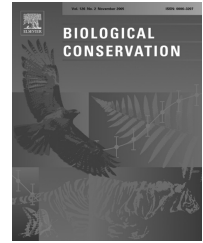


available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Review

Ungulate flight responses to human disturbance: A review and meta-analysis

Theodore Stankowich*

Organismic and Evolutionary Biology, University of Massachusetts, Morrill Science Center South, 611 N. Pleasant Street, Amherst, MA 01003, USA

ARTICLE INFO

Article history:

Received 24 January 2008

Received in revised form
26 June 2008

Accepted 28 June 2008

Available online 20 August 2008

Keywords:

Flight initiation distance

Escape behavior

Artiodactyla

Group size

Hunting

Habituation

Management

ABSTRACT

As human recreation in natural areas increases, so does the potential for disturbance to wildlife, and many factors (environmental, disturbance type, experience with humans) influence the impact of disturbance. However, there exists no comprehensive examination of the effects of human disturbance on ungulate escape responses. I conducted a comprehensive review of studies measuring Artiodactyl escape responses (e.g., flight initiation distance, distance moved) to experimental harassment by humans and vehicles, and meta-analyses aimed at predictive questions about the impact of human disturbance on ungulate behavior under an optimization framework. I found evidence across studies that ungulates pay attention to approacher behavior, have greater perceptions of risk when disturbed in open habitats, and females or groups with young offspring show greater flight responses than adult groups. Increased group size and the presence of hunting showed weak but positive heterogeneous effects on flight behavior both between and within species. Humans on foot were more evocative than other stimuli (vehicles, noises). Populations in areas with higher levels of human traffic showed reduced wariness but a lack of alternative sites to move to may explain some of this effect. Hunted populations showed significantly greater flight responses than non-hunted populations. Finally, I suggest five factors to consider when forming predictive models of ungulate flight behavior: (1) how seasonal variation in reproductive status and body condition effects wariness, (2) the relative impacts of lethal and non-lethal human contact, and (3) unique natural history traits that may cause differences in flight behavior between populations, (4) the availability of alternative sites, and (5) shorter distances between feeding sites and refugia can reduce the impact of other factors on flight responses.

© 2008 Elsevier Ltd. All rights reserved.

Contents

1. Introduction	2160
2. Materials and methods	2161
3. Results	2166

* Tel.: +1 413 545 0035.

E-mail address: teds@bio.umass.edu

0006-3207/\$ - see front matter © 2008 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2008.06.026

3.1.	Are ungulates sensitive to changes in speed and directness of approach of disturbing stimuli?	2166
3.2.	Are larger or smaller groups more sensitive to disturbance?	2166
3.3.	Do environmental factors influence the impact of disturbance stimuli on ungulates?	2166
3.4.	Does human disturbance negatively impact certain sex, age, or reproductive classes more than others?	2166
3.5.	What types of stimuli cause the greatest amount of disturbance and should thus be minimized?	2166
3.6.	Do individuals habituate or sensitize to regular exposure to non-lethal human disturbance or hunting activity?	2166
4.	Discussions and conclusions	2166
4.1.	Interactions between factors and unresolved questions	2168
4.2.	Management implications	2169
	Acknowledgement	2169
	References	2169

1. Introduction

With increasing urbanization, hunting, eco-tourism, and off-road recreation, opportunities for engaging wild animals in an inadvertently threatening manner as well as intentional harassment have increased substantially in the last century. However, some activities have a more negative impact than others (Boyle and Samson, 1985; Pomerantz et al., 1988; Knight and Cole, 1995). Anthropogenic stressors have sweeping effects on wildlife species (Miller and Gunn, 1979; reviewed by Kuss et al., 1990a; Knight and Gutzwiller, 1995; Olliff et al., 1999; Festa-Bianchet, 2003; Reimers and Colman, 2006), including short-term behavioral patterns (e.g., likelihood of flight response: Stankowich and Blumstein, 2005; foraging and maternal behavior: Fitzgibbon, 1998), long-term behavioral patterns (e.g., distribution, mother-offspring behavior patterns, activity patterns, habituation: Batcheler, 1968; Dorrance et al., 1975; Swenson, 1982; Jeppesen, 1987; Kufeld et al., 1988; Kilgo et al., 1998), and species biology (e.g., physiology, reproduction, physical health: Geist, 1971a,b, 1978; Gabrielsen and Smith, 1995). The generality of these impacts both within and between ungulate species is unknown (n.b., a great deal of attention has been paid to impacts on caribou and reindeer, *Rangifer tarandus*: reviewed in Reimers and Colman, 2006), and managers are often left wondering if information about disturbance effects in one species or population is relevant or useful for making management decisions about another species or population (Knight and Temple, 1995).

