

Behavioral Ecology VOLUME 17 NUMBER 2 MARCH/APRIL 2006

ISSN 1045-2249

Behavioral Ecology

VOLUME 17 NUMBER 2 MARCH/APRIL 2006

www.beheco.oxfordjournals.org



OXFORD

The official journal of the
International Society for Behavioral Ecology



OXFORD JOURNALS
OXFORD UNIVERSITY PRESS

Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer

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In predator-prey encounters, many factors influence risk perception by prey and their decision to flee. Previous studies indicate that prey take flight at longer distances when they detect predators at longer distances and when the predator's behavior indicates the increased likelihood of attack. We examined the flight decisions of Columbian black-tailed deer (*Odocoileus hemionus columbianus*) using an approaching human whose speed, directness of approach, directness of gaze, and simulated gun carrying varied. Deer fled at greater distances when approached more quickly and directly, and there was a concave-down quadratic trend in the relationship between the distances at which the predator began its approach and at which the deer became alert (alert distance [AD]), indicating that deer have a zone of awareness beyond which there is a delay in detecting an approaching predator. Time spent assessing the approacher (assessment time) was shorter during faster approaches and was positively related with AD. Deer fled at longer distances and had shorter assessment times when they were already alert to the predator at the initiation of approach. Males fled at shorter distances than females when approached during the gun-holding condition, and males had shorter assessment times than females when the approacher averted his gaze. Such sex differences in risk assessment might reflect male motivation during the mating season as well as exposure to human hunting. We suggest that risk assessment is affected by the predator's behavior, the state of awareness of the prey, and the distance at which they detect the predator. *Key words*: antipredator behavior, deer, flight initiation distance, risk assessment, start distance. [*Behav Ecol* 17:246–254 (2006)]

The decision of when to flee from a potential threat is subject to a high degree of natural selection given that the consequences of making an incorrect decision (i.e., failure to react quickly) can cost an animal its life. Flight initiation distance (FID) is the distance from an approaching threat at which a prey animal moves away/takes flight (see Table 1 for definitions of all terms; Hediger, 1964). According to optimality models (Ydenberg and Dill, 1986), prey animals should minimize the cost of escape by remaining where they are until the potential cost of staying (e.g., potentially being captured and killed) exceeds the costs of escape (e.g., lost feeding and mating opportunities and energy expenditures). The comprehensive review and meta-analyses of the FID literature of Stankowich and Blumstein (2005) suggest that characteristics of predators (e.g., approach speed, directness, predator size), prey (e.g., group size, morphology, experience), and the environment (e.g., distance to refuge) equally affect the perceived level of risk during a given encounter.

One major category of factors that influences FID is the perceived intensity of the predatory threat. Animals may trade off predator avoidance behavior against other activities in a manner that reflects the perceived magnitude of the predatory threat; this has been termed the "threat sensitivity hypothesis" (Helfman, 1989). More specifically, FID should expand progressively with increasing levels of perceived risk, and this relationship is affected by many factors, such as predator and prey traits and behaviors and environmental conditions (Caro, 2005; Stankowich and Blumstein, 2005; Ydenberg and Dill, 1986). It is widely known that predatory animals are not always hunting actively, and their physical posture can

provide clues to their current activity state (e.g., hunting, searching for a mate, resting). To date, one study has directly tested the effects of subtle postural differences in predator behavior (cf., speed and directness) that may indicate "intent" or "motivation" on FID and escape decisions in general but found no effect (Helfman and Winkelman, 1997). Nevertheless, animals can sometimes distinguish between predatory and nonpredatory species with similar appearances (Peckarsky and Dodson, 1980) and between active and inactive predators (Coss and Ramakrishnan, 2000; Dill, 1974). The ability to detect such physical and behavioral variations in predator motivation would be important to risk perception and flight decisions and would likely be adaptive.

FID has been a primary metric in the study of optimal escape theory and risk assessment in general, perhaps due to the ease of measurement, its use as a tool for wildlife managers in developing buffer and setback distances between animal nesting/feeding areas and human visitors (Fernández-Juricic et al., 2001, 2002, 2005; Rodgers and Smith, 1995, 1997), and their use in the assessment of animal welfare states as an indicator of fear or distress (e.g., Dwyer, 2004). However, the amount of time a prey animal spends assessing a potential threat might allow us to gain more insight into how dangerous a prey animal perceives any given threat to be. Many terrestrial animals have distinct alert postures that permit measurement of the actual time spent attending to the approaching threat (i.e., elapsed time between alert posture and flight); we will call this term "assessment time" (Table 1). Fernández-Juricic et al. (2001, 2002) have developed a similar metric "buffer distance," which is the distance between the predator's position when the prey becomes alert and the predator's position when the prey takes flight. Temporal aspects of risk assessment have been measured previously (loom rate: Dill, 1974; time to reach cover: Bonenfant and Kramer, 1996; Dill, 1990; time left before approacher reaches target: Cárdenas et al., 2005), but no study has yet examined the role of assessment time in flight decisions.

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Received 13 June 2005; revised 2 November 2005; accepted 11 November 2005.

Table 1
Definitions of terms used in text and figures

Term	Definition
SD	The distance between the predator and prey at which the predator begins its approach
AD	The distance between the predator and prey at which the prey becomes alert to the predator
FID	The distance between the predator and prey at which the prey initiates flight
Assessment time	The elapsed time between alert posture and flight by the prey
D_{\max}	Distance beyond which animals will not move away from an approaching predator
D_{\min}	Distance less than which animals are constantly aware of and flee from all potential threats
Scanning rate (α)	Rate at which animals make one complete scan of the environment for predators

While continuously monitoring an approaching predator, animals are likely to accrue costs due to time lost foraging, searching for mates, or guarding against intruding conspecifics (Blumstein, 2003). Therefore, we would predict that when a prey animal detects a predator at a greater distance, it should take flight at a greater distance (except in the case of ambush foragers: Cooper, 2005). While the distance between the predator and prey at the initiation of an intruder's approach, termed the "start distance" (SD) (Table 1), positively correlates with FID (64/68 species of Australian birds: Blumstein, 2003); the shape of the relationship is less clear (in 32 and 36 species, respectively, linear and logarithmic functions provided the best fit in species-specific regression models). Previous regression models of the relationship between FID and SD (Blumstein, 2003) have suggested that there are two critical distances (and three resulting zones of response; see Figure 1): (1) a minimum distance (D_{\min} ; Table 1) less than which (Zone I) prey are constantly aware of what other animals are around at all times and will always flee immediately due to an innately triggered flight response (Ellis, 1982) and (2) a maximum distance (D_{\max} ; Table 1), more than which (Zone III) prey will not move away from an approaching pred-

ator due to the following reasons: lack of perceptual capabilities, simply not being attentive to activities beyond this distance, or that they perceive the predator but do not treat it as dangerous. While the relationship between FID and SD is constrained by the fact that FID must be less than SD, optimality theory predicts that FID will increase with SD in a second zone (Zone II) spanning D_{\min} and D_{\max} (Figure 1, Zones I and III; Blumstein, 2003). However, there is no prevailing theory for how prey respond to a predator starting its approach in Zone III.

