

A critical examination of indices of dynamic interaction for wildlife telemetry studies

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Running Head: indices of dynamic interaction

1 **Summary / Abstract**

- 2 1. Wildlife scientists continue to be interested in studying ways to quantify how the
3 movements of animals are inter-dependent – *dynamic interaction*. While a number of
4 applied studies of dynamic interaction exist, little is known about the comparative
5 effectiveness and applicability of available methods used for quantifying interactions
6 among animals.
- 7 2. We highlight the formulation, implementation, and interpretation of a suite of eight
8 currently available indices of dynamic interaction. Point- and path-based approaches are
9 contrasted to demonstrate differences between methods and underlying assumptions on
10 telemetry data.
- 11 3. Correlated and biased-correlated random walks were simulated at a range of sampling
12 resolutions to generate scenarios with dynamic interaction present and absent. We
13 evaluate the effectiveness of each index at identifying differing types of interactive
14 behaviour at each sampling resolution. Each index is then applied to an empirical
15 telemetry dataset of three white-tailed deer (*Odocoileus virginianus*) dyads.
- 16 4. Results from the simulated data show that three indices of dynamic interaction reliant on
17 statistical testing procedures are susceptible to Type I error, which increases at fine
18 sampling resolutions. In the white-tailed deer examples, a recently developed index for
19 quantifying local-level cohesive movement behaviour (the *di* index) provides revealing
20 information on the presence of infrequent and varying interactions in space and time.
- 21 5. Point-based approaches implemented with finely sampled telemetry data over-estimate
22 the presence of interactions (Type I errors). Indices producing only a single global
23 statistic (7 of the 8 indices) are unable to quantify infrequent and varying interactions

24 through time. The quantification of infrequent and variable interactive behaviour has
25 important implications for the spread of disease, and the prevalence of social behaviour in
26 wildlife. Guidelines are presented to inform researchers wishing to study dynamic
27 interaction patterns in their own telemetry datasets. Finally, we make openly available
28 our code, in the statistical software R, for computing each index of dynamic interaction
29 presented herein.

30

31 **Keywords:** contact rate, static interaction, proximity, simulation, biased random walk, sampling
32 resolution, *Odocoileus virginianus*, GPS telemetry

33 **1 – Introduction**

34 The development of GPS tracking technologies is revolutionizing wildlife movement and
35 behaviour research (Cagnacci *et al.* 2010), and has led to increased interest in the study of
36 interactions among individual animals (e.g., mating behaviour, Stenhouse *et al.* 2005; and
37 predator-prey dynamics, Eriksen *et al.* 2008). Interactive behaviour can be characterized as either
38 static or dynamic (Macdonald, Ball & Hough 1980). Static interaction can be defined simply as
39 the joint-space use between two individuals, ignoring the temporal information of location fixes,
40 (Kernohan, Gitzen & Millspaugh 2001), and is typically measured by an index of home range
41 overlap or volume of intersection using utilization distributions (Millspaugh *et al.* 2004; Fieberg
42 & Kochanny 2005). Alternatively, dynamic interaction refers to how the movements of two
43 individuals are related (Macdonald *et al.* 1980), or as the inter-dependency in the movement of
44 two individuals (Doncaster 1990). Strictly speaking, the presence of dynamic interaction implies
45 some degree of static interaction, while the converse may or may not be true. Tests for dynamic
46 interaction can be used to examine attraction or avoidance behaviour (Doncaster 1990),
47 simultaneous joint-space use (Minta, 1992), or cohesiveness in the movements of two individuals
48 (Long & Nelson 2013). A number of techniques for studying dynamic interactions have been
49 developed and adopted widely in wildlife telemetry studies (see Table 1), but little is known
50 about the effectiveness of each at identifying true dynamic interaction patterns. Similarly, it is
51 difficult for researchers to compare results among existing methods because most applied studies
52 typically implement only a single method.

53 < Approximate location of Table 1 >

54 Novel tracking technologies (e.g., GPS, Argos, Platform terminal transmitters (PTTs),
55 global satellite Iridium systems, etc.) are changing the manner in which wildlife telemetry data

56 are recorded and transmitted. A wide variety of systems can be programmed to collect telemetry
57 fixes at variable sampling resolutions (Tomkiewicz *et al.* 2010). Sampling resolutions (the
58 frequency at which telemetry fixes are collected) previously unattainable are now routinely
59 implemented in modern tracking studies. However, many studies still employ coarser resolution
60 telemetry systems (e.g., VHF telemetry), which have a lower unit cost in order to monitor a
61 greater number of individuals (Girard *et al.* 2006). In addition to the wide range of technologies,
62 study objectives typically dictate sample size, sampling resolution, and study design, all of which
63 may influence the ways in which data are analyzed and interpreted. Therefore, researchers are
64 often left with the difficult task of identifying which, of a suite of available analytical techniques,
65 are appropriate for meeting study objectives.

66 The overall goal of this study is to demonstrate the effectiveness of eight available
67 indices for measuring dynamic interaction common to wildlife telemetry data using both
68 simulated and empirical data. Our objectives were to: 1) review the formulation and
69 interpretation of each of the eight indices, 2) detect present vs. absent dynamic interaction using
70 simulated data at varying sampling resolutions, 3) evaluate each method using empirical data
71 collected on white-tailed deer fitted with GPS collars, 4) highlight the advantages and
72 disadvantages of each approach, and 5) provide guidance on the selection, use, and interpretation
73 of dynamic interaction indices common to analysis of wildlife telemetry data. Areas of future
74 research are discussed to encourage the development of additional tools and algorithms that can
75 be used in association with dynamic interaction analysis. Last, we provide code for the R
76 statistical computing environment that allows researchers to implement each of the eight indices
77 of dynamic interaction presented herein.

78 **2 – Indices of Dynamic Interaction**

79 Indices of dynamic interaction can be broadly categorized as point-based or path-based,
80 depending on how they represent telemetry data (as points, or as connected segments – paths).
81 Clear conceptual differences in the calculation and interpretation of the eight dynamic indices are
82 apparent from their individual formulation (see below and Table 2), but also between point- and
83 path-based approaches. Point-based indices typically examine attraction/avoidance behaviour,
84 while path-based indices look at cohesive movement behaviour. Of the eight currently available
85 indices of dynamic interaction, six are point-based, while two are path-based (Table 2). The
86 terminology and notation used for describing telemetry data and concepts relating to
87 measurement of dynamic interaction is introduced in Table 3.

88 < Approximate location Table 2 >

89 < Approximate location Table 3 >

90 2.1 – Proximity analysis

91 Dynamic interaction is most simply quantified as a measure of nearness in space. Researchers
92 have used proximity analysis (Prox) to understand the frequency at which two individuals are
93 near each other. The simplest such index is the proximity rate:

$$94 \text{ Prox} = \frac{ST_{\alpha\beta}}{T_{\alpha\beta}}$$

95 where Prox measures the proportion of simultaneous fixes ($T_{\alpha\beta}$ – defined using temporal
96 threshold – t_c) that are spatially proximal ($ST_{\alpha\beta}$ – based on spatial threshold d_c). The value of
97 implementing Prox is that it is easily interpreted and gives an estimate of the proportion of time
98 animals are proximal in space (within d_c distance units), given the fixes that are close in time
99 (based on temporal threshold t_c) (Table 2). Further analysis can examine temporally the binary
100 sequence of proximal and non-proximal fixes. Prox has been used as an indicator of attraction
101 between individuals (e.g., Bertrand *et al.* 1996), and as an estimate of contact rates, which is

102 useful when studying disease spread dynamics (Baker & Harris 2000). The requirement of a
103 distance threshold is both advantageous and problematic. In some cases, such as with contact
104 rates, a biologically motivated spatial distance may be used. However, in many cases, it will be
105 chosen subjectively by the researcher, owing to previously used thresholds in the literature, or
106 some other property of the data such as error or sampling interval. In these cases, the subjectivity
107 of the chosen threshold will impact the results as various choices for d_c will change Prox results.

108 2.2 – Coefficient of association

109 The coefficient of association (Ca) was first introduced by Cole (1949) for measuring
110 interspecific associations in field samples and has since been identified as a potential measure of
111 dynamic interaction in wildlife telemetry data (Bauman 1998). Coefficient of association is
112 calculated as:

$$113 \text{Ca} = \frac{2ST_{\alpha\beta}}{n_{\alpha} + n_{\beta}}$$

114 where n_{α} (resp. n_{β}) is the total number of all fixes in α (resp. β). Ca is similar to Prox, only Ca
115 measures the rate of all fixes that are $ST_{\alpha\beta}$, not just the simultaneous fixes; thus Ca is measuring
116 the same phenomenon as Prox. Typically, $\text{Ca} > 0.5$ indicates attraction, while $\text{Ca} < 0.5$ indicates
117 no association (Kernohan *et al.* 2001; Table 2). Like Prox, Ca is a useful indicator of attraction
118 and contact rates, as defined by the threshold d_c . However, it is similarly affected by the
119 subjectivity with which d_c is determined.

120 2.3 – Coefficient of sociality

121 The coefficient of sociality (Cs) was proposed by Kenward *et al.* (1993) as an alternative
122 measure of attraction using the raw distances between fixes, rather than a user-defined threshold.
123 The formulation of Cs is a variant of Jacobs' index (Jacobs 1974), a metric originally proposed
124 for measuring food selection by wildlife. Cs is calculated as:

125
$$C_s = \frac{d_E - d_o}{d_E + d_o}$$

126 where d_o is the mean spatial distance between $T_{\alpha\beta}$ fixes and d_E is the expected mean distance,
127 based on n^2 permutations of the $T_{\alpha\beta}$ fixes. The statistic is symmetric (on [-1, 1]) where positive
128 values suggest attraction while negative values suggest avoidance. A Wilcoxon signed-rank test
129 can be used to examine the significance of the resulting C_s value (Table 2). A major limitation is
130 determining a reasonable expectation of mean distance to test against. Generally, the distribution
131 of distances of the n^2 permutations of all $T_{\alpha\beta}$ telemetry fixes is used to determine d_E . Others have
132 suggested that d_E can be determined via simulations using, for example, correlated random walks
133 (Miller 2012).

