

**Predator Recognition, Risk Assessment, and Antipredator Behavior in
Columbian Blacktailed Deer**

By

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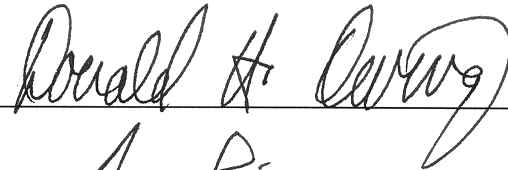
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ABSTRACT

During any encounter with a predator, prey animals must recognize the predator as potentially dangerous, assess the threat level imposed by that individual predator, decide when to flee, and flee in a manner that provides the best probability of successful escape. Natural selection acts on each aspect of prey antipredator behavior, and variation in predator appearance and behavior interact dynamically with individual variation in prey reactivity to produce significant variation in antipredator responses on which selection can act. When a previously common predator disappears due to local extinction, selection on recognition of that predator becomes relaxed, and systems involved in predator recognition can disintegrate. In Chapter 1, using predator models, I show that Columbian blacktailed deer (*Odocoileus hemionus columbianus*) exhibit a more rapid and stronger antipredator response to their current predator, the puma, than to a leopard displaying primitive rosettes similar to a locally extinct felid predator, an early jaguar. Presentation of a novel tiger with a striped coat engendered an intermediate speed of predator recognition and strength of antipredator behavior. The response to the leopard model slightly exceeded that of a nonthreatening deer model, suggesting that thousands of years of relaxed selection have led to the loss of recognition of the spotted coat as a jaguar-recognition cue, and that the spotted coat has regained its ability to camouflage the felid form. Many studies have used flight initiation distance (the distance between predator and prey at which the prey flees) as a proxy for fearfulness and examined the factors influencing the decision to flee. In Chapter 2, I conducted an extensive review and formal meta-analysis of the flight initiation distance literature, and I found that predator traits that were associated

with greater risk (speed, size, directness of approach), increased prey distance to refuge, and experience with predators consistently amplified the perception of risk. While fish tolerated closer approach when in larger schools, other taxa had greater flight initiation distances when in larger groups. The presence of armored and cryptic morphologies decreased perception of risk. I find that selection generally acts on prey to be sensitive to predator behavior, as well as on prey to modify their behavior and morphology. In an attempt to test a subset of these results empirically, in Chapter 3, I examined the flight decisions of blacktailed deer using an approaching human that varied in speed, directness of approach, directness of gaze, and simulated gun carrying. Deer fled at greater distances when approached more quickly and directly, and there was a concave-down quadratic trend in the relationship between starting distance and alert distance, indicating that deer have a zone of awareness beyond which there is a delay in detecting an approaching predator. Assessment time was shorter during faster approaches and was positively related with alert distance. Deer fled at longer distances and had shorter assessment times when they were already alert to the predator at the initiation of approach. These results suggest that risk assessment is affected the by the predator's behavior, the state of awareness of the prey, and the distance at which they detect the predator. Finally, the relationship between risk assessment by prey and the escape behaviors they perform while fleeing from predators is relatively unexplored. In Chapter 4, I examined escape angle, distance moved during flight, duration of trotting and stotting behavior, and change in elevation during flight in blacktailed deer. At short flight initiation distances, deer fled relatively greater distances and took flight paths at more acute angles, a property that

would force a real predator to change direction suddenly. My results indicate that distance moved and flight initiation distance are linked by the traits of reactivity and habituation: more reactive or unhabituated 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, and deer tended to flee uphill and into taller vegetation, using these landscape features as refuge from danger. In summary, by focusing on risk assessment across the attack sequence and on relaxation in selection on visual predator recognition, this dissertation elucidates the ecological and evolutionary factors that influence the cognitive processes involved in cervid antipredator behavior.

PREFACE

Animals have evolved a wide variety of morphological adaptations and behavioral tactics to help them avoid predators, warn conspecifics about the presence of predators, deter their attack, and escape during pursuit. The past twenty-five years of antipredator research have taught us about the evolution and economics of vigilance behavior, about how prey animals use specific cues to recognize their predators, and even about the sometimes dramatic strategies prey use to flee during an attack. Much of this research has been reviewed in recent books on antipredator behavior (Barbosa & Castellanos 2005; Caro 2005; Lima 1998; Lima & Dill 1990). While we know a great deal about how prey assess ambient predation risk (*e.g.*, dynamic hazard assessment: Bouskila & Blumstein 1992; giving up densities: Brown 1988; reviewed in Lima & Steury 2005) there have actually been relatively few advances in recent years in our knowledge of *how* prey recognize and assess risk during actual encounters with predators (but see the elegant series of papers on ground squirrel risk assessment during encounters with rattlesnakes: Rowe & Owings 1990; Rowe & Owings 1996; Swaisgood *et al.* 1999a; Swaisgood *et al.* 1999b; Swaisgood *et al.* 2003). In this dissertation, I have focused on these processes in Columbian blacktailed deer (*Odocoileus hemionus columbianus*), specifically the visual cues used in predator recognition and the factors that influence risk assessment.

Lima and Dill (1990) outlined stages in a theoretical predator attack sequence (summarized in Fig. 0.1) and suggested that prey aim to halt the attack sequence at each stage while predators aim to proceed until a capture has been made. Initially, when prey detect another animal in their environment, they must process what they

see, smell, or hear and match its characteristics with those of the species that it knows to be either safe or dangerous. The more closely the animal's configuration matches known species, the more quickly recognition will occur. Speed and accuracy in recognition of predators is crucial for successfully avoiding capture and we can measure recognition speed using the latency to perform relevant antipredator behaviors (*e.g.*, Coss & Ramakrishnan 2000). Chapter 1 discusses the role of predator camouflage in predator recognition and how relaxation of selection from a particular predator for thousands of generations can result in loss of visual predator recognition.

Once the predator has been recognized as a potential threat, if there is sufficient distance between them, the prey animal will begin to assess the potential threat posed by this predator using factors like predator behavior, distance to the predator and to refuge, the size of their own group, and even their own physical condition. Some animals may perform antipredator behaviors (like alarm calling or visual displays) that reflect fearful emotions and, in the simplest context, provide cues available for assessment by eavesdroppers. Other displays are targeted towards conspecifics to warn them of the presence of a predator, are directed at the predator to dissuade it from attacking, or lead the predator away from vulnerable offspring, as in distraction display. If the predator continues to approach, the prey must, at some point, make the decision to flee. Chapter 2 presents a formal review and meta-analysis of the literature on flight initiation distance, a common metric for studying fear and flight decisions (Ydenberg & Dill 1986). In collaboration with Dr. Daniel Blumstein of the University of California, Los Angeles, this chapter has been published in full in the *Proceedings of the Royal Society B* (Stankowich & Blumstein 2005). Chapter 3

then builds on this work by testing the effect of variation in predator behavior on flight decisions in deer. This chapter has also been published in full in *Behavioral Ecology* (Stankowich & Coss 2006) and a photograph I took of a blacktailed deer appears on the cover of that issue of the journal (Vol. 17, Issue 2). During flight, prey use a variety of tactics to successfully avoid capture and reach safety. Chapter 4 explores these escape tactics in deer and how their performance might be linked to pre-flight risk assessment.

Clearly, this attack sequence is very general and the true sequence of events varies widely based on the species involved. One of the general goals of this dissertation is to illustrate how the different stages are all linked, earlier events like predator behavior and their response to antipredator behaviors surely influence the choices prey make during escape. However few studies have actually examined these links and their effects on behavior. I have done so, inferring such early-sequence cognitive processes as recognition and risk assessment by measuring variation in behavior later in the sequence and correlating it with the animal's initial experiences during the encounter (Lima & Steury 2005). I hope this work will serve as a springboard for future work on predator recognition, risk assessment, and the role of individual variation in the expression of behavior. More specifically, there is an important need to integrate information on how individual variation in temperament or more complex behavioral syndromes affect the expression of antipredator behavior during encounters with familiar and novel predators.

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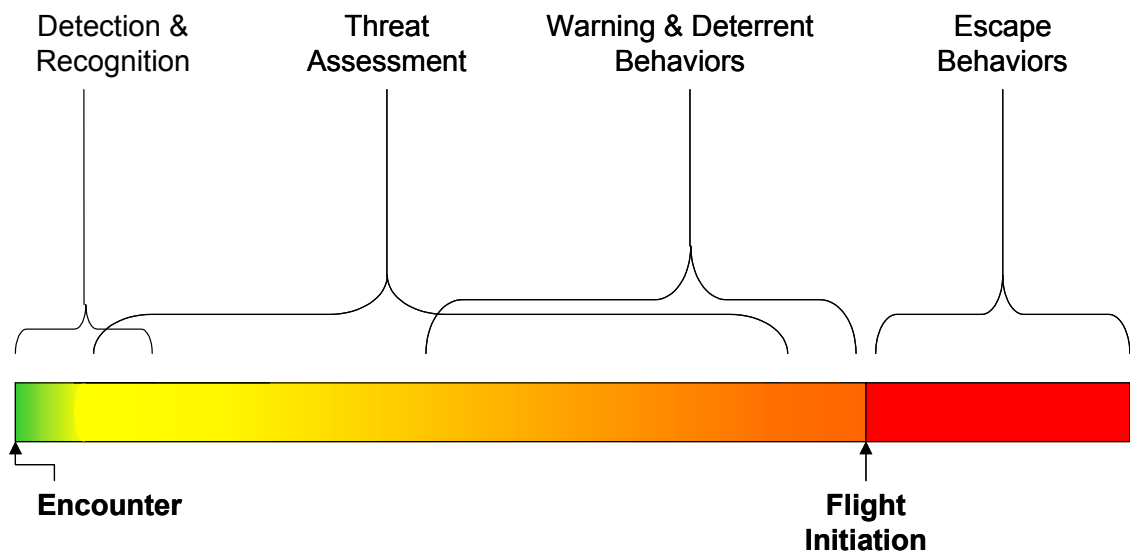
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FIGURE 0.1



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CHAPTER 1

The Re-emergence of Felid Camouflage With the Decay of Predator Recognition Under
Relaxed Natural Selection

ABSTRACT

Consistent predation by a particular predator exerts a strong source of natural selection on prey to rapidly recognize that predator and behave appropriately. When a previously common predator disappears due to local extinction, selection on visual, olfactory, and auditory recognition of that predator becomes relaxed, and sensory modalities involved in predator recognition may be more susceptible to disintegration. At present, we do not know the extent to which recognition of a specific predator is generalized to similar looking predators or how a specific predator recognition cue, such as coat pattern, degrades under prolonged relaxed selection. Using predator models, I show that deer exhibit a more rapid and stronger antipredator response to their current predator, the puma, than to a leopard displaying primitive rosettes similar to a locally extinct felid predator, an early jaguar. Presentation of a novel tiger with a striped coat engendered an intermediate speed of predator recognition and strength of antipredator behavior. The response to the leopard model slightly exceeded that of a nonthreatening deer model, suggesting that thousands of years of relaxed selection have led to the loss of recognition of the spotted coat as a jaguar recognition cue, and that the spotted coat has regained its ability to camouflage the felid form. My results shed light on the evolutionary arms race between adoption of camouflage to facilitate hunting and the ability of prey to quickly recognize predators by their formerly camouflaging patterns.

INTRODUCTION

Ungulates are morphologically and behaviorally adapted to react quickly to the presence of predators and escape capture using effective flight strategies. While morphological adaptations for rapid, prolonged flight appear to be retained for thousands of generations despite the local extinction of most major predatory species (Byers 1999), olfactory and auditory recognition appear to disintegrate rapidly in the absence of predators (Blumstein 2002). Berger and colleagues found that populations of moose (*Alces alces*) that were lacking predators for as few as 50 to 130 years showed reduced responses to auditory and olfactory predator cues compared with predator-experienced moose (Berger *et al.* 2001). Similarly, predator-naïve tammar wallabies (*Macropus eugenii*) and red-necked pademelons (*Thylogale thetis*) did not alter feeding behavior in the presence of formerly-relevant predator odors compared with control conditions (Blumstein *et al.* 2002). However, both studies suggested that these sensory abilities can be restored in as little as one generation, presumably by learning about predators. When presented with purely visual stimuli, some mammals show evolutionary persistence of predator recognition after an estimated 300 thousand years (kyr) of prolonged relaxed selection (Coss 1991; Coss 1999), albeit with complete decay of predator recognition in 3 to 5 million years (Myr) (Goldthwaite *et al.* 1990). However, there is evidence that tammar wallabies that have been isolated from predators for only 130 years showed a loss of visual predator recognition (Blumstein *et al.* 2004).

The multi-predator hypothesis (Blumstein 2006; Blumstein *et al.* 2004) predicts that antipredator behavior toward a particular predator may be maintained if prey continue to encounter a similar predatory species. While there is evidence to support

the multi-predator hypothesis (Blumstein & Daniel 2003; Blumstein *et al.* 2004), selection from specific predators can be unbalanced in contexts in which one of two historical predators disappears. For instance, wild-caught California ground squirrels (*Spermophilus beecheyi*) that recently colonized a rattlesnake-rare site did not differentiate the venomous rattlesnake (*Crotalus oreganus*) and nonvenomous gopher snake (*Pituophis melanoleucus*), whereas ground squirrels whose ancestors had experienced more prolonged relaxed selection from rattlesnakes were more aggressive toward their extant gopher snake predator (Coss *et al.* 1993). My present research on Columbian blacktailed deer (*Odocoileus hemionus columbianus*) examines a similar phenomenon in which one of two large, distinctively looking felid predators becomes extinct locally, yielding prolonged relaxed selection on recognition of the extinct predator in a time frame spanning hundreds of thousands of years.

Time scale of relaxed selection on predator recognition

In North America, the late Hemphillian fossil record (Barnosky & Shabel 2005; Morgan & Lucas 2003; Woodburne & Swisher 1995) suggests a long history of felid-deer interactions and strong natural selection for rapid recognition of danger by deer. The first wave of immigration of Odocoileini cervids from Asia to North America via Beringia occurred during the late Hemphillian about 5.5 Myr ago followed by the immigration of true *Odocoileus* during the early Blancan (Morgan & Lucas 2003; Woodburne & Swisher 1995). These early North American immigrants would have encountered several of their former Asian felid predators (*Homotherium*, *Machairodus* and *Megantereon*). *Odocoileus* deer have been in contact with extant pumas (*Puma concolor*) almost continuously since the middle Pleistocene (Barnosky & Shabel 2005;

Simpson 1941; Stock 1918). However, a genetic study suggests that North American pumas became extinct during the end of the Pleistocene, an event followed by rapid recolonization by a small number of founders (Culver *et al.* 2000). If this extinction event did occur, then blacktailed deer might have experienced a brief period of relaxed selection from all large felid predators.

Ancestral jaguars (*Panthera* aff. *P. gombaszoegensis*) immigrated from Asia during the early Pleistocene and co-occur with *Odocoileus* ~1.6 million years ago in California (Firby 1968; Kurtén & Anderson 1980; Sarna-Wojcicki 1976; Savage 1951). Some contact between jaguars and the ancestors of blacktailed deer might have occurred in Washington ~610 kya and Oregon during the late Irvingtonian to early Rancholabrean (Elftman 1931; Gustafson & Fry 1974; Simpson 1941), but sympatry this recent is ambiguous at best. The distribution of fossil sites exhibiting the large jaguar (*P. onca augusta*) indicates a progressive regression of the distribution of jaguars from the Northwestern USA in the late Irvingtonian to the Southwestern USA in more recent times (Daggett & Henning 1974; Seymour 1989). Genetic analysis coupled with the fossil record suggests that the mule deer (*O. hemionus*) progenitor of blacktailed deer diverged from whitetailed deer (*O. virginianus*) approximately 2.8 Myr ago (Pitra *et al.* 2004), following which *Odocoileus* along the Northern and Southern California coast were isolated by the onset of drainage of the Sacramento River through the San Francisco Bay, ~725 kyr ago (Smith & Coss 1984). Such a barrier to gene flow led to the genetic divergence of mule deer (*O. h. californicus*), blacktailed deer (*O. h. columbianus*), and pumas along the California coast (Carr & Hughes 1993; Ernest *et al.* 2003) and the isolation of blacktailed deer in Northwestern California and jaguars in Southern California where they were already rare in the late Pleistocene (Jefferson

1983). Viewed together with the jaguar fossil record, the mule deer ancestors of blacktailed deer were likely prey of early jaguars for possibly 1 Myr before gene flow along the California coast was disrupted.

Camouflage and Predator Recognition

Studies of the camouflaging properties of felid coats (Cott 1940; Mottram 1915; Ortolani 1999) suggest that vertical stripes should afford concealment in habitats where tall grass or reeds predominate. “Obliterative shading” is produced by a darker dorsal and lighter ventral coat to diminish perception of the cylindrical form. However, the obliterative shading of jaguars and leopards is much less pronounced than tigers, but the rosettes of these cats might produce the functional equivalent of obliterative shading by a dorsal-to-ventral lightening of color patches within the center of these rosettes (Mottram 1915). Ironically, rather than acting as camouflage, the repetitive texture of the leopard’s spotted coat is highly salient to a variety of prey, including cervids, suggesting that an evolutionary arm’s race has unfolded in which the presumed original camouflaging function the spotted coat has now become a major leopard-recognition cue by prey. For example, presentations of realistic models of a spotted leopard generated rapid and vigorous alarm calling by wild sambar deer (*Cervus unicolor*), chital deer (*Axis axis*), Malabar giant squirrel (*Ratufa indica*), Nilgiri langurs (*Trachypithecus johni*), and Hanuman langurs (*Semnopithecus entellus*), and even captive-born female rhesus macaques (*Macaca mulatta*) and inexperienced urban bonnet macaques (*M. radiata*) (Coss & Ramakrishnan 2000; Hollis-Brown 2005; Ramakrishnan & Coss 2000a; Ramakrishnan & Coss 2000b). Further, bonnet macaques recognized leopards partially obscured by vegetation predominantly by their

spotted, yellow coat (Coss *et al.* 2005). Together, these results suggest that rather than having camouflaging properties, the pattern regularity of the spotted yellow coat is highly conspicuous among species that have coevolved with leopards for thousands of generations. Therefore, a 1 Myr time frame of predation by jaguars on deer was probably sufficient for the evolution of jaguar-specific recognition in which the jaguar's coat pattern of flecks and rosettes would have become an important jaguar recognition cue.

Rationale and Hypotheses

The difference in selective history of predation from large cats with a uniform coat pattern (current exposure) and a cat with a presumed coat pattern of flecks and rosettes (now absent) was used to develop the hypothesis that, due to prolonged relaxed selection possibly spanning up to 0.7 Myr, blacktailed deer should show much weaker antipredator behavior during exposure to a realistic looking model of a spotted cat than to a model of a puma. Similarly, if coat texture disrupts felid recognition as proposed for the vertical stripes of tigers (Mottram 1915), a completely novel tiger model, a species with no historical relevance and opportunity for selection for rapid recognition, should elicit an even weaker antipredator response. To understand the roles of coat pattern and relaxation of selection due to predators on visual predator recognition, I compared antipredator behaviors of adult blacktailed deer in Northern California, where the only large felid predator is the puma, during and after systematic exposure to life-sized, 2-dimensional models (Fig. 1.1) of a puma, tiger, and leopard with a coat pattern of smaller, primitive rosettes as the reasonable coat texture of early jaguars (Werdelin & Olsson 1997). A model female mule deer (*O. h. hemionus*) was used as a

nonthreatening control. Since coat pattern is only one perceptual cue complementing the general felid form, I predicted that all the felid models would be more provocative than the mule deer control due to the multi-million year history that deer have experienced predation by large felids.

METHODS

Field Sites and Sampling Procedures

All trials were performed on free-living adult deer at Point Reyes National Seashore (PRNS) in Marin, County, California, and on the Bodega Peninsula (BP) in Sonoma County, California between June and September in 2004 and 2005. Vegetation ranged from grassland pasture (height < 10 cm) to a mixture of scrub and tall grass and no tree cover, and terrain consisted of low rolling hills. Deer of PRNS and BP have been protected from human hunting for 30-40 years and the deer of BP have become highly habituated to humans. Confirmed puma sightings and kill carcasses are sporadic but not unusual at PRNS; there have been several reliable puma sightings in the last 20 years at BP (P. Conners, pers. comm.). The size of BP, puma homerange size, the stealthy habits of pumas, and the presence of pumas in surrounding areas suggest that pumas do occasionally visit BP. Similar to most studies of wild deer, individuals were neither marked nor identifiable by physical characteristics. However, I strengthened confidence that replication of focal sampling was rare by avoiding resampling of what appeared to be the same group within 1-2 weeks, by conducting trials in different locations, and by attempting to sample different focal individuals within the group if it was likely that group had been studied previously.

Model Construction and Presentation

Images for the models were electronically scanned from high-quality color photographs in books and digitally tailored to: (1) achieve the same body and head orientation (*i.e.*, lateral view of the body, head turned to face the observer, and body in a stalking position with scapula forming a hump behind the head), (2) increase coat pattern regularity, (3) remove shadows falling on the head, and (4) remove blemishes. The images were printed on heavyweight matte paper on a Designjet 800 poster printer, permanently mounted on foamboard with a flexible horizontal hinge in the center, spray-painted green camouflage on the reverse side, and sprayed with a matte finish polyurethane water-repellant. Because of the aforementioned logistics of testing deer unfamiliar with the models, only one model of each species was constructed. To avoid differences in perceptual loading, all models have approximately the same total surface area and the felid models have similar body lengths (head to base of tail).

Animals in relatively open areas with little occlusive scrub were targeted for exposure. The location of the model relative to the deer had to fit several criteria. The model was positioned 15-70 m from the focal individual; a closer position may result in the deer being surprised by the sudden appearance of an object and deer would have had greater difficulty discerning the shape and pattern of the model from distances beyond this range. The location had to provide sufficient visual cover for the experimenter and model so the deer would not naturally know what was behind the object (*e.g.*, hillside or bush). All trials were conducted so that the model was downwind of the deer group to avoid confounding results with odor cues. Finally, a position was selected that provided direct sunlight on the image of the model, to avoid a backlit silhouette that would make the image/coat pattern less visible. Using a slowly moving car as temporary cover, the

experimenter, hiding under a green camouflage mesh sheet, covertly positioned himself with the model behind the protective cover so that the deer did not know he was there; if he was detected prematurely, the trial was aborted. All behavior was videotaped by a second observer using a Panasonic model PV-DV601D mini digital video recorder from a greater distance shown not to influence deer activity in a previous study (Chapter 3; Stankowich & Coss 2006). The experimenter erected the model into view and once the focal deer detected the model, it was held in view for 30 sec before it was concealed again. The model was exposed up to 4 times per trial with approximately 1-min intervals between each exposure. Once the last exposure was completed, the experimenter laid on the ground silently under the green tarp, and video recording continued until the deer were out of visual contact or began feeding continuously for more than 2 min.

Behavioral Quantification

I recorded: (1) the distance between the model and the focal individual for each exposure using a Bushnell Yardage Pro laser rangefinder accurate to the nearest 1 m, (2) group size and composition, and (3) environmental factors (temperature, wind speed/direction, and weather). Both the experimenter and video camera operator counted the number of snorts (audible expulsions of air through the nose) heard during the course of the trial; since most snorts were not audible on the videotape, I only analyzed the total number of snorts I heard during the trial. It was not possible to identify which individual emitted each snort nor was it possible to record the timing of each snort. The time of each foot-stamp performed by the focal deer was determined from the digital video. When deer were alarmed by the models, I often observed a behavior called “alarm walking” where the deer walk more slowly and the limbs are

raised in the air in an exaggerated fashion. This behavior has been observed in the same predator-prey circumstances in mule deer (*O. h. hemionus*: V. Geist, pers. comm.) but due to the rarity of observing these encounters, the behavior has never been described or quantified before in the literature. Alarm walking is a qualitatively different style of walking than the normal deer gait (Stankowich and Coss, in preparation). The time and duration of each bout of alarm walking by the focal deer was recorded from digital video. Body and head positions (*e.g.*, head up at model, head up looking elsewhere, head down feeding), times, and durations were recorded from digital video. The time when the focal deer first detected the model when it was exposed was recorded and all latency measurements (foot-stamping, alarm walking, and return to feeding) were calculated relative to this time. Snorting and foot-stamping rates were calculated by dividing the total number of each behavior by the duration of the trial, from the moment of first detection through 10 min past the end of the final model exposure.

Subjective Ratings of Antipredator Behavior

To get composite scores of responses to the models, I asked two individuals to watch videotapes of each trial and rate the behavior of the focal deer on four different measures. Individuals had all available information about the trials (*e.g.*, when each exposure occurred, number of deer in group, *etc.*) except which model was assigned to each trial. I asked them: (A) “At which exposure did ‘recognition of threat’ occur (if at all)?”; (B) “Score the overall ‘fearfulness’ or ‘level of perceived threat’ of the deer” on an interval scale of 1-10 (1 = no fear at all; 10 = extremely fearful); (C) “Score the degree of focused attention on the model” on a scale of 1-10 (1= paid no attention to the model; 10 = constantly attentive); and (D) “Score the overall strength of response to the

model” on a scale of 1-10 (1 = no response; 10 = very strong antipredator behavior and/or rapid flight). Individual scores were initially analyzed with the intraclass correlation coefficient (ICC) (Bravo & Potvin 1991) to determine inter-observer reliability. Individual scores from the reliably correlated measures were then averaged and the mean scores were treated as dependent variables for further statistical analyses.

Statistical Analyses

Preliminary inspection of the data revealed that there were no differences in antipredator responses between the two sites, so that sites were not compared. The effect of the models on the frequency of deer snorting, foot-stamping, and alarm walking was examined using multinomial loglinear analysis with maximum likelihood estimation and partitioned χ^2 tests for specific model comparisons (Agresti 1990). Latencies to foot-stamp and alarm walk to each model type were compared with Kaplan-Meier Survival Analysis using the log-rank statistic (L) for pairwise model comparisons. Proportions of total time in camera view spent in each body/head position (head toward model, head away from model, feeding) were arcsine transformed. These proportions were grouped together, rates of snorting and foot-stamping behaviors were natural log transformed and grouped together, and each group was analyzed using backward elimination MANCOVA (*i.e.*, all factors were initially introduced into the model and the least significant factor was removed at each step until a final model was achieved with all factors significant at the 0.10 level). Initial factors included in the analyses were model type, presence/absence of a fawn in the group, group size, initial distance between the model and focal deer, and time between final exposure and end of trial (included in the analysis of time proportions only), and the interaction between

model and fawn presence/absence. The difference in foot-stamping rates between the time periods when the exposures were occurring and the 10-min period after the final model exposure was analyzed with the Wilcoxon signed ranks test. The difference in frequency of foot-stamps during the exposure period between when the model was exposed and the 30-sec period after exposures was also analyzed with the Wilcoxon signed ranks test. The effect of model type on the subjective scores of latency to recognize the model as dangerous (question A) was analyzed with Kaplan-Meier Survival Analysis using the log-rank statistic (L) for pairwise model comparisons. The effect of model type on the subjective scores of the three other measures (questions B-D) was analyzed as a group using MANOVA. Post-hoc multiple comparisons of behavior rates and subjective scores were performed with Tamhane's correction when error variances were unequal (as determined by Levene's tests), and with Bonferroni's correction when error variances were equal. All analyses were performed with SPSS 10.0, and statistical significance for all tests was reached at $\alpha = 0.05$.

