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# Localized Removal Affects White-Tailed Deer Space Use and Contacts

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**ABSTRACT** Transmission and impact of infectious diseases can be altered if host social structure is disrupted by disease outbreaks or lethal management. Specifically, if remnants of depopulated groups join or increase contact with neighboring groups, between-group transmission may increase even as population density decreases. We tested whether this phenomenon could apply to diseases of white-tailed deer (*Odocoileus virginianus*) by using a before-after-control-impact design. We monitored space use and contacts among adult female and juvenile deer in southern Illinois during 2011–2014; midway through each study season, we removed all members except 1 collared deer from centrally located groups and left control

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groups intact. After group removal, remnant adult females shortened duration of contacts with neighboring groups, whereas remnant juveniles responded with greater shifts in space use and appeared to join neighboring groups. Together, our study points to potential age-specific responses of deer to social disruption, with evidence that juveniles respond in ways that could shift disease transmission dynamics toward frequency dependence. These findings highlight the need for focused research into the importance of social disruption in disease dynamics, and lend support for complete group removal (if possible) when culling for disease management.

**KEY WORDS** chronic wasting disease, contact rate, direct transmission, disease management, indirect transmission, infectious disease, *Odocoileus virginianus*, sharpshooting, social behavior.

Social behavior shapes contact patterns and, as a result, disease transmission opportunities within host populations (Anderson et al. 1986, Altizer et al. 2003, Nunn et al. 2015). Although there are costs to group-living (e.g., competition for food and mates, increased parasite burdens) benefits of social behavior (e.g., anti-predator defenses, increased access to food, thermoregulation) often outweigh these costs (Krebs and Davies 1997, Krause and Ruxton 2002). The costs and benefits of social behavior, and therefore the level of sociality, differ by species, season, age, and sex because of varying physiological needs and availability of food, cover, and mates (Caraco 1979, Krause and Ruxton 2002). Social interactions can be so important to a species like the domestic goat that a radio-collared "Judas goat" can be used to seek out and eliminate all other feral goats on an island (Taylor and Katahira 1988). Such a strong social proclivity can be problematic for disease control if it increases the chances of pathogen transport into new, susceptible groups (Cross et al. 2005, Nunn et al. 2008).

Social grouping can disconnect within-group contact patterns from overall population density, so that disease transmission is often modeled as frequency-dependent with the force of infection dependent on the proportion of infected individuals in the population (de Jong et al. 1995, Begon et al. 2002). In extreme cases, frequency-dependent diseases can cause hosts to become locally extinct because individuals seek each other even as the population decreases (e.g., devil facial tumor disease; McCallum et al. 2009). Unlike the case with density-dependent transmission, holding host density below a threshold may not be an effective management strategy when transmission is frequency-dependent (Getz and Pickering 1983).

Density- and frequency-dependent transmission mechanisms represent somewhat unrealistic extremes of the transmission mechanism continuum (Lloyd-Smith et al. 2005, Storm et al. 2013). Such simple models of disease transmission fail to acknowledge the impact of social disruption (due to disease mortality or management interventions) on host behavior, which can be highly problematic. For example, attempts to control bovine tuberculosis (bTB) in cattle by culling European badgers (*Meles meles*), the wildlife reservoir, reduced bTB incidence in cattle in cull areas but increased incidence in adjoining areas (Donnelly et al. 2006). Disruptions to badger social structure increased dispersal and increased contact rates with neighboring groups (Tuyttens et al. 2000, Donnelly et al. 2006, Vicente et al. 2007).

Understanding contact patterns of white-tailed deer (*Odocoileus virginianus*) is important to understand and predict dynamics of bTB and chronic wasting disease (CWD) in free-living deer populations (Gross and Miller 2001, Williams et al. 2002, Conner et al. 2008). White-tailed deer have an intermediate level of sociality; adult female and young deer form relatively stable social groups (typically described as matrilines) from September through June (Hawkins and Klimstra 1970, Hirth 1977, Nelson and Mech 1981, Lingle 2003), with distinct within-group and between-group interactions (Schauber et al. 2007, 2015; Tosa et al. 2015). Specifically, direct contact rates are greater within social groups than predicted based on joint space use alone (Schauber et al. 2007, 2015). In contrast, members of different social groups avoid close contact even when in the general vicinity of each other (Tosa et al. 2015). If group membership is stable, disease transmission compartmentalized based on group membership can be modeled similar to that of species that are more solitary (e.g., moose [*Alces alces*]), where each deer group is analogous to an individual. If disease mortality or management efforts destabilize group membership, however, that could enhance between-group transmission independent of changes in population density.

The importance of contact compartmentalization based on group membership for disease transmission is supported by evidence that having a closely related female infected with CWD nearby is a far stronger predictor of CWD infection than the number of unrelated, infected females nearby (Grear et al. 2010). Because deer infected with bTB and CWD rarely show clinical signs during early stages, targeted removal of infected deer is difficult (Williams et al. 2002, Wolfe et al. 2004). Moreover, the long incubation periods of these diseases can allow infected juveniles to outlive older, earlier-infected group members, which may lead to social disruption (e.g., orphaning, temporary isolation; Gross and Miller 2001, Williams et al. 2002). Because infected animals are difficult to identify, managers have implemented non-selective sharpshooting in and around core disease areas and increased hunting opportunities for the public; these efforts appear to have maintained low disease prevalence compared to areas with no culling (Williams et al. 2002, Bollinger et al. 2004, Mateus-Pinilla et al. 2013, Manjerovic et al. 2014). Still, how social disruption affects disease transmission and the remaining population is poorly understood (Wasserberg et al. 2009).

Localized removal of white-tailed deer has generated conflicting results, depending on whether entire groups were removed or remnant animals were left. After removal of entire deer social groups in the Adirondack Mountains in New York, remaining groups adjacent to the removal area did not alter their home ranges, even after 5 years (Porter et al. 1991, McNulty et al. 1997, Oyer and Porter 2004). Ozoga and Verme (1984) similarly reported that isolated females remaining after localized removal stayed within their original home ranges despite being surrounded by areas of lower deer density. In other studies, orphaned juveniles had smaller home ranges than unorphaned juveniles (Woodson et al. 1980, Marchinton and Hirth 1984, Giuliano et al. 1999). Partial group removal may cause remaining deer to group together (Ozoga and Verme 1984, Williams et al. 2008), where individuals initially from separate social groups attempt to form groups (Woodson et al. 1980, Etter et al. 1995, Giuliano et al. 1999, Comer et al. 2005). This behavior has also been observed in red deer (*Cervus elaphus*), where orphaned females more frequently joined and left groups than those whose mothers were still alive (Clutton-Brock et al. 1982). Although removal of deer may decrease density of deer in the area, partial group removal could cause greater movement of deer (and their pathogens) from group to group. Movement of deer between groups due to incomplete removal of groups by disease epidemics or management strategies can maintain efficient between-group transmission even as overall population density decreases. Furthermore, greater movement of deer or movement of deer into areas previously occupied by infected individuals that were removed can be problematic if pathogens can persist in the environment and be transmitted indirectly (Sauvage et al. 2003, Miller et al. 2004, Almberg et al. 2011). Similar to other transmissible spongiform encephalopathies, the prions that cause CWD can remain infectious for years in the environment. Chronic wasting disease can be transmitted directly and indirectly by contact with contaminated blood, saliva, feces, carcasses, or soil (Mathiason et al. 2009, Walter et al. 2011). As such, indirect transmission can further decouple between-group transmission of disease from the density of infected animals (Almberg et al. 2011).

