2-2007

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Recommended Citation
Schauber, Eric M., Storm, Daniel J. and Nielsen, Clayton K. "Effects of Joint Space Use and Group Membership on Contact Rates Among White-Tailed Deer." *Journal of Wildlife Management* 71, No. 1 (Feb 2007): 155-163. doi:10.2193.2005-546.

23 August 2006
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EFFECTS OF JOINT SPACE USE AND GROUP MEMBERSHIP ON CONTACT RATES AMONG WHITE-TAILED DEER

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

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

JOURNAL OF WILDLIFE MANAGEMENT 00(0):000-000; 2006

Key words: contact rate, disease, Global Positioning System, home range, Illinois, *Odocoileus virginianus*, social behavior, space use, transmission, white-tailed deer.

Contact rates fundamentally influence the establishment and spread of infectious diseases, and are sensitive to ecological setting (Anderson and May 1986). Some diseases, such as bovine tuberculosis (Cheeseman et al. 1988*a*, Lugton et al. 1998, O'Brien et al. 2002), require close physical proximity or near-simultaneous use of a site for transmission. The agent of chronic wasting disease (CWD) can similarly be transmitted directly (Miller and Williams 2003) but also appears to be transmitted indirectly, remaining infective for months to years in the environment (Miller et al. 1998, Williams et al. 2002, Miller et al. 2004). Whether transmission occurs primarily via direct or indirect contact, contact rates among wild animals can be elevated by high population density (Dietz 1982, de Jong et al. 2002, Ramsey et al. 2002), spatially concentrated resources such as cover or food (Totton et al. 2002, Palmer et al. 2004), and living in a social group (Altizer et al. 2003). Because contact rates are so important in the ecology of wildlife diseases, methods to measure contact rates would be useful to researchers and managers. Past researchers have quantified contact rates by observing contacts visually (Totton et al. 2002) or using telemetry to infer how often animals come in close proximity (White and Harris 1994, Caley et al. 1998, Ramsey et al. 2002, White et al. 2003, Ji et al. 2005).

Global Positioning System (GPS) telemetry may be particularly useful for quantifying direct and indirect contact rates in large mammals, because it can provide large numbers of locations of high spatial and temporal precision (Di Orio et al. 2003) for individual animals. Researchers using GPS telemetry can compare locations of multiple animals simultaneously with high precision, enabling measurement of direct contact rate. Researchers can also measure indirect contact rates by measuring how often each animal approaches sites visited in the past by other animals. Of course, close proximity of 2 hosts (either simultaneously or separated in time) or even physical touching does not necessarily indicate that contact sufficient for disease transmission has occurred. However, probability of disease transmission should logically increase as the frequency at which hosts come in close proximity increases.

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

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

STUDY AREA

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

METHODS

Capture and Collaring

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

We fitted deer with GPS collars (Model TGW-3500, weight 700 g; Telonics, Mesa, Arizona, USA) that stored location data internally. Pilot data (n = 1214 locations) from these collars at fixed locations under closed-canopy conditions indicated a median position error of 8.8 m and a 95th percentile error of 30 m. Pre-programmed release mechanisms caused the collars to drop off the deer at particular times and dates. Collars deployed in 2002 and 2003 recorded locations hourly and we programmed them to drop off after 4-5.5 months. Collars deployed in January-February 2004 recorded locations at 2-hour intervals until January 2005, during November and December 2004 when they recorded locations hourly. We set fix timeout at 3 min, so all collars achieving fixes at a given hour (concurrent fixes) did so ≤3 min of one another. We checked data from each animal for errors, and excluded locations from analyses if the estimated elevation was >100 m different from the typical elevation on the study area (ca. 100 m). We also excluded all data from the first 3 d after collaring to avoid including aberrant behaviors resulting from capture and immobilization.

