data). A temporal threshold is also needed, but this is more often a direct function of the temporal resolution.

Path-based interaction metrics use movement trajectories as the basic unit of analysis and measure similarity or coherence in derived movement parameters such as direction and step length for two individuals. While individuals are unlikely to move in straight lines from one recorded location to the next (with movement uncertainty increasing as the time between fixes increases), movement parameters are estimated based on this assumption. Although the derivation of movement parameters is sensitive to temporal resolution (Laube & Purves, 2011), path-based metrics involve fewer subjective decisions and may be more reflective of interaction behaviors compared to point-based metrics, especially as the temporal resolution of movement data increases. However, since existing path-based metrics measure the correlation of movement parameters for two individuals at the same time, they can only be used to detect a narrow set of interaction behaviors (e.g., positive interaction must be symmetric). Path metrics also do not consider the distance between the two individuals or their location relative to designated spaces such as home range overlap, therefore proximity is either implicit in the study (e.g., football players) or is addressed separately.

While few studies have compared multiple dynamic interaction metrics, when both point- and path-based metrics were used they were generally found to be complementary rather than redundant (Joo et al., 2018; Long, 2015; Long et al., 2014). Nevertheless, there have been few attempts to combine point- and path-based metrics in order to harness their respective strengths while reducing their respective limitations (but see Konzack et al., 2017; Zhang, Beernaerts, & Van de Weghe, 2018).

As noted previously, while derived movement parameters may more accurately reflect movement behaviors associated with interactions, the current path-based metrics in which they are used to analyze interactions are limited in their ability to robustly detect dynamic interactions. The correlation between two individuals' step length or azimuth irrespective of proximity is the basis of the most commonly used path-based dynamic interaction metrics (Long & Nelson, 2012; Shirabe, 2006). Other approaches that measure the relative motion of individuals in groups incorporate proximity as well as movement parameters that may be more characteristic of interactions such as increased speed or change in direction (Andersson, Gudmundsson, Laube, & Wolle, 2008; Laube, Imfeld, & Weibel, 2005; Merki & Laube, 2012; Zhang et al., 2018). However, these frameworks require interaction patterns such as "pursuit and escape" to be algorithmically defined a priori, and are therefore not as useful for studies in which this information is not well known.

Potential sources of uncertainty in the process of measuring interactions from location points are illustrated in Figure 1. Figure 1a shows three simultaneous (occurring at the same time) locations for two individuals, a and β, and a bar showing the threshold distance (dc) within which an interaction would be considered to occur. While none of the simultaneous location pairs was within the distance criterion, the hypothetical crossed paths of a and β in Figure 1b show that the two individuals could have been close but not empirically detected, an example of "step bias" (Creel, Winnie, & Christianson, 2013). The dashed green line in Figure 1b represents the movement of an uncollared individual γ, with whom both a and β are close enough to interact but no empirical evidence will exist, an example of "scatter bias" (Creel et al., 2013). Both of these sources of bias or uncertainty result in underestimated interactions, but point-based metrics are more susceptible to step bias than path-based metrics. Path-based metrics measure similarity in simultaneous movement parameters, and this may not characterize many types of interaction; for example, the step length and azimuth of $a1$ are not similar to those parameters for $\beta1$ (nor are $a2$ and $\beta2$ or $a3$ and $\beta3$ similar), so a path-based dynamic interaction metric would likely show no indication of interaction.

Path-based dynamic interaction metrics have not extended to more sophisticated movement parameters that might be more sensitive to behavioral changes, as well as more robust to varying temporal resolution of fixes being
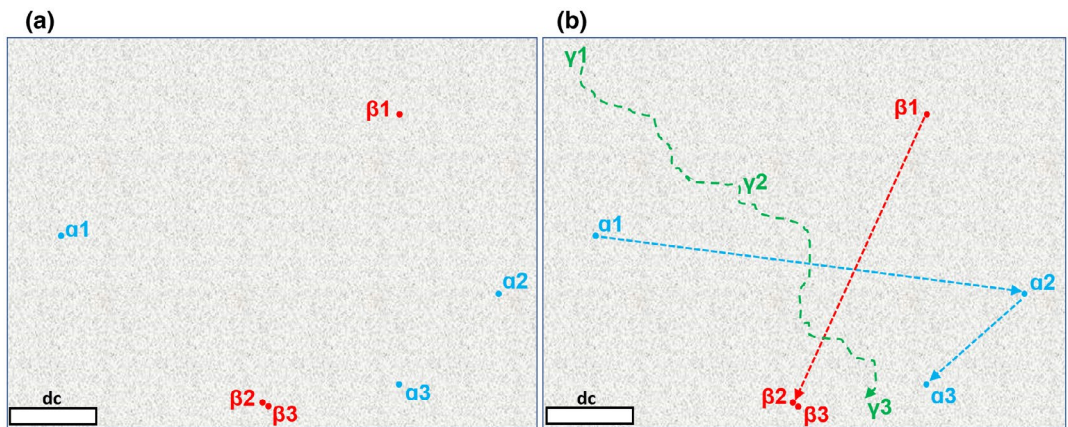
FIGURE 1 Potential sources of uncertainty for measuring dynamic interactions. (a) Map of three sequential locations for two individuals, a and β. (b) Inferred trajectories for a and β as well as a third individual, γ, whose location was not tracked. Using the distance criterion (dc), no interactions between a and β would be detected, but they could have interacted when they crossed paths (step bias) and either individual could have interacted with γ (scatter bias)

used. In a paper that introduced behavioral change point analysis, a type of path segmentation, Gurarie, Andrews, and Laidre (2009) noted the importance of describing three primary descriptive features of movement—speed, directional persistence, and variability/change—for identifying behavior-related movement. Interactions between individuals can be associated with many different behaviors occurring at various spatial and temporal scales, which makes measuring interactions from movement parameters more challenging than measuring individual behavior. Rather than attempting to identify interaction behaviors from movement parameters, the objective of this research was to test whether an individual's movement when it was near another individual was distinguishable from movement when it was not close.

This research addressed the general question of whether movement parameters can be used to measure interaction-related differences in dyadic movement. The specific components of this general question tested here were:

- Are there measurable differences in movement parameters for an individual when it is close to another individual?
- How do these differences vary across movement parameters, individuals, and proximity to other individuals?
- Which movement parameters differ the most with respect to proximity?

These questions were explored using simulated movement data as well as GPS data of black-backed jackals (*Canis mesomelas*) in Etosha National Park (Borchering, Bellan, Flynn, Pulliam, & McKinley, 2017). Black-backed jackals are monogamous and territorial, and their social structure is comprised of solitary residents, transients, and pair/pack members. The individuals whose locations were tracked in this dataset showed a range of different spatial interactions and make an excellent case study for these methods.

