Alternative Feeding Strategies and Potential Disease Transmission in Wisconsin White-Tailed Deer

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ABSTRACT We conducted experimental feeding using 3 feeding methods (pile, spread, trough) and 2 quantities (rationed, ad libitum) of shelled corn to compare deer activity and behavior with control sites and evaluate potential direct and indirect transmission of infectious disease in white-tailed deer (Odocoileus virginianus) in central Wisconsin, USA. Deer use was higher at 2 of the feeding sites than at natural feeding areas (P ≤ 0.02). Deer spent a higher proportion of time (P < 0.01) feeding at pile (49%) and spread (61%) treatments than at natural feeding areas (36%). We found higher deer use for rationed than ad libitum feeding quantities and feeding intensity was greatest at rationed piles and lowest at ad libitum spreads. We also observed closer pairwise distances (<0.3 m) among deer when corn was provided in a trough relative to spread (P = 0.03). Supplemental feeding poses risks for both direct and indirect disease transmission due to higher deer concentration and more intensive use relative to control areas. Concentrated feeding and contact among deer at feeding sites can also increase risk for disease transmission. Our results indicated that restrictions on feeding quantity would not mitigate the potential for disease transmission. None of the feeding strategies we evaluated substantially reduced the potential risk for disease transmission and banning supplemental feeding to reduce transmission is warranted. (JOURNAL OF WILDLIFE MANAGEMENT 72(2):416–421; 2008)

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Supplemental feeding contributes to transmission of several wildlife diseases, including bovine tuberculosis (TB) and brucellosis in cervids, mycoplasmal conjunctivitis in house finches (Carpodacus mexicanus), and trichomoniasis in birds (Thorne and Herriges 1992, Fisher et al. 1997, Miller et al. 2003, Höfte et al. 2004). Supplemental feeding, including baiting of white-tailed deer (Odocoileus virginianus) results in undesirable ecological effects (Casey and Hein 1983, Doenier et al. 1997, Cooper and Ginnett 2000) and increases indirect (environment-to-animal) and direct (animal-to-animal) transmission of infectious disease (Schmitt et al. 1997, Williams et al. 2002, Bartelt et al. 2003, Dunkley and Cattet 2003). Supplemental feeding likely promotes indirect and direct transmission of bovine TB in Michigan’s (USA) wild deer population (Schmitt et al. 1997, Garner 2001, Miller et al. 2003) because aggregation of deer at feeding sites results in more face-to-face contacts. Most contact among deer occurs within familial social groups (Marchinton and Hirth 1984); however, increased contact may occur because unrelated groups congregate at feeding sites (Blanchong et al. 2006). Indirect transmission of bovine TB likely occurs at feeding sites when infected animals deposit saliva and nasal droppings on frozen feed piles (Garner 2001).

Chronic wasting disease (CWD), a fatal prion disease of cervids, is the only transmissible spongiform encephalopathy known to cause contagious disease in wild animals (Williams et al. 2002). First recognized in captive mule deer (O. hemionus) in Colorado, USA, during the 1960s, CWD is currently found in western, midwestern, and eastern states and in Canada (Williams et al. 2002). Interspecies transmission of CWD is possible and CWD has subsequently been found in elk (Cervus elaphus), white-tailed deer, and moose (Alces alces). Management efforts have failed to eradicate or prevent geographic spread of this disease, which can be transmitted directly between animals and indirectly through an environmental source of infectious prions (Miller et al. 1998, 2004; Miller and Williams 2003). Infectious prions are shed through the alimentary tract via saliva or feces and potentially urine (Sigurdson et al. 1999, Spraker et al. 2002, Miller and Williams 2003, Kariv-Inbal et al. 2006, Mathiason et al. 2006). Prions deposited in soil remain infectious and are extremely resilient, persisting up to 3 years in experimental studies and >15 years in domestic situations (Brown and Gajdusek 1991, Johnson et al. 2006, Mathiason et al. 2006, Seidel et al. 2007). Supplemental feeding sites may harbor and concentrate disease agents deposited by infected animals, creating an environmental reservoir of contaminated feed or infectious excreta that poses a risk for indirect disease transmission (Miller et al. 2004, Palmer et al. 2004).