134 *2.4 – Doncaster’s non-parametric test*

135 Doncaster (1990) proposed a non-parametric test for interaction (Don) by examining the
136 separations between the n $T_{\alpha\beta}$ fixes and the unpaired $n^2 - n$ permutations of the $T_{\alpha\beta}$ fixes, and is
137 analogous to the Knox test for space-time clustering (Knox 1964). The cumulative distribution of
138 the $T_{\alpha\beta}$ fix distances can be compared graphically with the cumulative distribution of the $n^2 - n$
139 permuted distances. For example, Don is useful for determining a suitable distance threshold
140 (d_c) by identifying where the $T_{\alpha\beta}$ plot is above the expected line based on the permutations. Upon
141 selecting a suitable d_c value, a contingency table can be constructed, identifying the number of
142 $T_{\alpha\beta}$ and non- $T_{\alpha\beta}$ (termed ‘unpaired’) fix distances that are above and below the threshold d_c . A χ^2
143 test (with 1 d.f.) or a binomial test can be used to examine the statistical significance of the
144 counts of $T_{\alpha\beta}$ and non- $T_{\alpha\beta}$ distances above and below d_c (Table 2). A modified version of Don
145 replaces the expectations derived from the $n^2 - n$ permutations of the $T_{\alpha\beta}$ fixes with a simulation
146 procedure based on correlated random walks (White & Harris 1994).

147 *2.5 – Minta’s test for spatial and temporal interaction*

148 Minta (1992) introduced three statistics (L_{AA} , L_{BB} , and L_{ixn}) for examining the spatial and
 149 temporal interactions between two individuals. L_{AA} and L_{BB} ignore the temporal information
 150 from fixes and represent only spatial measures of interaction. Here, we focus on L_{ixn} , which is a
 151 statistic for examining temporal interaction. L_{ixn} requires the calculation of individual home
 152 ranges, typically from the collected telemetry data, which are then divided (using a spatial
 153 intersection) into three areas: 1) used by α only, 2) used by β only, and 3) shared by α and β
 154 (often termed the overlap zone; see Table 1 for notations). The number of fixes contained in each
 155 area (i.e., used by α only, used by β only, and the shared area) are tested against expectations
 156 representing the probability of finding the animal in each of these areas. Expectation
 157 probabilities can be derived by using either the proportions of all fixes contained in each area, or
 158 the overlap area percentages (see Minta 1992). In the case of overlap area percentages, it is
 159 assumed the relative areas associated with space used by α only, by β only, and the shared area,
 160 are proportional to the amount of use.

161 The L_{ixn} statistic is a function of the ratio of simultaneous use and avoidance of the
 162 shared area to that of the solitary use of the shared area, and is calculated by:

$$163 \quad L_{ixn} = \log \left[\frac{\left(\frac{n_{\alpha\beta}}{p_{\alpha\beta}} + \frac{n_{00}}{p_{00}} \right)}{\left(\frac{n_{\alpha 0}}{p_{\alpha 0}} + \frac{n_{0\beta}}{p_{0\beta}} \right)} \right]$$

164 where n represents the number of observed fixes, p is the expectation probability, and the
 165 subscripts α and β signify each individual's presence in the shared area, while the subscript 0
 166 signifies absence from the shared area. Thus, L_{ixn} measures the simultaneous use (defined using
 167 temporal threshold t_c) of the shared area. Positive L_{ixn} values suggest simultaneous use of the
 168 shared area (attraction), while negative values indicate solitary use of the shared area

169 (avoidance). Lixn near 0 indicates indifference or random use of the shared area. The Lixn
170 statistic can be tested for significance using a χ^2 test with 1 df from the contingency table of
171 observed and expected frequencies of use within the shared area (Table 2).

172 2.6 – Half-weight association index

173 The half-weight association index (HAI - Brotherton *et al.* 1997) represents a companion test to
174 the Minta (1992) Lixn temporal interaction statistic (Atwood & Weeks 2003). As in Lixn, HAI is
175 based on the shared area between the two individual home ranges (the overlap zone). The HAI
176 statistic is however a more localized approach, focusing only on those fixes contained in the
177 shared area (or only on the area of static interaction). HAI is calculated as:

$$178 \text{ HAI} = \frac{ST_{\alpha\beta}}{ST_{\alpha\beta} + \frac{(x + y)}{2}}$$

179 where x and y are the number of solitary fixes (for α and β , respectively) within the shared area.
180 Values near 1 indicate attraction (within the shared area) and values near 0 indicate avoidance
181 (within the shared area; Table 2). HAI is computed identically to C_a , but only for those fixes
182 contained in the shared area of the home range. Thus, for a dyad consisting of two individuals
183 with identical home ranges, $C_a = \text{HAI}$.

184 2.7 – Correlation index

185 Shirabe (2006) introduced a correlation index (Cr) for analyzing movement data, which can be
186 considered a type of path-based measure of dynamic interaction. The Cr index takes the form of
187 a Pearson product-moment correlation statistic for multivariate data (in this case bivariate in the
188 two spatial dimensions, X and Y). With Cr, movement data are represented as time-series with
189 vectors corresponding to movement segments that connect consecutive fixes (see Table 3). Cr

190 measures differences in corresponding vectors with respect to overall path means to determine
 191 the correlation structure of the data. Cr is calculated as:

$$192 \quad Cr = \frac{\sum_{t=1}^{n-1} (v_t - \bar{v}) \cdot (w_t - \bar{w})}{\sqrt{\sum_{t=1}^{n-1} |v_t - \bar{v}|^2} \sqrt{\sum_{t=1}^{n-1} |w_t - \bar{w}|^2}}$$

193 where v_t and w_t represent movement vectors (for α and β) corresponding to time t , and \bar{v} and \bar{w}
 194 are mean vectors. Cr is interpreted similarly to other correlation statistics; values range from -1
 195 to 1 where positive values indicate stronger correlation (cohesive movement), negative values
 196 indicate negative correlation (opposing movement), and values near 0 indicate random
 197 movement with respect to the other individual (Table 2). The mean vectors (\bar{v} and \bar{w}) represent
 198 the average speed and direction of travel of an object, which may or may not have relevance in
 199 the context of measuring and interpreting the presence of dynamic interactions, but strongly
 200 influence the results from Cr.

201 2.8 – Dynamic interaction index

202 Recently, Long & Nelson (2013) introduced a dynamic interaction index (DI) based on path-
 203 based methods, similar to earlier attempts of Shirabe (2006). The DI index attempts to measure
 204 the cohesiveness of corresponding movement vectors. DI is constructed as the mean of a
 205 localized version (termed di). Here, di is calculated as

$$206 \quad di = \left(1 - \frac{|d_t^\alpha - d_t^\beta|}{d_t^\alpha + d_t^\beta} \right) \times \cos(\theta_t^\alpha - \theta_t^\beta) \text{ whereas DI is calculated by}$$

$$207 \quad DI = \frac{1}{n-1} \sum_{i=1}^{n-1} di$$

208 where d is displacement and θ (the direction) of vector t for individual α or β . The localized di is
 209 simply the product of terms measuring cohesiveness in displacement and direction for each

210 corresponding segment. Thus, d_i is capable of separately measuring cohesiveness in the distance
211 and direction components (d_{i_d} and d_{i_θ} respectively), which can be averaged into global statistics
212 (see Long & Nelson 2013 for more details). Temporal trends in d_i can be used to identify periods
213 of cohesive, opposing, and random movement within a dyad. The DI approach, as in Cr,
214 measures cohesiveness irrespective of proximity between corresponding movement vectors
215 (Table 2). Thus, to justify DI analysis, the researcher is required to have some *a priori*
216 expectation of cohesive movement, which for example, can be based on proximity (defined by
217 distance threshold d_c), a measure of static interaction (e.g., home range overlap), or simultaneous
218 capture (e.g., familial groups). DI can then be set to 0 when these conditions are not met.

219 **3 – Testing Indices**

220 *3.1 – Simulated Data*

221 In order to test methods of dynamic interaction, we simulated situations where dynamic
222 interaction would be present vs. absent. Generating movement dyads without dynamic
223 interaction can be accomplished by simulating two independent correlated random walks (CRW)
224 (White & Harris 1994; Miller 2012). When we simulated the absence of dynamic interaction, the
225 origin of the second independent CRW was chosen to be a random location within the bounding
226 box of the first CRW to offer the potential for static interaction (see Figure 1a). CRW's are
227 governed by two parameters – h and r . The step-length parameter ($h > 0$) controls movement
228 distances, and represents a multiplicative value for random draws from a step-length distribution
229 (e.g., $l = h \times d$, d a random draw from a step-length distribution). The turning correlation
230 parameter (r) governs the amount of correlation in turning direction, which is interpreted simply
231 as a sliding scale from $r = 0$ (no correlation) to $r = 1$ (complete correlation in turning direction).
232 Turning angles then were drawn from a circular distribution with $\mu = 0$, and $\sigma = f(r)$. Here we

233 use `simm.crw` function in the `adehabitatLT` package in R (Calenge 2006), which employs the chi
234 distribution for step-lengths and a wrapped normal distribution for turning direction. In our
235 simulations, h was varied across the range 1 – 5, and r between 0 and 0.5 to produce a range of
236 scenarios with low to moderate amounts of correlation.

237 Unfortunately, no studies have simulated the presence of dynamic interaction in wildlife
238 dyads. Therefore, we use the following procedure for simulating trajectories where dynamic
239 interaction is present. Two trajectories are simultaneously generated, the first a CRW (as in the
240 absent scenario), the second a random walk consisting of combinations (McClintock *et al.* 2012)
241 of CRW and biased correlated random walks (BCRW; Barton *et al.* 2009). To emulate
242 interactive behaviour, we modeled the bias towards the current position of the first CRW (i.e.,
243 the movement direction of the BCRW at time t is towards the position of the first CRW at time
244 $t+1$). If we had biased the CRW throughout the entire second simulated trajectory, it would have
245 produced a strong level of dynamic interaction at all times, which is unrealistic for many wildlife
246 scenarios. A more realistic scenario is one where behaviour may shift between interactive and
247 non-interactive phases. In the second trajectory, we simulate behaviour switches from non-
248 interactive into interactive phases (CRW to BCRW and vice-versa) with transition probability p ,
249 resulting in varied amounts of time spent in the interactive phase. The range of values chosen for
250 p ($0.001 \leq p \leq 0.005$) was appropriate for producing a realistic behaviour in our simulations
251 given that we simulated trajectories with $n = 2000$ to 3000 fixes. During the interactive phase,
252 step-lengths of the second trajectory were constrained so that the difference in step-lengths
253 between the first and second trajectories was $\leq 25\%$, producing realistic patterns of interaction in
254 movement speed as well as movement direction.

