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11 RH: Tosa et al. • Impact of Localized Removal on Deer Behavior

12 **Localized Removal Affects White-Tailed Deer Space Use and Contacts**

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

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

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

37

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

50 Social grouping can disconnect within-group contact patterns from overall population
51 density, so that disease transmission is often modeled as frequency-dependent with the force of
52 infection dependent on the proportion of infected individuals in the population (de Jong et al.
53 1995, Begon et al. 2002). In extreme cases, frequency-dependent diseases can cause hosts to
54 become locally extinct because individuals seek each other even as the population decreases (e.g.,
55 devil facial tumor disease; McCallum et al. 2009). Unlike the case with density-dependent
56 transmission, holding host density below a threshold may not be an effective management
57 strategy when transmission is frequency-dependent (Getz and Pickering 1983).

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

67 Understanding contact patterns of white-tailed deer (*Odocoileus virginianus*) is important
68 to understand and predict dynamics of bTB and chronic wasting disease (CWD) in free-living
69 deer populations (Gross and Miller 2001, Williams et al. 2002, Conner et al. 2008). White-tailed
70 deer have an intermediate level of sociality; adult female and young deer form relatively stable
71 social groups (typically described as matriline) from September through June (Hawkins and
72 Klimstra 1970, Hirth 1977, Nelson and Mech 1981, Lingle 2003), with distinct within-group and

73 between-group interactions (Schauber et al. 2007, 2015; Tosa et al. 2015). Specifically, direct
74 contact rates are greater within social groups than predicted based on joint space use alone
75 (Schauber et al. 2007, 2015). In contrast, members of different social groups avoid close contact
76 even when in the general vicinity of each other (Tosa et al. 2015). If group membership is stable,
77 disease transmission compartmentalized based on group membership can be modeled similar to
78 that of species that are more solitary (e.g., moose [*Alces alces*]), where each deer group is
79 analogous to an individual. If disease mortality or management efforts destabilize group
80 membership, however, that could enhance between-group transmission independent of changes
81 in population density.

82 The importance of contact compartmentalization based on group membership for disease
83 transmission is supported by evidence that having a closely related female infected with CWD
84 nearby is a far stronger predictor of CWD infection than the number of unrelated, infected
85 females nearby (Gear et al. 2010). Because deer infected with bTB and CWD rarely show
86 clinical signs during early stages, targeted removal of infected deer is difficult (Williams et al.
87 2002, Wolfe et al. 2004). Moreover, the long incubation periods of these diseases can allow
88 infected juveniles to outlive older, earlier-infected group members, which may lead to social
89 disruption (e.g., orphaning, temporary isolation; Gross and Miller 2001, Williams et al. 2002).
90 Because infected animals are difficult to identify, managers have implemented non-selective
91 sharpshooting in and around core disease areas and increased hunting opportunities for the
92 public; these efforts appear to have maintained low disease prevalence compared to areas with no
93 culling (Williams et al. 2002, Bollinger et al. 2004, Mateus-Pinilla et al. 2013, Manjerovic et al.
94 2014). Still, how social disruption affects disease transmission and the remaining population is
95 poorly understood (Wasserberg et al. 2009).

96 Localized removal of white-tailed deer has generated conflicting results, depending on
97 whether entire groups were removed or remnant animals were left. After removal of entire deer
98 social groups in the Adirondack Mountains in New York, remaining groups adjacent to the
99 removal area did not alter their home ranges, even after 5 years (Porter et al. 1991, McNulty et al.
100 1997, Oyer and Porter 2004). Ozoga and Verme (1984) similarly reported that isolated females
101 remaining after localized removal stayed within their original home ranges despite being
102 surrounded by areas of lower deer density. In other studies, orphaned juveniles had smaller home
103 ranges than unorphaned juveniles (Woodson et al. 1980, Marchinton and Hirth 1984, Giuliano et
104 al. 1999). Partial group removal may cause remaining deer to group together (Ozoga and Verme
105 1984, Williams et al. 2008), where individuals initially from separate social groups attempt to
106 form groups (Woodson et al. 1980, Etter et al. 1995, Giuliano et al. 1999, Comer et al. 2005).
107 This behavior has also been observed in red deer (*Cervus elaphus*), where orphaned females
108 more frequently joined and left groups than those whose mothers were still alive (Clutton-Brock
109 et al. 1982). Although removal of deer may decrease density of deer in the area, partial group
110 removal could cause greater movement of deer (and their pathogens) from group to group.
111 Movement of deer between groups due to incomplete removal of groups by disease epidemics or
112 management strategies can maintain efficient between-group transmission even as overall
113 population density decreases. Furthermore, greater movement of deer or movement of deer into
114 areas previously occupied by infected individuals that were removed can be problematic if
115 pathogens can persist in the environment and be transmitted indirectly (Sauvage et al. 2003,
116 Miller et al. 2004, Almberg et al. 2011). Similar to other transmissible spongiform
117 encephalopathies, the prions that cause CWD can remain infectious for years in the environment.
118 Chronic wasting disease can be transmitted directly and indirectly by contact with contaminated