RESULTS

Antipredator Responses

Responses to the deer model were minimal: there were no occurrences of snorting and only three occurrences of foot-stamping when exposed to the deer model. A larger proportion of deer snorted and foot-stamped in the presence of the predator models than with the nonthreatening deer model (Fig. 1.2; Loglinear χ^2 : snorting: $\chi^2_3 = 23.840$, $P < 0.001$, foot-stamping: $\chi^2_3 = 14.853$, $P = 0.002$). When compared individually, each predator model elicited snorting in a larger proportion of deer than the deer model (all $P \leq 0.005$), and a larger proportion of deer snorted at the puma

model than at the leopard ($\chi^2_1 = 4.773$, $P = 0.029$). The frequency of deer snorting in the presence of the tiger was intermediate to that of the leopard and puma, but not significantly different from either ($P > 0.05$). In contrast to the frequency of deer snorting, only the tiger and puma models elicited foot-stamping in a larger proportion of deer than the deer model (Fig. 1.2; tiger: $\chi^2_1 = 4.314$, $P = 0.038$, puma: $\chi^2_1 = 10.872$, $P < 0.001$), while the deer and leopard had nearly identical frequencies of foot-stamping ($\chi^2_1 = 0.008$, $P > 0.500$). There was a nearly statistically significant effect of model type on the presence/absence of alarm walking ($\chi^2_3 = 7.758$, $P = 0.051$). A larger percentage of deer alarm walked in the presence of the tiger model than the deer ($\chi^2_1 = 4.918$, $P = 0.027$) and leopard models ($\chi^2_1 = 4.134$, $P = 0.042$), whereas the tiger model did not differ appreciably from the puma model ($\chi^2_1 = 0.131$, $P > 0.500$). While there was a trend for a larger percentage of deer to alarm walk more in the presence of the puma than the deer ($\chi^2_1 = 3.503$, $P = 0.061$) and leopard models ($\chi^2_1 = 2.824$, $P = 0.093$), neither effect was statistically significant. There was no reliable difference between the leopard and the deer models ($\chi^2_1 = 0.048$, $P > 0.500$).

To measure the reaction time of predator recognition, I examined the latency to foot-stamp and alarm walk from the time of first detection of the model. Latency to foot-stamp was much faster in response to the tiger and puma models than to the leopard and deer models (Fig. 1.3a). Deer foot-stamped to the puma model significantly sooner than to both the deer (survival analysis, $L = 10.83$, $P = 0.001$) and leopard models ($L = 10.97$, $P = 0.001$). There was a trend for faster reaction to the tiger model than to both the deer ($L = 3.44$, $P = 0.064$) and leopard models ($L = 3.14$, $P = 0.076$), but neither pairwise comparison was reliably different. There were no

statistically significant differences in reaction time between the leopard and deer models ($L = 0.00$, $P = 0.966$) and the puma and tiger models ($L = 1.90$, $P = 0.168$). The same trends were apparent for alarm walking reaction times: latency to alarm walk was much faster in response to the tiger and puma models than to the leopard and deer models (Fig. 1.3b). Deer alarm walked to the puma model significantly sooner than to both the deer (survival analysis, $L = 4.56$, $P = 0.033$) and leopard models ($L = 4.99$, $P = 0.025$). Likewise, the latency to alarm walk was also much shorter to the tiger model than to the deer ($L = 5.76$, $P = 0.016$) and leopard models ($L = 5.58$, $P = 0.018$). There were no reliable differences between the puma and tiger models ($L = 0.00$, $P = 0.976$) and between the deer and leopard models ($L = 0.04$, $P = 0.841$).

The size of the deer group had no effect on antipredator behavior rates (MANCOVA, $F_{2, 62} = 0.311$, $P = 0.734$), and, in the range of values tested, the initial distance between the deer and the model did not influence behavior (MANCOVA, $F_{2, 66} = 0.556$, $P = 0.576$). Deer foot-stamped at a higher rate when there were no fawns present (mean \pm SE, 0.717 ± 0.237 ; $n = 25$) than when there was a fawn present in the group (0.223 ± 0.084 , $n = 48$; MANCOVA, between-subjects $F_{1, 68} = 5.366$, $P = 0.024$, power = 0.627).

Models differed significantly in their effect on overall response strength (Fig. 1.4; MANCOVA, $F_{6, 136} = 3.575$, $P = 0.003$) and individually on snorting rate (between-subjects $F_{3, 68} = 4.603$, $P = 0.005$) and foot-stamping rate (between-subjects $F_{3, 68} = 4.066$, $P = 0.010$). Deer snorted at a higher rate to the puma and tiger than to the deer (Fig. 1.4; puma-deer: $P = 0.012$, tiger-deer: $P = 0.046$). The tiger and puma models elicited similar snort rates, and the leopard did not differ from any of the other models (all $P > 0.05$). Deer foot-stamped at a higher rate when exposed to the puma than when

exposed to the deer ($P = 0.030$) or leopard models ($P = 0.049$). There were no other pairwise differences in foot-stamping rates among the models (all $P > 0.05$). Deer foot-stamped more when the model was actively appearing and disappearing than after the model disappeared from view for the last time (Wilcoxon: $Z = -3.175$, $P = 0.001$); however, there was no difference in the frequency of foot-stamps during the exposure period between when the model was exposed and when it was concealed (Wilcoxon: $Z = -0.420$, $P = 0.675$).

In the analyses of the proportion of time the focal deer spent looking in the direction of the model, looking in other directions, and feeding I found no effect of trial duration (MANCOVA, $F_{3, 56} = 0.042$, $P = 0.989$), type of model (MANCOVA, $F_{9, 186} = 0.876$, $P = 0.548$), initial distance between the focal deer and the model (MANCOVA, $F_{3, 63} = 1.667$, $P = 0.183$), group size (MANCOVA, $F_{3, 64} = 1.892$, $P = 0.140$), or the interaction between presence of fawn and model type (MANCOVA, $F_{9, 177} = 0.836$, $P = 0.584$). The presence/absence of a fawn in the group did affect time allocation (MANCOVA, $F_{3, 65} = 2.961$, $P = 0.039$); specifically, deer spent a greater proportion of time feeding when there was a fawn present in the group (mean \pm SE, 0.276 ± 0.046 ; $n = 44$) compared to when no fawn was present (0.089 ± 0.020 , $n = 25$; MANCOVA, between-subjects $F_{1, 67} = 8.962$, $P = 0.004$, power = 0.839). While there was a trend for deer to resume feeding sooner after being exposed to the leopard and deer models than to the puma and tiger models (survival analysis, $0.15 > P > 0.07$), none of the pairwise differences reached the criterion for statistical significance.

Subjective Ratings of Antipredator Behavior

Individual subjective scores of deer responses to the models for all four questions (A-D) exhibited reliable intraclass correlation coefficients (A: ICC = 0.649, $r = 0.510$; B: ICC = 0.902, $r = 0.824$; C: ICC = 0.825, $r = 0.702$; D: ICC = 0.897, $r = 0.897$; all $P < 0.001$); therefore, I averaged the individual scores and examined the effect of model type on each composite variable. Recognition of danger was rated as occurring faster to the puma and tiger models than to the deer model (Fig 1.5a; puma-deer: $L = 9.78$, $P = 0.002$; tiger-deer: $L = 9.17$, $P = 0.003$), but there was no reliable difference between the deer and leopard models ($L = 0.59$, $P = 0.442$). The leopard model was recognized as dangerous more slowly than the puma model ($L = 4.51$, $P = 0.034$) and the tiger model ($L = 3.79$, $P = 0.052$), although this latter comparison was not statistically significant. There was no reliable difference between the tiger and puma models ($L = 0.07$, $P = 0.788$).

Model type had a reliable affect on the three other subjective measures of deer antipredator behavior (Fig 1.5b; B-D: MANCOVA, $F_{9, 204} = 3.420$, $P = 0.001$, all between-subjects $P < 0.001$), and all three measures were highly correlated with the total number of snorts, total number of foot-stamps, and total time spent alarm walking decoded from digital video (all r values > 0.341 , all $P \leq 0.003$). All subjective ratings were positively correlated reliably with the proportion of time the focal deer spent looking at the model (all r values > 0.40 , all $P \leq 0.001$) and reliably negatively correlated with proportion of time the focal deer spent feeding (all r values < -0.40 , all $P \leq 0.001$). Deer were more fearful (question B) of the puma than they were the deer ($P < 0.001$) and leopard models ($P = 0.004$), but not the tiger model ($P = 0.366$). The tiger also evoked more fear than the deer model ($P = 0.003$), but not the leopard model ($P =$

0.537). There was no reliable difference in fear between the leopard and deer models ($P = 0.107$). Deer were more attentive (question C) to the puma ($P < 0.001$) and tiger models ($P = 0.004$) than they were to the deer model. There was a trend for the deer to be more attentive to the puma model compared with the leopard ($P = 0.059$), however this result was not statistically significant. There were no other statistically significant pairwise differences (all $P > 0.05$). Deer had an overall stronger response (question D) to the puma ($P < 0.001$) and tiger models ($P = 0.002$) than to the deer model, and there was a trend for the deer to respond more strongly to the leopard model than the deer model ($P = 0.082$), however this result was not statistically significant. The puma elicited a stronger response than the leopard model ($P = 0.006$) but not the tiger ($P = 0.431$). There was no reliable difference in response strength between the leopard and tiger models ($P = 0.552$).

DISCUSSION

Both snorting and foot-stamping have been found to be indicators of recognition of danger and alarm in many ungulate species (Caro 2005). Likewise, a larger proportion of deer snorted and foot-stamped in the presence of the predator models than with the nonthreatening deer model. Both snorting and foot-stamping were strongly associated with the presence of a predator and absent when a nonthreatening model was displayed; albeit, the antipredator response to the leopard model was markedly less than both the tiger and puma models. Additionally, responses to the deer were much slower and weaker compared with the tiger and puma models and, to some extent, the leopard model. These results indicate that the presentation protocol and 2-dimensionality of the models likely had little effect on the results and any differences between the predator

models is due to their appearance and not other motion, auditory, olfactory, or environmental cues.

In nearly all analyses, the puma showed the strongest effect on deer responses. With the exception of the frequency of foot-stamping and alarm walking, the tiger was intermediate to but not reliably different from the leopard and puma models. Deer were most fearful of the puma and the puma elicited the strongest overall response of any of the predator models, suggesting that the individuals tested either occasionally came into contact with pumas directly (we know this to be the case with PRNS) or have retained rapid recognition of pumas via vertical inheritance of puma recognition ability from recent generations that did encounter pumas directly. While mean strengths of behavior toward the tiger model were consistently equal to or below those for the puma model, I found no reliable differences between responses to the tiger and puma models in any statistical comparison. The fact that there was no reduction in speed and strength of recognition of the tiger model, despite the lack of any historical experience with a vertically-striped predator, suggests that the tiger's vertical stripes did not sufficiently disrupt its general felid appearance and that deer were able to generalize the more familiar threatening puma configuration with a uniform coat to the novel striped cat.

My results suggest that threat recognition occurs much more rapidly and is strongest for the puma and tiger models compared with the leopard model. Given current evidence for rapid recognition of and strong responses to spotted felids by mammalian prey (Coss & Ramakrishnan 2000; Coss *et al.* 2005; Ramakrishnan & Coss 2000b), I would expect *O. hemionus* to have had similarly refined recognition capabilities of spotted felids when jaguars were active predators of deer historically throughout North America. However, relaxation in selection due to the local extinction

of a large spotted predator appears to have resulted in significant loss of recognition capability of the spotted coat as dangerous. Albeit, the snorting measure clearly indicates that some deer still perceived the leopard as dangerous, which suggests that the spotted coat did not obliterate the leopard's felid form completely. Therefore, the spotted coat appears to have regained its assumed earlier camouflaging properties by disrupting the general felid configuration (Mottram 1915), resulting in a reduction in speed and strength of felid recognition. As such, there appears to be two competing perceptual processes at work in this system: (1) relaxation of selection leading to the loss of recognition of a formerly salient coat pattern as characterizing danger and (2) the re-emergence of the edge-disruptive, blending properties of a spotted, camouflage pattern (Mottram 1915).

Effects of other factors on the performance of antipredator behaviors were minimal. The lack of effects of group size and initial model distance on snorting and foot-stamping rates and head/body time allocations suggests that antipredator behavior is not assuaged in larger groups and that as long as detection/recognition occurs, longer distances to the predator do not influence the strength of the antipredator response. The presence of fawns in the group reliably decreased the rate of foot-stamping and increased the proportion of time adults spent feeding (*n.b.*, additionally fawns may have remained hidden in nearby vegetation throughout the trial and while post-trial measurements were taken). If foot-stamping functions as a conspecific warning signal (Caro *et al.* 2004), I would expect increased foot-stamping when fawns were present so as to warn them of the potential danger or to potentially sensitize them to the threat (Stankowich & Sherman 2002). This evidence appears contradictory to previous results (Caro *et al.* 2004) showing that foot-stamping occurs more often in species living in

intermediate and large groups. I suggest that foot-stamping may function as a pursuit deterrent by drawing the attention of the predator and communicating that it has been spotted; deer may be less likely to foot-stamp to draw attention from a predator when fawns, which are less able to flee effectively, are present. Also, adults may have spent a greater proportion of the time feeding when fawns were present if they were the mothers of the fawns; female deer typically devote more energy to feeding after giving birth and while nursing young (Geist 1981).

Conclusion

In light of previous findings on the role of conspicuous spots as salient rather than camouflaging patterns (Coss & Ramakrishnan 2000; Coss *et al.* 2005; Hollis-Brown 2005; Mottram 1915; Ramakrishnan & Coss 2000a; Ramakrishnan & Coss 2000b), our results suggest that the spotted felid coat evolved initially to disrupt recognition of the felid form. As prey experienced a consistent source of natural selection when they failed to recognize spotted felid predators, adaptive changes in felid-recognition systems began to capitalize on the regularity of the spotted coat as a conspicuous predator-recognition cue. The apparent loss of recognition of the spotted coat as dangerous and the re-emergence of spots as an effective camouflage suggests that visual predator recognition is evolutionarily labile and that an evolutionary arms race exists between predator camouflage and prey recognition of predators. While the multipredator hypothesis (Blumstein 2006) predicted that deer should retain recognition of the major felid form because pumas remain as a source of predation, we see that unique camouflaging patterns may limit an animal's ability to generalize current predators to those of the past. As such, I recommend that future research focus on the

dynamics between more recent relaxed selection and predator camouflage strategies and should attempt to use more complex predator models to learn what specific features of predators disrupt their recognition by prey.

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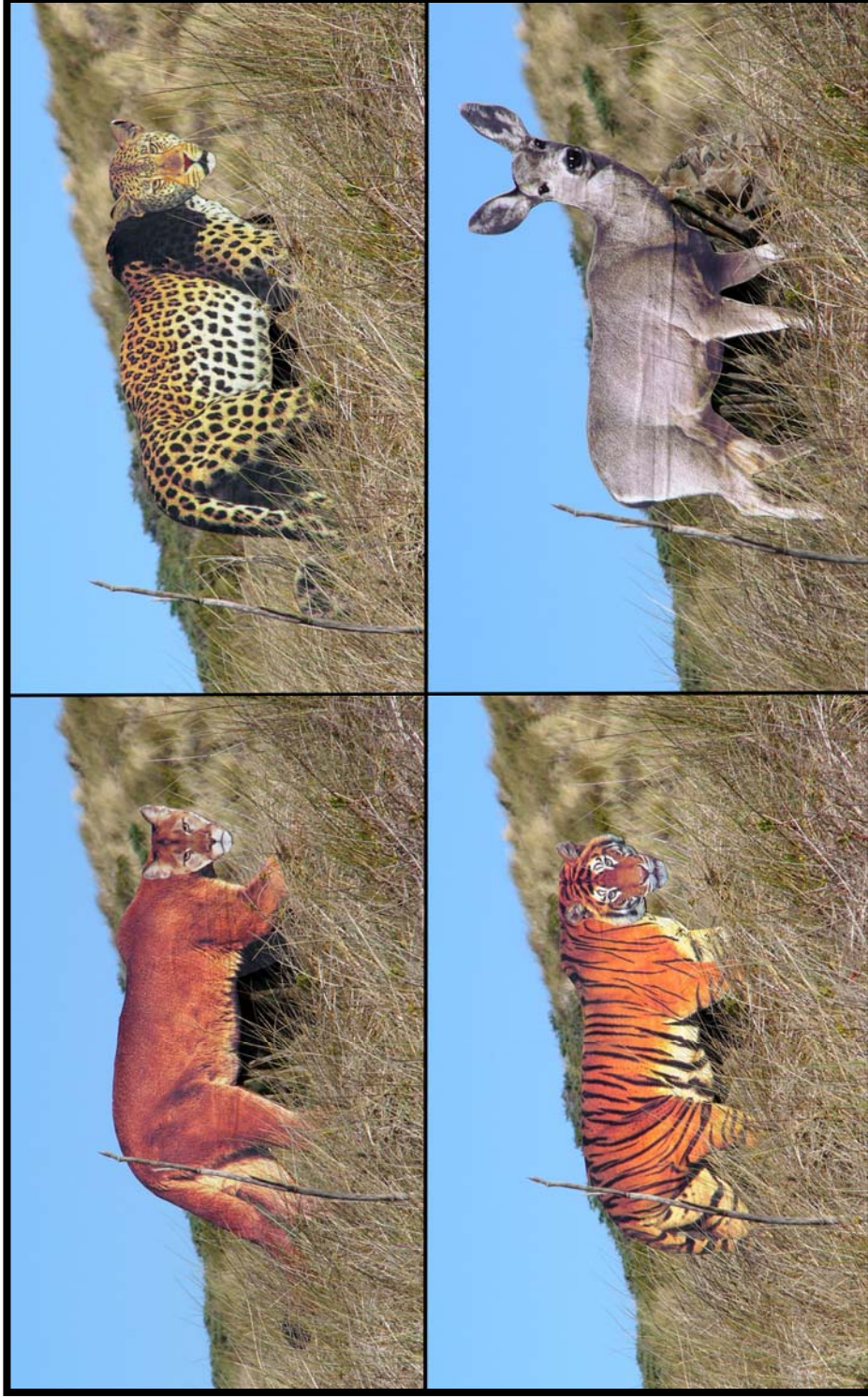
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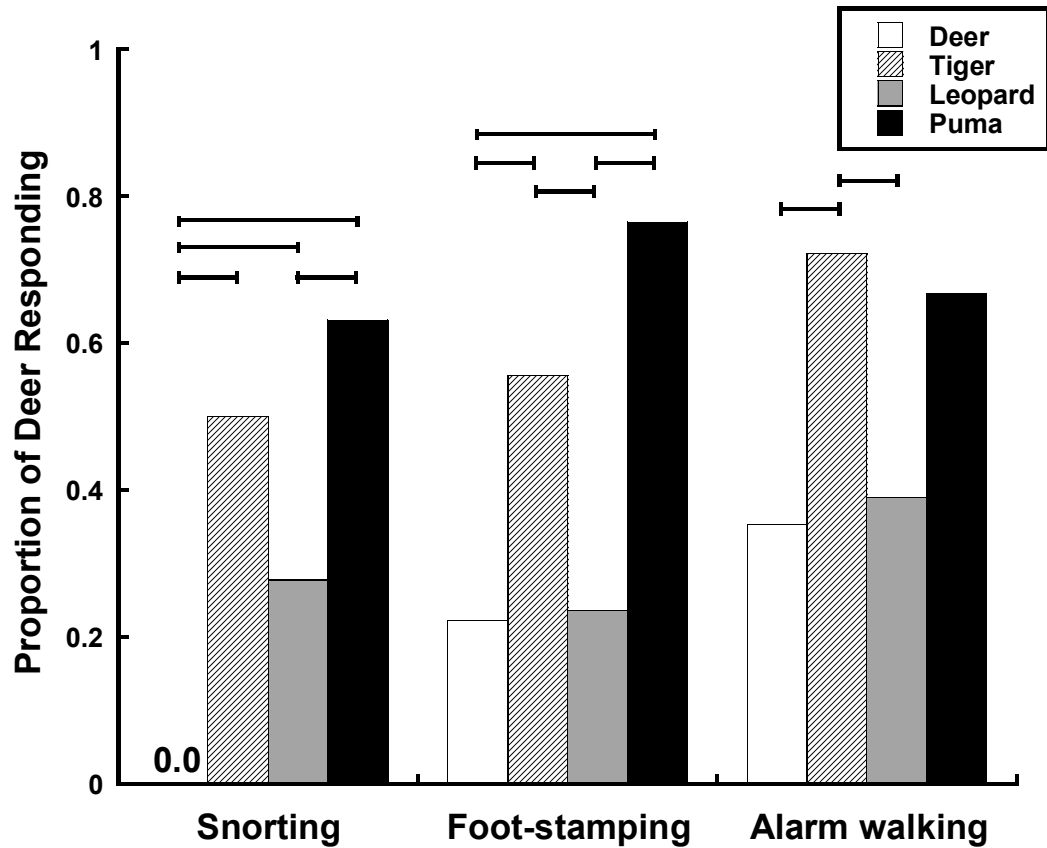
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FIGURE 1.1



Models presented to blacktailed deer shown to scale: clockwise from top left: puma, leopard, mule deer, and tiger.

FIGURE 1.2



Proportions of deer snorting, foot-stamping, and alarm walking. Lines above the bars indicate statistically significant pairwise differences between models ($P < 0.05$).

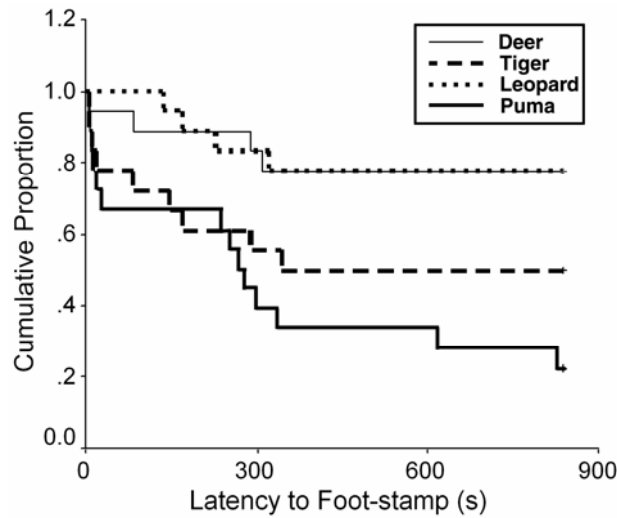
Snorting: $n_{\text{deer}} = n_{\text{tiger}} = n_{\text{leopard}} = 18$, $n_{\text{puma}} = 19$

Foot-stamping: $n_{\text{deer}} = n_{\text{tiger}} = 18$, $n_{\text{leopard}} = n_{\text{puma}} = 17$

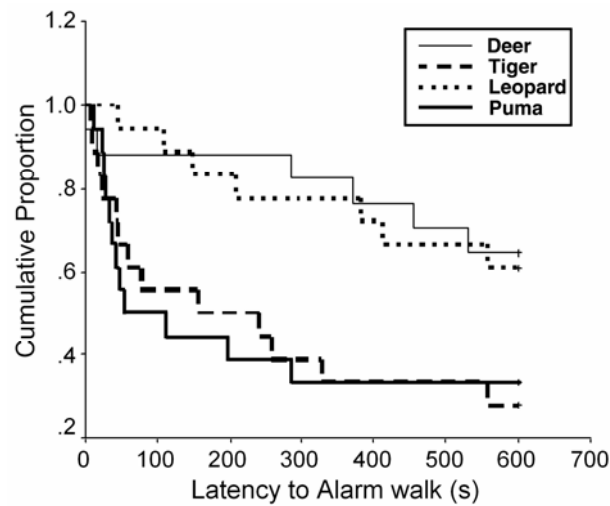
Alarm walking: $n_{\text{deer}} = 17$, $n_{\text{tiger}} = n_{\text{leopard}} = n_{\text{puma}} = 18$.