2 | DATA

2.1 | Simulated movement data

The ability to identify interactive movement was first tested using simulated data with known parameters. Long et al. (2015) simulated movement data to represent three types of interaction commonly observed in animals: grouping, leading/following, and shared resource use. The leader/follower simulation, illustrated in Figure 2, was
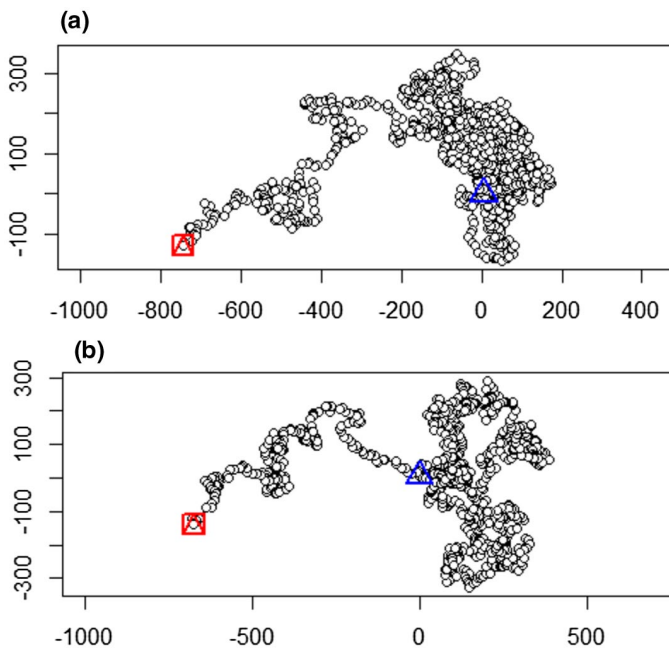
FIGURE 2 (a) Leader trajectory originating at (5,0) and simulated as *n* = 1,000 locations; *h* (step-length scaling factor) = 10; *r* and *ρ* (correlation concentration) = 0.4. (b) Follower trajectory originating at (0,5) simulated with additional bias parameters: *b* (bias strength) = 20; *c* (distance decay effect on bias) = −0.8. Trajectories start at the blue triangle and end at the red square

used here so that each dyad was comprised of an individual moving independently (leader) and an individual with dependent movement (follower). The follower was biased toward the location of the leader, the effect of which varied inversely with distance, and in order to mimic the sporadic nature of real leader–follower movement, the transition probability was defined so that approximately 60% of the follower's locations were biased and the remainder were simulated with a correlated random walk independent of the leader (see Long et al., 2015 for details).

Twenty-five simulated leader–follower dyads that met the following criteria were used in the analysis: mean distance between simultaneous observations (proximity) > 150 and at least 10 "contacts" (number of times a pair was within a temporal and distance threshold) within a distance of 10 (Table 1). Locations for the two individuals in a dyad are considered to be "simultaneous" when they occur at the same time (or within a temporal threshold). The simulated data occurred at one-unit intervals, therefore all 1,000 fixes were simultaneous. These criteria were used to ensure that there were a sufficient number of observations to test for differences and to ensure that pairs were reasonably spread out.

2.2 | Black-backed jackal data

To explore whether differences in proximity-related movement could be detected in "real" movement data, I used a dataset containing approximately hourly GPS locations for black-backed jackals (*C. mesomelas*) in Etosha National Park, Namibia in 2009–2010 (Belland & Getz, 2017; Borchering et al., 2017). I analyzed 10 dyads comprised of 10 different individuals for which there were at least three contacts within 100 m of each other (Figure 3). Individuals were identified as "cm" followed by a unique number; however, no information on their age or sex was provided.

TABLE 1 Descriptions of the simulated leader–follower dyads. The mean proximity or distance apart of the two individuals as well as the number of simultaneous contacts at two distance thresholds, 10 and 250, are given

Sim LF dyad	Mean proximity	No. contacts (10)	No. contacts (250)
1	323	14	619
2	208	38	642
3	304	12	442
4	225	30	581
5	254	25	436
6	477	15	248
7	165	45	701
8	414	12	383
9	303	19	609
10	428	11	326
11	203	29	666
12	467	13	303
13	437	13	392
14	328	14	529
15	557	14	432
16	316	22	537
17	312	19	614
18	203	17	616
19	192	33	671
20	309	19	541
21	242	15	496
22	184	17	781
23	266	19	557
24	194	18	713
25	277	25	494

Table 2 lists the dyads and the constituent individuals, the number of simultaneous fixes, the mean distance between them, and the number of times the two individuals were within a proximity distance threshold (see Section 3). The temporal threshold used to define simultaneous fixes was 1,800 s (most fixes were hourly, but the recorded time usually varied by a few minutes).

3 | METHODS

3.1 | Proximity distances

Movement parameters for each individual in a dyad were divided into two sets, "contacts" and "other," based on proximity distance thresholds, and statistical tests were used to determine whether they were significantly different. For the simulated data, distances of 10 and 250 were used; the distance of 250 should represent a diminished level of interaction but because the bias effect is somewhat stochastic and this threshold includes all simultaneous fixes for which proximity ranges from 0 to 250, it does not represent the distance at which no interaction is
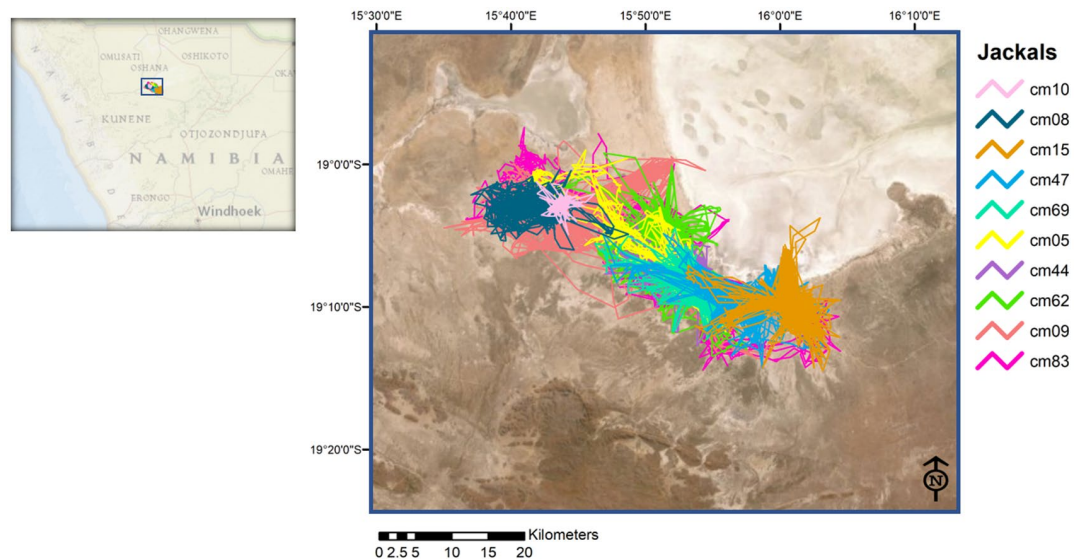
FIGURE 3 Trajectories of the 10 black-backed jackals in Etosha National Park in Northern Namibia

TABLE 2 Description of jackal dyads used. Number of fixes (GPS locations with duplicates removed) for each jackal individual; simultaneous fixes are the number of GPS locations for which both individuals were recorded at the same time (within 1,800 s); the number of contacts show the number of simultaneous fixes at which the individuals were within the specified distance

Dyad	No. simultaneous/ mean proximity (m)	No. contacts (100 m)	No. contacts (500 m)	No. contacts (1,000 m)	No. contacts (5,000–5,500 m)
cm05 and cm44	427/6,903	5	9	11	11
cm08 and cm09	3,269/2,932	169	616	1,103	120
cm08 and cm10	1,220/4,702	3	10	37	51
cm09 and cm10	1,168/2,156	3	22	76	5
cm09 and cm83	3,806/18,971	3	9	28	49
cm15 and cm47	8,431/4,353	37	103	189	387
cm44 and cm69	3,542/3,024	7	64	366	65
cm44 and cm83	3,882/8,760	30	47	80	193
cm47 and cm83	3,227/15,954	3	14	21	26
cm62 and cm83	5,503/8,526	39	146	356	153

expected. As each dyad was comprised of a leader and a follower, the results for each of the leaders represented the null expectation: "contact" movement parameters would not differ from "other" movement parameters irrespective of the proximity used to define them. The alternative hypothesis tested was that the "contact" movement parameters for the follower differed from the "other" parameters, and the difference would be greater for the shorter distance threshold.