Supplemental feeding is discouraged or banned in most states having CWD or bovine TB, due to risk of disease transmission (Bartelt et al. 2003, Dunkley and Cattet 2003). Despite many detrimental effects of feeding (including baiting) for wildlife, feeding bans remain controversial (Heberlein 2004). Proponents of supplemental feeding claim that changing feeding regimes (feeding quantity and feeding method) can mitigate the risk of disease transmission. Our objective was to assess the potential for indirect and direct transmission of infectious disease for different feeding quantities and methods based on deer use.

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and behavior patterns at experimental feeding sites and natural feeding areas.

**STUDY AREA**

Our study occurred during winter (Dec–Mar) of 2003–2004 and 2004–2005 at Sandhill Wildlife Area (SWA), located in central Wisconsin, USA. A 2.7-m fence, limiting deer movement and human access, enclosed this 37-km² research facility. Overwinter deer density at SWA was estimated at 13 (2003–2004) and 7 deer/km² (2004–2005) during the study period (W. Hall, Wisconsin Department of Natural Resources, unpublished data). Prior to our study, baiting or feeding did not occur on SWA. Controlled public hunts occurred annually from late October through early November with mandatory CWD testing of harvested adult deer. Chronic wasting disease had not been detected at SWA. Public use was minimal and limited to foot traffic during the study.

**METHODS**

We selected 4 upland feeding sites (northeast, northwest, southeast, southwest) separated by approximately 3.2 km to provide site independence because Kilpatrick and Stober (2002) found no effect of temporary baiting on deer home range size and home ranges were expected to be <3.2 km in diameter (Skuldt 2005). To determine natural deer use and feeding behavior, we also monitored 3–6 control sites (without food) where deer traditionally concentrated during winter. If a control site had no deer activity for >2 weeks, we selected a new control area with recent deer activity (snow tracks and sign of browsing) to increase data collection.

We conducted 6 experimental treatments at each feeding site. Treatments varied in both feeding quantity and method. Quantity was either rationed (8.8 L) or ad libitum (max. 44 L) shelled corn, replenished daily. Feeding methods were raised (0.85 m) feeding troughs (0.3-m² feeding area), spread feed (2–3-m² feeding area), or feed piles (0.1–0.4-m² feeding area). We used a randomized complete block design (RCBD) with feeding trial as the experimental unit and randomized treatment order within each feeding site and year. Feeding trials lasted for 12 days followed by an 8-day nonfeeding period to de-habituate deer and achieve independence between trials (Henke 1997). We separated the field season into early (1 Dec–1 Jan), mid- (10 Jan–10 Feb), and late winter (19 Feb–21 Mar; Ozoga 1972).

We used Silent Image® (Reconyx, LLP, LaCrosse, WI) motion-sensing digital cameras to continuously monitor feeding and control sites. We programmed cameras to capture images at 15-second intervals for 15 minutes when triggered by a deer or other animals and to record time-lapse images at 15-minute intervals. We used digital images to calculate deer-use minutes \( DUM = [(\text{no. of deer in image } \times 0.25 \text{ min/camera-day})] \) for each feeding trial (Beringer et al. 2003). We partitioned DUM by categories of behavioral interactions and distances between deer. We standardized DUM data by camera effort (min/day camera was functioning) from time-lapse images to account for occasional camera failure. We determined average deer group size for each trial and behavioral state of each deer: artificial feeding (corn feeding), natural feeding (noncorn feeding), other, or unknown.

We used DUM to infer potential direct and indirect disease transmission by contact among deer (no. of deer present at feeding site) or deposition of infectious agents (time deer spent) at the site. We measured feeding intensity (DUM spent artificially feeding/unit area of treatment) to assess potential indirect disease transmission. We also assessed differences in feeding behavior by comparing the proportion of time spent foraging during trials at feeding and control sites. We used distance and behavioral interactions between deer to infer potential direct disease transmission. We recorded pairwise distance between deer for >1 deer (e.g., 2 deer = 1 distance, 3 deer = 3 distances) in categories of ≤0.3 m, within 1 m (≥0.3 m), and ≥1 m (LaGory et al. 1981). We classified behavioral interactions between deer as nose touching, mutual grooming, striking, flailing, rushing, or chasing (Forand and Marchinton 1989). We considered close interactions (nose touch, mutual grooming) high risk for CWD transmission whereas agonistic interactions (striking, rushing, flailing, chasing) correspond to a lower risk. We considered deer in close proximity (distance category ≤0.3 m) at higher risk for direct transmission.

