

Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer

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The relationship between preflight risk assessment by prey and the escape behaviors they perform while fleeing from predators is relatively unexplored. To examine this relationship, a human observer approached groups of Columbian black-tailed deer (*Odocoileus hemionus columbianus*), varying his behavior to simulate more or less threatening behavior. We measured the focal deer's angle of escape, distance moved during flight, duration of trotting and stotting behavior, and change in elevation during flight. Analyses revealed positive relationships between the distance moved during flight and the distance at which they fled. When flight was initiated when the approacher was close, deer fled relatively shorter distances and took flight paths at more acute angles, a property that would force a real predator to change direction suddenly. Our results indicate that deer do not compensate for allowing the observer to approach more closely by fleeing greater distances. Rather, distance moved and flight initiation distance are linked by level of reactivity and habituation: more reactive or less habituated deer both flee at a greater distance and move away to a greater distance during flight. More threatening behavior by the approacher led to longer durations of rapid flight behavior (e.g., trotting and stotting), and deer tended to flee uphill and into taller vegetation, using these landscape features as refuge from danger. Finally, we provide the first evidence for Pitcher's untested "antiambush" hypothesis for the function of stotting and discuss its significance. In general, both preflight predator behavior and habitat features influence both duration and direction of escape. *Key words*: deer, distance moved, escape angle, escape behavior, flight initiation distance, stotting. [*Behav Ecol* 18:358–367 (2007)]

As predatory encounters escalate, animals must make a series of assessments and decisions regarding 1) predator recognition and species recognition (Curio 1993; Coss and Ramakrishnan 2000; Payne et al. 2004), 2) the level of threat posed by the predator (Helfman 1989; Rowe and Owings 1990, 1996; Swaisgood, Owings, et al. 1999a; Swaisgood Rowe, et al. 1999b), 3) when to flee based on the distance to the predator (Ydenberg and Dill 1986; Stankowich and Blumstein 2005) and access to refuge (Kramer and Bonenfant 1997), and 4) the optimal escape strategy based on the predator's mode of attack (e.g., Papouchis et al. 2001) and prey's physiological/morphological limitations (e.g., life stage; Cromarty et al. 2000; reproductive state; Bauwens and Thoen 1981; temperature; Losos 1988; wing morphology; Fernández-Juricic et al. 2006). Although selection acts on each stage of the predatory encounter sequence (Endler 1986; Lima and Dill 1990), animals may be able to compensate for increased risk in one domain with reduced risk in another (DeWitt et al. 1999; Lind and Cresswell 2005; Ajje et al. 2007). For instance, a lizard approached by a predator while basking in a more exposed area on the ground initiates flight at a greater distance (Cooper 2000) or runs a greater distance before stopping (Blamires 1999) than in conditions where refuge is more immediately available.

Although many studies have focused on the decision of when to flee from predators (reviewed in Stankowich and

Blumstein 2005), very little attention has been paid to relating escape behavior to preflight risk assessment and predator approach behavior (Caro 2005; Stankowich 2006). Flight initiation distance, the distance between the predator and prey at which the prey takes flight (Figure 1), has been shown to be 1) a reliable measure of fearfulness in animals (e.g., Dwyer 2004) and 2) strongly correlated positively with both the distance at which the predator begins its approach and the distance at which the prey becomes alert to the predator (respectively, "starting distance" and "alert distance"; birds: Blumstein 2003; Blumstein et al. 2005; lizards: Cooper 2005; deer: Stankowich and Coss 2006). Although the fact that flight initiation distance must be less than alert and starting distances and could alone generate these strong correlations, from a functional perspective these relationships imply that animals incur time costs (in the form lost feeding and mating opportunities) for sustaining high rates of antipredator vigilance (Blumstein 2003) and maintaining a zone of awareness within which they will treat any predator detected as a potential threat (Stankowich and Coss 2006). In addition to affecting flight behavior, the distance at which an animal becomes alert to a predator can also mediate the predator's decision to continue its approach/pursuit (Lingle and Wilson 2001). Nevertheless, animals that flee at very short distances are, all else being equal, at greater risk than animals that flee while the predator is farther away. It is surprising, therefore, that few investigators have attempted to relate preflight features of behavior to characteristics of escape behavior, such as distance moved, escape speed and direction, and style of escape.

The distance a prey animal flees from an approaching predator before stopping ("distance moved": Taylor and Knight 2003a; Figure 1) is commonly used as an indicator of the impact that any one predatory encounter has on an animal and is a reliable measure of fear (Miller et al. 2006). Distance

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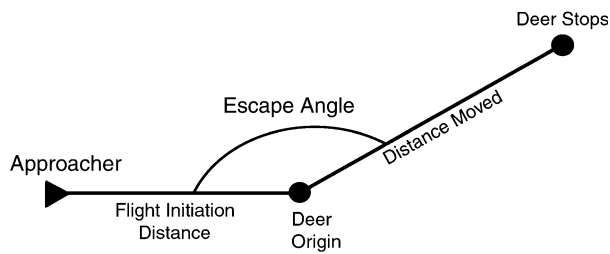


Figure 1

Plan view of deer flight initiation distance from an approaching human, escape angle, and distance traveled during flight. The approacher is represented by a black triangle indicating the direction of approach. The positions of the focal deer before and after flight are represented by black circles.