119 blood, saliva, feces, carcasses, or soil (Mathiason et al. 2009, Walter et al. 2011). As such,
120 indirect transmission can further decouple between-group transmission of disease from the
121 density of infected animals (Almberg et al. 2011).

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

129 **STUDY AREA**

130 We conducted our study at 4 sites in southern Illinois, USA (UTM zone 16N): a private property
131 (Johnson Farms; 309572E, 4175040N), Touch of Nature Environmental Center (TON; 309169E,
132 4166864N), Crab Orchard National Wildlife Refuge (CONWR; 311628E, 4166427N), and Rend
133 Lake (324803E, 4215562N; Fig. 1). This study area is located on the glacial border where there
134 is a sharp transition from rolling agricultural land in the north to rough unglaciated areas in the
135 south; elevations range from 118 m to 199 m. The region had hot, humid summers and mild
136 winters; monthly high temperatures ranged from 5°C in January to 32°C in July and monthly low
137 temperatures ranged from -5°C in January to 20°C in July (National Oceanic and Atmospheric
138 Administration 2010). Study sites were primarily oak (*Quercus* spp.)-hickory (*Carya* spp.) forest
139 with some crop fields, grasslands, and residential areas (Schauber et al. 2007). Bobcats (*Lynx*
140 *rufus*), coyotes (*Canis latrans*), and domestic dogs (*Canis familiaris*) are the primary predators
141 in this region (Rohm et al. 2007). Sites had relatively high deer densities (>15 deer/km²;

142 Anderson et al. 2013) and low mortality rates (87% annual survival rate of adult F; Storm et al.
143 2007). All sites were closed to hunting during this study with the exception of a deer hunt for
144 handicapped persons at TON (archery) and Rend Lake (gun) in November.

145 **METHODS**

146 **Deer Capture and Handling**

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

162 We calibrated detection distances by placing collars in the same orientation facing each
163 other to represent direct contact between collared deer. Detection distances differed by phase: ≤ 1
164 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

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

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

206 **Contact Rate Analysis**

207 To quantify the effect of social group removal on behavior of remnant deer, we used a before-
208 after-control-impact (BACI) design (Stewart-Oaten et al. 1986) to compare temporal changes in
209 measures of indirect and direct contact between control (i.e., from non-removal groups) and
210 remnant collared deer in each study site. We designed the study so that we would have ≥ 8 weeks

211 of data in both pre- and post-removal periods during the time when grouping behavior is
212 strongest. We censored data from all deer ≤ 3 days of capture and during the period of deer
213 removal at each site to account for altered behavior due to capture and presence of bait during
214 removal efforts, respectively (Kjær et al. 2008, Schaubert et al. 2015). Therefore, the pre-removal
215 period started 4 days following capture for each deer and ended when the site was baited (i.e.,
216 typically the week before removal; 18 Mar 2012, 13 Mar 2013, and 10 Mar 2014). The post-
217 removal period started the day bait was no longer at the site (i.e., typically a few days following
218 removal; 6 Apr 2012, 3 Apr 2013, and 1 Apr 2014) and lasted until the collars dropped off (i.e., 1
219 Jun). We excluded any GPS locations with an altitude < 0 m or > 400 m. We conducted all data
220 analyses in program R. We analyzed data for adult and juvenile phases separately and excluded
221 data from collared deer that died during the data collection period. We excluded 2 incomplete
222 removal groups (i.e., group size remained > 1) from the analysis. In addition, based on high
223 dynamic interaction index values (Long et al. 2014), we identified 4 groups that each had 2
224 collared deer (Fig. S1, available online in Supporting Information); we excluded data from 1
225 collar (chosen at random) from each of these within-group dyads from the analysis. Lastly, we
226 excluded contact data between 1 dyad consisting of 2 control deer whose dynamic interaction
227 index fluctuated between within-group and between-group levels over the study period.

