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Deciphering interactions between white-tailed deer and approaching vehicles

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ABSTRACT

Deer-vehicle collisions are a major transportation hazard, but factors affecting deer escape decision-making in response to vehicle approach remain poorly characterized. We made opportunistic observations of deer response to vehicle approach during daylight hours on a restricted-access facility in Ohio, USA (vehicle speeds were ≤ 64 km/h). We hypothesized that animal proximity to the road, group size, vehicle approach, and ambient conditions would affect perceived risk by white-tailed deer (*Odocoileus virginianus*) to vehicle approach, as measured by flight-initiation distance (FID). We constructed *a priori* models for FID, as well as road-crossing behavior. Deer responses were variable and did not demonstrate spatial or temporal margins of safety. Road-crossing behavior was slightly and positively influenced by group size during winter. Deer showed greater FIDs and likelihood of crossing when approached in the road; directionality of approach likely increased the perceived risk. These findings are consistent with antipredator theory relative to predator approach direction.

1. Introduction

Animal-vehicle collisions are an ever-increasing human and wildlife safety concern (Stankowich, 2008). White-tailed deer (*Odocoileus virginianus*) pose one of the greatest threats to human safety on roads in the USA via deer-vehicle collisions (DVCs), particularly considering their body size, abundance, and vagility in urban landscapes. Between July 1, 2016 and June 30, 2017, State Farm[®] Insurance Company estimated 1.35 million DVCs occurred in the USA, causing approximately \$4179 in damage per incident or approximately \$5 billion in total annually (State Farm[®] Mutual Automobile Insurance Company, 2018). Multiple mitigation techniques have been proposed and explored to prevent DVCs (e.g., roadside vegetation management, wildlife overpasses and underpasses, road warning signs; Blackwell and Seamans, 2009; Huijser and McGowen, 2010), but these methods range in effectiveness (0–100%) and are often region-specific (Huijser et al., 2008; Snow et al., 2018). Further, our understanding of animal perception of risk posed by oncoming vehicles, as well as subsequent escape decision-making, remains limited relative to informing mitigation efforts (Blackwell et al., 2014; Lima et al., 2015). Considering human safety and economic concerns associated with DVCs and limited research on this problem, we investigated deer responses to approaching vehicles using opportunistic observations in an antipredator

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framework to improve the current understanding of deer escape decisions.

Over the last two decades there has been an increased focus on quantifying animal response to human disturbance (as per the Risk Disturbance Hypothesis; Frid and Dill, 2002), including means of quantifying perceived risk to animals posed by static objects, human approach, and vehicle approach (DeVault et al., 2015; Lima et al., 2015). Traditionally, prey response to predators or other risks has been visualized through economic modeling in which prey begin to evade a predator when the cost of fleeing is equal or less than the cost of not fleeing (Ydenberg and Dill, 1986). The Risk Disturbance Hypothesis is a variation on the Ydenberg and Dill (1986) model that incorporates risk associated with predator approach relative to opportunity costs (Blumstein, 2003), and includes considerations of costs to fitness by remaining within a patch (Cooper and Blumstein, 2015). Hence, the failure of prey to accurately and efficiently assess risk over a prolonged period can result in a range of outcomes, such as metabolic costs of flight from an area, decreased foraging, capture, or death (Blumstein, 2006).

Speed and directness of a predator approach can influence the degree of risk perceived by prey (Stankowich and Blumstein, 2005; Stankowich and Coss, 2006), as measured by the distance from an approaching predator when the prey initiates escape, or the flight-initiation distance (FID; Ydenberg and Dill, 1986; Blumstein, 2003; Cooper and Frederick, 2007). As noted by Blackwell et al. (2019), there is comparatively less information available on responses by free-ranging animals to vehicle approach than to predators (or humans serving as predator surrogates) in investigations of escape behavior. Multiple factors could affect perceived risk posed by a vehicle. Blackwell et al. (2014) concluded that under typical roadway conditions at night, deer perceived little risk from approaching vehicles until vehicles were within 470 m, regardless of vehicle speed. Observed deer responses varied substantially among individuals, but deer FIDs \leq 470 m strongly indicated a zone of awareness. However, within this zone of awareness neither higher approach speeds or longer approach distances elicited earlier escape responses (Blackwell et al., 2014).

Quantifying deer behavioral responses to vehicle approach is further complicated by multiple biological and anthropogenic factors affecting perceived risk posed by the approaching vehicle, with many factors unmeasurable or difficult to relate to anti-predator behaviors (Blackwell et al., 2014; Lima et al., 2015). For instance, most DVCs mirror deer activity patterns of changes throughout the day and peak movements during crepuscular periods (Carbaugh et al., 1975; Allen and McCullough, 1976). Changes in photoperiod and temperature trigger hormonal changes in white-tailed deer resulting in the autumn rut breeding season (McMillin et al., 1980), which correspond with more DVCs (Carbaugh et al., 1975; Allen and McCullough, 1976). Herd group size, sex, and season influenced white-tailed deer vigilance behavior in response to natural predators (Lashley et al., 2014). Daily and seasonal changes in human activity often occur concomitantly to biological shifts such as traffic volume increases during crepuscular periods (Brown et al., 2012). Interestingly, elk (*Cervus canadensis*) and pronghorn (*Antilocapra americana*) were less responsive to vehicles in areas with high traffic volume than in areas with less traffic (Brown et al., 2012). Habituation to moving vehicles in many animal species likely occurs because of the omnipresence of these objects in the environment (Lima et al., 2015; DeVault et al., 2017). Further, there is evidence that birds, for example, can learn to gauge risk based on the directionality of approach by ground-based vehicles (Mukherjee et al., 2013; DeVault et al., 2018). Anthropogenic and natural hunting pressure also alter deer behavior in terms of vigilance and flight behavior (Stankowich, 2008; Lashley et al., 2014).