moved has been shown to be positively associated, negatively associated, or unassociated to flight initiation distance in lizards (positively associated: Bauwens and Thoen 1981; Schwarzkopf and Shine 1992; negatively associated: Martín and López 2003; unassociated: Blamires 1999; Cooper 1997a) and ungulates (positively associated: Taylor and Knight 2003b; negatively associated: Hamr 1988; Andersen et al. 1996; unassociated: Taylor and Knight 2003b). If animals compensate for risky behavior in one context with conservative behavior in another (Lind and Cresswell 2005), then we would expect a negative relationship between distance moved and flight initiation distance. Conversely, if behavioral responses were correlated across stages of the attack sequence, implying a reactivity syndrome, then we would expect a positive relationship. Distance moved also is affected by the directness of predator approach (Bratton 1990) and predator approach speed (Cooper 1997b), 2 reliable indicators of the level of threat posed by the predator. Additionally, environmental factors (e.g., amount of food present: Cooper et al. 2006) and contextual factors influence the distance an animal flees. For example, when approached by humans, animals flee longer distances when the human is off of a trail rather than on a trail (Miller et al. 2001; Taylor and Knight 2003b), when animals are in areas with more human disturbance or hunting (King and Workman 1986), when animals are farther from refuge (Cassirer et al. 1992; Cooper 1997a; Martín and López 2003; Fernández-Juricic et al. 2006), and when animals are in larger groups (Aastrup 2000; Taylor and Knight 2003b). Mule deer (*Odocoileus hemionus hemionus*) move greater distances in response to people than to snowmobiles (Freddy et al. 1986). Finally, features of the prey animal, such as sex (Hamr 1988) and reproductive state (Aastrup 2000), can affect distance moved.

In addition to the distance an animal moves during flight, escape responses can also vary in the angle at which the animal flees. The “escape angle” is the angular deviation away from the direction from which the predator approaches (Figure 1), where flight directly away from the predator is 180° and flight directly toward the predator is 0°. Cooper (1997a, 1997b) found that approach speed and flight initiation distance had no effect on escape angle in broad-headed skink (*Eumeces laticeps*), but he did find an effect of the angle to nearest cover. Stotting behavior allows mule deer to rapidly change directions during flight and flee at extreme angles (Geist 1981), which forces the predator to suddenly change directions during approach and may allow the prey to put more distance between itself and the predator.

Numerous studies across the animal kingdom have demonstrated that animals exhibit many forms of escape, but the extent to which many of these forms are associated with different environmental factors or different predators is poorly

understood (Caro 2005). Running speed is clearly affected by habitat (Lima and Dill 1990; Blumstein 1992; Blumstein et al. 2004), and Kramer and Bonenfant (1997) found that woodchucks (*Marmota monax*) fled at higher speeds when the distance to refuge was greater. Behrend and Lubeck (1968) reported that, in response to approaching humans, a larger proportion of white-tailed deer (*Odocoileus virginianus*) ran versus walked in hunted and high human traffic areas than in unhunted and low-traffic areas. Escape speed in mule deer was unaffected by disturbance type (human vs. snowmobile: Freddy et al. 1986). Animals may also use the surrounding habitat differently during their escape depending on the style of escape, predator approach behavior, or other environmental characteristics, and even closely related species may show differences in preferred refuge type. When confronted by coyotes, mule deer move uphill and toward slopes whereas white-tailed deer move downhill and away from slopes (Geist 1981; Lingle 2002). Such striking differences between sister species in terrain use during predatory encounters suggest that a variety of factors influence risk assessment and escape behavior in prey animals.

We examined the responses of Columbian black-tailed deer (*Odocoileus hemionus columbianus*) to an approaching human as a method of investigating the relationships between preflight risk factors (i.e., flight initiation distance, assessment time, predator behavior, environmental factors) and parameters of escape behavior (e.g., distance moved, escape angle, escape style). Approaching humans are often used as a predatory stimulus in studies of flight decisions and risk assessment (for review, see Stankowich and Blumstein 2005). Deer predators often will continue to pursue their prey even after the prey have become alert or begun to flee (Beier 1991; Smallwood 1993), but deer will also display clear antipredatory deterrent behaviors when confronted by predators but not pursued (Stankowich and Coss 2007). Although previous studies suggest that there is wide interspecific variation in how features of pre- and postflight behavior are related, it is clear that prey alter their escape behaviors based on degree of perceived risk, distance to the predator, and distance to safety. We hypothesized that more threatening approaches will result in greater escape distances because predator behavior has been shown to impact significantly flight initiation distance and assessment time (time elapsed between alert and flight behavior) in deer (Stankowich and Coss 2006). Additionally, we predicted that when the approacher is closer to the prey at flight initiation, the prey will flee at a more acute angle to force the approacher to alter its course rapidly and potentially lose ground on the prey. We then examined the effects of a variety of factors on the presence/absence and duration of different types of flight (e.g., trotting, stotting, and galloping) and how black-tailed deer made use of the local topography during escape. Determination of the relationships of these escape behaviors with preflight decision making and other environmental factors will fill a large gap in our understanding of how behavior at the first stage of a predatory encounter affects the initiation and expression of antipredator behavior in subsequent stages (Lima and Dill 1990; Lind and Cresswell 2005; Stankowich 2006).

METHODS

A single human observer conducted approaches on free-living adult deer in Point Reyes National Seashore (PRNS) in Marin County, California, USA from June–September 2003 (although most trials were conducted in the months of August and September) and August–September 2004. Vegetation cover was minimal and consistent during the times of data collection, consisting of open grasslands and pastures with no tree cover

and sparse scrub, and topographical features were limited to rolling hills with a few steep hillsides. Trials were conducted in the months when fawns are no longer in hiding and outside the seasons when males are in the rut and females are pregnant. Hunting has been banned in the park since 1971, although there are scattered reports of illegal poaching, and park management culled herds of nonnative deer in the pastures until 1994 using guns. The ranchland pastures of PRNS are not high-traffic park areas where deer–human interactions would be frequent. The deer are not completely habituated to humans and readily perform escape responses with a high state of arousal (e.g., stotting, tail flagging, galloping); albeit, they are not as wary of humans as deer in actively hunted populations. Therefore, humans are likely seen as potential threats to these deer but there would have been little, if any, opportunity for individuals to learn to associate guns with danger.

