Effects of human state park visitation rates on escape behavior of white-tailed deer

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Abstract: State parks are typically established to preserve natural or native habitats for wildlife while simultaneously providing recreational experiences for humans. However, because of their proximity to urban centers, the level of human visitation associated with state parks may be highly variable. Little information has been published regarding the effect of human visitation levels on wildlife escape behavior in state parks. We evaluated flight initiation distances (FIDs) and buffer distances (i.e., the difference between alert and flight distances) for white-tailed deer (*Odocoileus virginianus*; deer) from September 2013 to August 2014 at 3 state parks in east-central Illinois with different human visitation rates. Deer FIDs were lower in a high-visitation park and higher in a low-visitation park. The buffer distances were higher in a high-visitation park and lower in a low-visitation park. Other social (sex, group size, presence of juveniles) and environmental (cover, weather, season) variables that might affect escape behavior did not account for the relationships with park attendance. These results suggest that deer within state parks either habituate to human activity or spatially segregate based on personality (e.g., degree of shyness or boldness). Based on our findings, high levels of human visitation in parks can have a significant impact on the behavior of local wildlife.

Key words: escape behavior, flight initiation distance, human–wildlife interaction, *Odocoileus virginianus*, state parks, white–tailed deer

WHERE LAND CONVERSION for urban development or agricultural uses is extensive, wildlife habitat persists primarily in largely disconnected protected areas such as state or national parks and forests or in small tracts of privately-owned land (Goetz et al. 2009). Because of access, services, marketing, and proximity to urban areas, human visitation and the effects of visitation rates on wildlife that also may inhabit these areas may vary considerably (Boyle and Samson 1985, Neuvonen et al. 2010). Differences in the frequency of human–wildlife encounters among parks used for both human recreation and wildlife conservation also may lead to variation in animal responses to human activity (e.g., Ciuti et al. 2012).

Wildlife may respond to human activity by altering their behavior. In many cases, animals have a tendency to become less wary of humans when human disturbance is nonlethal (reviewed in Stankowich 2008), often leading to changes in habitat and resource use as well as antipredator behavior (e.g., North American elk [*Cervus canadensis*]: Thompson and Henderson 1998; grizzly bears [*Ursus arctos*]: Jope 1985, Olson et al. 1997, Herrero et al. 2005;

pumas [*Puma concolor*]: Sweanor et al. 2008; and reindeer [*Rangifer tarandus*]: Hansen and Aanes 2015). In contrast, lethal or highly disruptive human disturbance can result in increased sensitivity or dispersal. For example, many animals increase their wariness during hunting seasons (e.g., white-tailed deer [*Odocoileus virginianus*]: Behrend and Lubeck 1968; North American elk: Bender et al. 1999; and red deer [*Cervus elaphus*]: Jayakody et al. 2008). Elk are more vigilant when closer to roads (Ciuti et al. 2012), and bottlenose dolphins (*Tursiops truncatus*) may decline in abundance in response to increased activity of tour boats (Bejder et al. 2006). Differences in wariness can be detected by measuring the escape behavior of wildlife. A common measure of escape behavior and wariness in wildlife is the flight initiation distance (FID), or how close an animal can be approached by a human before it flees (Stone et al. 1994, Adams et al. 2006, Stankowich 2008, Weston et al. 2012). An individual's FID should occur when the perceived cost of remaining in an encounter becomes greater than the cost of fleeing from an encounter (Ydenberg and Dill 1986). When wildlife become less wary of

humans, the decision to remain in an encounter seems less costly, leading to smaller FIDs. These changes in FID are considered to reflect the fitness consequences of flight decisions. Fleeing when the risk of predation is low wastes energy, reduces foraging time, and can lead to decreases in fitness if done often, but if wildlife fail to flee when predation risk is high, they risk death. Wildlife therefore are expected to adjust their decision-making process based on the frequency and perceived risk of encounters (Cooper and Frederick 2007).

Two alternative mechanisms may explain variation in site-specific measurements of wariness in relation to the rate of encounters with humans. The first is habituation. When an individual repeatedly encounters humans without negative consequences, that individual may come to perceive little risk in remaining and thus have lower FIDs. To establish habituation as the mechanism underlying differences in behavior, wildlife in parks must be shown to adjust their escape behavior over time in response to experience. The second mechanism is that individuals could differ in their innate perception of and response to risk. Recent studies have examined consistent behavioral syndromes in wildlife, called personalities (Sih et al. 2004, Bell 2007), particularly aggressive and dispersal syndromes, via considering a bold-shy continuum (e.g., bighorn sheep [*Ovis canadensis*]: Reale et al. 2000, three-spined sticklebacks [*Gasterosteus aculeatus*]: Bell and Sih 2007, and sunfish [*Lepomis macrochirus*]: Wilson and Godin 2009). Bold individuals might perceive a lower risk of remaining than shy or cautious individuals and thus have lower FIDs. Shy individuals also may be more likely to disperse from areas with greater human activity, altering the behavioral landscape. For example, Møller (2012) suggested that urban birds have shorter flight distances (i.e., lower FIDs) than rural birds of the same species because tame (i.e., bold, in the parlance of personality) birds have invaded urban areas.