Joint Space Use and Group Membership

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

We measured joint space use by the volume of intersection of utilization distributions (VI; Millspaugh et al. 2004), which takes values ranging from 0 (no joint space use) to 1 (perfect concordance of utilization distributions). For each seasonal period, we estimated home range of each deer from 200 randomly selected locations (Seaman et al. 1999, Girard et al. 2002). We applied a fixed kernel estimator, with smoothing parameter determined by least-squares cross-validation (Seaman and Powell 1996). We then calculated VI for each pair of deer by calculating the approximate spatial integral of the square root of the product of their kernels, following the raster approach of Millspaugh et al. (2004). To assess the repeatability of VI calculations, we selected 1 pair of deer from each of 5 seasonal time periods (Fall-Spring 2002-2003, Summer 2003, Fall-Spring 2003-2004, Summer 2004, Fall-Spring 2004-2005) with mid-range VI values (0.25 to 0.75, where variance should be maximal), and calculated the standard deviation of 10 replicate VI values from separate random samples of 200 locations from each of those deer and seasons.

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

Calculating Contact Rates

We based our analysis of direct contact rate on the assumptions that the frequency at which 2 animals come close enough that their GPS-estimated locations are within a critical distance (δ) from one another is a positive predictor of the probability of direct transmission of a disease between them, and that smaller values of δ are likely to provide stronger predictors. Thus, our unit of study was the deer pair (deer i and j), for which we defined a direct contact as occurring when their concurrent (at time t) GPS-estimated locations were $<\delta$ m apart. Because GPS locations are not perfectly precise in space or time, we quantified direct contact rates for a range of δ (10, 25, 50, and 100 m). Direct contact rate for a deer pair in a given season was simply the proportion of concurrent location pairs in that season that constituted contacts (contingent on δ). Similarly, we defined an indirect contact as occurring when the GPS location of donor deer i at time t and a subsequent (at time $t+\Delta t$) GPS location of a recipient deer j were $< \delta$ m apart, and indirect contact rate was the proportion of lagged donor-recipient location pairs (contingent on Δt) that constituted contacts. We based this approach on the assumption that the probability of disease transmission via environmental contamination has a positive relationship with the frequency at which a recipient animal comes near a site previously occupied by a donor animal. We used the same set of δ for indirect as for direct contacts and a range of time lags (Δt = 1, 3, 10, and 30 d). Note that a direct contact is equivalent to an indirect contact with $\Delta t = 0$. At a given value of Δt, we excluded pairs of deer from analysis if <100 pairs of valid locations were available.

Statistical Analysis

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

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

We expected that the contact probability of each deer pair would have a positive (and perhaps nonlinear) relationship with their level of joint space use (VI). In addition, we sought to test whether pair type (i.e., whether the 2 deer were in the same vs. different social groups) could explain additional among-pair variation in contact probability. We assumed that any additional variation among deer pairs after accounting for VI and pair type could be modeled by a normal distribution (i.e., deer pair has a random effect whereas pair type has a fixed effect). We considered measurement errors in VI to be negligible (see Results: Space Use), so we did not use an errors-in-variables approach.

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

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

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

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

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

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

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

RESULTS

Collar Performance

We used GPS collars to monitor 20 females (2 fawns, 4 yearlings, and 14 adults) and 3 males (1 fawn, 1 yearling, 1 adult) between October 2002 and January 2005. Each collar collected between 235 and 10,493 valid locations over periods ranging from 2 weeks to >14 months before it dropped off or the animal was killed (Fig. 1). Monthly mean fix success was >98% during winter and ranged from 92-95% during late spring and summer. Minimum monthly mean fix success among collars was 81%. Collars deployed in January-February 2004 exhibited a greater mean frequency of high-precision (position dilution of precision < 5) fixes (73% in summer, 82% in winter) than collars deployed at other times (55% in summer, 62% in winter), even during concurrent periods, perhaps due to updated hardware or software in the collars. There were only 28 suspect locations due to anomalous altitude, with a maximum of 8 such suspect locations for an individual animal. Median time to fix ranged among collars from 38 to 66 sec, and the central span (5th to 95th percentile) of time to fix for all collars was 15 to 149 sec.