Like most studies of wild deer, we were unable to mark or identify individuals based on variation in coloration or coat patterns, and PRNS has no recent estimate of population size (although it is likely in the range of 500–1500 individuals). However, many stable groups [congregations of individuals within 30 m of their nearest neighbor (Stankowich 2003) that were cited reliably in the same location on multiple days] were identifiable by size, sex ratio, and location within the park. If we tested the same group more than once, we waited at least 2 weeks between trials and selected a member of the opposite sex or an individual with evident phenotypic differences (e.g., longer antlers, different size, different shade of coat color, etc.) than the previously sampled deer. We are, therefore, confident that replication on the same animal was rare.

A single observer conducted approaches as described in Stankowich and Coss (2006), whereas a second observer recorded the interactions on video. A focal deer was chosen in the group; typically, this was the animal nearest to us because we wanted the focal to perceive that it was the direct target of approach, and we did not want an animal between the focal and the approacher to flee first, which could confound the focal deer's decision to flee. Typically from the roadside, T.S. (1.85 m tall, Caucasian male, wearing tan pants, green coat, and a baseball hat) emerged from an automobile, moved into a position (usually within 20 m of the automobile and in view of the focal) where he had a direct line of approach to the focal deer (fawns, ≤ 1 year of age, were not selected as focal individuals), and then began to approach solitary or small groups of deer at a constant pace (speed described below), using a stopwatch and dropping weighted flags on the ground as markers to keep track of when response events occurred and the location of the approacher when each occurred. The approacher marked his location when he began the approach, when the deer became alert (i.e., standing with its head and neck upright and looking at the approacher), when the deer fled (defined as movement by walking, trotting, stotting, or galloping), and the original location of the deer. He noted the deer's path of escape and its final location (either where it stopped or where it disappeared from sight). Distances between each weighted marker were measured with a Bushnell Yardage Pro laser range finder and were accurate to the nearest 1 m.

After the end of each trial, we measured the angle of escape by laying 2 poles of known length on the ground, one in-line with the direction of approach (side 1), one in-line with the direction of escape (side 2), and the origin of the deer as the intersection. We then measured the distance between the free ends of the poles (side 3) to create a triangle and used the lengths of all 3 sides and a geometric formula to calculate the angle of escape (the angle between the direction of approach and direction of escape: Figure 1). We recorded as ordinal values differences (>5 m) in elevation between the

approacher's starting position, the deer's origin, and the deer's final location. We recorded the type (grass, scrub, or grass + scrub) and height (to the nearest foot) of the vegetation at the focal deer's origin and whether the vegetation at the deer's stopping point or place it disappeared was shorter, taller, or equal in height (to the nearest foot) to the vegetation at its origin. We noted the sex of the focal deer, if it was alert at the start of approach, and the size of the deer group. We also recorded several environmental variables (e.g., temperature, wind speed/direction, light level). Consistently, high winds and the long distances at which approaches started greatly minimized any olfactory cues the deer may have detected from the approacher, and these cues do not affect flight decisions in this population (Stankowich and Coss 2006). A Panasonic model PV-DV601D mini digital video recorder with 20 \times optical zoom lens was used by the second observer to record the trials from a much greater distance than the starting distance—a process that did not noticeably affect the deer's behavior. We noted from these video recordings the presence or absence of trotting, stotting, and galloping behaviors (defined by: Hildebrand 1977; Lingle 1992) during escape and the duration of each bout of these behaviors. When there were multiple bouts of the same type of flight behavior, we calculated the average bout duration. We discarded trials if the distances or times measured were questionable or if passing cars or other provocative situations alarmed any members of the group. Auditory cues (e.g., car doors closing and talking) were minimal to absent. We did not conduct trials if any members of the group took flight at a trotting speed or faster prior to the start of the approach.

Approaches were varied in 4 ways as described in Stankowich and Coss (2006). T.S. varied 1) approach speed by jogging versus walking toward the deer, 2) directness of approach by moving toward a point approximately 30 m to the left or right of the focal animal versus moving directly toward the focal, 3) predator intent by averting his gaze toward the ground during approach (n.b., when gaze was averted, the eye's of the approacher were completely concealed by the brim of a hat, and the second observer quietly told the approacher what the deer were doing via 2-way radio) versus staring directly at the focal deer, and 4) presence of a "gun" by holding a long black rod up at his eyes to simulate aiming a rifle at the focal versus walking normally with his arms swinging at his side.

Analyses

Prior to analyses, all continuous variables were subjected to Kolmogorov–Smirnov one-sample normality tests, and assessment time was natural log-transformed to satisfy normality assumptions. Distance moved (when the animals stayed in view), escape angle, trotting duration, and stotting duration were subjected to forward entry stepwise regression analyses (Neter et al. 1996) with a probability to enter of <0.10 , 2-tailed significance reached at $\alpha = 0.05$, and the most significant predictor entered at each step. The predictors consisted of predator speed, directness of approach, presence or absence of gun, predator intent, whether or not the focal deer was alert prior to the start of approach (alert prior), sex, group size, flight initiation distance, assessment time, escape angle (except in the analysis of escape angle), vegetation type, vegetation height, presence of stotting, presence of galloping (except in the analysis of stotting duration), deer's change in elevation during flight (down, no change, up), approacher's change in elevation from start to flight (down, no change, up), and the initial elevation of the approacher relative to the deer (uphill, no difference, downhill). Other environmental variables were excluded from final analyses due to their lack of predictive potential on antipredator behavior (Stankowich and Blumstein 2005) and/or their lack of effect on flight

decisions in this population (Stankowich and Coss 2006). The durations of stotting and trotting were not included in the analysis of escape angle because the decision of how long to perform these behaviors should not influence the initial angle of escape. Interactions were not included as candidate predictors to increase the potential explanatory power of each main-effect factor. We calculated partial correlation coefficients (*r*) for each factor in the analysis as measures of effect size; however, when the factor was not included in the final model, the reported *r* was the value that would result if the variable was entered into the model equation at the next step. We used binary logistic regression (forward entry using Wald statistic; $P < 0.10$ to enter) to measure the effects of the same factors on the presence or absence of stotting behavior. Changes in elevation during flight and changes in vegetation height during flight were analyzed with chi-squared tests. We analyzed separately the effect of alert and flight initiation distances on changes in elevation during flight using ordinal regression. Suspected outlying data points were analyzed with Grubb's test statistic for outliers at the $\alpha = 0.05$ level (2-tailed; Sokal and Rohlf 1995). All data are presented in means \pm standard errors. All statistical analyses were conducted in SPSS 10.0.