Because parks may differ in their degree of human activity, wildlife in some parks may be less wary of humans. However, few studies have examined the relationship between park visitation rates and wildlife behavior. This is in part due to the difficulty in distinguishing causal relationships between FID and variables in addition to encounter rates with humans that also could affect wariness (Stankowich 2008). For example, FIDs may be affected by social contexts such as group size (Lagory 1987, Stankowich and Coss 2007), age (Walther 1969, Calef et al. 1976), sex (Bergerud 1974, Recarte et al. 1998), and whether young are present (Bergerud 1974, Mahoney et al. 2001), as well as environmental conditions such as vegetation cover (de Boer et al. 2004, Stankowich and Coss 2007), time of year (Manor and Saltz 2005, Reimers et al. 2006), and weather. Variation in these social and environmental contexts must be considered when evaluating a relationship between frequency of park use and wildlife FIDs.

The goal of our study was to determine if state park visitation, used here as an indicator of how frequently wildlife encounter humans in parks, predicts wariness in white-tailed deer (hereafter, deer). We hypothesized that deer that experience more contact with humans will be less wary than deer that experience less contact with humans because they perceive encounters as less risky (i.e., habituation) or due to spatial segregation of personality types. If our hypothesis is true, then deer FIDs in a high-visitation park will be lower than deer FIDs in a low-visitation park. A second measure of escape behavior, buffer distance (i.e., the difference between alert and flight distances; Fernández-Juricic et al. 2001, 2002), should show the opposite relationship in response to park visitation.

Methods
Study areas

Our study was conducted in 3 state parks in east-central Illinois that differed in park visitation rates and size but permitted the same types of human activities (e.g., hiking, boating, camping, hunting, fishing, and cross-country skiing). Kickapoo State Recreation Area (KP; Vermilion County, IL, USA, 40.1167° N, 87.7544° W) is a 1,150-ha park consisting of 22 deep-water ponds, a bottomland sycamore (*Platanus occidentalis*) and silver maple (*Acer saccharinum*) forest, and several areas of upland black oak (*Quercus velutina*), white oak (*Quercus alba*), sugar maple (*Acer saccharum*), and hickory (*Carya* spp.) forest. Human activities at KP also included mountain biking and scuba
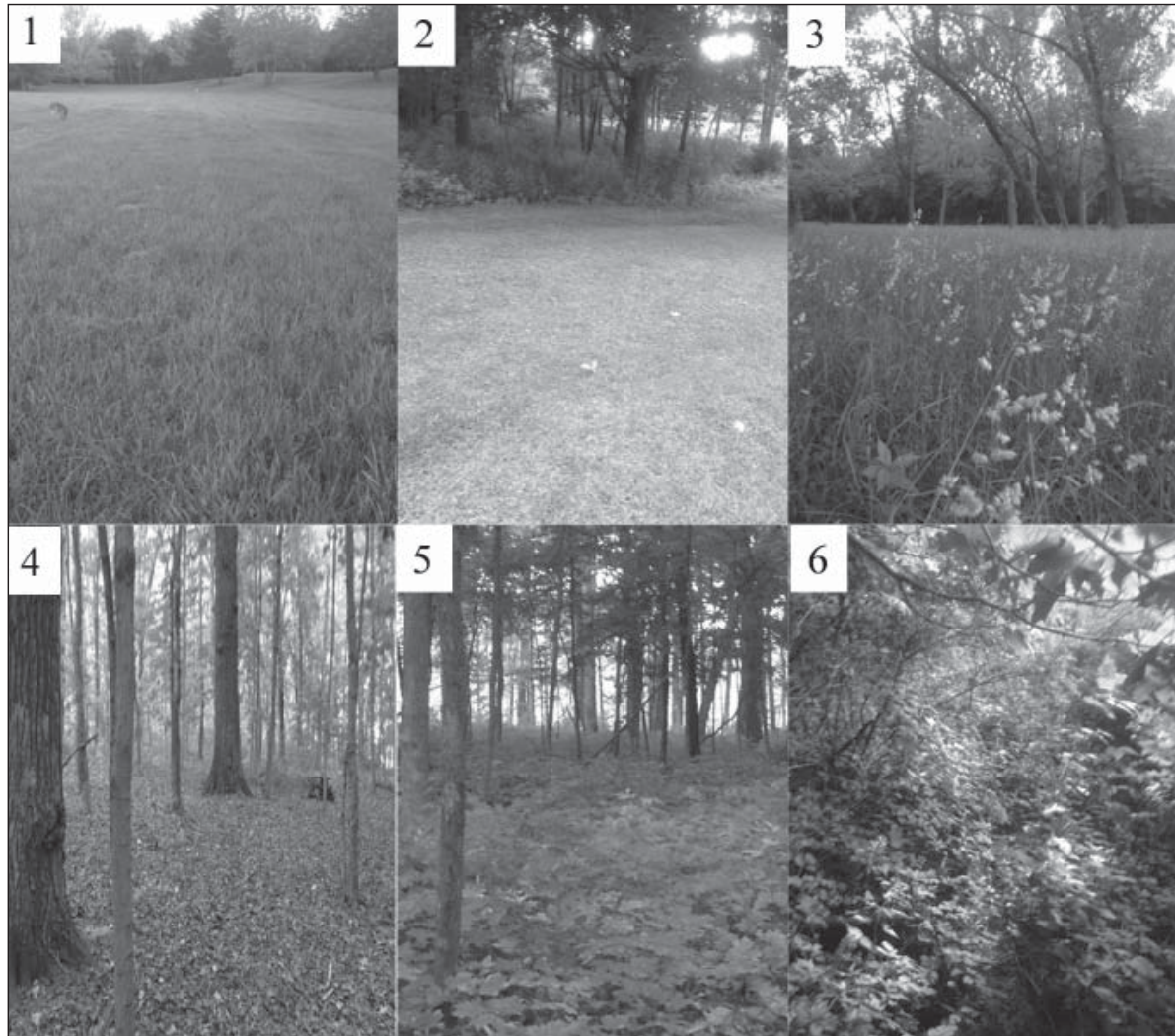
Figure 1. Vegetation cover categories used in our analyses of escape behavior of white-tailed deer (*Odocoileus virginianus*) in 3 state parks in east-central Illinois, USA, September 2013 to August 2014: 1 = >30 m from forest canopy cover; 2 = <30 m from forest canopy cover; 3 = in grass ≥ shoulder height of deer or shrubby cover; 4 = under forest canopy with open understory; 5 = under forest canopy with moderate understory cover; and 6 = under forest canopy with dense understory cover.