In recent years, wildlife managers and conservation biologists have developed several measures of human-induced stress and fitness reductions (e.g., breeding success, mate choice, flight response distances, glucocorticoids, and cardiac response: Tarlow and Blumstein, 2007) and of ecological and demographic impacts of human disturbance (e.g., changes in time budgets: Duchesne et al., 2000; probability of response: Borkowski et al., 2006; changes in space use: Manor and Saltz, 2005). For example, several research teams recently have focused their studies on the negative effects of human infrastructure development and power lines on space use by reindeer in Scandinavia and Finland (Nellemann et al., 2000; Nellemann et al., 2001; Vistnes et al., 2001; Nellemann et al., 2003; Skarin et al., 2004; Vistnes et al., 2004; Reimers and Colman, 2006, but see Reimers et al., 2007). Of the many studies on the short-term effects of human activities on wildlife, most utilize flight response distances (Knight and Cole,

1995; Miller et al., 2001), and it is not uncommon for species to show short-term effects on flight behavior but suffer no ill long-term effects (Richens and Lavigne, 1978). Nevertheless, more systematic research is needed on long-term effects to fill in those knowledge gaps (Knight and Cole, 1995).

Flight initiation distance (FID), the distance between the predator and prey when the prey flees, and other distance metrics are accurate indices of fear in animals (Miller et al., 2006) and are useful in the assessment of an animal's welfare state (Dwyer, 2004). However, the simple detection of a disturbance can induce increased alertness and heart rate, so the "range of disturbance" is likely to be much greater than FID (Ward and Cupal, 1979). Some researchers (Gill and Sutherland, 2000; Gill et al., 2001) suggest that behavioral measurements like FID may not be the most accurate indicator of human disturbance on wildlife because populations differ in the quality of the disturbance site and the availability of alternative sites. For example, animals living in an area where there are no alternative sites to move to when disturbed (Pop1), will, all else being equal, allow closer approach than animals from an area with alternative sites (Pop2). However, without knowledge of alternative site availability, the impact of human disturbance will be perceived as less in Pop1 than in Pop2, and the reduced flight responses in Pop1 may lead to the incorrect assumption that the animals in this population have habituated to the disturbance. For these reasons, composite metrics (e.g., buffer zones) take into account multiple measures including alert distance (AD: distance at which the prey becomes alert), FID, distance to roads, and resource use levels (Gill et al., 1996; Fernández-Juricic et al., 2001, 2002).

Many factors influence the decision to flee in animals, and flight decisions are economic inasmuch as animals flee when the costs of staying (i.e., not fleeing) exceed the benefits of staying (Ydenberg and Dill, 1986; Frid and Dill, 2002; Stankowich and Blumstein, 2005; Cooper and Frederick, 2007). Animals optimize this tradeoff in very general ways across taxa, but the factors that influence flight decisions and the disturbance level of a particular stimulus can vary both spatially (with population and human density differences) and temporally (with life history and seasonal differences in vulnerability), potentially leading to over- or under-mitigation of human activity on wildlife populations. High levels of inter or intra-species variation in the effect sizes of these factors suggests that animals pay attention to multiple factors and responses likely depend on the interactive effects of many factors (Frid, 1997, 2003). However, very few studies explicitly

quantify these interactive effects. Before exploring how these factors interact with each other and to predict *a priori* which factors are likely to be important and to interact in ungulate flight decisions, we must understand (1) the relative importance of each factor in ungulate flight decisions, and (2) the heterogeneity in the effects of each factor across species. A provocative interaction that causes anxiety or distress in members of one species or population, may be of little concern for members of another species or population due to differences in ecology or biology (Geist, 1978; Kuss et al., 1990a; Whittaker and Knight, 1998).

Here, I review the extensive literature on ungulate flight responses and ask questions based on optimization theory and impacts of human disturbance:

- (1) Prey pay attention to variation in the behavior of predators to judge the relative level of threat that it poses (Ydenberg and Dill, 1986). Given that the threat level of humans to ungulates varies greatly temporally, spatially, and between individual encounters, do ungulates pay attention to changes in speed and directness of approaching humans to judge their intent or level of threat?
- (2) Larger groups of ungulates may flee at greater distances because they probably detect disturbances at greater distances (increased collective vigilance) or are more likely to contain a particularly wary/reactive individual. On the other hand, individuals in larger groups may have greater perceptions of safety and flee at shorter distances (dilution effect) (discussed in Stankowich and Coss, 2006, 2007). Are larger groups more sensitive to disturbance than small groups and solitary animals, or are solitary individuals and small groups more responsive to disturbing stimuli?
- (3) Different levels of vulnerability to human persecution are associated with changes in the environment over time and space, and habitat selection is one way an animal might behaviorally mediate the effects of human interaction. Do environmental factors (e.g., season, amount of cover, time of day) influence the impact of disturbance stimuli on ungulates?
- (4) Human disturbances might be particularly detrimental during certain developmental periods, when males are forced to give up defending or searching for mates to flee, and when pregnant or guarding young offspring. Does human disturbance negatively impact certain sex, age, or reproductive classes more than others?
- (5) There is variation in the relative levels of disturbance caused by different types of anthropogenic stressors (Kuss et al., 1990a; Knight and Cole, 1995; Reimers and Colman, 2006). What types of stimuli cause the greatest amount of disturbance and should thus be minimized or more strictly regulated?
- (6) Animals show decreased flight responses in areas with larger human populations (Stankowich and Blumstein, 2005), and variation in disturbance typically is correlated with the intent of activity: hunting and nature-viewing individuals seek out direct interactions with wildlife, as opposed to hiking, biking, or snowmobiling individuals whose chief intent is not necessarily to

interact directly with wildlife. Do individuals habituate or sensitize (i.e., perceive greater risk) to regular exposure to non-lethal human disturbance or hunting activity?