We hypothesized that variables that likely increased the conspicuity of vehicles to deer (Blackwell et al., 2014) and variables thought to increase perceived risk (Lima et al., 2015) of the approaching vehicle would elicit greater FIDs and frequency of road crossings/erratic escape behavior. Considering the context of animal-vehicle collisions, the act of an animal crossing the road would likely increase the collision likelihood (Lee et al., 2010). In this study, we specifically assessed five predictions, following Blackwell et al. (2014):

- (1) deer would respond to vehicle approach based on a spatial margin of safety, but relative to vehicle start distance (Blackwell et al., 2014). Alternatively, vehicle approach during diurnal hours might allow deer to better assess risk relative to the vehicle or, possibly, recent events that might have elevated vigilance (e.g., predation), as per the *Threat Sensitivity Hypothesis* (Helfman, 1989). As such, deer might respond to vehicle approach soon after detection (Samia and Blumstein, 2015).
- (2) deer FID would increase with increasing vehicle approach speeds because of enhanced perceived risk due to the reduced time required for the approach (Blumstein, 2010; Lee et al., 2010; Cooper and Blumstein, 2014). Alternatively, vehicle approach speed might have little effect on deer escape decision-making (Blackwell et al., 2014);
- (3) deer FID would increase with proximity to the road and thus a more direct approach (Frid and Dill, 2002; Stankowich and Coss, 2007);
- (4) FID would increase with group size because of collective detection (Krause and Ruxton, 2002). Alternatively, FID might correlate negatively with group size, particularly during winter, as shown by Blackwell and Seamans (2009), or be subject to a group size-season (reflecting sex effects) interaction (e.g., LaGory, 1987); and
- (5) erratic behavior of deer, as defined by crossing the road, would correlate positively with proximity of deer to the road (e.g., decreasing likelihood of road crossing by deer near-road relative to individuals off-road at the beginning of the observation) and decreasing approach speeds and FID (*sensu* Lee et al., 2010). Alternatively, group size alone would correlate positively with the likelihood of crossing due to herd behavior, particularly during rutting season (Blackwell and Seamans, 2009).

2. Materials and methods

2.1. Study area

We observed free-ranging white-tailed deer at the National Aeronautics and Space Administration (NASA) Plum Brook Station

(PBS) in northern Ohio, USA (41° 21' N, 82° 38' W). The location consists of limited-access research facilities dispersed throughout a wide range of habitats (see below) and was considered to represent local biological reserves because it contains large portions of undeveloped and managed natural habitats within a larger agricultural and suburban matrix (Bowles and Arrighi, 2004). PBS comprises 2200 ha of land enclosed by a 2.4-m-high chain link fence, which was permeable to deer in several areas. Undeveloped land at PBS includes old fields and grasslands (31%), canopy-dogwood (*Cornus* spp.; 39%), open woodlands (15%) and mixed hardwood forests (11%) (Blackwell et al., 2014). Facilities at PBS are connected by approximately 60 km of roads with varying amounts of vehicle traffic (speed limit of 64 km/h or 40 mi/h). The majority of roads on PBS are bordered by a mown strip approximately 30 m in width on either side in an effort to reduce DVCs and increase road visibility (Blackwell et al., 2014). Estimated deer density between 2015 and 2016 was 15 individuals/km² (0.15 individuals/ha; United States Department of Agriculture, Wildlife Services, Ohio program, unpublished data). Controlled, lottery white-tailed deer hunts occur on PBS approximately five to six days each year during which hunters are on foot and in vehicles (Blackwell et al., 2014).

2.2. Protocol

Our experimental protocol was opportunistic, and not standardized by route, time of day, vehicle type (i.e., index of vehicle size, such as automobile or truck), start distance, or vehicle speed (max speed on PBS was 64 km/h). We made observations of deer responses to vehicle approach from June 2015 through December 2016. We recorded observations from moving vehicles whenever a deer was sighted < 5 m from a road. Deer were never chased with the vehicle, nor approached when deer were bedded or the driver identified fawns with the group (Blackwell et al., 2014). Per observation, driver and vehicle behavior remained relatively consistent with oncoming vehicles adhering to well-defined roads and exhibiting no erratic behavior to trigger earlier responses of deer located off-road (Walther, 1969; Stankowich, 2008; Mukherjee et al., 2013). However, drivers would brake to avoid collision.

Observers completed a standardized datasheet (Table S1) following an encounter (i.e., either by the driver of the vehicle after arriving at a safe spot along the side of the road or by a passenger familiar with the datasheet). We separated data into three general categories: (1) habitat and environmental characteristics, (2) approach characteristics and description, and (3) animal reaction data (see Table S2 for data descriptions). Given the opportunistic nature of our study, no data were collected relative to distance to concealing cover (for deer; Blackwell et al., 2014) or the type of cover to which animals escaped. We minimized error and potential uncertainty in estimates of the ambient temperature and distance of animals from the approach vehicle by using wide estimate bins (see Table S2). We also visually approximated in meters, by vehicle lengths, starting distances (SDs; maximum distance between detected deer and vehicle) and FID when a solitary deer or middle deer of a group (hereafter, focal deer) started moving to avoid the oncoming vehicle; here, the focal deer's FID represented the group FID (e.g., one FID measurement per observation). Similar to Blackwell et al. (2014), we assumed deer flight behaviors were in response to the oncoming vehicle if they were an obvious motion to flee in response to the approaching vehicle, and were not discerned to be in response to other factors (i.e., conspecifics, foraging, etc.). Also, like Blackwell et al. (2014), we were unable to quantify alert distance (AD), evident when the deer raises its head in the direction of the approaching vehicle (Stankowich and Coss, 2006), because of the difficulty identifying this behavior at a distance from a moving vehicle. We therefore use SD as a surrogate for AD (Blumstein, 2003). In addition to these metrics, we also recorded whether or not a deer crossed the road ahead of the car (Lee et al., 2010) as indicative of a greater chance of a deer-vehicle collision. To account for potential measurement error, we grouped FID into bins following the distance categories of the standardized data sheet (Table S1). We concluded an observation after the vehicle passed the initial location of the focal deer. When no deer reacted (i.e., vehicle had to stop/swerve before deer moved or deer did not initiate escape), we recorded 0 m for FID. Although FID = 0 m and no reaction are different from a behavioral perspective, for our purposes they both indicate low assessments of risk and thus are treated the same in our analysis. More specifically, we include an analysis of all observations so as to understand broadly, and from a management perspective, how deer respond to vehicle approach.