255 In a BCRW, three parameters (b , c , and ρ) govern different aspects of the bias effect
256 (Barton *et al.* 2009). We randomly varied the bias strength parameter (b) across a range of
257 acceptable values ($0.5 \leq b \leq 4$; Barton *et al.* 2009; Fronhofer, Hovestadt & Poethke 2013). The
258 shape parameter (c) governs how the proximity of the two individuals influences the magnitude
259 of the bias, which was varied randomly across a range of realistic values ($-0.3 \leq c \leq 0.3$). Finally,
260 ρ is a correlation parameter for the turning distribution, similar to r from the CRW, which we
261 also varied following previous studies ($0.8 \leq \rho \leq 0.9$; Barton *et al.* 2009; Fronhofer *et al.* 2013).
262 For more information see the Supplementary Material which contains the R code used for
263 simulating the presence of interaction with the BCRW, alongside a figure that demonstrates a
264 dyad with interaction present and a dyad with interaction absent. In total, 1000 simulated
265 scenarios were created to serve as a testing dataset, each containing two simulated dyads, one
266 with dynamic interaction present and one with dynamic interaction absent.

267 In order to examine the effect of varying sampling resolutions on indices of dynamic
268 interaction, we systematically down-sampled the simulated trajectories representing high
269 resolution telemetry data at four coarser levels (50%, 33%, 20%, and 10% of the original fixes).
270 This resulted in 1000 scenarios at each of five sampling resolutions (i.e., 100%, 50%, 33%, 20%,
271 and 10% of original fixes), each containing one dyad with dynamic interaction absent, and one
272 with dynamic interaction present.

273 3.2 – Empirical Data: White-tailed Deer GPS Telemetry Data

274 We collected data on a number of white-tailed deer from two study areas in south-central
275 Oklahoma, USA. Study site 1 was 1,214 ha in size, and was surrounded by a 15-strand, high-
276 tensile electric fence, thus restricting movement across property boundaries (2.5-m tall; Webb *et*
277 *al.* 2009). Study site 2 was 1,861 ha and consisted of 5-strand barbed-wire fences, which

278 allowed deer to cross property boundaries unrestricted. Vegetation on both study sites was
279 consistent with that of the Cross Timbers and Prairies ecoregion (Gee *et al.* 1994). On both
280 study sites, we captured deer during January–March (1998–2005 on study site 1; 2010–2012 on
281 study site 2) using modified drop-net systems (Gee, Holman & Demarais 1999). We sedated
282 deer using intramuscular injections of telazol (4.4 mg/kg) and xylazine (2.2 mg/kg), and used
283 yohimbine as an antagonist at 0.125 mg/kg. We fitted deer with GPS collars (ATS G2000
284 remote-release collars; Advanced Telemetry Systems, Inc., Isanti, MN) programmed to collect
285 1 fix every 15 (study site 1) or 30 minutes (study site 2). On study site 1, collars were capable of
286 collecting data for ~3 months, and on study site 2, collars collected data for ~6 months. All
287 capture, handling, and marking procedures were consistent with the guidelines of the American
288 Society of Mammalogists (Gannon *et al.* 2007) and were approved by permit from the Oklahoma
289 Department of Wildlife Conservation.

290 Three dyads of white-tailed deer (dyad 1 and 3 from study site 1 and dyad 2 from study
291 site 2) were selected to further demonstrate the performance of each index of dynamic interaction
292 using empirical telemetry data. We began with high-resolution GPS data recorded at a 30 min
293 sampling resolution¹, but systematically resampled data to reflect coarser fix intervals (i.e., 6 and
294 24 hours); which is a common practice (Webb *et al.* 2010). Final evaluation of dynamic
295 interaction measures occurred at three sampling resolutions: 30 min, 6 hour, and 24 hours.

296 We delineated 95% volume contour home ranges using the kernel density estimate
297 (Worton 1989) and the *ad hoc* bandwidth, which assumes the resulting density surface is
298 bivariate normal (Silverman 1986). For each dyad, we calculated the area of overlap of the two
299 home ranges (interpreted as the proportion of home range overlap - AOP; Millspaugh *et al.*

¹ Dyads 1 and 3 were tracked using a 15 min sampling resolution, but here we resampled the temporal resolution to 30 min for consistency with dyad 2.

2004) as a measure of static interaction that can be used as an *a priori* indicator of the potential for dynamic interaction in dyads. Similar to other studies, our hypothesis on the presence of dynamic interaction behaviour is based on a hierarchical approach where we first examine static interaction (home range overlap) between individuals (Figure 1), and subsequently look at finer resolution dynamic interactions. We predict little dynamic interaction in dyad 1 (AOP = 0.17), but greater dynamic interaction in dyads 2 and 3 (AOP = 0.67 and 0.57, respectively). We test these *a priori* predictions at all three sampling resolutions.

< Approximate location Figure 1 >

3.3 – Calculating measures of dynamic interaction

All eight indices of dynamic interaction (Table 2) were computed for each of the dyads in the simulation study and using empirical GPS data from white-tailed deer. Several of the indices required the selection of parameter thresholds for identifying $T_{\alpha\beta}$ fixes and $S_{\alpha\beta}$ fixes. A t_c threshold of $\frac{1}{2}$ the sampling resolution was used to determine simultaneous fixes, for example $t_c = 15$ min was used with the 30 min white tailed deer telemetry data. In the simulation study, a distance threshold parameter of $d_c = 2 * h$ was used, where h is the step-length parameter in the CRW. Previous research on deer interactions has used $d_c = 24$ m (Bertrand *et al.* 1996). We selected a more conservative value of $d_c = 50$ m based on visual observations of deer and because there would be greater potential for identifying dynamic interactions at this spatial resolution for testing purposes. However, depending on specific hypotheses to test, the spatial threshold may be adjusted higher or lower, and comparison across spatial thresholds could help identify the scale at which processes are occurring across the landscape. Validating identified thresholds for d_c using independent dyads will provide evidence as to whether a given threshold is appropriate.

323 We evaluate results of the 1000 simulations, examining the mean and standard deviation
324 of results from each index, for both the present and absent scenarios, along with significance of
325 statistical tests where appropriate. Histograms of index values for both the present and absent
326 scenarios are shown to highlight the distribution of results. Where statistical tests are employed
327 (i.e., in Don, Lixn, and Cs), we use an α -level of 0.01 to identify significant values. Results are
328 used to explore the effect of sampling resolution on each dynamic interaction index and to
329 compare among the various indices for measuring dynamic interaction in telemetry studies. The
330 relationship between index values and the amount of time spent in the interactive phase (in those
331 dyads with interaction simulated as present) is investigated using scatterplots and correlation
332 coefficients to quantify the effectiveness of indices for characterizing interactive behaviour, and
333 to identify scenarios where misleading results may occur. In those dyads where no interaction
334 was simulated (absent scenarios), the relationship between index values is compared to the level
335 of static interaction (AOP) in the dyad to discover how the level of static interaction influences
336 misleading inferences when interaction is absent. We chose one pair of dyads (see the
337 Supplementary Material) to examine in finer detail the performance of each index in scenarios
338 where interaction is present or absent. We compute index values at each resolution, along with
339 time-series plots to demonstrate how local analysis facilitates a finer treatment of interactive
340 behaviour.

341 In the white-tailed deer examples, we examine each index in finer detail for each
342 individual dyad. We explore the use of the local d_i statistic (Sec. 2.8) to examine temporal
343 variations in dynamic interaction behavior in these three dyads. At the finest sampling interval
344 (such as the 30 min sampling resolution here), the time-series plots of d_i can be noisy, making

345 interpretation of patterns difficult. To circumvent this problem, we present the time-series plot of
346 di for the 30 min data using a 24 hour moving average.

347 **4 – Results**

348 *4.1 Simulated Data*

349 Using simulated data to generate scenarios where dynamic interaction is present and
350 absent provided a useful means for assessing the differences and similarities between the eight
351 indices of dynamic interaction. Histograms for Prox, Ca, and HAI reveal that these three indices
352 are each capable of identifying cases where dynamic interaction was present and absent (Figure
353 2). All three indices are comparable in terms of interpretation, but the Prox and Ca indices are
354 essentially identical. The Prox, Ca, and HAI indices all appear to be robust to changes in
355 sampling resolution (Figure 2). The Don statistic also performed well, identifying interaction
356 (i.e., attraction) in all 1000 of the present scenarios, at each sampling resolution (Figure 2).
357 However, at all sampling resolutions, Don produced unexpectedly high Type I error; for
358 example, given that an α -level of 0.01 was used in the Don test, the number of falsely identified
359 occurrences of dynamic interaction identified in the absent simulations was higher than expected
360 (e.g., 98 of 1000 simulations at the 100% sampling resolution; Figure 2).

361 < Approximate Location of Figure 2 >

362 The Cs index also was successful at identifying correctly the presence of dynamic
363 interaction in all of the simulated scenarios (Figure 2). However, Cs was highly susceptible to
364 Type I error, which was more severe than Don in that Cs identified 380 of 1000 absent cases as
365 having significant dynamic interaction at the 100% sampling resolution, down to 222 of 1000
366 significant cases at the coarsest resolution (Figure 2). However, raw Cs index values were

367 relatively consistent across sampling resolutions, which suggests C_s , as an index, may be useful
368 without the formal statistical testing through the calculation of p -values.

369 The Lixn statistic performed poorest of all eight indices in that it was highly susceptible
370 to both Type I and Type II errors (Figure 2). Lixn failed to correctly identify dynamic
371 interactions in many of the present scenarios (Type II error), but this problem tended to be
372 reduced at finer sampling resolutions (e.g., 736/100 correctly identified as present at the 100%
373 sampling resolution vs. only 83/1000 at the 10% sampling resolution – Figure 2). More
374 problematic is the fact that Lixn also produces a high level of Type I errors; between 262 and
375 380 of 1000 of the absent scenarios were identified as having significant dynamic interaction.
376 The rate of Type I error also appears to increase at finer sampling resolutions, making the use of
377 Lixn problematic with modern high-resolution telemetry systems (e.g., GPS collars). The raw
378 Lixn values appear to be robust to changes in sampling resolution, but are hindered by high
379 variability in output results (and overlap of index distributions between present and absent
380 scenarios) leading to confusion in quantitative assessments (e.g., p -values).

381 As a path-based index of cohesive movement, C_r appears to be robust to changes in
382 sampling resolution (Figure 2). DI, on the other hand, was more sensitive to changes in sampling
383 resolution than C_r ; lower DI values occurred at finer sampling resolutions (Figure 2). However,
384 DI may be easier to interpret because of a relatively low variation in output values, and accurate
385 assignment to dynamic interaction when one actually is present (conversely, no dynamic
386 interaction for absent cases). Thus, at the global analysis level, it appears both C_r and DI provide
387 relatively robust and similar results.