After answering these broad questions, I examine the role of learning and habituation in ungulate flight responses, discuss our lack of knowledge of interaction effects and other important gaps in ungulate escape theory, and provide recommendations for the development of predictive models for ungulate responses to disturbing stimuli.

2. Materials and methods

I first gathered studies on Artiodactyls cited in Ydenberg and Dill's (1986) original review of flight behavior and searched the Web of Science (isiknowledge.com) for all references citing the review. I then searched Web of Science for papers using the terms 'flight distance,' 'flight initiation distance,' 'approach distance,' 'reaction distance,' 'escape distance,' and 'flush distance,' since these are all common ways of measuring flight responses on wild animals (Taylor and Knight, 2003a; Stankowich and Blumstein, 2005). All papers collected were mined for older references that appeared to measure flight responses in Artiodactyls but may not show up on the searches performed. In total, I found 59 references that examined the effects of different factors that directly addressed the questions outlined above on flight responses in Artiodactyls (Tables 1–3). I included studies that presented empirical tests of the factors and studies that simply reported an observational effect of a factor on flight behavior. The collection of papers is fairly exhaustive but there are likely many studies that simply fell outside the search parameters, are published in lesser-known volumes, or have not been cited by later works. Results were organized into three tables: (1) Biological factors (e.g., approacher behavior, group size, sex, habitat), (2) Disturbance types (e.g., humans, automobiles, and aircraft), and (3) Experience with humans (e.g., hunting status and human activity level). For each study, where appropriate, I report the effect (or no effect), the target species, the type of harassment, and if the population was actively hunted (if reported). Even though reindeer and caribou are all part of *R. tarandus*, I noted the subspecies and origin of reindeer populations and the location of caribou populations in the table because different populations have different histories of domestication and exposure to humans. To avoid confusion, all distance terms used in the studies were converted to 'alert distance,' 'flight initiation distance,' and 'distance moved' (DM). The most common response metrics were AD, FID, and DM, however others are reported as well. AD is positively correlated with FID (Colman et al., 2001; Stankowich and Coss, 2006) because animals likely accrue time costs (e.g., lost foraging or mating opportunities) while continuously monitoring an approacher (Blumstein, 2003; Cooper and Frederick, 2007), but there is considerable interspecies variation in the direction of the relationship between FID and DM (reviewed in Stankowich and Coss, 2007). Nevertheless, I associate greater AD, FID, and DM with greater response to a stimulus.

