Human activity affects the perception of risk by mule deer

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Abstract Human activity has been shown to influence how animals assess the risk of predation, but we know little about the spatial scale of such impacts. We quantified how vigilance and flight behavior in mule deer *Odocoileus hemionus* varied with distance from an area of concentrated human activity—a subalpine field station. An observer walked trails at various distances away from the station looking for deer. Upon encounter, the observer walked toward the focal animal and noted the distance at which it alerted and directed its attention to the approaching human (Alert Distance; AD), and the distance at which it fled (Flight Initiation Distance; FID). AD and FID both increased nonlinearly with distance from the center of the field station, reaching plateaus around 250 m and 750 m, respectively. Deer also tended to flee by stotting or running, rather than by walking, when far from the station but they walked away when near the station. These results indicate that deer perceive lower risk near a focused area of human activity, and that vigilance and flight behaviors respond on somewhat different spatial scales. The concept of a spatial "human footprint" on behavior may be useful for understanding how human activities affect wildlife [*Current Zoology* 60 ( ) : − , 2014]. .

Keywords Flight initiation distance, Alert distance, Predation risk assessment, Human disturbance, Mule deer, *Odocoileus hemionus*, Vigilance

Human presence can influence the quality of habitat for wild animals, even in the absence of activities such as agricultural and urban development that replace natural with anthropogenic landscapes (e. g., Miller et al., 2001; Taylor and Knight, 2003; Stankowich, 2008). The effect may be negative, if animals perceive humans themselves as a threat, or areas of human activity as risky. Bald eagles *Haliaeetus leucocephalus*, for example, shift their distribution in response to human activity (Stalmaster and Newman, 1978), and desert bighorn sheep *Ovis canadensis mexicana* avoid construction activity by traveling to more-distant water sources (Campbell and Remington, 1981). Conversely, the effect may be positive if humans increase the availability of food or if their activities decrease the risk from predators that avoid humans. Wolves *Canis lupus*, for example, avoid parts of Canada's Banff National Park that are heavily used by humans, and densities and survival of elk *Cervus canadensis* are higher in those areas (Hebblewhite et al., 2005). We

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know that humans affect wildlife behavior and demography, but less is known about the spatial scale of human impacts on wildlife.

Indeed, the effects of human activity may extend well beyond the boundaries of high-use areas. Western gulls *Larus oxidentalis*, for example, gradually become less tolerant to human approach up to 2000 m away from a tourist destination (Webb and Blumstein, 2005), and Gunther's dik-diks *Madoqua guentheri* distinguish between predator calls and non-threatening birdsong within 500 m of human settlement but not at greater distances (Coleman et al., 2008). More such studies are needed, however, to improve our ability to estimate the scale of human impacts on natural ecosystems.

The objective of this study was to identify the spatial scale over which humans affect mule deer's *Odocoileus hemionus* predation risk assessment because risk assessment has consequences for habitat use (Waser et al., 2014). To accomplish this, we asked (1) whether distance from a biological field station affects vigilance of deer and their propensity to flee, and (2) over what spatial scales any changes in behavior occur.

1 Materials and Methods

1. 1 Study site and species

We worked around the Rocky Mountain Biological Laboratory (RMBL), a biological field station that occupies the site of the former mining town of Gothic (38°58' N, 106°59' W, 2,900 m a. s. l.) in the Upper East River Valley of western Colorado, USA. RMBL hosts a maximum of 160 people during the snow-free season (May through September), and public recreational use of the Valley also peaks during this season. The vast bulk of human activity in the Valley occurs within a radius of approximately 300 m around the center of the Gothic "townsite" that contains the 75 residential cabins and other buildings of the field station. Gothic residents spend most of their time within the townsite, and the focus of visitor activity is at a visitor center in the middle of town. Human activity density decreases rapidly outside of the townsite; activity beyond townsite limits occurs primarily during daylight hours, unlike activity within the townsite, and is concentrated along a few foot trails and dirt roads that extend into neighboring undeveloped public lands. These paths and roads serve as access routes to RMBL research sites, which are clustered near the field station: in 2013 the density of research plots (1,063 in all) decreased rapidly with distance from the townsite center. Thirty-one percent of plots occurred within 500 m of the center, another 13% between 500 m and 1,000 m, and the rest were spread out in a long "tail" up to 150 km away. Plots > 5 km distant are generally accessed by vehicle using the single dirt road that runs the length of the Valley, which also provides tourist access to primitive dispersed campsites and to hiking and biking trailheads in the Valley.