RESULTS

Escape angle

Deer fled at an average angle of $135.9^\circ \pm 3^\circ$ away from the approacher, with a range of 70° – 180° . When deer fled at greater distances, they took flight paths at a greater angle from the approacher ($N = 82$, $P = 0.049$, $r = 0.217$; Table 1, Figure 2). We tested the fit of linear, logarithmic, and power models for the relationship between flight initiation distance and escape angle and, in the range of values tested, there was little variance in the overall fit of the models ($0.047 \leq R^2 \leq 0.057$). Therefore, a simple linear relationship between flight initiation distance and escape angle was deemed to be most parsimonious (Figure 2). There were no effects of any aspect of predator behavior, group size, sex, vegetation, or elevation on escape angle ($P > 0.05$), and the final regression model explained relatively little of the overall variance in escape angle (adjusted $R^2 = 0.049$).

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Distance moved

Deer fled an average of 105 ± 12 m ($N = 40$), with deer moving out of sight of the approacher in the remaining 48 trials. Flight initiation distance had the strongest association with distance moved ($N = 32$, $P = 0.002$, $r = 0.444$; Table 1, Figure 3a); deer fled to greater distances when they initiated flight at greater distances. Larger groups of deer fled greater distances ($P = 0.007$, $r = 0.489$, Figure 3b), and deer that initially were in only grass fled longer distances than deer that were in grass mixed with scrub ($P = 0.018$, $r = -0.435$, Figure 3c). There was no statistically significant effect of sex on distance moved ($P > 0.05$). Although distance moved was not reliably associated with predator speed, directness of approach, or presence of gun ($P > 0.05$), deer tended to flee greater distances when the approacher averted his gaze compared with when the approacher stared directly at the deer; however, this trend was not statistically significant ($P = 0.066$, $r = 0.346$). There were no statistically significant effects of vegetation height, elevation changes, or presence of stotting or galloping ($P > 0.05$). The final regression model included 4 terms (Table 1) and explained nearly 50% of the variance in distance moved (adjusted $R^2 = 0.488$, $P < 0.001$).

Escape style

Deer were observed trotting during flight in 59 of 71 trials, but in only 39 trials was trotting the only type of flight behavior observed. Deer stotted in 28 of 71 trials but galloped during escape in only 4 trials. The presence of stotting was most strongly affected by the height of the vegetation at the deer's

Table 1
Results of forward stepwise regression analyses on escape angle, distance moved, trotting, and stotting durations

Factor	Escape angle		Distance moved		Trot duration		Stot duration	
	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>
Predator behavior								
Approach speed	0.374	-0.099	0.392	-0.168	0.048	-0.266	0.972	-0.007
Directness of approach	0.806	0.028	0.639	0.093	0.067	-0.246	0.747	0.065
Predator intent	0.725	-0.039	0.066	0.346	0.626	-0.067	0.868	-0.034
Presence of 'Gun'	0.415	-0.091	0.946	-0.014	0.545	0.083	0.056	0.365
Group size	0.305	0.115	0.007	0.489	0.385	0.120	0.483	-0.142
Sex	0.826	0.025	0.514	0.129	0.216	0.169	0.952	-0.012
Alert prior	0.758	-0.035	0.233	0.233	0.990	-0.002	0.536	-0.125
Flight initiation distance	0.049	0.217	0.002	0.444	0.926	0.013	0.758	0.062
Assessment time	0.773	-0.032	0.799	0.050	0.457	-0.102	0.522	0.129
Escape angle			0.795	-0.051	0.380	-0.121	0.620	-0.100
Presence of stotting			0.547	0.119	0.289	-0.146		
Presence of galloping			0.943	-0.014	0.566	-0.079		
Vegetation height	0.305	0.115	0.338	0.188	0.058	-0.255	0.573	0.114
Vegetation type	0.107	0.179	0.018	-0.435	0.745	-0.045	0.852	-0.038
Change in flight elevation	0.253	0.128	0.213	-0.243	0.067	0.247	0.255	-0.227
Change in approach elevation	0.633	-0.053	0.442	0.151	0.953	-0.008	0.980	0.005
Initial difference in elevation	0.726	0.039	0.835	-0.041	0.965	-0.006	0.705	0.076
Final model								
Adjusted R^2	0.035		0.488		0.171		0.100	
df	1, 81		4, 27		4, 54		1, 26	
<i>P</i>	0.049		<0.001		0.007		0.056	

Results in bold signify that the factor was included in the final model. Partial correlations (*r*) of each factor are listed; when the factor was not entered into the final model, values are what would result if the variable were entered into the equation at the next step.