228 *Indirect contact.*—We compared 3 metrics of indirect contact, indicating potential for
229 environmental transmission, between remnant and control deer: 1) changes in home range size,
230 2) space use fidelity (i.e., overlap between pre- and post-removal space use of the same animal),
231 and 3) shifts in space use toward neighboring deer. We calculated home range size and space use
232 overlap using the AdehabitatHR package (Calenge 2006). For each individual in each time
233 period (i.e., pre- or post-removal), we used 500 randomly selected GPS locations and reference

234 bandwidths to calculate the fixed-kernel utilization distribution (UD; Seaman and Powell 1996,
 235 Seaman et al. 1999). To compare changes (from pre- to post-removal periods) in home range
 236 (Δ HR) and core area size (Δ CA) between control and remnant deer, we calculated home range
 237 (95% isopleth) and core area (50% isopleth) sizes from the pre- and post-removal fixed-kernel
 238 UDs for each deer.

239 We used volume of intersection (VI; Seidel 1992, Millspaugh et al. 2004, Fieberg and
 240 Kochanny 2005) to calculate space use overlap between 2 estimated UDs: \hat{f}_i and \hat{f}_j . For space
 241 use fidelity (VI_{fidelity}), \hat{f}_i and \hat{f}_j represent the estimated UDs of the same deer from the pre- and
 242 post-removal periods, respectively. To compare shifts in space use overlap toward neighboring
 243 deer, we calculated 2 VIs for each dyad (i,j), 1 pre-removal ($VI_{\text{pre}, ij}$) and 1 post-removal ($VI_{\text{post}, ij}$),
 244 where \hat{f}_i and \hat{f}_j represent the estimated UDs of 2 deer during the same time period. For each
 245 possible dyad in each study area, we calculated the difference in VI between periods ($\Delta VI_{ij} =$
 246 $VI_{\text{pre}, ij} - VI_{\text{post}, ij}$). Then, for each deer, we selected its greatest ΔVI value (ΔVI_{max} ; $\Delta VI_{\text{max}, i} =$
 247 ΔVI_{i1} if $\Delta VI_{i1} > \Delta VI_{i2}, \Delta VI_{i3}, \dots \Delta VI_{ij}$) and compared ΔVI_{max} between control and remnant deer.
 248 We excluded dyads with remnant deer when calculating ΔVI_{max} for control deer.

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

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

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

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

276 *Regrouping.*—Our metrics of indirect and direct contact are based on data only from deer
277 carrying GPS-proximity logger collars, but remnant deer might attempt to join or form groups
278 with un-collared deer. Therefore, we assessed evidence of grouping by remnant animals by
279 examining the frequency of observation (visual or via remote cameras) alone versus with other

280 deer post-removal. Specifically, we used a 2-sample t -test to test the post-hoc hypothesis that the
 281 proportion of post-removal observations of remnant animals alone was greater for adult than for
 282 juvenile remnants.

283 **RESULTS**

284 We captured and tagged 105 deer (46 in adult phase: 30 adults, 16 juveniles, 59 in juvenile
 285 phase: 21 adults, 38 juveniles), and we collared 20 females (16 adults, 4 juveniles) during the
 286 adult phase and 14 females (6 adults, 8 juveniles) and 8 juvenile males during the juvenile phase
 287 (Table 3). From 587 visual observations and 40,807 trail camera photographs, we identified 63
 288 social groups (27 in 2011–2012, 18 in 2012–2013, and 18 in 2013–2014), consisting of 1–5
 289 group members. Of these groups, we collared 42 social groups (20 in 2011–2012, 7 in 2012–
 290 2013, and 15 in 2013–2014). Of these, we were able to remove all but the collared animal
 291 successfully from 8 social groups, 4 in each phase (Table 1). We compared their responses with
 292 those of 34 collared animals in unmanipulated (i.e., control) groups (16 in adult phase, 18 in
 293 juvenile phase; Table 2). Overall mean GPS error was 5.78 m (SE = 0.01, $n = 292,278$); GPS
 294 error for each deer ranged from 5.40–6.26 m.