We hypothesize that the relationship between SD and FID in Zone II might increase initially up to a maximum FID but with the slope leveling off (i.e., an asymptote) or even taking a negative turn (i.e., a concave-down quadratic trend) in Zone III past the SD corresponding to a maximum FID (Figure 1; see solid curves with $D_{\max\text{-low}}$). Depending on the scanning rate (α ; Table 1), predators initiating an approach from outside Zone II are not detected until the prey rescans the area/direction from which the predator is approaching. With the optimal scanning rate (α_1), the prey animal would be able to constantly monitor the surrounding environment in all directions to D_{\max} so that, all else being equal, the prey animal would flee at the maximum FID for any predator SD greater than D_{\max} . Optimal scanning typically does not occur immediately on the predator entering the zone because lone prey or even small groups cannot maintain constant vigilance in all directions at all times. When the scanning rate is suboptimal (α_2), detection may not occur until the predator has come to within a markedly closer distance within Zone II, and because alert distance (AD) is correlated with FID (Blumstein et al., 2005), animals should then take flight at a shorter distance. This would result in a negative relationship between SD and FID at starting distances past D_{\max} (Figure 1; see range of values between α_1 and α_2). Additionally, there may be individual variation in D_{\max} so that some animals may treat a predator as dangerous at longer ($D_{\max\text{-high}}$) or shorter distances ($D_{\max\text{-low}}$) than others. This assessment process might be manifested in ways where some more reactive or less habituated animals are more likely to become alert prior to the initiation of approach at longer distances (Figure 1; dashed line corresponding to $D_{\max\text{-high}}$) than less reactive or more habituated animals (Figure 1; solid line corresponding to $D_{\max\text{-low}}$). We suggest that analyses of risk assessment using FID and assessment time should examine different regression models, both linear and curvilinear, to best describe the relationships between SD, AD, FID, and assessment time (Table 1).

While predator behavior and its effects on FID have been studied in detail in many species, only recently have the effects of interactions among specific predator behaviors on FID been analyzed. As predicted, Cooper et al. (2003) found that Bonaire whiptail lizards (*Cnemidophorus murinus*) had longer FIDs when approached quickly and directly than when approached quickly and indirectly. However, when approached slowly, lizards had longer FIDs during indirect approaches

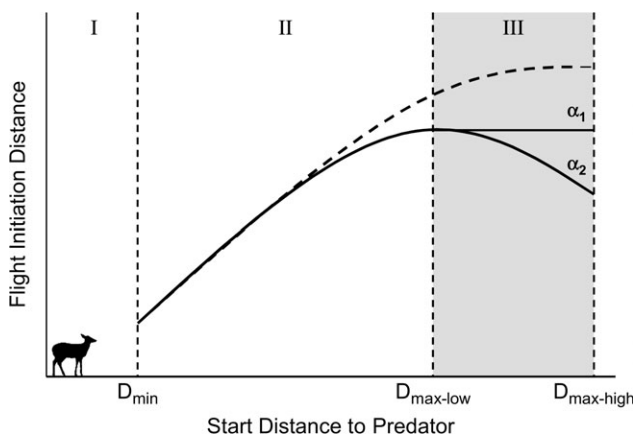


Figure 1
 Predicted relationship between FID and SD (Table 1). Less reactive animals have a shorter distance at which point they begin to treat predators as dangerous (Zone II up to $D_{\max\text{-low}}$) and are depicted by the solid lines that approach a local maximum at $D_{\max\text{-low}}$. Animals vary in their scanning rate from constantly aware of all predators in Zone II (α_1) to slower scanning rates (α_2) where they do not detect an approaching predator until it is further inside Zone II. More reactive animals are more likely to be alert prior to approach at long SDs and are depicted by the dashed line that approaches a local maximum at $D_{\max\text{-high}}$. The range of D_{\max} is depicted in gray, and the three zones described in the text are labeled at the top (I–III) and separated by dashed vertical lines. Note: Zone III extends indefinitely beyond $D_{\max\text{-high}}$.

than direct approaches. In addition to interactions between predator behaviors, we would also expect there to be interactions between prey sex and predator behavior due to sex differences in risk perception (Braña, 1993; Bulova, 1994; Johnson, 1970; Snell et al., 1988). Due to historical sources of selection mainly on male deer by human hunters, many have found that cervids (both male and female) have longer FIDs in areas where hunting activity is greater (de Boer et al., 2004), during the local hunting season (e.g., Behrend and Lubeck, 1968; Dasmann and Taber, 1956), and in response to humans compared to motorized vehicles (e.g., Eckstein et al., 1979; Kucera, 1976; but see Taylor and Knight, 2003).

We conducted experimental human approaches toward Columbian black-tailed deer (*Odocoileus hemionus columbianus*) to determine the degree to which perceived risk and predator motivation affect FID and assessment time. Humans are commonly used as predators in studies of flight decisions and risk assessment (for review, see Stankowich and Blumstein, 2005). While theory would suggest that deer should increase FID in response to increased perceived risk, there is evidence that animals might maintain both spatial and temporal margins of safety (flight decisions based on how far away the predator is and how long it will take for the predator to reach the prey, respectively) and use both in a dynamic way to make flight decisions (Cárdenas et al., 2005). We hypothesize that the typical hunting techniques of modern humans (guns and bows) make the distance between a human and a deer a less reliable metric for deer when making escape decisions. The influence of specific aspects of the predator's approach are likely specific to individual predator-prey relationships (Stankowich and Blumstein, 2005), but general qualitative relationships between SD, AD, FID, and assessment time may be universal for most predators of a given prey species or taxon (e.g., birds; Blumstein, 2003). We also aimed to test several interactions of predator behavior as well as the interaction of prey sex with different human threat postures (approaching while aiming a gun or with an averted gaze) to determine if males and females vary their responses to different kinds of human encounters.