The Upper East River Valley is a typical U-shaped glacial valley, with a relatively gentle bottom that rises to flanking mountains. Vegetation around the RMBL is a mosaic of willow (*Salix* spp.) thickets along streams, sagebrush *Artemisia tridentata* scrub on dry rocky slopes, subalpine meadows dominated by herbaceous vegetation, aspen *Populus tremuloides* woodland, and conifer stands dominated by Engelmann spruce *Picea engelmannii* and subalpine fir *Abies bifolia*.

Mule deer are abundant in and around RMBL during the summer months. They migrate from their lower-elevation winter range after snowmelt, generally in June, and settle into relatively stable summer home ranges. Does give birth in June and remain close to their hidden fawns until these emerge in July. After that, does and fawns range over larger areas (ca. 200 ha) for the rest of the summer. During the summer bucks remain in small groups that also range over relatively large areas (ca. 400 ha); these male groups dissolve during the autumn breeding season. Although summer

home ranges are relatively restricted, they are larger than the Gothic townsite; this, and their seasonal migration, gives mule deer knowledge of the much larger region around the townsite.

Deer are hunted in the Upper East River Valley, but hunting is limited to autumn, when RMBL is not in session, and is prohibited on RMBL property, as is wildlife feeding by RMBL residents. Natural predators in the area include mountain lions *Felis concolor*, black bears *Ursus americanus*, and coyotes *Canis latrans*. The former two species prey on adult mule deer, while coyotes prey primarily on fawns. These predators tend to avoid humans and are rarely seen near the Gothic townsite; as a probable consequence, mule deer does and their fawns are especially common in the townsite during summer months (Waser et al., 2014).

Mule deer are known to habituate to human presence—that is, to decrease their vigilance or avoidance responses to humans upon repeated exposure in a non-threatening context (Geist, 1981). Such habituation may reflect a learned shift in an animal's assessment of the risk that humans in particular pose, or of the overall predation environment when humans are present. Even deer from populations that are hunted can habituate to humans following sufficient non-threatening contact with them (Stankowich, 2008).

1. 2 Behavioral observations

Between 12 July and 28 August 2011 an observer (EHS) wearing dark blue or black clothing walked along trails within and around the Gothic town site for 2.5 hours at dawn or dusk, when mule deer are most active (Elbroch and Rinehart, 2011). The sampling schedule and routes were designed to equalize dawn and dusk observations as much as possible over the range of distances, and to avoid areas where cattle were present. Routes traversed the relatively uniform and gentle topography of the lower Valley slopes.

Once a deer was sighted, the observer recorded variables that may influence detection of a threat or that may influence vigilance and escape behavior. These included: time of day, temperature, wind speed and direction, distance of the animal to cover (willow, aspen or conifer patches at least 16 m^2 in area), sex of the focal individual, group size (number of deer within 50 m of the focal individual), and presence of fawns. The observer then walked at a speed of 1 m/s directly toward the focal individual, counting the number of 1-m paces taken until the deer assumed an alert posture, the number taken until it began to flee, and the total number to reach the deer's initial location. This initial location was recorded with a Garmin model 12 GPS (Garmin Ltd., Olathe, KS). Paces were then converted into three distances: the Starting Distance (SD = distance between the observer and the deer when it was sighted), Alert Distance (AD = distance from the observer at which the deer lifted its head and directed its attention to the approaching human), and Flight Initiation Distance (FID = distance from the observer at which the deer began to move away). When distances were very long or uneven terrain caused variable pace length, we measured distances with an optical rangefinder (Rangematic MK5 1200, Rochester NY, USA) instead of paces. We also noted the gait used by fleeing deer. No observations were taken if a deer was fleeing when first sighted.