295 **Indirect Contact**

296 Control and remnant deer exhibited similar decreases in core area and home range sizes from
 297 pre- to post-removal periods in both the adult phase (ΔCA $t_{5,1} = -1.06$, 1-tailed $P = 0.17$; ΔHR
 298 $t_{4,8} = -1.30$, 1-tailed $P = 0.13$) and the juvenile phase (ΔCA $t_{3,5} = 0.30$, 1-tailed $P = 0.39$; ΔHR
 299 $t_{3,7} = -0.12$, 1-tailed $P = 0.46$; Table 2, Fig. 2A). We found no evidence that group removal
 300 affected space use fidelity of remnant adults (remnant $\overline{VI_{\text{fidelity}}} = 0.63$, SE = 0.03, $n = 4$, vs.
 301 control $\overline{VI_{\text{fidelity}}} = 0.62$, SE = 0.02, $n = 16$; $t_{6,19} = -0.32$, 1-tailed $P = 0.38$), but remnant

302 juveniles had lower space use fidelity than control deer (remnant $\overline{VI} = 0.48$, SE = 0.05, $n = 4$ vs.
 303 control $\overline{VI} = 0.67$, SE = 0.02, $n = 18$; $t_{4,14} = 3.40$, 1-tailed $P = 0.013$; Fig. 2B).
 304 Similarly, we found no evidence that group removal caused remnant adults to shift space use
 305 toward neighboring groups (remnant $\overline{\Delta VI_{max}} = 0.04$, SE = 0.03, $n = 4$ vs. control $\overline{\Delta VI_{max}} = 0.04$,
 306 SE = 0.01, $n = 16$; $t_{4,30} = 0.05$, 1-tailed $P = 0.48$). Observed space-use shift by remnant juveniles
 307 toward neighbors after group removal was nearly 4 times greater than observed for controls, but
 308 this difference was not statistically significant (remnant $\overline{\Delta VI_{max}} = 0.15$, SE = 0.06, $n = 4$ vs.
 309 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
 310 evidence that apparent responses by remnant juveniles were caused by a difference in sex:
 311 comparisons between remnant males and control males during the juvenile phase (remnant
 312 $\overline{VI_{fidelity}} = 0.50$, SE = 0.07, $n = 3$ vs. control $\overline{VI_{fidelity}} = 0.68$, SE = 0.02, $n = 5$; $t_{2,47} = 2.53$, 1-
 313 tailed $P = 0.05$; remnant $\overline{\Delta VI_{max}} = 0.19$, SE = 0.06, $n = 3$ vs. control $\overline{\Delta VI_{max}} = 0.08$, SE = 0.03,
 314 $n = 5$; $t_{3,14} = -1.59$, 1-tailed $P = 0.10$; Fig. S2) were quantitatively and qualitatively similar to
 315 results obtained from juveniles of both sexes.

316 **Direct Contact**

317 Proximity loggers recorded 29,499 consolidated contacts (25,734 within-group, 3,765 between-
 318 group; Fig. 3). Only 37 of the between-group contacts were recorded during the adult phase. We
 319 did not find main or interactive BACI effects of treatment (remnant vs. control) and period (pre-
 320 vs. post-removal) on direct contact rates of adult females ($F_{1,404} \leq 2.33$, $P \geq 0.13$; Table 2, Fig.
 321 4A). Similarly, the BACI effect (treatment \times period interaction) on direct contact rates during the
 322 juvenile phase was not statistically significant ($F_{1,423} = 0.64$, $P = 0.43$). Remnant juveniles had
 323 similar overall contact rates to control deer ($F_{1,423} = 2.53$, $P = 0.11$), and contact rates of both

324 control deer and remnant juveniles were higher before than after the removal event ($F_{1,423} =$
325 15.18, $P \leq 0.001$; Fig. 4B).

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

333 **Regrouping**

334 Post-removal, adult remnant deer were nearly always observed alone (Fig. 5). In contrast, 3 of 4
335 juvenile remnants were observed more often with other deer than alone and the 1 other juvenile
336 remnant was observed alone only about half the time (Fig. 5). A post hoc test of this difference
337 between age classes in mean frequency of being observed alone indicated statistical significance
338 ($\bar{x} = 89.9\%$, $SE = 7.1$, $n = 4$ for adults vs. $\bar{x} = 39.8\%$, $SE = 5.5$, $n = 4$ for juveniles; $t_{5,67} = 5.59$, P
339 $= 0.002$).