Table 1 – Factor effects on different types of harassment on ungulates

Factor effects	Species	Metric (r)	Disturbance	Status	References	
<i>Approacher behavior</i>						
– Fast > Slow	Black-tailed deer	FID (0.21)	M	NH	Stankowich and Coss (2006)	
	Moose	FID	M	NH	McMillan (1954)	
	Elk	AD	M	H	McCullough (1969)	
– Direct > Indirect	Black-tailed deer	FID (0.31)	M	NH	Stankowich and Coss (2006)	
	Dall's sheep	ProbFlt (0.31)	A	NH	Frid (2003)	
– No effect of directness of approach	NL Caribou	AD, FID, DM	S	NH	Mahoney et al. (2001)	
– No effect of directness of gaze	Black-tailed deer	FID (0.03)	M	NH	Stankowich and Coss (2006)	
<i>Prey group size (r = 0.13; N = 10118)</i>						
– Large > Small/Solitary	AL, YT Caribou	Scale	A	U	Klein (1974), McCourt (1974)	
	GD Caribou	AD, FID, DM	M	H	Aastrup (2000)	
	NT Caribou	Scale	A	NH	Miller and Gunn (1979)	
	Black-tailed deer	DM (0.49)	M	NH	Stankowich and Coss (2007)	
	White-tailed deer	ProbFlt (0.11)	M	U	Lagory (1987)	
	Fallow & Roe deer	FID (0.20)	M	H	de Boer et al. (2004)	
	Muskoxen	Scale (0.35)	A	NH	Miller and Gunn (1979)	
	Dall's Sheep	ProbFlt (0.31)	A ^{helicopter}	NH	Frid (2003)	
	Mouflon	FID (0.18)	M	NH	Ciuti et al. (2008)	
	– No effect	YT Caribou	FID (0.01) FDr (0.27)	C	U	Horejsi (1981)
		AL Caribou	FID	A	U	Calef et al. (1976)
		Svalbard reindeer	AD (0.02)	M	H	Colman et al. (2001)
		R.t.p. – unknown origin	FID (0.03) DM (0.09)			
Black-tailed deer		FID (0.05)	M	NH	Stankowich and Coss (2006)	
Muskoxen		AD (–0.12)	S	NH	McLaren and Green (1985)	
Moose		FID	M	H	Altmann (1958)	
Guanacos		FID (0.05)	M	H	Donadio and Buskirk (2006)	
Gazelles		FID	M	NH	Manor and Saltz (2005)	
Dall's Sheep		ProbFlt (–0.11) FID	A ^{airplane} A ^{helicopter}	NH	Frid (2003)	
– Small/Solitary > Large	Vicuñas	FID (–0.03)	M	H	Donadio and Buskirk (2006)	
	Feral reindeer	FID (–0.19) DM (–0.23)	M	H	Reimers et al. (2006)	
	R.t.t.					
	Chamois	FID (–0.13)	M	NH	Cederna and Lovari (1985)	
	Impala	FID (–0.24)	M	H	Matson et al. (2005)	
	Bighorn sheep	Scale	M	NH	Hicks and Elder (1979)	
	Mountain sheep	HR (–0.36)	M	H	MacArthur et al. (1982)	
	Fallow deer	ProbFlt (–0.23)	M	NH	Recarte et al. (1998)	
	<i>Season</i>					
	– Summer > Spring	AL Caribou	Scale	A	U	Klein (1974)
– Early > Late summer	Feral reindeer	FID (0.54)	M	H	Reimers et al. (2006)	
	R.t.t.					
	GD Caribou	DM	M	H	Aastrup (2000)	
– Midsummer > Early & Late Summer	Mouflon	FID (0.24)	M	NH	Ciuti et al. (2008)	
	NT Caribou	Scale (0.29)	A	NH	Miller and Gunn (1979)	
	Feral reindeer	DM (0.45)	M	H	Reimers et al. (2006)	
	R.t.t.					
– Calving = Winter > Other seasons	AL Caribou	FID	A	U	Calef et al. (1976)	
	Wild reindeer	Scale	Various	U	Thomson (1972)	
– Rut = Other seasons	R.t.t.					
	Blesbok	FID	M	U	Rowe-Rowe (1974)	
– Winter < Other seasons	Blesbok	FID	M	U	Rowe-Rowe (1974)	
	Chamois	FID, DM	Various	H	Hamr (1988)	
– No effect	Gazelles	FID (0.89)	M	NH	Manor and Saltz (2005)	
	Svalbard reindeer	Scale	A	U	McCourt (1974)	
	R.t.p. – unknown origin					
<i>Habitat Type (r = 0.15; N = 1580)</i>						
– Open > Closed terrain	Svalbard reindeer	FID (0.25)	S	U	Tyler (1991)	
	R.t.p. – unknown origin					
	Blesbok	FID (0.58)	M	U	Rowe-Rowe (1974)	
	Moose	FID	M	H	Altmann (1958)	
	YT Caribou	FID (0.25) FDr (0.10)	C	U	Horejsi (1981)	
	Fallow & Roe deer	FID (0.43)	M	H	de Boer et al. (2004)	
	NT Caribou	Scale	A	NH	Miller and Gunn (1979)	
– Closed > Open terrain						