FIGURE 1.3

A)

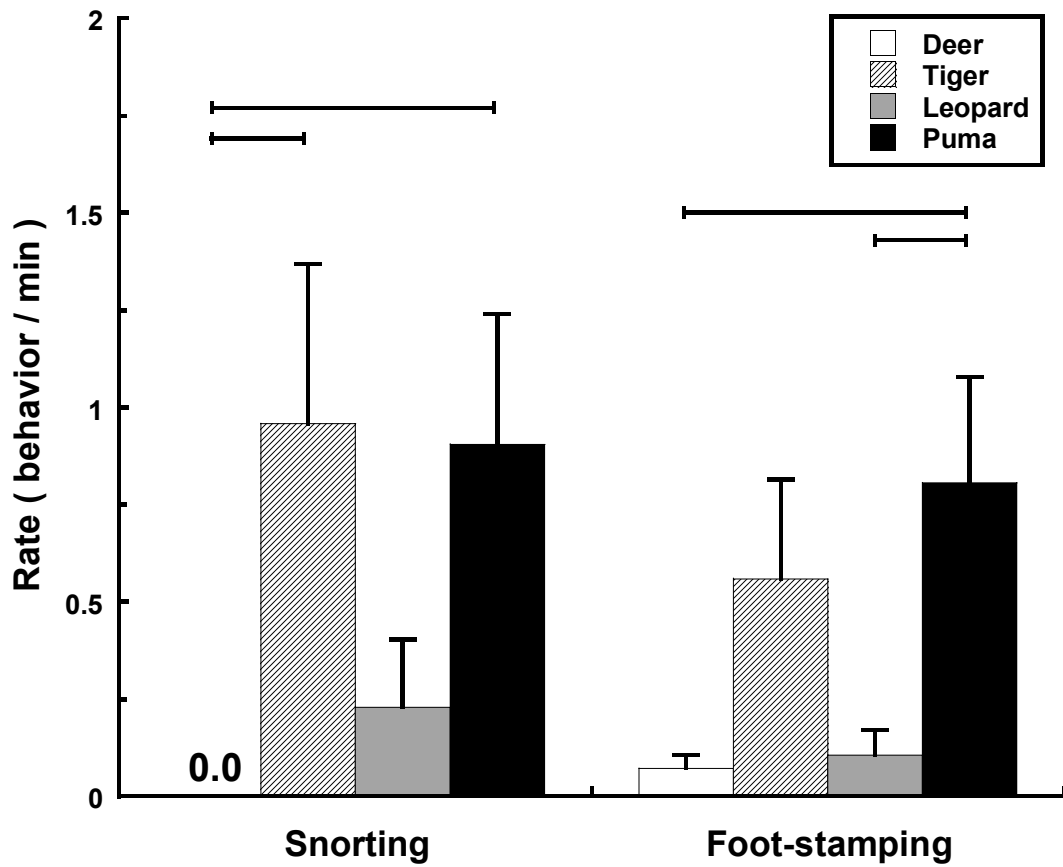


B)



Plots of Kaplan-Meier survivorship functions of latencies to (A) foot-stamp and (B) alarm walk to each model. (A) Pairwise comparisons for indicate statistically significant differences ($P < 0.05$) between the puma and deer models and between the puma and leopard models ($n_{\text{deer}} = n_{\text{tiger}} = n_{\text{leopard}} = 18$, $n_{\text{puma}} = 19$). (B) Pairwise comparisons indicate the puma and tiger models are each statistically significantly different ($P < 0.05$) from both the deer and leopard models ($n_{\text{deer}} = 17$, $n_{\text{tiger}} = n_{\text{leopard}} = n_{\text{puma}} = 18$).

FIGURE 1.4

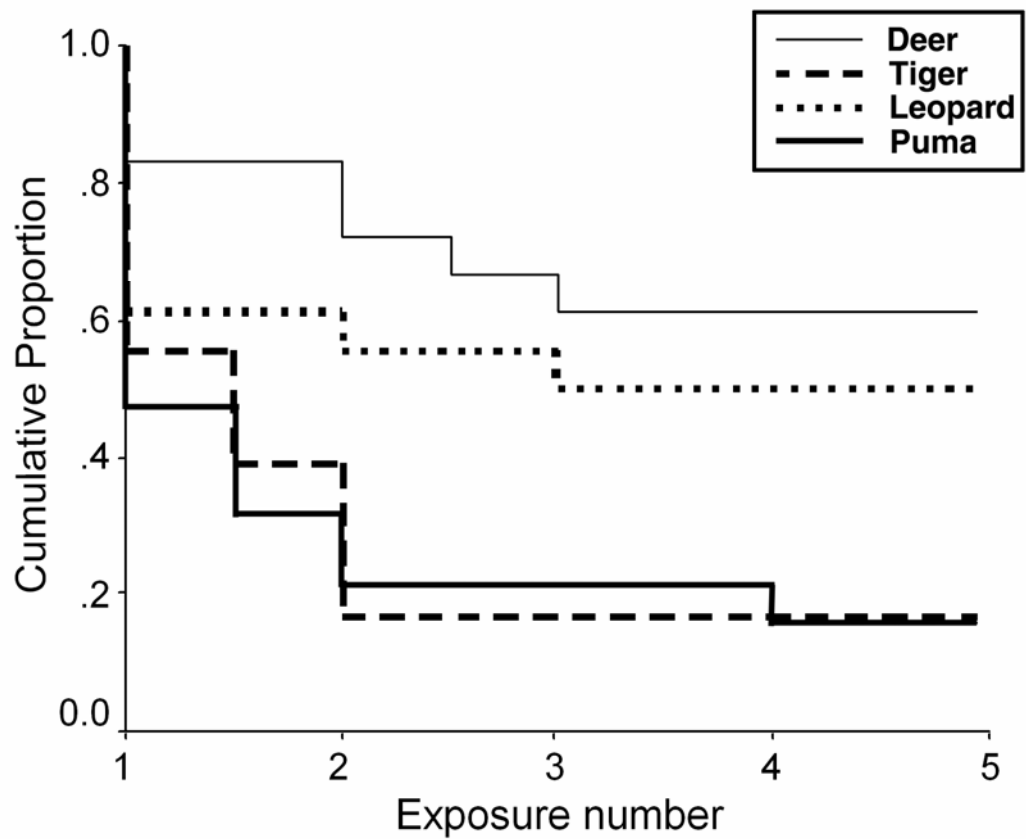


Mean \pm SE rates (behaviors / min) of snorting and foot-stamping observed. Black lines above the bars indicate statistically significant pairwise differences between models ($P < 0.05$).

Snorting and foot-stamping: $n_{\text{deer}} = n_{\text{tiger}} = n_{\text{leopard}} = 18$, $n_{\text{puma}} = 19$.

FIGURE 1.5

A)

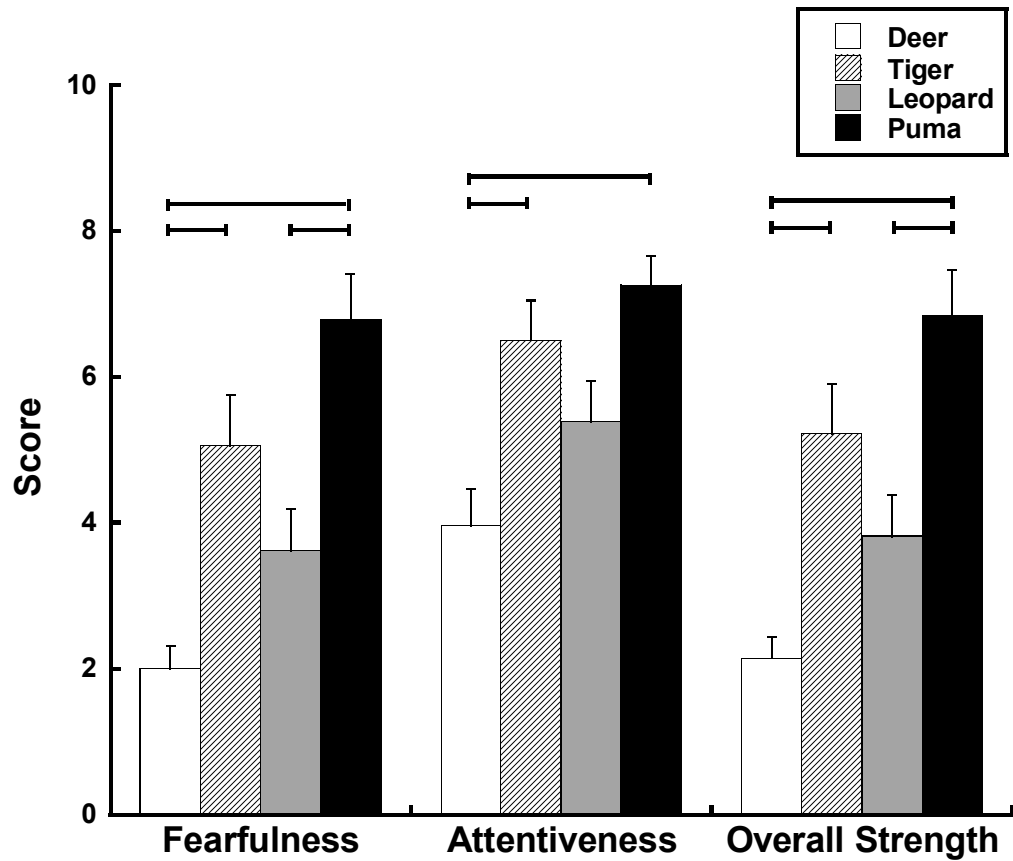


Plots of Kaplan-Meier survivorship functions of latencies to recognize each model as dangerous. Pairwise comparisons for indicate statistically significant differences ($P < 0.05$) between the puma and deer models, between the puma and leopard models, and between the tiger and deer models.

Sample sizes: $n_{\text{deer}} = n_{\text{tiger}} = n_{\text{leopard}} = 18$, $n_{\text{puma}} = 19$

FIGURE 1.5 ctd...

B)



Mean \pm SE scores (on a scale of 1-10) of fearfulness, attentiveness, and overall response in each trial to each model as judged by two independent observers. Black lines above the bars indicate statistically significant pairwise differences between models ($P < 0.05$)

Sample sizes: $n_{\text{deer}} = n_{\text{tiger}} = 18$, $n_{\text{leopard}} = n_{\text{puma}} = 17$

CHAPTER 2

Fear in Animals: A Meta-Analysis and Review of Risk Assessment

ABSTRACT

The amount of risk animals perceive in a given circumstance (*i.e.*, their degree of “fear”) is a difficult motivational state to study. While many studies have used flight initiation distance as a proxy for fearfulness and examined the factors influencing the decision to flee, there is no general understanding of the relative importance of these factors. By identifying factors with large effect sizes, we can determine whether antipredator strategies reduce fear, and we gain a unique perspective on the co-evolution of predator and antipredator behavior. Based on an extensive review and formal meta-analysis, I found that predator traits that were associated with greater risk (speed, size, directness of approach), increased prey distance to refuge, and experience with predators consistently amplified the perception of risk (in terms of flight initiation distance). While fish tolerated closer approach when in larger schools, other taxa had greater flight initiation distances when in larger groups. The presence of armored and cryptic morphologies decreased perception of risk, but body temperature in lizards had no robust effect on flight initiation distance. I find that selection generally acts on prey to be sensitive to predator behavior, as well as on prey to modify their behavior and morphology.

INTRODUCTION

Flight initiation distance is the distance at which an animal begins to flee from an approaching predator (Ydenberg & Dill 1986). Because it is relatively easy to systematically approach animals until they flee, and because flight initiation distance is correlated with other key aspects of escape behavior (*e.g.*, scanning rate—Fernández-Juricic & Schroeder 2003; alert distance (*i.e.*, distance at which prey become alert to an approaching threat)—Blumstein *et al.* 2005), flight initiation distance is an excellent metric with which to quantify an individual's fearfulness in a particular circumstance. This easy-to-measure metric has spawned a considerable theoretical literature, with a main goal being to evaluate hypotheses about optimal escape theory (Ydenberg & Dill 1986). Wildlife managers also use flight initiation distance to identify setback zones—areas beyond which species are not impacted by humans (Rodgers & Smith 1995; Fernández-Juricic *et al.* 2005).

Despite this large literature, there has been no attempt at a synthesis to identify the relative importance of various factors that influence fearfulness in animals. Thus, we do not generally know the degree to which prey behavior or conditional changes (*e.g.*, in morphology or experience) reduce perceptions of risk (*i.e.*, the current probability of being captured during a predatory encounter) compared to changes in predator behavior. If prey defenses co-evolve with predator hunting tactics, we might expect them to have similar effect sizes. Moreover, we currently do not know how prey respond to changes in predator behavior (Lima 2002).

We do know that there are species-specific effects for many factors, and it is thus difficult to draw generalizations about these factors. For instance, some reptiles

tolerate closer approach when warm (*Anolis lineatopus*: Rand 1964; *Tropidurus oreadicus*: Rocha & Bergallo 1990), which is consistent with greater agility and a greater ability to escape; other species, when cool, tolerate closer approach before fleeing (*Lophognathus temporalis*: Blamires 1999), which itself is consistent with another strategy of relying on crypsis when the cost of locomotion is high. At this point it is premature to conclude how temperature influences flight. Another issue is identifying the effect of group size on fearfulness. Do animals generally feel safer in large groups, as would be predicted by some models of predation hazard assessment (e.g., risk dilution models: Foster & Treherne 1981; Godin 1986)? Empirical evidence is mixed because some species tolerate a closer approach when in larger groups (Spottail shiner *Notropis hudsonius*: Seghers 1981), while other species are seemingly better able to detect approaching threats in groups and thus initiate flight at a greater distance (House sparrow *Passer domesticus*: Barnard 1980; Brent geese *Branta bernicla*: Owens 1977; *Macaca spp.*: Schaik *et al.* 1983). The high variance in the effect of group size on flight initiation distance has been attributed to the fact that many other variables contribute to optimal group size (Ydenberg & Dill 1986).

I conducted a formal meta-analysis where I estimated the effect sizes of various factors known to influence flight initiation distance. I asked the following broad questions.

- 1) Are animals relatively more responsive to characteristics associated with their predators, or with external factors, such as group size and the distance they are from a refuge, over both of which they have control? This is an important

question because it identifies the degree to which factors like habitat selection impact the effectiveness of different antipredator strategies.

- 2) How important are physical condition and morphological adaptations like armor or crypsis in explaining variation in flight initiation distance? While it is generally assumed that crypsis and armor make animals safer, do these morphological adaptations generally increase the perceived level of safety?
- 3) A large literature has examined the effects of body temperature or ambient temperature on reptile escape behavior. How important is this? Are reptiles at less or greater at risk as temperature increases and locomotor ability increases?
- 4) How important is experience with predators for flight initiation distance? Individuals may habituate or sensitize (*i.e.*, perceive greater risk) to repeated exposure. Can any generalizations be drawn about the effect of experience with predators?

By answering these four broad questions, I attempt to identify general factors that influence fearfulness in animals, and the degree to which they are generally important across taxa. I will identify those taxa in which homogeneous effects are found, and I will identify species or studies that have idiosyncratic results. Thus, my review and meta-analysis allow me to begin to identify those factors that influence the evolution of flight initiation distance and fearfulness in animals in general, and determine the relative importance of each effect in predicting flight responses.

METHODS

Data Collection

To obtain data, I first gathered the studies cited in Ydenberg & Dill's (1986) original review of flight initiation distance and searched the Web of Science (isiknowledge.com) for all references citing the review. In the literature, flight initiation distance has also been termed "flight distance" (*e.g.*, Hediger 1964), "approach distance" (*e.g.*, Cooper 1997), "reaction distance" (*e.g.*, Hurley & Hartline 1974), "escape distance" (*e.g.*, Handeland *et al.* 1996), and "flush distance" (*e.g.* Holmes *et al.* 1993), and the ambiguity in the literature regarding these terms has come under recent scrutiny (Taylor & Knight 2003). I searched BIOSIS reviews for papers citing these terms and extracted relevant citations from papers gathered through these means. I found 116 publications, published prior to 31 December 2003, which examined the influence of any environmental, predatory, or prey condition-based factor on flight initiation distance. I included both studies that presented empirical tests of each factor and their statistical results and studies that simply reported an observational effect of a factor on flight distance. I then pre-identified a list of factors (see Appendix A: "Factors investigated") to be analyzed with meta-analysis. For the analysis, I selected factors that: (1) have been studied in a wide range of species, (2) seemed to have some consistency (*i.e.*, low experimental variation: Osenberg *et al.* 1999) in the way they were measured (*e.g.*, consistent: predator speed usually contrasted fast versus slow approaches; inconsistent: numerous measures of habitat type), and (3) were likely to be targets of natural selection based on the economic theory of flight (Ydenberg & Dill 1986), specifically, factors that directly and most

strongly should affect variation in the level of threat posed during predatory encounters. The final list included: predator speed, predator size, directness of approach, prey distance to refuge, prey group size, presence of armor or crypsis, temperature in reptiles, predator population density, and sequential approaches by the predator. A full description and rationale for each factor studied is described in Appendix A. Sixty-one (53%) of the original 116 studies were used in my meta-analyses. Full tables of all relevant references collected, their findings, and the r and n values gathered from each are given in the Appendices (B-E).

Statistical Analyses

The Pearson's product-moment correlation coefficient, r , was chosen as an appropriate measure of effect size (Hunter *et al.* 1982; Rosenthal 1991) since it has been shown recently to be appropriate for analyzing results from behavioral and psychological studies (Fiske *et al.* 1998; Segerstrom & Miller 2004; Møller & Saino 2004) and the question being addressed in this study concerned an immediate effect (Osenberg *et al.* 1999) on flight decisions. For my studies, r is the magnitude of the effect on perceived risk of moving from a low-risk condition (control) to a high-risk condition (treatment). *Sensu* Segerstrom & Miller (2004), coefficients were obtained for each study, when possible, in the following ways (in order of preference): (1) direct reporting of r , R^2 , or partial correlation; (2) mean and variance data (SE or SD) reported in the text or figures converted to r using methods in Rosenthal (1991); (3) other test statistics (*e.g.*, F , U , t , χ^2) converted to r using methods in Rosenthal (1991); (4) exact P -values converted to r using *Meta-Analysis 5.3* (R. Schwarzer:

http://userpage.fu-berlin.de/~health/meta_e.htm). Studies that simply reported that there “was an effect” or there “was no effect,” $P > 0.05$ or $P < 0.05$, or only stated observationally that there was or was not a difference in flight initiation distance were excluded from analyses.

I performed meta-analyses by the Schmidt-Hunter method (Hunter & Schmidt 1990), where effect sizes from individual studies are weighted by their sample size to the proportion of the total sample size of the meta-analysis; weighted tests are the most precise and powerful meta-analytic procedures (Gurevitch & Hedges 1999). I estimated the observed standard deviation of effect sizes (Hunter & Schmidt 1990) and tested the significance of results using the Z test (Rosenthal 1984). Some studies report flight initiation data broken down by year, site, or other treatment effect; when combination of results across categories was inappropriate or not possible, I treated these results as independent studies in my analyses (*sensu* Fiske *et al.* 1998). For each weighted mean r , I calculated the fail-safe number of studies with an overall mean effect size equal to zero that would need to be filed away (*i.e.*, unpublished) in order to reduce the observed effect size to a non-significant level ($P < 0.05$; Rosenthal 1991). To test for the homogeneity (*i.e.*, the amount of constancy or variation in r -scores) of results across studies, I calculated the I^2 statistic (following Higgins *et al.* 2003). Negative values of I^2 were set to 0% so that I^2 varied between 0% (no heterogeneity = little variation in individual r -scores) and 100% (large heterogeneity = high variation in individual r -scores). I also used the rank correlation test of Begg and Mazumdar (1994) to examine the relationship between standardized effect size and sample size; negative correlations indicate that there were fewer than expected studies with

negative effects at low sample sizes, another indication of heterogeneity in effect size. When results were found to be heterogeneous, I examined individual study effect sizes using cluster analyses. For these, I used *Meta-Analysis 5.3* and interpreted clusters at the 5% level of significance. When appropriate, I subdivided taxonomic groups either by exclusion or inclusion of certain taxa. I then reran the meta-analyses as described above. All meta-analyses were computed using *Meta-Analysis 5.3*.

RESULTS

In most cases I found medium (Cohen 1988) estimates of effect size (Table 2.1) and my analyses were robust in that fail-safe numbers were substantial. Below I address my main questions.

(1) Are animals more responsive to characteristics associated with their predators, or with external factors over which they have more control, such as group size, or their distance from a refuge?

In general, animals are sensitive to both predator behavior and external factors over which they have more control when assessing predation risk. The distance of prey from their refugia had a large ($r = 0.43$), significant ($P < 0.0001$), and positive effect on flight initiation distance: animals far from their refugia systematically fled at greater distances. I also found a number of studies reporting effects of patch quality and costs of leaving. Typically, non-territorial animals and non-feeding animals initiate flight sooner (*i.e.*, they have larger flight initiation distances) than individuals engaged in combat, guarding territories or mates, or feeding (Appendix C). The effect

of refuge distance was larger than the effects of predator speed ($r = 0.38$), or directness ($r = 0.29$), or all predatory effects combined ($r = 0.32$; Tab. 2.1). However, reptiles were exceptionally sensitive to the speed at which predators approached them ($r = 0.67$). Relative predator size had a modest effect size ($r = 0.34$) with larger predators inducing greater flight initiation distances than smaller predators. Many studies also reported an effect of predator species or type on flight initiation distance (Appendix B), however since most were comparisons between humans and animals or machines, conclusions about the degree of threat posed are less clear. Overall, while group size had no significant effect size ($r = -0.01$, $P > 0.05$), when group size was subdivided along taxonomic lines, I found that fish tolerated closer approach when grouped ($r = -0.42$, $P < 0.001$), and other taxa were more sensitive when grouped and fled at greater distances ($r = 0.15$, $P < 0.001$).

(2) How important are physical condition and morphological adaptations like armor or crypsis in explaining variation in flight initiation distance?

Morphological and behavioral defenses against predators effectively reduce prey's perception of risk. I found a medium-sized effect ($r = 0.34$) when I combined defenses and consistent results for both the presence of armor and crypsis when examined alone. Additionally, the majority of studies found that large animals and animals in good condition (*i.e.*, lizards with intact tails) have longer flight initiation distances than shorter animals or those in poor condition (Appendix D). There appeared to be no cross-taxon effects of sex or reproductive state of the animal on flight initiation distance.

(3) How generally important is body or ambient temperature in lizards?

There was no consistent effect of body or ambient temperature in lizards ($r = 0.05$). Some species fled at greater distances when warm, others at shorter distances. There were no consistent effects in other taxa (Appendix D).

(4) How important is experience with predators on flight initiation distance?

Overall, experience with predators increased the perception of risk by 38%. Prey were more sensitive to predators when predator density is reduced ($r = 0.33$), and when they were sequentially approached by predators ($r = 0.47$). Also there are consistent observational reports in avian species of greater flight initiation distances during hunting seasons than during other months (Appendix E).

DISCUSSION

The results of both the review and the meta-analyses suggest that predatory, environmental, conditional, and experiential factors all have significant effects on flight initiation distance and that prey's responses to predator's threats are sensitive to variation in predator behavior. While some specific effects are ubiquitous (*e.g.*, refuge distance), others are taxon-, or species-specific (*e.g.*, group size). I summarize the results of my review graphically, and identify how each factor directly and/or indirectly influences flight decisions in animals (Fig. 2.1). The combination of factors that are influential for any given species likely differs because prey can pay attention only to a limited number of external variables. Selection favors paying attention to one or a few factors by weighting or de-emphasizing factors to streamline decision-

making (Bernays & Weislo 1994). Certainly, rapid assessment and decision-making are important when confronted by a potential predator (Bouskila & Blumstein 1992). I have grouped factors into four main categories for analysis and review: aspects of the predator, physical condition of the organism, environmental factors, and effects of experience and learning.

Effects of Predator Behavior/State

Predatory effects combined were found to contribute significantly and substantially to prey flight decisions because attributes of a predator directly relate to the perceived threat of the situation. Specifically, the non-mammalian prey are particularly sensitive to the increased speed of an approaching predator: the perceived risk of non-mammals increases by 60% when a predator increases its speed – a strong cue that it poses a significant threat. Curiously, I found no empirical evidence in the literature that this effect holds in mammals. However, this result is not convincing. For example, Hutson (1982) found no effect of variable approach speed when Merino sheep (*Ovis aries*) were tightly enclosed in a pen, which left only one study of no effect on which to base conclusions (see also Chapter 3; Stankowich & Coss 2006). I also found ubiquitous, homogeneous effects of directness of approach: perception of risk decreased by 31% when a predator appeared to be on a trajectory that bypassed the target prey. Directness of the path of approach is a strong indicator of the intent of the predator to attack or to bypass the focal animal. Interestingly, since I conducted my extensive literature review, new data have become available showing that in alpine birds found in an open tussock grass community, four out of five species initiated

flight at *greater* distances in response to an indirect approach (Fernández-Juricic *et al.* 2005). However, the publication of four negative results would be insufficient to overcome the original, large fail-safe number of studies (84) that would be required to eliminate or change my conclusion. The body size of the threat increases perceived risk. Larger size will emphasize the apparent size differences between predator and prey and can significantly increase the perceived loom rate of the predator (*i.e.*, “the rate of change of the angle subtended by the predator at the prey’s eye”: Dill 1974a: 711), a proposed mechanism of speed assessment by prey.

Other possible measures of predator threat level are less supported in my review and meta-analysis. There is no evidence that predator posture during approach affects perceived risk. The only empirical study included in the review of number of predators (Scrimgeour *et al.* 1997) found no effect (but see Geist *et al.* 2005), and most studies comparing types of predators focused on the response to humans rather than natural predators.

Two studies, however, found that the degree of exposure of a predator’s face can affect perceived risk (Burger & Gochfeld 1993), and that prey assign different levels of risk to different predator species, potentially based on hunting styles (Walther 1969). Prey seem also to evaluate the distance at which a predator begins its approach (Blumstein 2003). This nearly universal phenomenon is seen by the significant relationship between alert distance and flight initiation distance in many species (Fernández-Juricic *et al.* 2001; Blumstein 2003; Blumstein *et al.* 2004; Blumstein *et al.* 2005; Chapter 3; Stankowich & Coss 2006). Aspects of the predator’s behavior have a significant effect on the perceived risk of prey.

Environmental Factors

The meta-analysis clearly suggests that species that use refugia to escape from danger take into account the distance between themselves and safety when making flight decisions. Perceived risk increases by 43% when prey are far from rather than near a potential refuge. While the effect sizes were heterogeneous, the effect indicates that prey have some zone of safety around refugia, and when they venture farther from those refugia, their assessment of fear increases. This refuge-based perception of safety is strengthened by numerous studies showing longer flight initiation distances in more open habitats than when cover is greater (see “Habitat Type / Amount of Cover”: Appendix C). Modeling and empirical data suggest that this positive relationship between refuge and flight initiation distance is stronger (greater slope) when the refuge is between the predator and prey, and weaker (smaller slopes) when the prey is between the predator and refuge (Kramer & Bonenfant 1997).

While the effect of refuge distance on flight initiation distance is highly consistent, the effect size of group size is varied to an equal extent: effect sizes ranged from -0.49 to $+0.81$. There are many confounding effects on group size: dilution and food density effects have negative impacts on flight initiation distance, and increased vigilance levels of a group have positive effects. There is no consensus among the studies, but looking at how fish respond, we can see that larger groups resulted in smaller flight initiation distances: individuals gained an increased perception of safety when aggregated. Perhaps fish use coordinated shoaling behavior to systematically decrease risk differently than do other species: shoaling fish, in response to an increase in predation risk, perform a compaction response (Seghers 1974; Magurran & Pitcher

1987). If so, species that use coordinated defense (*e.g.*, musk ox: *Ovibos moschatus*) against predators should feel safer when in larger groups and tolerate closer approach (*n.b.*, however, there I found no examples of this effect), while other species, that use conspecific behavior as cues about predation risk (*e.g.*, water birds) should flush at greater distances when in larger groups (*e.g.*, Owens 1977).