388 To further examine simulation results, we explored the relationship between index values
389 and the proportion of time spent in the interactive phase (P_{int}) in present scenarios and level of

390 static interaction (AOP) in absent scenarios, focusing on the 100% sampling resolution. Several
391 patterns emerged from the correlation analysis (Figure 3; top row). Prox, Ca, Cs, HAI, Cr, and
392 DI all showed a strong, positive relationship with P_{int} ($r \geq 0.6$; Figure 3). Lixn on the other hand
393 showed a very weak positive relationship with P_{int} ($r = 0.209$; Figure 3). Further, by plotting
394 significant vs. non-significant results, we can see that with with Lixn, Type II error occurred
395 across the range of P_{int} scenarios suggesting that Lixn produces misleading interpretations even
396 when substantial interaction is present. The correlations associated with Don were ignored
397 because we only were able to plot p-values, which are not meaningful in this context.

398 < Approximate location Figure 3 >

399 In the absent scenarios, all indices showed a relatively weak relationship (Figure 3;
400 bottom row) with the level of static interaction (AOP) in the scenario (ignoring Don, since we
401 can only plot p -values). With those indices not employing statistical tests (Prox, Ca, HAI, Cr,
402 DI), index values were near 0 in all cases, correctly identifying no interaction. For Don, Lixn,
403 and Cs, Type I errors were produced across the range of AOP values (Figure 3), which is
404 problematic because it infers that a range of static interaction levels can result in misleading
405 interpretations.

406 We take one pair of dyads from the simulation to examine, in finer detail, the nature in
407 dynamic interaction, and the presence of Type I & II error. In the present case, the proportion of
408 time in the interactive phase was 0.53, and predictably, the level of static interaction was also
409 higher in the present case (AOP = 0.75) than in the absent case (0.30) (see the Supplementary
410 Material). First, looking at the dyad with interaction present, we see that Prox, Ca, and HAI
411 provide consistent results across all sampling resolutions (Table 4). Cr and DI both show
412 substantial interaction is present, but as seen before, the values are influenced by sampling

413 resolutions, increasing with coarser sampling data (Table 4). Cs and Don both successfully
414 identify significant interaction at all scales, while Lixn identifies significant interaction only at
415 the 100% and 33% resolutions (Table 4). In the absent scenario, Prox, Ca, HAI, Cr, and DI, all
416 identify no interaction in the data, each index ~ 0 . Don and Lixn, correctly identify the absence
417 of interaction; however, Cs incorrectly identifies significant interaction at all five scales (Type I
418 error – Table 4).

419 < Approximate location Table 4 >

420 To demonstrate how varying phases of dynamic interaction occur throughout simulated
421 trajectories, we plotted time series of di (along with proximity) to graphically investigate the
422 temporal phases of interactive behaviour of the two simulated dyads (Figure 4). Based on the
423 simulation parameters (see Supplementary Material) we know that the proportion of time in the
424 interactive phase was $P_{int} = 0.53$, which occurred across multiple phases. From the localized
425 time-series graphs, we identify when (and for how long) interactive behaviour occurs. In the
426 absent scenario, we see several instances later in the trajectories where the two objects become
427 proximal, but throughout the level of di remains near 0, correctly identifying no interactive
428 behaviour.

429 < Approximate location Figure 4 >

430 4.2 – Empirical Data: White-tailed Deer

431 Based on computed indices of static interaction (AOP) we predict little dynamic
432 interaction in dyad 1 (AOP = 0.17), but greater dynamic interaction in dyads 2 and 3 (AOP =
433 0.67 and 0.57, respectively). For dyad 1, 3 of the 8 indices indicated dynamic interaction in at
434 least one sampling resolution (i.e., either 30 min or 6 hr), but no interaction at the coarsest
435 sampling interval (24 hour) for all eight indices (Table 5). In general, indices did not show a

436 strong or consistent indication that these two individual deer were exhibiting dynamic
437 interaction. Also, for this particular dyad, indication of dynamic interaction appeared to
438 disappear as sampling resolution became coarser when using Don, Cs, and Lixn; otherwise,
439 indices did not reveal any interaction.

440 < Approximate location of Table 5 >

441 In dyad 2, the results showed much conflicting interpretation of whether dynamic
442 interaction was present at the different sampling resolutions and with each index (Table 5). The
443 Don and Cs indices identified significant attraction at all three sampling resolutions, Lixn
444 indicated random use, and Prox, Ca, HAI, Cr and DI showed the absence of any dynamic
445 interaction behaviour (Table 5). However, as Cr is similar to interpreting correlations, the values
446 (from 0.095-0.16) might be interpreted as minimal correlation in movements. Thus, in dyad 2, it
447 is particularly difficult to conclude whether or not dynamic interaction exists, which underscores
448 the difficulty in selecting an appropriate index.

449 With dyad 3, results indicated substantial and consistent dynamic interaction among
450 seven of the indices and at each sampling resolution (Table 5). Lixn suggested that there was
451 random use of the shared area across the three sampling resolutions. Given the ubiquitous
452 identification of dynamic interaction by 7 of the 8 indices, at all three sampling resolutions, we
453 conclude that positive interactive behaviour (i.e., both attraction and cohesive movement) does
454 exist in dyad 3.

455 While DI provides an overall index of cohesive movement, the local index d_i can be used
456 to examine spatial and temporal variations in cohesive movement behaviour. Due to varying
457 levels of dynamic interaction among the 3 dyads of deer, we plotted time series of d_i (and
458 temporal patterns of proximity between the two deer in meters) to graphically investigate the

459 spatial and temporal patterns of: 1) no interaction (top plot; dyad 1), 2) infrequent or minimal
460 interaction (middle plot; dyad 2), and 3) strong dynamic interaction (bottom plot; dyad 3) (Figure
461 4). In the plot of dyad 1, we first observe that distance between this dyad never exceeds 800 m.
462 However, the observed separation between the dyad appears random because there is little
463 variation in the plot of d_i (minimal variation around $d_i = 0$). In the plot for dyad 2, most
464 simultaneous locations were within 1000 m of each other; however, in a few instances, locations
465 of the two deer were >3000 m apart. Global statistics for the 8 indices revealed discrepancies in
466 the dynamic interaction behaviour in dyad 2. However, plotting d_i revealed that dyad 2 did in
467 fact exhibit dynamic interaction on multiple occasions. Finally, the plot for dyad 3 revealed
468 definitively the presence of strong dynamic interaction. Across much of the 3-month sampling
469 period, the dyad of male deer remained proximal for extended periods of time, with
470 corresponding cohesive movement. Although dynamic interaction is occurring across most of the
471 sampling period, this graph reveals periods of variable levels of dynamic interaction through
472 time.

473 < Approximate location Figure 4 >

474 **5 – Discussion**

475 The simulated data (and subsequent analysis) allowed the identification of several indices
476 that will be useful when applied to empirical wildlife telemetry data; including high resolution
477 data such as those collected from GPS collars. The case study on white-tailed deer revealed that
478 minimal AOP resulted in minimal dynamic interaction, but higher levels of AOP did not
479 necessarily equate to dynamic interaction behaviour because AOP relies on a 2-dimensional
480 home range that does not account for the simultaneous use of these areas, which is inferred using
481 both point- and path-based measures of interaction. The results from all eight indices

482 corroborated what is known about the seasonal biology of white-tailed deer; dyad 3 was a dyad
483 of male deer of ~3 years of age that were part of the same bachelor group. Although we used
484 white-tailed deer as a case study to assess various indices of dynamic interaction and behaviour;
485 the indices and guidelines we discuss can be applied much more broadly to animal behaviour
486 studies, and even for the analysis of any two moving objects in space and time (e.g., dyads of
487 vehicles, cell-phone users, athletes, etc.).

488 *5.1 – Comparison across indices*

489 The Prox, Ca, and HAI indices produce nearly identical values in all cases, owing to the
490 similarity in their derivation. In our examples, HAI produced similar values to Prox and Ca and
491 identical interpretation of attraction in both the simulation study, and in the white-tailed deer
492 case study. Our results also suggest that three of the classical indices of dynamic interaction
493 (Don, Cs, and Lixn) can be misleading, especially with high-resolution telemetry data.
494 Misleading results are due to statistical testing procedures being especially susceptible to Type I
495 error. Type II error was only problematic in the case of Lixn, as Don and Cs were only not-
496 significant in those present scenarios where interaction was low ($P_{int} < 0.2$; Figure 3). Plots and
497 contingency tables accompanying the Don statistic may be more useful for interpretation than
498 computed p -values; for instance, when examining the effect of the d_c parameter. Similarly, the
499 Cs index may still be a useful measure of dynamic interaction (despite the high type I error rate
500 when used in a hypothesis testing framework) because it was able to adequately separate
501 between the presence and absence of dynamic interaction. In the simulation experiment, Cs
502 showed a direct relationship with the proportion of time spent in the interactive phase. Further,
503 Cs measures a unique property of the data apart from other indices by utilizing the raw distances
504 between fixes rather than a subjectively defined distance threshold (d_c). Unlike the other indices,

505 Lixn index tests for dynamic interaction based on simultaneous use of the shared area (Minta,
506 1992). However, despite examining co-occurrence of the shared area, Lixn appears to be poorly
507 suited for measuring dynamic interaction in wildlife telemetry datasets.

508 Cr and DI measure dynamic interaction as the cohesiveness in movement using a path-
509 based approach. Cr values were consistent across sampling intervals, making it a suitable
510 candidate for measuring dynamic interaction with modern telemetry datasets. The primary
511 limitation of Cr is that it is dependent on measuring correlations relative to a mean path vector,
512 which is typically not meaningful in the context of dynamic interaction analysis. DI was
513 sensitive to changes in sampling resolution producing a lower index value at the highest
514 resolution. The advantage of the DI approach is in examining spatial variation in dynamic
515 interactions through the local level statistic – di.

516 *5.2 – Static vs. dynamic interaction*

517 We looked at three white-tailed deer dyads containing static interaction levels of AOP =
518 0.17, 0.67, and 0.57, respectively. However, only dyad 3 (AOP = 0.57) showed substantial
519 dynamic interaction, which agrees with the seasonal biology of male deer during this time; male
520 deer form bachelor groups during spring and summer (Hirth 1977). Thus, we were able to
521 identify a dyad of deer belonging to the same bachelor group using dynamic interaction metrics,
522 particularly di (see Figure 4). Further, while the converse may be true (i.e., no static interaction
523 implies no dynamic interaction), our analysis suggests that the relationship between the level of
524 static interaction and presence of dynamic interaction is complex and inferring dynamic
525 interaction from static interaction can be misleading. For example, with our simulations, we
526 produced a range of AOP values, from which no interaction was present. Incorrect inferences
527 may be most problematic for species inhabiting relatively large home range areas, where joint

528 space use (i.e., home range overlap) can occur without individuals ever encountering one another
529 from a temporal standpoint. Quantitative indices of dynamic interaction allow researchers to
530 examine a wide range of questions relating to animal behaviour and general ecology, and go
531 beyond typical measures of static interaction (e.g., home range overlap). Current methods (e.g.,
532 those outlined here) only begin to scratch the surface of the potential for space-time analysis in
533 wildlife systems where multiple animals are tracked simultaneously with high resolution tracking
534 devices.