340 **DISCUSSION**

341 Following general sharpshooting where individuals rather than groups were removed, Williams
342 et al. (2008) reported that remaining white-tailed deer increased their home range overlap, and
343 suspected that remnant deer had an inherent need to join new social groups of unrelated
344 individuals. In our study, experimental group removal caused shorter contacts and little change
345 in contact rates or space use of remnant adult females. In contrast, remnant juveniles reduced
346 their space use fidelity and appeared to increase spatial overlap with neighbors following group

347 removal. Visual observations with uncollared deer further suggested that juvenile deer may have
348 sought out interactions with neighbors following removal of group members. Similar to this
349 study, Williams et al. (2008) conducted their study in an area with high deer densities (i.e., 78–
350 83 deer/km²), little to no hunting pressure, and little predation pressure. Williams et al. (2008),
351 however, collared both male and female deer and did not distinguish between adults and
352 juveniles in their analysis. What is more, Williams et al. (2008) conducted their removal efforts
353 in January and did not account for social groups during removal; this may have resulted in partial
354 group removal or even left some collared groups intact. Our findings suggest that responses by
355 deer to social disruption differ by age, due in part to greater familiarity of adult females with
356 their surroundings and their more established social status with their neighbors relative to
357 juveniles (Hirth 1977, Nelson and Mech 1981, Taillon et al. 2006). Juveniles may also lose
358 social status with neighboring groups when group members are removed if social status is
359 derived from the group, similar to the manner in which calves derive social status from females
360 in red deer (Hall 1983). Whereas adult females may have previously reared and parted with their
361 offspring because of dispersal, predation, hunting mortality, or disease, juveniles have
362 experienced group member loss for the first time. For these reasons, juveniles may benefit more
363 from being social than adult females and may seek out opportunities to join other groups or
364 establish themselves, thereby increasing their contact rates with neighbors (Woodson et al. 1980,
365 Marchinton and Hirth 1984, Giuliano et al. 1999).

366 An increase in direct and indirect contact rates with other social groups by remnants
367 following group removal would facilitate pathogen spread and provide a potential mechanism
368 for frequency-dependent transmission, confounding attempts at disease management (Potapov et
369 al. 2012). We found no evidence that loss of group members drives adult females to increase

370 opportunities for direct or indirect contact with neighboring groups; rather, our findings indicate
371 that remnant adult females will remain in their home ranges, shorten duration of contacts, and
372 stay isolated until the fawning season and thereby limit spread of disease to neighboring groups.
373 Remnant juveniles, however, showed lower home range fidelity than controls and were observed
374 more often with other deer than were remnant adults. The effect of removal on space use shifts of
375 juveniles was not statistically significant, despite large observed effect sizes. Thus, our results on
376 how juveniles respond to group removal were inconclusive (i.e., consistent with small as well as
377 biologically significant effect sizes; Steidl et al. 1997). For diseases with long incubation times,
378 such as bTB and CWD, adult females typically have higher infection prevalence than juveniles
379 and continue to contaminate the environment by shedding pathogens (Delahay et al. 2000,
380 Conner et al. 2008). The potential of juveniles to spread pathogens between groups, however,
381 could be more problematic because younger infected animals are likely to outlive older infected
382 animals during epizootics (Conner et al. 2008). Further research into social prospects of remnant
383 juvenile deer would enhance our understanding of disease transmission and management in
384 group-living wildlife.

385 Among juveniles, we found that direct contact rates were higher before than after
386 removal. As winter progresses to spring, growth of vegetation increases cover in addition to
387 forage quantity and quality for deer (Beier and McCullough 1990). Because large feeding groups
388 are common during late winter and early spring (Hawkins and Klimstra 1970) and because direct
389 contacts appear to occur mainly during feeding (Kjær et al. 2008), this increase in vegetation
390 may decrease deer densities at each foraging location and thereby decrease opportunities for
391 direct contact. We expected that remnant juveniles would have higher direct contact rates overall
392 than control juveniles because we specifically chose removal groups located in the center of the

393 study sites, surrounded by other collared animals, and most control animals were located on the
394 periphery with fewer collared groups around them. The lack of statistical difference between
395 overall contact rates between control and remnant deer suggests that a number of control groups
396 were also surrounded by other collared deer.