Varying levels of investment in a particular site or high heterogeneity in patch quality can also impact flight decisions (Ydenberg & Dill 1986). Animals defending territories, mates, or young were more likely to have reduced flight initiation distances but this effect was not universal (*e.g.*, Rodgers & Smith 1997). Males engaged in combat have reduced flight initiation distances due to reduced vigilance/attention to predators. There was very little empirical evidence for territory defense, but territory-guarding individuals allowed closer approach than non-territorial animals (Shallenberger 1970; Walther 1969). Patch quality is also dependent upon how much food it holds. When there are large or numerous food items available, an animal will be less likely to leave since it is less likely to find such a resource elsewhere (Cooper *et al.* 2003). Between the strong effect of refuge distance in most species and more species-specific evidence of effects of group size, habitat type, and patch quality, there is significant evidence that the state of the surrounding environment can have a profound effect on the perception of fear by prey animals in predatory encounters.

Physical Condition/State of Prey

Many physical aspects of prey have been hypothesized to affect flight initiation distance and risk perception in general. Meta-analyses showed that the presence of

defensive armor and cryptic coloration decrease the amount of risk perceived by an animal in a given predatory encounter. There is also related evidence that increased crypsis via low lighting (Appendix D: Effect of Time & Light) and greater habitat cover (Appendix C: Effect of Habitat) can also decrease perceived risk and flight initiation distance. Clearly, the perception of having not been seen reduces fear in prey, and cryptic prey act as though potential predators will not detect them if they remain still. The physical condition of the animal affects its normal ability to escape in terms of speed, agility, and endurance. Very few studies have directly addressed measures of condition (good vs. poor). There is evidence from studies of tail autotomy in lizards suggesting that individuals with intact tails have longer flight initiation distances than those with autotomized tails, however some studies found no effect of tail autotomy. The presence of a tail facilitates flight, and those lacking tails should have slower escape speeds; tail loss might thus result in a switch to a crypsis-based anti-predator strategy (but for further debate, see Burger & Gochfeld 1990; Kelt *et al.* 2002; Cooper 2003a). Conversely, Kenward (1978) found that woodpigeons (*Columba palumbus*) in poor overall condition had longer flight initiation distances than those in good overall condition; this may indicate that in species where crypsis is not a viable strategy, animals with reduced ability to escape must flee sooner than those that are fully capable.

Other evidence for effects of the physical state of the animal on risk assessment are less robust: there is some consistency in the effect of large animals having longer flight initiation distances than small animals (larger animals may be at greater risk due to increased visibility, higher quality as potential prey, or reduced

escape speeds) and there is no consistent effect of sex, age, stress or temperature. An individual's reproductive state may indeed play a role in perception of risk: in reptiles, gravid females had shorter flight initiation distances than other animals, and in mammals, females with young had longer distances than others. These results may indicate that a switching of anti-predator strategy occurs when pregnant or immediately after having given birth due to decreased locomotor abilities (gravid reptiles) or the need to encourage young with undeveloped escape tactics to flee sooner, allowing more time to reach safety. While some aspects of an animal's physical state have clear effects on risk perception (armor, cryptic coloration/habitat, and physical condition), most other factors that have been studied show marginal, if any, impacts on an animal's state of fear.

Habituation and Experience

Habituation and experience with a predator significantly influences the perception of fear. While inter-species variation was high ($I^2 = 89.3\%$), there was a moderate effect ($r = 0.33$) of predator density on flight initiation distance. Typically, populations with few predators flushed at longer distances than those where predators were common. All of the predator density studies classified humans as the predator and measured differences in flight initiation distance between populations that differed in human density. If these populations with high human density have become habituated to humans in a non-threatening context (*e.g.*, in a park or recreation area), they are likely to perceive less risk when approached by a human than would an individual from a population where contact with humans is rare. However, if the prey

have not become habituated to the predator, and the predatory species, whether at high density or low density, is always a potential threat, animals that are more experienced or live in higher density areas should perceive higher risk and have higher flight initiation distances. Dill's (1974b) study of zebra danios (*Brachydanio rerio*) demonstrates this point: fish with more experience with predators had longer flight initiation distances than fish with less experience. Likewise, most studies of populations where hunting by humans occurs, found that animals have longer flight initiation distances during months when hunting was permitted (Appendix D: for reviews see Fox & Madsen 1997, and Smit & Visser 1993). Therefore, in times or places where human presence is typically non-threatening, animals have generally lower flight initiation distances. While there is evidence of genetic effects on fear (beef cattle breeds had longer flight initiation distances than dairy breeds and switching rearing type had no effect on this outcome, Murphey *et al.* 1980), risk assessment appears to be a plastic process for predator-savvy prey. Similarly, the more certain an animal is that the approaching predator intends to attack, the more risk it will perceive: most animals have longer flight initiation distances on the subsequent approaches than they do on the initial approach ($r = 0.47$). However this effect is not universal (Paulissen 1995; Rogers & Smith 1995).

Using meta-analyses of a systematic literature review, I have identified key factors associated with risk perception in animals. I have shown that prey can reduce their perception of risk and fear via behavioral, morphological, or experiential modifications to the same degree that predator behavior can increase the perception of risk in prey. Life history experience with predators and natural selection sensitize

prey to cues from predator behavior that reveal something about the predator's intent or motivation, and to modify their own behavior and morphology to reduce the level of threat a given predator poses. It is likely that an animal pays attention to a small subset of the factors I have reviewed to generate an estimate of the relative risk in any given predatory encounter.

Future studies should focus on this complex decision making process and identify the trade-offs individuals make when assessing risk. Specifically, future research must be aimed at studying the interactions between these factors (*e.g.*, Cooper *et al.* 2003) and must go beyond simply identifying significant factors to examine the relative importance of significant factors. Additionally, I believe that attention should be given to modeling risk assessment and flight decisions using Bayesian or dynamic state techniques in order to elucidate how the continuous influx of information about an approaching predator (*e.g.*, behavior, state, *etc.*) affects the likelihood that an animal will flee.

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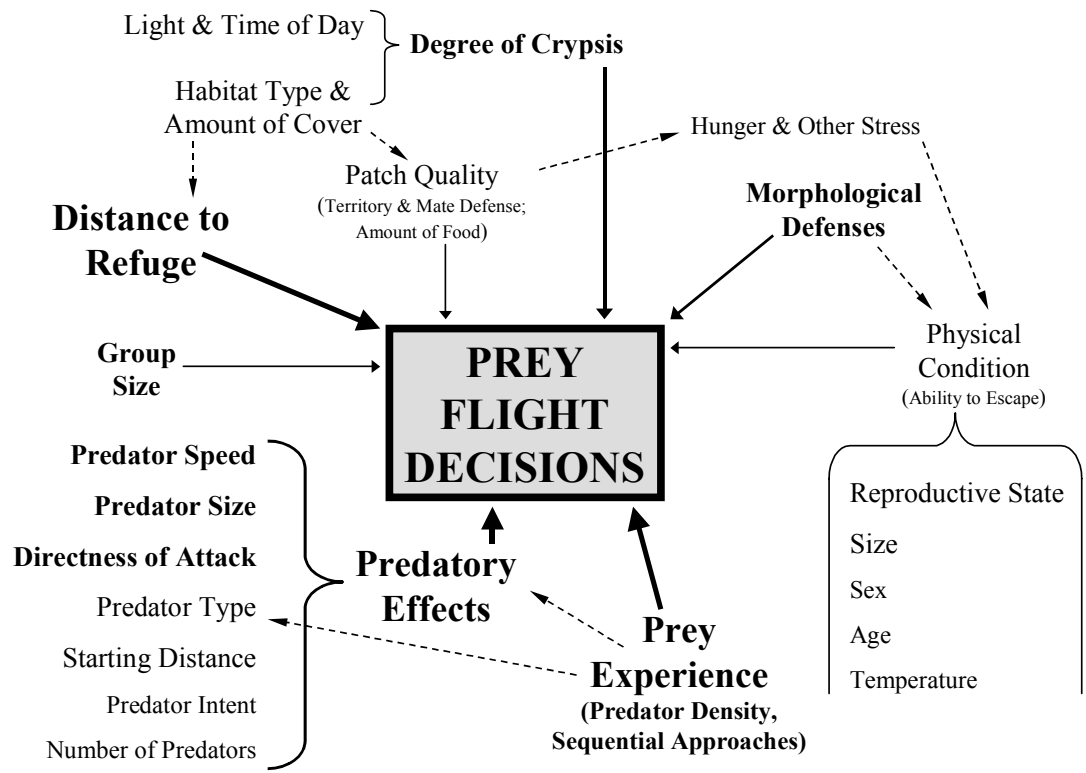
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TABLE 2.1

Factor	<i>r</i>	SD	<i>Z</i>	<i>I</i> ²	<i>K</i>	Total <i>N</i>	Fail- safe no.	Spear <i>ρ</i>
Predatory effects (total)	0.32	0.26	10.24**	68.7%	28	958	902 [†]	0.05
Predator speed	0.38	0.36	6.89**	84.1%	10	315	140 [†]	0.03
Exclude mammals	0.60	0.17	9.66**	32.0%	8	210	171 [†]	0.44
Reptiles only	0.67	0.07	9.75**	0.0%	4	159	102 [†]	-0.80
Predator directness	0.29	0.19	5.49**	32.0%	11	356	84 [†]	0.21
Excluding outlier	0.31	0.14	5.90**	0.0%	10	344	112 [†]	0.10
Predator size	0.34	0.10	5.75**	0.0%	7	277	66 [†]	0.04
Refuge Distance	0.43	0.26	13.59**	87.3%	17	907	1302 [†]	-0.48
Group Size	-0.01	0.31	-0.33	82.4%	16	964	-5	-0.41
Exclude fish	0.15	0.19	4.00**	60.0%	12	689	100 [†]	-0.69*
Fish only	-0.42	0.07	-7.22**	0.0%	4	275	48 [†]	-0.60
Prey Defense (total)	0.34	0.09	8.66**	0.0%	7	613	181 [†]	-0.46
Presence of Armor	0.33	0.16	3.99**	55.8%	3	138	17	na
Crypsis	0.34	0.05	15.28**	0.0%	4	475	82 [†]	-0.60
Temp in Lizards	0.05	0.31	1.72*	87.2%	18	1096	-18	0.37
Experience (total)	0.38	0.26	28.42**	92.0%	44	5141	8997 [†]	-0.01
Predator Density	0.33	0.24	20.65**	89.3%	30	3701	3893 [†]	-0.11
Sequential approach	0.47	0.41	8.96**	93.7%	7	330	99 [†]	0.21

Effect size (*r*), standard deviation of effect size (SD), *Z* score to test for significant differences from zero, *I*² to judge degree of heterogeneity in effect sizes, total number of studies (*K*), total combined sample size for all studies (total *N*), fail-safe number: the number of studies with a mean effect of zero to make the observed effect insignificant ($P < 0.05$), and a correlation between the effect size and log (*n*) of each study to test for heterogeneity of results (Spearman's *r*). (*N*, total sample size of all studies combined; *n*, sample size of an individual study.) * $P < 0.05$, ** $P < 0.001$; na: sample size too small for test; † - robust effect (Rosenthal 1991)

FIGURE 2.1



Summary of potential factors identified to influence flight initiation distance in animals. Boldness and size of solid lines and fonts indicate the relative strengths of statistical and theoretical support for each relationship (*i.e.*, bold and larger fonts indicate more important factors). Dotted lines indicate possible indirect relationships between factors.

CHAPTER 3

Effects of Predator Behavior and Proximity on Risk Assessment by Columbian
Blacktailed Deer

ABSTRACT

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. I examined the flight decisions of Columbian blacktailed deer (*Odocoileus hemionus columbianus*) using an approaching human that varied in speed, directness of approach, directness of gaze, and simulated gun carrying. 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), 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 alert distance. 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. I 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.

INTRODUCTION

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 is the distance from an approaching threat at which a prey animal moves away/takes flight (see Tab. 3.1 for definitions of all terms; Hediger 1964). According to optimality models (Ydenberg & 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). Chapter 2's and Stankowich and Blumstein's (2005) comprehensive review and meta-analysis of the flight initiation distance literature suggests 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.

Threat Sensitivity and Flight Decisions

One major category of factors that influences flight initiation distance 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, flight initiation distance 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 & Blumstein 2005; Ydenberg & Dill 1986; Chapter 2). 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, *etc.*). To date one study has directly tested the effects of subtle postural differences in predator behavior (*c.f.*, speed and directness) that may indicate ‘intent’ or ‘motivation’ on flight initiation distance and escape decisions in general, but found no effect (Helfman & Winkleman 1997). Nevertheless, animals can sometimes distinguish between predatory and nonpredatory species with similar appearances (Peckarsky & Dodson 1980) and between active and inactive predators (Dill 1974; Coss & Ramakrishnan 2000). The ability to detect such physical and behavioral variations in predator ‘motivation’ would be important to risk perception, flight decisions, and would likely be adaptive.

Alternative Measures of Risk Assessment

Flight initiation distance 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 & 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” (Tab. 3.1). Fernández-Juricic and colleagues (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: Dill 1990; Bonenfant & Kramer 1996; time left before approacher reaches target: Cárdenas *et al.* 2005), but no study has yet examined the role of assessment time in flight decisions.

Spatial Dynamics of Risk Assessment

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” (Tab. 3.1), positively correlates with flight initiation distance (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 flight initiation distance and start distance (Blumstein 2003) have

suggested that there are two critical distances (and three resulting zones of response: see Fig. 3.1): 1) a minimum distance (D_{\min} ; Tab. 3.1) below 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} ; Tab. 3.1), above which (Zone III) prey will not move away from an approaching predator due to: lack of perceptual capabilities, simply not being attentive to activities beyond this distance, or that they perceive the predator but don't treat it as dangerous. While the relationship between flight initiation distance and start distance is constrained by the fact that flight initiation distance must be less than start distance, optimality theory predicts that flight initiation distance will increase with start distance in a second zone (Zone II) spanning D_{\min} and D_{\max} (Fig. 3.1: 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.

I hypothesize that the relationship between start distance and flight initiation distance in Zone II might increase initially up to a maximum flight initiation distance, 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 start distance corresponding to a maximum flight initiation distance (Fig 3.1; see solid curves with $D_{\max\text{-low}}$).

Depending on the scanning rate (α ; Tab. 3.1), 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(s) would be able to constantly monitor the surrounding environment in all directions to D_{\max} so that, all else being equal, the prey animal(s) would flee at the maximum flight

initiation distance for any predator start distance greater than D_{\max} . Optimal scanning typically does not occur immediately upon the predator entering the zone since 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 since alert distance is correlated with flight initiation distance (Blumstein *et al.* 2005), animals should then take flight at a shorter distance. This would result in a negative relationship between start distance and flight initiation distance at starting distances past D_{\max} (Fig. 3.1; 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 which some more reactive or less habituated animals are more likely to become alert prior to the initiation of approach at longer distances (Fig. 3.1; dashed line corresponding to $D_{\max\text{-high}}$) than less reactive or more habituated animals (Fig. 3.1; solid line corresponding to $D_{\max\text{-low}}$). I suggest that analyses of risk assessment using flight initiation distance and assessment time should examine different regression models, both linear and curvilinear, to best describe the relationships between start distance, alert distance, flight initiation distance, and assessment time (Tab. 3.1).

Interactions Between Factors Influencing Flight Decisions

While predator behavior and its effects on flight initiation distance have been studied in detail in many species, only recently have the effects of interactions among

specific predator behaviors on flight initiation distance been analyzed. As predicted, Cooper and colleagues (2003) found that Bonaire whiptail lizards (*Cnemidophorus murinus*) had longer flight initiation distances when approached quickly and directly than when approached quickly and indirectly. However, when approached slowly, lizards had longer flight initiation distances during indirect approaches 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 flight initiation distances in areas where hunting activity is greater (de Boer *et al.* 2004), during the local hunting season (*e.g.*, Behrend & Lubeck 1968; Dasmann & Taber 1956), and in response to humans compared to motorized vehicles (*e.g.*, Eckstein *et al.* 1979; Kucera 1976; but see Taylor & Knight 2003).

Hypotheses

I conducted experimental human approaches towards Columbian blacktailed deer (*Odocoileus hemionus columbianus*) to determine the degree to which perceived risk and predator “motivation” affect flight initiation distance and assessment time. Humans are commonly used as predators in studies of flight decisions and risk assessment (for review see Appendices; Stankowich & Blumstein 2005). While theory would suggest that deer should increase flight initiation distance in response to increased perceived risk, there is evidence that animals might maintain both spatial

and temporal margins of safety (respectively, flight decisions based on how far away the predator is and how long it will take for the predator to reach the prey) and use both in a dynamic way to make flight decisions (Cárdenas *et al.* 2005). I 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 (Chapter 2; Stankowich & Blumstein 2005), but general qualitative relationships between start distance, alert distance, flight initiation distance, and assessment time may be universal for most predators of a given prey species or taxon (*e.g.*, birds: Blumstein 2003). I 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

Field Site and Subjects

I 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 over 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.*, galloping, stotting, tail flagging, *etc.*) 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. I was 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, *etc.*) 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 I have confidence that replication on the same animal was rare.

Approach Methodology

To measure flight initiation distance, alert distance, and assessment time, I identified solitary or small groups of deer from the roadside and positioned myself so I would have a direct line of approach to the deer. I (1.85 m tall, Caucasian male) conducted all approaches and wore the same outfit (green coat, tan pants, dark baseball hat) for each trial. I 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, I 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 alert distance was recorded for that trial. Flight consisted of movement away from the deer's original location, ranging from a slow walk to trotting, galloping or sprinting. 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.*, flight initiation distance \approx alert distance). After flight, I 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 20X 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, I 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, turning on camera, or while I moved to the starting position).

Approaches were varied in four ways: (1) I varied the speed of approach by conducting walking approaches and jogging approaches. (2) I varied the directness of approach by approaching the focal deer on a direct line ("direct") or an indirect line ("indirect") where I aimed my approach to a point approximately 30 m to the left or

right of the focal individual. My threat level as 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 approach and simulate lack of interest toward the deer (low threat), “gaze-averted” trials were conducted where I looked side-to-side at the ground during the approach and my eyes were never visible to the deer—an assistant notified me of when each event occurred using a 2-way radio. (4) To simulate hunting behavior (high threat), I 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 (B. McClure, pers. comm.).

Analyses

Prior to analyses, all dependent variables were subjected to a Komolgorov-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 start distance and alert distance separately as the independent variables (*strictu sensu* Blumstein 2003; Blumstein *et al.* 2005); each relationship was fitted to linear, quadratic, and cubic models sequentially. If the quadratic term achieved significance (ANOVA *t*-test, $P < 0.05$), 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 (*strictu sensu* Blumstein 2003; *n.b.*, R^2 statistics could not be used to compare

quadratic and cubic models to logarithmic and linear models since 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 since: (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 start distances, 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, I made the resulting model equation linear by transforming the variables prior to subsequent analyses. I winnowed my list of candidate predictors (*e.g.*, temperature, light level, vegetation type, *etc.*) for flight initiation distance and assessment time by examining their predictive properties for ungulates in the literature (Chapter 2; Stankowich & 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 start distance. Due to the large number of possible interactions among factors, I chose to select a subset of interactions of interest that would directly test my initial predictions of sex difference in risk assessment and interactions among predator behaviors (*e.g.*, Cooper *et al.* 2003). I 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 ANCOVA model with a probability to remove of 0.10 (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 (AD)

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 start distance (SD) (Pearson's $r = 0.596$, $R^2 = 0.355$, $P < 0.001$, $n = 48$), but the cubic function provided the best fit ($R^2 = 0.471$; cubic term: $t = -2.396$, $P = 0.021$; Fig. 3.2a). 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 a start distance of 222 m where the predicted alert distance is 138 m. Since start distance and alert distance are highly correlated and there are many more available observations with start distance than alert distance, I used start distance as a covariate in all subsequent analyses of factors influencing flight initiation distance and assessment time.

Flight initiation distance (FID)

Deer fled from the approacher in every trial ($n = 78$) and flight initiation distance was correlated linearly to start distance (Pearson's $r = 0.364$, $R^2 = 0.132$, $P = 0.001$, $n = 78$) and alert distance ($r = 0.689$, $R^2 = 0.475$, $P < 0.001$, $n = 48$). The concave-down quadratic function provided the best fit with start distance ($R^2 = 0.182$; quadratic term: $t = -2.132$, $P = 0.036$, $n = 78$; Fig. 3.2b, 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 a start distance of 219 m where the predicted flight initiation distance is 87 m. When trials where deer were alert prior and not alert prior to the start of the approach are analyzed separately, flight initiation distance showed a quadratic fit when deer were not alert prior ($R^2 = 0.186$; quadratic term: $t = -2.146$, $P = 0.037$, $n = 48$; function: $FID = -2.78 + 0.76(SD) - (1.95 \times 10^{-3})(SD^2)$; maximum: $SD = 194$ m, $FID = 71$ m; Fig. 3.2b, solid thin curve) and a logarithmic fit when deer were already alert ($R^2 = 0.178$; $\ln SD$ term: $t = 2.44$, $P = 0.020$, $n = 30$; function: $FID = 41.36(\ln SD) - 116.72$; Fig. 3.2b, thin dashed curve). A quadratic function provided the best fit with alert distance ($R^2 = 0.52$; quadratic term: $t = -2.081$, $P = 0.043$; Fig. 3.2c). 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 alert distance of 162 m where the predicted flight initiation distance is 84 m.

In a backward-elimination ANCOVA where all data were included, five terms were removed (Tab. 3.2; $P > 0.10$) including intent (Fig 3.3: direct gaze: 73 ± 6 m, $n = 19$, gaze averted: 63 ± 8 m, $n = 16$). Both covariates SD and SD^2 remained in the final model and were significant (Tab. 3.2; $P < 0.05$). 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 (Fig. 3.3; Tab. 3.2; $P < 0.05$) 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 presence of gun (Fig. 3.3: 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 ($P > 0.05$), but remained in the final model (Tab. 3.2) because we found a statistically significant interaction between them (Fig. 3.4; Tab. 3.2; $P = 0.038$). 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: $t = -0.477$, $P = 0.639$), but males had shorter flight initiation distances when approached holding a simulated gun (holding ‘gun’: 46 ± 5 m, $n = 6$, no ‘gun’: 71 ± 16 m, $n = 2$; $t = -2.222$, $P = 0.068$; *n.b.*, only two walking, direct approach, direct gaze, no ‘gun’ trials were conducted on males, which influenced the level of significance). While there were no sex differences in flight initiation distance when the approacher did not have a simulated gun ($t = -0.151$, $P = 0.883$), males had shorter flight initiation distances than females when the approacher was carrying a simulated gun ($t = -2.115$, $P = 0.056$).

Assessment Time (T_{assess})

At longer start distances, 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 start distance (quadratic term: $t = -0.499$, $P = 0.670$) or alert distance (quadratic term: $t = -$

0.426, $P = 0.672$). Of the other models analyzed, the linear model was judged to provide the best fit for start distance (Fig. 3.2d: $R^2 = 0.216$) with the model $\ln(T_{\text{assess}}) = 0.79 + 0.004(\text{SD})$. When trials where deer were alert prior and not alert prior to the start of the approach are analyzed separately, flight initiation distance showed a logarithmic fit when deer were not alert prior ($R^2 = 0.194$; ln SD term: $t = 3.331$, $P = 0.002$, $n = 48$; function: $\ln(T_{\text{assess}}) = -1.05 + 0.46(\ln \text{SD})$; Fig. 3.2d, thin solid curve) and a linear fit when deer were already alert ($R^2 = 0.237$; SD term: $t = 2.946$, $P = 0.006$, $n = 30$; function: $\text{FID} = 0.99 + 0.003(\text{SD})$; Fig. 3.2d, thin dashed curve). The linear model was judged to provide the best fit for alert distance (Fig. 3.2e: $R^2 = 0.379$) with the model $\ln(T_{\text{assess}}) = 0.62 + 0.006(\text{AD})$. Assessment time was not correlated with flight initiation distance (Fig. 3.2f: $R^2 = 0.003$, $P = 0.649$, $n = 78$).

In a backward-elimination ANCOVA where all data were included, five terms were removed (Tab. 3.2; $P > 0.10$) including presence of gun (Fig. 3.5: 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, start distance and group size, remained in the model (Tab. 3.2), and while group size approached statistical significance ($P = 0.085$), start distance was strongly associated with assessment time ($P < 0.001$). I found statistically significant main effects for (Fig. 3.5; Tab. 3.2) 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, $n = 48$). 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 ($P > 0.05$), but remained in the final model (Tab. 2) because I found a

statistically significant interaction among them (Fig. 3.6: $P = 0.017$). 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: $t = 1.522$, $P = 0.189$; *n.b.*, only seven walking, direct approach, 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, $n = 13$; $t = -0.217$, $P = 0.830$).

Additionally, males assessed an approacher significantly shorter than females when the approacher’s gaze was averted ($t = -2.414$, $P = 0.030$), but not when his gaze was directed at them ($t = -0.526$, $P = 0.606$).

DISCUSSION

As was predicted, flight initiation distance varied widely depending on the style of predator approach, the start distance of the approacher, the alert distance in response to the approacher, and the state of awareness of the deer. Within the range of starting distances tested, I found that alert distance and flight initiation distance increased with starting distance then decreased slightly or leveled off at the longest starting distances tested (Fig. 3.2a,b). The presence of the local maximum in the final cubic model (Fig. 3.2a) and a maximum observed alert distance (169 m) indicates that deer maintain vigilance in an approximate ‘zone of awareness’ (Zones I & II). At very long start distances, deer that were not alert prior actually took flight at distances below the maximum flight initiation distance (Fig. 3.2b, thin solid line). When deer were alert prior to the start of the approach the relationship between flight initiation distance and start distance was logarithmic with flight initiation distance beginning to

asymptote at greater start distances (Fig 3.2b, thin dashed line). This contrast in relationships suggests that there is individual variation in D_{\max} (Fig. 3.1) where possibly more reactive or less habituated animals (*i.e.*, those that were already alert prior to approach from long start distances) may treat predators appearing at very long distances ($D_{\max\text{-high}}$; Fig. 3.1) 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 flight initiation distances (Fig. 3.3) and a qualitatively different flight response at long start distances (Fig. 3.2b) 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 don't treat them as dangerous. It is apparent that assessment time has a positive linear relationship with both start distance (Fig. 3.2d) and alert distance (Fig. 3.2e); 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 start distances measured. Since assessment time and flight initiation distance are not correlated reliably (Fig. 3.2f), then the relationship between flight initiation distance and alert distance follows a similar quadratic trajectory (Fig. 3.2c) and levels off at greater alert distances. Cárdenas *et al.* (2005) found that galahs (*Cacatua roseicapilla*), once alerted, permitted approach to almost half the alert distance; our finding of a nonlinear relationship between alert distance and flight initiation distance suggests that deer maintain a spatial margin of safety in a qualitatively different way.