535 Recent research has suggested that measures of static interaction (like AOP) can be used
536 to estimate contact-rates and levels of dynamic interaction between wildlife, important in
537 modeling disease transmission (Robert, Garant & Pelletier 2012). Our analysis reveals the flaws
538 in this assumption, as even moderate levels of static interaction may have highly variable contact
539 rates and levels of dynamic interaction (e.g., Figure 3). However, some disease transmission
540 occurs via mechanisms that simply relate to spatial overlap, through feces or saliva (e.g., chronic
541 wasting disease, Williams *et al.* 2002), or intermediate hosts (e.g., West Nile virus, Marra *et al.*
542 2004). Thus, the nature of disease transmission will be important in identifying whether
543 measures of static or dynamic interaction are appropriate.

544 5.3 – Scale

545 Our simulation study outlined a key problem commonly encountered in wildlife
546 movement analysis; inferences made at one scale of analysis do not necessarily hold at other
547 scales (see Laube & Purves 2011 for a more thorough discussion of this). Indices that do not
548 formally test statistical significance appear to be less sensitive to varying scales (i.e., Prox, Ca,
549 HAI, Cr, DI) when compared to indices that implement statistical tests (i.e., Don, Cs, Lixn).
550 Beyond scale, inference among indices is impacted by the nature or level of dynamic interaction

551 present. Most methods appear to successfully identify strong dynamic interaction when present
552 (e.g., simulations, and deer dyad 3) with greater inconsistencies occurring for infrequent or low
553 levels of dynamic interaction (e.g., deer dyad 2). Our guidelines will help inform the selection of
554 appropriate indices given varying scales and levels of dynamic interaction.

555 The implementation of the local-level statistic (i.e., d_i), along with time-series plots of
556 proximity (e.g., in Figure 4 and Figure 5), reveals information on infrequent (e.g., deer dyad 1),
557 variable (e.g., deer dyad 2), and frequent (e.g., deer dyad 3) interactions. The prevalence of
558 infrequent and variable interactions in wildlife is unknown, which typically is the motivating
559 factor for assessing the level of dynamic interaction, and the d_i index represents a new metric for
560 revealing both frequent and infrequent interactive behaviour. Animals are now routinely tracked
561 for an extended duration (e.g., several months) with fine resolution telemetry fix rates (e.g., sub-
562 hour sampling intervals), allowing the identification of rare and periodic interactive behaviour,
563 which has important implications on a wide range of studies such as disease spread (Böhm *et al.*
564 2008), patterns of sociality (Gorman *et al.* 2006), and predator-prey dynamics (Eriksen *et al.*
565 2008).

566 We only superficially examine the temporal local dynamics in d_i . More sophisticated
567 analysis could involve other temporal variables to investigate more complex problems, such as
568 circadian rhythms, seasonality, and weather factors. Variations in the level of dynamic
569 interaction (measured through d_i) may be a result of different behaviour states that can relate to
570 resting, foraging, or travelling behaviour (Dzialak *et al.* *Unpublished data*). Including a
571 quantitative characterization of movement behaviour (e.g., Morales *et al.* 2004; Jonsen,
572 Flemming, & Myers 2005; Gurarie, Andrews, & Laidre 2009) for comparison could enhance
573 interpretation of changes in dynamic interaction when using the d_i measure. Similarly, by

574 mapping the local statistic d_i , one can investigate the role of fine scale landscape and
575 environmental variables on the observed patterns of dynamic interaction. For example, in
576 northern Alberta, Canada, high levels of anthropogenic disturbance are causing increased
577 permeability in the landscape, resulting in a higher potential for caribou predation by wolves
578 (Latham *et al.* 2011). To assist in maintaining the caribou population, the Government of Alberta
579 has promoted the culling of wolves. Novel dynamic interaction analysis, through local d_i , could
580 help reveal the landscape characteristics (e.g., habitat, fragmentation, topography) associated
581 with predation in order to better inform land management policies (e.g., Dzialak *et al.* 2011;
582 Wasser *et al.* 2011), rather than adopt more extreme measures such as culling.

583 5.4 – Statistical testing

584 In wildlife telemetry research, the effects of sampling resolution and autocorrelation are
585 well documented (e.g., home range delineation – Swihart & Slade 1985; Seaman & Powell 1996,
586 habitat selection models – Otis & White 1999; Nielsen *et al.* 2002, behaviour analyses – Boyce
587 *et al.* 2010). Yet, little is known about the effects of autocorrelated data and sampling resolution
588 on indices of dynamic interaction. Serial autocorrelation in successive fixes of telemetry data
589 increases with higher sampling frequency (Dray, Royer-Carenzi & Calenge 2010) and hinders
590 the use of methods where independence is assumed (Swihart & Slade 1985), as standard errors
591 will typically be underestimated. In the presence of highly autocorrelated data, statistical tests
592 can be overly sensitive, producing false positives more frequently as the degree of
593 autocorrelation increases. While some have argued that the autocorrelation problem can be
594 overcome by down-sampling telemetry data until it is functionally independent (Swihart & Slade
595 1997), this procedure has been criticized due to loss of biologically relevant data (de Solla,
596 Bonduriansky & Brooks 1999). Alternately, it may be more effective to implement statistical

597 methods that accommodate (de Solla *et al.* 1999; Nielsen *et al.* 2002), are less sensitive to
598 autocorrelated structures (Fieberg 2007), or adjust the null distribution so that it is appropriate
599 for autocorrelated data (White & Harris 1994). With dynamic interaction analysis, it is pragmatic
600 to think of the autocorrelation problem from a sampling strategy perspective, that is, more
601 (autocorrelated) data provides a better representation of the animals true movement path (Fieberg
602 2007). Finer space-time analysis is possible with greater sampling resolution, enabling better
603 estimates of true dynamic interaction and contact rates between individuals.

604 Several of the indices we examined use formal statistical tests for the presence of
605 dynamic interaction that require the generation of null distributions in order to test the
606 expectation of no interaction. In Don and Cs, these null distributions are generated by permuting
607 the observed fixes of the two animals and measuring the distance between the two permuted
608 fixes. Generating null distributions through permutations of observed data assumes that the data
609 are independent and identically distributed within individual trajectories, but also that the two
610 individuals move independently of one another. As such, permutations typically result in an
611 incorrect expectation leading to increased Type I error when data are autocorrelated (White &
612 Harris 1994). Further, Cs is more susceptible to Type I errors than Don, owing to the use of raw
613 distance values in its calculations. More appropriate methods for generating null expectations for
614 statistical tests are warranted, either using random walk simulations (e.g., White & Harris 1994;
615 Miller 2012) or by developing more appropriate mechanistic models.

616 With Lixn the statistical test is based on expectations derived from the relative area
617 values of each home range overlap section (inhabited by α only, β only, and overlapping area).
618 We initially thought that if the area of home range overlap is relatively large, Lixn is susceptible
619 to Type I error; conversely, if the overlap is relatively small, Lixn may be susceptible to Type II

620 error. However, from the simulation study, we revealed that Lixn was susceptible to Type I error
621 across a range of overlap values (Figure 3). Given that Lixn relies explicitly on the calculation
622 of individual home ranges, Lixn is further confounded by problems associated with producing
623 reliable home range estimates (e.g., Hemson *et al.* 2005; Börger *et al.* 2006; Downs & Horner
624 2008). Thus, Lixn represents a measure of simultaneous home range use, somewhere in between
625 typical measures of static interaction (like AOP) and the other measures of dynamic interaction.
626 Animals typically use their home range in a non-homogenous fashion (Samuel, Pierce & Garton
627 1985); therefore expectations derived from the overlap of home ranges may be misleading
628 relative to actual space use intensity patterns – typically represented by a utilization distribution
629 (Worton 1989). An improved formulation for Lixn could derive the expected values as a function
630 of the joint distribution of two individual utilization distributions (see Powell 2000; Fieberg &
631 Kochanny 2005), assuming the animals move independently of one another.

632 5.5 – Guidelines

633 The role of classical hypothesis testing in ecological analysis continues to be questioned
634 (e.g., Hobbs & Hilborn 2006), and in the context of measuring dynamic interactions, our results
635 suggest that procedures avoiding null hypothesis testing provide greater insight into interactive
636 behaviour patterns. Most times, statistical hypothesis testing is not the goal; rather it is the
637 identification of an ecological mechanism (e.g., why are animals interactive at a given point?).
638 The usefulness of Prox, Ca, and HAI owe to the simplicity of their (near identical) calculation
639 and interpretation, and as demonstrated produce nearly identical results. The Don and Cs indices
640 suffer from the susceptibility of their statistical testing procedures to Type I errors, and in the
641 case of Cs, a problem magnified with high resolution GPS telemetry data. Cs, due its formulation
642 based on raw distances, may still be useful to examine this separate property of the data;

643 however, we suggest that a subjective interpretation be employed. The Don index measures
644 attraction similar to Prox, Ca, and HAI, and we advocate the use of those methods over the Don
645 index. The Lixn index suffers from the same statistical problems as Don and Cs, but also from
646 the configurational problems related to the general task of home range delineation. Lixn
647 performed poorly when viewed as a stand-alone index and provided contrasting results in the
648 white-tailed deer case study, and as such we do not recommend its use.

649 Novel path-based measures of dynamic interaction (i.e., Cr, DI) examine the
650 cohesiveness in movement segments, rather than proximity or arrangement of fixes represented
651 as spatial points. Of these two metrics, Cr appeared to be least sensitive to sampling resolution,
652 but did suffer from high variation in index values. DI provides novel insight into the spatial
653 variation in dynamic interaction behaviour through the use of the local di statistic. Thus, di is
654 most useful with high resolution GPS telemetry data because of the ability to examine spatial and
655 temporal changes in dynamic interaction behaviour. Neither Cr or DI consider the spatial
656 distance between individuals, and analyzing dyads alongside some measure of proximity (e.g.,
657 Figure 4) provides added context for these path-based measures of dynamic interaction.