Space Use

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

Group Membership

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

Direct Contact Rates

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

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

Indirect Contact Rates

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

DISCUSSION

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

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

Relative to direct contacts, indirect contacts showed greater variability around the relationship with VI. This variability may reflect the importance of excursions outside the home range. Based on average home range size for deer in our study, the median excursion distance of 2.7 km represents a trek equivalent to nearly 5 home-range radii. A deer that temporarily travels outside its home range into unfamiliar territory may avoid direct, and potentially aggressive, contact with resident deer. However, persistent pathogens left behind could substantially accelerate the spread of disease among social groups. Rare, long-distance movements are particularly important in the spread of invading populations (Kot et al. 1996) and gene flow (Nelson 1993). Thus, temporary excursions could play a disproportionate role in geographic spread of diseases in white-tailed deer, especially diseases like CWD that are more prevalent among adults than among yearlings (Miller et al. 2000, Gross and Miller 2001, Williams et al. 2002, Joly et al. 2003), the primary age-class of dispersers (Hawkins et al. 1971, Kammermeyer and Marchinton 1976, Nelson and Mech 1992, Nixon et al. 1994).

Our results have bearing on the debate over whether disease transmission among wildlife is best characterized as density-dependent or frequency-dependent (de Jong et al. 1995, McCallum et al. 2001, de Jong et al. 2002, McCallum et al. 2002, Schauber and Woolf 2003). Density-dependent transmission implies that force of infection drops as host population decreases, allowing the population to rebound and potentially resulting in population stability (Anderson and May 1978). If transmission is strictly frequency-dependent, however, force of infection stays high even as the population crashes (Getz and Pickering 1983). Researchers have proposed transmission within social groups as a mechanism for frequency-dependent transmission (Altizer et al. 2003) because animals within a social group make frequent contacts regardless of the density of the surrounding population. However, within-group contacts alone cannot perpetuate an epizootic, so between-group transmission is critical to the impact on host persistence. Some researchers have found that group size in deer increases only weakly with population density (Thirgood 1996, Shankar Raman 1997, Borkowski 2000), supporting the hypothesis that direct transmission within social groups is largely frequency-dependent. However, if group size is relatively constant, then population density must be largely determined by the number of social groups per unit area. Thus, overall direct contact rate between one group and all neighboring groups is likely to increase with population density. Our finding that indirect contact rates are similar within and between groups suggest that transmission of persistent pathogens via environmental contamination is very likely to be density dependent. However, high pathogen persistence is likely to produce delayed density dependence, which can increase the amplitude of disease-driven fluctuations in host abundance (May and Anderson 1978).

Caveats

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

Our measurements of contact rates are imperfect measurements of true contact probabilities, which are imperfect measurements of the probability of transmission of particular pathogens. The ideal proximity criterion (δ) to indicate contact would be zero, but limits of precision of GPS-derived locations in space and time set a lower bound on meaningful values of δ. However, the within:between odds-ratio of direct contact rates was greatest for a proximity criterion of 10 m, so 10 m appears to be a suitable criterion for defining direct contacts from GPS collar data. In our pilot data (described in Methods), location errors typically caused observed distances between nearby GPS collars to exceed the true distance, so the observed frequency of contacts based on GPS locations apart almost certainly underestimates the true frequency. Simulations indicate that the relative magnitude of this bias increases as δ decreases, and the true contact rate increases (E. Schauber, Southern Illinois University Carbondale, unpublished data). Therefore, the effect of group membership on contact rates may be greater than we report here.

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

Our statistical analyses rely on some assumptions that may be violated. We used deer pairs rather than individual deer as the sampling units, but contact rates for deer pair A-B may not be independent of those for deer pairs B-C or A-C. For example, deer B might be more (or less) sociable than average, so its presence affects the contact rates of pair A-B and B-C in the same direction. Thus, we based our analysis on the assumption that non-independence arises solely through group membership and joint space use, not through behavioral characteristics of individual animals. Also, we assumed that missing data are a random subset of all possible data for each deer pair and season. Fix success and precision of GPS collars vary with animal behavior (e.g., bedded vs. standing), cover type, topography, and season (Rempel et al. 1995, Moen et al. 1996, Dussault et al. 1999, D'Eon et al. 2002, Di Orio et al. 2003). Thus, sites, times, and behaviors associated with low fix success are likely to be underrepresented in data collected for a given individual, and could bias estimates of contact rates. GPS collars generally had high fix success in our relatively flat study area, but spatially varying fix success or precision could be a major consideration when estimating contact rates in areas of more rugged terrain.