diving, with snowmobiling and horseback riding nearby. Park visitation from September 2013 to August 2014 was 1,124,910 visitors. Park visitation data were provided by the Illinois Department of Natural Resources (Division of Parks and Recreation, Springfield IL, USA).

Moraine View State Recreation Area (MV; McLean Co., IL, USA, 40.4109° N, 88.7313° W) is a 682-ha park with a 63-ha lake and several moraines covered with white and black oak, black walnut (*Juglans nigra*), sugar maple, hickory, ash (*Fraxinus* spp.), and elm (*Ulmus* spp.) trees. Human activities also included swimming, horseback riding, and snowmobiling. Park visitation from September 2013 to August 2014 was 272,550 visitors.

Walnut Point State Park (WP; Coles Co., IL,

USA, 39.6983° N, 88.0357° W) is a 271-ha park with a 23-ha multi-fingered lake and woodland dominated by ash, oak, hickory, maple, walnut, black locust (*Robinia pseudoacacia*), and sassafras (*Sassafras albidum*) trees. Park attendance from September 2013 to August 2014 was 198,716 visitors.

Although we did not have population estimates for deer in the parks, and parks differed considerably in total area, we conducted our study in the areas of each park where visitor activity was concentrated (N. M. Sutton [NMS], personal observation). Thus, deer that were encountered in these areas likely experienced rates of contact with humans that reflected park visitation rates; our high-visitation park had >5 times the number

of visitors than our lowest-attendance park. Adult deer in these parks had no nonhuman predators, although coyotes (*Canis latrans*) are ubiquitous in this region (Rosenblatt et al. 1999) and prey on deer fawns in spring and early summer (Cypher et al. 1993).

Measuring escape behavior

We recorded FIDs and buffer distances for deer at each site once per month from September 2013 to May 2014 and 3 times per month from June to August 2014 following protocols published by Stankowich and Coss (2006). To minimize bias related to the variation in the behavior and appearance of the researcher, all field data were collected by NMS (hereafter, researcher), and the same attire was worn during each site visit. During each site visit, we began searching for deer 1 hour before sunset and ended the survey 30 minutes after sunset. We conducted our surveys primarily in high-traffic areas of parks (e.g., roadsides, hiking, and horseback trails) to ensure that any deer encountered were likely to be deer that also encountered park visitors. When deer were located, we selected a focal deer if the deer occurred in a group, and then we moved in a clear, straight-line path toward the deer. We chose focal deer such that the deer being approached was always an adult and not alert to the researcher at the start of the encounter. We used a weighted flag to mark this as the initial distance (ID), then walked toward the deer at a constant speed. When the focal deer became alert (i.e., head upright and pointed in our direction), we dropped a second weighted flag to mark the alert distance (AD). Finally, when the deer fled, we dropped a third weighted flag to mark the FID. We then measured the distance from each flag to the location of the focal deer prior to flight using a Nikon Prostaff 3 laser rangefinder (Nikon, Inc., Melville, NY, USA). We calculated the buffer distance, or how long a deer waited to flee after becoming alert (Fernández-Juricic et al. 2001, 2002), as AD minus FID. Because we were unable to identify individuals, it is possible that some individuals were resampled. However, Runyan and Blumstein (2004) determined that individual identity was not a strong enough factor to obscure environmental influences on FID, and that a moderate degree of pseudoreplication
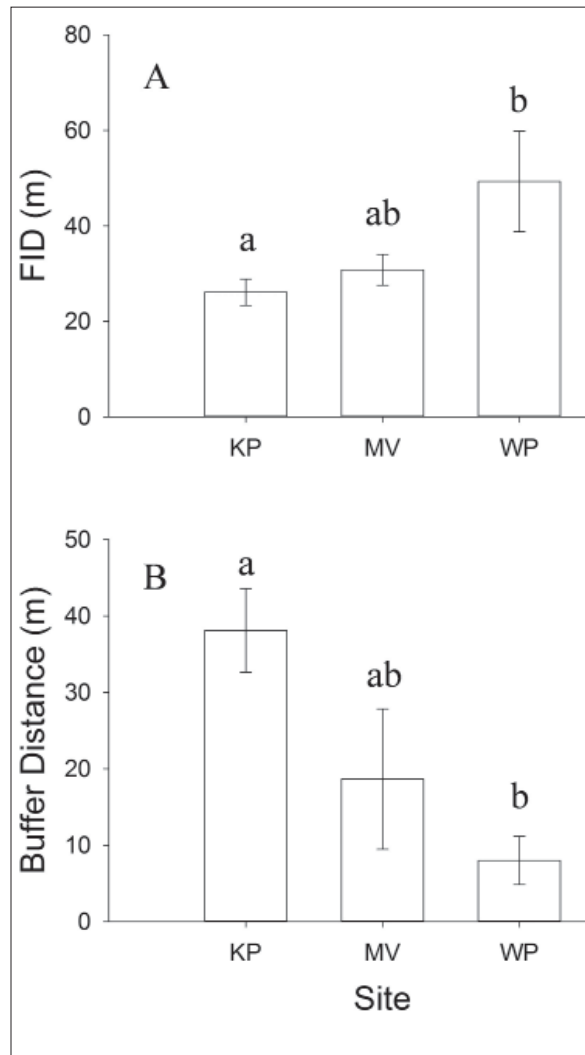
did not affect results of analyses in their study of yellow-bellied marmots (*Marmota flaviventris*). We censored any data if the encounter was interrupted at any stage by other park visitors.