658 The following points can be used to guide decisions when studying dynamic interaction
659 in wildlife telemetry datasets. First, it is necessary to identify the presence of temporal overlap in
660 α and β to assess if a dyad offers potential for interactive behaviour. A measure of static
661 interaction (e.g., AOP, as used here) can be used to assess joint space use. Second, Prox, Ca, or
662 HAI can be used as an index of attraction or avoidance behaviour. Alternatively, Cs can be used
663 as a measure of attraction or avoidance that is based on raw distances; however statistical
664 inference should be avoided. Third, Cr or DI can be used as an index of the overall level of

665 cohesion in movement segments. Finally, d_i can be used to further investigate local-level
666 variations in the cohesiveness of movement, especially within proximal episodes.

667 *5.6 – Future Directions*

668 The development of more sophisticated simulation models that emulate the complex
669 nature of dynamic interactions present in wildlife dyads is required to further advance
670 understanding of the capability of current and future methods aimed at measuring dynamic
671 interaction behaviour. Here we provide a simple and straightforward procedure for simulating
672 the presence of dynamic interaction in movement dyads using biased correlated random walks
673 (Codling *et al.* 2004), where the bias component is set to be the current location of the other
674 individual. We vary parameters related to distance-decay between individuals and bias-strength
675 over ranges that have been tested in studies looking at correlated random walks biased towards
676 favorable habitat patches (e.g., Barton *et al.* 2009; Fronhofer *et al.* 2013). Further testing is
677 required to examine the role of these parameters in the context of interactive behaviour.

678 Agent-based models (Bennett & Tang 2006) offer the opportunity to incorporate
679 increasingly detailed and sophisticated interactive behaviour patterns into simulations. New
680 technologies are now integrating robotic agents into real-world scenarios that are capable of
681 interacting with live organisms (Krause, Winfield & Deneubourg 2011). Programming different
682 movement patterns with robotic agents may provide novel opportunities to study new and unique
683 problems looking at different interactive behaviour in robot-organism dyads.

684 Researchers are now capable of directly measuring animal contacts through the use of
685 proximity collars. Proximity collars utilize ultra-high frequency radio (UHF) to detect when two
686 (or more) collars are within a pre-programmed distance of another (Prange *et al.* 2006).
687 Specifically, proximity collars measure contact rates directly, as opposed to inferring contact as

688 is done with telemetry data through the use of the temporal threshold t_c and measures such as
689 Prox. This direct measurement of contact is especially important in the study of disease
690 transmission, where existing tracking systems are hindered by the lack of information between
691 fixes (Böhm, Hutchings & White 2009). Traditional tracking technologies also have been limited
692 in studying dynamic interactions and contact rates in smaller animals due to the combined effect
693 of their fine-scale movements and the positional error of VHF or GPS sensors. Also, missing
694 telemetry fixes are often prevalent due to the cryptic habitats frequented by smaller animals (e.g.,
695 nests, burrows, and man-made structures) further motivating the use of alternative sensors. For
696 example, interesting social behaviour has been revealed in possums (Ji, White & Clout 2005) and
697 raccoons (Prange, Gehrt & Hauver 2011) using proximity collars. Proximity collars are limited
698 in that they provide no location information on where contacts occur, but can be analyzed with
699 temporal variables, or additional bio-sensors (e.g., Laske, Garshelis, & Iaizzo 2011), to study
700 timing patterns and rates of contacts. A combined tracking-proximity collar system would be
701 advantageous in order to simultaneously investigate contacts along with location (Davis *et al.*
702 2013) and to provide validation data for tracking-based dynamic interaction indices.

703 The future of dynamic interaction research likely lies with modifying more complex
704 mechanistic movement models (e.g., Morales *et al.* 2004; Jonsen *et al.* 2005) for studying
705 interactive behaviour patterns. Given the flexible inferential framework under which most of
706 these models are developed (see Patterson *et al.* 2008), incorporating the effects of mobile con-
707 or cross-specifics in order to study dynamic interactions is imperative to further advancing
708 mechanistic movement models (Haydon *et al.* 2008; McClintock *et al.* 2012). For example, in
709 studying grey seals, McClintock *et al.* (2012) utilize a small number of known ‘centres of
710 attraction’ in order to model seal movements. Extension of a similar model to the study of

711 dynamic interactions might assume, for example, that during an interactive phase, centers of
712 attraction would be the locations of another individual based on biased random walks, as in our
713 simulation study. In predator-prey situations, this relationship would be further complicated by
714 the attraction of predators to prey, and the avoidance of prey to predators. As they are able to
715 explicitly accommodate environmental covariates (e.g., Patterson *et al.* 2009), mechanistic
716 movement models are primed to take dynamic interaction analysis to the next phase, whereby the
717 combined effect of habitat and other environmental covariates on dynamic interaction is explicit
718 within the analysis framework.

719

720 **6 – Conclusion**

721 There still is much to be learned about animal behaviour. Despite recent technological
722 advances, much research builds on early studies that relied on visual observations of animals
723 (Hirth 1977), which is limited by animal activity patterns, habitat use, and observation bias. For
724 example, early accounts on the breeding behaviour of white-tailed deer were based on visual
725 observations, but recent molecular genetic techniques have revealed greater insight into the
726 breeding biology of deer (e.g., DeYoung *et al.* 2009). Then, indices of dynamic interaction can
727 be leveraged to further study rare behavioural interactions that are not readily observed visually
728 while in the field. Other avenues of research that may benefit from recently developed
729 techniques to study dynamic interactions and contact rates (e.g., contact at d_c) include: studies of
730 behaviour and ecology, territory defense, determining mating and reproduction events, assessing
731 disease spread through direct contact, interspecific competition for resources, and intra- and
732 interspecific interactions. One of the most pervasive topics deals with potential for disease
733 spread, particularly when wild animal species come into contact with domestic livestock

734 (Wyckoff *et al.* 2009). Combining behavioural indices with spatially-explicit landscape data or
735 genetic data will provide greater insight into unobservable phenomena that shape animal
736 populations (demographics and dynamics) and long-term fitness measures (e.g., reproductive
737 success).

738 In summary, the calculation of contact rates and measures of dynamic interaction offer
739 promise in studying dynamically moving objects in a wide range of fields from pure scientific
740 discovery and ethology to application and management. Herein, we have provided general points
741 on the formulation, interpretation, and use of dynamic interaction indices that can be used to
742 guide future research. Specifically, we have found existing techniques relying on significant-tests
743 to be misleading (e.g., Don, Cs, and Lixn) due largely to the propensity to falsely identify
744 dynamic interaction when it is absent. Further, local-level analysis provides more illuminating
745 evidence of the complex nature of interactive behaviour in wildlife dyads; especially with
746 modern high-resolution telemetry systems. In future research, it will prove useful to combine
747 local-level measurements of dynamic interaction (e.g., di, Long & Nelson 2013) with landscape
748 data to determine where interactions are linked to; for example, to determine preferred resources
749 on the landscape, dietary or niche overlap (within and between species), and the potential for
750 disease spread. To make these methods and indices as widely available as possible, we have
751 implemented each of the eight indices in the R statistical computing environment, and made this
752 code openly available to other users <Website Link>.

753 **Acknowledgements**

754 < TBD >

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Table 1: Selected examples of applications involving the study of dynamic interactions using wildlife telemetry data.

Index	Species	Data	Study Objective	Citation
Prox	white-tailed deer (<i>Odocoileus virginianus</i>)	VHF	Parturition	(Bertrand <i>et al.</i> 1996)
	maned wolves (<i>Chrysocyon brachyurus</i>)	GPS	Familial bonds	(Bandeira de Melo <i>et al.</i> 2007)
Ca	maned wolves (<i>Chrysocyon brachyurus</i>)	VHF	Inter- & intra-sex behaviour	(de Almeida Jácomo <i>et al.</i> 2009)
	red wolves (<i>Canis rufus</i>)	GPS	Sociality, group behaviour	(Karlin & Chadwick 2011)
Don	wood mice (<i>Apodemus sylvaticus</i>)	VHF	Mating	(Tew & Macdonald 1994)
	raccoons (<i>Procyon lotor</i>)	VHF	Philopatry	(Gehrt & Fritzell 1998)
	coyote (<i>Canis latrans</i>)	VHF	Inter- & intra-sex behaviour	(Chamberlain, Lovell & Leopold 2000)
	badgers (<i>Meles meles</i>)	VHF	Sociality, group behaviour	(Böhm <i>et al.</i> 2008)
Cs	lynx (<i>Lynx canadensis</i>)	VHF	Inter- & intra-sex behaviour	(Poole 1995)
	red & grey squirrels (<i>Sciurus vulgaris</i> & <i>carolinensis</i>)	VHF	Interspecific	(Kenward & Hodder 1998)
	wolves & moose (<i>Canis lupus</i> & <i>Alces alces</i>)	GPS	Interspecific	(Eriksen <i>et al.</i> 2008)
Lixn	badgers (<i>Taxidea taxus</i>)	VHF	Inter- & intra-sex behaviour	(Minta 1993)
	grizzly bear (<i>Ursus arctos</i>)	VHF	Inter- & intra-sex behaviour	(Mace & Waller 1997)
	mountain lion (<i>Puma concolor</i>)	VHF	Familial bonds	(Nicholson <i>et al.</i> 2011)
HAI	coyote (<i>Canis latrans</i>)	VHF	Management and control	(Bromley & Gese 2001)
	coyote (<i>Canis latrans</i>)	VHF	Habitat relations	(Atwood & Weeks 2003)
Cr	caribou (<i>Rangifer tarandus</i>)	VHF	Sociality, group behaviour	(Shirabe 2006)
DI	grizzly bear (<i>Ursus arctos</i>)	GPS	Mating	(Long & Nelson 2013)

Table 2: Eight indices of dynamic interaction for wildlife telemetry data. Refer to Table 3 for terminology. In all indices, except for Lixn, simultaneous fixes ($T_{\alpha\beta}$) are determined using a temporal threshold (t_c) and d_c is a threshold distance for proximal fixes ($S_{\alpha\beta}$).

