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8 RH: Contact rates in white-tailed deer • *Schauber et al.*

9 **EFFECTS OF JOINT SPACE USE AND GROUP MEMBERSHIP ON CONTACT**
10 **RATES AMONG WHITE-TAILED DEER**

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17 **Abstract:** Establishment and spread of infectious diseases are controlled by the frequency
18 of contacts among hosts. Although managers can estimate transmission coefficients from
19 the relationship between disease prevalence and age or time, they may wish to quantify or
20 compare contact rates before a disease is established or while it is at very low prevalence.
21 Our objectives were to quantify direct and indirect contacts rates among white-tailed deer
22 (*Odocoileus virginianus*) and to compare these measures of contact rate with simpler

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23 measures of joint space use. We deployed Global Positioning System (GPS) collars on 23
24 deer near Carbondale, Illinois from 2002 to 2005. We used location data from the GPS
25 collars to measure pairwise rates of direct and indirect contact, based on a range of
26 proximity criteria and time lags, as well as volume of intersection (VI) of kernel utilization
27 distributions. We analyzed contact rates at a given distance criterion and time lag using
28 mixed-model logistic regression. Direct contact rates increased with increasing VI and
29 were higher in fall-spring than in summer. After accounting for VI, the estimated odds of
30 direct contact during fall-spring periods were 5.0 to 22.1-fold greater (depending on the
31 proximity criterion) for pairs of deer in the same social group than for between-group
32 pairs, but for direct contacts during summer the within:between-group odds ratio did not
33 differ significantly from 1. Indirect contact rates also increased with VI, but the effects of
34 both season and pair-type were much smaller than for direct contacts and differed little as
35 the time lag increased from 1 to 30 d. These results indicate that simple measures of joint
36 space use are insufficient indices of direct contact because group membership can
37 substantially increase contacts at a given level of joint space use. With indirect
38 transmission, however, group membership had a much smaller influence after accounting
39 for VI. Relationships between contact rates and season, VI, and pair type were generally
40 robust to changes in the proximity criterion defining a contact, and patterns of indirect
41 contacts were affected little by the choice of time lag from 1 to 30 d. The use of GPS
42 collars provides a framework for testing hypotheses about the form of contact networks
43 among large mammals and comparing potential direct and indirect contact rates across
44 gradients of ecological factors, such as population density or landscape configuration.

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46 **Key words:** contact rate, disease, Global Positioning System, home range, Illinois,

47 *Odocoileus virginianus*, social behavior, space use, transmission, white-tailed deer.

48 -----

49 Contact rates fundamentally influence the establishment and spread of infectious diseases,

50 and are sensitive to ecological setting (Anderson and May 1986). Some diseases, such as

51 bovine tuberculosis (Cheeseman et al. 1988a, Lugton et al. 1998, O'Brien et al. 2002),

52 require close physical proximity or near-simultaneous use of a site for transmission. The

53 agent of chronic wasting disease (CWD) can similarly be transmitted directly (Miller and

54 Williams 2003) but also appears to be transmitted indirectly, remaining infective for

55 months to years in the environment (Miller et al. 1998, Williams et al. 2002, Miller et al.

56 2004). Whether transmission occurs primarily via direct or indirect contact, contact rates

57 among wild animals can be elevated by high population density (Dietz 1982, de Jong et al.

58 2002, Ramsey et al. 2002), spatially concentrated resources such as cover or food (Totton

59 et al. 2002, Palmer et al. 2004), and living in a social group (Altizer et al. 2003). Because

60 contact rates are so important in the ecology of wildlife diseases, methods to measure

61 contact rates would be useful to researchers and managers. Past researchers have

62 quantified contact rates by observing contacts visually (Totton et al. 2002) or using

63 telemetry to infer how often animals come in close proximity (White and Harris 1994,

64 Caley et al. 1998, Ramsey et al. 2002, White et al. 2003, Ji et al. 2005).

65 Global Positioning System (GPS) telemetry may be particularly useful for

66 quantifying direct and indirect contact rates in large mammals, because it can provide large

67 numbers of locations of high spatial and temporal precision (Di Orio et al. 2003) for
68 individual animals. Researchers using GPS telemetry can compare locations of multiple
69 animals simultaneously with high precision, enabling measurement of direct contact rate.
70 Researchers can also measure indirect contact rates by measuring how often each animal
71 approaches sites visited in the past by other animals. Of course, close proximity of 2 hosts
72 (either simultaneously or separated in time) or even physical touching does not necessarily
73 indicate that contact sufficient for disease transmission has occurred. However, probability
74 of disease transmission should logically increase as the frequency at which hosts come in
75 close proximity increases.

76 The high cost of GPS collars can severely limit the number of animals that
77 managers can monitor with such high precision and intensity. An alternative approach
78 would be to use joint space use (e.g., home range overlap or volume of intersection of
79 utilization distributions; Millspaugh et al. 2004) as a measure of potential contact between
80 pairs of hosts. For example, Conner and Miller (2004) evaluated potential contact between
81 2 mule deer (*Odocoileus hemionus*) population units by the frequency at which members
82 of 1 unit were located within the home range of the other unit. Because joint space use
83 may be cheaper and easier to quantify than the frequency at which 2 animals come in close
84 proximity, such an index of potential contact may provide an efficient metric for
85 management decisions. However, social structure can also affect contact rates, and may
86 preclude the utility of joint space use as an index of contact.

87 Group-living animals are more likely to contact other individuals within their social
88 group than those from other groups. In cases where group membership is stable and

89 well-defined, as with European badgers (*Meles meles*; Cheeseman et al. 1988b), managers
90 could treat groups as if they were individuals, with the assumption that 1 infected member
91 is likely to infect the entire group. However, lethal population control can disrupt social
92 cohesion (Tuytens et al. 2000). For wildlife species with more fluid group membership,
93 such as white-tailed deer (*Odocoileus virginianus*; Hawkins and Klimstra 1970, Nixon et
94 al. 1994, Comer et al. 2005), the task of understanding disease transmission may be greatly
95 complicated. Therefore, joint space use may not provide a reliable indicator of potential
96 contact between two animals when social group membership also has a large effect on
97 contact rates. Our objective was to assess the relative effects of joint space use and group
98 membership on pairwise direct and indirect contact rates among white-tailed deer.
99 Specifically, we sought to test whether elevated contact rates within social groups are
100 simply explained by their high degree of joint space use.