2.3. Analysis

We considered each vehicle approach an experimental unit. We converted FID bins to ascending multinomial groups (e.g., 1, 2, 3, 4, 5, 6, and 7). We then defined whether a deer crossed the road in front of the vehicle (1) or not (0) as a binary response. Prior to model evaluation, we investigated relationships between starting distance and FID or vehicle speed by visualizing them graphically. Blumstein (2003) suggested an overall positive relationship between SD and FID. This relationship was further supported by Stankowich and Coss' (2006) investigation of prey responses to approaching predators and their findings of potential for no response beyond a maximum, species-specific FID (i.e., a spatial margin of safety). Vehicle speed and SD could also interact to affect time-to-collision, thus affecting estimation of a temporal margin of safety (Cárdenas et al., 2005). However, we found no relationship between FID and SD, nor vehicle speed and SD (see below) and, therefore, did not include SD in our models.

We evaluated two *a priori* models reflecting our predictions by using cumulative link mixed models for ordinal FID bins and generalized linear mixed models for crossing behavior in program R (R Core Development Team, 2017). We developed an *a priori* full model for each response variable (Eqs. (1) and (2)) examining fixed effects of deer proximity to the road, interaction of vehicle speed and type, and interaction of season and deer group size. We designated 3 seasons including deer rut (September–November), post-rut (December–April), and calving/pre-rut (May–August, Cheatum and Morton, 1946; Blackwell et al., 2014). We also included the midpoint of each FID bin as a fixed effect for deer crossing. Because vehicle speed and group size were numerical fixed effects, we centered and scaled both variables, respectively. We investigated random effects of weather, location, time of day, and temperature. We used location data (i.e. road name) to account for potential inherent bias associated with repeated routes despite our random

sampling design. We incorporated time of day and temperature because of potential differences in deer activity throughout the day. Because opportunistic observations were made during daytime hours, we did not have time periods equivalent to all crepuscular periods. Instead, we designated diurnal periods of early morning (2 h before and after sunrise), mid-morning (two hours after sunrise to one hour prior to solar noon), noon (one hour prior to one hour after solar noon) and afternoon (anytime time greater than one hour after solar noon to 1600 h). We determined sunrise, solar noon and sunset times using *sunrise* and *solarnoon* functions in R package *maptools* by supplying latitude, longitude, and date (R Core Development Team, 2017).

$$\text{FID} \sim \text{proximity to road} + (\text{vehicle speed} \times \text{vehicle type}) + (\text{group size} \times \text{season}) + (1|\text{weather}) + (1|\text{road name}) + (1|\text{diurnal period}) + (1|\text{temperature}) + (1|\text{Julian date}) + 1 \quad (1)$$

$$\text{Deer crossing road} \sim \text{proximity to road} + \text{FID} + \text{vehicle speed} + (\text{group size} \times \text{season}) + (1|\text{weather}) + (1|\text{road name}) + (1|\text{diurnal period}) + (1|\text{temperature}) + (1|\text{Julian date}) + 1 \quad (2)$$

We developed cumulative link mixed models, appropriate for ordinal or rank data, for FID bins using function *clmm* in R package *ordinal* (Christensen, 2015; R Core Development Team, 2017). We determined which link function best described our data by comparing the log-likelihood of the full model among different link functions and chose the link function associated between structured (e.g., equidistant) and unstructured thresholds or cut points (e.g., flexible). After choosing the best threshold for model fit, we assessed the importance and contribution of random effects by investigating their standard deviations and compared reduced random effects models to the full model, again via greatest log-likelihood (Christensen, 2015). Next, we evaluated fixed effects by comparing models within a nested model set (e.g., full model, interaction terms, simple effects, null model). We used the likelihood ratio statistic for all model comparisons and developed an analysis of deviance table for investigating fixed effects of the final model. More accurate than Wald tests, the likelihood ratio statistic is similar to the chi-square distribution with degrees of freedom based on the differences in number of parameters among compared models (Christensen, 2015). We used deviance because of its close relation to sums of squares for linear models (McCullagh and Nelder, 1989). We determined directional influences of fixed effects based on estimated regression coefficients and their associated 95% confidence intervals ($\alpha = 0.05$).

We used generalized linear mixed models for binomial logistic regression to investigate the binomial response of whether or not a deer crossed the road using *glmer* in R package *lme4* (R Core Development Team, 2017). We began by fitting the full model (Bolker et al., 2009) using mid-distances for FID bins. We then checked model singularity and collinearity of variables and removed variables with $r^2 \geq 0.7$. We also checked model fit among multiple optimization packages and then restarted the full model using the ideal optimizer at 10,000 interactions. We checked the full model for over dispersion using Pearson's residuals and chi-square analysis. We assessed the importance and contribution of each random effect, then removed random effects with minimal influence according to their diagonal elements and standard deviations. After assessing random effects, we compared fixed effects models by Akaike's Information Criterion (AIC). We developed a list of reduced candidate models based on our prediction. We considered models with $\Delta\text{AIC} \geq 4.0$ to the model with the least AIC to be least contributing (Burnham and Anderson, 2002). We checked assumptions of the final model including graphs of correlation matrices, probability curves of odds ratios, and QQ-plot of remaining random effects. We compared odds ratios and confidence intervals of main effects using $\alpha = 0.05$.