We used ArcMap 10/ ArcInfo (ESRI, Redlands CA, USA) software to map buildings, terrain, and locations of observed deer relative to the town center. Because deer were not individually marked, we do not know how many individuals were approached, but we minimized resampling of individuals by including a large area that spanned multiple home ranges and by avoiding repeated observations of distinctive individuals or groups (e.g., Blumstein et al., 2003).

1.3 Statistical analyses

We used Alert Distance (AD) and Flight Initiation Distance (FID) as indicators of how deer assessed the risk posed by an approaching human (Ydenberg and Dill, 1986; Blumstein, 2003; Blumstein et al., 2005). To answer our first

question—whether these indicators are affected by distance from the town center (DTC)—we fitted general linear models that included DTC and other variables that could affect risk detection or vigilance behavior. We began with exploratory ANOVA or regression analyses to identify variables that seemed to have no relationship with AD or FID— our sample size was insufficient for a thorough overall analysis that included all variables. These preliminary analyses indicated that time of day, weather variables, and habitat could be excluded. Fawns were too rare to include in analyses. To see what variables influenced vigilance behavior, we then fitted General Linear Models for AD and FID, using a forward stepwise procedure and Akaike Information Criterion. In all models, residuals were normally distributed. Variables included in the models were Distance to the Town Center (DTC), sex (SEX), distance to nearest cover (COV), group size (GRP), and constraining variables, plus their two-way interactions; data were too sparse to estimate higher-order interactions. In the case of AD, Start Distance (SD) was the constraining variable because AD logically cannot exceed SD (Blumstein, 2003, 2010. In the case of FID, AD was the constraining variable because FID logically cannot exceed AD (Blumstein, 2003, 2010).

To assess the spatial "footprint" of human activity (our second question), we took residuals from a regression of each response variable on its constraining variable and compared average residuals "near" vs. "far" from the RMBL townsite, using a sliding distance partition to assign observations to "near" vs. "far" DTC categories. We used the best-fit partition (that which maximized the difference in "near" vs. "far" group means and the explained variance) to judge the spatial scale over which human activity affected AD and FID. We did not do this analysis on residuals from the best models minus DTC because some of those variables—group size, for example—themselves varied with DTC, and we wanted to estimate the total spatial footprint through all causal pathways. Analyses were performed with R (R Development Core Team, 2011) and JMP (SAS Institute, 2002). Throughout, p-values < 0.05 were considered statistically significant.

2 Results

We obtained 42 FID observations overall during 17 days of trail-walking, including 28 of does and 14 of bucks. We encountered deer most often in dry meadows (78. 6% of encounters). Deer usually were feeding when first sighted. After alerting to the observer (head up, head and ears directed toward observer), they rarely returned to feeding. Instead, they continued to watch the approaching observer until they fled. Deer often fled directly toward the closest cover or, in sloping terrain, headed uphill, walking or stotting. As deer moved away, they often paused periodically to look in the direction of the approaching observer.

As expected, constraining variables were the best predictors of AD and FID. AD increased significantly with SD (AD = 5. 635 + [0. 821 × SD]; $F_{1,40} = 378. 53$, $p < 0. 001$, $R^2_{adj} = 0. 90$), and FID increased significantly with AD (FID = 14. 934 + [0. 365 × AD]; $F_{1,40} = 28. 59$, $P = 0. 001$; $R^2_{adj} = 0. 40$). Neither of these constraining variables was significantly linearly related to DTC ($p > 0. 300$ in both cases)