101 **STUDY AREA**

102 Our study took place approximately 4 km southeast of Carbondale, Illinois, USA
103 (37° 42' 14" N, 89° 9' 2" E), an area primarily in the Central Hill Plains ecological unit,
104 oak-hickory section (Keys, Jr. et al. 1995). The climate was characterized by relatively
105 short winters and hot, humid summers, with mean annual precipitation of 116.5 cm, mean
106 January low temperature of -6.2°C, and mean July high temperature of 31°C (Midwestern
107 Regional Climate Center 2006). The study area consisted of relatively contiguous patches
108 of oak-hickory forest (57%), hay fields and other grasslands (26%), and row crop
109 agriculture (primarily soybeans, 12%), with minor components of human habitation and
110 old fields.

111 **METHODS**

112 **Capture and Collaring**

113 We focused on capturing adult and yearling females, although we also captured and
114 monitored some fawns and males. We captured most deer at sites baited with corn and
115 apples by using dart projectors (Pneu-Dart, Inc., Williamsport, Pennsylvania, USA) to fire
116 3-cc barbed darts containing a mixture of Telazol HCl (4 mg/kg) and xylazine HCl (2
117 mg/kg), based on a 50-kg deer (Kilpatrick and Spohr 1999). Each dart contained a radio
118 transmitter for locating immobilized animals. We also used rocket-propelled or drop nets
119 at baited sites, and we immobilized deer captured in nets with an intramuscular injection of
120 10 mg/kg ketamine HCl. We blindfolded all deer during handling; aged them by tooth
121 eruption as fawn, yearling, or adult; sexed; and fitted them with a GPS collar. The
122 Southern Illinois University Carbondale Institutional Animal Care and Use Committee
123 (protocol #03-003) approved deer capture and handling methods.

124 We fitted deer with GPS collars (Model TGW-3500, weight 700 g; Telonics, Mesa,
125 Arizona, USA) that stored location data internally. Pilot data ($n = 1214$ locations) from
126 these collars at fixed locations under closed-canopy conditions indicated a median position
127 error of 8.8 m and a 95th percentile error of 30 m. Pre-programmed release mechanisms
128 caused the collars to drop off the deer at particular times and dates. Collars deployed in
129 2002 and 2003 recorded locations hourly and we programmed them to drop off after 4-5.5
130 months. Collars deployed in January-February 2004 recorded locations at 2-hour intervals
131 until January 2005, during November and December 2004 when they recorded locations
132 hourly. We set fix timeout at 3 min, so all collars achieving fixes at a given hour

133 (concurrent fixes) did so ≤ 3 min of one another. We checked data from each animal for
134 errors, and excluded locations from analyses if the estimated elevation was >100 m
135 different from the typical elevation on the study area (ca. 100 m). We also excluded all
136 data from the first 3 d after collaring to avoid including aberrant behaviors resulting from
137 capture and immobilization.

138 **Joint Space Use and Group Membership**

139 Adult does nearing parturition (which begins ca. 1 June in southern Illinois, Rohm
140 2005) sequester themselves from their family groups and maintain small, exclusive
141 territories for 1-2 mo (Nixon et al. 1992, Bertrand et al. 1996). Because we expected
142 contacts to be less frequent during this period, we calculated contact rates and joint space
143 use separately for summer (15 May to 31 Aug) and fall-spring (1 Sep to 14 May) periods.

144 We measured joint space use by the volume of intersection of utilization
145 distributions (VI; Millspaugh et al. 2004), which takes values ranging from 0 (no joint
146 space use) to 1 (perfect concordance of utilization distributions). For each seasonal period,
147 we estimated home range of each deer from 200 randomly selected locations (Seaman et
148 al. 1999, Girard et al. 2002). We applied a fixed kernel estimator, with smoothing
149 parameter determined by least-squares cross-validation (Seaman and Powell 1996). We
150 then calculated VI for each pair of deer by calculating the approximate spatial integral of
151 the square root of the product of their kernels, following the raster approach of Millspaugh
152 et al. (2004). To assess the repeatability of VI calculations, we selected 1 pair of deer from
153 each of 5 seasonal time periods (Fall-Spring 2002-2003, Summer 2003, Fall-Spring
154 2003-2004, Summer 2004, Fall-Spring 2004-2005) with mid-range VI values (0.25 to 0.75,

155 where variance should be maximal), and calculated the standard deviation of 10 replicate
156 VI values from separate random samples of 200 locations from each of those deer and
157 seasons.

158 We identified pairs of deer in the same social groups based on both high levels of
159 joint space use and highly correlated movements. Location is a multivariate quantity (x , y
160 coordinates), so Ramsey et al. (2002) used canonical correlation analysis to measure the
161 correlation of a linear combination of x and y between animals. However, spatial
162 coordinates are inherently orthogonal and measured on the same scale for all animals, so
163 we simply took the sum of the universal transverse mercator (UTM) x - (easting) and y -
164 (northing) coordinates for each location of each deer and calculated the univariate
165 correlation (Pearson's r) between the coordinate sums for each pair of deer with >100
166 concurrent locations ($n = 115$ pairs). After identifying social groups based on outlying
167 correlation coefficients ($r \geq 0.5$), we then compared direct and indirect contact rates within
168 versus between groups as a function of VI. If contact rates are especially high within
169 social groups, we predicted that within-group pairs would exhibit higher contact rates than
170 predicted based on VI alone.