3. Results

We conducted 328 vehicle approaches toward groups of 2.0 deer on average ($\sigma = 1.53$, 1–15 deer per observation). Most approaches occurred during the early morning period (45.1% of observations) in a Ford Ranger (47.8%) on a 2-lane road with a 64 km/h speed limit at an average speed of 51.5 km/h. Cloudy (59.4%) and sunny (34.3%) weather from -0.56°C to 27.22°C ($\bar{x} = 5.66^\circ\text{C}$, $\sigma = -10.48^\circ\text{C}$) predominated approach conditions, and most approaches (50.2%) were made during post-rut (winter). Most (91.1%) of our start distances were ≤ 300 m ($\bar{x} = 157.02$ m, $\text{SE} = 4.14$ m based on median distances per distance bins, excluding the " > 300 m" bin), and we found no significant correlation between FID standardized by start distance of the vehicle compared to start distance and speed (Fig. 1; Blackwell et al., 2014; DeVault et al., 2015).

Deer FID increased from deer off the road (FID median $\bar{x} = 34.01$ m, $\text{SE} = 5.20$ m) to deer in the road (FID median $\bar{x} = 51.17$ m, $\text{SE} = 6.06$ m), with deer on road edges showing intermediate escape responses (FID median $\bar{x} = 37.62$ m, $\text{SE} = 2.81$ m; Tables 1 and 2). These findings support our third prediction of greater FID when deer proximity to the road results in a more direct vehicle approach. Other variables had minimal contributions to deer FID (Tables 1 and 2). Vehicle speed also had no apparent effect on deer escape decision-making (i.e., lack of temporal margin of safety) whether independent of or interacting with vehicle size. As vehicle size increased (i.e. different vehicle types), deer responses demonstrated no changes in FID, and weather variables were excluded from the final model due to a lack of contribution to model performance. Lastly, deer FID did not vary among season or group size.

Deer behavior recorded as crossing the road or not was best represented by FID, proximity to road, vehicle speed, and a group size-by-season interaction with random effects of ambient temperature and Julian day (Table 3). However, confidence intervals overlapping 1.00 for many variables in the top model suggested minimal influence. Deer were slightly more likely to cross the road as FID increased (Table 4). Deer also demonstrated greater probability of crossing the road as group size increased during post-rut (December-April), which was composed mostly of winter months (September-November). Deer positioned on the road were also more likely to cross the road when approached by a vehicle, with the exception of six instances when a deer was approached on the road and did not engage in crossing behavior.

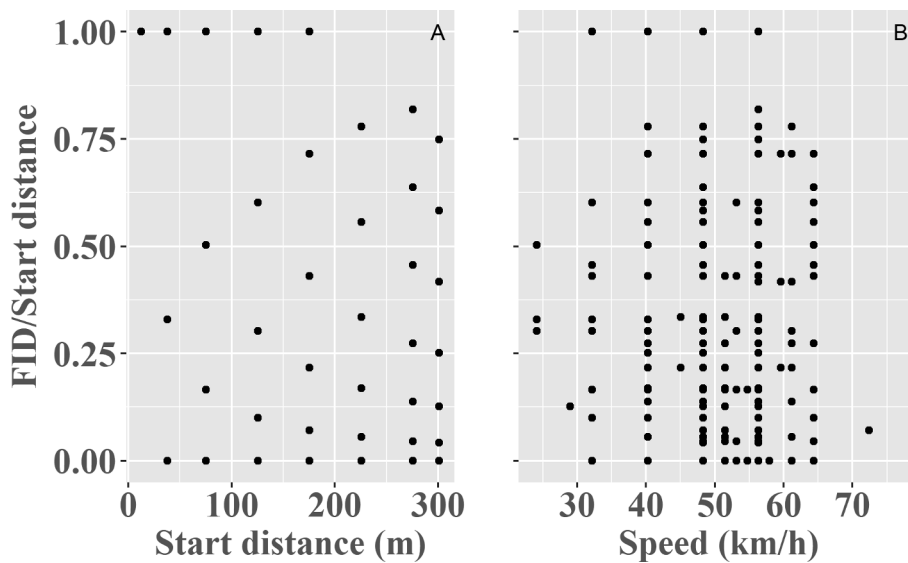


Fig. 1. Flight-initiation distance (FID) responses by white-tailed deer (*Odocoileus virginianus*) standardized by vehicle start distances at Plum Brook Station (PBS), Ohio, USA in relation to (A) vehicle start distance and (B) vehicle speed.

Table 1

Deviance explained by a cumulative link mixed model investigating factors affecting white-tailed deer (*Odocoileus virginianus*) flight-initiation distances (FID) during opportunistic observations from vehicles at Plum Brook Station (PBS) in northern Ohio, USA, 2015–2016.

Source	df	deviance	P-value
Total	23	76.27	< 0.001
Treatment	14	63.20	≤ 0.001
Group × season	2	4.15	0.126
Speed × vehicle type	3	0.93	0.818
Group	1	0.21	0.643
Season	2	4.38	0.112
Speed	1	0.35	0.553
Vehicle type	3	1.75	0.626
Proximity to road	2	56.34	≤ 0.001
Residual	9	13.07	0.159

Table 2

Regression coefficients from cumulative link mixed models regarding white-tailed deer (*Odocoileus virginianus*) flight-initiation distances (FIDs) in response to vehicles during opportunistic observations at Plum Brook Station (PBS) in northern Ohio, USA, 2015–2016.