Understanding how social structure disruption affects remnant animals is crucial to understanding disease transmission and improving disease management. Therefore, our goal was to quantify the effect of social group removal on remnant white-tailed deer behavior. Our objectives were to compare changes in direct contact rates between control and remnant deer, compare changes in indirect contact rates between control and remnant deer, and compare behavioral responses (i.e., those changes in direct and indirect contact) of remnant adult females to remnant juveniles.

## STUDY AREA

We conducted our study at 4 sites in southern Illinois, USA (UTM zone 16N): a private property (Johnson Farms; 309572E, 4175040N), Touch of Nature Environmental Center (TON; 309169E, 4166864N), Crab Orchard National Wildlife Refuge (CONWR; 311628E, 4166427N), and Rend Lake (324803E, 4215562N; Fig. 1). This study area is located on the glacial border where there is a sharp transition from rolling agricultural land in the north to rough unglaciated areas in the south; elevations range from 118 m to 199 m. The region had hot, humid summers and mild winters; monthly high temperatures ranged from 5°C in January to 32°C in July and monthly low temperatures ranged from −5°C in January to 20°C in July (National Oceanic and Atmospheric Administration 2010). Study sites were primarily oak (*Quercus* spp.)-hickory (*Carya* spp.) forest with some crop fields, grasslands, and residential areas (Schauber et al. 2007). Bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and domestic dogs (*Canis familiarus*) are the primary predators in this region (Rohm et al. 2007). Sites had relatively high deer densities (>15 deer/km$^2$;

Anderson et al. 2013) and low mortality rates (87% annual survival rate of adult F; Storm et al. 2007). All sites were closed to hunting during this study with the exception of a deer hunt for handicapped persons at TON (archery) and Rend Lake (gun) in November.

## METHODS

### Deer Capture and Handling

To characterize between-group interactions, we captured and marked adjacent social groups of adult female and juvenile white-tailed deer. To record contacts and movements, we equipped 1 deer/group with a proximity logger (SirTrack, Havelock North, New Zealand) affixed to a store-on-board global positioning system (GPS) collar (TGW-4500, Telonics, Mesa, AZ, USA). During the adult phase of the study (2011–2012), we focused on collaring females >1 year old. During the juvenile phase (2012–2014), we focused on collaring male and female juveniles. We programmed collars to record deer locations at 1-hour intervals during the adult phase and at 30-minute intervals during the juvenile phase. We set fix timeouts to 3 minutes so that all collars achieved fixes simultaneously. Collars were equipped with a very high frequency (VHF) transmitter with a mortality signal programmed for 4 hours of inactivity. We scheduled the collar drop-off mechanisms to detach on 1 June each year (6–8 months of data collection). Proximity loggers continuously emitted and detected ultra high frequency (UHF) signals to and from other devices, respectively; they recorded identity, date, time, and duration of interactions with other devices. We programmed proximity loggers to record a new interaction if separated by >30 seconds.

We calibrated detection distances by placing collars in the same orientation facing each other to represent direct contact between collared deer. Detection distances differed by phase: ≤1 m during the adult phase and ≤2 m during the juvenile phase (Prange et al. 2006, Walrath et al.

2011). We adjusted this distance following the adult phase because 1 m was too short (i.e., within-group contacts totaled only 58.5 per week; SE = 6.4); 2 m was still a biologically relevant distance where 2 animals could physically touch, and proximity loggers recorded contacts >1 m even if they were oriented in different directions. We captured and aged white-tailed deer (juveniles [~0.5 yr] or adults [>1.5 yr]) between October to January of 2011–2014 using methods described in Tosa et al. (2015). During capture, we anesthetized deer using intramuscular injections of Telazol® and xylazine HCl. We marked each individual using a metal ear tag and 2 plastic ear tags with unique color and number combinations. Capture, handling, and removal methods were approved by the Southern Illinois University Carbondale Institutional Animal Care and Use Committee (protocol no. 11-027).

### Delineating Groups and Localized Removal

We determined social group size and composition by visual observations from vehicles, elevated stands, and photographic records during capture and monitoring. We defined an association as animals that were ≤25 m of each other and moving in a coordinated fashion during a particular observation (Hirth 1977, Aycrigg and Porter 1997, Lingle 2003, Miller et al. 2010); we also considered behavioral cues (e.g., aggressive actions) when recording associations. We positioned remote cameras (Excite C2000, Cuddeback, De Pere, WI, USA) on bait piles (during trapping) and in areas of high deer activity to supplement visual observations. For remote camera photographs, we recorded marked deer (identified using color and number combinations of the ear tags) and number and sex of untagged deer. If we were unable to determine sex of untagged deer, whether the deer was marked, or the identity of the tagged deer, we recorded those deer as unsure.

Because photographs of social groups are often incomplete and because multiple photographs of the same social group were taken frequently (especially at bait piles while deer were feeding), we condensed information from photographs taken at the same location within 15 minutes of each other into 1 record. We defined sampling periods as 1 day to account for uneven sampling between days. For each tagged deer, we selected the group size observed in the most sampling periods (i.e., the mode). To determine which tagged deer belonged to the same group, we calculated the percentage of total sampling periods each tagged individual was photographed together with each other tagged deer. With these values, we conducted hierarchical cluster analysis between tagged deer using the hclust function in the stats package in program R (R Development Core Team 2014), and created dendrograms to visualize the results.

During March–April, we selected for removal treatment 1–3 centrally located groups at each study site that contained collared animals and whose group composition was well-documented. We determined the number of groups for the removal treatment based on the number of social groups collared at each site; generally, we selected 1 removal group for every 6 social groups that were collared so that the removal group was surrounded by the control groups. We baited identified groups with corn, and targeted all their members except for 1 collared deer (hereafter referred to as the remnant) per group for simultaneous removal using centerfire rifles (Table 1). Once we removed deer, we continued to monitor remnant deer via radio-telemetry, visual observations, and trail cameras.

## Contact Rate Analysis

To quantify the effect of social group removal on behavior of remnant deer, we used a before-after-control-impact (BACI) design (Stewart-Oaten et al. 1986) to compare temporal changes in measures of indirect and direct contact between control (i.e., from non-removal groups) and remnant collared deer in each study site. We designed the study so that we would have ≥8 weeks of data in both pre- and post-removal periods during the time when grouping behavior is strongest. We censored data from all deer ≤3 days of capture and during the period of deer removal at each site to account for altered behavior due to capture and presence of bait during removal efforts, respectively (Kjær et al. 2008, Schauber et al. 2015). Therefore, the pre-removal period started 4 days following capture for each deer and ended when the site was baited (i.e., typically the week before removal; 18 Mar 2012, 13 Mar 2013, and 10 Mar 2014). The post-removal period started the day bait was no longer at the site (i.e., typically a few days following removal; 6 Apr 2012, 3 Apr 2013, and 1 Apr 2014) and lasted until the collars dropped off (i.e., 1 Jun). We excluded any GPS locations with an altitude <0 m or >400 m. We conducted all data analyses in program R. We analyzed data for adult and juvenile phases separately and excluded data from collared deer that died during the data collection period. We excluded 2 incomplete removal groups (i.e., group size remained >1) from the analysis. In addition, based on high dynamic interaction index values (Long et al. 2014), we identified 4 groups that each had 2 collared deer (Fig. S1, available online in Supporting Information); we excluded data from 1 collar (chosen at random) from each of these within-group dyads from the analysis. Lastly, we excluded contact data between 1 dyad consisting of 2 control deer whose dynamic interaction index fluctuated between within-group and between-group levels over the study period.