171 **Calculating Contact Rates**

172 We based our analysis of direct contact rate on the assumptions that the frequency
173 at which 2 animals come close enough that their GPS-estimated locations are within a
174 critical distance (δ) from one another is a positive predictor of the probability of direct
175 transmission of a disease between them, and that smaller values of δ are likely to provide
176 stronger predictors. Thus, our unit of study was the deer pair (deer i and j), for which we

177 defined a direct contact as occurring when their concurrent (at time t) GPS-estimated
178 locations were $< \delta$ m apart. Because GPS locations are not perfectly precise in space or
179 time, we quantified direct contact rates for a range of δ (10, 25, 50, and 100 m). Direct
180 contact rate for a deer pair in a given season was simply the proportion of concurrent
181 location pairs in that season that constituted contacts (contingent on δ). Similarly, we
182 defined an indirect contact as occurring when the GPS location of donor deer i at time t
183 and a subsequent (at time $t + \Delta t$) GPS location of a recipient deer j were $< \delta$ m apart, and
184 indirect contact rate was the proportion of lagged donor-recipient location pairs (contingent
185 on Δt) that constituted contacts. We based this approach on the assumption that the
186 probability of disease transmission via environmental contamination has a positive
187 relationship with the frequency at which a recipient animal comes near a site previously
188 occupied by a donor animal. We used the same set of δ for indirect as for direct contacts
189 and a range of time lags ($\Delta t = 1, 3, 10, \text{ and } 30$ d). Note that a direct contact is equivalent to
190 an indirect contact with $\Delta t = 0$. At a given value of Δt , we excluded pairs of deer from
191 analysis if < 100 pairs of valid locations were available.

192 **Statistical Analysis**

193 By definition, members of a social group are not independent in their interactions
194 with other individuals. Therefore, we retained only 1 randomly selected deer from each
195 social group for analysis of between-group contact rates. Similarly, indirect contact rates
196 with each deer in a pair as donor (i.e., with deer i as donor and deer j as recipient, and vice
197 versa) are not independent of each other, so we randomly selected 1 for inclusion.

198 Our objectives were to quantify the relationship between probability of contact
199 (direct or indirect) for a deer pair and their level of joint space use, and to test whether
200 within-group pairs exhibited higher contact rates than expected on the basis of joint space
201 use alone. Our data for each deer pair (i), proximity criterion (δ), and time lag (Δt)
202 consisted of a time series of 1s and 0s indicating whether each location pair at time t met
203 the criterion of a contact. We expected contact rates to differ among pairs of deer and
204 times. To account for time effects, we classified each record (pair of locations for deer pair
205 i at time t) into a time period (Fall-Spring 2002-2003, Summer 2003, Fall-Spring 2003-
206 2004, Summer 2004, or Fall-Spring 2004-2005). The time periods were themselves
207 classified into seasons: summer vs. fall-spring, as we expected the rates of contact to be
208 generally different between summer and fall-spring. Within a time period, we assumed
209 that contact rate was constant (after accounting for other effects), except that we expected
210 first-order autocorrelation in contact probability (i.e., elevated probability of contact for
211 deer pair i at time t if the pair was in contact at time $t-1$ or $t-2$ hrs). We assumed that any
212 other variation in contact rate among time periods having accounted for season can be
213 modeled using a normal distribution (i.e., period has a random effect whereas season has a
214 fixed effect).

215 We expected that the contact probability of each deer pair would have a positive
216 (and perhaps nonlinear) relationship with their level of joint space use (VI). In addition,
217 we sought to test whether pair type (i.e., whether the 2 deer were in the same vs. different
218 social groups) could explain additional among-pair variation in contact probability. We
219 assumed that any additional variation among deer pairs after accounting for VI and pair

220 type could be modeled by a normal distribution (i.e., deer pair has a random effect whereas
 221 pair type has a fixed effect). We considered measurement errors in VI to be negligible (see
 222 Results: Space Use), so we did not use an errors-in-variables approach.

223 We conducted this analysis using mixed-model logistic regression (SAS Macro
 224 Glimmix; Littell et al. 1996). For each value of δ and Δt , and using i to index deer pair ($i =$
 225 1 to 115) and t to index the time of the donor location ($t = 1$ to 19,271 hrs), we modeled
 226 contact probability using the following response and explanatory variables (Table 1):

227 $\text{logit}(\pi_{it}) =$

$$228 \beta_0 + \beta_1 V_{i,s(t)} + \beta_2 V_{i,s(t)}^2 + (\beta_3 S(t) + e_{s(t)}) + \beta_4 Y_{i,t-1} + \beta_5 S(t) Y_{i,t-1} + (\beta_6 P_i + \beta_7 S(t) P_i + e_i)$$

229 To directly estimate seasonal odds ratios of within- vs. between-group contact, with
 230 associated confidence intervals, we also fitted the following equivalent model:

231 $\text{logit}(\pi_{it}) =$

$$232 \beta_0 + \beta_1 V_{i,s(t)} + \beta_2 V_{i,s(t)}^2 + (\beta_3 S(t) + e_{s(t)}) + \beta_4 Y_{i,t-1} + \beta_5 S(t) Y_{i,t-1} + (\beta_6 (1 - S(t)) P_i + \beta_8 S(t) P_i + e_i)$$

233

234 where β_6 is the effect of being a within-group pair (after accounting for other variables) on
 235 the log-odds of contact in summer and β_8 is the pair type effect in fall-spring.

236 RESULTS

237 Collar Performance

238 We used GPS collars to monitor 20 females (2 fawns, 4 yearlings, and 14 adults)
 239 and 3 males (1 fawn, 1 yearling, 1 adult) between October 2002 and January 2005. Each
 240 collar collected between 235 and 10,493 valid locations over periods ranging from 2 weeks
 241 to >14 months before it dropped off or the animal was killed (Fig. 1). Monthly mean fix

242 success was >98% during winter and ranged from 92-95% during late spring and summer.
243 Minimum monthly mean fix success among collars was 81%. Collars deployed in
244 January-February 2004 exhibited a greater mean frequency of high-precision (position
245 dilution of precision < 5) fixes (73% in summer, 82% in winter) than collars deployed at
246 other times (55% in summer, 62% in winter), even during concurrent periods, perhaps due
247 to updated hardware or software in the collars. There were only 28 suspect locations due
248 to anomalous altitude, with a maximum of 8 such suspect locations for an individual
249 animal. Median time to fix ranged among collars from 38 to 66 sec, and the central span
250 (5th to 95th percentile) of time to fix for all collars was 15 to 149 sec.