Factor	Contrasts between factors	β	SE	z	P	95% Confidence interval ^a	
						Lower	Upper
Proximity to road	edge vs. on-road	-0.39	0.175	-2.26	0.024	-0.74	-0.05
	off-road vs. on-road	-1.35	0.217	-6.25	≤ 0.001	-1.78	-0.93
Vehicle speed		-0.03	0.065	-0.51	0.610	-0.16	0.09
Vehicle type	SUV vs. small truck	-0.10	0.324	-0.31	0.754	-0.74	0.53
	truck vs. small truck	0.08	0.151	0.51	0.612	-0.22	0.37
	van vs. small truck	0.25	0.205	1.23	0.220	-0.15	0.65
Group size		-0.03	0.064	-0.53	0.598	-0.16	0.09
Season	calving/pre-rut vs. rut	0.19	0.214	0.90	0.368	-0.23	0.61
	post-rut vs. rut	0.26	0.203	1.28	0.199	-0.14	0.66

^a 95% Confidence intervals not overlapping 0 suggested strong directional responses.

4. Discussion

Opportunistic observations of white-tailed deer reactions to approaching vehicles during daylight hours indicated that perceived risk (as indexed by FID) was influenced by proximity of deer to the road, with the longest FIDs recorded for deer encountered in the

Table 3

Model selection results of binomial logistic regression models of variables potentially affecting whether or not white-tailed deer (*Odocoileus virginianus*) crossed the road in response to oncoming vehicles during opportunistic observations of deer at Plum Brook Station (PBS) in northern Ohio, USA, 2015–2016.

Model ^a	k	AICc	ΔAICc	AICc weight	Cumulative weight	Log-likelihood	Evidence ratio
~FID + proximity to road + speed + group size × season	12	430.73	0.00	1.00	0.999	−202.95	1.00
~FID + proximity to road + speed	7	448.50	17.77	1.38E−04	1.000	−217.11	7.22E+03
~FID	6	458.15	27.42	1.11E−06	1.000	−222.97	8.99E+05
~Proximity to road + speed	4	519.22	88.48	6.11E−20	1.000	−255.56	1.64E+19
~Group size × season	8	519.92	89.19	4.30E−20	1.000	−251.77	2.33E+19
~Group size	4	520.67	89.93	2.96E−20	1.000	−256.28	3.38E+19
Null model (~1)	3	542.53	111.79	5.30E−25	1.000	−268.23	1.89E+24

^a Candidate models were based on the prediction of a positive correlation between whether or not a deer crossed the road and the proximity of the deer to the road), decreasing vehicle speed, and decreasing distance between the deer and the vehicle (e.g., flight-initiation distance (FID); *sensu* Lee et al., 2010). Group size alone was also predicted as potentially increasing the likelihood of deer crossing, especially during the rutting season (Blackwell and Seamans, 2009).

Table 4

Odds ratio of fixed effects from top binomial logistic regression model regarding whether or not white-tailed deer (*Odocoileus virginianus*) crossed the road in response to oncoming vehicles as recorded from opportunistic observations of deer at Plum Brook Station (PBS) in northern Ohio, USA, 2015–2016.

Factor	Contrasts between factors	Odds ratio ^a	SE	z	P-value	95% Confidence interval	
						Lower	Upper
FID		1.01	0.003	3.58	≤0.001	1.00	1.02
Proximity to road	road edge vs. on-road	0.08	0.039	−5.26	≤0.001	0.03	0.21
	off-road vs. on-road	0.03	0.018	−6.32	≤0.001	0.01	0.10
Vehicle speed		0.81	0.102	−1.67	0.095	0.63	1.04
Group size		1.02	0.440	0.05	0.958	0.44	2.38
Season	calving/pre-rut vs. rut	1.01	0.383	0.02	0.983	0.48	2.12
	post-rut vs. rut	0.85	0.324	−0.43	0.664	0.40	1.79
Group size × season	calving/pre-rut vs. rut	1.49	0.811	0.72	0.469	0.51	4.33
	Post-rut vs. rut	2.71	1.350	2.00	0.045	1.02	7.20

^a Odds ratios of 1.00 indicate no difference between levels of a factor (e.g., on the road, off the road, or on the road edge) or in relation to incremental changes of a continuous or discrete variable (e.g., as vehicle speed increases, the probability of a deer crossing the road decreases).

road on a direct or near-direct approach. However, erratic behavior, as defined by road crossing, was influenced by proximity of deer to the road and group size during winter, with minimal influence by vehicle speed or FID.

In contrast to our predictions, we observed no evidence of a fixed spatial or dynamic spatial margin of safety in the distribution of FIDs. This finding contrasts somewhat with Blackwell et al. (2014), wherein a zone of awareness within 470 m of the animal was found. However, we note that unlike Blackwell et al. (2014), most (82.68%) observed deer FIDs in this study were initially observed ≤100 m from the vehicle and approximately a third (33.43%) were ≤25 m. Therefore, it is possible that our start distances were too short to discern a fixed spatial margin of safety from deer responses. However, like Blackwell et al. (2014), we found no temporal aspect to deer responses to vehicle approaches, despite observed FIDs allowing deer approximately 1.7–7.0 s to react to vehicles before collisions, traveling the average local speed of 51.5 km/h in this study. As our data are opportunistic in nature, it is possible that the deer became aware of the vehicle (e.g. by hearing it) before they were detected by the driver. In Blackwell et al. (2014), deer were detected up to ~800 m away with the use of a FLIR thermal imaging system. However, our observers were trained to recognize escape behavior, so any errors associated with FID are likely negligible.

In support of our prediction, we found that deer FID and crossing probability increased with proximity to the road, suggesting an increased perception of risk of oncoming vehicles when vehicle approaches are more direct than tangential, which is consistent with antipredator theory (Frid and Dill, 2002; Stankowich and Coss, 2007). Black-tailed deer (*Odocoileus hemionus columbianus*) displayed similar responses when approached by human observers directly or indirectly (Stankowich and Coss, 2006, 2007). Also, Blackwell et al. (2019) found that across 5 bird species observed in bird-aircraft interactions, birds exposed to direct aircraft approach were twice as likely to initiate escape as those approached tangentially. Although we interpret deer perception of risk based on the proximity of deer to the direct path of the vehicle (i.e., angle of approach), we also acknowledge that the road itself could be a key component of risk perception. In other words, deer may perceive the road surface as a riskier location than the side of the road, regardless of the angle to the approaching vehicle, because deer mainly observe vehicles on the road.