Table 1 – continued

Factor effects	Species	Metric (r)	Disturbance	Status	References
– Grass > Grass with scrub	Black-tailed deer	DM (0.44)	M	NH	Stankowich and Coss (2007)
	AL Caribou	FID	A	U	Calef et al. (1976)
– No effect	Feral reindeer	FID, DM	M	H	Reimers et al. (2006)
	R.t.t.				
	NL Caribou	AD, FID, DM	S	NH	Mahoney et al., 2001
	White-tailed deer	FID	C	NH	Halloran (1943)
– Rugged > Flat terrain	White-tailed deer	ProbFlt (0.03)	M	U	Lagory (1987)
	Fallow deer	ProbFlt (0.16) [†]	M	NH	Recarte et al. (1998)
<i>Time of day</i>					
– Dusk/Dawn > Other times	Moose	FID	M	H	Altmann (1958)
	Elk	FID	M	H	Altmann (1958)
	Mule deer	FID	M	H	Altmann (1958)
– Evening > Morning	Gazelle	FID	C	NH	Walther (1969)
	Mule deer	AD	M, B	NH	Taylor and Knight (2003b)
– Morning > Evening	Mule deer	DM	M, B	NH	Taylor and Knight (2003b)
	Bison	FID	M, B	NH	Taylor and Knight (2003b)
– Day > Night	White-tailed deer	ProbFlt	S	U	Eckstein et al. (1979)
	Elk	FID (0.10)	M, C	NH	Schultz and Bailey (1978)
– Positive effect of min after sunrise	Chamois	DM (0.76)	B, M _{jog}	NH	Gander and Ingold (1997)
– Negative effect of min after sunrise	Chamois	DM (–0.84)	M _{hike}	NH	Gander and Ingold (1997)
– No effect	Chamois	FID (0.11)	B,M	NH	Gander and Ingold (1997)
<i>Age/Sex</i>					
– Calves > Other Ages	AL Caribou	FID	A	U	Calef et al. (1976)
– Calves = ♀♀ > Bulls	NT Caribou	Scale	A	NH	Miller and Gunn (1979)
	Muskoxen	Scale (0.10)	A	NH	Miller and Gunn (1979)
	Elk	FID (–0.12)	M	H	Bender et al. (1999)
– ♂♂ > ♀♀	NL Caribou	FID	M	H	Bergerud (1974)
– ♀♀ > ♂♂	Wild reindeer	Scale	Various	U	Thomson (1972)
	R.t.t.				
	Gazelle	FID (0.23)	C	NH	Walther (1969)
	Fallow deer	ProbFlt (0.18)	M	NH	Recarte et al. (1998)
	Chamois	FID, DM	Various	H	Hamr (1988)
	Gazelle	FID (–0.23)	C	NH	Walther (1969)
	Chamois	DM (0.81)	M	NH	Gander and Ingold (1997)
	Elk	FID (0.07)	M, C	NH	Schultz and Bailey (1978)
	YT Caribou	FDr (0.31)	C	U	Horejsi (1981)
			FID (0.13)		
– Adult ♂ < Subadult ♂	Chamois	FID (0.10)	B,M	NH	Gander and Ingold (1997)
– Adult ♂ > Subadult ♂		DM (0.47)	B	NH	Gander and Ingold (1997)
– No effect of sex	Elk	FID (0.07)	M, C	NH	Schultz and Bailey (1978)
	YT Caribou	FDr (0.31)	C	U	Horejsi (1981)
– No effect of age	Chamois	FID (0.10)	B,M	NH	Gander and Ingold (1997)
		DM (0.47)	B	NH	Gander and Ingold (1997)
<i>Reproductive status</i>					
– ♂: In Velvet > Pre-rut > In Rut	Moose	FID	M	H	Altmann (1958)
– ♂: Wandering > Bachelor > Territorial	Gazelle	FID (0.23)	C	NH	Walther (1969)
– ♀♀ w/calves > ♂♂	AL Caribou	Scale	A	U	Klein (1974)
	NT Caribou	Scale	A	NH	Miller and Gunn (1979)
	Mouflon	FID (0.17)	M	NH	Ciuti et al. (2008)
	Moose	FID	M	H	Altmann (1958)
– ♀ w/newborn > ♀ w/calf	NL Caribou	AD (0.24)	M	H	Bergerud (1974)
– ♀♀ groups w/calves > w/o calves		FID (0.70)			
	Mouflon	FID (0.14)	M	NH	Ciuti et al. (2008)
	NL Caribou	FID (0.21)	S	NH	Mahoney et al., 2001
– Groups w/calves < w/o calves	Gazelle	FID (0.23)	C	NH	Walther (1969)
– ♀ w/young < Other ♀♀	Chamois	FID	M	NH	Cederna and Lovari (1985)
– Groups w/more young > w/fewer young	NL Caribou	AD (0.12)	S	NH	Mahoney et al., 2001
– No effect of group composition		DM (0.04)			
		FDr (0.08)			
	Dall's Sheep	ProbFlt (0.06)	A _{helicopter}	NH	Frid (2003)
	ProbFlt (–0.04)	A _{airplane}			

Abbreviation Key:

Metrics: AD (Alert distance), AT (Assessment time) DM (Distance moved), FID (Flight initiation distance), FDr (Flight duration), Fspeed (Flight speed), HR (Heart rate), Obs (Observational report), ProbFlt (Probability of flight), Scale (Artificial scale of flight response: e.g., no reaction – rapid flight). Statistics: *r* = effect size (given when available for individual studies and the total for all studies in the analysis), *N* = sum of sample sizes of all studies included in the analysis. Disturbance Type: A (Airplane and/or Helicopter), Various (multiple harassment types including humans, animals, and moving vehicles), B (Bicycle), C (Car/Automobile), D (Dog), M (Human; when explicitly tested, M was split into two groups: M_{jog} = Jogger, M_{hike} = Hiker), S (Snowmobile), Pred (Predatory model or different real predators). Hunting Status: F (Commercially/farm raised), H (Hunted); NH (Not hunted), U (Unspecified in the paper). Species: R.t.t. (Rangifer tarandus tarandus), R.t.p. (R. t. platyrhynchus), AL (Alaska), GD (Greenland), NL (Newfoundland), NT (Northwest territories) YT (Yukon). [†]Not included in meta-analysis for this section.

Table 2 – Effects of different types of harassment on flight responses of ungulates