Environmental and social variables

We recorded temperature at the beginning and end of each site visit and categorized weather during each visit as 1 of 5 possibilities: sunny, partly cloudy, cloudy (i.e., fully overcast), rainy, or snowy. For each encounter, we recorded group size, sex of the focal deer, and absence or presence of juvenile deer. We pooled group size into 1 of 3 categories: solitary, average, and large. The solitary class consisted of focal deer that were not in a group. The average group class consisted of focal deer in groups of 2–6 deer. We chose this range based on the average group size observed ±1 SD. Focal deer in groups >6 were assigned to the large group class. We could not determine age of deer beyond adult and juvenile, but all focal deer were adults. We also ranked the vegetation cover where the deer was initially observed from 1 to 6: 1 = >30 m from forest canopy cover in open habitat with low cover; 2 = <30 m from forest canopy cover but still in open habitat with low cover; 3 = in tall grass (≥shoulder height of deer) or shrubby cover; 4 = under forest canopy with open understory; 5 = under forest canopy with moderate understory cover; and 6 = under forest canopy with dense understory cover (Figure 1). We considered categories 1–3 to represent increasing perceived security by deer in open habitats (closer to escape habitat [forest] for 2, greater height of horizontal cover provided by tall grasses or shrubs for 3), and categories 4–6 to represent increasing perceived security by deer in closed-canopy habitats (greater horizontal cover provided by understory vegetation).

Data analyses

We used analysis of variance (ANOVA) and post-hoc Tukey's HSD to test for the effects of park (as a proxy for encounter rate), group size, cover, and weather on FID and buffer distance. We used Pearson's product-moment regression to evaluate the relationship between temperature and FID and buffer distance, and a t-test to determine the effect of presence of juveniles on FID and buffer distance. Because

Figure 2. Comparison of mean (±SE) FID (A) and buffer distance (B) of white-tailed deer (*Odocoileus virginianus*) in 3 state parks in east-central Illinois, USA, September 2013 to August 2014. KP = Kickapoo, MV = Moraine View, and WP = Walnut Point. Lower-case letters above bars in figures indicate categories that did not differ significantly in post-hoc Tukey's HSD tests.