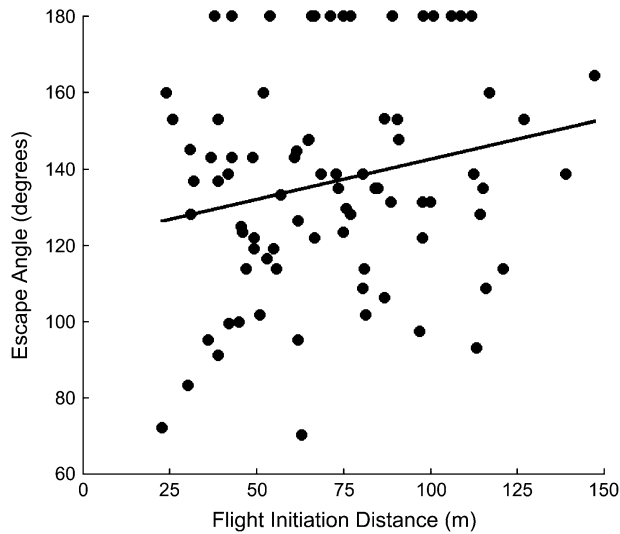


Figure 2

The relationship of escape angles and flight initiation distances taken by Columbian black-tailed deer during flight in response to approaches by a human ($N = 82$) (line is linear regression with partial correlation $r = 0.217$).

origin, where stotting was more likely to occur with increased vegetation height [Wald $\chi^2 = 10.084$, degree of freedom (df) = 1, $P = 0.001$; Table 2]. Moreover, there was a trend for increased probability of stotting when deer fled at greater escape angles (Wald $\chi^2 = 3.110$, df = 1, $P = 0.078$); deer that fled directly away from the approacher were more likely to stot during flight. No other factor contributed reliably to the likelihood of stotting; therefore, vegetation height and escape angle were the only factors entered into the final logistic regression model ($\chi^2 = 16.298$, df = 2, $P < 0.001$; Nagelkerke $R^2 = 0.278$). There were insufficient instances of galloping (4) to analyze probability or duration of galloping behavior, and because trotting was observed in more than 80% of flights, we did not analyze the probability of its occurrence. The duration of trotting (overall mean 8 ± 1 s) was reliably dependent on predator behavior, with more threatening approaches yielding a longer duration of trotting. In this context, more rapid approaches yielded a longer duration of trotting ($P = 0.048$, $r = -0.266$; Table 1, Figure 4a), and there was a trend for a shorter duration of trotting in response to indirect approaches ($P = 0.067$, $r = -0.246$; Figure 4a). Trotting duration also was impacted to a small degree by environmental factors. Shorter vegetation at the deer's point of origin led to a longer duration of trotting ($P = 0.058$, $r = -0.255$; Figure 4b), and deer that fled uphill tended to trot for longer periods ($P = 0.067$, $r = 0.247$; Figure 4c), however, neither of these effects was statistically significant. No other factor significantly contributed to the final model of trotting duration (adjusted $R^2 = 0.171$, $P = 0.007$). The only factor to contribute to the explanation of variation in the duration of stotting (overall mean 6.0 ± 1.0 s; adjusted $R^2 = 0.100$, $P = 0.056$) was the presence of a simulated gun under which circumstances deer stotted for longer periods when the approacher carried a gun ($P = 0.056$, $r = 0.365$; Figure 4a); however, this effect was not statistically significant.

Habitat use during flight

In 88 trials, deer fled uphill (32 trials) or did not change elevation (43 trials) more often than expected and fled downhill (13 trials) less often than expected ($\chi^2 = 15.705$, $P < 0.001$).

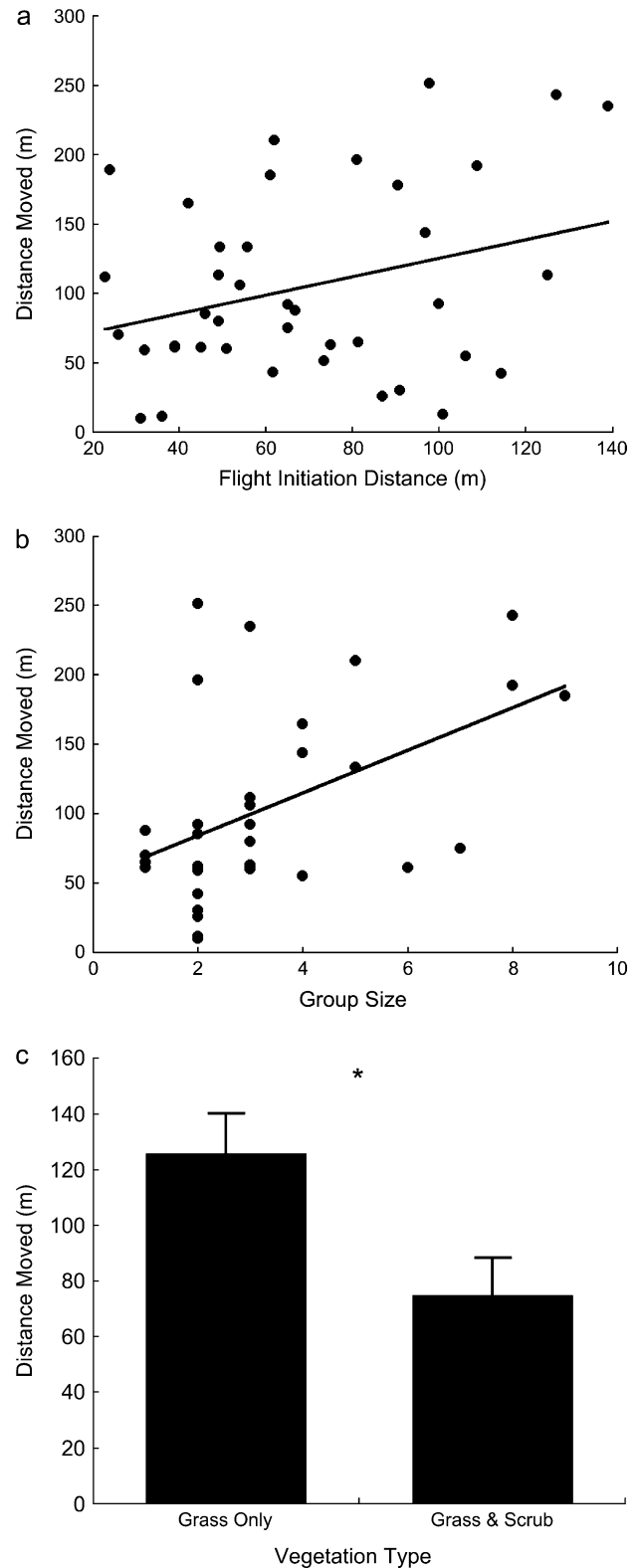


Figure 3

The distance Columbian black-tailed deer moved during flight in response to approaches by a human ($N = 31$) before stopping in view. (a) Scatter plot of distance moved and flight initiation distance (line is linear regression with partial correlation $r = 0.444$). (b) Scatter plot of distance moved and group size (line is linear regression with partial correlation $r = 0.489$). (c) Distance moved as a function of vegetation type at the deer's point of origin (mean and standard errors values are shown: * $P < 0.05$).