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

413 Our findings are limited to populations of female and juvenile deer with little or no
414 hunting pressure during winter and spring, outside of breeding and fawning seasons. Areas with
415 strong hunting or predation pressure or severe winter weather may have different grouping

416 responses to removal because protection from predators and access to resources are important
417 influences for grouping behavior (Krause and Ruxton 2002). We did not measure contact rates of
418 adult male deer or differentiate between behavior of remnant juveniles that were male or female.
419 Contact rates of adult male deer are especially important for disease transmission during the
420 mating season when males provide additional pathways for pathogens to spread to other female
421 social groups (Geist 1981, Koutnik 1981, Miller and Conner 2005), and male and female
422 juveniles may respond differently to disturbances in social structure (Nixon et al. 2007).
423 Although sex could account for behavioral differences in remnant juveniles, our analyses using
424 only male juveniles produced results similar to those for the full dataset (Fig. S2). Obviously,
425 there are variations in behavior by individual (Fig. S4). However, the female remnant juvenile
426 (deer 2206) was most active in contacting other groups before group removal and 1 male
427 remnant juvenile (deer 0516) was most active in contacting other groups following group
428 removal (Fig. S4D). We specifically chose to monitor deer during winter and spring because
429 white-tailed deer matrilineal exhibit the greatest social interaction during these seasons (Hawkins
430 and Klimstra 1970), when between-group transmission is most likely. Moreover, our study does
431 not measure the transmission of pathogens. Rather, our study measures the potential for pathogen
432 transmission using various metrics; transmission of pathogens depends heavily on the disease in
433 question. Diseased individuals may have different social behavior (Krumm et al. 2005, Webster
434 2007). For instance, Salazar et al. (2016) reported that mule deer (*Odocoileus hemionus*) with
435 clinical CWD were less likely to be observed in groups with other deer than were apparently
436 healthy individuals. In spite of these limitations, our findings elucidate the behavioral differences
437 between remnant juveniles and adults in response to social group removal and can be used to
438 strengthen our understanding of social behavior and disease dynamics of white-tailed deer.

439 **MANAGEMENT IMPLICATIONS**

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

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669 *Associate Editor: James Cain.*

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

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

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

681 Fig. 4. Direct contact metrics of white-tailed deer before and after the removal period during
682 2011–2014 in southern Illinois, USA. We present mean direct contact rates (no.
683 contacts/dyad/week; A and B) and mean duration of direct contact (seconds; C and D) of control
684 (black) and remnant (gray) deer during adult (A and C) and juvenile (B and D) phase. Error bars
685 represent standard error.

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

689

690 Table 1. Collared white-tailed deer in treatment groups in southern Illinois, USA, 2011–2014.
 691 We removed all group members, except the one listed as remnant, during March–April in 2012–
 692 2014. We determined group sizes using visual observations and trail camera photographs.
 693

Phase	Remnant deer ID	Site	Age	Sex	Group size		Date removed	Group size post-removal
					pre-removal	No. deer removed		
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		

694 ^aTouch of Nature Environmental Center.

695 ^bCrab Orchard National Wildlife Refuge.

696 Table 2. Hypotheses and results of statistical tests used to evaluate responses of remnant white-tailed deer to group member removal
 697 in southern Illinois, USA, 2011–2014. Indirect contact metrics were change in core area (ΔCA), change in home range (ΔHR), space
 698 use fidelity measured by volume of intersection (VI_{fidelity}), and maximum space use shift toward neighbors (ΔVI_{max}). Direct contact
 699 metrics were contact rate (no. contacts/dyad/week) and duration of contacts (seconds).
 700

		Adult phase		Juvenile phase	
	Metric	Prediction	Observed	Prediction	Observed
Indirect contact	ΔCA	Remnant > Control	Remnant > Control	Remnant > Control	Remnant < Control
	ΔHR	Remnant > Control	Remnant > Control	Remnant > Control	Remnant > Control
	VI_{fidelity}	Remnant < Control	Remnant > Control	Remnant < Control	Remnant < Control**
	ΔVI_{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

701 ** One-tailed $P < 0.05$.

702 * 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.

Year	Phase	Site	Control				Removal			
			M	F	F	Group sizes	M	F	F	Initial group sizes
			Juvenile	Juvenile	Adult		Juvenile	Juvenile	Adult	
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

^aTouch of Nature Environmental Center.

^bCrab Orchard National Wildlife Refuge.

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.