251 **Space Use**

252 Among females for which we were able to estimate home range for both fall-spring
253 and summer seasons ($n = 11$), mean (\pm SE) home range size was 105 ± 13 ha in fall-spring
254 and 45 ± 4 ha in summer. Deer 19, an adult female, had 2 separate home ranges with
255 centers ca. 1 km apart, which it switched between at 1- to 3-month intervals. All other
256 females made ≥ 1 distinct excursion outside their home ranges during the monitoring
257 period, but did not establish new home ranges. These excursions typically lasted <1 d, and
258 straight-line distance from the home-range centroid to the furthest excursion point ranged
259 from 1.0 to 7.9 km (median = 2.7 km). Replicate VI values for deer pairs with mid-range
260 VI had SD ranging from 0.025 to 0.055 (median SD = 0.031), which is quite small relative
261 to the range of VI among pairs (0 to 0.8).

262 **Group Membership**

263 Mean (\pm SE) pairwise correlation of movement was 0.033 ± 0.014 . We identified 3
264 within-group pairs based on extensive home-range overlap ($VI > 0.6$) and highly correlated
265 movements ($r \geq 0.5$, $Z \geq 3.2$). Deer 8 and 9 were fawns (male and female) collared
266 simultaneously in March 2003, which we presumed to be siblings. The other 2
267 within-group pairs were composed of females, either adult-adult (deer 16 and 17) or
268 adult-yearling (deer 21 and 22). Another pair of adult females (deer 18 and 19) did not
269 exhibit characteristics of a social group during spring 2004, but did in fall 2004 during
270 periods when deer 19 inhabited its southwestern home range. Therefore, we treated this
271 pair as a between-group pair until fall 2004, and as a within-group pair thereafter. In
272 general, VI was lower for between- than within-group pairs, but 7 between-group pairs had
273 $VI > 0.7$ and 2 within-group pairs had $VI < 0.7$.

274 **Direct Contact Rates**

275 Across a range of proximity criteria ($\delta = 10$ to 100 m), the log-odds of direct
276 contact showed strong, but nonlinear, positive relationships with VI (Fig 2A, Fig. 3A-B),
277 with direct contact rates very close to zero for $VI < 0.5$. Direct contact rates were lower in
278 summer than in fall-spring and showed strong temporal autocorrelation (Fig. 2B).
279 Within-group direct contact rates were significantly greater than expected based on season
280 and VI alone (Fig. 3A-B), and the pair-type \times season interaction was significant for all
281 values of δ (Fig. 2B). The effect of group membership was much greater in fall-spring
282 than in summer. Based on logistic regression coefficients, the odds of direct contact
283 during fall-spring were 22.1-fold greater for within-group than between-group pairs at $\delta =$

284 10 m after accounting for VI, and this odds ratio declined to 5.0 but remained significantly
285 >1 out to $\delta = 100$ m (Fig. 4A). In contrast, within:between-group odds ratios for direct
286 contacts during summer had 95% CIs that included 1 for all values of δ (Fig. 4A).
287 Qualitative patterns emerging from analysis of direct contact rates were generally
288 unaffected by the value of δ , although temporal autocorrelation generally increased and
289 pair type effects became smaller with increasing δ (Fig. 2A-B).

290 **Indirect Contact Rates**

291 As with direct contact rates, the log-odds of indirect contact increased significantly,
292 but nonlinearly, with VI and showed strong temporal autocorrelation with little qualitative
293 or quantitative change in these relationships as Δt ranged from 1 to 30 d (Fig. 2C-J, Fig.
294 3C-F). The relationship between indirect contact rates and VI was more variable than for
295 direct contact rates, with some between-group pairs with VI > 0.6 having similar indirect
296 contact rates to pairs with VI ~ 0.3 (Fig. 3C-F). In general, coefficients related to pair-type
297 effects on indirect contact rates were much smaller in magnitude than was the case for
298 direct contacts, although point estimates of the pair-type main effect on indirect contacts
299 tended to be positive (Fig. 2C-J). Effects of pair type on indirect contacts were only
300 evident at $\delta = 10$ with $\Delta t = 1$ and $\Delta t = 10$ (Fig. 2D-J); otherwise, estimated within:between-
301 group odds ratios for indirect contacts during fall-spring were generally close to and not
302 significantly different from 1, except for $\delta = 10$ with $\Delta t = 1$ and $\Delta t = 10$ (Fig. 4B-C). For
303 indirect contacts in summer, estimated within:between-group odds ratios did not differ
304 significantly from 1 for any value of δ or Δt , although they were sometimes extremely
305 imprecise (Fig. 4B-C). At a given value of δ , logistic regression coefficients differed little

306 as Δt varied from 1 to 30 d (Fig. 2C-J), and this robustness to variations in Δt was apparent
307 in the relationship between indirect contact rates and VI (Fig. 3C-F).

308 **DISCUSSION**

309 In analyzing contacts rates measured from GPS-collared white-tailed deer, our
310 primary finding is that joint space use alone does not appear to be a reliable indicator of
311 either group membership or likely levels of direct contact among white-tailed deer. Some
312 pairs of deer had high levels of overlap in their utilization distributions without their
313 movements being strongly correlated, indicating that they were not acting as a social
314 group. Even after accounting for the fact that within-group pairs had high VI, the odds of
315 direct contact with $\delta = 10$ m were ca. 20 times greater for within- than between-group
316 pairs. The large discrepancy in direct contact rates between within- and between-group
317 pairs of white-tailed deer suggests that directly transmitted diseases should spread much
318 more rapidly within than between deer social groups. Thus, realistic models of disease
319 transmission should treat intra- and inter-group transmission differently. However, in
320 areas where deer social groups are stable and few females move between groups, the
321 discrepancy in contacts implies that managers could simplify models of disease spread by
322 treating groups as individuals and focusing on inter-group transmission. After all, if a
323 disease infects all members of 1 group, but is unable to spread to another group, that
324 epizootic fails as surely as if only 1 individual had become infected. We found that
325 between-group direct contacts had a strong relationship with VI, suggesting that joint space
326 use by different deer groups could be a valid indicator of inter-group direct contact, as
327 assumed by Conner and Miller (2004).