Table 2
Number of trials where stotting behavior was present or absent partitioned by vegetation height

		Vegetation height					
		0–1 ft	1–2 ft	2–3 ft	3–4 ft	4–5 ft	Total
Presence of stotting	Absent	30	10	2	0	1	43
	Present	7	10	10	1	0	28
	Total	37	20	12	1	1	71

Binary logistic regression: Wald $\chi^2 = 10.084$, $df = 1$, $P = 0.001$.

Alert and flight initiation distance had no effect on changes in elevation during flight (alert distance: Wald = 0.158, $df = 1$, $P = 0.691$; flight initiation distance: Wald = 0.268, $df = 1$, $P = 0.608$). Initial differences in elevation between the approacher and the deer were equal in frequency (observer lower than deer: 27 trials, equal in elevation: 30 trials, above deer: 31 trials; $\chi^2 = 0.295$, $P = 0.863$). There were many more trials than expected ($\chi^2 = 28.932$, $P < 0.001$) with no change in elevation during approach (51 trials) and fewer than expected where the approacher traveled uphill (27 trials) or downhill (10 trials); deer traveled uphill more often than downhill. Too many cells with fewer than 5 cases precluded further analyses (e.g., logistic regression or chi-squared analysis) on the relationship between these variables. In a survey of 72 trials, deer fled to taller vegetation more often (21 trials) than to shorter vegetation (7 trials; $\chi^2 = 29.083$, $P < 0.001$), although in most cases, there was no difference in vegetation height spanning from where the deer originated to its final destination (44 of 72 trials). It should be noted that in the analyses of changes in elevation during flight, we are assuming that deer had equal opportunities to flee uphill, downhill, or to stay at the same elevation in each trial (this also applies for analyses of vegetation height). To confirm this, however, would be a logistically and statistically daunting task.

DISCUSSION

Deer escape responses were deeply dependent on variation in approach behavior, environmental characteristics, and their proximity to the approaching human. Escape angles (Figure 1) were more acute when the deer allowed closer approach by the human, as if to disrupt the continuity of approach and to force energetically costly shifts in direction by the approacher if he were to follow in pursuit. Additionally, distance moved increased with increasing flight initiation distance. Larger groups of deer and deer that were in unprotective grassy cover moved longer distances. More threatening approaches led to reliably longer durations of trotting and stotting behavior. Habitat characteristics predictably influenced escape angle and flight duration, and generally deer fled uphill more often and to areas with more protective cover.

Escape angle

The angle of escape away from the approacher was impacted significantly by the distance at which the deer fled. The effect was relatively weak ($r = 0.217$), but there are a plethora of other factors that might influence strongly the direction of flight (e.g., contagious following of other group members, known sources of refuge, locating a hidden fawn). To our knowledge, this is the first empirical evidence that flight initiation distance affects flight angles in ungulates. Geist (1981, p. 171) states that “when a predator closes in, a mule deer can