Disturbance effects	Species	Metric (r)	Status	References
<i>Anthropogenic disturbance (r = 0.58; N = 3171)</i>				
– Human = Mine Noise > Undisturbed	Elk calves	DM (0.38)	U	Kuck et al. (1985)
– Human > Military Noise	Moose	FID (0.72)	H	Andersen et al. (1996)
– Human = Military Noise	Moose	DM (0.26)	H	Andersen et al. (1996)
– Human = Car	Elk	FID	NH	Schultz and Bailey (1978)
– Human > Car	Giraffe	Obs	U	Kearton (1929)
– Human or Car w/light < w/o light	Elk	FID (0.10) [†]	NH	Schultz and Bailey (1978)
– Human > Horseback = Car	White-tailed deer	FID (0.46)	NH	Kucera (1976)
– Human > Bicycle = Cars	Bighorn sheep	DM (0.83)	NH	Papouchis et al. (2001)
		FDr (0.99)		
		ProbFlt (0.13)		
– Human > Bicycle	Mule deer	FID	NH	Taylor and Knight (2003b)
– Human = Bicycle	Bison, Pronghorn	AD, FID, DM	NH	Taylor and Knight (2003b)
– Jogger = Hiker = Bicycle	Chamois	FID (0.30)	H	Gander and Ingold (1997)
– Skier > Snowmobile	Reindeer	FID (0.26)	NH	Reimers et al. (2003)
		DM (0.33)		
– Snowmobile > Skier	Reindeer	AD (–0.38)	NH	Reimers et al. (2003)
– Gunshots = Humans > Cars = Airplanes=	Elk	HR, ProbFlt	F	Ward and Cupal (1979)
<i>Motorcycles</i>				
– Airplane = Helicopter	AL Caribou	Scale	U	Klein (1974)
– Airplane > Helicopter	AL Caribou	FID	U	Calef et al. (1976)
– Helicopter > Airplane	AL, YT Caribou	Scale	U	McCourt (1974)
– Airplanes/Helicopters > Humans	Muskoxen	Obs	NH	Gray (1973)
– No effect of maternal stress type	Sheep	FID	F	Roussel et al. (2006)
<i>Aircraft altitude</i>				
– Low > High	AL, YT Caribou	Scale	U	Klein (1974), McCourt et al. (1974)
	NT Caribou	Scale (0.37)	NH	Miller and Gunn (1979)
	Muskoxen	Scale (0.23)	NH	Miller and Gunn (1979)
	Moose	Scale	U	McCourt (1974)
– No effect	Dall's Sheep	ProbFlt (0.14)	NH	Frid (2003)
<i>Animals</i>				
– Human > Wolves	NL Caribou	FID	H	Bergerud (1974)
– Human > Dogs	Chamois	DM	H	Hamr (1988)
	Muskoxen	Obs	H	Hone (1934)
– Human = Dog	Elk	FID (0.27)	NH	Kloppers et al. (2005)
– Human w/dog > w/o dog	Mule deer	AD, DM	NH	Miller et al. (2001)
	Mouflon	FID (0.31)	H	Martinetto and Cugnasse (2001)
	Muskoxen	Obs	H	Hone (1934)
– Human w/dog = w/o dog	Chamois	Obs	H	Hamr (1988)
– Carnivores > Non-threatening stimuli	Sheep	DM (0.46)	F	Hansen et al. (2001)
– Wild dog > Cheetah > Lion > Hyena > Jackal	Gazelle	FID (0.16)	NH	Walther (1969)
<i>Humans in context</i>				
– Human off trail > on trail	Mule deer	DM	NH	Miller et al. (2001), Taylor and Knight (2003b)
– Human off trail = on trail	Mule deer	AD, FID	NH	Miller et al. (2001)
– Human w/dog off trail > on trail	Mule deer	FID	NH	Miller et al. (2001)
– Human w/dog off trail = on trail	Mule deer	AD	NH	Miller et al. (2001)
– Familiar < Unfamiliar human	Moose	FID	NH	McMillan (1954)

See Table 1 for Abbreviation and Reference Keys.

I then identified a list of factors to be analyzed with meta-analysis. For the analyses, I identified factors that (i) seemed to have some consistency (i.e., low experimental variation; Osenberg et al., 1999) in the way they were measured (e.g., consistent: the factor 'group size' is typically a simple correlation between number of individuals in the group and the degree of flight response; inconsistent: numerous ways of classifying of age and sex groups) and (ii) had empirical data available from at least 5 studies. The final list of factors on

which I ran formal meta-analyses included: Group size, habitat type, anthropogenic disturbances, human activity, and hunting.

Following Stankowich and Blumstein (2005), I selected the Pearson's product-moment correlation coefficient, r , as the appropriate measure of effect size (Hunter et al., 1982; Rosenthal, 1991). The r coefficient has been shown to be appropriate for analyzing results from psychological and behavioral studies (Fiske et al., 1998; Møller and Saino, 2004; Segerstrom