For the jackal data, three distance thresholds were used to represent "contact" or hypothetical interaction that occurs at different scales (e.g., direct contact or shared fine-scaled resources such as carcasses; and interaction such as awareness, territoriality, or shared coarse-scaled resources such as watering holes): 100, 500, and 1,000 m. In addition to detecting different types of interaction, using a range of distances helps account for the

hourly temporal resolution and potential missed contacts that are not detected empirically due to "step bias" (Creel et al., 2013). For example, 1,000 m would not be considered a distance within which meaningful interaction between jackals might occur, but is used here to help address these sources of measurement uncertainty.

A fourth distance threshold was used here as a null expectation; "contacts" were defined as fixes occurring with proximity between 5,000 and 5,500 m, while "other" were fixes that occurred at proximity distances greater than 5,500 m. Movement parameters for these two sets would not be expected to have significant proximity-based differences; however, in practice they may indicate different movement behaviors that coincided with those distances or "scatter bias" (Creel et al., 2013), or interaction with uncollared individuals.

3.2 | Movement parameters

The movement parameters tested here were selected because they have been used previously in movement ecology studies and can be calculated locally for each step (excepting relative angle and its derivatives for the first and last step and absolute angle, speed, and its derivatives for the last step). Ten movement parameters were tested here: seven describe an individual's movement and three are indices that measure similarity of movement of two individuals in a dyad. The parameters, their range of values for the 10 jackal individuals, and their capability to represent speed, directional persistence, and variability/change are listed in Table 3 and briefly described below.

The two measures of direction used here were *absolute angle* and *relative angle*, and they were calculated using AdehabitatLT (Calenge, 2006). Absolute angle measures the azimuth relative to the *x* direction and may be related to interactions when they involve movement toward or away from fixed resources (waterholes, dens, roads, or paths). Relative angle measures the turning angle or change in direction. *Speed* is redundant with *step length* when the fixes are at uniform time intervals, but is more robust than step length when intervals are variable. *Persistence index* (PI) is the cosine of the relative angle and measures how direct movement is; values close to 1 represent the most direct movement (i.e., small turning angles), while values close to 0 show uncorrelated movement (i.e., turning angles close to 90°). PI approaching −1 would indicate oscillating movements (i.e., turning angles close to 180°) (Laidre et al., 2013). *Persistence velocity* (Vp) is the product of speed and PI, and therefore the interpretation for PI remains roughly the same, except that higher speed translates into more direct movements and high speed with oscillating direction results in smaller negative values (and is less likely to occur) (Gurarie et al., 2009, 2016). *Turning velocity* (Vt) is the product of speed and sine of the relative angle, so can be interpreted as the tendency to move in a perpendicular direction (Gurarie et al., 2009).

Finally, the three path-based dynamic interaction metrics were calculated for each simultaneous fix for each dyad (as opposed to the global mean of each index in Tables 2 and 3) using WildlifeDI (Long et al., 2014). DI.theta measures the correlation between the individuals' absolute angle or azimuth; DI.dist measures the correlation in step lengths; and the product of those two values describes correlation in both direction and distance (DI). For all three of these metrics, a value close to 1 indicates that the direction, distance, or both are very similar, respectively. The lowest value for DI and DI.theta is −1, indicating negative correlation (e.g., movement in opposite directions), while the lowest value for DI.dist is 0, indicating that the two individuals had extremely different step lengths.

3.3 | Statistical tests for differences in movement parameters

Each distance threshold resulted in two sets of fixes for each individual in a dyad (the DI metrics were the same for each individual in a dyad): "contacts," which included the step before, during, and after a contact; and "other" fixes, which included all of the other fixes. To test the hypothesis that an individual's movement differs when it is near (and presumably interacting with) another individual, the following nonparametric tests of difference were used: Watson's U^2 statistic (for absolute and relative angle), the Kolmogorov–Smirnov statistic (speed, step length,

TABLE 3 Description of movement parameters (with range of values for the jackals) tested in this study

Parameter	Calculation	Reference	Range of values (units)	Incorporate change, direction, speed?
Absolute angle (abs.angle)	Azimuth between x direction and steps i and i + 1	Calenge (2006)	$-\pi$ to π (rad)	Direction
Relative angle (rel.angle)	Change of direction from i − 1 to i to i + 1	Calenge (2006)	$-\pi$ to π (rad)	Change, direction
Step length	Distance traveled between fixes	Calenge (2006)	0 to 15,612 (m)	_Speed (indirectly)_
Speed	Distance traveled between fixes divided by time between fixes	Gurarie et al. (2016)	0–4.2 (m/s)	Speed
Persistence index (PI)	Cos(relative angle)	Laidre et al. (2013)	−1 to 1 (n/a)	Change, direction
Persistence velocity (Vp)	Speed × cos(relative angle)	Gurarie et al. (2016)	−3.8 to 3.4 (n/a)	Change, direction, speed
Turning velocity (Vt)	Speed × sin(relative angle)	Gurarie et al. (2016)	−3.4 to 4.1 (n/a)	Change, direction, speed
Dynamic interaction (DI)	(DI.theta) × (DI.distance)	Long and Nelson (2013)	−1 to 1 (n/a)	Direction, _speed_ (indirectly through step length)
Dynamic interaction for direction (DI.theta)	Cos(absolute angle for individual 1 at i − absolute angle for individual 2 at i)	Long and Nelson (2013)	−1 to 1 (n/a)	Direction
Dynamic interaction for displacement (DI.dist)	1 − ((absolute value of difference between step lengths for two individuals at i)/(sum of the step lengths for two individuals at i))	Long and Nelson (2013)	0 to 1 (n/a)	_Speed_ (indirectly through step length)

PI, Vp, and Vt), and the Wilcoxon rank sum test (DI, DI.theta, and DI.dist). A bootstrap analysis (k = 1,000) was used to determine the significance of each statistic, so that the size of "contact" and "other" remained constant across dyad–distance combinations. As this research was aimed at exploring whether there were differences in movement associated with proximity, there were no a priori assumptions about the nature of the differences (e.g., that an individual will move faster or more directly when another individual is close), so two-sided tests were used for the Watson and Kolmogorov–Smirnov tests. The three DI metrics are indices that measure correlation, so a one-sided test, the Wilcoxon rank sum test, was used instead to determine whether movement correlation was greater when the individuals were close. This test compares all possible pair combinations from each dataset and the resulting statistic, W, is the number of times an observation from "other" was greater than "contacts" (out of number m × number of others). A similar bootstrap permutation was used to compare the observed W statistic to 1,000 permutations, and the (pseudo) p-value was recorded. Figure 4 gives an overview of these methods. All analyses were done in R (R Core Team, 2020).