We used Dunnett’s test to compare deer use, average group size, and proportion of time spent foraging between feeding and control sites (SAS Institute 2006). Control-site values were mean values for control sites grouped by trial period. We assessed effects of year, season, quantity, method, and the interaction of quantity–method on deer use (DUM), average group size, feeding intensity, and proportion of time spent in foraging, behavioral interactions, or pairwise distances using analysis of variance (ANOVA) with Type III sum of squares (SAS Institute 2006). We used Box–Cox transformations to meet assumptions of normality and homogeneity of errors in ANOVA (Box and Cox 1964). We used Fisher’s protected least significant difference for multiple comparisons of least-square means when a significant \( F \)-test was found by ANOVA. We compared the DUM and proportions of different behaviors between all feeding sites with the control site using a 2-sample \( t \)-test with Levene’s test for equality of variance, but we excluded trials with insufficient data (<50 DUM/trial) to determine behavioral interactions.

We also evaluated potential fecal ingestion at pile and trough treatments by randomly selecting 2 days per trial to present corn mixed with deer fecal pellets (6.25% pellets for rationed and 2.5% pellets for ad libitum quantities) during the second year. We recovered pellets after 24 hours and quantified dry-weight mass of pellet disappearance. We did not use spread treatments because pellet recovery was not reliable. We evaluated fecal ingestion using a selection index (% pellets consumed/% corn consumed) to quantify relative
consumption of corn and pellets. We excluded from our analysis experimental trials with minimal corn consumption (<2.2 L) during the 24-hour treatment period. We used 2-sample 𝑡-tests to compare selection indices between different feeding quantities and methods.

We fed shelled corn with a different colored metallic flake bait markers (detectable in fecal pellets) at each feeding site to assess animal use of >1 feeding site and test site independence (Thompson 2006). We conducted pellet surveys to record deposition of bait markers, evaluate deer movement among feeding sites, and determine deer use at sites. Pellet transects, surveyed before (autumn) and after (spring) experimental feeding, extended 600 m in cardinal directions with 4-m² circular plots surveyed at 50-m intervals at each feeding and control site (Doenier et al. 1997). Autumn surveys removed old pellet groups and spring surveys measured deposition of new pellets and collected pellet groups containing bait markers >1 m from transects and >30 m from feeding sites. We analyzed effect of site, distance from site center, year, and annual site DUM on spring pellet density using linear regression.

**RESULTS**

We provided 1,184 L of corn in 2003–2004 and 668 L in 2004–2005. In 2 years, we recorded 127,262 digital images of deer during experimental feeding trials. Model selection using Akaike’s Information Criterion indicated that DUM and year + DUM were the best models for prediction of spring fecal-pellet density (Thompson 2006). We found spring pellet density increased with DUM at feeding sites in 2003–2004 (𝑟² = 0.99, 𝑑𝑓 = 2, 𝑃 = 0.005) and appeared to increase in 2004–2005 (𝑟² = 0.93, 𝑑𝑓 = 2, 𝑃 = 0.06). The most active feeding sites also yielded the highest recovery of marked pellet groups (Table 1). We found only 1 of 360 marked pellet groups, collected during both study years, contained 2 distinct bait markers, indicating feeding from 2 feeding sites, likely within a 48-hour period (Thompson 2006). All other recovered marked pellet groups corresponded to the closest feeding site.