MANAGEMENT IMPLICATIONS

For directly transmitted diseases, our results indicate that managers should not assume that measurements of joint space use (home range overlap or VI) among animals provide reliable information about contact rates; the composition and size of social groups also need to be known in order to make inferences about the potential direct transmission of disease. Because we found a strong effect of group membership on direct contact rates, we suggest that disease management by lethal population control could reduce the ability of directly transmitted diseases to become established or persist in deer groups (due to reduced group size and cohesion), but simultaneously increase the opportunity for an already-established disease to spread among groups (due to reduced social cohesion). For indirectly transmitted, diseases, on the other hand, our results indicate that joint space use is a reliable indicator of potential contact rate among white-tailed deer, even if pathogens only persist for as short as 1 d. Researchers commonly report home range overlap or VI in field studies of deer, so data required for management decisions regarding indirectly transmitted diseases may be readily available from published literature or acquired at lower expense than is necessary for studies involving GPS collars.

ACKNOWLEDGMENTS

Constructive criticism from R. Barker, 2 anonymous reviewers, and M. Eichholz greatly improved this manuscript. We thank C. and M. Bloomquist, V. Carter, L. J. Kjær, P. McDonald, A. Nollman, J. Rohm, and J. Waddell for field assistance. We are indebted to J. McDonald for initiating this project. We also thank the staff and graduate students of the SIUC Cooperative Wildlife Research Laboratory for volunteering. Federal Aid in Wildlife Restoration Project W-87-R, with additional support from the SIUC Graduate School provided primary funding for this research. The late A. Woolf served as principal investigator of this project until his death in April 2004.

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Associate Editor: Barker

TABLES

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

Term	Definition
logit(π_{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 logit(π_{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 logit(π_{it}) and $V_{i,s(t)}$
β_2	Quadratic term of the relationship between logit(π_{it}) and $V_{i,s(t)}$
β_3	Amount by which logit(π_{it}) is increased in summer
β_4	Amount by which logit(π_{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 logit(π_{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 logit(π_{it}) among periods after accounting for season
e_i	Mean-zero independent normal random error for describing unexplained differences in logit(π_{it}) among deer pairs after accounting for the combined effects of pair-type and season