*Indirect contact.*—We compared 3 metrics of indirect contact, indicating potential for environmental transmission, between remnant and control deer: 1) changes in home range size, 2) space use fidelity (i.e., overlap between pre- and post-removal space use of the same animal), and 3) shifts in space use toward neighboring deer. We calculated home range size and space use overlap using the AdehabitatHR package (Calenge 2006). For each individual in each time period (i.e., pre- or post-removal), we used 500 randomly selected GPS locations and reference bandwidths to calculate the fixed-kernel utilization distribution (UD; Seaman and Powell 1996, Seaman et al. 1999). To compare changes (from pre- to post-removal periods) in home range ($\Delta$HR) and core area size ($\Delta$CA) between control and remnant deer, we calculated home range (95% isopleth) and core area (50% isopleth) sizes from the pre- and post-removal fixed-kernel UDs for each deer.

We used volume of intersection (VI; Seidel 1992, Millspaugh et al. 2004, Fieberg and Kochanny 2005) to calculate space use overlap between 2 estimated UDs: $\hat{f}_i$ and $\hat{f}_j$. For space use fidelity ($\mathrm{VI}_{\mathrm{fidelity}}$), $\hat{f}_i$ and $\hat{f}_j$ represent the estimated UDs of the same deer from the pre- and post-removal periods, respectively. To compare shifts in space use overlap toward neighboring deer, we calculated 2 VIs for each dyad (*i*,*j*), 1 pre-removal ($\mathrm{VI}_{\mathrm{pre,\ ij}}$) and 1 post-removal ($\mathrm{VI}_{\mathrm{post,\ ij}}$), where $\hat{f}_i$ and $\hat{f}_j$ represent the estimated UDs of 2 deer during the same time period. For each possible dyad in each study area, we calculated the difference in VI between periods ($\Delta\mathrm{VI}_{\mathrm{ij}} = \mathrm{VI}_{\mathrm{pre,\ ij}} - \mathrm{VI}_{\mathrm{post,\ ij}}$). Then, for each deer, we selected its greatest $\Delta$VI value ($\Delta\mathrm{VI}_{\mathrm{max}}$; $\Delta\mathrm{VI}_{\mathrm{max,\ i}} = \Delta\mathrm{VI}_{\mathrm{i1}}$ if $\Delta\mathrm{VI}_{\mathrm{i1}} > \Delta\mathrm{VI}_{\mathrm{i2}}, \Delta\mathrm{VI}_{\mathrm{i3}}, \ldots \Delta\mathrm{VI}_{\mathrm{ij}}$) and compared $\Delta\mathrm{VI}_{\mathrm{max}}$ between control and remnant deer. We excluded dyads with remnant deer when calculating $\Delta\mathrm{VI}_{\mathrm{max}}$ for control deer.

For each indirect contact metric, we tested for differences between control and remnant deer with a Welch's 2-sample *t*-test for unequal variances ($\alpha = 0.05$). In the adult and juvenile phase, we predicted that $\Delta$HR and $\Delta$CA would be greater, $\mathrm{VI}_{\mathrm{fidelity}}$ would be smaller, and $\Delta\mathrm{VI}_{\mathrm{max}}$ would be greater for remnant deer than for control deer (Table 2).

*Direct contact.*—To test whether group removal affected direct contact patterns, we conducted a BACI analysis of variance (ANOVA) of contact rates and of duration of contacts recorded by proximity loggers, where we included treatment (i.e., control or remnant) and period (i.e., pre- or post-removal) as factors and deer and site as random effects in a mixed-effect

ANOVA using the nlme package (Pinheiro et al. 2012). We calculated direct contact rates (proximity logger records/week) among all possible dyads within the same site, beginning the week immediately following deployment of the last GPS collar at each site (11 Dec 2011 at Johnson, 8 Jan 2012 and 13 Jan 2013 at TON, 22 Dec 2013 at CONWR, and 19 Jan 2014 at Rend Lake). We combined proximity logger records between the same dyad that were <30 seconds apart into 1 consolidated record (Walrath et al. 2011). Although previous studies have censored 1-second contacts (Prange et al. 2006, 2011), we kept these interactions because short-duration contacts may still allow for disease transmission (Walrath et al. 2011).

For each individual deer, we calculated contact rate as mean number of contacts per dyad recorded per week (only including dyads that recorded ≥1 contact during the study period). We also calculated the mean duration of contacts made by each deer with all other collared deer (averaged over contact records). We excluded contacts with remnant deer when calculating contact rates and durations for control deer. We predicted a treatment×period interaction (i.e., BACI effect) such that contact rates and contact durations between groups would increase more (or decrease less) for remnant deer following removal of their social group than for control deer (Table 2). In addition, we assessed statistical support for the post hoc hypothesis that remnant juveniles increased their contact rate temporarily following the removal of their social group members by repeating the BACI analysis only using contact rate data 3 weeks pre- and post-removal event.

*Regrouping.*—Our metrics of indirect and direct contact are based on data only from deer carrying GPS-proximity logger collars, but remnant deer might attempt to join or form groups with un-collared deer. Therefore, we assessed evidence of grouping by remnant animals by examining the frequency of observation (visual or via remote cameras) alone versus with other deer post-removal. Specifically, we used a 2-sample *t*-test to test the post-hoc hypothesis that the proportion of post-removal observations of remnant animals alone was greater for adult than for juvenile remnants.

## RESULTS

We captured and tagged 105 deer (46 in adult phase: 30 adults, 16 juveniles, 59 in juvenile phase: 21 adults, 38 juveniles), and we collared 20 females (16 adults, 4 juveniles) during the adult phase and 14 females (6 adults, 8 juveniles) and 8 juvenile males during the juvenile phase (Table 3). From 587 visual observations and 40,807 trail camera photographs, we identified 63 social groups (27 in 2011–2012, 18 in 2012–2013, and 18 in 2013–2014), consisting of 1–5 group members. Of these groups, we collared 42 social groups (20 in 2011–2012, 7 in 2012–2013, and 15 in 2013–2014). Of these, we were able to remove all but the collared animal successfully from 8 social groups, 4 in each phase (Table 1). We compared their responses with those of 34 collared animals in unmanipulated (i.e., control) groups (16 in adult phase, 18 in juvenile phase; Table 2). Overall mean GPS error was 5.78 m (SE = 0.01, $n = 292{,}278$); GPS error for each deer ranged from 5.40–6.26 m.