4 | RESULTS

4.1 | Movement parameter comparison—Simulated data

The bootstrap test was used to determine statistical significance at a probability level of 0.05 (i.e., differences were considered significant if the observed statistic was greater [DI metrics] or less than at least 950 of the permuted values). The proportion of times the bootstrap test was significant is shown for the simulated trajectories
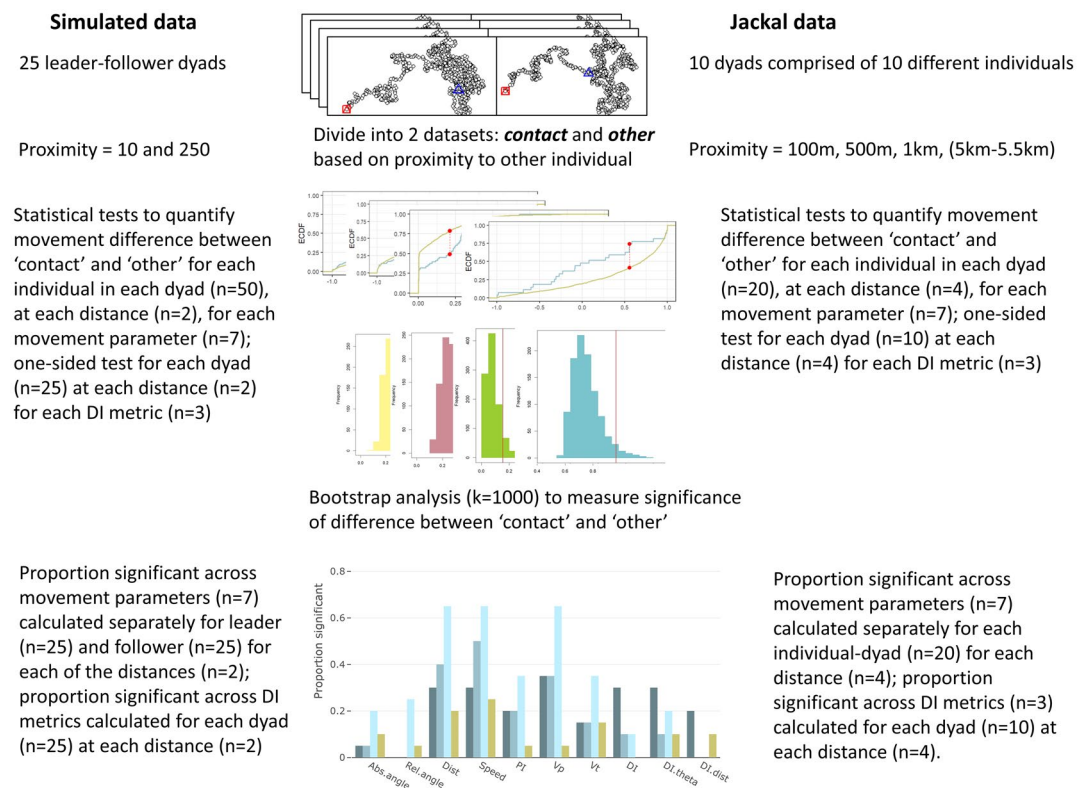

Simulated data

25 leader-follower dyads

Proximity = 10 and 250

Statistical tests to quantify movement difference between 'contact' and 'other' for each individual in each dyad (n=50), at each distance (n=2), for each movement parameter (n=7); one-sided test for each dyad (n=25) at each distance (n=2) for each DI metric (n=3)

Proportion significant across movement parameters (n=7) calculated separately for leader (n=25) and follower (n=25) for each of the distances (n=2); proportion significant across DI metrics calculated for each dyad (n=25) at each distance (n=2)

Divide into 2 datasets: **contact** and **other** based on proximity to other individual

Bootstrap analysis (k=1000) to measure significance of difference between 'contact' and 'other'

Jackal data

10 dyads comprised of 10 different individuals

Proximity = 100m, 500m, 1km, (5km-5.5km)

Statistical tests to quantify movement difference between 'contact' and 'other' for each individual in each dyad (n=20), at each distance (n=4), for each movement parameter (n=7); one-sided test for each dyad (n=10) at each distance (n=4) for each DI metric (n=3)

Proportion significant across movement parameters (n=7) calculated separately for each individual-dyad (n=20) for each distance (n=4); proportion significant across DI metrics (n=3) calculated for each dyad (n=10) at each distance (n=4).

FIGURE 4 Overview of data and methods

(Figure 5a) and the jackal data (Figure 5b). The proportions for the simulated data were out of 25 for each of the individual–distance combinations, with leaders measured separately from followers; the proportions for the three DI metrics in the graph are labeled for the follower trajectories but they are based on the 25 dyads comprised of both a leader and a follower. For the simulated data, high proportions were expected only for the follower trajectories, with higher proportions when proximity was less (F_10). The follower movement parameters had the highest proportions of significant differences for PI (23/25, or 0.92), Vp (0.88), and relative angle (0.76) at dc = 10, with the proportions for these parameters at dc = 250 around 0.4. The proportions for the leader trajectories were much lower for these parameters, though almost equal to the follower trajectories for the parameters of
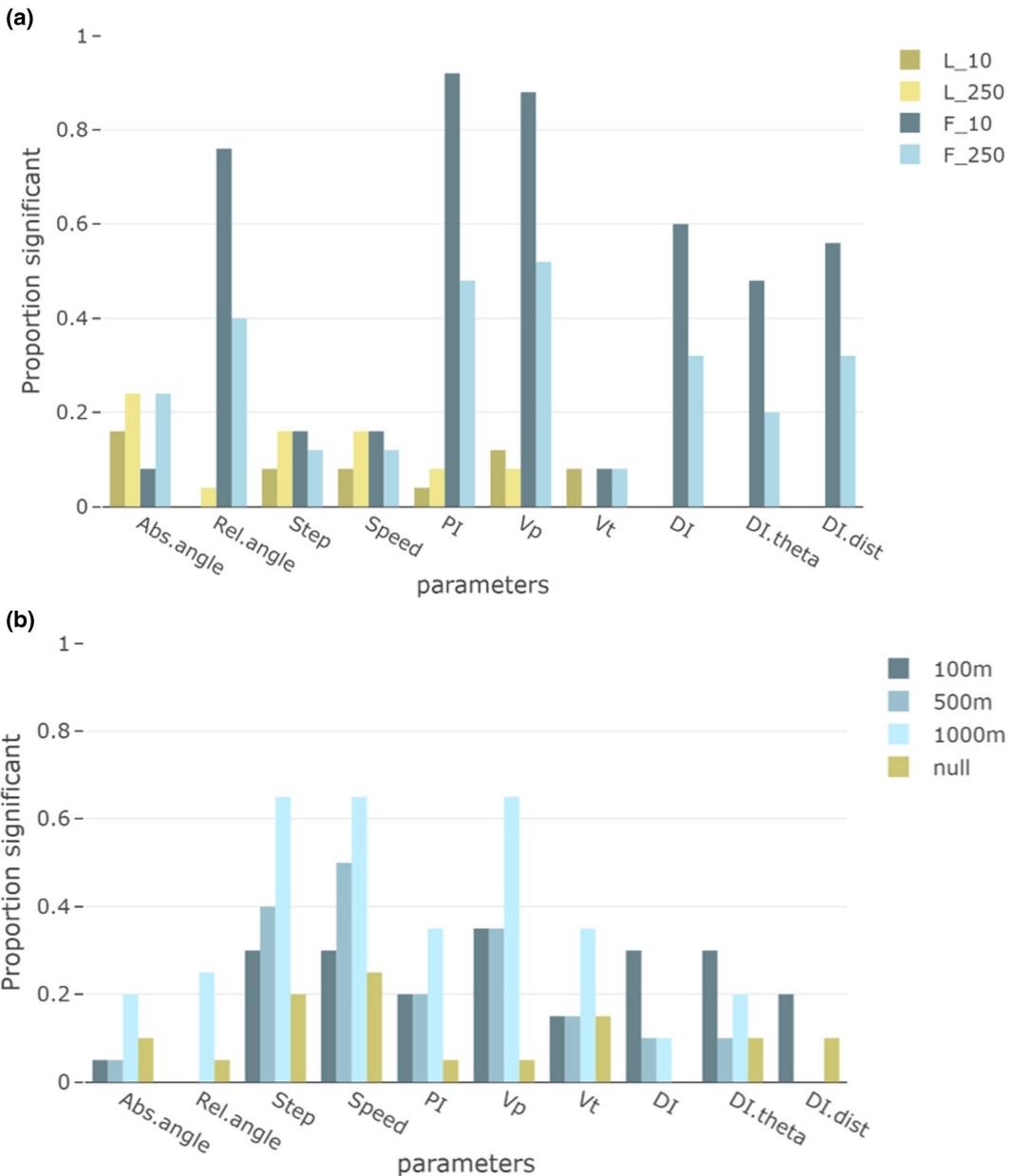