FIGURE LEGENDS

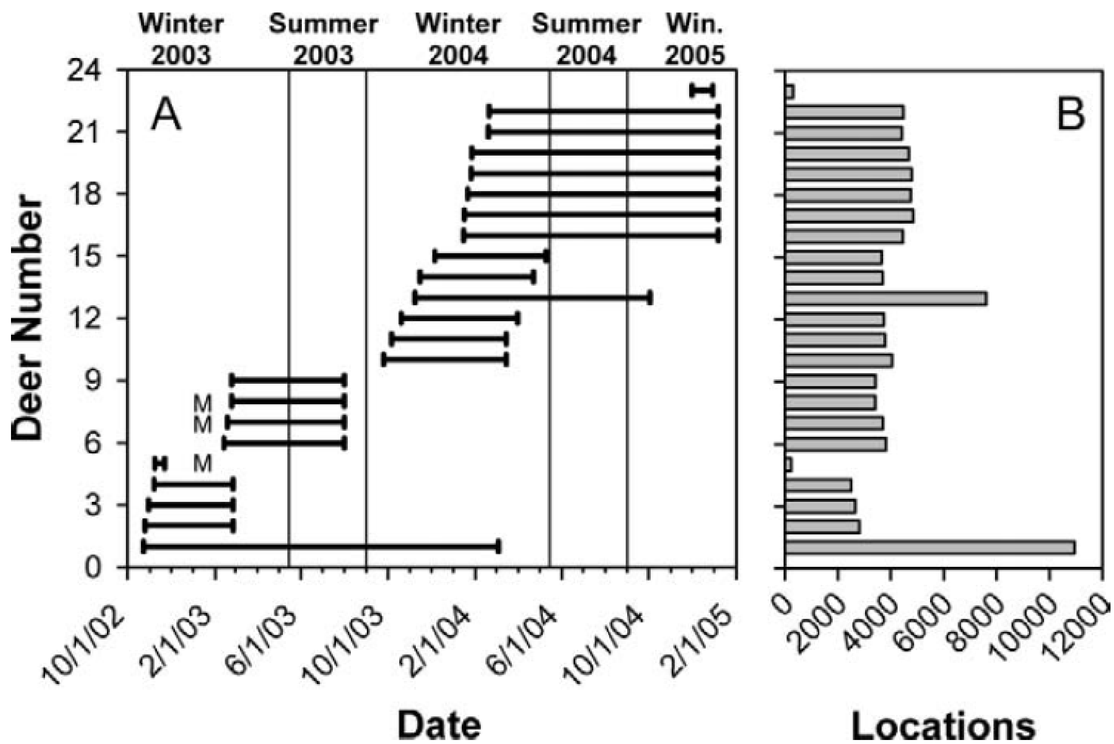
Figure 1. (A) Periods of monitoring and (B) number of valid locations for individual white-tailed deer collared with GPS collars near Carbondale Illinois, 2002-2005. Deer nos. 5, 7, and 8 (designated with "M") were fawn, yearling, and adult males, respectively. Vertical lines in (A) delineate seasons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

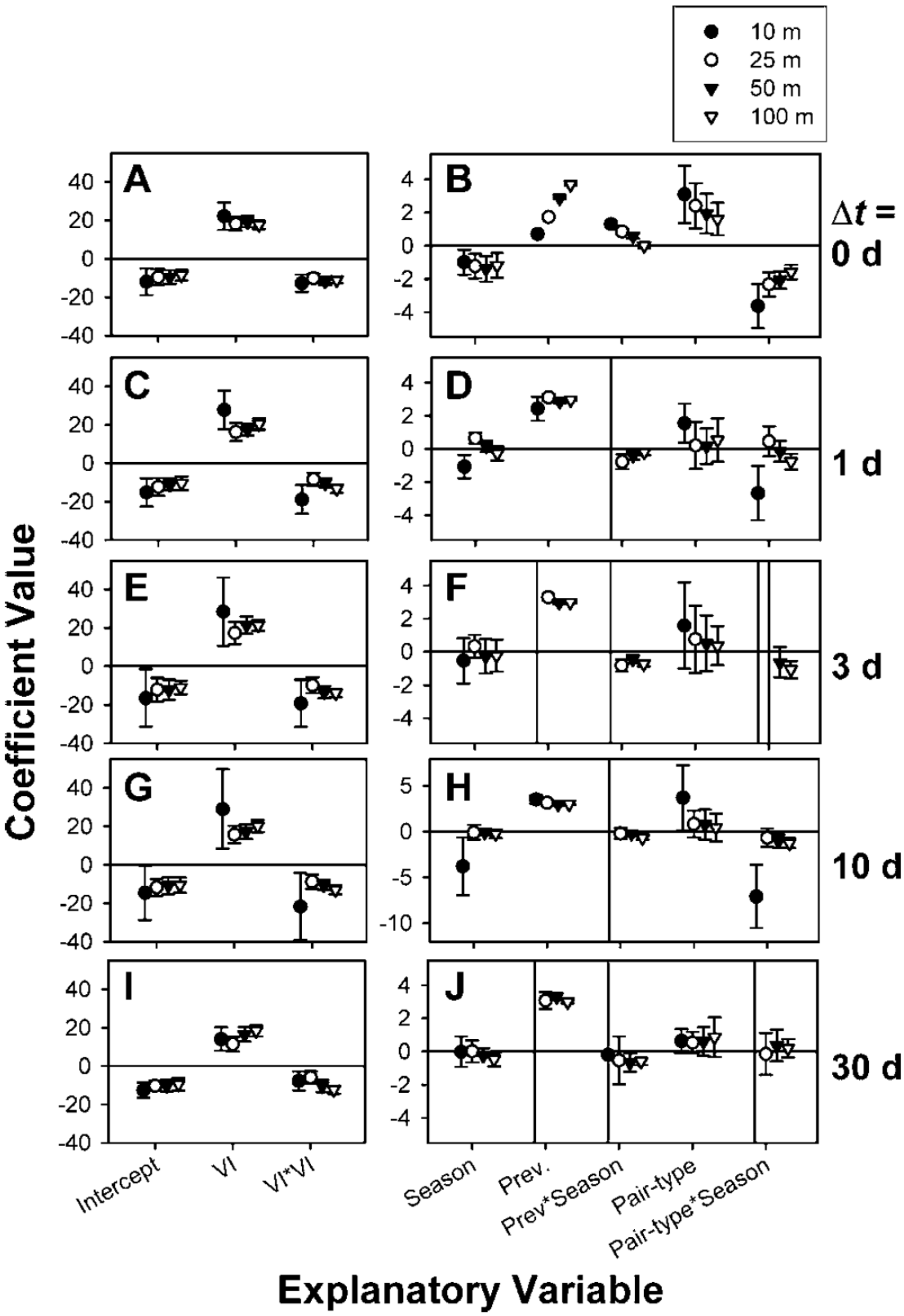
Figure 2. Estimated logistic regression coefficients ($\hat{\beta}$), with 95% CIs, from model fitting to contact rates between pairs of white-tailed deer near Carbondale, Illinois, 2002-2005. We included deer pair and period (e.g., Fall-Spring 2002-03) as random effects. Different symbols indicate different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