For both AD and FID, all of the best models included DTC as well as the constraining variable (Table 1). Both AD and FID increased with DTC once the effects of the constraining variables were removed: animals were more vigilant away from the townsite and both alerted and fled when the approaching human was farther away. Distance to cover and its interaction with SD, SEX, and GRP were included, along with SD and DTC, in various combinations among the equivalent models for AD. These interactions probably result from complex effects of habitat openness on cover and encounter distances (distance from cover was correlated with SD; $F_{1,40}=13. 478$, $P = 0. 0007$). There were also non-significant interactions involving sex: compared to does, bucks tended to be more vigilant, to be encountered farther from cover and from town, and to occur in smaller groups. The best models for FID included GRP and its interaction

with AD, and SEX, along with AD and DTC. This is probably because both AD and GRP were affected by DTC—deer density (and therefore group size) decreased with distance from the townsite ($F_{1,40} = 5.718$, $P = 0.022$), where bucks were uncommon, and where deer allowed closer approaches before alerting or fleeing. Bucks tended to flee at longer distances than does ($P = 0.053$ from a full factorial model of FID that included SEX).

DTC also seemed to affect escape gait: deer tended to flee by stotting, rather than walking, when far from the townsite (Logistic regression of effects of DTC on flight gait: $P = 0.081$).

AD and FID residuals from regression on SD and AD, respectively, both increased on average with DTC (Fig. 1A, B; Table 2) in a decelerating fashion, although the second-order polynomial term was not statistically significant in the case of FID residuals. The nonlinear effect of DTC suggests that there is indeed a finite spatial "footprint" of human activity. Variation in behavioral responses also appeared to be somewhat greater at shorter DTC, where some deer tolerated close approaches while others fled at distances resembling those for individuals found further from the town center (Fig. 1A, B).

The spatial "footprint" of human activity on deer vigilance and flight behaviors is suggested by the distances at which AD and FID residuals are most clearly partitioned into "near" and "far" categories. The difference in mean "near" vs. "far" AD residuals was greatest, and highly significant, at a partition distance of 250 m, and decreased with greater distances (Fig. 1A), suggesting that human activity affects vigilance behavior within 250 m from the town center. This distance roughly corresponds to the distance of the most peripheral summer-occupied cabins from the town center. The difference in mean "near" vs. "far" FID residuals was greatest, and was highly significant, at a partition distance of 750 m (Fig. 1B), suggesting that the influence of human activity on flight behavior extends to 750 m away from the town center.

3 Discussion

The result that DTC was included in all best-fit linear models of AD and FID indicates that mule deer increased their vigilance and decreased their tolerance to human approach with distance from a site of concentrated human activity (DTC). Other variables (e. g., sex and group size effects) that were included in at least some of the equivalent best-fit models were unsurprising given previous studies of ungulate behavioral responses to predation risk, or correlations within the dataset (e. g., between group size and DTC). We urge caution in over-interpreting these best-fit models, however, because correlations within the dataset (e. g., between group size and DTC) could obscure causal relationships.

Analysis of residuals from regression of AD and FID on their respective constraining variable (SD and AD, respectively) suggested that DTC effects were nonlinear (Fig. 1, Table 3), saturating at distances 250 m from the town center for AD and 750 m for FID. This suggests a human "footprint" of 250–750 m.

Several things may contribute to these differences in behavior near vs. far from human activity. First, deer whose home ranges included the field station, where encounters with humans are common and benign, may be habituated to human presence. In other words, they may have very different assessments of risk associated with an approaching human than do deer farther from the station that have had few encounters with humans, or possibly hostile encounters in a previous autumnal hunting season (see Kilgo et al., 1998). Deer may also know that coyotes and other predators are far more common away from the field station (see Waser et al., 2014 and as a result associate the approach of any heterospecific large mammal with risk when they are far from the town center. The greater variation in FID among deer observed close to the townsite may in turn represent individual differences in "shyness" and "boldness" (Wilson et al.,

1994; Runyan and Blumstein, 2004), or varying degrees of habituation—perhaps age-related—that are less likely to be expressed in riskier sites.

The spatial extent of human habituation effects has been called the "behavioral footprint" of anthropogenic impacts (Webb and Blumstein, 2005; Blumstein and Fernández-Juricic, 2010; Blumstein, 2014). Conservation efforts and wildlife managers are aided by knowledge of this "footprint" because perception of threat from humans has implications for how animals allocate time to feeding versus other activities, and thus for their interactions with other species. Given the reasonable agreement between the radius of 300 m around the RMBL town center that includes most of the field station buildings and the distances over which AD and FID behaviors changed (250 and 750 m, respectively), we suggest that a "footprint" for mule deer that experience benign encounters with humans, and perhaps associate human activity with fewer encounters with coyotes and other predators, corresponds to a discontinuity from high to low levels of human presence.