based on sex because we observed only 4 males in this study. However, male FIDs encompassed the range of female FIDs (t_{73} = 0.08, P = 0.94) and so were pooled with females for analyses. All analyses were performed in SAS version 9.4 at α = 0.05 (SAS Institute, Cary, NC, USA).
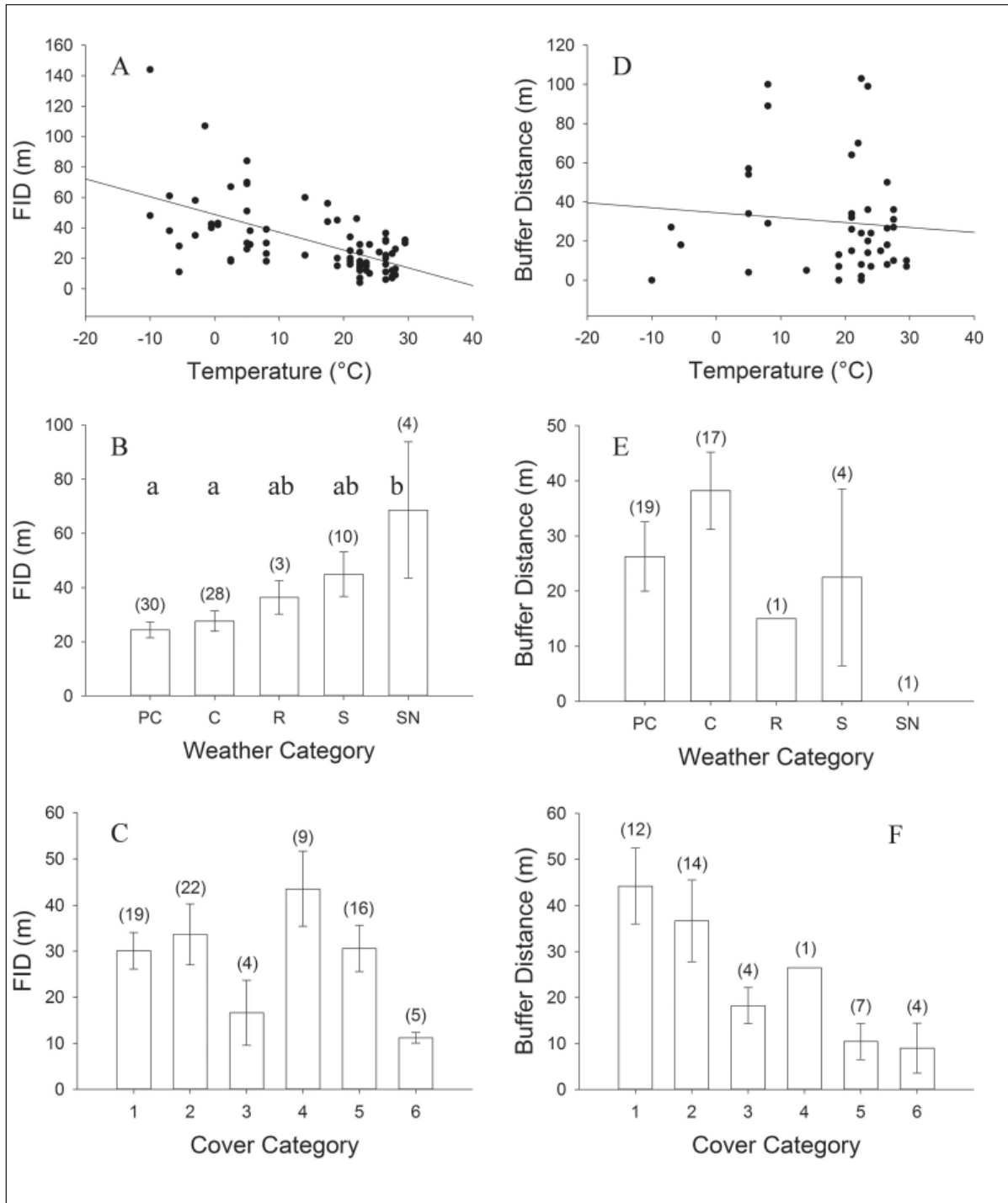
Results

We visited each park 18 times during our study and recorded FIDs for 75 deer encounters. Of these, 46 encounters were recorded at KP (range 1–6 per visit), 16 encounters were at MV (range 1–4 per visit), and 13 encounters were at WP (range 1–3 per visit). We calculated buffer distances for 42 of these 75 encounters (it was unclear when the deer became alert to the presence of the researcher in the other 33 cases). We observed 22 solitary deer, 44 average groups, and 9 large groups. At least 1 juvenile was present in 24 of the 75 observations. Twenty-eight observations were in cloudy, 30 in partly cloudy, 3 in rainy, 10 in sunny, and 4 in snowy weather. Nineteen observations were in cover type 1, 22 in type 2, 4 in type 3, 9 in type 4, 16 in type 5, and 5 in type 6.

Deer FIDs differed across sites ($F_{2,72}$ = 5.50, P = 0.006). Mean FID in KP was lower than that in WP ($P < 0.05$), whereas the mean FID in MV was intermediate in value and did not differ from that in the other 2 parks ($P > 0.05$; Figure 2a). Buffer distances also differed across sites ($F_{2,39}$ = 4.50, P = 0.02). Mean buffer distance in KP was greater than that in WP ($P < 0.05$), but did not differ between MV and the other 2 parks ($P > 0.05$; Figure 2b).

Deer FIDs decreased as temperature increased (R^2 = 0.34, $P < 0.0001$; Figure 3a) and differed across weather categories ($F_{4,70}$ = 5.14, P = 0.001; Figure 3b). Deer FIDs were higher in snowy weather than in cloudy or partly cloudy weather ($P < 0.05$). FIDs in sunny and rainy weather were intermediate and did not differ from each other or from other weather categories ($P > 0.05$). Buffer distance was not related to temperature (R^2 = 0.0001, P = 0.95; Figure 3d) and did not differ among weather categories ($F_{4,37}$ = 0.85, P = 0.50; Figure 3e). Vegetation cover was not related to deer FIDs ($F_{5,69}$ = 1.65, P = 0.16; Figure 3c) or to buffer distance ($F_{5,36}$ = 2.36, P = 0.06; Figure 3f).

Deer FIDs differed among group size classes ($F_{2,72}$ = 4.43, P = 0.02; Figure 4a), with focal

hunting activities could alter the perception of riskiness of encounters with humans (Behrend and Lubeck 1968, de Boer et al. 2004), we also used a *t*-test to compare FID and buffer distance between encounters during the hunting season (Oct. 1 to Jan. 18: inclusive dates for bow hunting season and firearm season) and the rest of the year. Finally, we used ANOVA to test for differences among parks in the temperature when deer encounters were recorded, and contingency table analyses with Pearson's chi square to test for differences among parks in the distribution of deer encounters in weather, cover, and group-size categories, and presence of juveniles. We did not analyze for differences