We found differences in DUM among feeding sites, supporting our RCBD (Table 1). Deer use at control sites was lower than at southeast (𝑃 < 0.001) and northeast (𝑃 = 0.02) feeding sites but similar to northwest (𝑃 = 0.78) and southwest (𝑃 > 0.90) feeding sites (Table 1). Eight days after removal of corn, DUM was reduced by 76–91% at feeding sites (Table 1). Average deer group size did not vary among years (𝐹₁,₂⁹ = 0.00, 𝑃 = 0.95), feeding methods (𝐹₂,₂⁹ = 0.28, 𝑃 = 0.76), or feeding quantities (𝐹₁,₂⁹ = 0.02, 𝑃 = 0.89). Although we observed apparent group-size differences among feeding sites (𝐹₂,₂⁹ = 2.77, 𝑃 = 0.06), with larger groups in southeast compared to southwest and northwest sites (Table 1), group sizes at feeding sites were not different than at control sites (𝑃 = 0.89). We also observed higher (𝐹₁,₃⁶ = 8.85, 𝑃 < 0.01) deer use (DUM) in 2003–2004 (least-squares means [lsmeans] = 72.02) than 2004–2005 (lsmeans = 33.14) and differences between feeding quantities (𝐹₁,₃⁶ = 4.36, 𝑃 = 0.04). Higher deer use occurred during rationed (lsmeans = 65.20) than ad libitum feeding (lsmeans = 39.96, 𝑃 = 0.08). We found no differences in deer use among feeding methods (𝐹₂,₃⁶ = 1.68, 𝑃 = 0.20), seasons (𝐹₁,₃⁶ = 0.89, 𝑃 = 0.35), or for quantity–method interaction (𝐹₂,₃⁶ = 1.28, 𝑃 = 0.29).

We recorded higher DUM at supplemental feeding than control sites for pairwise distances of ≤0.3 m (𝑡₃₀ = 4.03,