Index	Reference	Sig. Test	Data	Tests	Interpretation
Prox	-	-	Point	Ratio of $ST_{\alpha\beta}$ fixes to $T_{\alpha\beta}$ fixes, based on d_c .	Prox can be interpreted much like Ca (see below) and is similarly based on d_c .
Ca	Cole (1949)	-	Point	The proportion of all fixes that are $ST_{\alpha\beta}$ based on d_c .	Ca ~ 1 – attraction Ca ~ 0 – no association
Don	Doncaster (1990)	χ^2 test	Point	If the distribution of distances of $T_{\alpha\beta}$ is different than the distances of permutations of all fixes.	Based on the contingency table and a χ^2 test looks for significant attraction in $ST_{\alpha\beta}$ for a given d_c .
Lixn	Minta (1992)	χ^2 test	Point	The simultaneity of usage of the shared area of each home range.	$L_{ixn} > 0$, shared use is simultaneous (attraction) $L_{ixn} < 0$, shared use is solitary (avoidance) $L_{ixn} \sim 0$ shared use is random
Cs	Kenward (1993)	Wilcoxon signed-rank test	Point	For differences between distances of $T_{\alpha\beta}$ and distances of permutations of all fixes.	Cs ~ 1 – attraction Cs ~ -1 – avoidance
HAI	Atwood & Weeks (2003)	-	Point	Number of $ST_{\alpha\beta}$ fixes within the shared area of the home range against solitary use of shared area.	HAI ~ 1 – attraction HAI ~ 0 – avoidance
Cr	Shirabe (2006)	-	Path	Correlation of movement segments tested against respective path means. Identical to Pearson correlation statistic (r).	Cr ~ 1 – positive correlation (cohesion) Cr ~ -1 – negative correlation (opposition) Cr ~ 0 – no correlation (random)
DI	Long & Nelson (2013)	-	Path	Cohesion in individual movement segments (global and local), with respect to distance and direction.	DI ~ 1 – cohesive movement DI ~ -1 – opposing movement DI ~ 0 – random movement

Table 3: Terminology and notation used for describing telemetry data and dynamic interaction methods.

Term	Explanation
α or β	Individuals of a dyad (telemetry data)
dyad	Pair of individuals (α and β)
fix	A telemetry record (spatial location and time stamp)
t_c	Time threshold
d_c	Distance threshold
$T_{\alpha\beta}$	Temporally simultaneous fixes based on t_c
$S_{\alpha\beta}$	Spatially proximal fixes based on d_c
$ST_{\alpha\beta}$	Spatially proximal and temporally simultaneous fixes based on d_c and t_c
v_t, w_t	Movement segment, vector connecting two consecutive fixes
\bar{v}, \bar{w}	Mean movement segment for an entire path

Table 4: Index results from single scenario analysis in the simulation experiment, * denotes significant values ($p < 0.01$). A video, along with the parameterization, of these two dyads is available in the supplementary material.

		Prox	Ca	Don	Lixn	Cs	HAI	Cr	DI
Present	<i>100%</i>	0.427	0.427	0 *	0.626 *	0.607 *	0.456	0.324	0.277
	<i>50%</i>	0.427	0.427	0 *	0.586	0.608 *	0.452	0.364	0.287
	<i>33%</i>	0.435	0.435	0 *	0.765 *	0.609 *	0.458	0.359	0.305
	<i>20%</i>	0.413	0.413	0 *	0.343	0.608 *	0.432	0.409	0.332
	<i>10%</i>	0.427	0.427	0 *	-0.738	0.607 *	0.446	0.401	0.387
Absent	<i>100%</i>	0	0	0.262	-0.614	0.051 *	0	0.012	-0.002
	<i>50%</i>	0	0	0.582	-0.614	0.051 *	0	0.016	-0.001
	<i>33%</i>	0	0	0.791	-0.593	0.050 *	0	0.010	0.005
	<i>20%</i>	0	0	1	-0.538	0.051 *	0	-0.022	-0.010
	<i>10%</i>	0	0	1	-0.497	0.051 *	0	0.001	-0.016

Table 5: Results of dynamic interactions using empirical GPS data collected from white-tailed deer in Oklahoma, USA. Dynamic interactions were tested at three temporal resolutions (30 min, 6 hr, and 24 hr) for eight indices of dynamic interaction. Values highlighted in grey indicate significance at $p < 0.01$.

Dyad	Sampling Resolution			Interpretation
	30 min	6 hr	24 hr	
1	30 min	6 hr	24 hr	
Prox	0.017	0.030	0.018	No proximity
Ca	0.014	0.025	0.016	No attraction
Don (p-val.)	0	0.0042	0.66	Varies depending on scale, attraction at 30 min and 6hr
Cs	0.013	0.02	0.01	Varies depending on scale, attraction at 30 min and 6 hr
Lixn	-0.19	0.11	0.058	Simultaneous use of shared area at 30 min, but not at coarser scales
HAI	0.037	0.053	0.044	No attraction within shared area
Cr	-0.022	0.079	0.060	No correlation
DI	-0.004	0.021	-0.014	No dynamic interaction
2	30 min	6 hr	24 hr	
Prox	0.071	0.073	0.072	No proximity
Ca	0.069	0.07	0.07	No attraction
Don (p-val.)	0	0	0	Attraction
Cs	0.10	0.10	0.10	Attraction
Lixn	0.37	0.31	0.32	Random use of shared area
HAI	0.074	0.077	0.075	No attraction within shared area
Cr	0.095	0.16	0.11	Very low positive correlation
DI	0.029	0.11	0.028	No dynamic interaction
3	30 min	6 hr	24 hr	
Prox	0.57	0.57	0.58	Poximity
Ca	0.53	0.52	0.54	Attraction
Don (p-val.)	0	0	0	Attraction
Cs	0.40	0.39	0.36	Attraction
Lixn	0.11	0.21	0.21	Random use of shared area
HAI	0.60	0.60	0.61	Attraction within shared area
Cr	0.59	0.66	0.72	Positive correlation
DI	0.28	0.57	0.61	Positive dynamic interaction (cohesive movement)

Figure 1: Empirical GPS telemetry data for three white-tailed deer dyads ($n = 6$ deer). Contours (grey and black polygons) represent 95% volume contour home ranges using kernel density estimates, along with static interaction measured as the area of overlap proportion (AOP) of the two individual home ranges. AOP is depicted as the grey shaded region. Deer in dyads 1 and 3 were tracked for approximately 3 months; while in dyad 2, deer were tracked approximately 6 months.

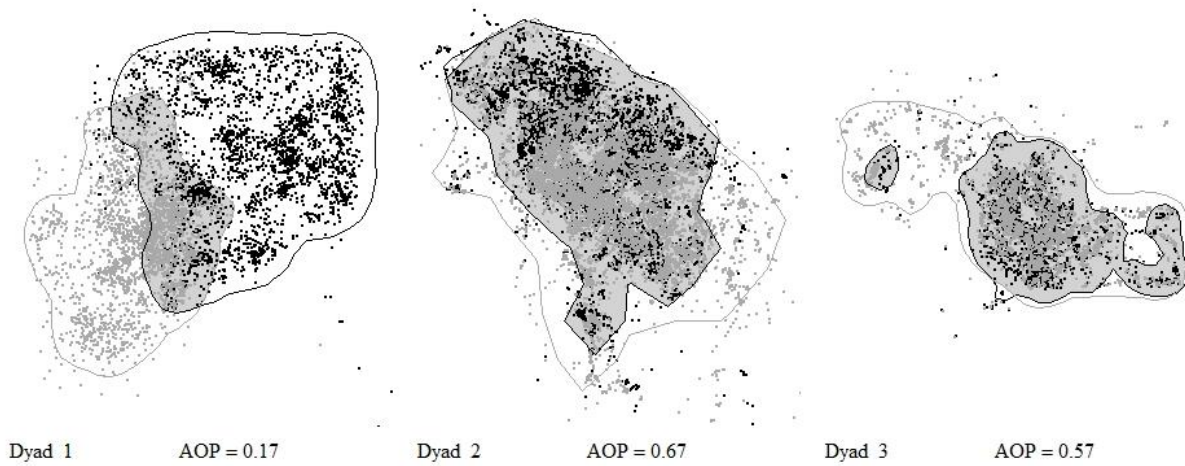


Figure 2: Results from simulations where 1000 scenarios were generated, each containing one dyad, under two circumstances: 1) dynamic interaction present (medium grey histogram) and 2) dynamic interaction absent (light grey histogram). Dark grey indicates where the index values overlap. Each scenario was examined at five sampling resolutions (100% , 50%, 33%, 20%, 10% of fixes). Along with the histogram of index values, we present the mean, standard deviation (in brackets), and number of significant results where appropriate ($p < 0.01$ – denoted by *). Note: values plotted for Don are simply p -values as no stand-alone index is generated with Don.

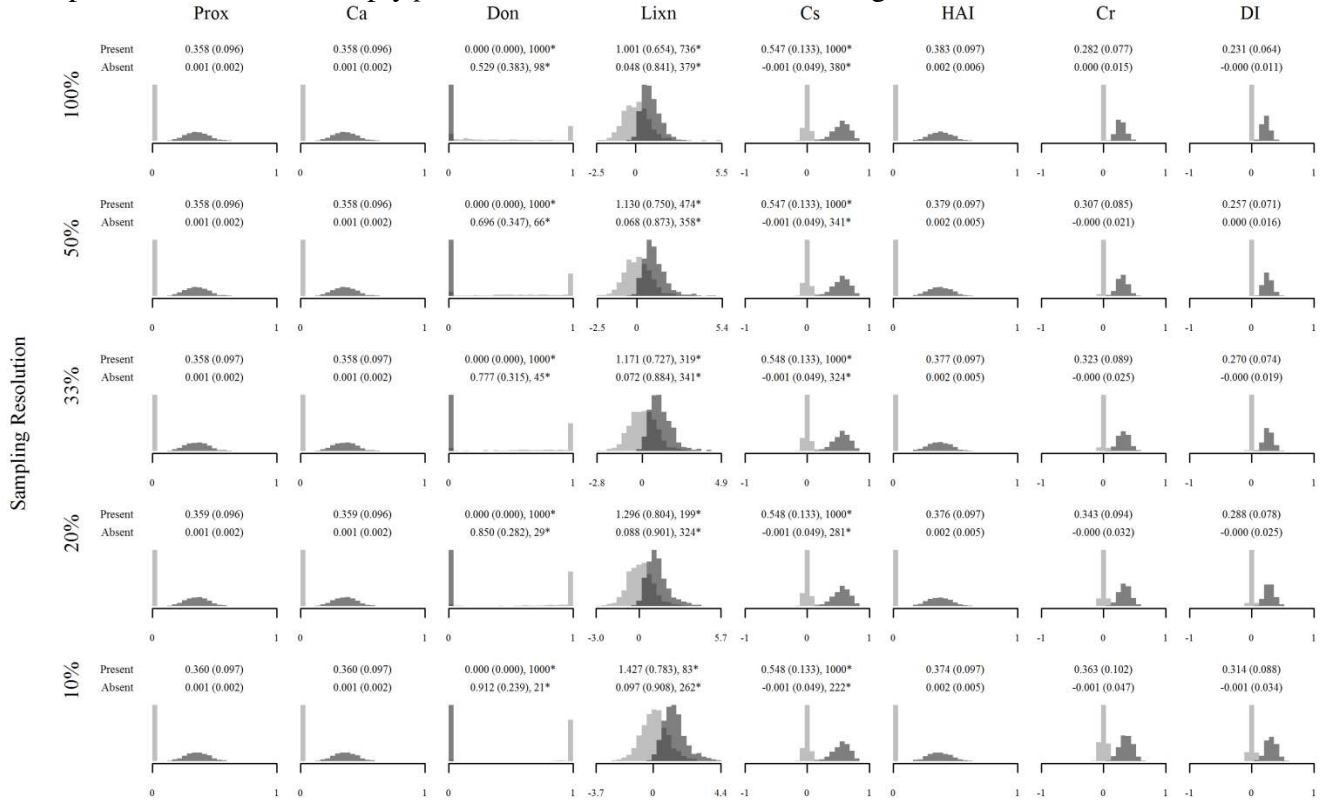


Figure 3: Correlation between indices of dynamic interaction and proportion of time in the interactive phase (P_{int}) from the scenarios where interaction was simulated as present (top row); and static interaction (AOP) from the dyads where interaction was simulated as absent (bottom row). Values plotted using an open circle denote Type II error in the top row (no significant interaction when present) and Type I error in the bottom row (significant interaction when absent).