Figure 3. Effect of environmental covariates on escape behavior of white-tailed deer (*Odocoileus virginianus*) in 3 state parks in east-central Illinois, USA, September 2013 to August 2014. At top, the relationship between temperature (°C) and a) FID and d) buffer distance. Middle, comparison of mean (±SE) b) FID and e) buffer distance across weather categories. At bottom, comparison of mean (±SE) c) FID and f) buffer distance across vegetation cover categories. Sample sizes given in parentheses. Lowercase letters above bars in figures indicate categories that did not differ significantly in post-hoc Tukey's HSD tests.
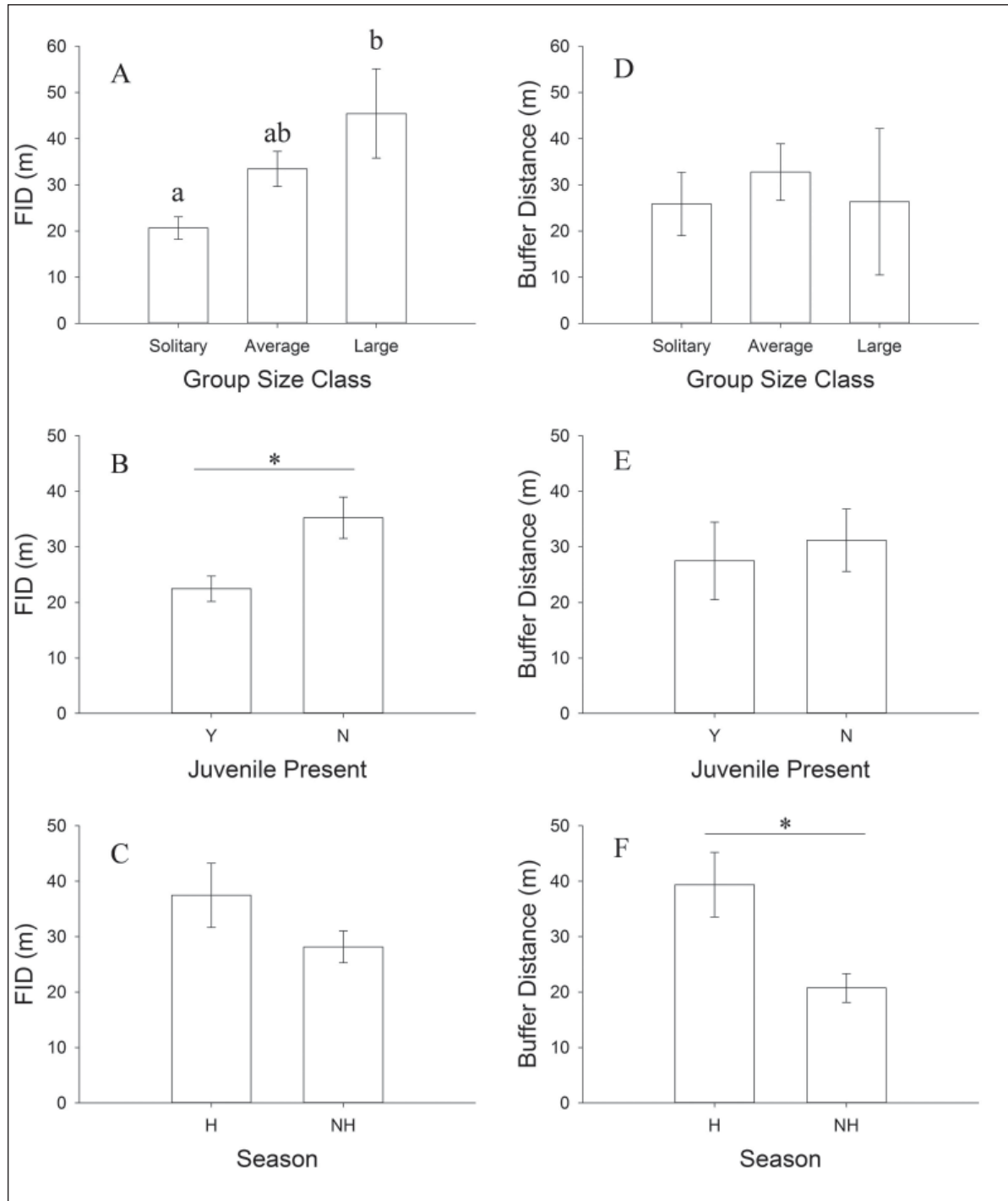
Figure 4. Effect of social covariates on escape behavior of white-tailed deer (*Odocoileus virginianus*) in 3 state parks in east-central Illinois, USA, September 2013 to August 2014. At top, comparison of mean (±SE) a) FID and d) buffer distance across group size classes. Middle, comparison of mean (±SE) b) FID and e) buffer distance between groups with (Y) and without (N) juveniles present. At bottom, comparison of mean (±SE) c) FID and f) buffer distance during (H) and outside of (NH) hunting season. Sample sizes given in parentheses. Lowercase letters above bars in panel A indicate categories that did not differ significantly in post-hoc Tukey's HSD tests. Asterisks (*) indicate significance ($P < 0.05$) in 2-sample tests.

deer in large groups having higher FIDs than solitary deer ($P < 0.05$). Deer FIDs were lower for deer in groups where juveniles were present than in groups without juveniles ($t_{73} = 2.25$, $P = 0.03$; Figure 4b). Deer FIDs did not differ between hunting and non-hunting seasons ($t_{73} = 1.61$, $P = 0.11$; Figure 4c). Buffer distance did not differ among group size classes ($F_{2,39} = 0.29$, $P = 0.75$; Figure 4d) or with the absence or presence of juveniles ($t_{40} = 0.40$, $P = 0.69$; Figure 4e). Buffer distance was greater during the hunting season than the non-hunting season ($t_{40} = 2.86$, $P = 0.007$; Figure 4f), although the number of buffer distance measurements taken during the hunting season was small ($n = 6$).