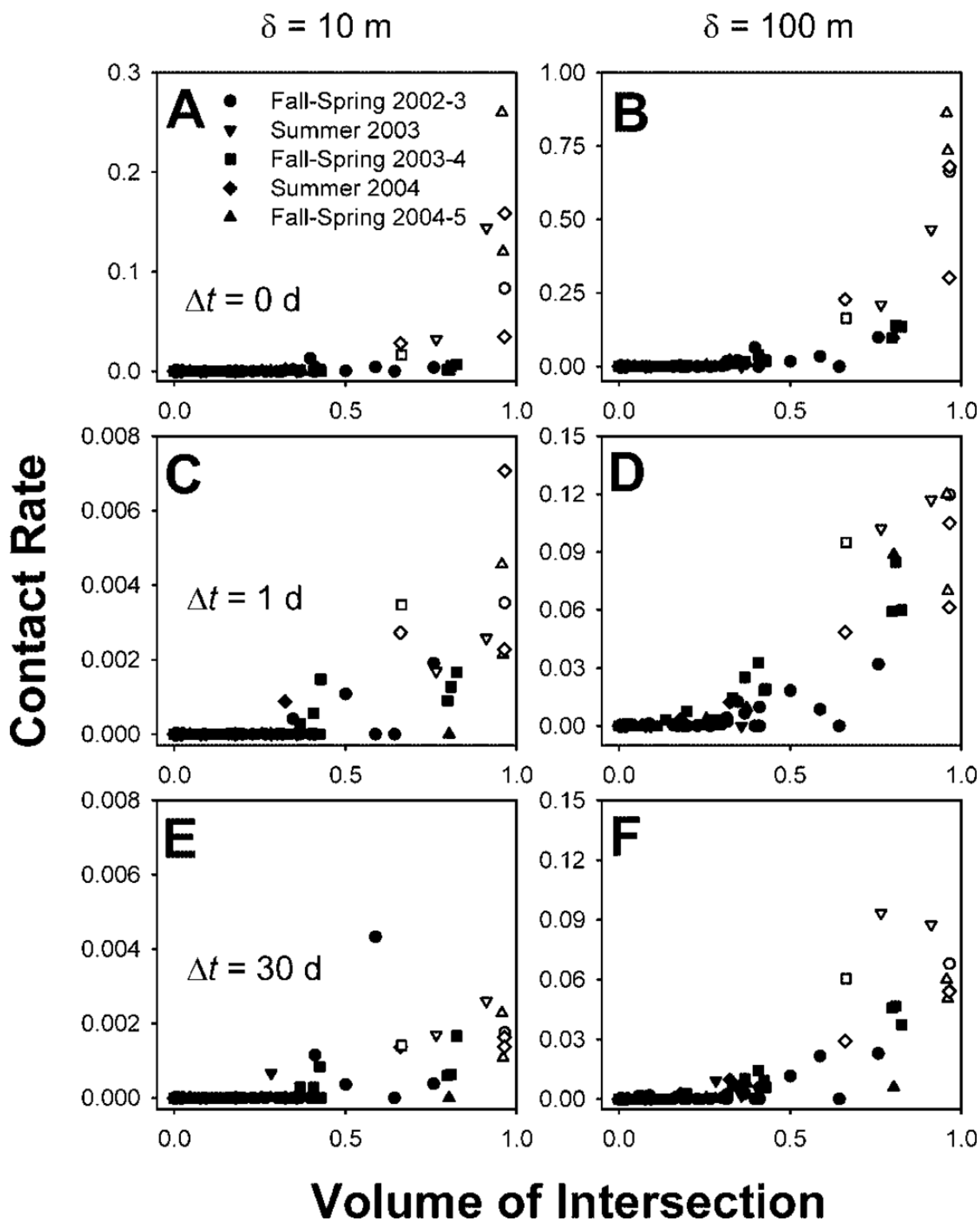
Figure 3. Relationship between seasonal contact rates and joint space use (volume of intersection) for between-group (filled symbols) and within-group (open symbols) pairs of white-tailed deer near Carbondale, Illinois, 2002-2005. Proximity criteria (δ) defining