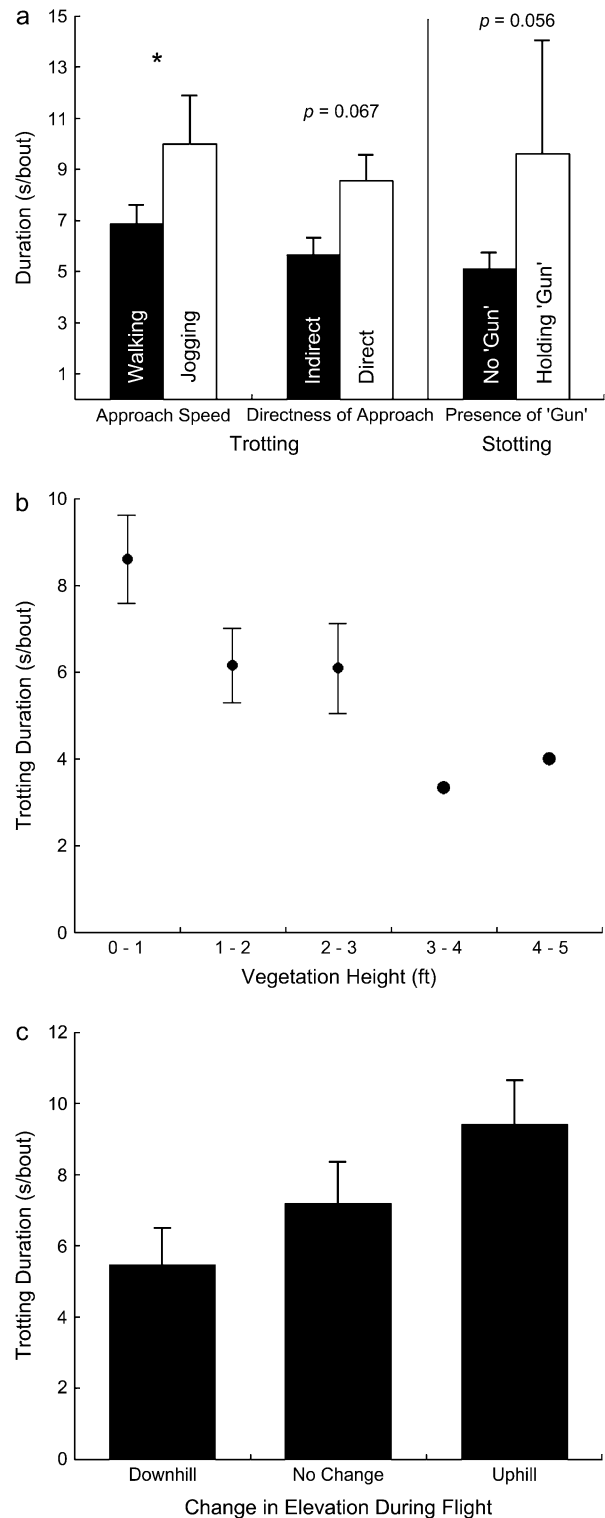


Figure 4
 (a) Duration of flight behavior of Columbian black-tailed deer in response to human approaches for trotting and stotting behavior included in the analyses of covariance (mean and standard error values are shown). Bars depict the effects of approach speed and directness of approach on trotting duration ($N = 59$) and the effect of the presence of a gun on stotting duration ($N = 28$, $*P < 0.05$). (b) Nose and whisker plot (mean \pm standard error) showing the effect of vegetation height on trotting duration ($N = 59$, $P = 0.058$; $r = -0.255$). (c) Bar chart showing trotting duration as a function of change in elevation during flight ($N = 59$, $P = 0.067$; $r = 0.247$).

initiate evasive maneuvers based on sudden unpredictable changes in direction and on placing obstacles between itself and the predator." When the predator is narrowing the distance between itself and its prey, the tactical close-range adoption of escape angles that deviate sharply from the predator's course of approach may function to increase effectively this distance during pursuit. In essence, the ability of the predator to track visually the evasive actions of prey at farther distances likely enhances the predator's ability to adjust its actions to correspond with sudden changes in prey flight trajectory. Additionally, taking an escape angle that does not maximize the absolute distance between the predator and prey (e.g., any angle less than 180°) at the onset of flight might signal to the predator that the prey can easily maintain a lead during a pursuit—thereby deterring further chase (Markl 1985). Similar to evasive moth behavior (Roeder and Treat 1961) and sideways jumping in ground squirrels (Owings and Coss 1977), our results suggest that deer use acute escape angles to hinder pursuit at close proximity and simply flee directly away from the approacher when they are farther away.

Distance moved

We found distance moved to be positively related to flight initiation distance. Stankowich and Coss (2006) found that flight initiation distance was positively correlated with both starting distance and alert distance in black-tailed deer. Together, these correlations indicate that pre- and postflight decision making are highly interdependent processes where animals that detect and flee from a predator at longer distances also flee longer distances. Taylor and Knight (2003b) found this same result in bison (*Bison bison*) and pronghorn (*Antilocapra americana*), but they found no relationship between distance moved and flight initiation distance in Rocky Mountain mule deer—a different subspecies of mule deer (*O. h. hemionus*) than studied herein (*O. h. columbianus*). A negative relationship between distance moved and flight initiation distance has been found in moose (*Alces alces*; Andersen et al. 1996) and chamois (*Rupicapra rupicapra*; Hamr 1988). A negative relationship would indicate compensation along the attack sequence, whereas a positive relationship indicates that behavior is correlated across situations where individuals that allow close approach also flee relatively short distances. Despite previous exposure to humans that would likely engender habituation, individual differences in flight behavior are probably a combination of the effects of human habituation and individual differences in deer personality or temperament in which general reactivity is an important component (cf., Capitanio 2004). Nevertheless, future tests of compensation and correlation of antipredator behavior across contexts should focus on 1) testing individuals repeatedly to reliably assign reactivity scores to individuals before testing flight responses and 2) testing individuals repeatedly at different alert distances.

Although the dilution of risk in larger groups should lead to shorter flight initiation distances and shorter distances moved, we found that larger groups of deer fled longer distances, a finding consistent with similar findings in caribou (*Rangifer tarandus*) and Rocky Mountain mule deer (respectively, Aastrup 2000; Taylor and Knight 2003b). Whereas Aastrup (2000) attributed this result to increased vigilance in larger groups, Taylor and Knight (2003b) noted that the first-group members to stop running often began running again to catch up with the rest of the group, and larger groups had a greater chance of containing a particularly wary animal that flees longer distances. Finally, Lingle and Wilson (2001) and Dasmann and Taber (1956) predict that larger groups of white-tailed deer and mule deer, respectively, will likely have more animals

that become alert by the behavior of their companions without detecting the predator themselves; this contagion may result in increased wariness in and earlier flight for larger groups. All 3 hypotheses explain why *O. hemionus* flee at greater distances when in larger groups (Taylor and Knight 2003b; Stankowich and Coss 2006), whereas the latter 2 hypotheses address not only the increased flight initiation distances but also the longer distances moved.

Deer that were initially located in grass with scrub fled shorter distances than deer in only grassy areas. Observations that mule deer tend to seek vegetative cover when moving away from a threat (Geist 1981) and that black-tailed deer (*O. h. columbianus*) use hiding during escape more than mule deer (*O. h. hemionus*; Linsdale and Tomich 1953) suggest that the deer examined herein might have fled shorter distances because they were already in relatively dense cover and were satisfactorily hidden from the approacher. Our finding that deer fled to areas with vegetative cover greater than or equal to their original location supports this conclusion and is in agreement with other studies (Linsdale and Tomich 1953; Geist 1981).

Escape style and predator behavior

More threatening approaches led to increased durations of rapid flight by deer (Figure 4a). Few studies have addressed flight duration with respect to level of threat, but Freddy et al. (1986) found that flight responses in mule deer lasted longer when they were approached by a human on foot than a human on a snowmobile; humans on foot were, in general, treated as much more threatening than humans on snowmobiles. More white-tailed deer ran versus walked when approached in hunted areas than in areas where no hunting occurred (Behrend and Lubeck 1968). Furthermore, there is an abundance of evidence that animals flee at greater distances when approached in a more threatening manner (as reviewed in Ydenberg and Dill 1986; Stankowich and Blumstein 2005), and certainly, an animal's flight duration will depend on the duration and intensity of subsequent pursuit by the predator. Nevertheless, our findings provide initial quantitative evidence that variation in preflight predator behavior can influence the duration of the flight response.