FIGURE 5 Proportion statistically significant based on bootstrap permutations for the simulated data (a) and the jackal data (b)

step length, speed, and Vt. The results for speed and step length were exactly the same, as was expected since the temporal interval was uniform and they were essentially redundant measures. The higher proportions for leader trajectories generally occurred at greater proximity (L_250), with the exception of Vp and Vt. Absolute angle had the highest proportion for the leader trajectories (0.16 for L_10 and 0.24 for L_250). The DI metrics were significantly different for about half of the dyads (0.48–0.6) at shorter proximity distance, and dropped to 0.2–0.32 proportion at dc = 250. Vt had the lowest proportion of differences overall, 0.08 for both follower proximities as well as for the leader trajectory at closer proximity and a proportion of 0 for L_250. While the proportion of differences for the leader trajectories was sometimes equivalent to that of the follower trajectories (absolute angle, distance/speed, Vt), they never exceeded the follower-trajectory proportions.

4.2 | Movement parameter comparison—Jackal data

The proportions for the jackals were out of 20 for each of the individual–distance combinations and the proportions for the three DI metrics were based on 10 dyads (Figure 5b). The highest proportions were usually when proximity was greatest (1,000 m), with step length, speed, and Vp the metrics that were most significant (0.65). These three parameters had the highest proportions at all three proximities, however, step length and speed also had the highest proportion of significant differences at the "null" distance (0.2 and 0.25). PI and Vt had the same proportion at 1,000 m (0.35), but PI had higher proportions for 100 and 500 m (0.2) and lower proportions for the null distance (0.05 compared to 0.15 for Vt). DI metrics were highest at the closest proximity (0.3 for DI and DI.theta; 0.2 for DI.distance). The combined metric, DI, showed no significant differences at the null proximity distance.

The proportion of differences at the null distance was always exceeded by the proportion for at least one of the shorter distances, but the differences were smallest for absolute angle and DI.dist. Vp had the greatest separation between proportions at 1,000 m (0.65) and the null distance (0.05).

In general, a parameter would be considered potentially useful for distinguishing contact-related movement if the proportions that were statistically significant for the three closer proximity distances representing meaningful interaction were greater than the proportions that were significant at the null distance. By those criteria, step length, speed, PI, Vp, and DI would be considered useful. The higher proportion of differences in contact movement at 1,000 m was not interpreted as evidence of broad-scale social interaction; it was more likely a result of potential step bias as well as an increased likelihood of statistically significant results associated with higher contact numbers.

With the exception of Vp performing well and absolute angle performing poorly, there was considerable disagreement in how well movement parameters differentiated between contact-related movement and other movement for both the simulated follower trajectories and the jackals. Relative angle and PI had much higher proportions for the simulated data than for the jackals, while step length and speed were much higher for the jackals. The relative angle is most directly impacted by the bias when the follower trajectory is simulated, so it makes sense that this parameter and its derivatives (PI, Vp) have high proportions in the simulated dyads. Vt is also calculated from the relative angle but is more difficult to interpret since it is based on the sine of the turning angle; a value of 0 indicates both direct movement (0° relative angle) as well as oscillating movement (180° relative angle). Step length and speed were more likely characteristics of behaviors associated with interactions between jackals (e.g., stopping or resting) that would not have been part of the follower simulations. In addition to small steps, contacts were also associated with no movement (individual was stationary for at least two consecutive time periods). When an individual showed no movement between fixes, none of the angle parameters or their derivatives could be calculated. All three DI values were 0 if only one of the individuals was stationary and all three DI values were 1 if both individuals were stationary.

Differences between contact and other movement were detected at a very high proportion for PI (0.92) and Vp (0.88) in the simulated follower movement. While none of the proportions in the jackal data exceeded 0.65, in addition to data and measurement uncertainties, it would be unrealistic to expect that two individuals in a dyad are interacting in a measurable way whenever they are within a certain distance of each other.

4.3 | Individual–dyad comparison

In addition to comparing the ability to distinguish between contact-related movement across parameters, differences across jackal individuals were also assessed (Figure 6). Since an individual had distance-based contacts in different dyads and likely different interaction behaviors reflected in its movement, dyad-specific individuals were considered separately here; the number of dyads a single individual was part of ranged from one (cm05, cm15, cm69, and cm62) to four (cm83). This resulted in 20 dyad-specific individuals for which the proportion of significant results for all distances less than or equal to 1,000 m (potential "meaningful" interaction) was combined and compared to the proportion of significant results at 5,000–5,500 m apart (the null expectation). For each of the 20 dyad-specific individuals, the proportion of significant results at "meaningful" distances was out of 21 (7 parameters × 3 distance thresholds), while the proportion for the null distance was out of 7 (7 parameters × 1 distance). The DI metrics were not included since they are dyad measures rather than individual measures.

There was substantial variation in the proportions; 16 individual dyads had higher proportions for the meaningful distances, while four had higher proportions for the null distance. Ten individuals had no significant differences at the null distance, while only one individual had no significant differences at the meaningful distances (cm47_83, proportion at null distance was 0.43). To illustrate how different the results for the same individual may be when they are paired with a different individual, cm47 was also in a dyad with cm15 where the opposite was true (0.47 for meaningful distance and 0 for null). In general, when an individual was part of multiple dyads, the differences between the contact and null proportions were quite different; cm08 was in two dyads and the contact proportions were 0.52 (with cm09) and 0.1 (with cm10), while the null proportions were 0.14 and 0.43, respectively. Cm83 was part of four dyads and the proportions for contact differences ranged from 0.19 to 0.29 while the proportions for null distances ranged from 0 to 0.43. With the exception of the dyad comprised of cm08 and cm09, for which individual proportions were exactly the same (0.52 for contact and 0.14 for null), there was very little similarity in results for individuals in the same dyad.
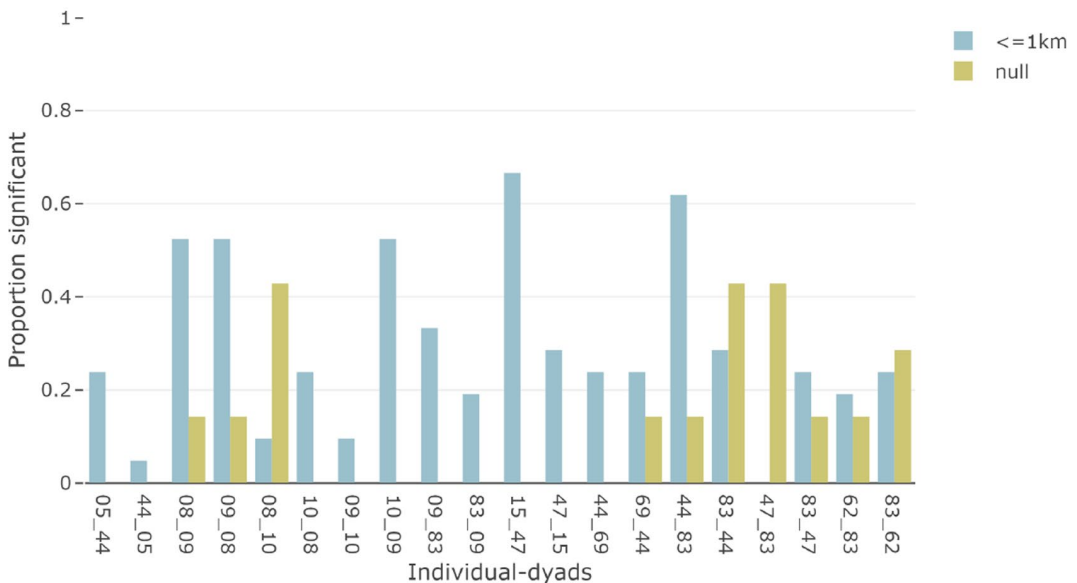