### Indirect Contact

Control and remnant deer exhibited similar decreases in core area and home range sizes from pre- to post-removal periods in both the adult phase ($\Delta$CA $t_{5.1} = -1.06$, 1-tailed $P = 0.17$; $\Delta$HR $t_{4.8} = -1.30$, 1-tailed $P = 0.13$) and the juvenile phase ($\Delta$CA $t_{3.5} = 0.30$, 1-tailed $P = 0.39$; $\Delta$HR $t_{3.7} = -0.12$, 1-tailed $P = 0.46$; Table 2, Fig. 2A). We found no evidence that group removal affected space use fidelity of remnant adults (remnant $\overline{\mathrm{VI}_{\mathrm{fidelity}}} = 0.63$, SE = 0.03, $n = 4$, vs. control $\overline{\mathrm{VI}_{\mathrm{fidelity}}} = 0.62$, SE = 0.02, $n = 16$; $t_{6.19} = -0.32$, 1-tailed $P = 0.38$), but remnant juveniles had lower space use fidelity than control deer (remnant $\overline{VI}$ = 0.48, SE = 0.05, $n$ = 4 vs. control $\overline{VI}$ = 0.67, SE = 0.02, $n$ = 18; $t_{4.14}$ = 3.40, 1-tailed $P$ = 0.013; Fig. 2B).

Similarly, we found no evidence that group removal caused remnant adults to shift space use toward neighboring groups (remnant $\overline{\Delta VI_{max}}$ = 0.04, SE = 0.03, $n$ = 4 vs. control $\overline{\Delta VI_{max}}$ = 0.04, SE = 0.01, $n$ = 16; $t_{4.30}$ = 0.05, 1-tailed $P$ = 0.48). Observed space-use shift by remnant juveniles toward neighbors after group removal was nearly 4 times greater than observed for controls, but this difference was not statistically significant (remnant $\overline{\Delta VI_{max}}$ = 0.15, SE = 0.06, $n$ = 4 vs. control $\overline{\Delta VI_{max}}$ = 0.04, SE = 0.01, $n$ = 18; $t_{3.32}$ = −1.79, 1-tailed $P$ = 0.08; Fig. 2C). We found no evidence that apparent responses by remnant juveniles were caused by a difference in sex: comparisons between remnant males and control males during the juvenile phase (remnant $\overline{\mathrm{VI}_{\mathrm{fidelity}}}$ = 0.50, SE = 0.07, $n$ = 3 vs. control $\overline{\mathrm{VI}_{\mathrm{fidelity}}}$ = 0.68, SE = 0.02, $n$ = 5; $t_{2.47}$ = 2.53, 1-tailed $P$ = 0.05; remnant $\overline{\Delta VImax}$ = 0.19, SE = 0.06, $n$ = 3 vs. control $\overline{\Delta VImax}$ = 0.08, SE = 0.03, $n$ = 5; $t_{3.14}$ = −1.59, 1-tailed $P$ = 0.10; Fig. S2) were quantitatively and qualitatively similar to results obtained from juveniles of both sexes.

## Direct Contact

Proximity loggers recorded 29,499 consolidated contacts (25,734 within-group, 3,765 between-group; Fig. 3). Only 37 of the between-group contacts were recorded during the adult phase. We did not find main or interactive BACI effects of treatment (remnant vs. control) and period (pre- vs. post-removal) on direct contact rates of adult females ($F_{1,404} \leq 2.33$, $P \geq 0.13$; Table 2, Fig. 4A). Similarly, the BACI effect (treatment × period interaction) on direct contact rates during the juvenile phase was not statistically significant ($F_{1,423}$ = 0.64, $P$ = 0.43). Remnant juveniles had similar overall contact rates to control deer ($F_{1,423}$ = 2.53, $P$ = 0.11), and contact rates of both control deer and remnant juveniles were higher before than after the removal event ($F_{1,423}$ = 15.18, $P \leq 0.001$; Fig. 4B).

For duration of contact during the adult phase, we found a significant BACI effect (i.e., treatment×period interaction; $F_{1,404} = 5.49$, $P = 0.02$), but the effect was opposite of our prediction; duration of contact was greater for remnant than control adults before the removal event, whereas contact durations for remnant and control adults were similar after the removal event (Fig. 4C). During the juvenile phase, neither the main nor interactive (BACI) effects of treatment and period on duration of contacts were statistically significant ($F_{1,423} \leq 0.51$, $P \geq 0.48$; Figs. 4D and S3).

### Regrouping

Post-removal, adult remnant deer were nearly always observed alone (Fig. 5). In contrast, 3 of 4 juvenile remnants were observed more often with other deer than alone and the 1 other juvenile remnant was observed alone only about half the time (Fig. 5). A post hoc test of this difference between age classes in mean frequency of being observed alone indicated statistical significance ($\bar{x}$ = 89.9%, SE = 7.1, $n = 4$ for adults vs. $\bar{x}$ = 39.8%, SE = 5.5, $n = 4$ for juveniles; $t_{5.67} = 5.59$, $P = 0.002$).

## DISCUSSION

Following general sharpshooting where individuals rather than groups were removed, Williams et al. (2008) reported that remaining white-tailed deer increased their home range overlap, and suspected that remnant deer had an inherent need to join new social groups of unrelated individuals. In our study, experimental group removal caused shorter contacts and little change in contact rates or space use of remnant adult females. In contrast, remnant juveniles reduced their space use fidelity and appeared to increase spatial overlap with neighbors following group removal. Visual observations with uncollared deer further suggested that juvenile deer may have sought out interactions with neighbors following removal of group members. Similar to this study, Williams et al. (2008) conducted their study in an area with high deer densities (i.e., 78–83 deer/km$^2$), little to no hunting pressure, and little predation pressure. Williams et al. (2008), however, collared both male and female deer and did not distinguish between adults and juveniles in their analysis. What is more, Williams et al. (2008) conducted their removal efforts in January and did not account for social groups during removal; this may have resulted in partial group removal or even left some collared groups intact. Our findings suggest that responses by deer to social disruption differ by age, due in part to greater familiarity of adult females with their surroundings and their more established social status with their neighbors relative to juveniles (Hirth 1977, Nelson and Mech 1981, Taillon et al. 2006). Juveniles may also lose social status with neighboring groups when group members are removed if social status is derived from the group, similar to the manner in which calves derive social status from females in red deer (Hall 1983). Whereas adult females may have previously reared and parted with their offspring because of dispersal, predation, hunting mortality, or disease, juveniles have experienced group member loss for the first time. For these reasons, juveniles may benefit more from being social than adult females and may seek out opportunities to join other groups or establish themselves, thereby increasing their contact rates with neighbors (Woodson et al. 1980, Marchinton and Hirth 1984, Giuliano et al. 1999).

An increase in direct and indirect contact rates with other social groups by remnants following group removal would facilitate pathogen spread and  provide a potential mechanism for frequency-dependent transmission, confounding attempts at disease management (Potapov et al. 2012). We found no evidence that loss of group members drives adult females to increase opportunities for direct or indirect contact with neighboring groups; rather, our findings indicate that remnant adult females will remain in their home ranges, shorten duration of contacts, and stay isolated until the fawning season and thereby limit spread of disease to neighboring groups. Remnant juveniles, however, showed lower home range fidelity than controls and were observed more often with other deer than were remnant adults. The effect of removal on space use shifts of juveniles was not statistically significant, despite large observed effect sizes. Thus, our results on how juveniles respond to group removal were inconclusive (i.e., consistent with small as well as biologically significant effect sizes; Steidl et al. 1997). For diseases with long incubation times, such as bTB and CWD, adult females typically have higher infection prevalence than juveniles and continue to contaminate the environment by shedding pathogens (Delahay et al. 2000, Conner et al. 2008). The potential of juveniles to spread pathogens between groups, however, could be more problematic because younger infected animals are likely to outlive older infected animals during epizootics (Conner et al. 2008). Further research into social prospects of remnant juvenile deer would enhance our understanding of disease transmission and management in group-living wildlife.