Effects of Predator Behavior

As predicted by the Threat Sensitivity Hypothesis (Helfman 1989), I found strong main effects for both approach speed and directness of approach on flight initiation distance (Fig. 3.3), with faster and more direct approaches eliciting flight at greater distances. But while flight initiation distances were greater in trials where gaze was directed (Fig. 3.3) 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 & Blumstein 2005; Ydenberg & Dill 1986).

Effects of Group Size

The finding of no reliable statistical effect of group size on flight initiation distance 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 (*Capreolus capreolus*) and 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 flight initiation distances for small groups of impala (*Aepyceros melampus*). Indeed, the effect of group size on flight initiation distance 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 (Chapter 2; Stankowich & Blumstein 2005). Further, we found a strong trend for lower assessment times in larger groups. One explanation for this result is that blacktailed deer are more “irritable” at greater population densities (Dasmann & Taber 1956), and the flight of one deer is typically contagious, initiating flight in the rest of the group (Stankowich, pers obs). 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.

Assessment Time and Perceived Risk

To my knowledge, my research on Columbian blacktailed deer is the first study to examine the role of assessment time in flight decisions. As predicted, I 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 (Fig. 3.5); 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.

Fear of Humans and Sex Effects

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 *et al.*, 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 flight initiation distances (but see Grau & Grau 1980). Many game bird species (Fox & Madsen 1997; Madsen 1985; Smit & Visser 1993) have longer flight initiation distances during months when hunting is permitted compared with other months; and whitetailed deer (*Odocoileus virginianus*) increase their avoidance response toward humans at progressively longer distances over the course of the hunting season (Grau & Grau 1980). Alpine marmots (*Marmota marmota*), moose (*Alces alces*), impalas, roe deer, and caribou in hunted areas have longer flight initiation distances than like individuals in areas where there is little or no hunting (respectively: Louis & Le Berre 2000; Altman 1958; Matson *et al.* 2005; de

Boer *et al.* 2004; Aastrup 2000). My 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 & Lubeck 1968; de Boer *et al.* 2004).

I found no statistically significant main effects for prey sex, the presence of a simulated gun, or predator intent on flight initiation distances or assessment time. Since 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, I found that males approached with an aimed 'gun' allowed the predator to approach closer than males approached without a 'gun' and females approached with a 'gun' (Fig. 3.4). 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 (Fig. 3.6; $P = 0.189$) due to small sample sizes. One possible explanation for the sex-differences in flight initiation distance in response to a 'gun' is that aiming a 'gun' while approaching results in a rigid upper body with fluid, moving legs, and since '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 gun-like 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.

Cooper and colleagues' (2003) findings 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 my study did not find any evidence in deer of an interaction between predator speed and directness of approach, the lizards' behavior may bear on my conclusions about male behavior during gaze-averted trials (Fig. 3.6). Changes in gaze might signify interest or lack of interest by both conspecifics and other species (*c.f.*, 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 flight initiation distance 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 my experimental manipulations, assessment algorithms involve more complex dynamics than simple cost-benefit relationships between distance to safety, speed of escape, and distance to predator.

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TABLE 3.1**Definitions of terms used in text and figures**

Term	Definition
Start Distance	The distance between the predator and prey at which the predator begins its approach
Alert Distance	The distance between the predator and prey at which the prey becomes alert to the predator
Flight Initiation Distance	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 below 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

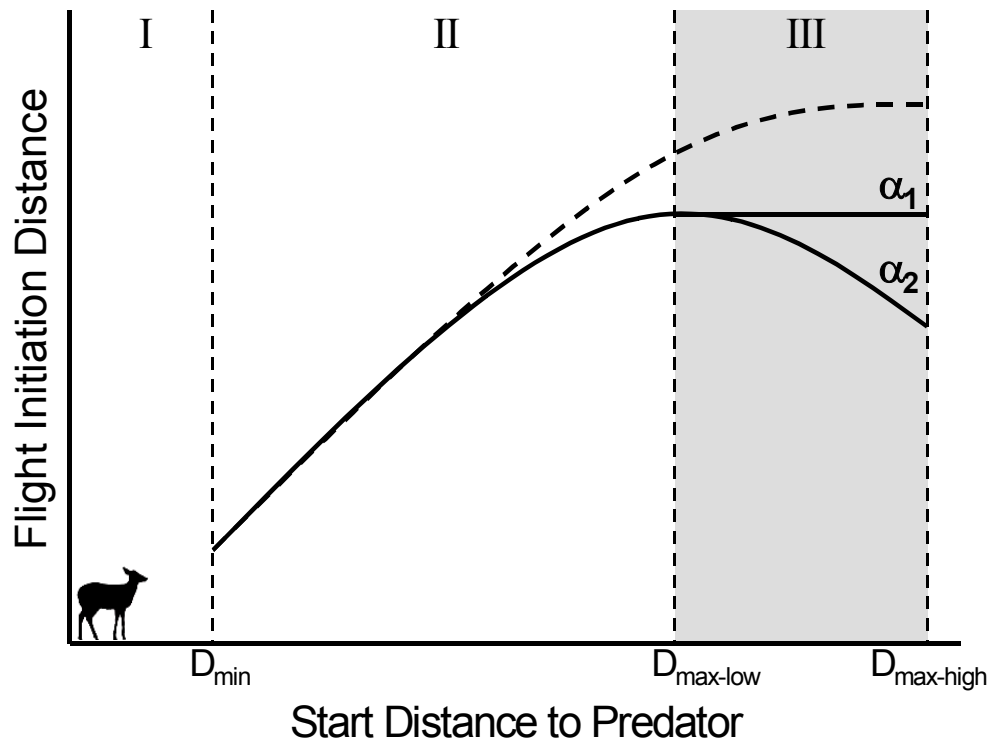
TABLE 3.2

Results of backward-elimination ANCOVAs on factors influencing flight initiation distance and assessment time. P to remove = 0.10

Factor	Order Removed	F	P	η^2
<u>Flight Initiation Distance</u>				
Group Size	1	0.191	0.664	0.003
Intent \times Sex	2	0.559	0.457	0.009
Speed \times Directness	3	0.706	0.404	0.011
Directness \times Intent	4	2.336	0.131	0.036
Intent	5	0.054	0.817	0.001
Presence of Gun		0.119	0.784	0.096
Sex		0.542	0.596	0.352
Approach Speed		3.421	0.069	0.050
Presence of Gun \times Sex		4.473	0.038	0.064
Directness of Approach		8.183	0.006	0.112
Start Distance ²		8.623	0.005	0.117
Start Distance		11.832	0.001	0.154
Alert Prior		20.229	< 0.001	0.237
<u>Assessment Time</u>				
Speed \times Directness	1	0.882	0.351	0.014
Directness \times Intent	2	0.611	0.438	0.010
Presence of Gun \times Sex	3	1.294	0.260	0.020
Presence of Gun	4	0.296	0.588	0.005
Directness of Approach	5	2.260	0.138	0.034
Intent		0.009	0.939	0.009
Sex		0.199	0.732	0.165
Group Size		3.054	0.085	0.044
Intent \times Sex		5.985	0.017	0.083
Alert Prior		25.745	< 0.001	0.281
Approach Speed		27.952	< 0.001	0.298
Start Distance		44.472	< 0.001	0.403

Statistics given for factors removed are reported from the step before they were eliminated from the model.

FIGURE 3.1



Predicted relationship between flight initiation distance and start distance (Tab. 3.1).

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 Zones 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 start distances 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 $D_{\max\text{-high}}$.

FIGURE 3.2

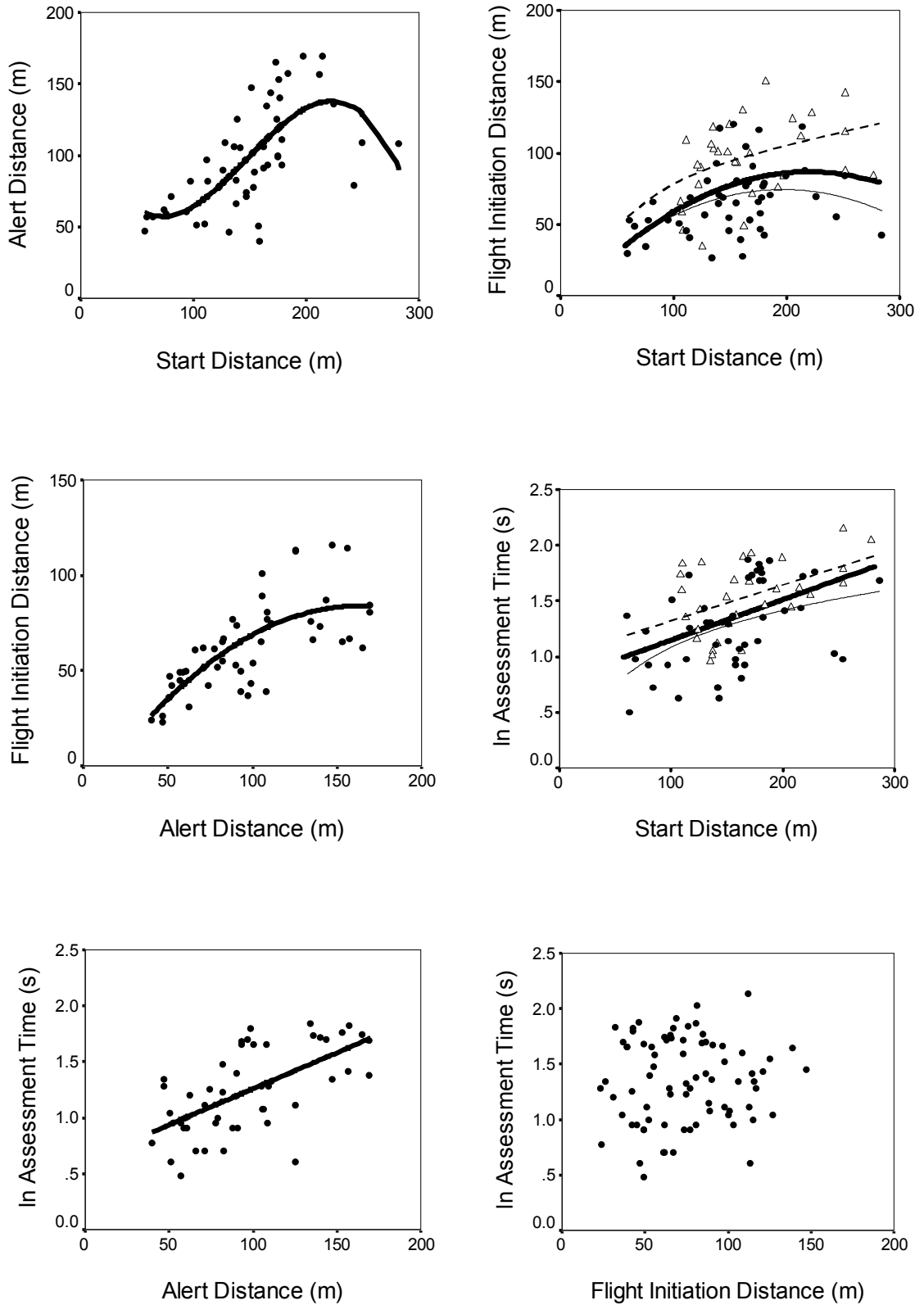
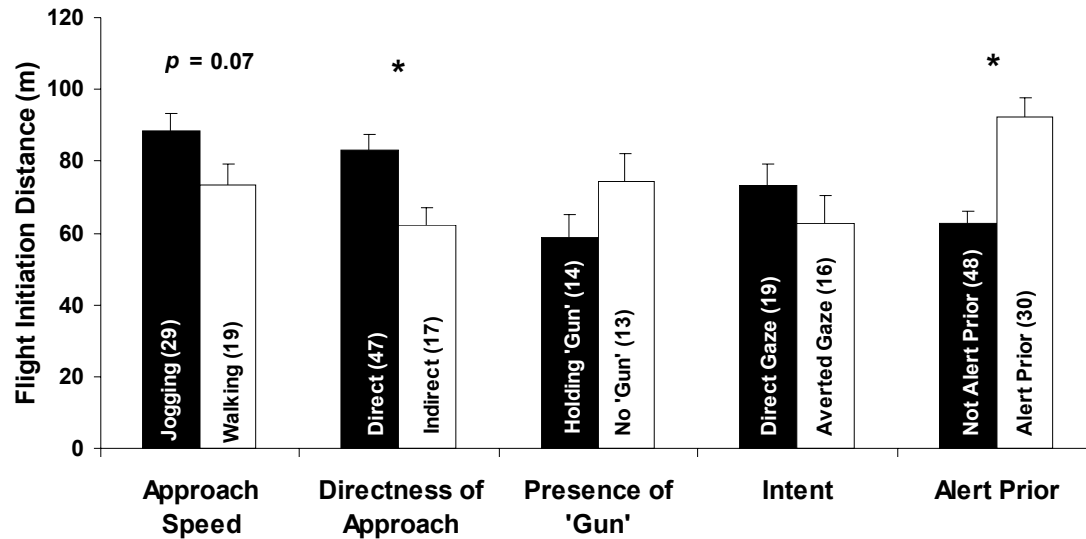


FIGURE 3.2 legend

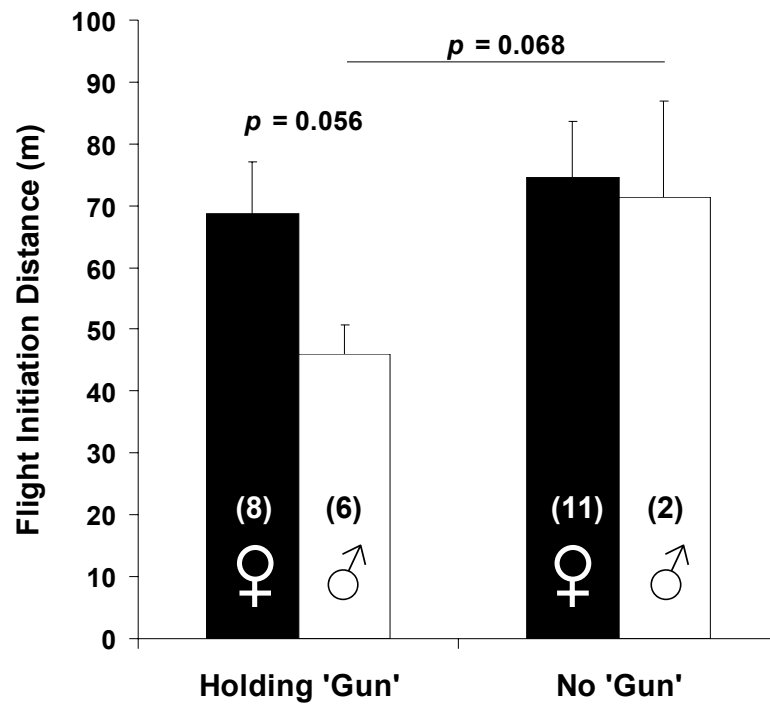
Scatterplots showing relationships between start distance, alert distance, flight initiation distance and ln assessment time (see Tab. 3.1 for definitions) of Columbian blacktailed deer responses to an approaching human. In (b) and (d) only, open triangles (\triangle : $n = 30$) are trials where the focal deer was alert prior to the start of the approach, and closed circles (\bullet : $n = 48$) 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): $n = 78$.

FIGURE 3.3



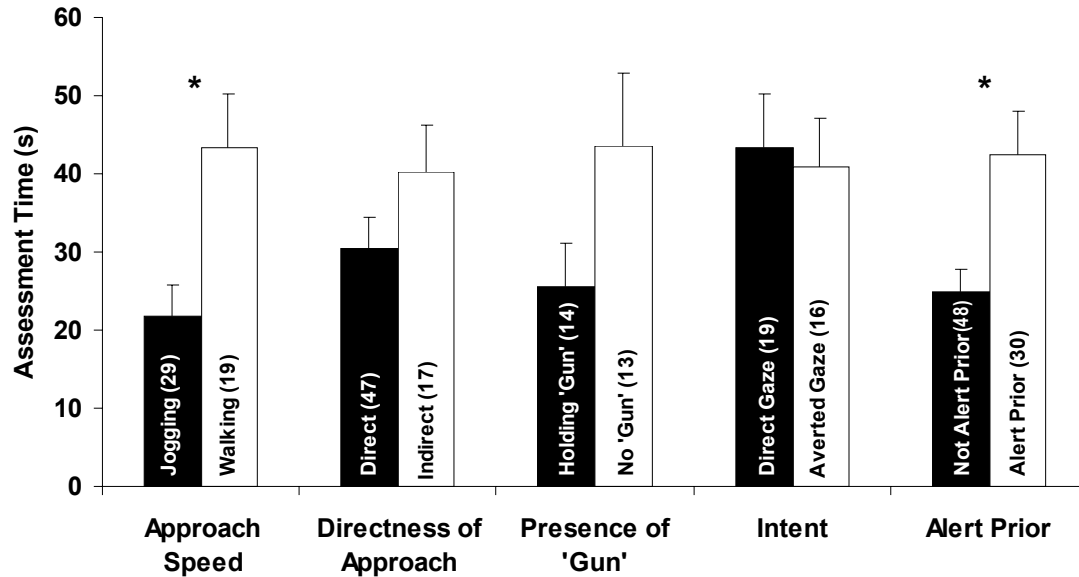
Mean \pm SE flight initiation distances (Tab. 3.1) of Columbian blacktailed deer in response to different types of approaches of a human; the figure shows responses to the different factors included in the ANCOVA analyses. Pairs of bars do not include multiple levels of other factors that were only examined in one member of the pair, *e.g.*, in 'approach speed', 'walking' only includes trials with 'no gun' and 'direct gaze' since 'presence of 'gun'' and 'intent' were only varied in walking trials. Sample sizes (*n*) for each bar are in parentheses inside the bar. * $P < 0.01$

FIGURE 3.4



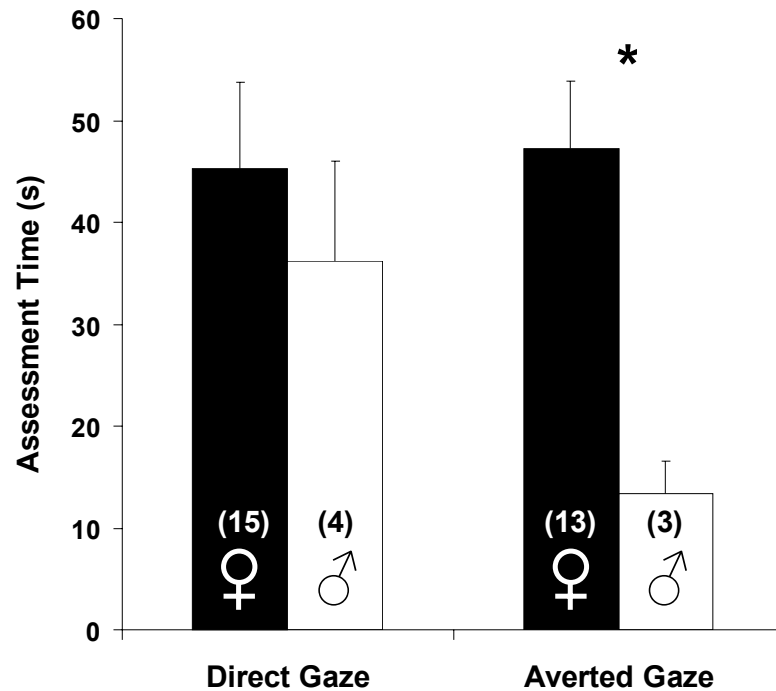
Mean \pm SE flight initiation distances (Tab. 3.1) of male and female Columbian blacktailed deer in response to the presence or absence of a simulated gun during the approach (walking directly with direct gaze) of a human. The overall interaction of sex and presence of 'gun' was statistically significant ($P = 0.038$). Sample sizes (n) for each bar are in parentheses inside the bar.

FIGURE 3.5



Mean \pm SE assessment times (Tab. 3.1) of Columbian blacktailed 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, *e.g.*, in “approach speed”, ‘walking’ only includes trials with ‘no gun’ and ‘direct gaze’ since ‘presence of ‘gun’ and ‘intent’ were only varied in walking trials. Sample sizes (*n*) for each bar are in parentheses inside the bar. * $P < 0.001$

FIGURE 3.6



Mean \pm SE assessment times (Tab. 3.1) of male and female Columbian blacktailed 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 ($P = 0.017$). Sample sizes (n) for each bar are in parentheses inside the bar. * $P < 0.05$

CHAPTER 4

Effects of Risk Assessment, Predator Behavior, and Habitat on Escape Behavior in
Columbian Blacktailed Deer

ABSTRACT

The relationship between pre-flight risk assessment by prey and the escape behaviors they perform while fleeing from predators is relatively unexplored. To examine this relationship, I approached groups of Columbian blacktailed deer (*Odocoileus hemionus columbianus*), varying my behavior to simulate more or less threatening behavior. I 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 greater distances and took flight paths at more acute angles, a property that would force a real predator to change direction suddenly. My 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 the traits 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 during my approach 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. In general, both pre-flight predator behavior and habitat features influence both duration and direction of escape.

INTRODUCTION

As predatory encounters escalate, animals must make a series of assessments and decisions regarding: (i) predator recognition and species recognition (Coss & Ramakrishnan 2000) (ii) the level of threat posed by the predator (Helfman 1989), (iii) when to flee based on the distances to the predator (Ydenberg & Dill 1986; Stankowich & Blumstein 2005; Chapter 2) and access to refuge (Kramer & Bonenfant 1997), and (iv) 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 & Thoen 1981; temperature: Losos 1988; wing morphology: Fernández-Juricic *et al.* 2006). While selection acts on each facet of the predatory encounter (Lima & Dill 1990), animals may be able to compensate for increased risk in one domain with reduced risk in another (Ajie *et al. In press*; DeWitt *et al.* 1999; Lind & Cresswell 2005). 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.

While many studies have focused on the decision of when to flee from predators (reviewed in Chapter 2; Stankowich & Blumstein 2005), very little attention has been paid to relating escape behavior to pre-flight risk assessment and predator approach behavior (Caro 2005). Flight initiation distance, the distance between the predator and prey at which the prey takes flight (Fig. 4.1), consistently has been found to be positively correlated 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: Chapter 3; Stankowich & Coss 2006). While the fact that flight initiation distance must be less than alert and starting distances could alone be driving these strong correlations, from a functional perspective, these relationships imply that animals incur time costs (in the form of 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 (Chapter 3; Stankowich & 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 & 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 pre-flight features of behavior to characteristics of escape behavior, such as distance moved, escape speed and direction, and style of escape.

Distance Moved

The distance a prey animal flees from an approaching predator before stopping (“distance moved”: Taylor & Knight 2003a; Fig. 4.1) 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. In press*). Distance moved has been shown to be positively associated, negatively associated, or unassociated to flight initiation

distance in lizards (positively associated: Bauwens & Thoen 1981; Schwarzkopf & Shine 1992; negatively associated: Martín & López 2003; unassociated: Blamires 1999; Cooper 1997a) and ungulates (positively associated: Taylor & Knight 2003b; negatively associated: Andersen *et al.* 1996, Hamr 1988; unassociated: Taylor & Knight 2003b). If animals compensate for risky behavior in one context with conservative behavior in another (Lind & 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 is also affected by the directness of predator approach (Bratton 1990) and predator approach speed (Cooper 1997b), two reliable indicators of the level of threat posed by the predator. Additionally, contextual factors influence the distance an animal flees. 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 & Knight 2003b), when animals are in areas with more human disturbance or hunting (King & Workman 1986), when animals are farther from refuge (Cooper 1997a; Martín & López 2003; Snell *et al.* 1988; Fernández-Juricic *et al.* 2006; Cassirer *et al.* 1992), and when animals are in larger groups (Taylor & Knight 2003b; Aastrup 2000). 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; Snell *et al.* 1988) and reproductive state (Aastrup 2000) can affect distance moved.

Escape Angle and Style

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 (Fig. 4.1) where flight directly away from the predator is 180° and flight directly towards the predator is 0°. Cooper (1997a,b) 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 (Blumstein 1992; Lima & Dill 1990; 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 (*O. 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 towards slopes, while 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 suggests that a variety of factors influence risk assessment and escape behavior in prey animals.

Hypotheses

I examined the responses of Columbian blacktailed deer (*O. h. columbianus*) to an approaching human as a method of investigating the relationships between pre-flight 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 Chapter 2; Stankowich & Blumstein 2005). While previous studies suggest that there is wide interspecific variation in how features of pre- and post-flight 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. I hypothesized that more threatening approaches will result in greater escape distances since predator behavior has been shown to significantly impact flight initiation distance and assessment time (time elapsed between alert and flight behavior) in deer (Chapter 3; Stankowich & Coss 2006). Additionally, I predicted that when the approacher is closer to the prey at flight initiation, the prey will flee at a more acute escape angle to force the approacher to

alter its course rapidly and potentially lose ground on the prey. I 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 blacktailed deer made use of the local topography during escape. Determination of the relationships of these escape behaviors with pre-flight decision making and other environmental factors will fill a large gap in our understanding of how behavior at the first stages of a predatory encounter affects the initiation and expression of antipredator behavior in subsequent stages (Lima & Dill 1990; Lind & Cresswell 2005).

METHODS

Field Site and Subjects

I conducted 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. Vegetation cover was minimal, 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. Hunting has been banned in the park since 1971, although there are scattered reports of illegal poaching. 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.

Like most studies of wild deer, I was unable to mark or identify individuals based on variation in coloration or coat patterns. However, many stable groups

(congregations of individuals within 30 m of their nearest neighbor (Stankowich 2003) that were sighted reliably in the same location on multiple days) were identifiable by size, sex ratio, and location within the park. If I tested the same group more than once, I waited at least two 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. I am, therefore, confident that replication on the same animal was rare.

Approach Methodology

I conducted approaches as described in Chapter 3 and Stankowich and Coss (2006). A focal deer was chosen in the group; typically this was the animal nearest to me because I wanted the focal to perceive that it was the direct target of approach, and I didn't want an animal between the focal and me to flee first, which could confound the focal deer's decision to flee. Typically from the roadside, I emerged from an automobile, moved into a position (usually within 20m of the automobile and in view of the focal) from which I had a direct line of approach to the focal deer (fawns (≤ 1 yr) 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 my location when each occurred. I marked my location when I began the approach, when the deer became alert (*i.e.*, standing with its head and neck upright and looking at me), when the deer fled (defined as movement by walking, trotting, stotting, or galloping), and the original location of the deer. I 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 rangefinder and were accurate to the nearest 1 m.