FIGURE 6 Proportion significant for each individual–dyad combination. Significance results for the seven movement parameters were combined for the three meaningful distances (100, 500, and 1,000 m) and compared to the proportion significant for the null distance

5 | DISCUSSION

This research used simulated leader–follower trajectories and GPS data for black-backed jackals (*C. mesomelas*) in Etosha National Park to illustrate how dynamic interactions between two individuals may be detected using movement parameters. Movement parameters associated with relatively close proximity were considered to represent potentially interaction-related movement, and movement parameters of simulated leader trajectories and individuals when proximity exceeded a distance within which meaningful interaction could occur were considered to represent independent movement. In the simulated data, follower trajectories in close proximity had significantly different movement based on persistence index (PI), persistence velocity (Vp), and relative angle compared to follower trajectories not in close proximity, as well as leader trajectories at all proximities. These three parameters are related (PI is the cosine of relative angle and Vp is the product of speed and PI) and measure *change in direction* (relative angle, PI) as well as *speed* (Vp). Both PI and Vp performed better than relative angle, suggesting that relative angle and PI are not redundant parameters, which could be a result of the cosine transformation as well as the use of two different tests to measure their differences (Watson for angles, Kolmogorov–Smirnov for PI).

In addition to Vp, speed and step length also differed considerably for the jackals, particularly when proximity was 1,000 m. While speed and step length would be redundant when the temporal resolution is constant (e.g., in the simulated data), there was some variation in the amount of time elapsed between fixes in the jackal data. Small (and sometimes zero) step lengths were often associated with contacts in the jackal data, and there are social behaviors such as resting or sharing resources that are consistent with little or no movement for several hours with the jackals that would not occur in the simulated leader–follower dyads. Persistence velocity (Vp), the product of speed and PI, was the most effective parameter with the jackal data, which may reflect the combined effects of speed and PI individually. Speed was a far less effective parameter for the simulated data and PI and Vp had very similar results, likely reflecting the lack of association between speed (and step length) and contacts in the simulated data compared to in the jackal data.

Persistence velocity (Vp) and turning velocity (Vt) were the only movement parameters capable of describing all three of change/variability, directional persistence, and speed. Persistence velocity (Vp) was able to identify contact-related movement when proximity between individuals was potentially meaningful and did not erroneously differentiate between contact and other movement at "null" distances for both the simulated and the jackal data. While turning velocity can also capture all three of change/variability, direction, and speed, it measures the tendency to make perpendicular turns and is not as powerful for measuring potentially interaction-related movement. In general, movement parameters that measure at least two of the three properties of change/variability, directional persistence, and speed were better able to distinguish contact-related movement.

While the DI metrics are indices of correlation rather than movement parameters, their results provide interesting insights into how they can be used to measure interactions. The combined DI metric equals 1 when both individuals were stationary for that time fix, but for the jackals, this was rarely evidence of interaction as the proximity in these cases often exceeded 1 km. Conversely, DI was 0 when only one of the individuals was stationary and this was more often associated with proximity less than 1 km. The scenario in Figure 9 later illustrates an example of potential interaction characterized by correlated movement (and high DI values), but it is worth considering the scenario in Figure 8 also, as an equally likely example of (positive) interaction characterized by DI values close to −1, which would be interpreted as negative interaction.

5.1 | Contact-related movement parameters

In path segmentation, basic movement behaviors can be inferred from trajectory sections in which specific movement parameters are distinctive and relatively uniform. For example, foraging would be associated with high relative angles and low speed, while resting might be characterized by low relative angles and low speed, sustained across multiple recorded locations (Edelhoff, Signer, & Balkenhol, 2016). Interactions between individuals can

result from many different behaviors, which makes empirically identifying interactions more problematic than identifying other (individual) movement behaviors. The objective of this research was to explore whether contact-related movement could be differentiated empirically from other movement rather than to determine specific movement parameter values associated with interactions, however, several consistencies emerged. In general, when two individuals were close to each other (proximity <500 m), some combination of the following movement characteristics was observed in the three steps around a contact for at least one individual:

- small step length (<20 m);
- extreme PI values (<−0.9 or >0.9), more often negative, but also alternating between the two extremes;
- consecutively high DI values (measured for the dyad).

The following examples illustrate different types of potential dynamic interactions and the derived movement parameters associated with them.

5.1.1 | Close proximity of short duration

Figure 7 illustrates an interaction marked by very close proximity but relatively short duration (e.g., the kind of direct contact required for disease spread). On February 17, 2010 cm44 and cm83 moved from almost 5 km apart at 2:00 to approximately 3 m apart at 3:00 and 135 m apart at 4:00, but were 5 km apart again by 5:00. Each individual moved a relatively large distance before and after the contact, and cm44 was relatively stationary when they were very close, while cm83 moved 143 m. However, the actual distances traveled at each fix were
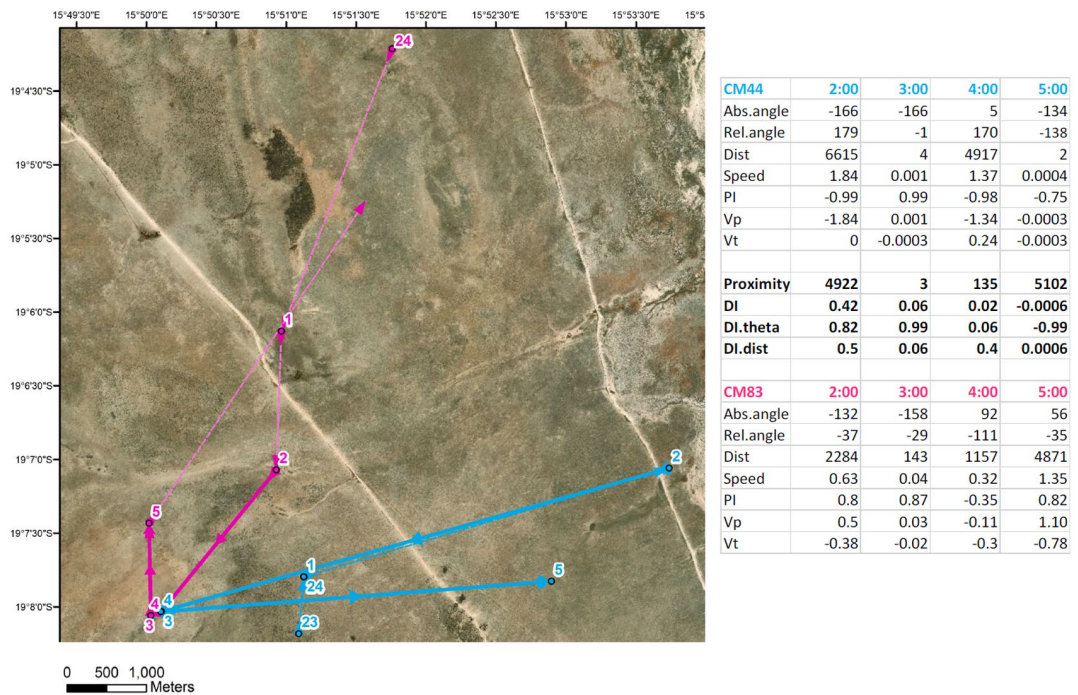