METHODS

We conducted all approaches on free-living adult deer in Point Reyes National Seashore in Marin County, California, USA, between June 2003 and September 2004, although most trials were conducted in the months of August and September. All trials were conducted in open grassland and pasture habitat with no tree cover. The topography of the area consisted of rolling hills with few steep hillsides. All animals in this park have been protected from human hunting for more than 30 years, although illegal poaching has been reported. Thus, while the deer are not as wary of humans as in actively hunted populations, they are not completely human habituated and readily exhibit escape responses (e.g., sprinting, bounding, tail flagging) when approached.

Similar to most studies of wild ungulates, deer were not marked or able to be identified by individual variation in coloration or coat patterns. We were able to distinguish many groups based on their size, composition, and location within the park. If the same group was approached more than once, a member of the opposite sex or a deer that had evident phenotypic differences (e.g., longer antlers, different size) from a previously sampled deer was selected as the new focal deer. Trials on the same group were separated by at least 1–2 weeks. Thus, we have confidence that replication on the same animal was rare.

To measure FID, AD, and assessment time, T.S. as the approacher identified solitary or small groups of deer from the

roadside and positioned himself so he would have a direct line of approach to the deer. T.S. (1.85-m-tall Caucasian male) conducted all approaches and wore the same outfit (green coat, tan pants, dark baseball hat) for each trial. T.S. approached the deer at a constant pace and, using a stopwatch, kept track of when alert and flight responses occurred. When one of these events occurred, T.S. would drop a weighted flag on the ground (for subsequent distance measurements) and record the time of the event keeping the same pace and direction. Alert behavior was defined as the focal deer standing with its head and neck upright and aimed directly at the approacher. The final bout of looking at the approacher before flight is used to measure alertness, and if a deer was already alert prior to the start of the approach, this was noted and no AD was recorded for that trial. Flight consisted of movement away from the deer's original location, ranging from a slow walk to trotting, sprinting, or bounding. Flight behavior necessarily followed alert behavior, although when the approacher was detected at very close distances, flight occurred almost instantly after the focal deer saw the approacher (i.e., FID \approx AD). After flight, the approacher marked the initial location of the focal deer and noted its final location (either where it stopped or where it disappeared from sight). Distances between each weighted flag were measured with a Bushnell Yardage Pro laser rangefinder and were accurate to the nearest 1 m. A second observer, using a Panasonic model PV-DV601D mini digital video recorder with 20 \times optical zoom lens, videotaped all trials from the roadside at a greater distance away in a manner that did not noticeably affect the subjects' behavior. At the end of each trial, we recorded the sex of each deer in the group. Trials were discarded if there was any doubt about the distances and times measured or if the deer were alarmed by a passing car or other provocative situations. Trials were not conducted if the focal deer took flight at a trotting speed or faster prior to the initiation of the approach (i.e., while parking or exiting the car, while turning on the camera, or while the approacher moved to his starting position).

Approaches were varied in four ways. (1) We varied the speed of approach by conducting walking approaches and jogging approaches. (2) We varied the directness of approach by approaching the focal deer on a direct line ("direct") or an indirect line ("indirect") where the approacher aimed his approach to a point approximately 30 m to the left or right of the focal individual. The threat level of the approacher was varied from the above-described walking style (staring directly at the focal deer with arms swinging at side) in two distinct ways. (3) To vary the apparent intent of the approacher and simulate lack of interest toward the deer (low threat), "gaze-averted" trials were conducted where the approacher looked side-to-side at the ground during the approach and his eyes were never visible to the deer—an assistant notified the approacher of when each event occurred using a two-way radio. (4) To simulate hunting behavior (high threat), the approacher aimed a long black rod (resembling a rifle) at the focal deer while walking directly at the focal deer; this was a common technique used by local hunters prior to the ban on hunting in the park (McClure B, personal communication).

Analyses

Prior to analyses, all dependent variables were subjected to a Kolmogorov-Smirnov one-sample normality test, and assessment time was natural log transformed to satisfy normality assumptions. All dependent variables were subjected to curvilinear regressions using SD and AD separately as the independent variables (*stricto sensu* Blumstein, 2003); each

relationship was fitted to linear, quadratic, and cubic models sequentially. If the quadratic term achieved significance (ANOVA *t* test, $p < .05$), the term remained in the model; a cubic model was then fitted, and the cubic term was tested for significance using the same criterion. If a quadratic term did not achieve significance, no cubic term was tested, and the relationship was fitted to linear and logarithmic functions (stricto sensu Blumstein, 2003; n.b., R^2 statistics could not be used to compare quadratic and cubic models to logarithmic and linear models because they contain different numbers of parameters). When comparing linear and logarithmic models, the best-fitted curve was judged first by the R^2 statistic, but if the R^2 statistics were identical, the model producing the most normal residuals (Kolmogorov-Smirnov one-sample normality test) was deemed the best fit. Curves were not forced through the origin because (1) we would expect qualitatively different antipredator responses (e.g., immediate flight) when predators started their approaches from extremely close distances, (2) no trials were conducted with short SDs, and (3) the coefficient of determination (R^2) is meaningless in models forced through the origin (Neter et al., 1996). Consequently, the best-fitted curves are only interpretable in the range of distances tested. When the best relationship was curvilinear, we made the resulting model equation linear by transforming the variables prior to subsequent analyses. We winnowed our list of candidate predictors (e.g., temperature, light level, vegetation type) for FID and assessment time by examining their predictive properties for ungulates in the literature (Stankowich and Blumstein, 2005). The final list of candidate factors were predator speed, directness of approach, presence or absence of an aimed “gun,” predator intent, whether or not the focal deer was alert prior to the initiation of approach, group size, sex, and SD. Due to the large number of possible interactions among factors, we chose to select a subset of interactions of interest that would directly test our initial predictions of sex difference in risk assessment and interactions among predator behaviors (e.g., Cooper et al., 2003). We included the following factor interactions: speed \times directness, directness \times intent, sex \times presence of gun, and sex \times intent. Finally, all factors were entered into a backward-elimination analysis of covariance (ANCOVA) model with a probability to remove of .10 (Neter et al., 1996) with two-tailed significance reached at $\alpha = 0.05$; the least significant available factor was removed at each step (a main effect cannot be removed if it was part of a more significant interaction effect). All data are presented in mean \pm SE. All statistical analyses were conducted in SPSS 10.0.