Deer also demonstrated greater probability of crossing the road as group size increased during the winter or post-rut (December–April), but the contribution of group size to crossing was minimal at best considering a lower 95% confidence interval of the odds ratio near 1.00 (i.e., no effect). This finding contrasts with prior work on PBS involving nocturnal approaches, where FIDs were negatively correlated with deer group size during winter (Blackwell and Seamans, 2009). Further, deer group size increases through

the fall and winter concomitant with hormonal changes and increased movement activity, all of which can affect deer road crossing behavior (Carbaugh et al., 1975; Allen and McCullough, 1976). As deer group size increases, threats can be detected earlier when at least one deer is vigilant (e.g., many-eyes hypothesis; Lima, 1995; Stankowich, 2008; Bonnot et al., 2017). Bonnot et al. (2017) observed such patterns with groups of roe deer (*Capreolus capreolus*) reacting to approaching humans sooner than solitary roe deer, despite less vigilance by individuals. However, Blackwell and Seamans (2009) noted that delays in individual reactions within the larger group might offset effects of enhanced vigilance (see also Lingle and Wilson, 2001). We suggest that during daylight approaches in this study, and without any visual obstruction and minimal changes to vehicles or approach behavior, deer perception of risk and subsequent vigilance were likely reduced (Lashley et al., 2014, Bonnot et al., 2017), thereby minimizing the effect of group size. Stankowich (2008) also hypothesized that group size effects on perceived risk can be context dependent.

Finally, sex and age can influence individual deer responses to potential threats (Lashley et al., 2014), but these potential effects were captured only indirectly in our study via the seasonal component. Future investigations could benefit from tracking individual movements (e.g., marked individuals) to reveal interactions of sex- and age-specific vigilance to predator threats (Lashley et al., 2014). Distance to escape cover and the position of cover in relation to the prey and predator can also influence a prey's FID (Cooper and Blumstein, 2015, Domenici and Ruxton, 2015), a pattern observed among multiple mammalian species and habitats (Lee et al., 2010, Hegland and Hamre, 2018, Snow et al., 2018). However, we did not compare habitats of initial observations to subsequent escape cover.

Most vehicle approaches were conducted in the absence of rain and all occurred within the same area where consistent traffic patterns throughout the year would support deer habituation, similar to Brown et al.'s (2012) observation of elk and pronghorn habituation to vehicles in high traffic areas. Low traffic volumes throughout our study area likely also provided ample opportunities for deer to successfully cross roads without incident, possibly diminishing perceived risk and increasing habituation to roads as safe zones (Jaeger et al., 2005, Lima et al., 2015, Stillfried et al., 2017a,b). Replication of this study in an area with higher traffic volume might result in lower deer FIDs and fewer road crossings, based on repetitive exposure to traffic volumes and speed (Brown et al., 2012). Despite our vehicle starting distances ranging from 0 to 25 m to over 300 m, any spatial margin of safety could have been relaxed due to few previous negative interactions with vehicles (low threat sensitivity) and ample time to assess oncoming risks. Less than 1% of vehicle approaches resulted in drivers stopping for deer, and drivers only slowed during 11.8% of approaches, which further supports the few negative interactions between deer and vehicles within our study area.

5. Conclusion

Without further refined experiments on deer behavioral responses at herd or individual levels to approaching vehicles, and relative to time of day/season, traffic volume, vehicle speeds, and surrounding habitat, mitigation recommendations should remain focused on coarse correlates of DVCs such as increasing human density and average daily traffic counts at landscape scales (Farrell and Tappe, 2007, Rytwinski et al., 2015, Snow et al., 2018), and deer visibility of oncoming traffic (Blackwell et al., 2014). Efforts that focus on human behavioral modifications are promising (Ng et al., 2008, Grace et al., 2017). For example, our findings provide additional support for vehicle operators to avoid swerving when a deer is in their path. Swerving to avoid the deer might cause the approaching vehicle to hit another vehicle in the opposite lane or a stationary object (New York State Department of Transportation, 2009). After all, a deviation of an oncoming car from a direct collision path with a deer does not guarantee a miss. Reductions in DVCs will be best achieved by integrating the aforementioned research areas with a better understanding of deer responses to oncoming vehicles.

CRedit authorship contribution statement

Morgan B. Pfeiffer: Methodology, Writing - original draft, Writing - review & editing. **Raymond B. Iglay:** Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Thomas W. Seamans:** Investigation, Data curation, Writing - review & editing. **Bradley F. Blackwell:** Methodology, Writing - review & editing. **Travis L. DeVault:** Conceptualization, Methodology, Writing - review & editing, Supervision.