328 We measured indirect contact rates among deer using a range of proximity criteria
329 and time lags separating donor and recipient locations. As with direct contacts, indirect
330 contact rates increased with increasing joint space use. However, the effect of group
331 membership after accounting for joint space use was much smaller and less consistent for
332 indirect than direct contacts, even for time lags as short as 1 d. Therefore, differences in
333 indirect contacts between within- and between-group pairs of white-tailed deer appear to
334 be driven primarily by the high level of joint space use between members of the same
335 group. Variations in the time lag between donor and recipient visits of the same location
336 ≥ 1 d had little effect. This implies that the effects of joint space use and group
337 membership on indirect contact rates among white-tailed deer are relatively robust to
338 variations in the expected persistence of pathogens. Of course, the probability of indirect
339 transmission is likely to increase if pathogens persist longer, but our point is that the
340 qualitative pattern of indirect contacts relative to joint space use and group membership
341 may be relatively unaffected by the duration of pathogen persistence.

342 Relative to direct contacts, indirect contacts showed greater variability around the
343 relationship with VI. This variability may reflect the importance of excursions outside the
344 home range. Based on average home range size for deer in our study, the median
345 excursion distance of 2.7 km represents a trek equivalent to nearly 5 home-range radii. A
346 deer that temporarily travels outside its home range into unfamiliar territory may avoid
347 direct, and potentially aggressive, contact with resident deer. However, persistent
348 pathogens left behind could substantially accelerate the spread of disease among social
349 groups. Rare, long-distance movements are particularly important in the spread of

350 invading populations (Kot et al. 1996) and gene flow (Nelson 1993). Thus, temporary
351 excursions could play a disproportionate role in geographic spread of diseases in
352 white-tailed deer, especially diseases like CWD that are more prevalent among adults than
353 among yearlings (Miller et al. 2000, Gross and Miller 2001, Williams et al. 2002, Joly et
354 al. 2003), the primary age-class of dispersers (Hawkins et al. 1971, Kammermeyer and
355 Marchinton 1976, Nelson and Mech 1992, Nixon et al. 1994).

356 Our results have bearing on the debate over whether disease transmission among
357 wildlife is best characterized as density-dependent or frequency-dependent (de Jong et al.
358 1995, McCallum et al. 2001, de Jong et al. 2002, McCallum et al. 2002, Schauber and
359 Woolf 2003). Density-dependent transmission implies that force of infection drops as host
360 population decreases, allowing the population to rebound and potentially resulting in
361 population stability (Anderson and May 1978). If transmission is strictly
362 frequency-dependent, however, force of infection stays high even as the population crashes
363 (Getz and Pickering 1983). Researchers have proposed transmission within social groups
364 as a mechanism for frequency-dependent transmission (Altizer et al. 2003) because
365 animals within a social group make frequent contacts regardless of the density of the
366 surrounding population. However, within-group contacts alone cannot perpetuate an
367 epizootic, so between-group transmission is critical to the impact on host persistence.
368 Some researchers have found that group size in deer increases only weakly with population
369 density (Thirgood 1996, Shankar Raman 1997, Borkowski 2000), supporting the
370 hypothesis that direct transmission within social groups is largely frequency-dependent.
371 However, if group size is relatively constant, then population density must be largely

372 determined by the number of social groups per unit area. Thus, overall direct contact rate
373 between one group and all neighboring groups is likely to increase with population density.
374 Our finding that indirect contact rates are similar within and between groups suggest that
375 transmission of persistent pathogens via environmental contamination is very likely to be
376 density dependent. However, high pathogen persistence is likely to produce delayed
377 density dependence, which can increase the amplitude of disease-driven fluctuations in
378 host abundance (May and Anderson 1978).

379 **Caveats**

380 Our results suffer from a number of weaknesses, which future research in this area
381 should consider. Foremost, we analyzed contacts between particular pairs of deer, but
382 spread of disease is controlled by the total contact rate between each individual and all
383 other individuals (Dietz 1982). GPS collars are costly, so researchers can generally only
384 use them to monitor a subset of a population. Thus, scaling up from pairwise to total
385 contact rates requires at a minimum knowing the number of groups inhabiting an area,
386 typical group sizes, and levels of joint space use among groups. These factors are all likely
387 to vary with population density and landscape configuration, and thus represent the
388 mechanistic link between such ecological factors and effects on epizootiology.

389 Our measurements of contact rates are imperfect measurements of true contact
390 probabilities, which are imperfect measurements of the probability of transmission of
391 particular pathogens. The ideal proximity criterion (δ) to indicate contact would be zero,
392 but limits of precision of GPS-derived locations in space and time set a lower bound on
393 meaningful values of δ . However, the within:between odds-ratio of direct contact rates

394 was greatest for a proximity criterion of 10 m, so 10 m appears to be a suitable criterion for
395 defining direct contacts from GPS collar data. In our pilot data (described in Methods),
396 location errors typically caused observed distances between nearby GPS collars to exceed
397 the true distance, so the observed frequency of contacts based on GPS locations apart
398 almost certainly underestimates the true frequency. Simulations indicate that the relative
399 magnitude of this bias increases as δ decreases, and the true contact rate increases (E.
400 Schauber, Southern Illinois University Carbondale, unpublished data). Therefore, the
401 effect of group membership on contact rates may be greater than we report here.