After the end of each trial, I measured the angle of escape by laying two poles of known length on the ground, one in-line with the direction of approach (side 1), one in-line with the initial direction of escape (side 2), and the origin of the deer as the intersection. I then measured the distance between the free ends of the poles (side 3) to create a triangle and used the lengths of all three sides and a geometric formula to calculate the angle of escape (the angle between the direction of approach and direction of escape: Fig. 4.1). I recorded as ordinal values differences (>5 m) in elevation between my starting position, the deer's origin, and the deer's final location. I 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. I noted the sex of the focal deer, if it was alert at the start of approach, and the size of the deer group. I 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 me, and these cues do not affect flight decisions in this population (Chapter 3; Stankowich & Coss 2006). A second observer video recorded the trials from a much greater distance than the starting distance and did not noticeably affect the deer's behavior, using a Panasonic model PV-DV601D mini digital video recorder with 20X optical zoom lens. From

videotapes, I noted the presence or absence of trotting, stotting, and galloping behaviors (defined by: Hildebrand 1976; 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, I calculated the mean bout duration. I discarded trials if the distances or times measured were questionable or if passing cars or other provocative situations alarmed any members of the group. I 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 four ways as described in Chapter 3 and Stankowich and Coss (2006). I varied: (1) approach speed by jogging versus walking toward the deer, (2) directness of approach by moving towards a point approximately 30 m to the left or right of the focal animal versus moving directly towards the focal, (3) predator intent by averting my gaze towards the ground during approach (*n.b.*, when gaze was averted, my eyes were completely concealed by the brim of a hat) versus staring directly at the focal deer, and (4) presence of ‘gun’ by holding a long black rod up at my eyes to simulate aiming a rifle at the focal versus walking normally with my arms swinging at my 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 ,

two-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), the deer's change in elevation during flight (down, no change, up), the my change in elevation from start to flight (down, no change, up), and my initial elevation 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 (Chapter 2; Stankowich & Blumstein 2005) and/or their lack of effect on flight decisions in this population (Chapter 3; Stankowich & 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. I 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 were entered into the model equation at the next step. I 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. I

analyzed separately the effects of alert and flight distance 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 (two-tailed: Sokal & Rohlf 1995). All data are presented in means \pm SEs. All statistical analyses were conducted in SPSS 10.0.

RESULTS

Escape Angle

Deer fled at an average angle of $135.9 \pm 3^\circ$ away from me, with a range of 70° to 180° . When deer fled at greater distances, they took flight paths at a greater angle from me ($N = 82$, $P = 0.049$; Tab. 4.1, Fig. 4.2). I 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 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 (Fig 4.2). 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 (Adj. $R^2 = 0.049$).

Distance Moved

Deer fled an average of 105 ± 12 m ($N = 40$) with deer moving out of sight of me in the remaining 48 trials. Flight initiation distance had the strongest association with distance moved ($N = 32$, $P = 0.002$; Tab. 4.1, Fig. 4.3a): deer fled to greater

distances when they initiated flight at greater distances. Larger groups of deer fled greater distances ($P = 0.007$; Fig. 4.3b) and deer that were initially in only grass fled longer distances than deer that were in grass mixed with scrub ($P = 0.018$; Fig. 4.3c). There was no statistically significant effect of sex on distance moved ($P > 0.05$). While 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 I averted my gaze compared to when I stared directly at the deer; however this trend was not statistically significant ($P = 0.066$). 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 four terms (Tab. 4.1) and explained nearly 50% of the variance in distance moved (Adj. $R^2 = 0.488$, $P < 0.001$).

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 origin, where stotting was more likely to occur with increased vegetation height (Wald $\chi^2 = 10.084$, d.f. = 1, $P = 0.001$; Tab. 4.2). Moreover, there was a trend for increased probability of stotting when deer fled at greater escape angles (Wald $\chi^2 = 3.110$, d.f. = 1, $P = 0.078$); deer that fled directly away from me 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, d.f. = 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 since trotting was observed in over 80% of flights, I 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 ($P = 0.048$; Tab. 4.1, Fig. 4.4a), and there was a trend for a shorter duration of trotting in response to indirect approaches ($P = 0.067$; Fig. 4.4a). Trotting duration was also impacted by environmental factors. Shorter vegetation at the deer's point of origin appeared to lead to a longer duration of trotting ($P = 0.058$; Fig. 4.4b), and deer that fled uphill tended to trot for longer periods ($P = 0.067$; Fig. 4.4c). No other factor significantly contributed to the final model of trotting duration (Adj. $R^2 = 0.171$, $P = 0.007$). The only factor to contribute to the explanation of variation in the duration of stotting (overall mean: 6.0 ± 1.0 s; Adj. $R^2 = 0.100$, $P = 0.056$) was the presence of a simulated gun under which circumstances deer stotted for somewhat longer periods when I carried a 'gun' ($P = 0.056$; Fig. 4.4a), 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 ($\chi^2 = 15.705$, $P < 0.001$). Alert and flight distance had no effect on changes in elevation during flight (alert distance: Wald = 0.158, d.f. = 1, $P = 0.691$; flight initiation

distance: Wald = 0.268, d.f. = 1, $P = 0.608$). Initial differences in elevation between the myself 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 when I 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).

DISCUSSION

Deer escape responses were deeply dependent on variation in approach behavior, environmental characteristics, and their proximity to the approaching human. Escape angles were more acute when the deer allowed closer approach by me, as if to disrupt the continuity of approach and to force me to make potentially energetically costly shifts in direction if I was 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 me was significantly impacted 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 strongly influence the direction of flight (*e.g.*, contagious following of other group members, known sources of refuge, locating a hidden fawn). To my 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 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 effectively increase this distance during pursuit. In essence, the ability of the predator to visually track 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 doesn’t maximize the absolute distance between the predator and prey (*e.g.*, anything 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). My results suggest that deer use acute escape angles to hinder

pursuit at close proximity and simply flee directly away from an approacher when they are farther away.

Distance Moved

I found distance moved to be positively related to flight initiation distance. Chapter 3 and Stankowich and Coss (2006) found that flight initiation distance was positively correlated with both starting distance and alert distance in blacktailed deer. Together, these correlations indicate that pre- and post-flight 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, while 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 (*c.f.*, Capitanio 2004). Nevertheless, future tests of

compensation and correlation of antipredator behavior across contexts should focus on testing individuals repeatedly to reliably assign reactivity scores to individuals before testing flight responses.

While the dilution of risk in larger groups should lead to shorter flight initiation distances and shorter distances moved, I found that larger groups of deer fled longer distances, a finding which is in agreement with similar findings in caribou (*Rangifer tarandus*) and Rocky Mountain mule deer (respectively, Aastrup 2000; Taylor & Knight 2003b). While 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 mule deer 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 three hypotheses are proximate explanations of why *O. hemionus* flee at greater distances when in larger groups (Chapter 3; Stankowich & Coss 2006; Taylor & Knight 2003b), but the latter two hypotheses address not only the increased flight initiation distances but also longer distances moved.

Deer that were initially located in grass + 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 blacktailed deer (*O. h. columbianus*) use hiding during escape more than mule deer (*O. h. hemionus*: Linsdale & 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 me. My 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 more descriptive accounts of deer behavior (Geist 1981; Linsdale & Tomich 1953).

Escape Style and Predator Behavior

More threatening approaches led to increased durations of rapid flight by deer (Fig. 4.4a). Few studies have addressed flight duration with respect to level of threat, but Freddy and colleagues (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 whitetailed deer ran versus walked when approached in hunted areas than in areas where no hunting occurred (Behrend & 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 Chapter 2; Stankowich & Blumstein 2005; Ydenberg & Dill 1986), and certainly an animal's flight duration will depend on the duration and intensity of subsequent pursuit by the predator. Nevertheless, my findings provide initial quantitative evidence that variation in pre-flight 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 (Fig. 4.4b) and were more likely to stot when in taller vegetation (Tab. 4.2), suggesting that stotting behavior in deer aids in traversing tall vegetation quickly and that when fleeing through short grass, trotting is more energy efficient. Bounding, stotting, and leaping by ungulates have been shown previously to serve as a means to clear obstacles (Geist 1981; Lingle & Pellis 2002) and as a potential signal to predators of physical ability (reviewed in Caro *et al.* 2004). Indeed, blacktailed deer aim their flight to put obstacles (*e.g.*, fences, uneven rocky surfaces) between themselves and the predator or flee to areas with deep vegetation that would both hinder the predator's advance and provide potential refuge (Dasmann & Taber 1956; Geist 1981; Linsdale & Tomich 1953). This supposition is evidenced in the high frequency of trials in which deer fled to taller vegetation and the shorter distances fled in denser vegetation. Additionally, evidence of longer trotting durations when fleeing uphill (Fig. 4.4c) suggest 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. While I found that deer moved up slopes more often than expected, deer that detected and fled from me at longer distances were not more likely to flee up slopes than deer

that detected the approacher and fled later. It should be noted that in the analyses of changes in elevation and vegetation height during flight, I am assuming that deer had equal opportunity to flee uphill, downhill, or to stay at the same elevation in each trial. To confirm this, however, would be a logistically and statistically daunting task. 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 may be a refuge with a better vantage point for *O. hemionus* in general, deter further pursuit by coyotes (Lingle 2002), and generally provide an increased perception of safety from predators. Still, woodchucks have faster escape speeds when they are far from refuge (Kramer & Bonenfant 1997), indicating that some species do 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 impacts on flight behavior and escape decisions. I 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 (Andersen *et al.* 1996; Hamr 1988). However, I 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 & Cresswell 2005), my evidence suggests that animals that are relatively wary may flee at greater distances and move greater distances while less wary animals may allow the predator to approach more closely and move shorter distances. I 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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TABLE 4.1

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								
	Adj. <i>R</i> ²	0.035	0.488	0.171	0.100			
	d.f.	1, 81	4, 27	4, 54	1, 26			
	<i>P</i>	0.049	<0.001	0.007	0.056			

Results in bold signify 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.

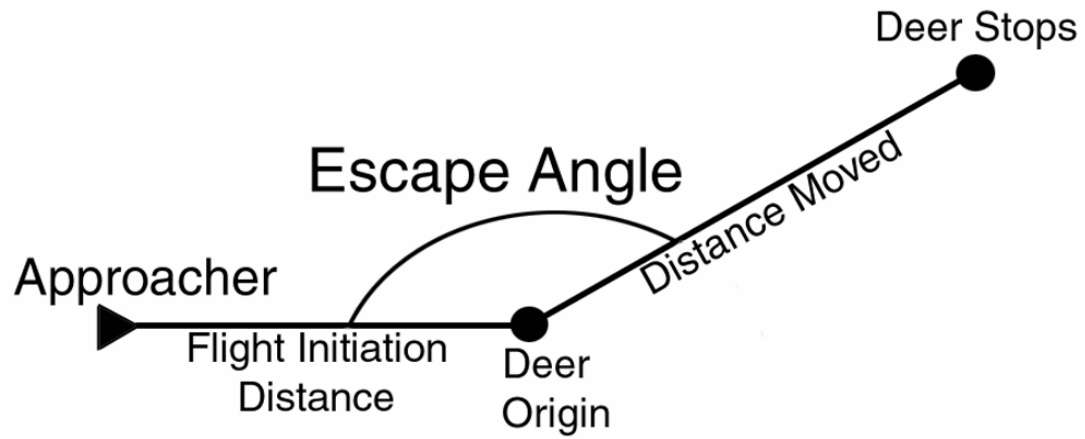
TABLE 4.2

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

		Vegetation Height (ft)					Total
		0 – 1	1 – 2	2 – 3	3 – 4	4 – 5	
Presence of Stotting	Absent	30	10	2	0	1	43
	Present	7	10	10	1	0	28
	Total	37	20	12	1	1	71

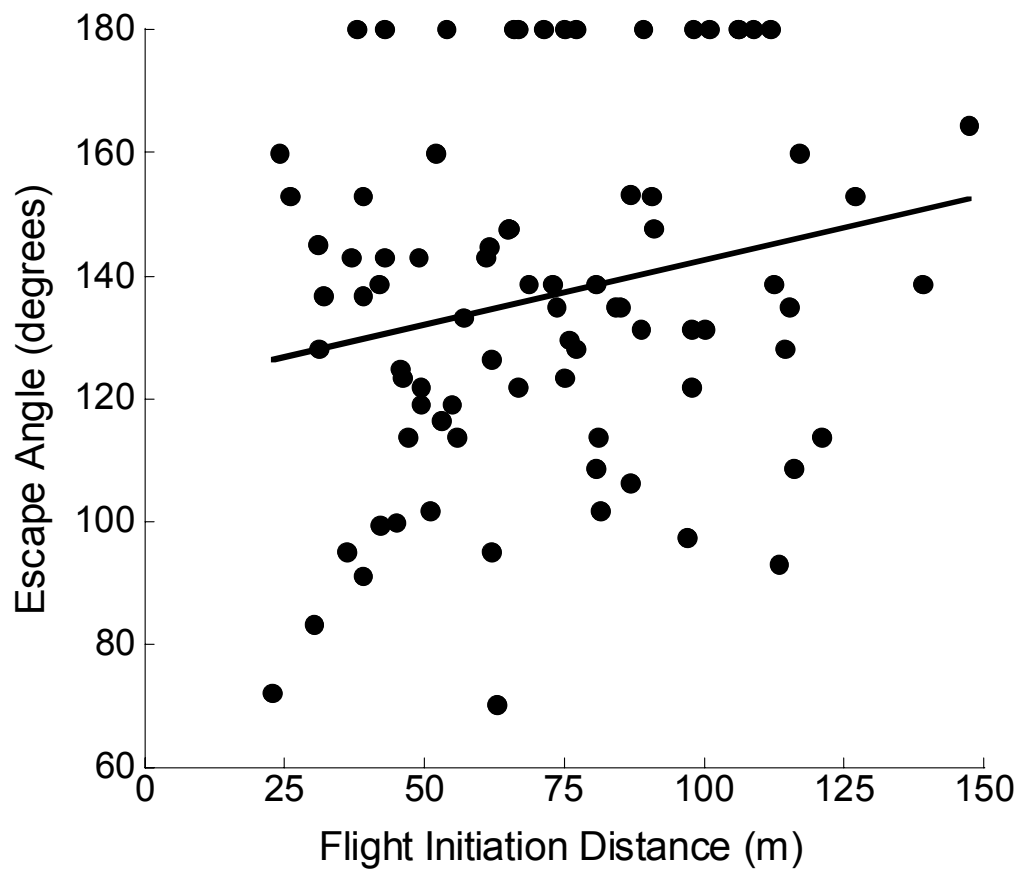
Binary Logistic Regression: Wald $\chi^2=10.084$, d.f.=1, $P=0.001$

FIGURE 4.1



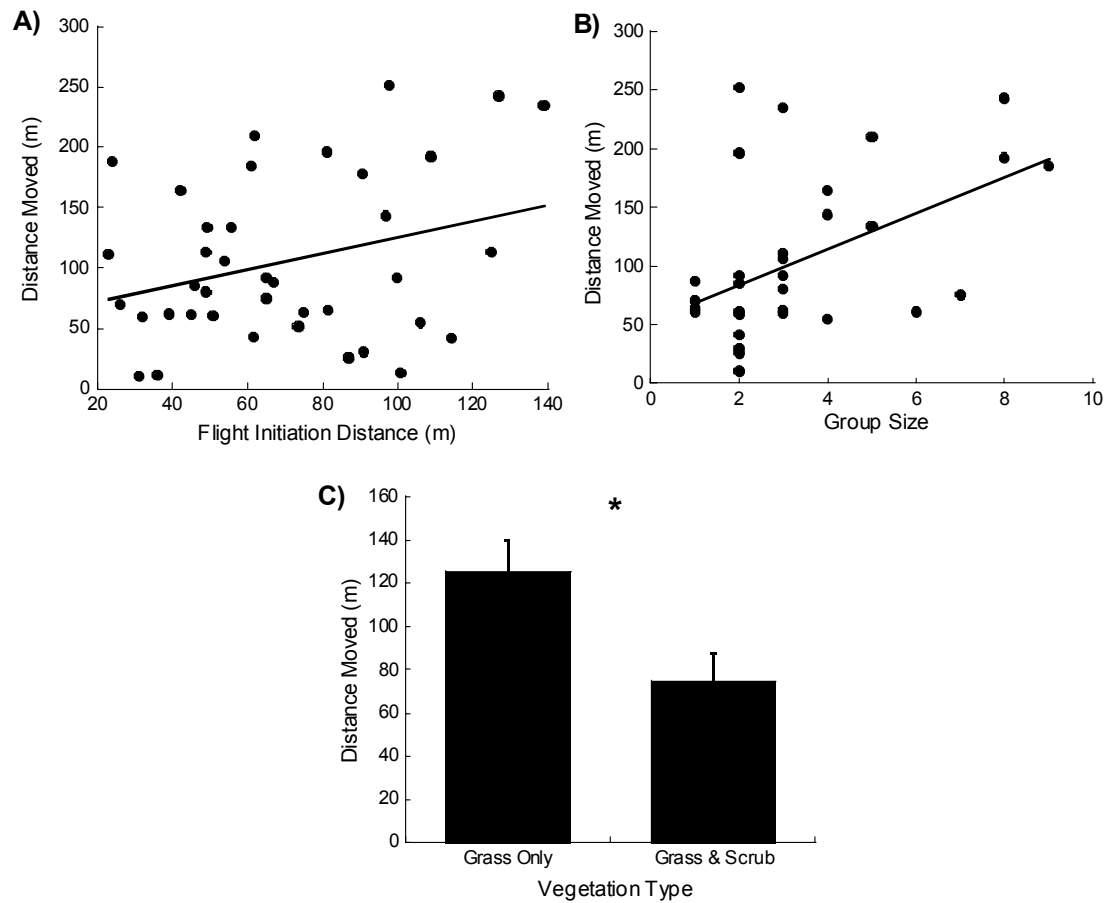
Plan view of deer flight initiation distance from an approaching human, escape angle, and distance traveled during flight. The approacher is represented by a black triangle indicating the direction of approach. The positions of the focal deer before and after flight are represented by black circles.

FIGURE 4.2



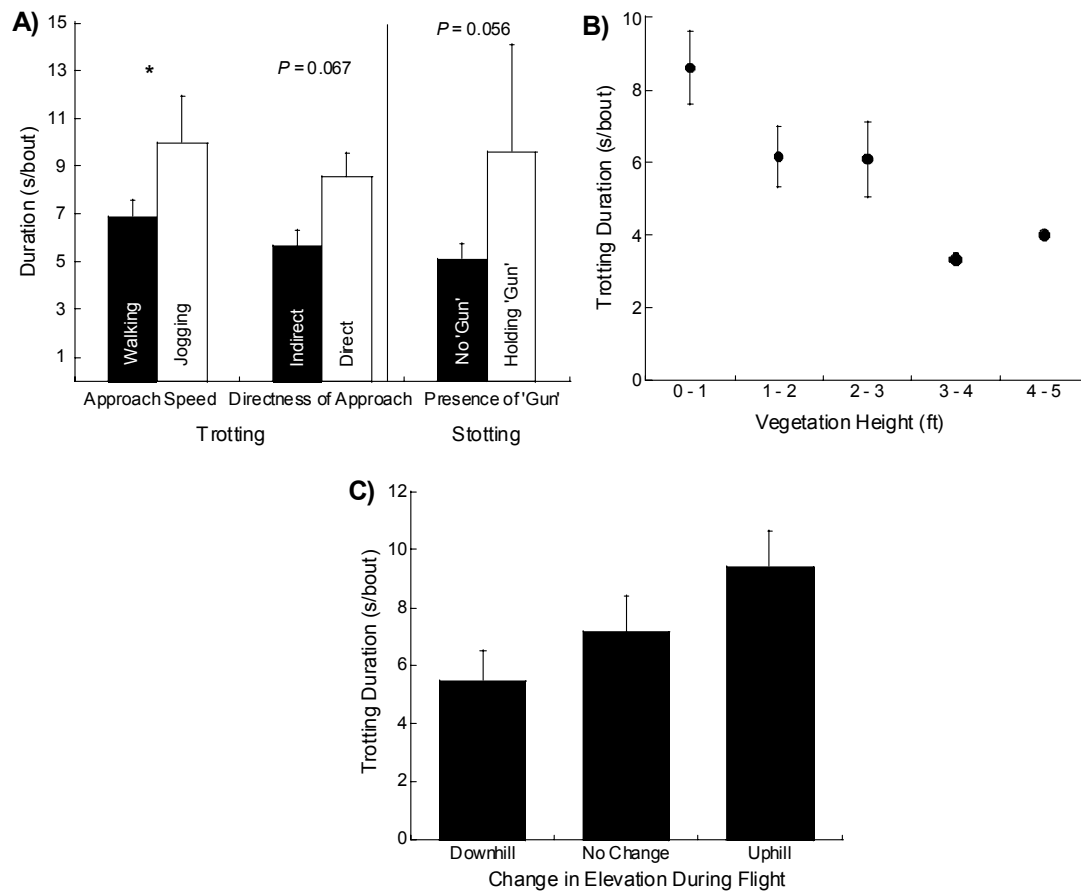
The relationship of escape angles and flight initiation distances taken by Columbian blacktailed deer during flight in response to approaches by a human ($N = 82$) (line is linear regression with partial correlation, $r = 0.217$).

FIGURE 4.3



The distance Columbian blacktailed deer moved during flight in response to approaches by a human ($N = 31$) before stopping in view. (A) Scatterplot of distance moved and flight initiation distance (line is linear regression with partial correlation ($r = 0.444$)). (B) Scatterplot 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: $*P < 0.05$).

FIGURE 4.4



(A) Duration of flight behavior of Columbian blacktailed deer in response to human approaches for trotting and stotting behavior included in the regression analyses (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 SE) 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 ($N = 59$; $P = 0.067$; $r = 0.247$).

CONCLUDING REMARKS

The ultimate goal of the research described in this dissertation was designed to demonstrate how we might gain insights into the cognitive processes of animals during encounters with predators by studying variation in their behavior in response to simulated predators. As animal biologists, we often talk about the problem of getting inside the “black box” of the animal’s mind: we are forced to use outward expressions of behavior to understand the perceptions, thoughts, and mental processes of animals. In order to survive and reproduce, animals must use the same cognitive processes that humans do: stimulus recognition, information acquisition, dynamic assessment of that information, and adaptively deciding on the best course of action. I wanted to show how environmental and evolutionary factors influence these processes and how, by studying different response to different stimuli, we can study each process.

This work benefited greatly from a large literature on the behavior, ecology, and evolution of mule deer and blacktailed deer. Several comprehensive monographs and book chapters (Cowan 1936; Dasmann & Taber 1956; Geist 1981; Linsdale & Tomich 1953; Taber & Dasmann 1958; Wallmo 1981) provided a wealth of information on mule deer natural history that helped shape the arguments in each chapter. More recent papers by Susan Lingle (Lingle 1992; Lingle 2000; Lingle 2001; Lingle 2002; Lingle & Pellis 2002; Lingle & Wilson 2001) and Taylor and Knight (2003) have advanced our knowledge of mule deer antipredator behavior and provided empirical support for much of the earlier more descriptive works of natural history. Chapter 4 builds on much of the knowledge put forth in this literature, and Chapters 1 and 3 address the cognitive aspects of antipredator behavior, which have been relatively unexplored to date.

In Chapter 1, I analyzed a behavior called “alarm walking,” which was previously undescribed in the literature. Valerius Geist and others have observed this form of high-step walking in Rocky Mountain mule deer when real predators are present, but since these live interactions are so rarely observed in nature, it was never quantified. In fact, in terms of its timing and kinematics, alarm walking is a quantitatively different style of walking (Stankowich & Coss, in preparation) than the normal walk of a cervid (Hildebrand 1976), and I hope to publish the first quantification of the footfall timing and leg lifting movements of this behavior with Richard Coss in a forthcoming manuscript.

The use of predator models to elicit antipredator responses in animals is a common practice in the study of behavior. The model presentations in Chapter 1 were inspired by previous work on primate responses to painted leopard models in the wild and in captivity (Coss & Ramakrishnan 2000; Coss *et al.* 2005; Hollis-Brown 2005; Ramakrishnan & Coss 2000a; Ramakrishnan & Coss 2000b; Ramakrishnan & Coss 2001), however, the use of full-sized poster photographs of the predators was novel to this study. I initially intended to base this entire dissertation on a comparative study of the responses to the models by Columbian blacktailed deer, Axis deer (*Axis axis*), and Fallow deer (*Dama dama*) at Point Reyes National Seashore. Logistical difficulties made it impossible to do the model presentations on the latter two species, however it provided the opportunity to study the flight decisions and escape behavior of blacktailed deer, which ended up filling up the bulk of the dissertation. When I began the model presentations on blacktailed deer, I expected to see the strongest response to the puma, a moderate response to the leopard, a weak response to the tiger, and no

response to the deer. The surprising result that deer hardly responded to the leopard at all and responded relatively strongly to the tiger suggested that the camouflaging properties of the leopard's spotted coat re-emerged after hundreds of thousands of years of relaxed selection. Given the length of allopatry between Columbian blacktailed deer and jaguars, the next logical follow-up study should examine the response of mule deer in the Southwest US, where local jaguar extinction is relatively recent, to the leopard and puma models to determine if any loss of visual recognition of the spotted coat as dangerous has occurred in these deer.

As evidenced by the abundance of studies found in Chapter 2 that examined the effects of different factors on flight initiation distance, many researchers are interested in measuring fear in animals and what influences animals' perceptions of risk. Recent literature has explored the role of starting and alert distance on flight initiation distance (Blumstein 2003; Blumstein *et al.* 2005; Cooper 2005; Stankowich & Blumstein 2005; Stankowich & Coss 2006), and I believe the next step in theoretical advancement of this field is to build a dynamic model of risk assessment during predatory encounters using Bayesian information updating. Additionally, studies of escape behavior can help inform management of wild populations and park design. These implications for management have already been described at length for avian species (Fernández-Juricic *et al.* 2001; Fernández-Juricic & Schroeder 2003; Fernández-Juricic *et al.* 2004; Fernández-Juricic *et al.* 2005). Through an understanding of how ungulates specifically are impacted by human activity we can design refugia with buffer zones between human roads/trails and prime animal habitat

so that animals have enough land where their “zones of awareness” (Chapter 3; Stankowich & Coss 2006) are not limited by human activity.