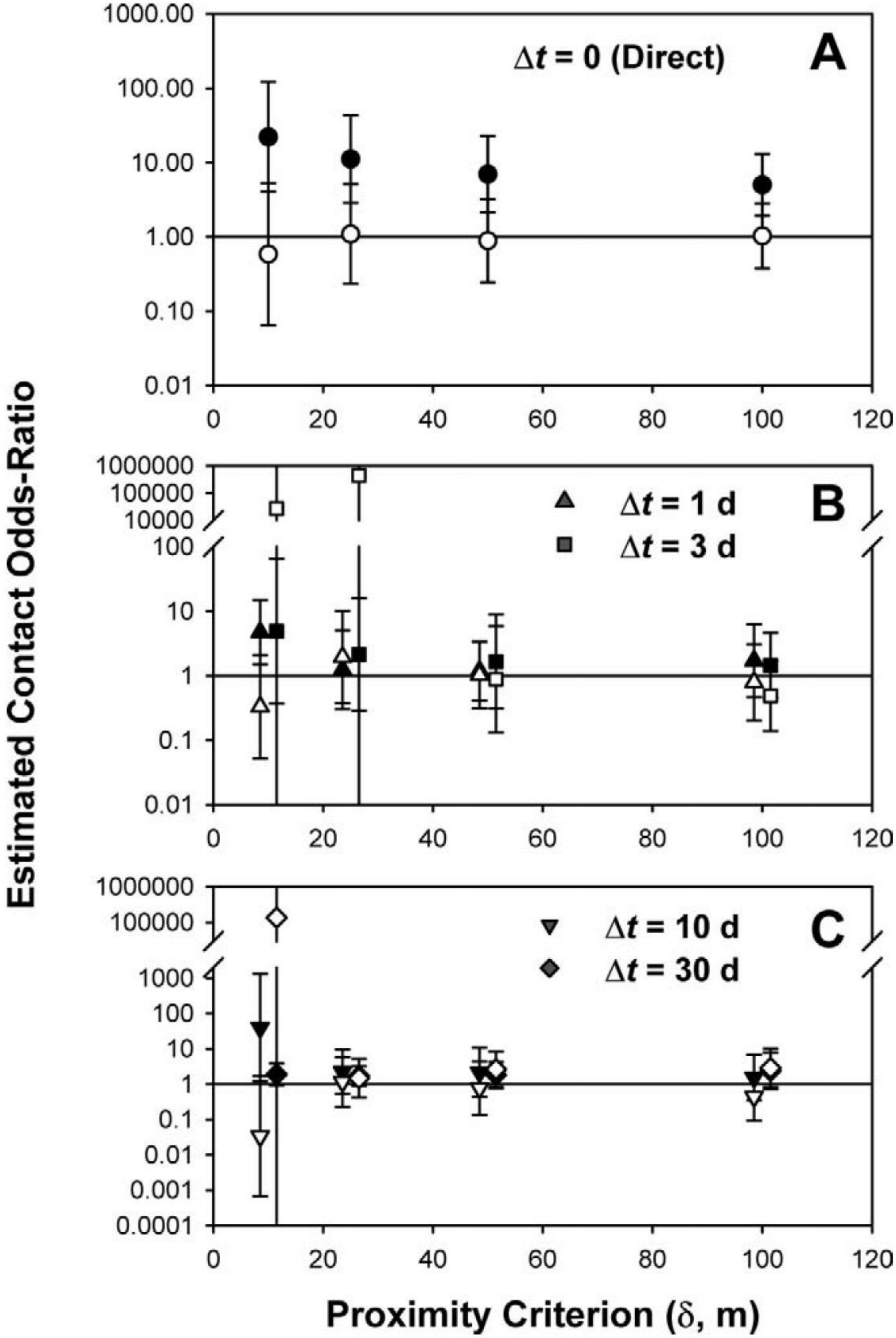
contacts were (A,C,E) 10 m and (B,D,F) 100 m. (A-B) Direct contacts (Δt = 0), (C-D) indirect contacts with Δt = 1 d, (E-F) indirect contacts with Δt = 30 d.