402 Our study focused mainly on adult females, so we were unable to examine
403 differences between inter- and intra-sex transmission. We studied contact between females
404 because: (1) few diseases of deer have been shown to be primarily spread to females from
405 males, (2) the female population controls population growth, and (3) collaring adult males
406 is problematic due to neck swelling during the rut. However, some diseases could be
407 spread by the act of copulation as well as sniffing and flehmening of urine and other
408 secretions during the mating season. For example, CWD tends to be much more prevalent
409 in adult male than female deer (Farnsworth et al. 2005), suggesting that males that attempt
410 to breed with large numbers of females may experience high levels of exposure.

411 Our statistical analyses rely on some assumptions that may be violated. We used
412 deer pairs rather than individual deer as the sampling units, but contact rates for deer pair
413 A-B may not be independent of those for deer pairs B-C or A-C. For example, deer B
414 might be more (or less) sociable than average, so its presence affects the contact rates of
415 pair A-B and B-C in the same direction. Thus, we based our analysis on the assumption

416 that non-independence arises solely through group membership and joint space use, not
417 through behavioral characteristics of individual animals. Also, we assumed that missing
418 data are a random subset of all possible data for each deer pair and season. Fix success and
419 precision of GPS collars vary with animal behavior (e.g., bedded vs. standing), cover type,
420 topography, and season (Rempel et al. 1995, Moen et al. 1996, Dussault et al. 1999, D'Eon
421 et al. 2002, Di Orio et al. 2003). Thus, sites, times, and behaviors associated with low fix
422 success are likely to be underrepresented in data collected for a given individual, and could
423 bias estimates of contact rates. GPS collars generally had high fix success in our relatively
424 flat study area, but spatially varying fix success or precision could be a major consideration
425 when estimating contact rates in areas of more rugged terrain.

426 **MANAGEMENT IMPLICATIONS**

427 For directly transmitted diseases, our results indicate that managers should not
428 assume that measurements of joint space use (home range overlap or VI) among animals
429 provide reliable information about contact rates; the composition and size of social groups
430 also need to be known in order to make inferences about the potential direct transmission
431 of disease. Because we found a strong effect of group membership on direct contact rates,
432 we suggest that disease management by lethal population control could reduce the ability
433 of directly transmitted diseases to become established or persist in deer groups (due to
434 reduced group size and cohesion), but simultaneously increase the opportunity for an
435 already-established disease to spread among groups (due to reduced social cohesion). For
436 indirectly transmitted, diseases, on the other hand, our results indicate that joint space use
437 is a reliable indicator of potential contact rate among white-tailed deer, even if pathogens

438 only persist for as short as 1 d. Researchers commonly report home range overlap or VI in
439 field studies of deer, so data required for management decisions regarding indirectly
440 transmitted diseases may be readily available from published literature or acquired at lower
441 expense than is necessary for studies involving GPS collars.

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451

452

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632 **TABLES**

633 Table 1. Definitions of terms involved in the statistical modeling of contact rate among
 634 white-tailed deer near Carbondale, Illinois, 2002-2005.

Term	Definition
$\text{logit}(\pi_{it})$	The logit (log-odds) of contact probability, based on distance criterion (δ) and time lag (Δt), for deer pair i at time t
β_0	Value of $\text{logit}(\pi_{it})$ in fall-spring for deer in different groups if there was no contact between the pair the previous time (1 or 2 hrs earlier)
β_1	Linear term of the relationship between $\text{logit}(\pi_{it})$ and $V_{i,s(t)}$
β_2	Quadratic term of the relationship between $\text{logit}(\pi_{it})$ and $V_{i,s(t)}$
β_3	Amount by which $\text{logit}(\pi_{it})$ is increased in summer
β_4	Amount by which $\text{logit}(\pi_{it})$ is increased in fall-spring if there was a contact between the pair i at the previous time (1 or 2 hrs earlier)
β_5	Amount to add to β_3 to obtain the effect of previous contact in summer
β_6	Amount by which $\text{logit}(\pi_{it})$ is increased in fall-spring if the 2 deer are in the same social group
β_7	Amount to add to β_6 to obtain the group effect in summer
$s(t)$	Time period (e.g., Fall-Spring 2002-2003) at time t ($s(t) = 1$ to 5)
$S(t)$	Indicator of season at time t ($S(t) = 0$ if Fall-Spring, 1 if summer)
$V_{i,s(t)}$	Volume of intersection of deer pair i in time period $s(t)$
$Y_{i,t}$	Indicator of contact for pair i at time t

P_i	Pair type of deer pair i ($P_i = 1$ if members of the same social group, $P_i = 0$ if members of different groups)
$e_{s(t)}$	Mean-zero independent normal random error for describing unexplained differences in $\text{logit}(\pi_{it})$ among periods after accounting for season
e_i	Mean-zero independent normal random error for describing unexplained differences in $\text{logit}(\pi_{it})$ among deer pairs after accounting for the combined effects of pair-type and season

636 **FIGURE LEGENDS**

637 Figure 1. (A) Periods of monitoring and (B) number of valid locations for individual
638 white-tailed deer collared with GPS collars near Carbondale Illinois, 2002-2005. Deer
639 nos. 5, 7, and 8 (designated with "M") were fawn, yearling, and adult males, respectively.
640 Vertical lines in (A) delineate seasons for statistical analyses.

641

642 Figure 2. Estimated logistic regression coefficients ($\hat{\beta}$), with 95% CIs, from model
643 fitting to contact rates between pairs of white-tailed deer near Carbondale, Illinois,
644 2002-2005. We included deer pair and period (e.g., Fall-Spring 2002-03) as random
645 effects. Different symbols indicate different distance criteria (δ) used to define contacts
646 (filled circle--10 m, open circle--25 m, filled triangle--50 m, open triangle--100 m). (A,
647 B) Direct contacts ($\Delta t = 0$), (C, D) indirect contacts with $\Delta t = 1$ d, (E, F) $\Delta t = 3$ d, (G, H)
648 $\Delta t = 10$ d, (I, J) $\Delta t = 30$ d. Note the different scale for the vertical axis of panel (H).
649 "Season" indicates the effect of summer, "Prev" indicates the effect of the pair of deer
650 being in contact 1 or 2 hrs before, and "Pair-type" indicates the effect of both members of
651 the pair being members of the same social group. Positive coefficients imply positive
652 effects on contact rates. Vertical lines spanning a panel indicate extremely imprecise
653 coefficient estimates (CIs extend beyond ± 240).