RESULTS

Alert distance

Focal deer became alert during the course of the approach in 48 out of 78 trials, with the focal deer already being alert before the approach began in the remaining 30 trials. The distance at which the focal became alert was correlated linearly with SD (Pearson's $r = .596$, $R^2 = 0.355$, $p < .001$, $n = 48$), but the cubic function provided the best fit ($R^2 = 0.471$; cubic term: $t = -2.396$, $p = .021$; Figure 2a). While extrapolation outside of the range of measured values is inadvisable, the curve is described by the function: $AD = 132 - 2.32(SD) + 0.02(SD^2) - (4.79 \times 10^{-5})(SD^3)$. The local maximum is located at an SD of 222 m where the predicted AD is 138 m. Because SD and AD are highly correlated and there are many more available observations with SD than AD, we used SD as a covariate in all subsequent analyses of factors influencing FID and assessment time.

Flight initiation distance

Deer fled from the approacher in every trial ($n = 78$), and FID was correlated linearly to SD (Pearson's $r = .364$, $R^2 = 0.132$, $p = .001$, $n = 78$) and AD ($r = .689$, $R^2 = 0.475$, $p = .000$, $n = 48$). The concave-down quadratic function provided the best fit with SD ($R^2 = 0.182$; quadratic term: $t = -2.132$, $p = .036$, $n = 78$; Figure 2b, thick solid curve). This curve is described by the function: $FID = -7.68 + 0.86(SD) - (1.96 \times 10^{-3})(SD^2)$, and the local maximum is located at an SD of 219 m where the predicted FID is 87 m. When trials where deer were alert prior and not alert prior to the start of the approach are analyzed separately, FID showed a quadratic fit when deer were not alert prior [$R^2 = 0.186$; quadratic term: $t = -2.146$, $p = .037$, $n = 48$; function: $FID = -2.78 + 0.76(SD) - (1.95 \times 10^{-3})(SD^2)$; maximum: SD = 194 m, FID = 71 m; Figure 2b, solid thin curve] and a logarithmic fit when deer were already alert [$R^2 = 0.178$; ln SD term: $t = 2.44$, $p = .020$, $n = 30$; function: $FID = 41.36(\ln SD) - 116.72$; Figure 2b, thin dashed curve]. A quadratic function provided the best fit with AD ($R^2 = 0.52$; quadratic term: $t = -2.081$, $p = .043$; Figure 2c). The curve is described by the function: $FID = -17.90 + 1.25(AD) + (3.85 \times 10^{-3})(AD^2)$, and the local maximum is located at an AD of 162 m where the predicted FID is 84 m.

In a backward-elimination ANCOVA where all data were included, five terms were removed (Table 2; $p > .10$) including intent (Figure 3; direct gaze: 73 ± 6 m, $n = 19$, averted gaze: 63 ± 8 m, $n = 16$). Both covariates SD and SD^2 remained in the final model and were significant (Table 2; $p < .05$). We found a strong main effect of approach speed (jogging: 88 ± 5 m, $n = 29$; walking: 73 ± 6 m, $n = 19$) and significant main effects (Figure 3; Table 2; $p < .05$) of directness of approach (direct: 83 ± 4 m, $n = 47$; indirect: 62 ± 5 m, $n = 17$) and alertness prior to approach (alert prior: 92 ± 5 m, $n = 30$; not alert prior: 63 ± 3 m, $n = 48$). The main effects of the presence of gun (Figure 3; holding gun: 59 ± 6 m, $n = 14$; no gun: 74 ± 8 m, $n = 13$) and sex (male: 61 ± 6 m, $n = 16$; female: 77 ± 4 m, $n = 58$) were not statistically significant ($p > .05$) but remained in the final model (Table 2) because we found a statistically significant interaction between them (Figure 4; Table 2; $p = .038$). The presence or absence of a simulated gun had no effect on females (holding gun: 69 ± 8 m, $n = 8$; no gun: 75 ± 9 m, $n = 11$; simple effects: $t = -0.477$, $p = .639$), but males had shorter FIDs when approached holding a simulated gun (holding gun: 46 ± 5 m, $n = 6$; no gun: 71 ± 16 m, $n = 2$; $t = -2.222$, $p = .068$; n.b., only two walking, direct approach, direct gaze, and no-gun trials were conducted on males, which influenced the level of significance). While there were no sex differences in FID when the approacher did not have a simulated gun ($t = -0.151$, $p = .883$), males had shorter FIDs than females when the approacher was carrying a simulated gun ($t = -2.115$, $p = .056$).

Assessment time (T_{assess})

At longer SDs, deer spent more time assessing the approacher than when he began his approach at closer distances. The quadratic term did not explain a significant additional portion of the covariation between assessment time and SD (quadratic term: $t = -0.499$, $p = .670$) or AD (quadratic term: $t = -0.426$, $p = .672$). Of the other models analyzed, the linear model was judged to provide the best fit for SD (Figure 2d; $R^2 = 0.216$) with the model $\ln(T_{\text{assess}}) = 0.79 + 0.004(SD)$. When trials where deer were alert prior and not alert prior to the start of the approach are analyzed separately, FID showed a logarithmic fit when deer were not alert prior [$R^2 = 0.194$; ln SD term: $t = 3.331$, $p = .002$, $n = 48$; function: $\ln(T_{\text{assess}}) = -1.05 + 0.46(\ln SD)$; Figure 2d, thin solid curve] and a linear