### Table 1. Number of trials, mean white-tailed deer-use minutes (DUM; for study yr, feeding quantities, and feeding methods), mean deer group size, proportional reduction in deer use (DUM) after removal of corn, spring pellet density, and total number of recovered bait-marker pellet groups at supplemental feeding and control sites (x ± SE) during December–March of 2003–2004 and 2004–2005 at Sandhill Wildlife Area, Babcock, Wisconsin, USA.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Northeast</th>
<th>Northwest</th>
<th>Southeast</th>
<th>Southwest</th>
<th>Control site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x ± SE</td>
<td>x ± SE</td>
<td>x ± SE</td>
<td>x ± SE</td>
<td>x ± SE</td>
</tr>
<tr>
<td>No. of trials</td>
<td>12 ± 0.06</td>
<td>11 ± 0.07</td>
<td>12 ± 0.03</td>
<td>12 ± 0.01</td>
<td>12 ± 0.01</td>
</tr>
<tr>
<td>DUM</td>
<td>59.17 ± 25.52</td>
<td>7.91 ± 5.24</td>
<td>142.7 ± 18.17</td>
<td>3.03 ± 1.40</td>
<td>2.16 ± 0.59</td>
</tr>
<tr>
<td>Yr (DUM)</td>
<td>2003–2004</td>
<td>101.4 ± 45.95</td>
<td>14.36 ± 9.08</td>
<td>171.8 ± 25.32</td>
<td>1.25 ± 0.73</td>
</tr>
<tr>
<td></td>
<td>2004–2005</td>
<td>16.93 ± 6.27</td>
<td>0.16 ± 0.10</td>
<td>113.7 ± 21.80</td>
<td>4.80 ± 2.62</td>
</tr>
<tr>
<td>Feeding quantity (DUM)</td>
<td>Ad libitum</td>
<td>33.58 ± 21.65</td>
<td>2.10 ± 1.04</td>
<td>126.9 ± 24.38</td>
<td>0.59 ± 0.38</td>
</tr>
<tr>
<td></td>
<td>Rationed</td>
<td>84.76 ± 46.19</td>
<td>12.74 ± 10.37</td>
<td>158.5 ± 27.54</td>
<td>5.46 ± 2.48</td>
</tr>
<tr>
<td>Feeding method (DUM)</td>
<td>Pile</td>
<td>26.15 ± 6.35</td>
<td>3.77 ± 2.41</td>
<td>128.0 ± 23.86</td>
<td>4.79 ± 3.51</td>
</tr>
<tr>
<td></td>
<td>Spread</td>
<td>88.68 ± 71.55</td>
<td>19.75 ± 19.74</td>
<td>194.3 ± 20.72</td>
<td>1.54 ± 0.90</td>
</tr>
<tr>
<td></td>
<td>Trough</td>
<td>62.69 ± 36.65</td>
<td>3.16 ± 1.73</td>
<td>106.0 ± 34.97</td>
<td>2.75 ± 2.61</td>
</tr>
<tr>
<td>Mean deer group size</td>
<td>1.23 ± 0.06</td>
<td>1.12 ± 0.05</td>
<td>1.32 ± 0.03</td>
<td>1.19 ± 0.09</td>
<td>1.20 ± 0.06</td>
</tr>
<tr>
<td>Proportional reduction in deer use (DUM) 8 days after corn removal</td>
<td>0.88 ± 0.04</td>
<td>0.76 ± 0.11</td>
<td>0.87 ± 0.02</td>
<td>0.91 ± 0.08</td>
<td></td>
</tr>
<tr>
<td>Spring pellet density (pellets/4 m²)</td>
<td>2003–2004</td>
<td>22.94 ± 2.40</td>
<td>8.72 ± 0.61</td>
<td>35.76 ± 8.13</td>
<td>2.81 ± 1.74</td>
</tr>
<tr>
<td></td>
<td>2004–2005</td>
<td>5.71 ± 5.99</td>
<td>0.67 ± 3.94</td>
<td>10.78 ± 13.54</td>
<td>3.07 ± 0.98</td>
</tr>
<tr>
<td>Total no. of recovered bait-marker pellet groups</td>
<td>2003–2004</td>
<td>113 ± 1</td>
<td>193 ± 0</td>
<td>0 ± 2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2004–2005</td>
<td>3 ± 0</td>
<td>46 ± 2</td>
<td>0 ± 0</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Behavioral interaction among white-tailed deer based on interaction proportions, deer-use minutes (DUM), distance proportions, and distance DUM at supplemental feeding sites and control sites ($x \pm SE$) at Sandhill Wildlife Area, Babcock, Wisconsin, USA, during December–March of 2003–2004 and 2004–2005. We analyzed close interactions (nose touching, grooming), agonistic interactions (striking, rushing, flailing, chasing), and distance categories at supplemental feeding sites and control sites using 2-sample $t$-tests.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Supplemental feeding sites</th>
<th>Control sites</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$x$</td>
<td>SE</td>
</tr>
<tr>
<td>Interaction proportions</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Close interactions</td>
<td>0.0004</td>
<td>0.0003</td>
</tr>
<tr>
<td>Agonistic</td>
<td>0.0008</td>
<td>0.0006</td>
</tr>
<tr>
<td>Interaction DUM</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Close interactions</td>
<td>0.573</td>
<td>0.39</td>
</tr>
<tr>
<td>Agonistic</td>
<td>1.246</td>
<td>4.87</td>
</tr>
<tr>
<td>Distance proportions</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\leq 0.3$ m</td>
<td>0.013</td>
<td>0.005</td>
</tr>
<tr>
<td>Within 1 m</td>
<td>0.239</td>
<td>0.04</td>
</tr>
<tr>
<td>$\geq 1$ m</td>
<td>0.619</td>
<td>0.06</td>
</tr>
<tr>
<td>Distance DUM</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\leq 0.3$ m</td>
<td>1.274</td>
<td>0.32</td>
</tr>
<tr>
<td>Within 1 m</td>
<td>62.15</td>
<td>13.29</td>
</tr>
<tr>
<td>$\geq 1$ m</td>
<td>165.5</td>
<td>36.70</td>
</tr>
</tbody>
</table>

$P = <0.001$, within 1 m ($t_{30.28} = 4.50$, $P = <0.001$), and $\geq 1$ m ($t_{31.08} = 3.90$, $P = <0.001$) but not for close behavioral ($t_{37} = 0.73$, $P = 0.47$) or agonistic interactions ($t_{37} = 0.71$, $P = 0.48$; Table 2). We found no differences between feeding and control sites in proportion of time spent in close ($t_{37} = 0.50$, $P = 0.62$) or agonistic interactions ($t_{37} = 0.73$, $P = 0.47$); however, we rarely observed deer at feeding sites in close (0.04% of the time) or agonistic interactions (0.08%; Table 2). The proportion of time we observed deer in close pairwise distances ($\leq 0.3$ m) at feeding sites was rare (1.3%) and was different from control sites ($t_{37} = 1.36$, $P = 0.18$; Table 2). In contrast, deer spent 23.9% of time within 1 m of other deer at feeding sites and 14.1% at control sites ($t_{37} = 1.26$, $P = 0.22$; Table 2). The proportion of time we recorded deer foraging at feeding and control sites differed by feeding method ($F_{2,20} = 29.77$, $P < 0.001$). Deer spent 36% of the time foraging at control sites, similar to trough treatments (34%) but less than spread (61%, $P < 0.001$ and piled (49%, $P = 0.007$) treatments.