The temperature at which encounters were recorded did not vary among sites ($F_{2,72} = 1.61$, $P = 0.21$); variation in temperature over the study primarily reflected seasonal changes rather than minor differences within each cycle of site visits. The weather conditions during which encounters were recorded differed among sites ($\chi^{2}_{8} = 37.11$, $P < 0.0001$) with more encounters than expected in snowy weather at WP and MV ($n = 2$ for both) than at KP ($n = 0$) and more encounters than expected in partly cloudy and cloudy weather at KP ($n = 24$ partly cloudy, 22 cloudy) than at WP ($n = 2$ partly cloudy, 2 cloudy) and MV ($n = 4$ partly cloudy, 4 cloudy). The number of encounters in different cover types also differed among sites ($\chi^{2}_{10} = 32.00$, $P = 0.0004$) with a higher proportion of observations in low cover at KP than at MV or WP. Neither the number of encounters in different group size classes ($\chi^{2}_{4} = 1.09$, $P = 0.91$) nor the number of encounters with juveniles present ($\chi^{2}_{2} = 4.27$, $P = 0.11$) differed among sites.

Discussion

Escape behavior of deer we studied varied among parks as predicted by our hypothesis; the likelihood of increased numbers of encounters with park visitors resulted in decreased wariness by white-tailed deer. Deer FIDs were lowest at a high-visitation park and highest at a low-visitation park. Buffer distance, a measure of how long deer waited between first alerting to a researcher and fleeing, was greatest at a high-visitation park and lowest at a low-visitation park. The weather conditions when encounters were recorded, size of the group in which a deer occurred, and presence of juveniles also were related to FID. Of these, the number of encounters recorded under different weather conditions was the only variable that also varied among sites and could have confounded our conclusion related to FIDs. However, the small number of encounters under snowy conditions (2 encounters each at MV and WP versus 0 encounters at KP), the only weather condition that differed significantly from the others in its relationship to FIDs, was unlikely to introduce enough bias to alter our findings on site effects. Surprisingly, we did not detect a relationship between cover and FIDs, and FIDs did not differ between hunting season and the rest of the year. None of the environmental or social variables we measured were related to buffer distance, although buffer distance was greater during hunting season. Thus, we are confident that, of the variables measured, park visitation best predicted deer escape behavior.

While we found strong support for an effect of park visitation on deer escape behavior, it was difficult to determine the mechanism responsible for the altered behavior without being able to identify individual deer to track changes in escape behavior over time. Habituation to humans has been demonstrated in many cases (elk: Thompson and Henderson 1998; Olympic marmots [*M. olympus*]: Griffin et al. 2007; wild boar [*Sus scrofa*]: Cahill et al. 2012; but see Lehrer et al. 2012 for woodchucks [*M. monax*]), and has been proposed as a process through which escape behavior is altered (anoles [*Anolis lineatopus*, *A. graham*]: Cooper 2010; Eurasian sparrowhawk [*Accipiter nisus*]: Møller and Ibáñez-Álamo 2012; and reindeer: Hansen and Aanes 2015). If higher park visitation correlates with a higher frequency of deer–human encounters, then deer in high-visitation parks would be expected to learn to perceive human activity as less dangerous than deer in low-visitation parks and alter their escape behavior accordingly (Cooper and Frederick 2007). From an economic perspective, fleeing less often when encounter rates are high also can result in energetic savings and fewer missed opportunities for foraging (Ydenberg and Dill 1986). Thus, habituation to humans seems a likely explanation for the observed differences

in FIDs and buffer distances.

Another explanation for differences in escape behavior among parks is that human activity within parks could result in selective dispersal of deer with different personality types. There is growing support for the existence of individual personalities, or behavioral syndromes, in many species (Sih et al. 2004, Bell 2007). Flight initiation distances have been implicated in personality studies (burrowing owl [*Athene cunicularia*]: Carrete and Tella 2010), and selective breeding experiments demonstrate that such behavioral syndromes are heritable and can be selected for (van Oers et al. 2004, Patrick et al. 2013, Dochtermann et al. 2015). Bold deer may be more likely to remain in high-visitation parks than shy deer, whereas both shy and bold deer could remain in low-visitation parks. Under a personality dispersal hypothesis, deer FIDs would be lower in high-visitation parks through selective dispersal of shy phenotypes. FIDs in low-visitation parks, however, would remain variable due to less motivation for shy phenotypes to disperse. Bejder et al. (2006) suggested that decreases in abundance of bottlenose dolphins in areas where tour boat activity increased, as well as simultaneous increases in dolphin abundance where tour boat activity was low, was likely due to dispersal of sensitive (i.e., shy) individuals away from areas of high disturbance. Møller (2012) also suggested that differences in flight distance between urban-dwelling and rural-dwelling individuals of the same bird species was most likely due to tame (i.e., bold) birds, which were more tolerant of human disturbance, being better able to colonize urban areas. Future research is needed to document the existence of persistent behavioral syndromes in deer and distinguish between mechanisms that can affect FIDs.