Among juveniles, we found that direct contact rates were higher before than after removal. As winter progresses to spring, growth of vegetation increases cover in addition to forage quantity and quality for deer (Beier and McCullough 1990). Because large feeding groups are common during late winter and early spring (Hawkins and Klimstra 1970) and because direct contacts appear to occur mainly during feeding (Kjær et al. 2008), this increase in vegetation may decrease deer densities at each foraging location and thereby decrease opportunities for direct contact. We expected that remnant juveniles would have higher direct contact rates overall than control juveniles because we specifically chose removal groups located in the center of the study sites, surrounded by other collared animals, and most control animals were located on the periphery with fewer collared groups around them. The lack of statistical difference between overall contact rates between control and remnant deer suggests that a number of control groups were also surrounded by other collared deer.

There are obvious limitations to this study. Our sample size is small, with only 4 removal groups in each phase, so we had statistical power to detect only large changes in behavior. We were only able to capture and collar a limited number of deer at each site, leaving some groups without collared or tagged members. Inevitably, we were unable to measure potential indirect or direct contacts with those unmarked groups. These data, nevertheless, allowed us to describe and compare changes in remnant deer behavior because remnant deer were in centrally located areas surrounded by collared deer. Another limitation is that our measurements of direct contact rates are not directly comparable between adult and juvenile phases because we increased the detection distance of the proximity loggers during the juvenile phase to increase the sample size of between-group proximity logger contacts. Still, the scarcity of direct contacts recorded during the adult phase (only 37 contacts among 126 possible dyads) may explain why we did not find a difference in direct contact rates between remnant and control deer. Although broad patterns of behavior among the deer we studied likely differed among years, the BACI design measures average behavioral differences between remnants to control animals from the pre- to post-removal period. Therefore, any changes caused by year should be reflected by both remnants and controls, and thereby offset one another.

Our findings are limited to populations of female and juvenile deer with little or no hunting pressure during winter and spring, outside of breeding and fawning seasons. Areas with strong hunting or predation pressure or severe winter weather may have different grouping responses to removal because protection from predators and access to resources are important influences for grouping behavior (Krause and Ruxton 2002). We did not measure contact rates of adult male deer or differentiate between behavior of remnant juveniles that were male or female. Contact rates of adult male deer are especially important for disease transmission during the mating season when males provide additional pathways for pathogens to spread to other female social groups (Geist 1981, Koutnik 1981, Miller and Conner 2005), and male and female juveniles may respond differently to disturbances in social structure (Nixon et al. 2007). Although sex could account for behavioral differences in remnant juveniles, our analyses using only male juveniles produced results similar to those for the full dataset (Fig. S2). Obviously, there are variations in behavior by individual (Fig. S4). However, the female remnant juvenile (deer 2206) was most active in contacting other groups before group removal and 1 male remnant juvenile (deer 0516) was most active in contacting other groups following group removal (Fig. S4D). We specifically chose to monitor deer during winter and spring because white-tailed deer matrilines exhibit the greatest social interaction during these seasons (Hawkins and Klimstra 1970), when between-group transmission is most likely. Moreover, our study does not measure the transmission of pathogens. Rather, our study measures the potential for pathogen transmission using various metrics; transmission of pathogens depends heavily on the disease in question. Diseased individuals may have different social behavior (Krumm et al. 2005, Webster 2007). For instance, Salazar et al. (2016) reported that mule deer (*Odocoileus hemionus*) with clinical CWD were less likely to be observed in groups with other deer than were apparently healthy individuals. In spite of these limitations, our findings elucidate the behavioral differences between remnant juveniles and adults in response to social group removal and can be used to strengthen our understanding of social behavior and disease dynamics of white-tailed deer.

## MANAGEMENT IMPLICATIONS

Because remnant juveniles tended to shift their space use and were observed more often with other deer than were remnant adults after group removal, our findings suggest that disease management should aim to remove entire social groups of deer instead of separate individuals, if feasible (Porter et al. 1991, McNulty et al. 1997, Oyer and Porter 2004). If removing whole social groups is not logistically possible, culling individuals may still have desired effects on disease control (Potapov et al. 2012, Mateus-Pinilla et al. 2013, Manjerovic et al. 2014), but further research is needed.

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Fig. 1. Study area where we captured, marked, and collared white-tailed deer during 2011–2014 in southern Illinois, USA to investigate space use and contacts after deer removal.

Fig. 2. Indirect contact metrics for collared control (white) and remnant (gray) white-tailed deer during 2011–2014 in southern Illinois, USA. Changes in indirect contact following the removal period were quantified by change in home range and core area size (A), space use fidelity measured by volume of intersection (B), and shift in space use toward neighbors measured by greatest change in volume of intersection (C). Error bars represent standard error.

Fig. 3. Mean direct contact rates (no. contacts/dyad/week) between white-tailed deer measured by proximity loggers during 2011–2014 in southern Illinois, USA, relative to time of group removal for control (black) and remnant (gray) white-tailed deer during the adult phase (A) and the juvenile phase (B). Error bars represent standard error.

Fig. 4. Direct contact metrics of white-tailed deer before and after the removal period during 2011–2014 in southern Illinois, USA. We present mean direct contact rates (no. contacts/dyad/week; A and B) and mean duration of direct contact (seconds; C and D) of control (black) and remnant (gray) deer during adult (A and C) and juvenile (B and D) phase. Error bars represent standard error.

Fig. 5. Histogram of white-tailed deer group size observations before and after the removal period during 2011–2014 in southern Illinois, USA. Each panel represents a remnant individual (identification of individual on top right): remnant adults (left) and remnant juveniles (right).

Table 1. Collared white-tailed deer in treatment groups in southern Illinois, USA, 2011–2014. We removed all group members, except the one listed as remnant, during March–April in 2012–2014. We determined group sizes using visual observations and trail camera photographs.

| Phase | Remnant deer ID | Site | Age | Sex | Group size pre-removal | No. deer removed | Date removed | Group size post-removal |
|---|---|---|---|---|---|---|---|---|
| Adult | 0115 | TON[a] | Adult | F | 2 | 1 | 27 Mar 2012 | 1 |
| Adult | 0410 | Johnson | Adult | F | 3 | 2 | 30 Mar 2012 | 1 |
| Adult | 0511 | TON[a] | Adult | F | 3 | 2 | 6 Apr 2012 | 1 |
| Adult | 0811 | TON[a] | Adult | F | 2 | 1 | 2 May 2012 | 1 |
| Juvenile | 0516 | Rend Lake | Juvenile | M | 3 | 2 | 18 Mar 2014 | 4 |
| Juvenile | 2206 | CONWR[b] | Juvenile | F | 2 | 1 | 29 Mar 2014 | 4 |
| Juvenile | 2308 | TON[a] | Juvenile | M | 3 | 2 | 1 Apr 2013 | 2 |
| Juvenile | 2404 | Rend Lake | Juvenile | M | 2 | 1 | 18 Mar 2014 | 2 |
| Total | 8 | | | | | 12 | | |

[a] Touch of Nature Environmental Center.

[b] Crab Orchard National Wildlife Refuge.