Figure 4. Estimated odds ratio of within- versus between-group contact rates for white-tailed deer near Carbondale, Illinois, 2002-2005, as a function of the proximity criterion and season (filled symbols for fall-spring, open symbols for summer). Error bars indicate 95% CI for estimated odds ratio from mixed-model logistic regression. (A) Direct contacts, (B) indirect contacts with Δt = 1 or 3 d, (C) indirect contacts with Δt = 10 or 30 d. Proximity criteria in (B) and (C) are offset by $\pm$1.5 m to avoid overlapping symbols for different values of Δt. CIs for summer odds ratios extending outside of graphs (B) and (C) extend from $<10^{-80}$ to $>10^{90}$.


Winter 2003
Summer 2003
Winter 2004
Summer 2004
Win. 2005
A
B
Deer Number
M
M
M
0
3
6
9
12
15
18
21
24
10/1/02
2/1/03
6/1/03
10/1/03
2/1/04
6/1/04
10/1/04
2/1/05
Date
0
2000
4000
6000
8000
10000
12000
Locations


10 m
25 m
50 m
100 m
A
B
C
D
E
F
G
H
I
J
Δt = 0 d
1 d
3 d
10 d
30 d
Coefficient Value
Intercept
VI
VI*VI
Season
Prev.
Prev*Season
Pair-type
Pair-type*Season
Explanatory Variable


δ = 10 m
δ = 100 m
A
B
C
D
E
F
Fall-Spring 2002-3
Summer 2003
Fall-Spring 2003-4
Summer 2004
Fall-Spring 2004-5
Δt = 0 d
Δt = 1 d
Δt = 30 d
Contact Rate
Volume of Intersection



Δt = 0 (Direct)
A
1000.00
100.00
10.00
1.00
0.10
0.01
Δt = 1 d
Δt = 3 d
B
1000000
100000
10000
100
10
1
0.1
0.01
Δt = 10 d
Δt = 30 d
C
1000000
100000
1000
100
10
1
0.1
0.01
0.001
0.0001
0
20
40
60
80
100
120
Estimated Contact Odds-Ratio
Proximity Criterion (δ, m)

677