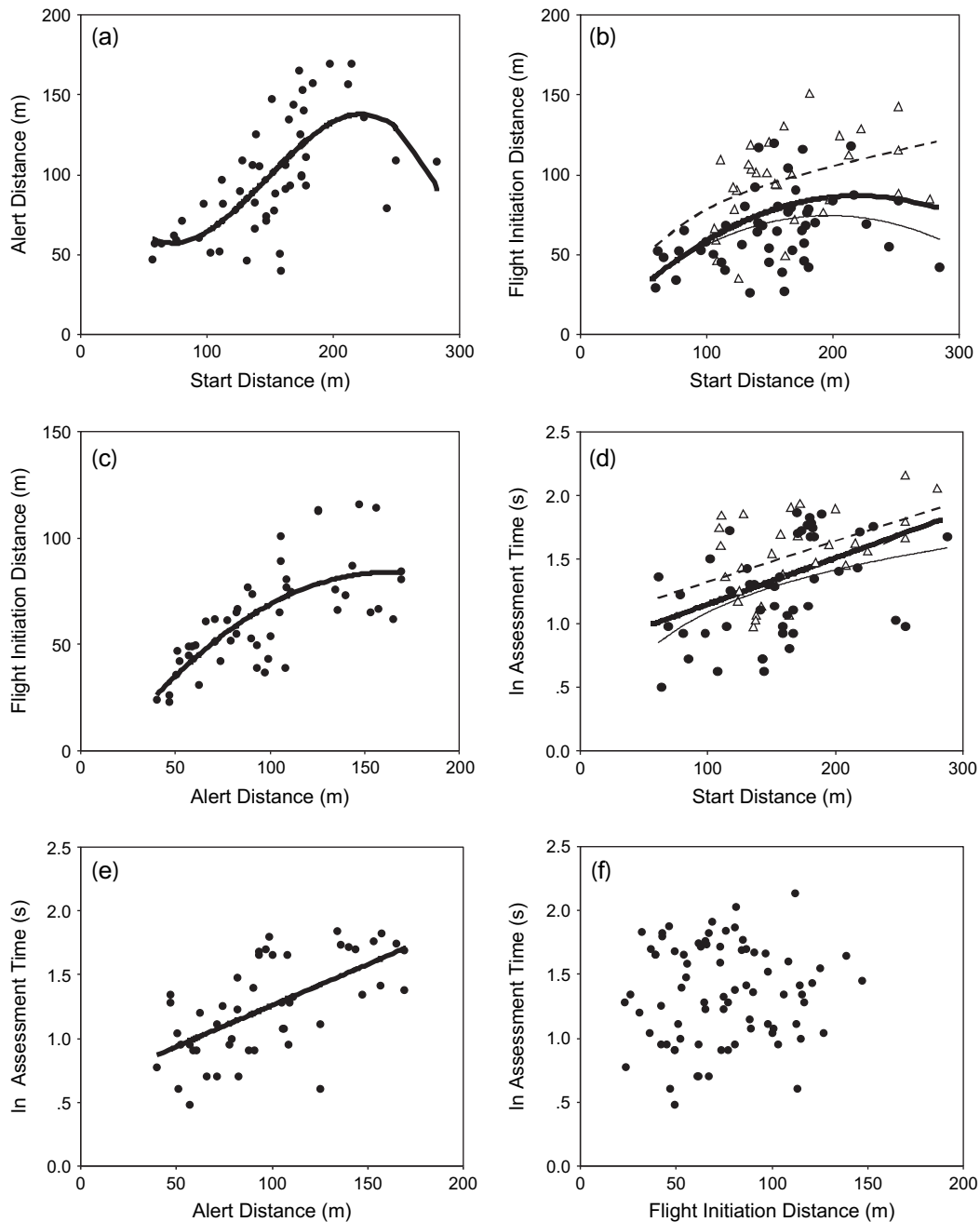


Figure 2

Scatterplots showing relationships between SD, AD, FID, and \ln assessment time (see Table 1 for definitions) of Columbian black-tailed deer responses to an approaching human. In (b) and (d) only, open triangles ($n = 30$) are trials where the focal deer was alert prior to the start of the approach, and closed circles ($n = 48$) indicate trials where the focal deer was not alert prior to the start of the approach. Thick solid curves indicate best-fitted lines of the function that most suitably explained the overall relationship between each pair of variables. Thin dashed curves and thin solid curves in (b) and (d) indicate the best-fitted lines of the functions that most suitably explained the overall relationship between the variables in trials where the focal deer was alert prior and not alert prior (respectively) to the start of the approach. Total sample sizes (n) for each figure are as follows—a, c, e: $n = 48$; b, d, f: $n = 78$.

fit when deer were already alert [$R^2 = 0.237$; SD term: $t = 2.946$, $p = .006$, $n = 30$; function: $FID = 0.99 + 0.003(SD)$; Figure 2b, thin dashed curve]. The linear model was judged to provide the best fit for AD (Figure 2e; $R^2 = 0.379$) with the model $\ln(T_{\text{assess}}) = 0.62 + 0.006(AD)$. Assessment time was not correlated with FID (Figure 2f; $R^2 = 0.003$, $p = .649$, $n = 78$).

In a backward-elimination ANCOVA where all data were included, five terms were removed (Table 2; $p > .10$) including presence of gun (Figure 5; holding gun: 26 ± 6 s, $n = 14$;

no gun: 44 ± 9 s, $n = 13$) and directness of approach (direct: 30 ± 4 s, $n = 47$; indirect: 40 ± 6 s, $n = 17$). Both covariates, SD and group size, remained in the model (Table 2), and while group size approached statistical significance ($p = .085$), SD was strongly associated with assessment time ($p < .001$). We found statistically significant main effects for (Figure 5; Table 2) approach speed (jogging: 22 ± 4 s, $n = 29$; walking: 43 ± 7 s, $n = 19$) and alertness prior to approach (alert prior: 42 ± 8 s, $n = 30$; not alert prior: 25 ± 3 s, $n = 48$).