Table 2. Hypotheses and results of statistical tests used to evaluate responses of remnant white-tailed deer to group member removal in southern Illinois, USA, 2011–2014. Indirect contact metrics were change in core area ($\Delta$CA), change in home range ($\Delta$HR), space use fidelity measured by volume of intersection ($VI_{fidelity}$), and maximum space use shift toward neighbors ($\Delta VI_{max}$). Direct contact metrics were contact rate (no. contacts/dyad/week) and duration of contacts (seconds).

| | | Adult phase | | Juvenile phase | |
|---|---|---|---|---|---|
| | Metric | Prediction | Observed | Prediction | Observed |
| Indirect contact | $\Delta$CA | Remnant > Control | Remnant > Control | Remnant > Control | Remnant < Control |
| | $\Delta$HR | Remnant > Control | Remnant > Control | Remnant > Control | Remnant > Control |
| | $VI_{fidelity}$ | Remnant < Control | Remnant > Control | Remnant < Control | Remnant < Control** |
| | $\Delta VI_{max}$ | Remnant > Control | Remnant < Control | Remnant > Control | Remnant > Control* |
| Direct contact | Rate | Negative BACI effect | Positive BACI effect | Negative BACI effect | Negative BACI effect |
| | Duration | Negative BACI effect | Positive BACI effect** | Negative BACI effect | Positive BACI effect |

** One-tailed $P < 0.05$.

* One-tailed $P = 0.08$.

Table 3. Demographic characteristics of white-tailed deer collared and monitored for experimental tests of behavioral response to social group disruption in southern Illinois, USA, 2011–2014. We determined group sizes using visual observations and trail camera photographs.

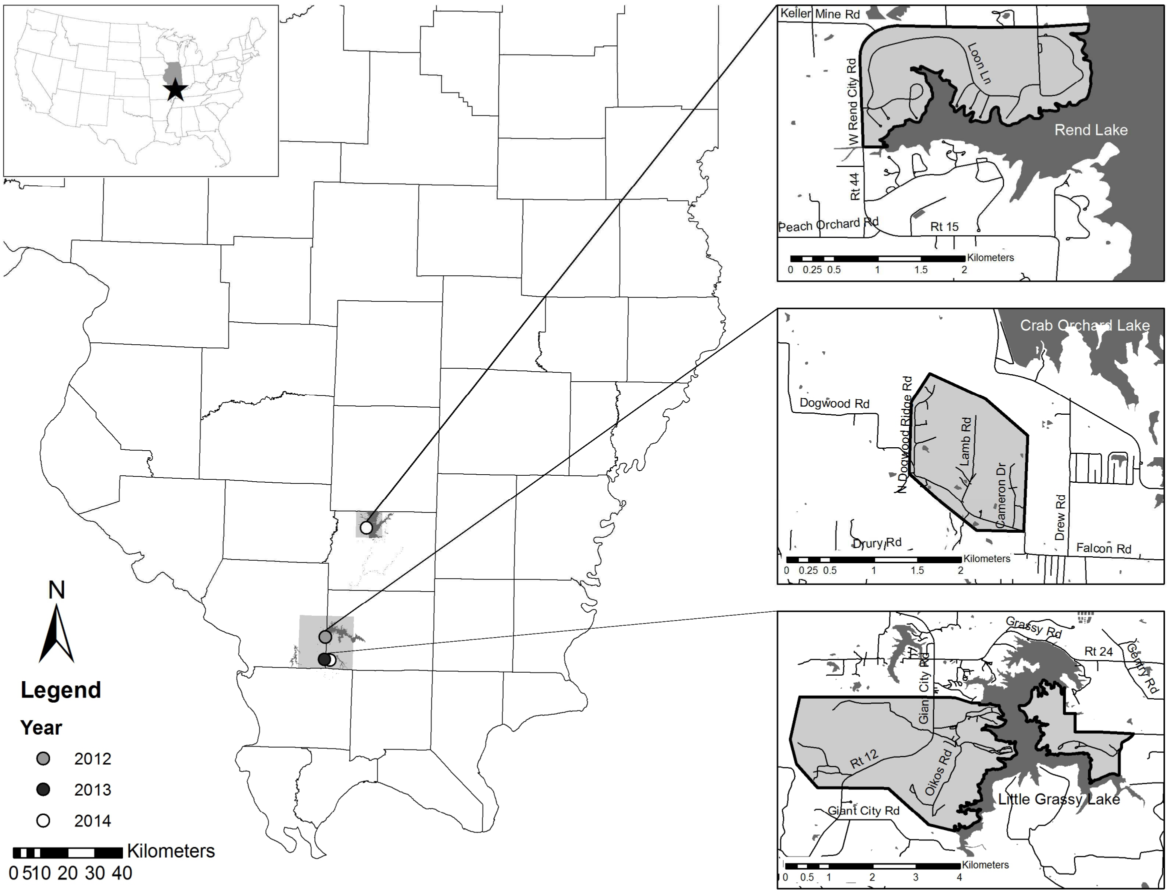
| | | | Control | | | | Removal | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Year | Phase | Site | M Juvenile | F Juvenile | F Adult | Group sizes | M Juvenile | F Juvenile | F Adult | Initial group sizes |
| 2011–2012 | Adult | Johnson | 0 | 1 | 3 | 1–3 | 0 | 0 | 1 | 3 |
| 2011–2012 | Adult | TON[a] | 0 | 3 | 9 | 1–5 | 0 | 0 | 3 | 2–3 |
| 2012–2013 | Juvenile | TON[a] | 1 | 1 | 4 | 1–8 | 1 | 0 | 0 | 3 |
| 2013–2014 | Juvenile | CONWR[b] | 0 | 3 | 2 | 1–4 | 0 | 1 | 0 | 2 |
| 2013–2014 | Juvenile | Rend Lake | 4 | 3 | 0 | 1–8 | 2 | 0 | 0 | 2–3 |