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Appendix A. Supplementary material

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References

- Allen, R.E., McCullough, D.R., 1976. Deer-car accidents in southern Michigan. *J. Wildl. Manag.* 40, 317–325. <https://www.jstor.org/stable/3800431>.
 Blackwell, B.F., Seamans, T.W., 2009. Enhancing the perceived threat of vehicle approach to deer. *J. Wildl. Manage.* 73, 128–135. <https://doi.org/10.2193/2008-014>.
 Blackwell, B.F., Seamans, T.W., Fernández-Juricic, E., DeVault, T.L., Outward, R.J., 2019. Response of birds to aircraft approach in an airport environment. *J. Wildl.*

- Manag. <https://doi.org/10.1002/jwmg.21650>.
- Blackwell, B.F., Seamans, T.W., DeVault, T.L., 2014. White-tailed deer response to vehicle approach: evidence of unclear and present danger. *PLoS ONE* 9, e109988. <https://doi.org/10.1371/journal.pone.0109988>.
- Blumstein, D.T., 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manag.* 67, 852–857. <https://www.jstor.org/stable/3802692>.
- Blumstein, D.T., 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Anim. Behav.* 71, 389–399. <https://doi.org/10.1016/j.anbehav.2005.05.010>.
- Blumstein, D.T., 2010. Flush early and avoid the rush: a general rule of antipredator behavior? *Behav. Ecol.* 21, 440–442. <https://doi.org/10.1093/beheco/ariq030>.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evolut.* 24, 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>.
- Bonnot, N.C., Hewison, A.M., Morellet, N., Gaillard, J.M., Debeffe, L., Couriot, O., Cargnelutti, B., Chaval, Y., Lourtet, B., Kjellander, P., Vanpé, C., 2017. Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Anim. Behav.* 124, 35–46. <https://doi.org/10.1016/j.anbehav.2016.11.031>.
- Bowles, M.D., Arrighi, R.S., 2004. NASA's nuclear frontier: the plum brook reactor facility. *Monogr. Aerospace History* 33, 150–151.
- Brown, C.L., Hardy, A.R., Barber, J.R., Fristrup, K.M., Crooks, K.R., Angeloni, L.M., 2012. The effect of human activities and their associated noise on ungulate behavior. *PLoS ONE* 7, e40505. <https://doi.org/10.1371/journal.pone.0040505>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second ed. Springer-Verlag, New York, USA.
- Carbaugh, B., Vaughan, J., Bellis, E., Graves, H., 1975. Distribution and activity of white-tailed deer along an interstate highway. *J. Wildl. Manag.* 39, 570–581. <https://www.jstor.org/stable/3800400>.
- Cárdenas, Y.L., Shen, B., Zung, L., Blumstein, D.T., 2005. Evaluating temporal and spatial margins of safety in galahs. *Anim. Behav.* 70, 1395–1399. <https://doi.org/10.1016/j.anbehav.2005.03.022>.
- Cheatum, E., Morton, G.H., 1946. Breeding season of white-tailed deer in New York. *J. Wildl. Manag.* 10, 249–263. <https://www.jstor.org/stable/3795841>.
- Christensen, R.H.B., 2015. Analysis of ordinal data with cumulative link models – estimation with the R-pacake ordinal. R-package version 2015.6-28.
- Cooper, W.E., Blumstein, D.T., 2015. Escape behavior: importance, scope, and variables. In: Cooper Jr., W.E., Blumstein, D.T. (Eds.), *Escaping From Predators An Integrative View of Escape Decisions*. Cambridge University Press, Cambridge, UK.
- Cooper Jr., W.E., Blumstein, D.T., 2014. Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. *Behav. Ecol.* 25, 44–52. <https://doi.org/10.1093/beheco/art083>.
- Cooper Jr., W.E., Frederick, W.G., 2007. Optimal flight initiation distance. *J. Theor. Biol.* 244, 59–67. <https://doi.org/10.1016/j.jtbi.2006.07.011>.
- DeVault, T.L., Blackwell, B.F., Seamans, T.W., Lima, S.L., Fernández-Juricic, E., 2015. Speed kills: ineffective avian escape responses to oncoming vehicles. *Proc. R. Soc. B* 282, 20142188. <https://doi.org/10.1098/rspb.2014.2188>.
- DeVault, T.L., Seamans, T.W., Blackwell, B.F., Lima, S.L., Martinez, M.A., Fernández-Juricic, E., 2017. Can experience reduce collisions between birds and vehicles? *J. Zool.* 301, 17–22.
- DeVault, T.L., Seamans, T.W., Blackwell, B.F., Lima, S.L., Fernández-Juricic, E., 2018. Individual variation in avian avoidance behaviours in response to repeated, simulated vehicle approach. *Can. J. Zool.* 96, 441–446. <https://doi.org/10.1139/cjz-2017-0142>.
- Domenici, P., Ruxton, G., 2015. Prey behaviours during fleeing: escape trajectories, signaling, and sensory defences. In: Cooper Jr., W.E., Blumstein, D.T. (Eds.), *Escaping From Predators: An Integrative View of Escape Decisions*. Cambridge University Press, Cambridge, U.K.
- Farrell, M.C., Tappe, P.A., 2007. County-level factors contributing to deer-vehicle collisions in Arkansas. *J. Wildl. Manag.* 71, 2727–2731. <https://doi.org/10.2193/2006-085>.
- Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6, 11. <http://www.consecol.org/vol6/iss1/art11/>.
- Grace, M.K., Smith, D.J., Noss, R.F., 2017. Reducing the threat of wildlife-vehicle collisions during peak tourism periods using a Roadside Animal Detection System. *Accid. Anal. Prev.* 109, 55–61. <https://doi.org/10.1016/j.aap.2017.10.003>.
- Hegland, S.J., Hamre, L.N., 2018. Scale-dependent effects of landscape composition and configuration on deer-vehicle collisions and their relevance to mitigation and planning options. *Landscape Urban Plann.* 169, 178–184. <https://doi.org/10.1016/j.landurbplan.2017.09.009>.
- Helfman, G.S., 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behav. Ecol. Sociobiol.* 24, 47–58. <https://link.springer.com/article/10.1007%2FBF00300117>.
- Huijser, M.P., McGowen, P.T., Fuller, J., Hardy, A., Kociolek, A., 2008. *Wildlife-vehicle collision reduction study: report to Congress*. U.S. Department of Transportation, Federal Highway Administration, McLean, Virginia, USA.
- Huijser, M.P., McGowen, P.T., 2010. Reducing wildlife-vehicle collisions. In: Beckmann, J.P., Clevenger, A.P., Huijser, M.P., Hilty, J.A. (Eds.), *Safe Passages Highways, Wildlife, and Habitat Connectivity*. Island Press, Washington, DC, USA.
- Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., von Toshowitz, K.T., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecol. Model.* 185, 329–348. <https://doi.org/10.1016/j.ecolmodel.2004.12.015>.
- Krause, J., Ruxton, G.D., 2002. *Living in Groups*. Oxford University Press, Oxford.
- LaGory, K.E., 1987. The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. *Anim. Behav.* 35, 20–25. [https://doi.org/10.1016/S0003-3472\(87\)80206-3](https://doi.org/10.1016/S0003-3472(87)80206-3).
- Lashley, M.A., Chitwood, M.C., Biggerstaff, M.T., Morina, D.L., Moorman, C.E., DePerno, C.S., 2014. White-tailed deer vigilance: the influence of social and environmental factors. *PLoS ONE* 9, e90652. <https://doi.org/10.1371/journal.pone.0090652>.
- Lee, E., Croft, D., Ramp, D., 2010. Flight response as a causative factor in kangaroo-vehicle collisions. In: Coulson, G., Eldridge, M. (Eds.), *Macropods: The Biology of Kangaroos, Wallabies and Rat-kangaroos*. CSIRO Publishing, Melbourne, pp. 301–311.
- Lima, S.L., 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behavior* 49, 11–20. [https://doi.org/10.1016/0003-3472\(95\)80149-9](https://doi.org/10.1016/0003-3472(95)80149-9).
- Lima, S.L., Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., 2015. Animal reactions to oncoming vehicles: a conceptual review. *Biol. Rev.* 90, 60–76. <https://doi.org/10.1111/brv.12093>.
- Lingle, S., Wilson, W.F., 2001. Detection and avoidance of predators in white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*). *Ethology* 107, 125–147.
- McCullagh, P., Nelder, J., 1989. *Generalized Linear Models*, second ed. Chapman and Hall/CRC Press LLC, Boca Raton, Florida, USA.
- McMillin, J., Seal, U., Karns, P., 1980. Hormonal correlates of hypophagia in white-tailed deer. *Federation Proc.* 39, 2964–2968. <https://europepmc.org/abstract/med/6998739>.
- Mukherjee, S., Ray-Mukherjee, J., Sarabia, R., 2013. Behaviour of American crows (*Corvus brachyrhynchos*) when encountering an oncoming vehicle. *Can. Field-Naturalist* 127, 229–233. <https://doi.org/10.22621/cfn.v127i3.1488>.
- New York State Department of Transportation, 2009. Don't become a statistic of New York's 65,000 annual deer-vehicle collisions, most occur October-December. State of New York.
- Ng, J.W., Nielsen, C., St. Clair, C.C., 2008. Landscape and traffic factors influencing deer-vehicle collisions in an urban environment. *Human-wildlife Conflicts* 2, 34–47. <https://www.jstor.org/stable/24875104>.
- R Core Team, 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://R-project.org/>.
- van der Rytwinski Ree, R., Cunningham, G.N., Fahrig, L., Findlay, C.S., Houlahan, J., Jaeger, J.A.G., Soanes, K., van der Grift, E.A., 2015. Experimental study designs to improve the evaluation of road mitigation measures for wildlife. *J. Environ. Manage.* 154, 48–64. <https://doi.org/10.1016/j.jenvman.2015.01.048>.
- Samia, D., Blumstein, D., 2015. Birds flush early and avoid the rush: an interspecific study. *PLoS One* 10. <https://doi.org/10.1371/journal.pone.0119906>.
- Snow, N.P., Zhang, Z., Finley, A.O., Rudolph, B.A., Porter, W.F., Williams, D.M., Winterstein, S.R., 2018. Regional-based mitigation to reduce wildlife-vehicle