I split up my analyses of starting distance, alert distance, flight distance, assessment time, distance moved, and escape style into two chapters and two manuscripts for publication in order to avoid an overwhelmingly long paper where details of each step in the attack sequence would be lost. However, I believe that this set of measurements would benefit from a single overall analysis to show direct and indirect links between each measure. Perhaps this could be achieved via path analysis showing directional effects between alert, flight, and escape decisions. Bulova (1994) used path analysis to study the direct and indirect effects of air temperature, the directness of the observer's approach, and distance to nearest cover when first sighted, wind, and time of day on the flight initiation distance and distance moved on zebra-tailed lizards (*Callisaurus draconoides*) and two populations of greater earless lizards (*Cophosaurus texcanus*). To my knowledge, this is the only study to use path analysis to study the relationships between flight initiation distance and distance moved. Currently, I can say that in blacktailed deer alert distance is positively correlated to flight initiation distance and flight initiation distance is correlated with distance moved. Future data sets on flight and escape decisions should consider using path analysis to judge the effects of different factors throughout the attack sequence and to quantify multi-level correlations between measures of flightiness.

In Chapters 3 and 4, I discussed at length the role of individual variation in reactivity on the decisions of when to flee and how to escape. Animals that were alert prior to the start of the approach fled at greater distances and assessed the approacher

for longer periods of time before fleeing (Figs. 3.3 & 3.5). Additionally, animals that fled at greater distances, fled greater distances (Fig. 4.3a). Summed together, I suggest that antipredator behavior is correlated across these contexts and there may be a reactivity syndrome in prey animals (Sih *et al.* 2004a; Sih *et al.* 2004b). Animals that are more wary or less habituated exhibit more conservative antipredator behavior across the board: becoming alert earlier, fleeing at greater distances, and fleeing greater distances. To bolster this argument would require observing individuals reliably and repeatedly over time in order to establish that individuals are consistent in their behavior across contexts over time. The results presented in Chapter 4 are contrary to the compensation hypothesis in antipredator behavior (Lind & Cresswell 2005) which states that animals that exhibit riskier behavior earlier in the attack sequence will be more conservative in their responses later in the attack sequence. Nevertheless, the inter-context correlation hypothesis would be more testable in a species that can be marked, controlled easily, and exhibits clear antipredator behavior at each stage of the attack sequence (*e.g.*, clear responses to an approaching stimulus, consistent flight behavior, *etc.*). Future study of reactivity syndromes in antipredator behavior should focus on how individual variation affects responses to familiar versus novel species – perhaps different behavioral types will adjust their antipredator responses to novel predators at different stages in the attack sequence.

In summary, I hope this dissertation helped demonstrate that we can gain insights into animal decision-making processes by observing their outward behavior in response to predators and that the decisions animals make during predatory encounters are correlated across the attack sequence. I am certainly not the first to make this

attempt and recent reviews of antipredator behavior have come to similar conclusions (Caro 2005; Lima & Dill 1990). I found that relaxation in selection pressure on visual recognition of a unique predator leads to the loss of recognition and the re-emergence of the camouflaging capabilities of coat patterns. While the finding of loss of visual recognition is not new (*e.g.*, Blumstein *et al.* 2004), I am the first to show that the loss of a once salient recognition cue (spotted coat) can regain its ability to camouflage the predator, demonstrating a predator-prey evolutionary arms race of visual recognition of the predator. Those studying the evolution of camouflage can gain a great deal of insight into the effectiveness of animal patterns over evolutionary time. In the very least, I hope I have provided a foundation for future research on visual predator recognition and prey decision-making across the attack sequence. I believe the animal behavior community still has much to learn about these topics and with advances in animal monitoring/observation technology (*e.g.*, remote digital video transmission, GPS, infrared video) and analytical statistics (*e.g.*, Bayesian updating, Path Analysis, Multilevel Modeling, AIC Model Selection Criteria), we can gain further insight into prey risk assessment and decision making during predatory encounters.

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APPENDICIES

APPENDIX A

Factors investigated

(i) Predatory effects

Many different aspects of a predator's approach toward prey have been studied for their role in influencing prey flight initiation distance. The speed at which the predator approaches is commonly included in analyses, and while, in reptiles, faster approaches nearly always elicited flight at a greater distance, the trend in other taxa was less clear. We included studies that measured the role of directness of approach on flight initiation distance. This factor is usually broken up into direct approaches or indirect approaches where the predator tangentially approaches the prey with a set bypass distance. Finally, we included studies examining the effect of relative predator size (*e.g.*, large vs. small predator) on flight initiation distance where the predator is classified simply as small or large. All three of these categories were then analyzed together to determine the overall importance of predator traits on the evolution of fear in prey. We identified high-risk approaches (fast, direct, large predator) as the treatment and low risk approaches as the control (*i.e.*, positive r values indicate that higher risk approaches led to animals initiating flight at greater distances).

ii) Refuge distance

The distance between an individual prey animal and safe locations has been shown both empirically (see Appendix B) and using theoretical models (Kramer & Bonenfant 1997) to play a significant role in the decision to flee. We examined

studies that correlated distance to nearest refuge with flight initiation distance to determine the strength of effect it has on flight decisions. Positive r -values indicate that longer distances to refuge lead to animals initiating flight at greater distances.

(iii) Group size

In their initial review of flight initiation distance, Ydenberg & Dill (1986) found no consistent effect of group sizes on flight distance and concluded that the large number of other species-specific influences on group size likely reduces our ability to make cross-taxa generalizations about its effect on flight initiation distance. We analysed studies where group size was compared with flight initiation distance to determine if (1) there is, indeed, a general effect of group size on flight, and (2) if there are significant effects within taxa that shed light on the role of other factors in its relationship with the decision to flee. Positive r -values indicate that animals in larger groups initiate flight at greater distances.

(iv) Prey defenses

We included studies that compared species with varying degrees of morphological defenses or varying degrees of morphological crypsis. The perception of risk by cryptic or heavily armored prey likely plays a large role in determining what strategy to use when confronted with a potential predator (Ydenberg & Dill 1986). After each factor was analyzed individually, we combined both types of studies into a single meta-analysis. We identified species lacking in

crypsis or morphological defenses as being at higher risk: positive r -values indicate that these unprotected animals initiate flight at greater distances.

(v) Temperature in reptiles

Air and body temperature have been shown to have profound impacts on reptile physiology and behavior, specifically, maximum escape speed. Hertz *et al.* (1982) found that at high body temperatures, two *Agamid* lizard species flee rapidly from predators but at lower body temperatures, they show reduced speeds, hold their ground, and attack predators aggressively. We examined the effect of temperature on cold-blooded organism, specifically reptiles. We included studies that measured the effects of air, body, substrate or water temperature on reptile flight initiation distance. Positive r -values indicate that colder reptiles allow closer approach than warmer reptiles.

(vi) Experience with and habituation to predators

We included studies that measured the degree of experience the prey had with the predator or predators in general. Studies were divided into two categories for meta-analyses. First, we analyzed studies that compared flight initiation distances in populations of prey that differed in the relative density of predators around them. Low-density areas were labeled as treatment areas and high-density areas as control areas: positive r -values indicate that prey fled sooner (*i.e.*, had greater flight initiation distances) in areas with low predator density. Second, we analyzed studies that did multiple sequential approaches towards prey and compared

the flight initiation distance from the first approach to that measured on subsequent approaches. We categorized the second approach as high risk and the first approach as low risk. Thus, positive r -values indicate that animals tolerated closer approaches on the first approach relative to subsequent approaches. After each factor was analyzed individually, we combined both types of studies into a single meta-analysis.

APPENDIX B: Factors contributing to perceived risk and their effects on flight initiation distance

Taxa	Prey Species	Predator(s)	Effect on Flight Distance	<i>n</i>	<i>R</i>	Source
Predator Approach Speed						
I	Ocean skater: <i>Halobates robustus</i>	White rectangle	No effect			Treherne & Foster 1980
F	Damselfish: <i>Chromis cyanea</i>	Circle Model	No effect	15	.24	Hurley & Hartline 1974
		Square Model	No effect	9	.20	
F	Zebra danio: <i>Brachydanio rerio</i>	Largemouth bass	Fast > Slow approach	12	.69	Dill 1973, 1974a
F	Reef-fish species	Grey shark	Fast > Slow approach			Eibl-Eibesfeldt 1965
R	Lizard: <i>Anolis lineatopus</i>	Human with stick	Fast > Slow approach			Rand 1964
R	Broad-headed skink: <i>Eumeces laticeps</i>	Human	Fast > Slow approach	52	.66	Cooper 1997b
R	Eastern brownsnake: <i>Pseudonaja textiles</i>	Human	No effect			Whitaker & Shine 1999
R	Desert iguana: <i>Dipsosaurus dorsalis</i>	Human	Fast > Slow approach	20	.82	Cooper 2003b
R	Keeled earless lizard: <i>Holbrookia propinqua</i>	Human	Fast > Slow approach	37	.71	Cooper 2003c
R	Bonaire whiptail lizard: <i>Cnemidophorus murinus</i>	Human	Fast > Slow approach	50	.61	Cooper <i>et al.</i> 2003
B	New Zealand dotterel: <i>Charadrius obscurus</i>	Human	Fast > Slow approach	15	.36	Lord <i>et al.</i> 2001
M	Gazelle spp: <i>Gazella thomsonii</i> ; <i>G. granti</i>	African wild dog	Run > walk > stalk			Estes & Goddard 1967
M	Enclosed Merino sheep: <i>Ovis aries</i>	Human	No effect	20	-.44	Hutson 1982
M	Woodchuck: <i>Marmota monax</i>	Human	No effect	85	.01	Bonenfant & Kramer 1996
Predator Size						
F	Zebra danio: <i>Brachydanio rerio</i>	Largemouth bass	Large > Small predator: spd1	12	.43	Dill 1974a
			Large > Small predator: spd2	12	.21	
			Large > Small predator: spd3	12	.30	
F	Bicolor damselfish: <i>Pomacentrus partitus</i>	Atlantic trumpetfish	Large > Small predator	64	.23	Helfman & Winkelman 1997
F	Blue chromis damselfish: <i>Chromis cyanea</i>	Plastic model: bar jack	Large > Small predator	38	.41	Hurley & Hartline 1974
F	Goby: <i>Cryptocentrus steinitzi</i>	Model Serranid fish	Large > Small predator	20	.64	Karplus & Tuvia 1979
R	Black iguana: <i>Ctenosaura similes</i>	Human wearing eye mask	Large > Small eye mask	119	.33	Burger <i>et al.</i> 1991
Predator Intent						
F	Bicolor damselfish: <i>Pomacentrus partitus</i>	Atlantic trumpetfish	No effect of predator orientation			Helfman & Winkelman 1997

Directness of Approach

R	Broad-headed skink: <i>Eumeces laticeps</i>	Human	Indirect < Direct approach	36	.47	Cooper 1997b
R	Zebra-tailed lizard: <i>Callisaurus draconoides</i>	Human	Indirect < Direct approach			Bulova 1994
R	Greater earless lizard: <i>Cophosaurus texanus</i>	Human	Indirect < Direct approach			Bulova 1994
R	Black iguana: <i>Ctenosaura similes</i>	Human	Indirect < Direct approach: a*	86	.20	Burger & Gochfeld
			Indirect < Direct approach: b	31	.23	1990
			Indirect < Direct approach: c	57	.30	
R	Desert iguana: <i>Dipsosaurus dorsalis</i>	Human	Indirect < Direct approach	9	.16	Cooper 2003b
R	Keeled earless lizard: <i>Holbrookia propinqua</i>	Human	Indirect < Direct approach	20	.69	Cooper 2003c
R	Bonaire whiptail lizard: <i>Cnemidophorus murinus</i>	Human	Indirect < Direct approach: fast	27	.28	Cooper <i>et al.</i> 2003
			Indirect < Direct approach: slow	22	-.45	
B	Herring gull: <i>Larus argentatus</i>	Human	Indirect < Direct approach	22	.22	Burger & Gochfeld 1981
B	Great black-backed gull: <i>Larus marinus</i>	Human	No effect (human naïve population)	26	.22	Burger & Gochfeld 1981
M	Gazelle spp: <i>Gazella thomsonii</i> ; <i>G. granti</i>	African wild dog	Indirect < Direct approach			Estes & Goddard 1967

Predator Species/Type

I	Brown shrimp: <i>Crangon crangon</i>	Cod	Cod < Wooden rod			Arnott <i>et al.</i> 1999
I	Hermit crab: <i>Pagurus acadianus</i>	Model lobster	Sponge < Lobster model			Scarratt & Godin 1992
F	Blue chromis damselfish: <i>Chromis cyanea</i>	Model bar jack	Dark model > Light model			Hurley & Hartline 1974
			No effect of model shape			
R	Black iguana: <i>Ctenosaura similes</i>	Human face	Hair over face < Face exposed			Burger & Gochfeld 1993
			Male face < Female face			
R	Ground skink: <i>Scincella lateralis</i>	Model lizard	No effect of predator species			Smith 1997
		Mounted blue jay				
		Mounted crow				
R	Eastern brownsnake: <i>Pseudonaja textiles</i>	Human	No effect of shade of clothes			Whitaker & Shine 1999
B	Herring gull: <i>Larus argentatus</i>	Human	Wolfhound > Human			Goethe 1937 (<i>as cited in Hediger 1964</i>)
		Wolfhound				
B	Wigeon: <i>Anas Penelope</i>	Boats, wind-surfers	Stationary boat < mobile boat < wind -surfers			Madsen <i>et al.</i> 1992 (<i>as cited in Fox & Madsen 1997</i>)
B	New Zealand dotterel: <i>Charadrius obscurus</i>	Human, Dog	Dog > Human			Lord <i>et al.</i> 2001
B	Brown pelican: <i>Pelecanus occidentalis</i>	Human, Boat	Boat < Human			Rodgers & Smith 1995
			Boat = Human			Rodgers & Smith 1997

B	Double-crested cormorant: <i>Phalacrocorax auritus</i>	Human, Boat	Boat < Human	Rodgers & Smith 1995
B	Great blue heron: <i>Ardea herodias</i>	Human, Boat	Boat < Human	Rodgers & Smith 1995
B	Tricolored heron: <i>Egretta tricolor</i>	Human, Boat	Boat < Human	Rodgers & Smith 1995
B	Great egret: <i>Casmerodius albus</i>	Human, Boat	Boat = Human	Rodgers & Smith 1995
B	Anhinga: <i>Anhinga anhinga</i>	Motor boat, Canoe	Motor boat = canoe	Rodgers & Smith 1995
B	Sanderling: <i>Calidris alba</i>	Human, ATV	No effect	Rodgers & Smith 1997
B	Willet: <i>Catoptrophorus semipalmatus</i>	Human, Car, ATV	Car = Human; Human = ATV; Car > ATV	Rodgers & Smith 1997
B	Ring-billed gull: <i>Larus delawarensis</i>	Human, Car, ATV	Human = ATV; Car < ATV; Car < Human	Rodgers & Smith 1997
B	American kestrel: <i>Falco sparverius</i>	Human, Car	No effect	Holmes <i>et al.</i> 1993
	Merlin: <i>F. columbarius</i>		No effect	
	Prarie falcon: <i>F. mexicanus</i>		No effect	
B	Rough-legged hawk: <i>Buteo lagopus</i>	Human, Car	Human > Car	Holmes <i>et al.</i> 1993
	Golden eagle: <i>Aguila chrysaetos</i>			
B	Ferruginous hawk: <i>Buteo regalis</i>	Human, Car	Car > Human	Holmes <i>et al.</i> 1993
M	Alpine marmot: <i>Marmota marmota</i>	Human, Dog	Human + Dog < Human only	Louis & Le Berre 2000
M	Thomson's gazelle: <i>Gazella thomsoni</i>	5 predators	Jackal < Hyena < Lion < Cheetah < Wild Dog	Walther 1969
M	Giraffe: <i>Giraffa camelopardalis</i>	Human, Automobile	Human > Automobile	Kearton 1929
Number of Predators				
M	Thomson's gazelle: <i>Gazella thomsoni</i>	Hyena	Solitary hyena < Pack	Walther 1969
I	Lotic mayfly: <i>Baetis tricaudatus</i>	Longnose dace Stonefly	No effect	Scrimgeour <i>et al.</i> 1997
Starting Distance of Approaching Threat				
B	68 Australian & Tasmanian bird spp.	Human	Positive Correlation: 64 of 68 spp.	Blumstein 2003

I = Invertebrate, F = Fish, B = Bird, R = Reptile, M = Mammal. If no *n* or *r*-value is given, sufficient data to calculate effect size was not reported, and the study was not included in the meta-analysis. No meta-analyses were conducted on "Predator Intent," "Predator Species/Type," "Number of Predators," "or Starting Distance of Approaching Threat," and these studies were not included in the "Predatory effects (combined)" meta-analysis. *Burger & Gochfeld 1990: a = heavy human exposure, b = minimal exposure, c = no exposure

APPENDIX C: Environmental and ecological factors influencing flight initiation distance

Taxa	Prey Species	Predator(s)	Effect on Flight Distance	N	r	Source
Group Size						
I	Water strider: <i>Gerris remigis</i>	Conspecific adults	Convex quadratic relationship	72	-.49	Dill & Ydenberg 1987
I	Ocean skater: <i>Halobates robustus</i>	White rectangle	Large groups > Small groups			Treherne & Foster 1980
F	Banded killifish: <i>Fundulus diaphanous</i>	Model white perch	No effect			Godin & Morgan 1985
F	Fathead minnow: <i>Pimephales promelas</i>	Yellow Perch	No effect	16	-.20	Abrahams 1995
F	Brook stickleback: <i>Culea inconstans</i>	Yellow Perch	Large groups < Small groups	11	-.35	Abrahams 1995
F	Atlantic salmon: <i>Salmo salar</i>	Cod	Solitary < Groups			Handeland <i>et al.</i> 1996
F	Bicolor damselfish: <i>Pomacentrus partitus</i>	Atlantic trumpetfish	Solitary > Groups			Helfman & Winkelman 1997
F	Spottail shiner: <i>Notropis hudsonius</i>	Fishing lure	Solitary > Groups	176	-.41	Seghers 1981
B	House sparrow: <i>Passer domesticus</i> L.	Human	No effect	18	.33	Barnard 1980
B	Sanderling: <i>Calidris alba</i>	Human	No effect.	57	.26	Roberts & Evans 1993
B	Barred ground dove: <i>Geopelia striata</i>	Human	Concave quadratic relationship	184	.17	Greig-Smith 1981
B	Woodpigeon: <i>Columba palumbus</i>	Goshawk	Large groups > Small groups	48	.34	Kenward 1978
B	Bald eagle: <i>Haliaeetus leucocephalus</i>	Human in canoe	Solitary < Groups: ground Solitary > Groups: perched	67 177	.01 -.10	Knight & Knight 1984
B	Brent geese: <i>Branta bernicla</i>	Human	Large groups > Small groups			Owens 1977
B	Pink-footed goose: <i>Anser brachyrhynchus</i>	Car	Large groups > Small groups	24	.43	Madsen 1985
B	Tufted duck: <i>Aythya fuligula</i> Pochard: <i>A. ferina</i>	Boat	Large groups > Small groups	6	.81	Batten 1977
M	Enclosed Merino sheep: <i>Ovis aries</i>	Human	Solitary > Groups			Hutson 1982
M	Moose: <i>Alces alces</i>	Human	Solitary > Groups			Altmann 1958
M	Thomas' leaf monkey: <i>Prebytis thomasi</i>	Human	No effect	25	.18	van Schaik <i>et al.</i> 1983
M	Long-tailed macaque: <i>Macaca fascicularis</i>	Human	Large groups > Small groups	45	.44	van Schaik <i>et al.</i> 1983
M	Pig-tailed macaque: <i>Macaca nemestrina</i>	Human	Large groups > Small groups	24	.46	van Schaik <i>et al.</i> 1983
M	Lar gibbon: <i>Hylobates lar</i>	Human	No effect	14	.26	van Schaik <i>et al.</i> 1983
Patch Quality/Cost of Leaving						
Territory & Mate Defense						
F	Cichlid: <i>Nannacara anomala</i>	Model predator fish	♂♂: Mouth-fighting pairs < Tail-beating pairs = single fish			Jakobsson <i>et al.</i> 1995 Brick 1998
R	Lizard: <i>Psammmodromus algirus</i>	Human	♂♂: Mate-guarding < Lone			Martín & López 1999

R	Broad-headed skink: <i>Eumeces laticeps</i>	Human	♂♂: Mate-guarding < Lone ♂ introduced to: Mate-guarding ♂♂ < Isolated ♂♂ < Control ♂♂ ♀ introduced to: Isolated ♂♂ < Mate-guarding ♂♂	Cooper 1997b Cooper 1999
R	Lizard: <i>Tropidurus hispidus</i>	Human	♂♂: Guarding territory > During encounter with intruder	Díaz-Uriarte 1999
R	Marine iguana: <i>Amblyrhynchus cristatus</i>	Human	♂♂: Territorial < Nonterritorial	Shallenberger 1970
B	Brown pelican: <i>Pelecanus occidentalis</i>	Human, Boat	Foraging > Nesting (both preds)	Rodgers & Smith 1997
B	Anhinga: <i>Anhinga anhinga</i>	Boat	Foraging > Nesting	Rodgers & Smith 1997
B	Double-crested cormorant: <i>Phalacrocorax auritus</i>	Human	No effect: Foraging = Nesting	Rodgers & Smith 1997
B	Great blue heron: <i>Ardea herodias</i>	Human	No effect: Foraging = Nesting	Rodgers & Smith 1997
B	Great egret: <i>Ardea alba</i>	Human Boat	Foraging > Nesting	Rodgers & Smith 1997
B	Tricolored heron: <i>Egretta tricolor</i>	Human	Foraging < Nesting	Rodgers & Smith 1997
B	Wood stork: <i>Mycteria americana</i>	Boat	Foraging > Nesting	Rodgers & Smith 1997
M	Thomson's gazelle: <i>Gazella thomsoni</i>	Car	♂♂: Territorial < Bachelor < Solitary	Walther 1969
Feeding Site				
I	Crayfish: <i>Procambarus clarkii</i>	Net	Large food items < small food items	Bellman & Krasne 1983
I	Hermit crab: <i>Pagurus acadianus</i>	Model lobster	No effect of food mass	Scarratt & Godin 1992
I	Lotic mayfly: <i>Baetis tricaudatus</i>	Longnose dace Stonefly	Low food reward > High food reward	Scrimgeour & Culp 1994
F	Brook trout: <i>Salvelinus fontinalis</i>	Human	High feed rate < Low feed rate	Grant & Noakes 1987
F	Guppy: <i>Poecilia reticulata</i>	Model pike cichlid	Nonforaging > Foraging	Krause & Godin 1996
R	Bonaire whiptail lizard: <i>Cnemidophorus murinus</i>	Human	Food present < No food present	Cooper <i>et al.</i> 2003
R	Broad-headed skink: <i>Eumeces laticeps</i>	Human	Feeding < Not feeding	Cooper 2000a
B	House sparrow: <i>Passer domesticus</i> L.	Human	High seed density > Low seed density	Barnard 1980
M	Moose: <i>Alces alces</i>	Human	Feed in water < Feed on land	Altmann 1958
M	Svalbard reindeer: <i>Rangifer tarandus platyrhynchus</i>	Snowmobile	Feeding < Lying down	Tyler 1991

Distance to Refuge (RD)

I	Fiddler crab: <i>Uca tangeri</i>	Human	♂♂: Long RD > Short RD ♀♀: No effect	5 8	.94 .24	Jordão & Oliveira 2001
F	African cichlid fish: <i>Melanochromis chipokae</i>	Black ball	Long RD > Short RD	18	.72	Dill 1990
F	Killifish: <i>Fundulus diaphanus</i>	Black object on rod	Long RD > Short RD	42	.45	McLean & Godin 1989
F	Threespine stickleback: <i>Gasterosteus aculeatus</i>	Black object on rod	No effect			McLean & Godin 1989
F	Ninespine stickleback: <i>Pungitius pungitius</i>	Black object on rod	No effect			McLean & Godin 1989
R	Iberian rock lizard: <i>Lacerta monticola</i>	Human	Long RD > Short RD	105 106	.31 .55	Martín & López 2000a; Martín & López 2003a
R	Keeled earless lizard: <i>Holbrookia propinqua</i>	Human	Long RD > Short RD	84	.42	Cooper 2000b Cooper 2003a
R	Broad-headed skink: <i>Eumeces laticeps</i>	Human	Long RD > Short RD While eating: Long RD > Short RD When not feeding: No effect	21	.54	Cooper 1997a Cooper 2000a
R	Wall lizard: <i>Podarcis muralis</i>	Human	Long RD > Short RD Long RD > Short RD: site 1 No effect: site 2	156 20 20	.34 .63 .35	Braña 1993 Diego-Rasilla 2003
R	Zebra-tailed lizard: <i>Callisaurus draconoides</i>	Human	Long RD > Short RD			Bulova 1994
R	Greater earless lizard: <i>Cophosaurus texanus</i>	Human	Long RD > Short RD			Bulova 1994
R	Lizard: <i>Psammotromus algirus</i>	Human	No effect	150	.01	Martín & López 2000b
R	Lizard: <i>Acanthodactylus erythrurus</i>	Human	Long RD > Short RD	18	.64	Martín & López 2003b
M	Woodchuck: <i>Marmota monax</i>	Human	Long RD > Short RD Long RD > Short RD: a* Long RD > Short RD: b	6 31 27	.92 .76 .83	Bonenfant & Kramer 1996 Kramer & Bonenfant 1997
M	Gray squirrel: <i>Sciurus carolinensis</i>	Motorized cat model	Long RD > Short RD	90	.86	Dill & Houtman 1989

Habitat Type / Amount of Cover				
F	Brook trout: <i>Salvelinus fontinalis</i>	Human	Low cover > High cover	Grant & Noakes 1987
R	Chameleon: <i>Chamaeleo chamaeleon</i>	Human	Low cover > High cover	Cuadrado <i>et al.</i> 2001
R	Broad-headed skink: <i>Eumeces laticeps</i>	Human	Bare ground > Leaf litter	Cooper 1998
R	Lizard: <i>Psammodromus algirus</i>	Human	Low cover > High cover	Martín & López 2000b
			Juveniles: Exposed = Covered	Martín & López 1995a
R	Broad-headed skink: <i>Eumeces laticeps</i>	Human	High in trees < Low in trees	Cooper 1997a
R	Lizard: <i>Psammodromus algirus</i>	Human	With refuge plants > No refuge plants	Martín & López 1995b
R	Northern water snake: <i>Nerodia sipedon</i>	Human	Low perch < High perch	
R	Lizards: <i>Anolis cybotes</i> , <i>A. distichus</i> , <i>A. coelestinus</i> , <i>A. bahorucoensis</i>	Human	Natural perch: High < Low	Schneider <i>et al.</i> 2000
			Fencepost: Low < High	
			No effect of perch diameter	
R	Northern water snake: <i>Nerodia sipedon</i>	Human	Lower perch < Higher perch	Weatherhead & Robertson 1992
R	Zebra-tailed lizard: <i>Callisaurus draconoides</i>	Human	Site w/ less cover > Other sites	Bulova 1994
R	Desert iguana: <i>Dipsosaurus dorsalis</i>	Human	Open sites > Semi-open > Bushy	Cooper 2003b
R	Keeled earless lizard: <i>Holbrookia propinqua</i>	Human	Open sites > Plant cover (incomplete cover)	Cooper 2003c
R	Striped plateau lizard: <i>Sceloporus virgatus</i>	Human	No effect (woods v. slide)	Smith 1996
R	Spiny chuckwalla: <i>Sauromalus hispidus</i>	Human	Dens > Rocks > Feeding areas	Shallenberger 1970
R	Lava lizards: <i>Tropidurus albemarlensis</i>	Human	Sparse cover > Heavy cover	Snell <i>et al.</i> 1988
B	House sparrow: <i>Passer domesticus</i> L.	Human	In open fields > Inside shed	Barnard 1980
B	Herring gull: <i>Larus argentatus</i>	Human	Open sites > Dense bush cover	Burger & Goch 1981
			Less vegetation cover > More cover	Burger & Gochfeld 1983
B	Great black-backed gull: <i>Larus marinus</i>	Human	No effect of % vegetation cover	Burger & Gochfeld 1983
B	Bald eagle: <i>Haliaeetus leucocephalus</i>	Human in canoe	Standing/feeding > Perched (p=0.06)	Knight & Knight 1984
		Human	Heavy vegetation < Open areas	Stalmaster & Newman 1978

B	American kestrel: <i>Falco sparverius</i> Prairie falcon: <i>F. mexicanus</i> Ferruginous hawk: <i>Buteo regalis</i>	Human	Perch Ht: High < Low	Holmes <i>et al.</i> 1993
B	Merlin: <i>Falco columbarius</i> Rough-legged hawk: <i>Buteo lagopus</i> Golden eagle: <i>Aquila chrysaetos</i>	Human	Perch Ht: No effect	Holmes <i>et al.</i> 1993
M	Enclosed Merino sheep: <i>Ovis aries</i>	Human	Enclosed: Narrow lane < Wide lane	Hutson 1982
M	Moose: <i>Alces alces</i>	Human	In open country > In forest/shrubs	Altmann 1958
			Moving < Feed in flat < Feed in H ₂ O	McMillan 1954
M	Blesbok: <i>Damaliscus dorcas phillipsi</i>	Human	More open terrain > Less open terrain	Rowe-Rowe 1974
M	Svalbard reindeer: <i>Rangifer tarandus platyrhynchus</i>	Snowmobile	Open terrain > Restricted view	Tyler 1991

I = Invertebrate, F = Fish, B = Bird, R = Reptile, M = Mammal, RD = Distance to refuge. If no *N* or *r*-value is given, sufficient data to calculate effect size was not reported and the study was not included in the meta-analysis. No meta-analyses were conducted on “Patch Quality / Cost of Leaving” or “Habitat Type / Amount of Cover.”