Table 2
Results of backward-elimination ANCOVAs on factors influencing FID and assessment time

Factor	Order removed	F	p	η ²
FID				
Group size	1	0.191	.664	0.003
Intent × sex	2	0.559	.457	0.009
Speed × directness	3	0.706	.404	0.011
Directness × intent	4	2.336	.131	0.036
Intent	5	0.054	.817	0.001
Presence of gun		0.119	.784	0.096
Sex		0.542	.596	0.352
Approach speed		3.421	.069	0.050
Presence of gun × sex		4.473	.038	0.064
Directness of approach		8.183	.006	0.112
SD ²		8.623	.005	0.117
SD		11.832	.001	0.154
Alert prior		20.229	<.001	0.237
Assessment time				
Speed × directness	1	0.882	.351	0.014
Directness × intent	2	0.611	.438	0.010
Presence of gun × sex	3	1.294	.260	0.020
Presence of gun	4	0.296	.588	0.005
Directness of approach	5	2.260	.138	0.034
Intent		0.009	.939	0.009
Sex		0.199	.732	0.165
Group size		3.054	.085	0.044
Intent × sex		5.985	.017	0.083
Alert prior		25.745	<.001	0.281
Approach speed		27.952	<.001	0.298
SD		44.472	<.001	0.403

Statistics given for factors removed are reported from the step before they were eliminated from the model. *p* to remove = .10.

The main effects of intent (direct gaze: 43 ± 7 s, *n* = 19 vs. averted gaze: 40 ± 6 s, *n* = 16) and sex (male: 33 ± 7 s, *n* = 16 vs. female: 32 ± 3 s, *n* = 58) were not statistically significant (*p* > .05) but remained in the final model (Table 2) because we found a statistically significant interaction among them (Figure 6; *p* = .017). There was no statistically significant effect of gaze aversion on assessment time in males (direct gaze: 36 ± 10 s, *n* = 4 vs. averted gaze: 13 ± 3 s, *n* = 3; simple effects: *t* = 1.522, *p* = .189; n.b., only seven walking, direct approach, and no-gun trials were conducted on males, which influenced the level of statistical significance) or females (direct gaze: 45 ± 8 s, *n* = 15 vs. averted gaze: 47 ± 7 s, *n* = 13;

t = -0.217, *p* = .830). Additionally, males assessed an approacher significantly shorter than females when the approacher's gaze was averted (*t* = -2.414, *p* = .030) but not when his gaze was directed at them (*t* = -0.526, *p* = .606).

DISCUSSION

As was predicted, FID varied widely depending on the style of predator approach, the SD of the approacher, the AD in response to the approacher, and the state of awareness of the deer. Within the range of starting distances tested, we found that AD and FID increased with starting distance then decreased slightly or leveled off at the longest starting distances tested (Figure 2a,b). The presence of the local maximum in the final cubic model (Figure 2a) and a maximum observed AD (169 m) indicates that deer maintain vigilance in an approximate “zone of awareness” (Zones I and II). At very long SDs, deer that were not alert prior actually took flight at distances less than the maximum FID (Figure 2b, thin solid line). When deer were alert prior to the start of the approach, the relationship between FID and SD was logarithmic with FID beginning to asymptote at greater SDs (Figure 2b, thin dashed line). This contrast in relationships suggests that there is individual variation in *D*_{max} (Figure 1) where possibly more reactive or less habituated animals (i.e., those that were already alert prior to approach from long SDs) may treat predators appearing at very long distances (*D*_{max-high}; Figure 1) as more dangerous than less reactive animals (i.e., those that were not alert prior to approach at long distances). This difference in behavioral type and alertness results in longer overall FIDs (Figure 3) and a qualitatively different flight response at long SDs (Figure 2b) in animals alert prior to the start of approach. Therefore, *D*_{max} is likely to vary in a given species where animals have different zones of awareness, beyond which they may detect predators but do not treat them as dangerous. It is apparent that assessment time has a positive linear relationship with both SD (Figure 2d) and AD (Figure 2e); albeit the difference in this relationship from when deer are alert prior versus not alert prior appears to be minor and difficult to interpret in the range of SDs measured. Because assessment time and FID are not correlated reliably (Figure 2f), then the relationship between FID and AD follows a similar quadratic trajectory (Figure 2c) and levels off at greater ADs. Cárdenas et al. (2005) found that galahs (*Cacatua roseicapilla*), once alerted, permitted approach to almost half the AD; our finding of a nonlinear relationship between AD and FID suggests that deer maintain a spatial margin of safety in a qualitatively different way.

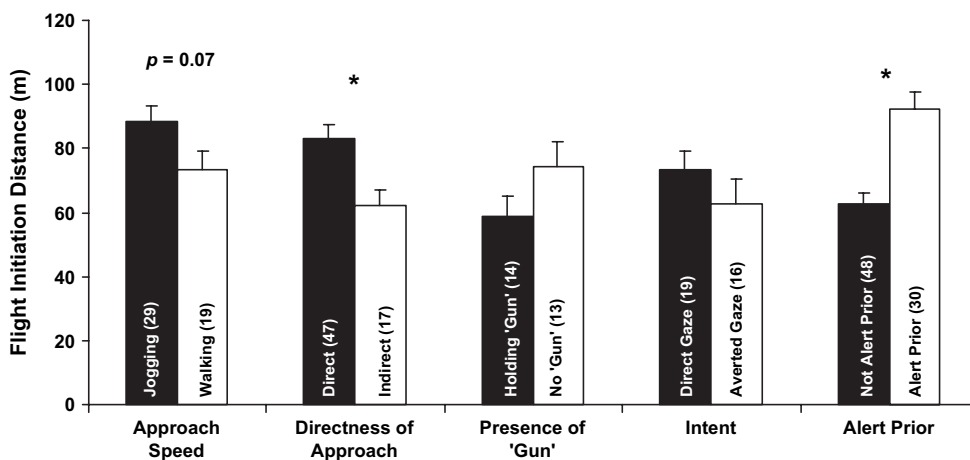


Figure 3
 Mean ± SE FIDs (Table 1) of Columbian black-tailed deer in response to different types of approaches of a human; the figure shows responses to the different factors included in the ANCOVA analyses. Pairs of bars do not include multiple levels of other factors that were only examined in one member of the pair; for example, in approach speed, walking only includes trials with no gun and direct gaze because the presence of gun and intent were only varied in walking trials. Sample sizes (*n*) for each bar are in parentheses inside the bar. **p* < .01