- collisions. *J. Wildl. Manag.* 82, 756–765. <https://doi.org/10.1002/jwmg.21420>.
- Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. *Biol. Conserv.* 141, 2159–2173. <https://doi.org/10.1016/j.biocon.2008.06.026>.
- Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proc. Roy. Soc. London B: Biol. Sci.* 272, 2627–2634. <https://doi.org/10.1098/rspb.2005.3251>.
- Stankowich, T., Coss, R.G., 2006. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behav. Ecol.* 17, 246–254. <https://doi.org/10.1093/beheco/arj020>.
- Stankowich, T., Coss, R.G., 2007. Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behav. Ecol.* 18, 358–367. <https://doi.org/10.1093/beheco/arl086>.
- State Farm® Mutual Automobile Insurance Company. 2018. Deer damage can be costly. <https://www.statefarm.com/simple-insights/auto-and-vehicles/deer-damage-can-be-costly> (accessed 24 August 2018).
- Stillfried, M., Gras, P., Boerner, K., Goeritz, F., Painer, J., Roellig, K., Wenzler, M., Hofer, H., Ortmann, S., Kramer-Schadt, S., 2017a. Secrets of success in a landscape of fear: urban wild boar adjust risk perception and tolerate disturbance. *Front. Ecol. Evolut.* 5, 157. <https://doi.org/10.3389/fevo.2017.00157>.
- Stillfried, M., Fickel, J., Börner, K., Wittstatt, U., Heddergott, M., Ortmann, S., Kramer-Schadt, S., Frantz, A.C., 2017b. Do cities represent sources, sinks or isolated islands for urban wild boar population structure? *J. Appl. Ecol.* 54, 272–281. <https://doi.org/10.1111/1365-2664.12756>.
- Walther, F.R., 1969. Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour* 34, 184–220. <https://doi.org/10.1163/156853969X00053>.
- Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. *Adv. Study Behavior* 16, 229–249. [https://doi.org/10.1016/S0065-3454\(08\)60192-8](https://doi.org/10.1016/S0065-3454(08)60192-8).