This suggestion is consistent with two other recent studies at the RMBL. First, Carrasco and Blumstein (2012) found that mule deer responded to marmot *Marmota flaventris* alarm calls but not to non-threatening birdsong within 500 m of the RMBL town center, whereas they fled in response to both stimuli beyond this distance. Second, over a decade of study, Waser et al. (2014) documented spatial patterns around the RMBL that suggest a trophic cascade involving coyotes, mule deer does, and preferred food plants of the deer. As one moves beyond a distance of approximately 250 m from the nearest summer-occupied building at the field station, coyote activity increases, activity density of does and fawns decreases, and browsing of food plants decreases. The spatial scale of these effects agrees with the 250–750 m DTC scale that we report here.

We contend that documenting the spatial scale over which humans affect wildlife will permit us to better understand and manage our impacts on wildlife (Blumstein, 2014). In this study spatial gradients in deer vigilance and flight behavior allowed us to document the human spatial footprint, but not to pinpoint the behavioral mechanisms behind this habituation response. Future studies are needed to explore more exactly what it is about areas of high *vs*. low human activity that affects the behavior of mule deer and other wildlife.

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Table 1 Best-fit explanatory models for Alert Distance (A) and Flight Initiation Distance (B)

Variable	Model	R^2_{adj}	F	P	AICc	K	ΔAICc
A) Alert Distance							
	SD+DTC−SD*COV−SEX*COV	0.943	170.22	0.0001	191.096	6	0
	SD+DTC−COV−SD*COV	0.944	214.61	0.0001	191.647	5	0.55
	SD+DTC−SD*COV+COV*GRP	0.941	165.24	0.0001	192.279	6	1.18
B) Flight Initiation Distance							
	AD+DTC−SEX+AD*COV−GRP **−AD*GRP**	0.673	15.04	0.0001	220.146	8	0
	AD+DTC−GRP−AD*GRP	0.642	19.36	0.0001	220.305	6	0.16
	AD+DTC+AD*COV−GRP −AD*GRP	0.655	16.55	0.0001	220.490	7	0.34
	AD+DTC−SEX+AD*COV−GRP −AD*GRP+DTC*GRP	0.682	13.58	0.0001	220.927	9	0.78

Models are arranged from lowest to higher AICc. Only the best-fit and equivalent models (ΔAICc < 2.00) are included. The best model is indicated in boldface. Signs of effect coefficients are indicated in the model column. AD = Alert Distance; SD = Start Distance; DTC = Distance from Town Center; COV = Distance to cover; GRP = Number of conspecifics within 50 m of focal individual; SEX = sex of focal individual (coded as does − bucks).

Table 2 Best-fit (lowest AICc) polynomial regressions for effects of distance from the town center (DTC) on A) Alert Distance (AD), and B) Flight Initiation Distance (FID) residuals from regressions with constraining variables

A) AD Residuals

		df	MS	F	P	t	Parameter Estimate
Model fit:				$R^2_{adj} = 0.124$; AICc = 203.59			
Model		2	457.97	3.91	0.028		
	intercept				0.134	−1.53	−3.847
	DTC	1		7.66	0.009	2.77	0.009
	DTC^2	1		2.90	$−7 \times 10^{-6}$	−1.70	0.096
Error		39	117.17				
C. Total		41					

B) FID residuals

		df	MS	F	P	t	Parameter Estimate
Model fit:				$R^2_{adj} = 0.188$; AICc = 227.53			
Model		1	2220.66	10.48	0.002		
	intercept	1			0.020	−2.41	−8.125
	DTC	1			0.002	3.24	0.010
Error		39	211.85				
C. Total		41					

Table 3 Analysis of the spatial scales over which human activity affects deer vigilance and flight behaviors