Habitat use during flight

Habitat factors had a significant impact on the type and duration of flight behavior exhibited by deer when approached. Deer trotted for longer periods when in shorter vegetation (Figure 4b) and were more likely to stot when in taller vegetation (Table 2). There are 2 possible explanations for this result: 1) stotting behavior in deer aids in traversing tall vegetation quickly and when fleeing through short grass, trotting is more energy efficient and 2) stotting is an "antiambush" tactic to avoid capture by predators that may be hiding in tall vegetation. Regarding the first possible explanation, bounding, stotting, and leaping by ungulates have been shown previously to serve as a means to clear obstacles (Geist 1981; Lingle and Pellis 2002) and as a potential signal to predators of physical ability (reviewed in Caro et al. 2004). Indeed, black-tailed deer aim their flight to put obstacles (e.g., fences, uneven rocky surfaces) between themselves and the approacher or flee to areas with deep vegetation that would both hinder the predator's advance and provide potential refuge (Linsdale and Tomich 1953; Dasmann and Taber 1956; Geist 1981). This supposition is supported by the high frequency of trials in which deer fled to taller vegetation and the shorter distances fled in denser vegetation.

Regarding the second explanation, Pitcher (1979) suggested that the height gained during stotting in gazelles allows fleeing individuals to more accurately scan the surrounding vegetation along the flight path; to date, this hypothesis remains untested. Caro (1986b; p. 657–658) proposed 7 predictions concerning this hypothesis, including 1) “individuals should not stot in short vegetation,” 2) “stotting should increase with vegetation height,” 3) “stotting should not necessarily occur in the presence of predators,” 4) “stotting should be less likely to occur in short flights,” 5) “stots should occur more frequently toward the end of a flight when prey move into a new area,” 6) stotting should be more common “in response to species of predators that use a concealed approach and that normally hunt in groups,” and 7) prey individuals that stot more should “escape capture more easily in medium or tall vegetation.” Our finding that deer stotted more often in taller vegetation provides strong evidence for prediction 2, and, because vegetation measurements were taken at the origin of the deer, we do not know if the 7 occurrences of stotting in 0–1 ft vegetation occurred at the beginning of the trials or later on when they may have reached deeper vegetation (i.e., our data may also support prediction 1). Our data does not support prediction 4 (there was no relationship between distance moved and presence of stotting; Table 1) or prediction 5 (stotting occurred within 5 s of flight initiation in 21 out of 28 cases), and predictions 3, 6, and 7 were not tested in our study. Notably, black-tailed deer mothers sometimes stot back and forth in one place (often around their fawns) while snorting when they have just been exposed to a model puma (Stankowich and Coss 2007) that is no longer visible (i.e., concealed in tall vegetation: Stankowich T, personal observation). In this case, stotting may function as a way to inspect the vegetation from an elevated vantage point in order to locate the ambush predator or even to locate fawns that may be hiding in the area. In sum, this is the first empirical support for the antiambush hypothesis for the function of stotting, but there are likely multiple benefits to stotting, including predator detection and health advertisement (Caro 1986a).

Additionally, evidence of longer trotting durations when fleeing uphill (Figure 4c) suggests that deer will expend the extra energy of longer rapid flight in order to gain an elevation advantage on the approaching predator, which likely affords better visibility as well as forcing the predator to tire more easily. Lingle (2002) found that coyotes were less likely to approach, attack, and capture mule deer that were at progressively higher elevations at the time of the initial encounter, and mule deer moved up slopes if they initially lacked an elevation advantage on coyotes. Although we found that deer moved up slopes more often than expected, deer that detected and fled from the approacher at longer distances were not more likely to flee up slopes than deer that detected the approacher and fled later. Nevertheless, mule deer use of terrain in response to a human will likely differ qualitatively from terrain use in response to coyotes. Therefore, increased elevation is likely to afford a better vantage point for *O. hemionus* in a manner that deters further pursuit by coyotes (Lingle 2002) and possibly pursuit by pumas.

Similar to our finding that deer trot for longer durations when fleeing uphill (presumably to use higher elevation as a refuge), woodchucks have faster escape speeds when they are far from refuge (Kramer and Bonenfant 1997), indicating that animals may not exhibit constant escape speeds when distance to safety is variable. Thus, it is reasonable to speculate that prey might employ a general rule of thumb to keep “time to reach refuge” at a minimum by 1) increasing their escape speeds when far from refuge and 2) reducing escape speeds when refuge is nearby and they are in less danger of being overtaken and captured. In more extreme instances, California

ground squirrels (*Spermophilus beecheyi*) will stop their flight near burrow entrances, turn and monitor the approaching predator, and then enter their burrows with a only few seconds to spare (Owings et al. 1986).

On the whole, this study has demonstrated that factors that influence the decision to flee (e.g., group size, environmental characteristics, and predator behavior) can also have significant impact on flight behavior and escape decisions; and decisions made in early stages of the attack sequence (Endler 1986; Lima and Dill 1990) can have effects on behavior in later stages (Stankowich 2006). We had expected animals that fled at shorter distances to compensate for their increased exposure to danger by fleeing greater distances, as has been found in moose and chamois (Hamr 1988; Andersen et al. 1996). However, we found a positive relationship between distance moved and flight initiation distance, indicating that animals that flee at greater distances move greater distances. Instead of compensatory behavior in the attack sequence (e.g., Lind and Cresswell 2005), our evidence suggests that animals that are relatively wary may flee at greater distances and move greater distances whereas less wary animals may allow the predator to approach more closely and move shorter distances. We found similar relationships between predator approach style/proximity and escape behavior in which deer take a more evasive escape angle when the predator is closer and employ more evasive flight behaviors for greater durations when the predator is approaching in a more threatening manner.

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