654

655 Figure 3. Relationship between seasonal contact rates and joint space use (volume of
656 intersection) for between-group (filled symbols) and within-group (open symbols) pairs
657 of white-tailed deer near Carbondale, Illinois, 2002-2005. Proximity criteria (δ) defining

658 contacts were (A,C,E) 10 m and (B,D,F) 100 m. (A-B) Direct contacts ($\Delta t = 0$), (C-D)

659 indirect contacts with $\Delta t = 1$ d, (E-F) indirect contacts with $\Delta t = 30$ d.

660

661 Figure 4. Estimated odds ratio of within- versus between-group contact rates for

662 white-tailed deer near Carbondale, Illinois, 2002-2005, as a function of the proximity

663 criterion and season (filled symbols for fall-spring, open symbols for summer). Error

664 bars indicate 95% CI for estimated odds ratio from mixed-model logistic regression. (A)

665 Direct contacts, (B) indirect contacts with $\Delta t = 1$ or 3 d, (C) indirect contacts with $\Delta t = 10$

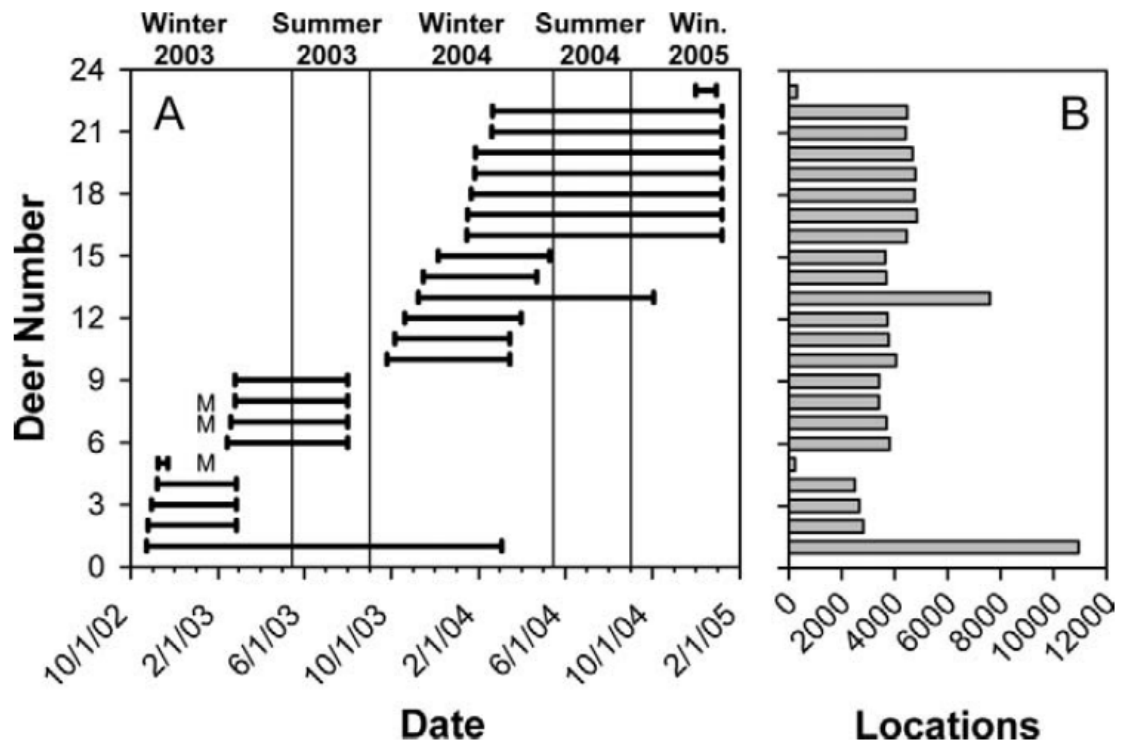
666 or 30 d. Proximity criteria in (B) and (C) are offset by ± 1.5 m to avoid overlapping

667 symbols for different values of Δt . CIs for summer odds ratios extending outside of

668 graphs (B) and (C) extend from $<10^{-80}$ to $>10^{90}$.