Variable	Statistic	Partition Distance from Town Center			
		250 m	500 m	750 m	1000 m
AD residual	Mean near	**−10.32**	−3.87	−0.55	−2.21
	Mean far	**4.12**	3.52	1.00	4.92
	$F_{1,40}$	**19.344**	4.657	0.170	3.627
	$p <$	**0.0001**	0.037	0.682	0.064
	R^2_{adj}	**0.283**	0.034	0.000	0.136
FID residual	Mean near	−6.48	−2.57	**−6.74**	−4.64
	Mean far	2.59	2.34	**12.14**	12.58
	$F_{1,40}$	2.828	0.969	**18.953**	15.435
	$p <$	0.100	0.331	**0.0001**	0.0003
	R^2_{adj}	0.217	0.178	**0.280**	0.242

Residuals were partitioned into "near" and "far" categories using different distances from the townsite center. Values in boldface indicate the best partition distance—the one that maximizes the difference between near and far means and the model explained variance.
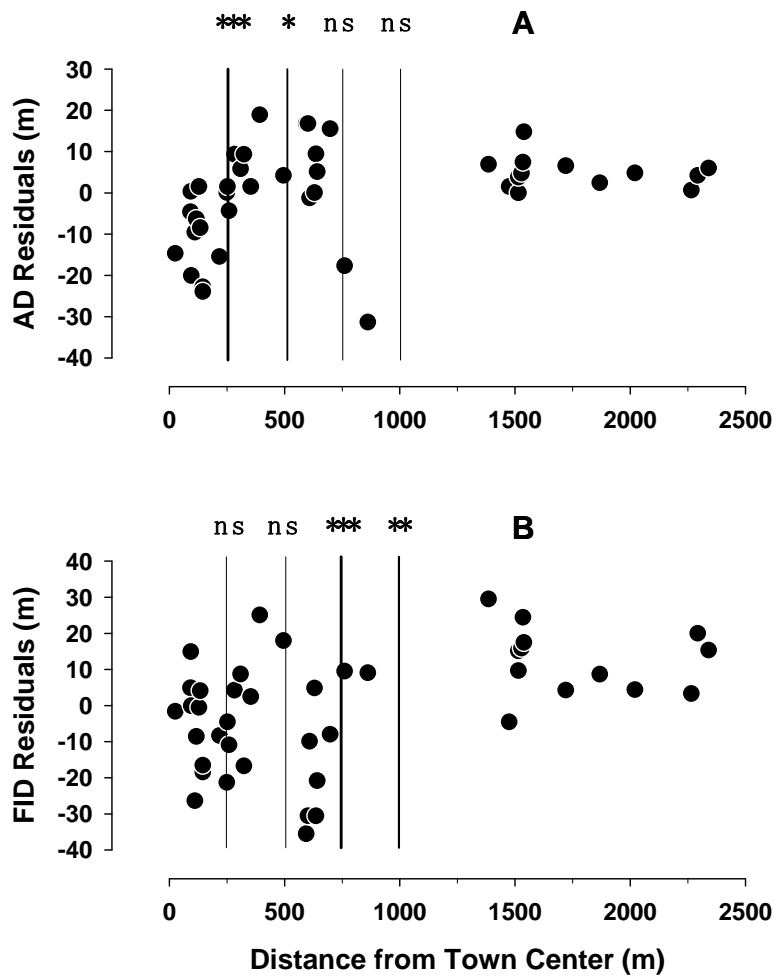
Fig. 1 A): Alert Distance (AD) residuals (from regression of AD on Start Distance) plotted over Distance from Town Center. B): Flight Initiation Distance (FID) residuals (from regression of FID on AD) plotted against Distance from Town Center

Vertical lines indicate tested partition distances used to compare mean residuals for "near" vs. "far" distances. The thickest lines indicate the best partition distance—the one that maximizes the difference in "near" vs. "far" means residuals and the explained variance. *** $P < 0.0001$; ** $P < 0.02$; * $P < 0.05$; ns = $P > 0.05$.