Table 3 – Effect of harassment experience on ungulate flight behavior

Status effects	Species	Metric (r)	Disturbance	References
<i>Human activity (r = -0.15; N = 2697)</i>				
- High < Low snowmobile traffic	Svalbard reindeer	FID (-0.20)	S	Tyler (1991)
	R.t.p. – unknown origin	DM (-0.21)		
- High < Low human traffic	Blesbok	FID (-0.58)	M	Rowe-Rowe (1974)
	Gazelle	FID	C	Walther (1969)
	Elk	FID (-0.86)	M	Cassirer et al. (1992)
	Moose	FID	M	Denniston (1956)
	Svalbard reindeer	AD (-0.21)	M	Colman et al. (2001)
	R.t.p. – unknown origin	FID (-0.36)		
		DM (-0.42)		
	Fallow deer	ProbFlt (-0.12)	M	Recarte et al. (1998)
- Low < High human traffic	Muskoxen	Obs	M	Hone (1934)
	Bighorn sheep	DM (0.30)	M	King and Workman (1986)
- No effect of human traffic level	Elk	DM (0.09)	M	Cassirer et al. (1992)
	Ibex	FID	M	Alados and Escos (1988)
- High < Low wolf activity	Elk	FID (0.47) [†]	M, D	Kloppers et al. (2005)
<i>Repeated exposure</i>				
- Later > Earlier exposures	Beef cattle	FID (0.33)	M	Kilgour et al. (2006)
	Dall's Sheep	ProbFlt (0.36)	A _{helicopter}	Frid (2003)
- Earlier > Later exposures	Wild reindeer	Scale	Various	Thomson (1972)
	R.t.t.			
	Moose	FID	M	McMillan (1954)
- No effect of exposure order	Dall's Sheep	ProbFlt (0.14)	A _{airplane}	Frid (2003)
	Svalbard reindeer	AD (0.00)	M	Colman et al. (2001)
	R.t.p. – unknown origin	FID (0.03)		
		DM (0.09)		
- Before < After harassment treatment	Elk	FID (0.67)	M, D	Kloppers et al. (2005)
<i>Hunting (r = 0.17; N = 2096)</i>				
- Experienced > Not experienced	Moose	FID	M	Altmann (1958)
	GD Caribou	AD, FID	M	Aastrup (2000)
- After hunting > Before hunting	Elk	FID (0.32)	M	Bender et al. (1999)
- More hunted > Less or non-hunted areas	White-tailed deer	FID (0.09)	M	Behrend and Lubeck (1968)
		FSpeed		
	Vicuñas	FIDrp (0.52)	M	Donadio and Buskirk (2006)
	Bighorn sheep	DM (0.30)	M	King and Workman (1986)
	Roe deer	FID (0.41)	M	de Boer et al. (2004)
	Impala	FID (0.71)	M	Matson et al. (2005)
- No effect of presence of hunting	Guanacos	FID (0.01)	M	Donadio and Buskirk (2006)
	White-tailed deer	FID	C	Grau and Grau (1980)
	Svalbard reindeer	AD (0.02)	M	Colman et al. (2001)
	R.t.p. – unknown origin	FID (-0.06)		
		DM (-0.11)		

See Table 1 for Abbreviation and Reference Keys.

and Miller, 2004) and this study addresses questions of immediate effects (Osenberg et al., 1999) on flight decisions. For this study, *r* typically is the magnitude on the effect on perceived risk of moving from a low-threat situation (control) to a high-risk situation (treatment). Coefficients were obtained for each study, when possible, in the following ways: (i) direct reporting of *r*, *R*², or partial correlation; (ii) mean and variance data (SE or SD) reported in the paper and converted to *r* using methods in Rosenthal (1991); (iii) other test statistics (e.g., *F*, *U*, *t*) and *P*-values converted to *r* using Meta-Analysis 5.3 (Ralf Schwarzer: http://userpage.fu-berlin.de/~health/meta_e.htm). Tests that reported that *P*-values were less than a stated value (e.g., *P* < 0.05; *P* < 0.001) were conservatively assigned that *P*-value (*P* < 0.01 was assigned *P* = 0.01) and converted to *r*. Studies simply stating that there ‘was an

effect’ or there ‘was no effect’, *P* > 0.05, or only stated observationally that there was or was not a difference in response were excluded from analyses. Effect sizes from all studies providing enough information to calculate *r* are listed in Tables 1–3. I performed formal weighted meta-analyses by the Schmidt–Hunter method on the five factors listed above (Hunter and Schmidt, 1990); weighted tests are the most precise and powerful meta-analytic procedures (Gurevitch and Hedges, 1999). I report the weighted mean *r* ± SD (Hunter and Schmidt, 1990), the results of *Z*-tests of significance (Rosenthal, 1984), the number of studies used in the analysis (*k*), and the sum of the sample sizes for all studies in the test (i.e., total sample size for the test: *N*). For each weighted mean *r*, I calculated the number of additional studies with an overall mean *r* ≈ 0 that would need to be filed away

(i.e., unpublished) in order to reduce the observed r to a critical 0.05 level (k_{fs} ; Orwin, 1983). While no formal guidelines exist for how large k_{fs} must be in order to achieve a robust effect, given the small number of studies in this review (59), I judged the effect to be robust if $k_{fs} > 2k$; therefore, it would take two times as many studies with a mean $r = 0$ than were found to reduce the overall effect size to 0.05. This is a subjective assessment as benchmarks of robustness using k_{fs} have not been set previously. All meta-analyses were computed using Meta-Analysis 5.3. To test for the heterogeneity (i.e. the amount of constancy or variation in r -scores) of results across studies, I calculated by hand the I^2 statistic (following Higgins et al., 2003), where 0% signifies no heterogeneity (little variation in individual r -scores) and 100% signifies great heterogeneity (high variation in individual r -scores).

3. Results

In most cases, I found weak (Cohen, 1988) estimates of effect size, little robustness, and high heterogeneity in individual r -scores. For factor effects not tested with meta-analyses, some appeared directionally consistent across species, while for others, there was wide variation in the direction of the effect. Below I discuss the results of the main questions.

3.1. Are ungulates sensitive to changes in speed and directness of approach of disturbing stimuli?

While very few studies have been conducted on the effects of approacher behavior on ungulate flight decisions, the consistency of the effects of approacher behavior on ungulate flight found here (Table 1) match those of previous reviews on other taxa (Ydenberg and Dill, 1986; Stankowich and Blumstein, 2005): when the approacher appears more threatening (faster, more direct), prey will flee at greater distances.