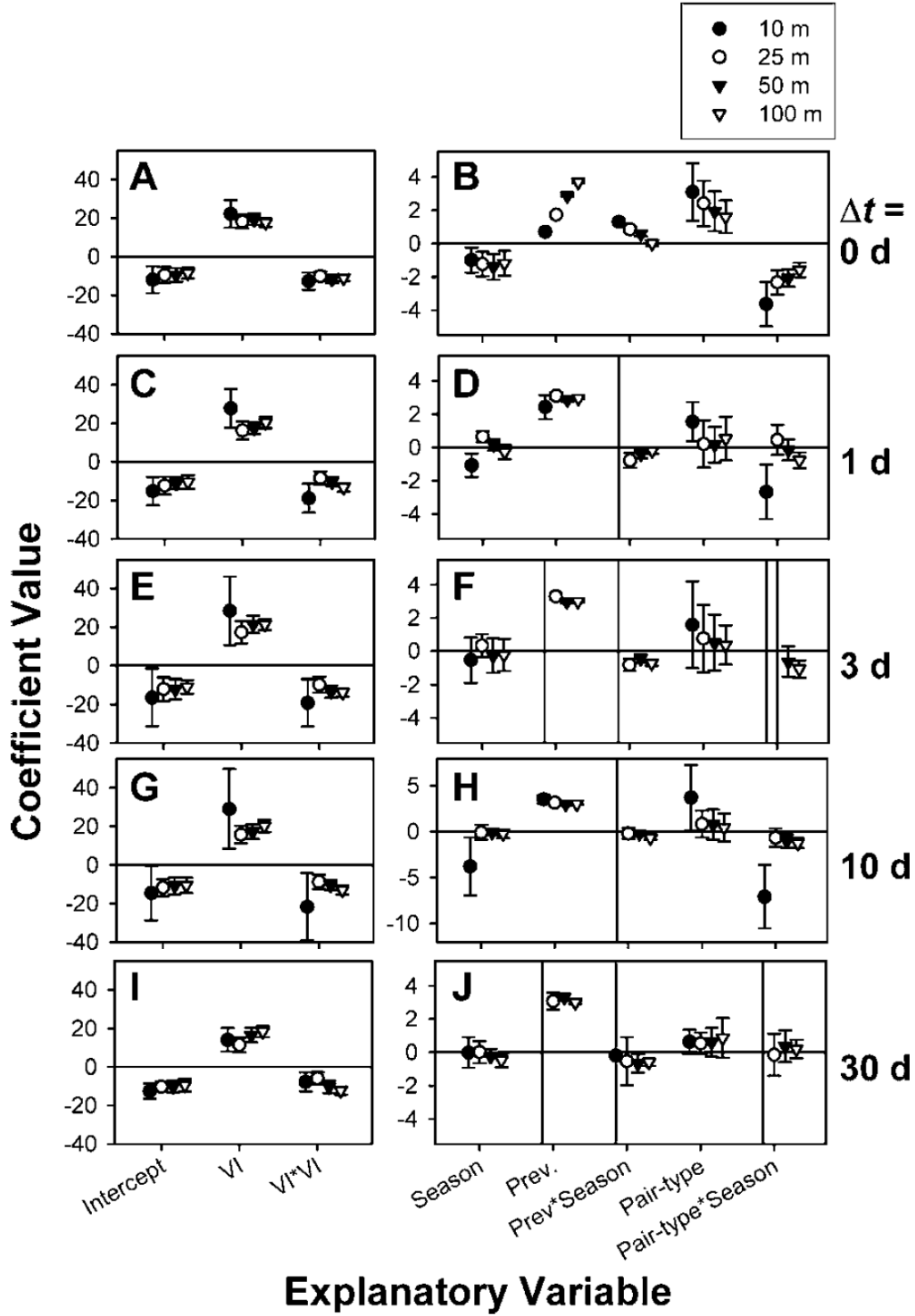
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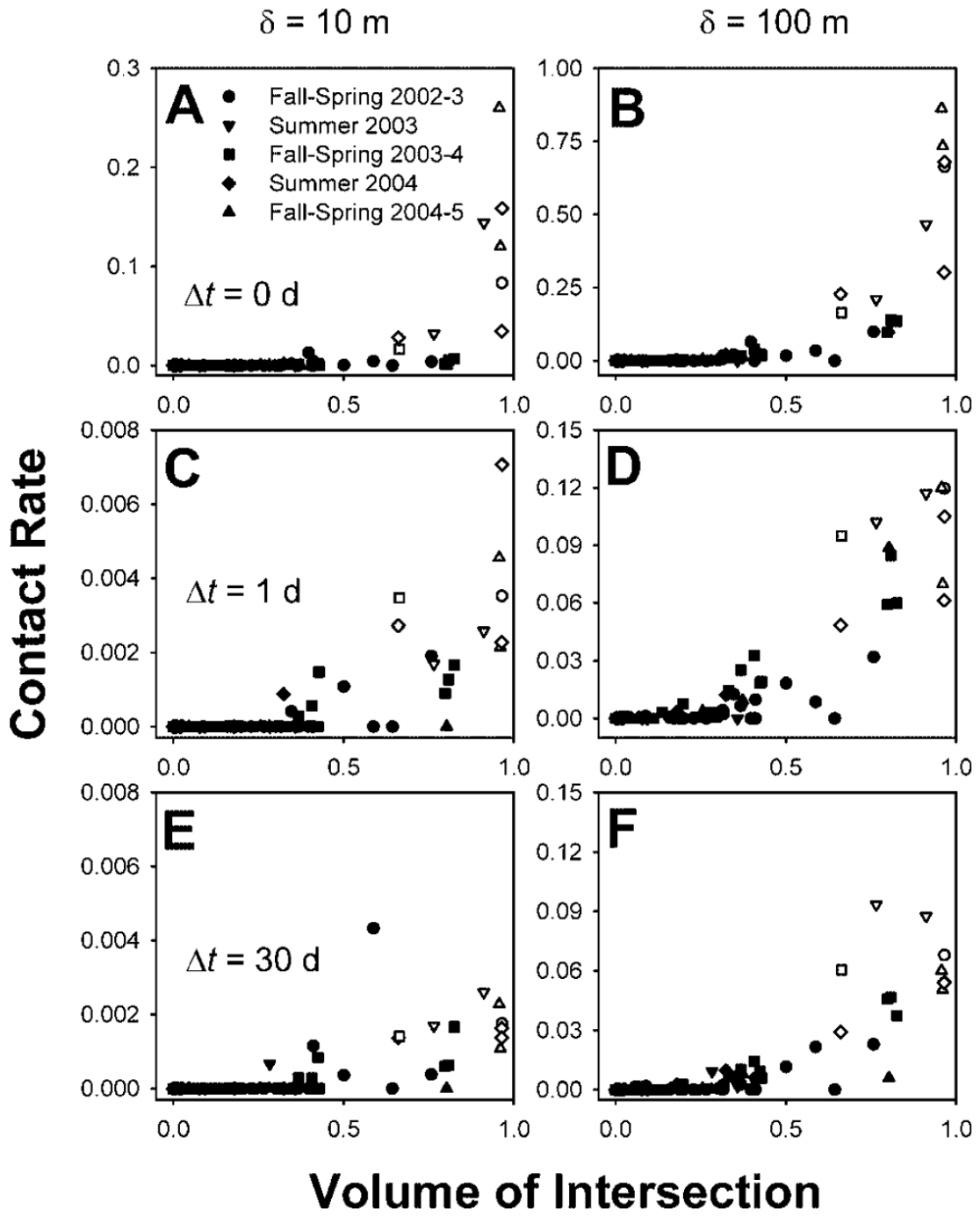


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