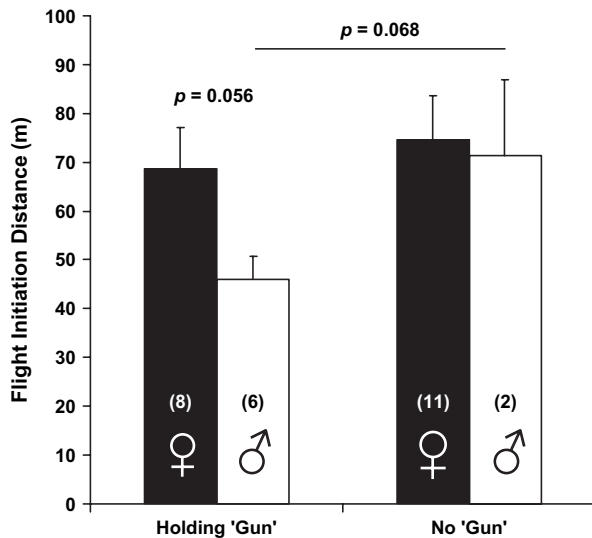


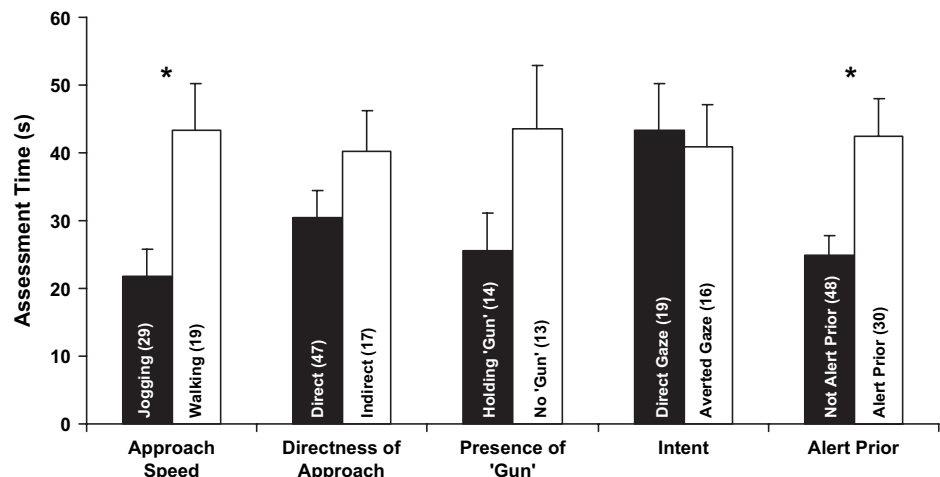
Figure 4
Mean \pm SE FIDs (Table 1) of male and female Columbian black-tailed deer in response to the presence or absence of a simulated gun during the approach (walking directly with direct gaze) of a human. The overall interaction of sex and the presence of gun was statistically significant ($p = .038$). Sample sizes (n) for each bar are in parentheses inside the bar.

As predicted by the threat sensitivity hypothesis (Helfman, 1989), we found strong main effects for both approach speed and directness of approach on FID (Figure 3), with faster and more direct approaches eliciting flight at greater distances. But while FIDs were greater in trials where gaze was directed (Figure 3) compared with gaze-averted approaches, this effect was not reliably distinguishable. On the whole, these findings indicate that some predatory behaviors are indeed perceived as threatening by prey. The prey, in turn, diminish levels of threat by immediately increasing their distance from the predator. This finding is ubiquitous in the literature across many taxa (Caro, 2005; Stankowich and Blumstein, 2005; Ydenberg and Dill, 1986). The finding of no reliable statistical effect of group size on FID is contrary to the results of nearly all ungulate studies. Large groups of mountain sheep (*Ovis canadensis*: MacArthur et al., 1982) and fallow deer (*Dama dama*: Recarte et al., 1998) were less frightened than small groups,

as measured, respectively, by their lower heart rates and decreased likelihood of flight. Large groups of roe deer (*Capreolus capreolus*), fallow deer (de Boer et al., 2004), and caribou (*Rangifer tarandus*: Aastrup, 2000) had greater flight distances than small groups or lone individuals, but Matson et al. (2005) found significantly greater FIDs for small groups of impala (*Aepyceros melampus*). Indeed, the effect of group size on FID varies widely across species and taxa; some species show a positive effect of group size, some show no effect, and still others show negative effects (Stankowich and Blumstein, 2005). Further, we found a strong trend for lower assessment times in larger groups. One explanation for this result is that black-tailed deer are more "irritable" at greater population densities (Dasmann and Taber, 1956), and the flight of one deer is typically contagious, initiating flight in the rest of the group (Stankowich T, personal observation). Thus, when vigilance duties are shared in a group and the likelihood of early detection increases, the increased probability of the presence of "reactive" or less habituated deer should result in earlier flight of that individual followed by the entire group.

To our knowledge, our research on Columbian black-tailed deer is the first study to examine the role of assessment time in flight decisions. As predicted, we found that deer spent reliably more time assessing an approaching threat when they perceived less risk. The mean assessment time was greater for each less threatening approach condition than its more threatening counterpart except for intent (Figure 5), although the effect was only statistically reliable for approach speed. Interestingly, the deer spent longer assessing the threat when they were alert prior to the initiation of the approach. The likely explanation for this effect is that, if deer observed the approacher during experimental setup (e.g., getting out of the car and getting into position), they would have received more information from the approacher in a nonthreatening context. This contradictory information might engender latent inhibitory properties (Mackintosh, 1973) that would require a longer reappraisal period to be overcome if the perceived context became threatening. Conversely, if the only knowledge of the new threat was that something large was suddenly approaching them, there would be no inhibition to counteract, and the surprising aspects of this encounter would be more immediately evocative. From a noncausal Bayesian perspective, this new information decreases the a priori probability that the human is a threat, and it takes more information (i.e., more time) to increase the probability that the human is a threat to the threshold level for flight.

Figure 5
Mean \pm SE assessment times (Table 1) of Columbian black-tailed deer in response to different types of approaches of a human; the figure shows responses to the different factors included in the ANCOVA analyses. Pairs of bars do not include multiple levels of other factors that were only examined in one member of the pair; for example, in approach speed, walking only includes trials with no gun and direct gaze because the presence of gun and intent were only varied in walking trials. Sample sizes (n) for each bar are in parentheses inside the bar. * $p < .001$.