*Kramer & Bonenfant 1997: a = burrow in front of animal, b = burrow behind animal

APPENDIX D: Physiological, morphological, and life history factors influencing flight initiation distance

Taxa	Prey Species	Predator(s)	Effect on Flight Distance	N	r	Source
Degree of Crypsis						
Morphological Aspects						
R	Lizard: <i>Psammmodromus algirus</i>	Human	Bright ♂♂ > Dull ♂♂ > ♀♀	84	.42	Martín & López 1999
R	Lizards: <i>Anolis cristatellus</i> & <i>A. stratulus</i>	Human	More cryptic sp. (<i>A. stratulus</i>) < Less cryptic sp. (<i>A. cristatellus</i>)	77	.38	Heatwole 1968
R	Lizard: <i>Sceloporus occidentalis</i>	Human	More cryptic females & juveniles <	169	.34	Johnson 1970
R	Lizard: <i>Sceloporus biserialis</i>	Human	Less cryptic males	145	.28	
Effect of Time & Light						
R	Black iguana: <i>Ctenosaura similes</i>	Human	No effect (time of day)			Burger & Gochfeld 1990
B	6 raptor spp.	Human, Car	No effect (time, cloud cover)			Holmes <i>et al.</i> 1993
M	Alpine marmot: <i>Marmota marmota</i>	Human, Dog	Late in day < Early in day			Louis & Le Berre 2000
M	Moose: <i>Alces alces</i>	Human	Dusk/dawn < Other times			Altmann 1958
M	Thomson's gazelle: <i>Gazella thomsoni</i>	Human or Car	Morning < Evening			Walther 1969
Effects of Habitat: See Appendix B						
Morphological Defenses						
F	Brook stickleback: <i>Culea inconstans</i> Fathead minnow: <i>Pimephales promelas</i>	Yellow perch	Armored sticklebacks < Unarmored minnows	16	.65	Abrahams 1995
F	Killifish: <i>Fundulus diaphanous</i> Threespine stickleback: <i>Gasterosteus aculeatus</i> Ninespine stickleback: <i>Pungitius pungitius</i>	Black object on rod	Armored threespine < Unarmored killifish Armored ninespine < Unarmored killifish	56 66	.41 .19	McLean & Godin 1989
Physical Condition / Ability to Escape						
R	Lizard: <i>Liolaemus nigromaculatus</i>	Human	Large: Intact tails > Autotomized Small: No effect of tail autotomy			Kelt <i>et al.</i> 2002
R	Ground skink: <i>Scincella lateralis</i>	Green plastic lizard	Intact tails > Autotomized			Formanwicz <i>et al.</i> 1990
R	Black iguana: <i>Ctenosaura similes</i>	Human	Intact tails > Autotomized			Burger & Gochfeld 1990
R	Keeled earless lizard: <i>Holbrookia propinqua</i>	Human	No effect of tail autotomy			Cooper 2003a
R	Striped plateau lizard: <i>Sceloporus virgatus</i>	Human	Intact tails > Autotomized			Smith 1996
B	Woodpigeon: <i>Columba palumbus</i>	Goshawk	Poor condition > Good condition			Kenward 1978

Size				
I	Fiddler crab: <i>Uca tangeri</i>	Human	No effect	Jordão & Oliveira 2001
I	Lotic mayfly: <i>Baetis tricaudatus</i>	Longnose dace	Large larvae < Small larvae	Scrimgeour <i>et al.</i> 1997
F	Brook stickleback: <i>Culea inconstans</i>	Yellow perch	Long body < Short body	Abrahams 1995
F	Brook trout: <i>Salvelinus fontinalis</i>	Human	Short body < Long body	Grant & Noakes 1987
F	Bicolor damselfish: <i>Pomacentrus partitus</i>	Atlantic trumpetfish	No effect	Helfman & Winkelman 1997
R	Lizard: <i>Liolaemus nigromaculatus</i>	Human	No effect	Kelt <i>et al.</i> 2002
R	Black iguana: <i>Ctenosaura similes</i>	Human	Long > Short snout-vent length	Burger & Gochfeld 1990
R	Queen snake: <i>Regina septemvittata</i>	Human	No effect	Layne & Ford 1984
R	Iberian Rock Lizard: <i>Lacerta monticola</i>	Human	Long > Short snout-vent length	Martín & López 2003a
R	Marine iguana: <i>Amblyrhynchus cristatus</i>	Human	Long > Short snout-vent length	Shallenberger 1970
R	Spiny chuckwalla: <i>Sauromalus hispidus</i>	Human	Dens: Large/med > Small Feeding grounds: No effect	Shallenberger 1970
R	Mojave Desert chuckwalla: <i>Sauromalus obesus</i>	Human	No effect	Shallenberger 1970
R	Piebald chuckwalla: <i>Sauromalus varius</i>	Human	No effect	Shallenberger 1970
R	Striped plateau lizard: <i>Sceloporus virgatus</i>	Human	No effect	Smith 1996
B	17 passerine spp.	Human	Small species < Large species	Cooke 1980
B	6 raptor spp.	Human, Car	Human: Small species < Large species Car: No effect	Holmes <i>et al.</i> 1993
Sex				
I	Fiddler crab: <i>Uca tangeri</i>	Human	No effect	Jordão & Oliveira 2001
F	Killifish: <i>Fundulus diaphanus</i>	Black object on rod	No effect	McLean & Godin 1989
F	Threespine stickleback: <i>Gasterosteus aculeatus</i>	Black object on rod	No effect	McLean & Godin 1989
F	Ninespine stickleback: <i>Pungitius pungitius</i>	Black object on rod	No effect	McLean & Godin 1989
R	Eastern brownsnake: <i>Pseudonaja textiles</i>	Human	No effect	Whitaker & Shine 1999
R	Lizard: <i>Podarcis muralis</i>	Human	Males > Females	Braña 1993
R	Zebra-tailed lizard: <i>Callisaurus draconoides</i>	Human	Males > Females	Bulova 1994
R	Greater earless lizard: <i>Cophosaurus texanus</i>	Human	Males > Females	Bulova 1994
R	Black iguana: <i>Ctenosaura similes</i>	Human	No effect	Burger & Gochfeld 1990
R	Keeled earless lizard: <i>Holbrookia propinqua</i>	Human	No effect	Cooper 2003a

R	Spiny chuckwalla: <i>Sauromalus hispidus</i>	Human	No effect				Shallenberger 1970
R	Mojave Desert chuckwalla: <i>Sauromalus obesus</i>	Human	No effect				Shallenberger 1970
R	Piebald chuckwalla: <i>Sauromalus varius</i>	Human	No effect				Shallenberger 1970
R	Queen snake: <i>Regina septemvittata</i>	Human	No effect				Layne & Ford 1984
R	Striped plateau lizard: <i>Sceloporus virgatus</i>	Human	No effect				Smith 1996
R	Lizard: <i>Sceloporus occidentalis</i>	Human	Males > Females				Johnson 1970
R	Lava lizard: <i>Tropidurus albemarlensis</i>	Human	Males < Females				Snell <i>et al.</i> 1988
R	Lava lizards: <i>Tropidurus</i> spp.	Human	Española: Males > Females All other islands: No effect				Stone <i>et al.</i> 1994
		Human	No effect				Watkins-Colwell 1997
B	American kestrel: <i>Falco sparverius</i> Merlin: <i>F. columbarius</i>	Human, Car	No effect				Holmes <i>et al.</i> 1993
M	Thomson's gazelle: <i>Gazella thomsoni</i>	Car	Males < Females				Walther 1969
Age							
R	Lizard: <i>Psammmodromus algirus</i>	Human	Juveniles > Adults				Martín & López 1995a
R	Lava lizards: <i>Tropidurus</i> spp.	Human	No effect				Watkins-Colwell 1997
B	Bald eagle: <i>Haliaeetus leucocephalus</i>	Human in canoe	No effect				Knight & Knight 1984
		Human	Adults > Subadults				Stalmaster & Newman 1978
B	Least terns: <i>Sterna antillarum</i> Black skimmer: <i>Rynchops niger</i>	Human	Adults > Nestlings				Rodgers & Smith 1995
B	Brown pelican: <i>Pelecanus occidentalis</i>	Human	No effect				Rodgers & Smith 1995
B	Golden eagle: <i>Aquila chrysaetos</i>	Human, Car	No effect				Holmes <i>et al.</i> 1993
M	Thomson's gazelle: <i>Gazella thomsoni</i>	Car	Adult male < Subadult male				Walther 1969
Body/Air Temp							
R	Iberian rock lizard: <i>Lacerta monticola</i>	Human	Low heating rate > High heating rate				Martín & López 2000a
			No effect (air temp)	106	-.02		Martín & López 2003a
			No effect (air temp)	150	.07		Martín & López 2000b
R	Lizard: <i>Lophognathus temporalis</i>	Human	Warm air temp > Cool air temp	278	.17		Blamires 1998

R	Keeled earless lizard: <i>Holbrookia propinqua</i>	Human	Warm soil temp > Cool soil temp	83	.52	Cooper 2000b
		Human	Warm substrate > Cool substrate	32	.54	Cooper 2003a
R	Lizard: <i>Psammmodromus algirus</i>	Human	No effect (air temp)	60	.18	Martín & López 1995a
R	Lizard: <i>Anolis lineatopus</i>	Human & stick	Cool > Warm body temp	32	-.57	Rand 1964
R	Lizard: <i>Tropidurus areadicus</i>	Human	Cool > Warm body temp	15	-.53	Rocha & Bergallo 1990
R	Ground skink: <i>Scincella lateralis</i>	Lizard model	Cool > Warm body temp	59	-.33	Smith 1997
R	Northern water snake: <i>Nerodia sipedon</i>	Human	No effect: air temp	55	.05	Weatherhead & Robertson
			No effect: water temp	55	.03	1992
R	Zebra-tailed lizard: <i>Callisaurus draconoides</i>	Human	High wind < Low wind			Bulova 1994
R	Greater earless lizard: <i>Cophosaurus texanus</i>	Human	Early & late in day (cooler) > midday (warmer)			Bulova 1994
R	Eastern brownsnake: <i>Pseudonaja textiles</i>	Human	Warm body temp > Cool body temp			Whitaker & Shine 1999
R	Queen snake: <i>Regina septemvittata</i>	Human	Warm body temp > Cool body temp	20	.66	Layne & Ford 1984
R	Black iguana: <i>Ctenosaura similes</i>	Human	No effect (air temp)			Burger & Gochfeld 1990
R	Desert iguana: <i>Dipsosaurus dorsalis</i>	Human	Warm air temp < Cool air temp			Cooper 2003b
R	Wall lizard: <i>Podarcis muralis</i>	Human	No effect: air temp – outcrop	20	.38	Diego-Rasilla 2003
			No effect: air temp – viewpoint	20	-.01	
R	Lava lizards: <i>Tropidurus</i> spp.	Human	“Non-linear” effect of air temp			Watkins-Colwell 1997
R	Marine iguana: <i>Amblyrhynchus cristatus</i>	Human	Cool > Warm body temp: Nonter ♂	9	-.88	Shallenberger 1970
			Cool > Warm body temp: ♂ & ♀	8	-.83	
R	Spiny chuckwalla: <i>Sauromalus hispidus</i>	Human	Cool > Warm body temp	46	-.71	Shallenberger 1970
R	Mojave Desert chuckwalla: <i>Sauromalus obesus</i>	Human	Cool > Warm body temp	48	-.03	Shallenberger 1970
B	House sparrow: <i>Passer domesticus</i> L.	Human	Cool > Warm (minimum air temp)			Barnard 1980
			No effect (current air temp)			
B	Herring gull: <i>Larus argentatus</i>	Human	No effect (air temp)			Burger & Gochfeld 1983
B	Great black-backed gull: <i>Larus meritus</i>	Human	No effect (air temp)			Burger & Gochfeld 1983
B	6 raptor spp.	Human, Car	No effect (air temp)			Holmes <i>et al.</i> 1993
M	Thomson’s gazelle: <i>Gazella thomsoni</i>	Human or Car	Warm air temp < Cool air temp			Walther 1969
Reproductive State						
R	Lizard: <i>Lacerta vivipara</i>	Human	Gravid ♀♀ < ♂♂			Bauwens & Thoen 1981
R	Lizard: <i>Podarcis muralis</i>	Human	Gravid ♀♀ < Non-pregnant ♀♀, ♂♂			Braña 1993

R	Southern water skink: <i>Eulamprus tympanum</i>	Human	Gravid ♀♀ < ♂♂ & Non-gravid ♀♀	Schwarzkopf & Shine 1992
R	Striped plateau lizard: <i>Sceloporus virgatus</i>	Human	No effect (gravid v. non-gravid)	Smith 1996
B	Herring gull: <i>Larus argentatus</i>	Human	No effect (day of incubation)	Burger & Gochfeld 1983
B	Great black-backed gull: <i>Larus meritus</i>	Human	No effect (day of incubation)	Burger & Gochfeld 1983
B	New Zealand dotterel: <i>Charadrius obscurus</i>	Human, Dog	No effect (day of incubation)	Lord <i>et al.</i> 2001
B	Alpine accentor: <i>Prunella collaris</i>	Human	Nesting > After Hatching	Barash 1975
B	Brown pelican: <i>Pelecanus occidentalis</i>	Human	No effect (incubating eggs = with nestlings)	Rodgers & Smith 1995
B	Double-crested cormorant: <i>Phalacrocorax auritus</i>			
M	Alpine marmot: <i>Marmota marmota</i>	Human, Dog	Pups outside burrow > No pups outside	Louis & Le Berre 2000
M	Thomson's gazelle: <i>Gazella thomsoni</i>	Car	♀♀: With fawns < Others	Walther 1969
M	Blesbok: <i>Damaliscus dorcas phillipsi</i>	Human	♀♀: Postpartum > Others	Rowe-Rowe 1974
M	Moose: <i>Alces alces</i>	Human	♂♂: No effect during rut ♀♀: With newborn > With calf ♂♂: Velvet > Prerut > Rut	Altmann 1958
Hunger & Other Stressors				
I	Lotic mayfly: <i>Baetis tricaudatus</i>	Longnose dace	Small: no effect of hunger Large: short starvation period > long starvation period	Scrimgeour <i>et al.</i> 1997
F	Atlantic salmon: <i>Salmo salar</i>	Cod: <i>Gadus morhua</i>	Osmotically stressed < Acclimated	Handeland <i>et al.</i> 1996
R	Adder: <i>Vipera berus</i>	Human	Nourished > Undernourished	Andrén 1982
M	Red deer: <i>Cervus elaphus</i>	Human	When irritable > Normal behavior	Darling 1937

I = Invertebrate, F = Fish, B = Bird, R = Reptile, M = Mammal. If no *N* or *r*-value is given, sufficient data to calculate effect size was not reported and the study was not included in the meta-analysis. No meta-analyses were conducted on “Effect of Time & Light” in Degree of Crypsis and “Physical Condition / Ability to Escape” excluding reptiles in “Body / Air Temp.”

APPENDIX E: The effect of prey experience and habituation on flight initiation distance

Taxa	Prey Species	Predator(s)	Effect on Flight Distance	N	r	Source
Predator Density						
R	Lizard: <i>Liolaemus monticola</i>	Human	Low Human Density (HD) > High HD	123	.29	Labra & Leonard 1999
R	Lizard: <i>Liolaemus fuscus</i>	Human	Low HD > High HD	41	.51	Labra & Leonard 1999
R	Lizard: <i>Liolaemus lemniscatus</i>	Human	Low HD > Med/High HD	104	.43	Labra & Leonard 1999
R	Black iguana: <i>Ctenosaura similes</i>	Human	Low HD > High HD	275	.51	Burger & Gochfeld 1990
R	Bonaire whiptail lizard: <i>Cnemidophorus murinus</i>	Human	Far from > near to human activity Low HD > High HD	61	.24	Cooper <i>et al.</i> 2003
R	Wall lizard: <i>Podarcis muralis</i>	Human	Low HD > High HD	40	.43	Diego-Rasilla 2003
R	Iguana: <i>Ctenosaura hemilopha</i>	Human	Low HD < High HD	57	-.59	Blázquez <i>et al.</i> , 1997
B	8 shorebird spp.	Human	Low HD > Med/High HD			Blumstein <i>et al.</i> 2003
B	Great tit: <i>Parus major</i>	Human	Low HD = High HD	27	.05	Cooke 1980
B	Blue tit: <i>Parus caeruleus</i>	Human	Low HD = High HD	51	-.11	Cooke 1980
B	Song thrush: <i>Turdus philomelos</i>	Human	Low HD > High HD	78	.72	Cooke 1980
B	Blackbird: <i>Turdus merula</i>	Human	Low HD > High HD	247	.36	Cooke 1980
B	Robin: <i>Erithecus rubecula</i>	Human	Low HD > High HD	49	.33	Cooke 1980
B	Dunnoek: <i>Prunella modularis</i>	Human	Low HD > High HD	74	.49	Cooke 1980
B	Starling: <i>Sturnus vulgaris</i>	Human	Low HD > High HD	112	.59	Cooke 1980
B	Greenfinch: <i>Carduelis chloris</i>	Human	Low HD > High HD	26	.60	Cooke 1980
B	Chaffinch: <i>Fringilla coelebs</i>	Human	Low HD = High HD	62	.25	Cooke 1980
B	House sparrow: <i>Passer domesticus</i>	Human	Low HD > High HD	324	.58	Cooke 1980
B	Herring gull: <i>Larus argentatus</i>	Human	Low HD > High HD	35	.59	Burger & Gochfeld 1981
			Low HD > High HD	181	.42	Burger & Gochfeld 1983
B	Great black-backed gull: <i>Larus marinus</i>	Human	Low HD > High HD	99	.55	Burger & Gochfeld 1983
B	New Zealand dotterel: <i>Charadrius obscurus</i>	Human, Dog	Low HD > High HD: Walk Low HD > High HD: Run	15 15	.66 .39	Lord <i>et al.</i> 2001

B	Great crested grebe: <i>Podiceps cristatus</i>	Human	Low HD > High HD	436	.14	Keller 1989
B	Curlew: <i>Numenius arquata</i>	Human	Low HD > High HD			Tensen & van Zoest 1983 (as cited in Smit & Visser 1993)
B	Brent goose: <i>Branta bernicla</i>	Human	High HD > Low HD			Owens 1977
B	Bald eagle: <i>Haliaeetus leucocephalus</i>	Human	Low HD > High HD	300	.17	Stalmaster & Newman 1978
M	Alpine marmot: <i>Marmota marmota</i>	Human, Dog	Low HD > High HD	322	.55	Louis & Le Berre 2000
M	Thomson's gazelle: <i>Gazella thomsoni</i>	Human or Car	High HD > Low HD (non-hunted)			Walther 1969
M	Svalbard reindeer: <i>Rangifer tarandus platyrhynchus</i>	Snowmobile	Low HD > High HD	99	.13	Tyler 1991
M	Moose: <i>Alces alces</i>	Human	Low HD > High HD			Denniston 1956
M	Blesbok: <i>Damaliscus dorcas phillipsi</i>	Human	Low HD > High HD	168	.22	Rowe-Rowe 1974
Sequential Approach						
R	Whiptail lizard: <i>Cnemidophorus tessellatus</i>	Human	1 st approach > 2 nd approach			Paulissen 1995
R	Whiptail lizard: <i>Cnemidophorus gularis</i>	Human	1 st approach > 2 nd approach			Paulissen 1995
R	Marine iguana: <i>Amblyrhynchus cristatus</i>	Human	1 st approach < 2 nd approach	98	.40	Shallenberger 1970
R	Spiny chuckwalla: <i>Sauromalus hispidus</i>	Human	1 st approach < 2 nd approach	46	.84	Shallenberger 1970
R	Mojave Desert chuckwalla: <i>Sauromalus obesus</i>	Human	1 st approach < 2 nd approach	65	.80	Shallenberger 1970
B	Laughing gull: <i>Larus atricilla</i>	Human	1 st approach > 2 nd approach			Rodgers & Smith 1995
B	Cattle egret: <i>Bubulcus ibis</i>	Human	1 st approach > 2 nd approach	12	-.81	Rodgers & Smith 1995
B	Black skimmer: <i>Rynchops niger</i>	Human	1 st approach < 2 nd approach: 1989	22	.81	Rodgers & Smith 1995
B	Brent goose: <i>Branta bernicla</i>	Human	1 st approach < 2 nd approach: 1990 1 st approach < 2 nd appr. < 3 rd appr.	56	.50	Owens 1977
Other Experiential Effects						
F	Zebra danio: <i>Brachydanio rerio</i>	Model largemouth bass	More experienced > Less experienced			Dill 1974b
F	Atlantic salmon: <i>Salmo salar</i>	Plastic heron model	Young wild salmon < farmed salmon Old wild salmon = farmed salmon			Johnsson <i>et al.</i> 2001
R	Striped plateau lizard: <i>Sceloporus virgatus</i>	Human	More handling < Less handling			Smith 1996

R	Lava lizards: <i>Tropidurus</i> spp.	Human	Isles w/ feral cats > w/o cats: pair 1 Isles w/ feral cats > w/o cats: pair 2 Isles w/ feral cats > w/o cats: pair 3 No effect of rat or snake presence	Stone <i>et al.</i> 1994
		Human	No effect of presence of introduced predators	Watkins-Colwell 1997
R	Lizard: <i>Lacerta vivipara</i>	Human	No effect of experience	Bauwens & Thoen 1981
B	Bean goose: <i>Anser fabalis</i>	Human	Hunting season > Other months	Gerdes & Reepmayer 1983
B	White-fronted goose: <i>Anser albifrons</i>	Human	Hunting season > Other months	Madsen 1985
B	Pink-footed goose: <i>Anser brachyrhynchus</i>	Human	Hunting season > Other months	Madsen 1988 (<i>as cited in Fox & Madsen 1997</i>)
B	Brent goose: <i>Branta bernicla</i>	Human	Hunting season > Other months	Rudfeld 1990 (<i>as cited in Smit & Visser 1993</i>)
B	Ducks: <i>Anas</i> spp.	Human	Hunting season > Other months	Arctander <i>et al.</i> 1984 (<i>as cited in Fox & Madsen 1997</i>)
B	Common snipe: <i>Gallinago gallinago</i>	Human	Hunting season > Other months	
B	Bald eagle: <i>Haliaeetus leucocephalus</i>	Human in canoe	No effect (boat traffic): perched No effect (boat traffic): on ground	Knight & Knight 1984
M	Alpine marmot: <i>Marmota marmota</i>	Human, Dog	Hunted > Nonhunted	Louis & Le Berre 2000
M	Cattle: <i>Bos taurus</i> , <i>B. indicus</i>	Human	Beef breeds > Dairy breeds (genetic) Switch rearing type: no effect	Murphey <i>et al.</i> 1980
M	Moose: <i>Alces alces</i>	Human	Hunted > Nonhunted Unfamiliar human > Familiar human	Altmann 1958 McMillan 1954

F = Fish, B = Bird, R = Reptile, M = Mammal, HD = Human Density. If no *N* or *r*-value is given, sufficient data to calculate effect size was not reported and the study was not included in the meta-analysis. Meta-analysis was not conducted on “Other Experiential Factors” but those studies were included in the “Experienced (combined)” meta-analysis.

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