CM44	2:00	3:00	4:00	5:00
Abs.angle	-166	-166	5	-134
Rel.angle	179	-1	170	-138
Dist	6615	4	4917	2
Speed	1.84	0.001	1.37	0.0004
PI	-0.99	0.99	-0.98	-0.75
Vp	-1.84	0.001	-1.34	-0.0003
Vt	0	-0.0003	0.24	-0.0003
Proximity	4922	3	135	5102
DI	0.42	0.06	0.02	-0.0006
DI.theta	0.82	0.99	0.06	-0.99
DI.dist	0.5	0.06	0.4	0.0006
CM83	2:00	3:00	4:00	5:00
Abs.angle	-132	-158	92	56
Rel.angle	-37	-29	-111	-35
Dist	2284	143	1157	4871
Speed	0.63	0.04	0.32	1.35
PI	0.8	0.87	-0.35	0.82
Vp	0.5	0.03	-0.11	1.10
Vt	-0.38	-0.02	-0.3	-0.78

FIGURE 7 Movement of cm44 (blue) and cm83 (pink) around a contact (proximity = 3 m at 3:00 and 135 m at 4:00) at February 17, 2010 (angles are in degrees, distance is in meters, speed is in meters per second, proximity is in meters)

not similar enough to result in a high DI.dist, and with the exception of the azimuth at the contact, the individuals showed little movement coherence as measured by the DI metrics. For this type of interaction, there was very little correlation in their movement parameters and the most notable movement pattern was the change in individual parameters: for cm44 in particular, PI changed from −0.99 to 0.99 to −0.98 (oscillating–direct–oscillating movement) in three consecutive steps. The other individual, cm83, had less extreme but still substantial changes in movement (PI ranged from −0.35 to 0.87).

5.1.2 | Dissimilar dyadic movement

An even more exceptional example of this is shown for the same individuals on April 21, 2010 (Figure 8). Each individual traveled more than 1.7 km in the previous step from opposite parts of the study area; they were 7 m apart at 3:00, then traveled almost back to where they started 3–4 hr earlier. The PI values for both individuals ranged from close to −1 to close to 1 and the DI values were all negative, reflecting in particular the movement in opposite directions. In this case, DI.theta values of −0.99 and −0.98 represent almost opposite movement but are more likely associated with positive interaction or attraction to each other as the two individuals are moving
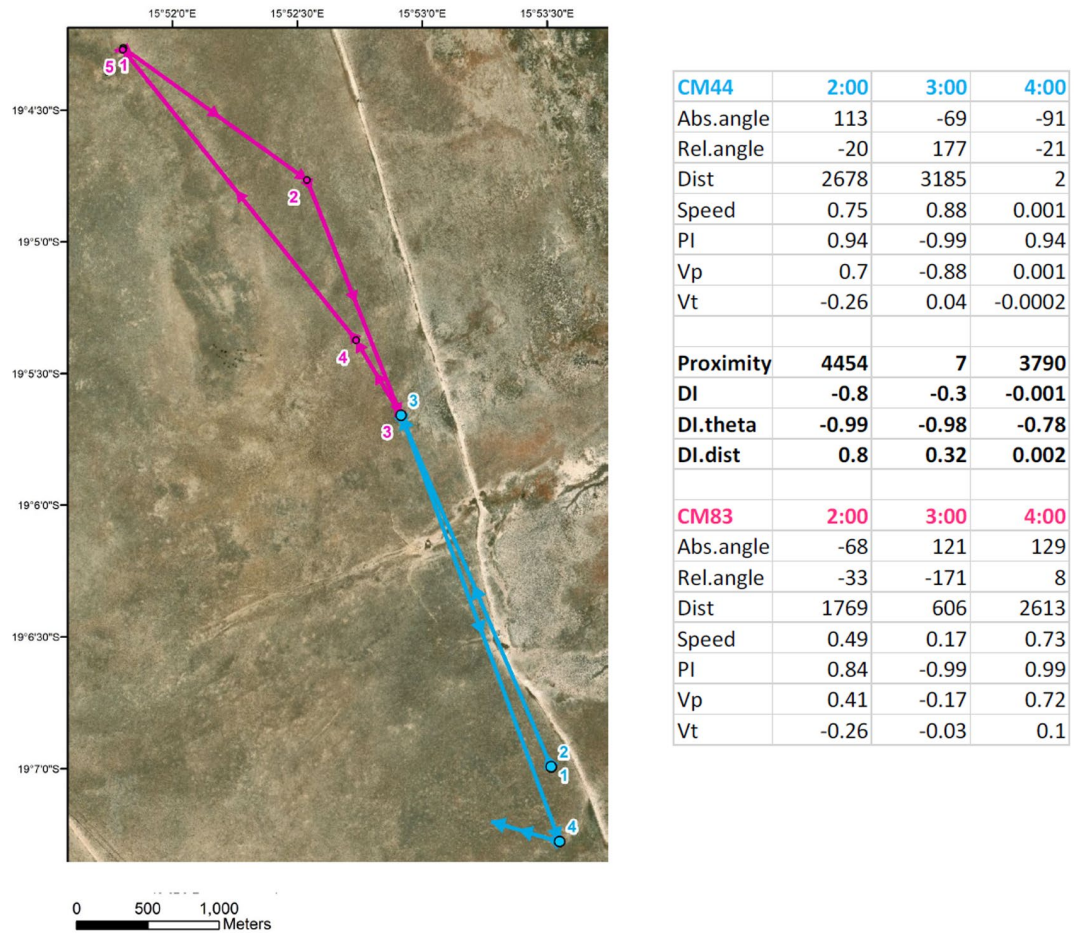

CM44	2:00	3:00	4:00
Abs.angle	113	-69	-91
Rel.angle	-20	177	-21
Dist	2678	3185	2
Speed	0.75	0.88	0.001
PI	0.94	-0.99	0.94
Vp	0.7	-0.88	0.001
Vt	-0.26	0.04	-0.0002
Proximity	4454	7	3790
DI	-0.8	-0.3	-0.001
DI.theta	-0.99	-0.98	-0.78
DI.dist	0.8	0.32	0.002
CM83	2:00	3:00	4:00
Abs.angle	-68	121	129
Rel.angle	-33	-171	8
Dist	1769	606	2613
Speed	0.49	0.17	0.73
PI	0.84	-0.99	0.99
Vp	0.41	-0.17	0.72
Vt	-0.26	-0.03	0.1

FIGURE 8 Movement of cm44 (blue) and cm83 (pink) around a contact (proximity = 7 m) at 3:00, April 21, 2010 (angles are in degrees, distance is in meters, speed is in meters per second, proximity is in meters)

toward each other rather than moving together. This example also helps to illustrate how temporal resolution impacts the measurement of interactions—if either individual's location had been recorded a few minutes earlier or later, proximity would have been much greater at 2:00 and 4:00.

5.1.3 | Sustained similar dyadic movement

In contrast, Figure 9 highlights a potential interaction of longer duration during which the individuals were farther apart but appeared to be traveling together. On May 10, 2010, the closest cm83 and cm62 were to each other (empirically) was 661 m at 8:00, however, their movements appear correlated as indicated by several high DI values in succession. Their trajectories from 5:00 to 6:00 in particular were quite similar in both direction and step length, resulting in DI values >0.9 for all metrics, in spite of their proximities being 1,758 m at 5:00 and 2,297 m at 6:00. They crossed paths between 7:00 and 8:00 and this could be an example of step bias, where an interaction is not detected as a result of the temporal resolution of fixes. In addition to the high DI values, their individual movements show considerable change in values and both have PI values close to 1 (moving at close to a straight line) as proximity decreases. Their step lengths and speed were relatively consistent for all four steps, except cm62 moved very little at 6:00 until cm83 gets closer. It is also possible they were following or pursuing another individual, a potential source of scatter bias.