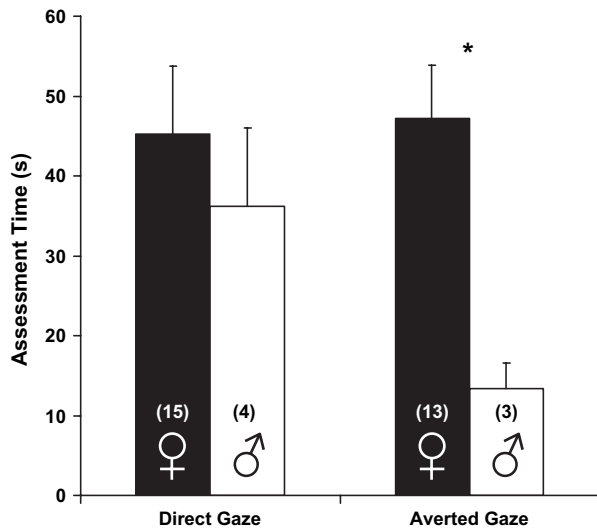


Figure 6
Mean \pm SE assessment times (Table 1) of male and female Columbian black-tailed deer in response to direct or averted gaze by a human approacher (walking without holding a gun). The overall interaction of sex and intent was statistically significant ($p = .017$). Sample sizes (n) for each bar are in parentheses inside the bar. * $p < .05$.

Red deer (*Cervus elaphus*) have been found to perceive humans in a recreational context as less threatening than humans in a hunting context and spend more time being vigilant and less time feeding during the hunting season (Jayakody S, Sibbald AM, Lambin X, Gordon IJ, unpublished data). Specifically, hunting activity should encourage targets of hunting to perceive greater risk from an approaching human and have shorter assessment times and longer FIDs (but see Grau GA and Grau BL, 1980). Many game bird species (Fox and Madsen, 1997; Madsen, 1985; Smit and Visser, 1993) have longer FIDs during months when hunting is permitted compared with other months, and white-tailed deer (*Odocoileus virginianus*) increase their avoidance response toward humans at progressively longer distances over the course of the hunting season (Grau GA and Grau BL, 1980). Alpine marmots (*Marmota marmota*), moose (*Alces alces*), impalas, roe deer, and caribou in hunted areas have longer FIDs than like individuals in areas where there is little or no hunting (Louis and Le Berre, 2000; Altmann, 1958; Matson et al., 2005; de Boer et al., 2004; Aastrup, 2000, respectively). Our findings, to some extent, contradict this evidence.

While the deer in this population are not currently under sex-based selection from human hunting (hunting of *O. h. columbianus* has been banned in the park since 1971), clearly there are sex-based differences in risk perception by other species when they are faced with an approaching human (Braña, 1993; Bulova, 1994; Johnson, 1970; Snell et al., 1988). In certain instances, female cervids appear to show more fear of approaching humans than males do (Bullock et al., 1993; Jeppesen, 1987), but this effect is not ubiquitous (Behrend and Lubeck, 1968; de Boer et al., 2004).

We found no statistically significant main effects for prey sex, the presence of a simulated gun, or predator intent on FIDs or assessment time. Because males historically were the main hunting targets, males should have fled at longer distances in response to a human holding a gun and assessed a gaze-averted approacher for a longer period of time. However, we found that males approached with an aimed gun allowed the predator to approach closer than males ap-

proached without a gun and females approached with a gun (Figure 4). While there were no sex differences in assessment time when the approacher's gaze was directed at the deer, males spent less time assessing than did females when gaze was averted and males when gaze was directed, although the latter result was not statistically significant (Figure 6; $p = .189$) due to small sample sizes. One possible explanation for the sex differences in FID in response to a gun is that aiming a gun while approaching results in a rigid upper body with fluid, moving legs, and because gun trials were conducted during the early stages of the male rut, males may have mistaken the approacher initially as another male deer or another displaying animal attempting to displace him from his territory or separate him from a group of females. If rutting males have a significant interest in maintaining rank and status among the other males in a particular area, they may allow closer approach to get a better look at the threat. Alternatively, males may allow closer approach when approached with a gun because they were unfamiliar with gunlike objects due to the absence of hunting and treated them as objects of curiosity; however, it is unclear why females should not show the same response.

Findings of Cooper et al. (2003) of interactions between predator approach speed and directness of approach demonstrated that prey lizards switch antipredator tactics and assessment algorithms depending on the behavior of the predator. When approached directly, no matter the speed, lizards may view themselves as a likely target of the predator. However, if approached slowly and indirectly, lizards might determine that they are not likely the target and flee at greater distances, wasting less time assessing the threat to avoid being located by the approacher at closer distances. While our study did not find any evidence in deer of an interaction between predator speed and directness of approach, the lizards' behavior may bear on our conclusions about male behavior during gaze-averted trials (Figure 6). Changes in gaze might signify interest or lack of interest by both conspecifics and other species (cf., Coss, 1978; Coss et al., 2005), with animals becoming much less concerned when another individual's attention is diverted elsewhere. If males view a gaze-averted approacher as a potential predator that has not seen them, they may forego prolonged assessment of the threat and decide to take flight before being seen. However, when the approacher directs its gaze at the male deer, normal assessment algorithms set in and they may decide to hold their ground for longer and evaluate the approacher's intentions. That this interaction was not present for FID suggests that, for males making flight decisions, perhaps the distance they are from the predator is less important than gaining an accurate assessment of the predator's motivational state. As apparent in our experimental manipulations, assessment algorithms involve more complex dynamics than simple cost-benefit relationships between distance to safety, speed of escape, and distance to predator.

This research was supported by a Humanities Research Grant and CAB Research Fellowship to T.S. and a faculty D-grant to R.G.C. from The University of California, Davis. We thank E. Arnett, J. Vargas, S. Evanger, J. Angus, L. Rabin, M. Wyman, and J. Wammock for assistance during data collection; M. Watnik and P. Burman for statistical advice; D. Blumstein, A. Bourke, L. Rabin, and two anonymous reviewers for providing comments on a previous version of this manuscript; all the ranches at Point Reyes National Seashore for permission to work on their land; and B. McClure, V. Geist, S. Lingle, and T. Caro for logistic and theoretical input during the planning stages. We are grateful to the National Park Service for providing space to stay while in the field. This work was conducted under research permits from the California Department of Fish and Game (803043-05) and the National Park Service (03-0024).

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