The amount of time (DUM) we observed deer at pairwise distances within 1 m ($F_{2,21} = 3.65$, $P = 0.04$) differed among feeding methods and appeared to differ for $\leq 0.3$-m distance ($F_{2,21} = 2.87$, $P = 0.08$). Close pairwise distances ($\leq 0.3$ m) were greater when corn was in a trough (lsmeans = 1.52) than when spread on the ground (lsmeans = 0.22, $P = 0.03$). Pairwise distances within 1 m were greater when food was spread (lsmeans = 81.81) than piled (lsmeans = 17.92, $P = 0.01$). We found no differences in proportion of time spent in close behavioral interactions, agonistic interactions, and pairwise distance categories among feeding treatments.

Feeding intensity varied between years ($F_{1,20} = 8.02$, $P = 0.01$), between feeding quantities ($F_{1,20} = 20.6$, $P < 0.001$), among feeding methods ($F_{2,20} = 12.7$, $P < 0.001$), and by quantity–method interaction ($F_{2,20} = 3.81$, $P = 0.04$). Similar to DUM, we found feeding intensity was higher in 2003–2004 (lsmeans = 73.86) than 2004–2005 (lsmeans = 20.83). Feeding intensity was higher at rationed (lsmeans = 70.86) than ad libitum treatments (lsmeans = 23.82). Pile treatments had the highest feeding intensity (lsmeans = 56.4) followed by trough treatments (lsmeans = 35.8), and both differed from spread treatments (lsmeans = 8.58, $P < 0.01$). Feeding intensity was highest at rationed piles (lsmeans = 111.0) and lowest at ad libitum spreads (lsmeans = 1.19) compared to other treatment combinations (lsmeans range 20–40, $P < 0.01$).

The mean fecal-ingestion selection index ($x = 0.28$, SE = 0.06) we measured indicated that fecal ingestion occurred during our feeding trials, but deer were able to avoid consumption of fecal pellets compared to corn. The selection index did not differ between pile ($x = 0.23$, SE = 0.08) and trough ($x = 0.37$, SE = 0.03; $t_{12} = 1.21$, $P = 0.25$) treatments or between ad libitum ($x = 0.27$, SE = 0.07) and rationed ($x = 0.29$, SE = 0.08; $t_{12} = 0.23$, $P = 0.82$) quantities.

DISCUSSION

We found deer use in 2003–2004 was twice as great as 2004–2005, following a substantial harvest in autumn 2004 at SWA, which decreased deer abundance. We believe lower deer abundance in the winter of 2004–2005 and subsequent reduced competition for natural browse may explain decreased deer use of feeding sites (Doenier et al. 1997). Nevertheless, higher deer use at the northeast and southeast feeding sites relative to control sites confirms that deer concentrate their activity around sites where supplemental food is provided (Williams et al. 1993, Fisher et al. 1997). Use of feeding sites may be a learned behavior, from mother to offspring, and lack of deer activity at northwest and southwest feeding sites may be a result of naïve deer at SWA (Anderson et al. 1975, Nelson and Mech 1984). The primary use of feeding sites is to attract deer; thus, feeding sites with low deer use would likely not be used as a place to attract deer in subsequent years. Although deer use at northwest and southwest sites was similar to control sites, we included these feeding sites in our analyses, making our...
comparisons between feeding and control sites a conservative evaluation of natural and artificial situations.