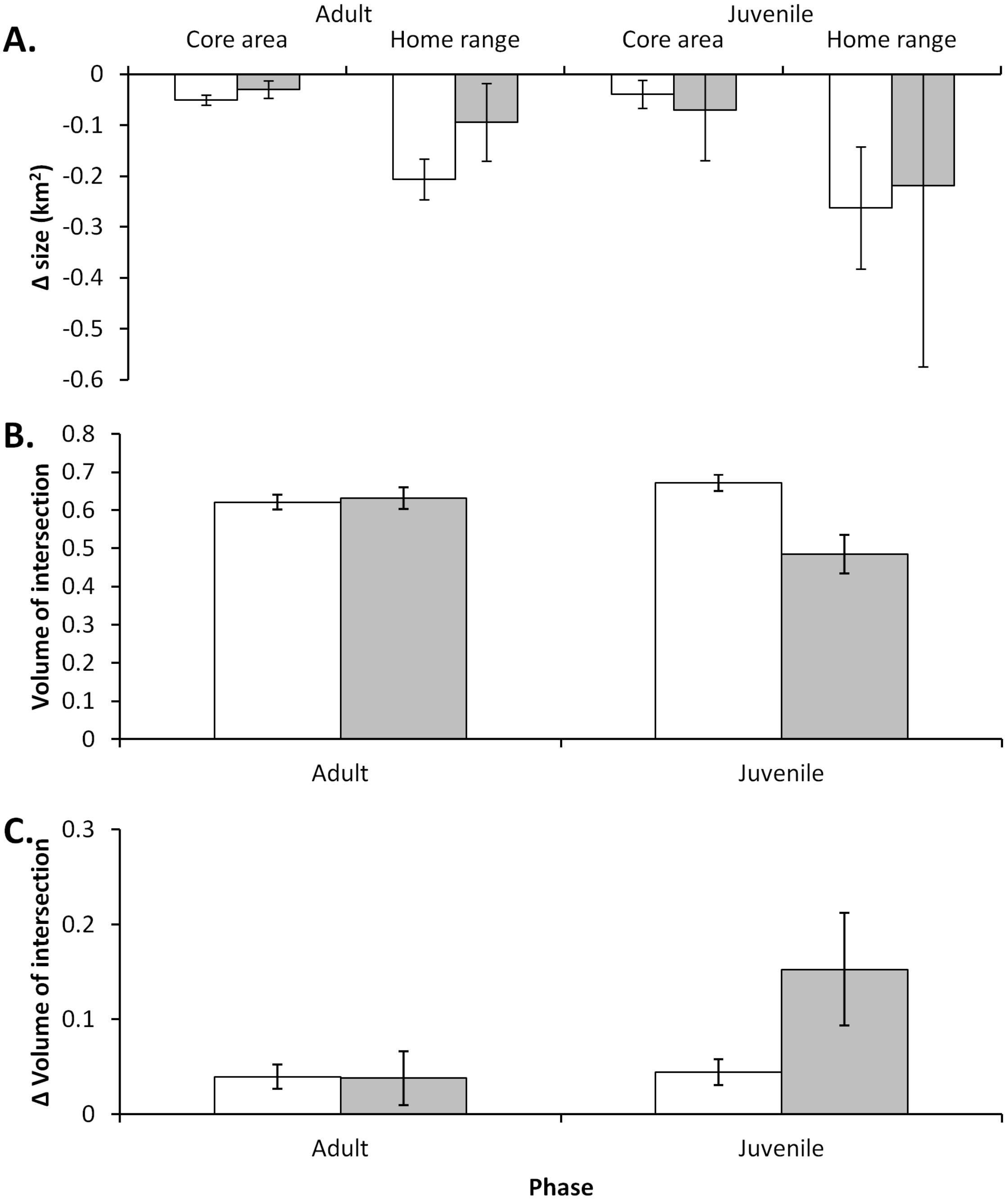
[a] Touch of Nature Environmental Center.

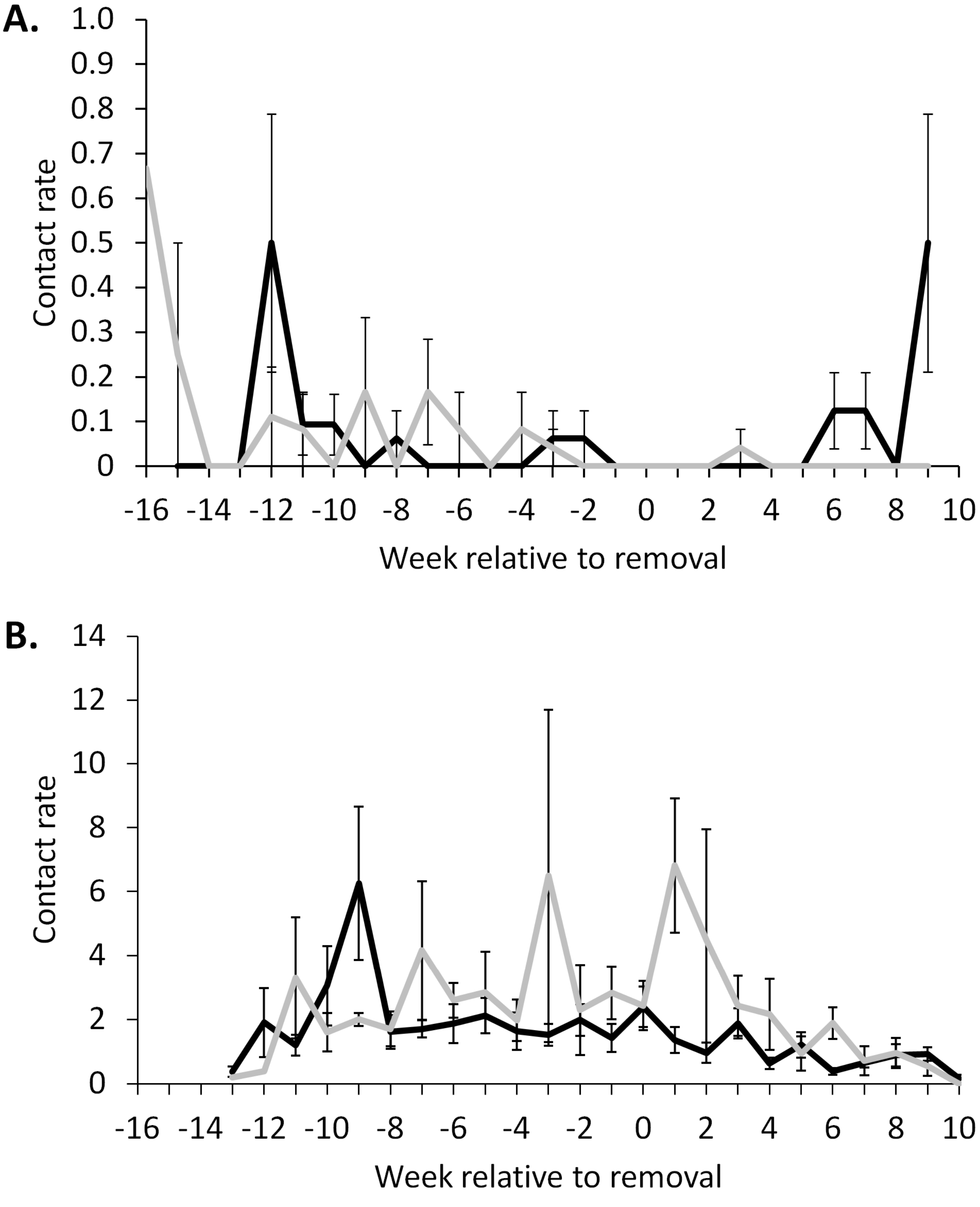
[b] Crab Orchard National Wildlife Refuge.