Focal deer in groups where ≥1 juvenile was present had significantly lower FIDs than focal deer in groups without juveniles. The effect of juveniles in groups on FID has not previously been examined for deer. For other ungulates, the relationship is inconclusive. Mahoney et al. (2001) reported that groups of caribou (*R. tarandus*) with juveniles had lower FIDs than groups without juveniles, whereas Bergerud (1974) found the opposite.

In ungulates, juveniles often have greater FIDs than adults (Thomson's gazelle [*Eudorcas thomsonii*]: Walther 1969; caribou: Calef et al. 1976). However, the juvenile deer we observed typically appeared uncertain about when to flee, looking to nearby adult deer rather than focusing on the researcher. Focal adult deer could act bolder to protect juveniles or be waiting for juveniles to move. Further study could help determine the relationship between age and escape behavior in deer.

Solitary deer had lower FIDs than deer in large groups. Lagory (1987) also found larger groups had higher FIDs than smaller groups of deer. When considering the probability of pursuit by a predator, the first deer to flee from a group may be less likely to be attacked than those lagging behind, whereas a single deer fleeing may trigger a predator to give chase. Results concerning the relationship between group size and escape behavior in other ungulates, including the closely related black-tailed deer (*Odocoileus hemionus*), have been mixed. Stankowich and Coss (2006) found no effect of group size on escape behavior of black-tailed deer, whereas a follow-up study (Stankowich and Coss 2007) found a relationship in black-tailed deer similar to both Lagory's (1987) and our studies of white-tailed deer.

Vegetation cover was not related to FID in our study, which is in agreement with previous studies on the effect of habitat type and cover on white-tailed deer flight responses (Halloran 1943, Lagory 1987). The effect of vegetation cover on buffer distance has not previously been examined for white-tailed deer, and we detected no relationship between our cover types and this metric of escape behavior. We recognize, however, that our sample sizes were small for the higher-cover categories (i.e., cover categories 3 and 6). Deer FIDs in these cover types, which offered the greatest concealment for deer in either the open (category 3) or under the forest canopy (category 6), were in fact lower than FIDs in other cover categories (Figure 3c), but the overall ANOVA was not significant. Sampling of FIDs in different vegetation cover categories did not vary significantly among sites, and therefore did not bias our main findings, but we suggest that increased sampling could

reveal decreased wariness under conditions of greater concealment. Habitat type was related to FID in a variety of other ungulates (Stankowich 2008), and it is unclear whether white-tailed deer behave differently or the different conclusions noted above are due to the studies assessing habitat at different spatial scales.

Deer FIDs were negatively related to temperature, indicating deer were less wary of humans in warmer temperatures. The warmest temperatures occurred during summer, a time when visitation rates to parks was highest and encounter rates with humans were likely highest as well. Concealment by tall grasses or leafed-out woody vegetation, or quick access to places with such concealment, is also more available in summer. The relationship with temperature also could reflect an effect of hunting season on deer FID, as hunting seasons occur during colder times of year, but FIDs did not differ significantly between hunting and nonhunting seasons. Behrend and Lubeck (1968) found that deer in areas hunted more frequently in Adirondack forests had higher FIDs than deer in less-hunted areas, whereas Grau and Grau (1980) found no significant change in deer FIDs prior to and during a controlled hunt held on the National Aeronautics and Space Administration (NASA) Plum Brook Station near Sandusky, Ohio, USA. The effect of hunting on deer FIDs was likely mediated by the context of the hunt. In recreational parks and NASA test facilities, deer likely encounter frequent human activity, whereas in large protected forests such as the Adirondacks, deer may not encounter humans as frequently. Since all of our sites were sampled equally throughout the year, however, any temperature-related effects did not bias our relationship between deer FIDs and park visitation rates.

Higher FIDs in snowy weather and lower FIDs in cloudy or partly cloudy weather suggest deer feel less at risk when cloud cover reduces glare for these typically crepuscular/nocturnal animals, and feel most at risk when snowfall reduces visibility. White-tailed deer rely on movement detection and brightness contrast for identifying predators, both of which could be hindered by snowfall, rain, or bright sunlight (VerCauteren and Pipas 2003). There was no significant accumulation of snow during our surveys, so greater FIDs on snowy days was more likely related to reduced visibility than difficulty with locomotion in snow. However, our results should be interpreted with caution as our data included small frequencies of certain weather categories.

Our study confirms that the escape behavior of deer can be affected by a variety of factors, as shown for other ungulates (Stankowich 2008). However, our study is the first to clearly demonstrate that both FID and buffer distance for deer may also vary with different levels of park visitation by humans. The lower wariness in KP is most likely related to greater park visitation because other variables that were related to deer flight behavior, such as presence of juveniles and group class, did not differ among parks. Differences among state parks may affect the extent of habituation to humans or affect the distribution of personality types within and around state parks. Future studies should attempt to identify individuals and track their level of wariness across time to obtain a better understanding of the mechanism by which site-specific changes in wariness occur and a more complete understanding of how recreation-oriented protected areas affect wildlife behavior.

It is not clear that decreased wariness toward humans by deer causes any concerns for park management, and decreased tendency to flee may actually increase the quality of the park experience for human visitors that enjoy viewing or photographing deer. Lower FIDs may be a mechanism to reduce fitness costs of escape behavior, but studies to determine how escape behavior affects the vital rates (e.g., recruitment or growth rates of juveniles, condition of adults) of deer remain to be conducted. Until such studies demonstrate a negative impact of human park visitation rates on deer populations, the consequences of escape behavior for deer management remain unclear.

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