Our camera surveillance suggested that deer use at control sites was diffuse rather than concentrated around a discrete food source. Although natural feeding behavior of deer can result in seasonal concentrations such as yarding, natural browse is diffusely distributed, held aloft, and not replaced after consumption, thereby reducing risk of indirect disease transmission from shared feed, fecal ingestion, or contamination of the environment with infectious agents. We found deer spend more time foraging at pile and spread treatments than at control sites, mostly feeding on corn, a behavior more likely to expose deer to infectious agents deposited by other deer (Garner 2001). Deer also spent more time close to other deer at feeding sites than at control sites, although relative time spent in close and agonistic interactions was similar. Increased time spent at feeding sites provides greater potential for direct and indirect disease transmission (Garner 2001). Unusually large groups at feeding sites suggest that deer may be more likely to interact with unrelated individuals (Garner 2001, Blanchong et al. 2006); however, the small group sizes in our study suggested that additional unrelated contacts were minimal.

Aggressive behavior of white-tailed deer at winter feeding sites suggests that artificial feeding promotes local competition and potentially increases disease-transmitting contacts among deer (Grenier et al. 1999). In our study, rates of direct contacts at feeding sites were similar to those at control sites but these interactions were rare compared with 2–4 aggressive contacts per hour observed in large groups (up to 200) of food-stressed deer (Ozoga 1972). We recorded a maximum of 240 images per hour and had lower deer use, reducing our likelihood of recording such interactions. We suspect that a more rigorous sampling regime incorporating continuous video surveillance would document higher rates of interaction at feeding sites compared with controls.

Closer pairwise distances among deer likely indicate more potential interactions or direct contacts (Bellhouse 1991). We observed closer pairwise distances (≤0.3 m) at troughs and suspected that multiple feeding spaces at troughs may enable deer to feed in closer proximity. In contrast, food piles could be monopolized by a few individuals (probably related), promoting greater pairwise distances. Although the amount of time (DUM) we observed deer at close distances (≤0.3 m) was reduced when feed was spread, deer were 2 times as likely to be within 1 m compared to other feeding methods.

Supplemental food and feeding sites could be contaminated through deposition of feces, saliva, or urine from infectious deer. Feed contaminated with nasal secretions or saliva is a source of indirect disease transmission of bovine TB and likely facilitates transmission of CWD (Miller et al. 2004, Palmer et al. 2004, Mathiason et al. 2006). We found the proportion of time spent foraging at spread treatments was higher than at other treatments, possibly because more dispersed food promotes higher tolerance of other feeding deer or reduced ability to prevent access by competitors. We believe greater use of rationed (8.8 L) quantities of corn may restrict food amounts but not reduce deer use and likely confers a greater risk for disease transmission through direct contact with other deer or with infectious agents in the environment. We used feeding intensity (artificial feeding DUM/unit area of treatment) as a better measure of potential indirect disease transmission by quantifying exposure at the food source, where an infectious agent is more likely. Feeding intensity at rationed piles was 2–5 times greater than at troughs, ad libitum piles, or rationed spread treatments, and 10 times greater than ad libitum spread methods. We found spread feeding appeared to pose the least risk because deer feed less intensely over a larger feeding area, possibly reducing likelihood of encountering disease agents deposited by infected deer. Although our study indicates piles and rationed feeding could increase potential risk for indirect transmission of infectious disease, none of the treatments eliminate potential disease transmission when shared feed contributes to disease transmission compared to a naturally dispersed resource.

Fecal–oral transmission is a likely mechanism of disease transmission of CWD (Miller et al. 2004). Fecal ingestion is not widely documented in white-tailed deer; however, a study of food habits of tame white-tailed deer reported consumption of deer pellets (Shedd 1981). Our data show that deer could not entirely avoid fecal consumption at supplemental feeding sites and even low-level consumption may be important if fecal material contains an infectious dose of disease agent. Consumption of fecal material, contaminated soil, and forage are potential modes of indirect disease transmission that require further research.

Management Implications
Supplemental feeding increased deer concentration at feeding sites and poses greater risk for direct and indirect disease transmission than does natural foraging. Repeated use of feeding areas poses long-term risk for indirect transmission of resilient disease agents (e.g., CWD) that may persist in food, fecal material, or soil (Johnson et al. 2006). Current disease management strategies have proposed restricting food quantities or changing feeding methods. However, our findings suggest that no feeding strategy (including restrictive feeding) appears to reduce the potential for disease transmission substantially. Banning supplemental feeding practices to reduce risks of disease transmission, especially in areas with infectious disease outbreaks, is warranted.

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