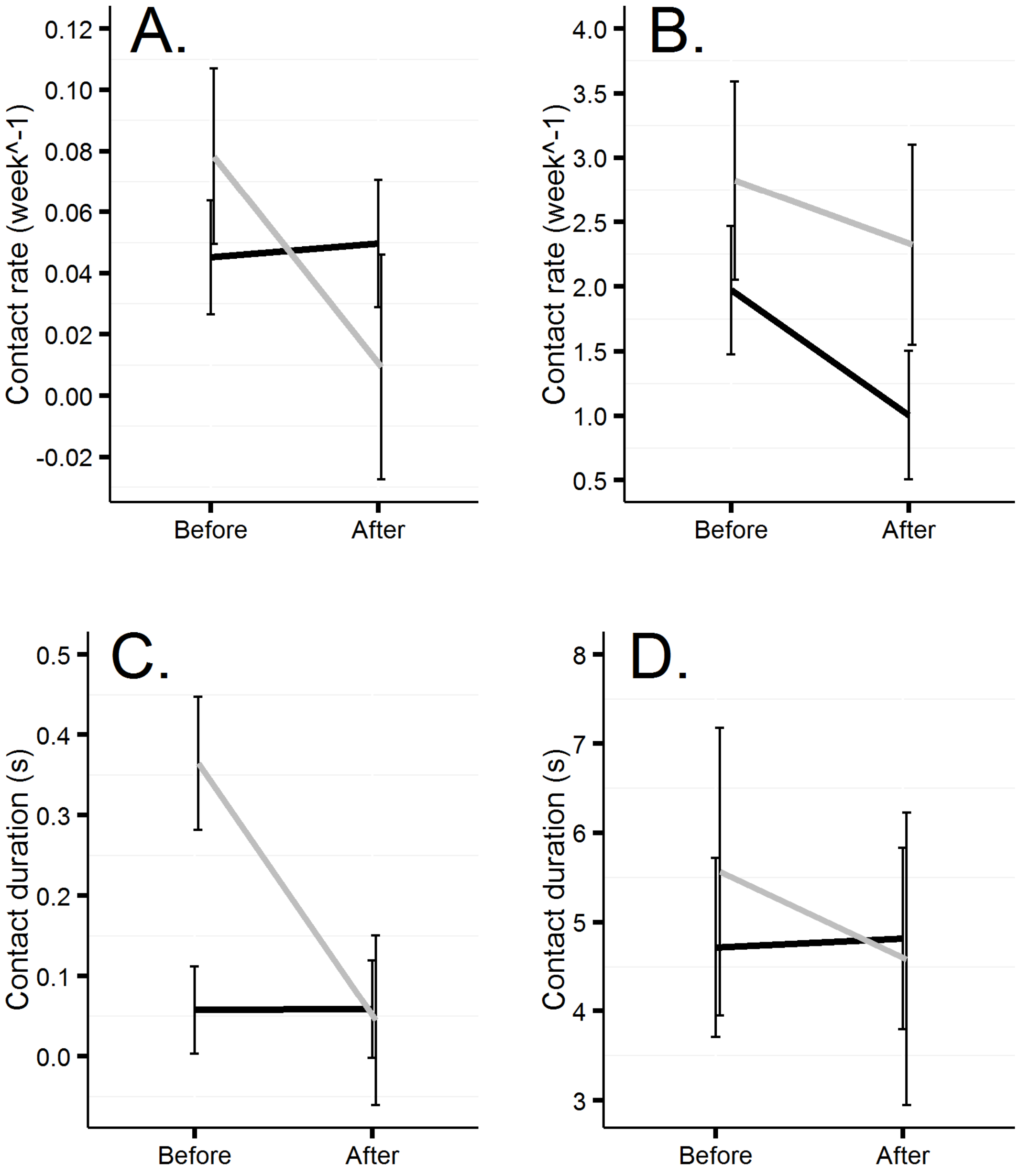
Tosa et al.

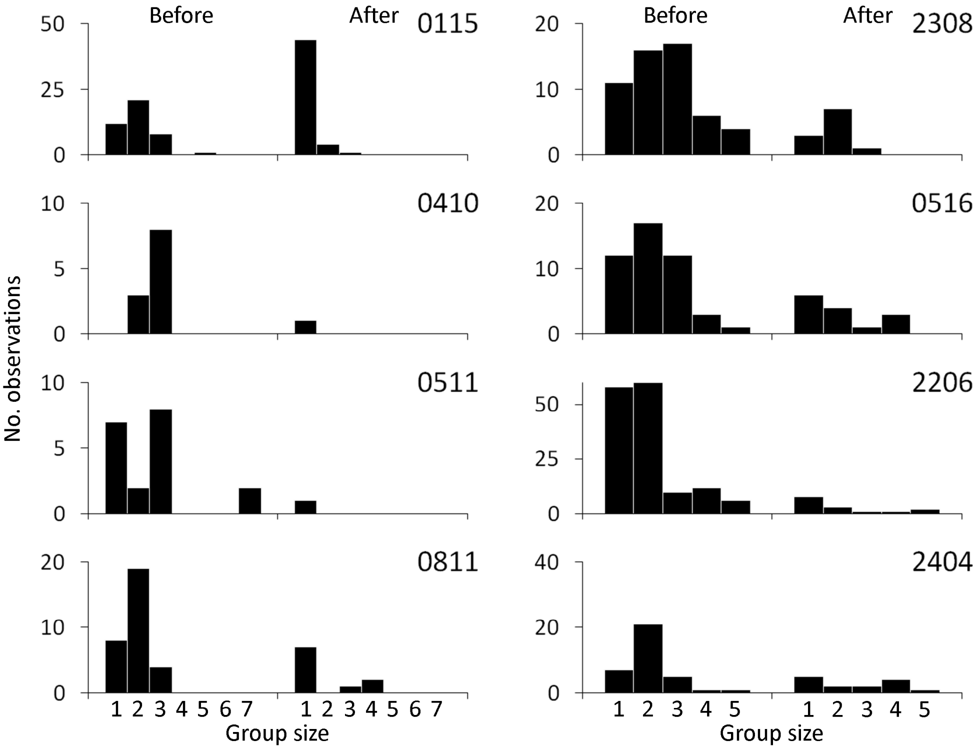
Article Summary: Transmission and impact of infectious diseases can be altered if host social structure is disrupted. By testing whether remnant white-tailed deer join or increase contacts with neighboring groups after group depopulation, we found age-specific responses to social disruption and support for complete group removal when culling for disease management.


Keller Mine Rd
Loon Ln
W Rend City Rd
Rend Lake
Rt 44
Peach Orchard Rd
Rt 15
Kilometers
0 0.25 0.5 1 1.5 2
Crab Orchard Lake
Dogwood Rd
N Dogwood Ridge Rd
Lamb Rd
Cameron Dr
Drury Rd
Drew Rd
Falcon Rd
Kilometers
0 0.25 0.5 1 1.5 2
Grassy Rd
Rt 24
Gent Rd
Giant City Rd
Rt 12
Oikos Rd
Little Grassy Lake
Giant City Rd
Kilometers
0 0.5 1 2 3 4
N
Legend
Year
2012
2013
2014
Kilometers
0 5 10 20 30 40


A.
Adult
Juvenile
Core area
Home range
Core area
Home range
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
Δ size (km²)
B.
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Volume of intersection
Adult
Juvenile
C.
0.3
0.2
0.1
0
Δ Volume of intersection
Adult
Juvenile
Phase


A.
Contact rate
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-16
-14
-12
-10
-8
-6
-4
-2
0
2
4
6
8
10
Week relative to removal
B.
Contact rate
14
12
10
8
6
4
2
0
-16
-14
-12
-10
-8
-6
-4
-2
0
2
4
6
8
10
Week relative to removal


A.
Contact rate (week^-1)
0.12
0.10
0.08
0.06
0.04
0.02
0.00
-0.02
Before
After
B.
Contact rate (week^-1)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
Before
After
C.
Contact duration (s)
0.5
0.4
0.3
0.2
0.1
0.0
Before
After
D.
Contact duration (s)
8
7
6
5
4
3
Before
After


Before
After
0115
2308
0410
0516
0511
2206
0811
2404
No. observations
50
25
0
20
10
0
10
5
0
20
10
0
10
5
0
50
25
0
20
10
0
40
20
0
1 2 3 4 5 6 7
1 2 3 4 5 6 7
1 2 3 4 5
1 2 3 4 5
Group size
Group size