The three scenarios shown here represent different types of potential interaction in terms of behavior, spatial scale, and movement associated with them, and illustrate how movement parameters might be used to detect
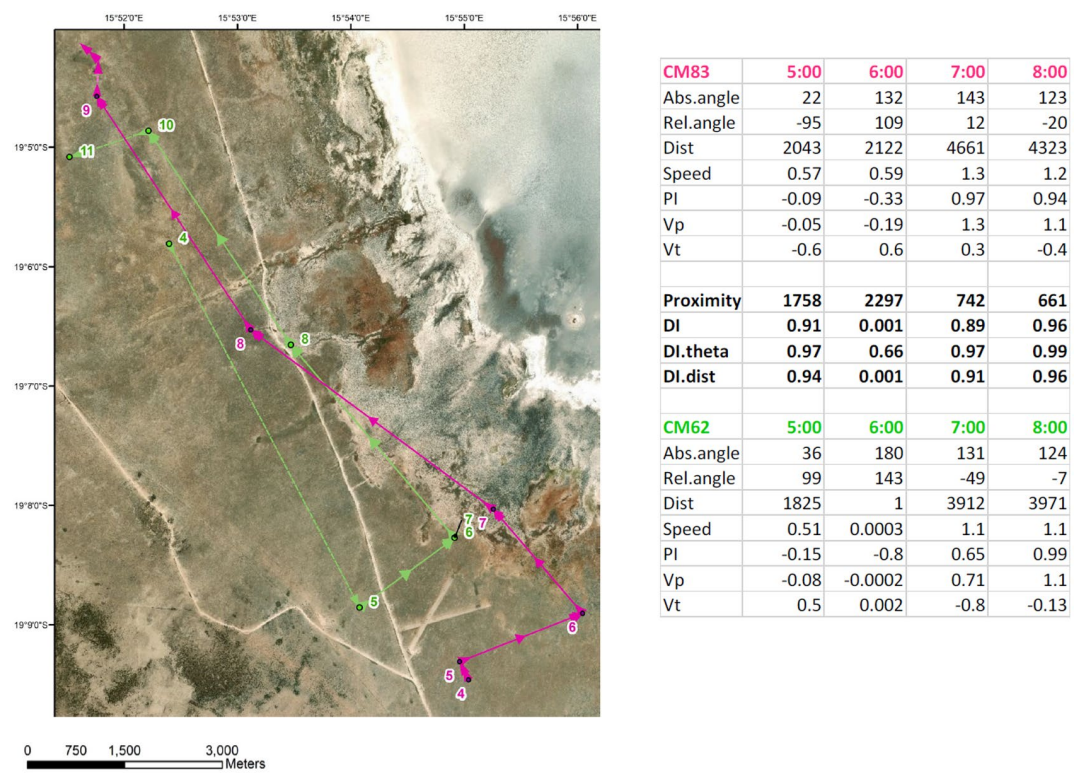

CM83	5:00	6:00	7:00	8:00
Abs.angle	22	132	143	123
Rel.angle	-95	109	12	-20
Dist	2043	2122	4661	4323
Speed	0.57	0.59	1.3	1.2
PI	-0.09	-0.33	0.97	0.94
Vp	-0.05	-0.19	1.3	1.1
Vt	-0.6	0.6	0.3	-0.4
Proximity	1758	2297	742	661
DI	0.91	0.001	0.89	0.96
DI.theta	0.97	0.66	0.97	0.99
DI.dist	0.94	0.001	0.91	0.96
CM62	5:00	6:00	7:00	8:00
Abs.angle	36	180	131	124
Rel.angle	99	143	-49	-7
Dist	1825	1	3912	3971
Speed	0.51	0.0003	1.1	1.1
PI	-0.15	-0.8	0.65	0.99
Vp	-0.08	-0.0002	0.71	1.1
Vt	0.5	0.002	-0.8	-0.13

FIGURE 9 Movement of cm83 (pink) and cm62 (green) on May 10, 2010. While their proximity was not closer than 661 m (at 8:00), their movement appears to be correlated (angles are in degrees, distance is in meters, speed is in meters per second, proximity is in meters)

them. Oscillating extreme PI values and short step lengths may be more characteristic of the short and close interactions needed for disease spread. Consecutive DI values close to 1 may better identify individuals traveling together, while DI values approaching −1 may actually indicate positive interaction when two individuals move toward each other.

The wide variation across individual jackals' results showed that interaction-related movements are typically not symmetric for both individuals in a dyad. This is important as point- and path-based interaction metrics currently used are based on pairwise measures, which assume interaction is symmetric. Focusing on individual movement can not only help to capture asymmetric interaction, but is also extensible beyond dyadic interaction.

6 | CONCLUSIONS

While often viewed as equally appropriate for measuring dynamic interactions, the significant conceptual (as well as practical) differences between existing point- and path-based metrics warrant deeper consideration about which method is more appropriate for measuring different types of interactions. Since point-based metrics consider proximity, they may be more appropriate for studying positive interactions that require direct contact and may be of short duration, such as mating or spreading of disease. However, the inability to consider the path between two points may decrease the number of "contacts" quantified as a result of, for example, step bias. Focusing on the path between points can reduce these potential "false negatives" from point-based approaches, and may also provide a more appropriate framework for detecting interaction-related movement.

However, existing path-based dynamic interaction metrics measure movement similarity based on relatively basic parameters such as azimuth and step length. Consequently, these metrics are suitable for measuring a very narrow type of positive interaction (e.g., two individuals traveling together), and empirically detected negative interaction could actually be evidence of positive interaction (e.g., two individuals moving in opposite directions toward each other). This work highlights the potential for using more complex movement parameters capable of representing direction, speed, and change to identify interaction-related movement.

Unlike path analytics in which movement behaviors such as foraging can be inferred from relatively uniform and distinct parameters such as low speed and high relative angle, interaction-related movement is far more complex and unlikely to be associated with a narrow set of uniform parameter values. For the black-backed jackals, there were several consistent movement characteristics that were observed when two individuals in a dyad were in close proximity, such as extreme persistence index values or consecutive DI values close to 1. The movement these values describe—oscillating from straight-line movement and sustained movement similarity, respectively—might generally be associated with interactions in other animals and types of individuals.

These results provide more evidence that dynamic interactions comprise a wide variety of behaviors and movement characteristics at different temporal and spatial scales, and more research is needed on how to analyze them. A range of distance and temporal thresholds should also be used to address different types of interaction, as well as issues related to empirical measurement such as step bias. Negative interactions have been far less studied in general, and complex movement parameters may be more appropriate for detecting them than existing point- and path-based dynamic interaction metrics. It may be unrealistic to expect dynamic interaction indices to be able to measure both positive and negative interactions, and new metrics focused solely on the range of negative interactions and how they might be detected is an important research focus.

Simulated data with known movement parameters can help to provide a baseline for exploring these dynamic interaction metrics, but they will always represent overly simplified movement processes. With animal-borne videos and cameras becoming more common, there will soon be better ways to confirm details about interactions in the field. In addition to testing this approach with other types of moving objects that might exhibit interaction-related movement differences, future research will address explicitly combining proximity with complex movement parameters to generate new indices of dynamic interaction. Understanding the nature and magnitude of

dynamic interactions in wildlife is crucial to better understand spatial processes and phenomena related to interactions, ranging from resource use to mating to disease spread. The ability to detect interactions based on movement characteristics will make measuring interactions in large animal movement databases more accurate and efficient.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST

The author has no conflict of interest to declare.

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