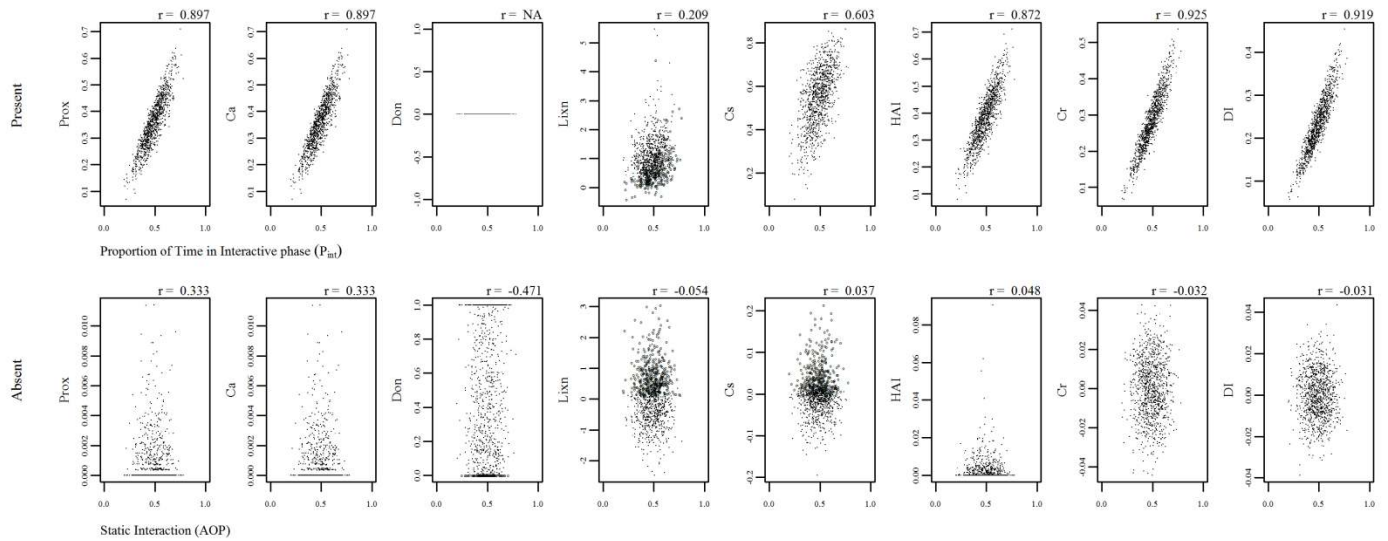


Figure 4: Time series plot of the local d_i statistic (in black; developed by Long and Nelson 2013) and proximity (meters; in grey) for the 100% sampling resolution from a single pair of dyads from the simulation study (see Supplementary Material A), one with interaction absent (top) and one with interaction present (bottom). The black dotted line represents random interaction at $d_i=0$, whereas the grey dotted line represents the critical threshold for identifying proximal fixes ($d_c = 50$ m).

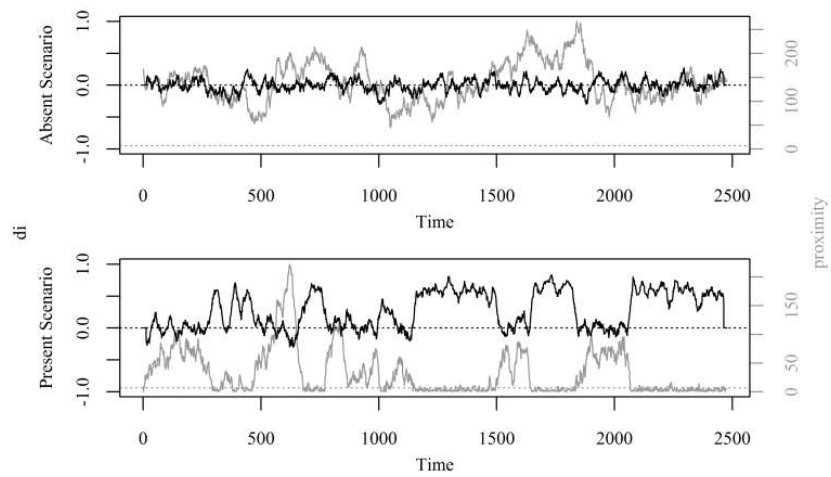
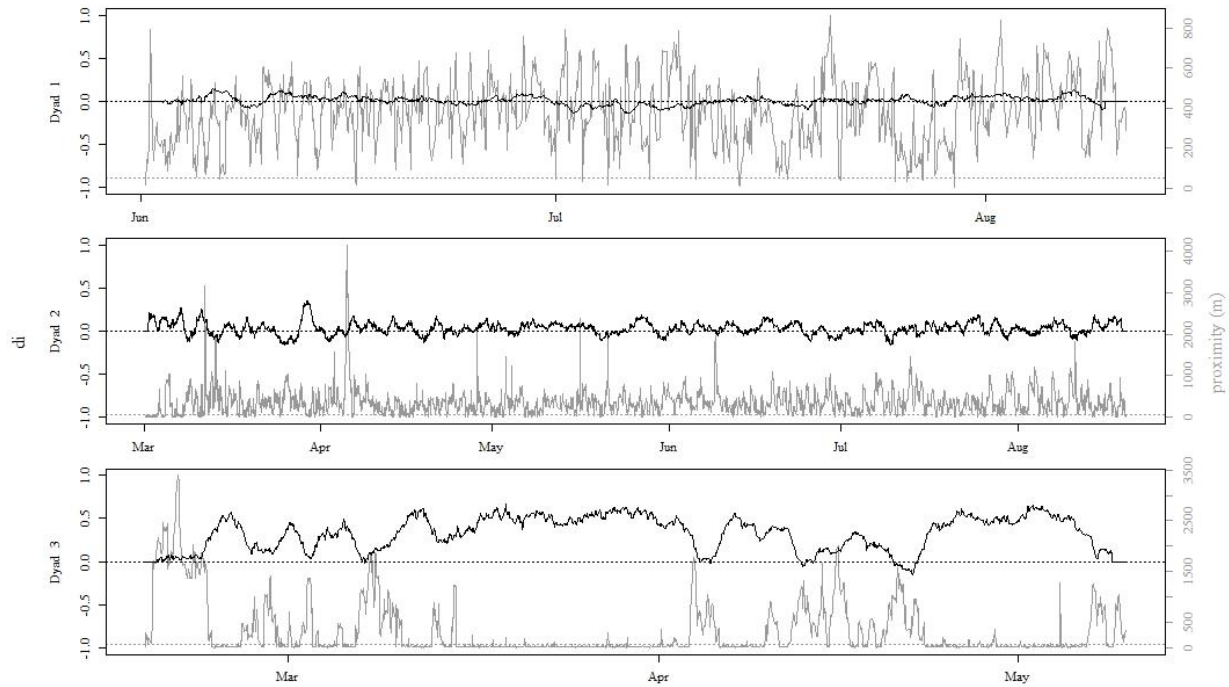


Figure 5: Time series plot of the local d_i statistic (in black; developed by Long and Nelson 2013) and proximity (meters; in grey) for the 30 min sampling interval for three white-tailed deer dyads ($n = 6$ deer). A 24 hr moving window average of d_i was used to minimize noise. The index d_i is presented on y-axis 1 and proximity (m) on y-axis 2. The black dotted line represents random interaction at $d_i=0$, whereas the grey dotted line represents the critical threshold for identifying proximal fixes ($d_c = 50$ m).



Supplementary Material:

1. Figure showing two simulated dyads along with 95% kernel home range estimates; a) interaction present, b) interaction absent. These two scenarios were used for finer treatment of dynamic interaction in the simulation study. The parameters used were:

$$n = 2475$$

$$h = 3.46$$

$$r = 0.19$$

$$p = 0.004$$

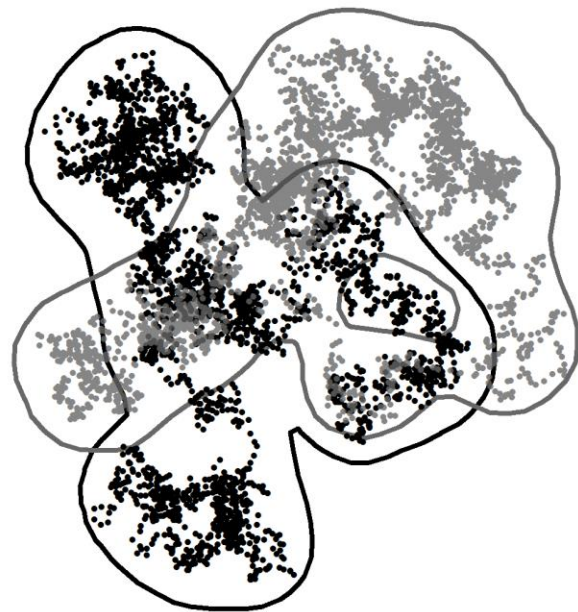
$$b = 3.9$$

$$\rho = 0.87$$

This resulted in a $P_{int} = 0.53$ for the present case (a) with an AOP = 0.75 and in the absent case (b) AOP = 0.30.



a) Interaction Present



b) Interaction Absent

2. R Code (function) for producing the biased correlated random walk (BCRW) used to simulate the presence of dynamic interaction.

< Attach R code as file for uploading >