3.2. Are larger or smaller groups more sensitive to disturbance?

There was a very weak, non-robust overall effect for larger groups to show greater flight responses (Table 1; $r = 0.13 \pm 0.22$, $Z = 12.70$, $P < 0.00001$, $k = 21$, $N = 10118$, $k_{fs} = 32$, $I^2 = 96\%$), and there was extremely high heterogeneity across studies and both between and within species.

3.3. Do environmental factors influence the impact of disturbance stimuli on ungulates?

Individuals in more open habitats fled more readily than individuals in closed, wooded habitats (Table 1; $r = 0.15 \pm 0.18$, $Z = 6.09$, $P < 0.00001$, $k = 7$, $N = 1580$, $k_{fs} = 14$, $I^2 = 90\%$), however this effect was weak, only somewhat robust, and highly heterogeneous. The effect of season showed little consistency across studies, but the variation in the manner in which it has been categorized makes generalization even more difficult. In hunted populations, individuals appeared to be more fearful at dusk and dawn compared to other times of the day, while in non-hunted populations, there is no clear effect of time of day on flight responses.

3.4. Does human disturbance negatively impact certain sex, age, or reproductive classes more than others?

There was no consistent qualitative effect of age or sex across studies (Table 1: Age/Sex), but females and young animals appear to flee at greater distances than males. Similarly, females with more vulnerable offspring by their side exhibit greater flight responses than males and other females (Table 1: Reproductive Status).

3.5. What types of stimuli cause the greatest amount of disturbance and should thus be minimized?

There was a strong, highly robust, yet heterogeneous effect of the type of disturbance on flight behavior (Table 2; $r = 0.58 \pm 0.37$, $Z = 35.93$, $P < 0.00001$, $k = 11$, $N = 3171$, $k_{fs} = 116$, $I^2 = 100\%$), where humans on foot were far more evocative than terrestrial vehicles, aircraft, or anthropogenic noise (Anthropogenic Disturbances). Low-flying aircraft were nearly universally more disturbing than high-flying aircraft (Table 2: Aircraft Altitude), and humans had more or equally evocative effects on ungulates than Canids (Table 2: Animals). Finally, humans in a predictable hiking context (i.e., on trails) were less threatening than humans hiking off trails (Table 2: Humans in Context; Miller et al., 2001).

3.6. Do individuals habituate or sensitize to regular exposure to non-lethal human disturbance or hunting activity?

Overall, there was a weak yet robust habituation response of ungulates to increased human activity (Table 3; $r = -0.15 \pm 0.18$, $Z = -8.06$, $P < 0.00001$, $k = 10$, $N = 2697$, $k_{fs} = 21$, $I^2 = 90\%$), where ungulates in areas with higher rates of exposure to humans had reduced flight responses. There was high variation in responses to repeated exposures: some species showed greater responses on later exposures, some on earlier exposures, and some showed no difference in response between sequential exposures to humans. Hunting had a weak yet robust effect on flight responses (Table 3; $r = 0.17 \pm 0.22$, $Z = 7.89$, $p < 0.00001$, $k = 10$, $N = 2096$, $k_{fs} = 24$, $I^2 = 93\%$), where ungulates in areas with hunting activity had greater flight responses than non-hunted areas. However, this effect was highly heterogeneous and several studies found very little or no effect of hunting on flight behavior.

4. Discussions and conclusions

The results of both the review and the meta-analyses suggest that environmental factors, and experience with humans and their recreational activities have significant impacts on ungulate behavior. However, a large degree of heterogeneity in the size and direction of the effects make generalizations about many factors difficult for ungulates in general. This heterogeneity is likely due, in part, to interactive effects of different factors where the effect size of one factor changes non-additively with changes in another factor (e.g., Frid, 1997); this is discussed further below. While some specific effects are ubiquitous (e.g., approacher behavior), others are species- or population-specific (e.g., group size).

When approachers behaved in a more threatening manner, ungulates fled at greater distances. Relative to other taxa (Stankowich and Blumstein, 2005), this effect is understudied in ungulates, but nearly all studies indicated that rapidly or directly approaching humans are more evocative than slowly or indirectly approaching humans. Clearly, animals pay attention to the behavior of the approacher, looking for cues as to whether or not it has spotted the individual or intends to attack.

While a large number of studies have measured the effect of group size on flightiness in ungulates, the overall trend for larger groups to have greater flight responses was very weak and not at all robust (Table 1: Group Size). Individual studies showed strong responses in either direction (e.g., large > small groups: Stankowich and Coss, 2007, $r = 0.49$; small > large groups: MacArthur et al., 1982, $r = -0.36$) and many showed no effect at all. Looking within the directional effects, there is no apparent effect of stimulus type, type of measurement of flight response, or hunting status on group size effects, and there are even disagreements within species on the presence and direction of the effect. For example, in hunted populations of *R. tarandus* (caribou and reindeer) that were harassed by humans on foot and where measurements of FID and DM were taken, Aastrup (2000) found larger groups to be more wary, Reimers and colleagues (2006) found smaller groups to be more wary, and Colman and colleagues (2001) found no effect at all. While these results were from different populations with different histories with humans, there were no major differences in the levels of hunting or recreation described in these reports; however, there was often an interaction between group size and season where group size effects changed during the hunting season and when tourism rates were greater. Larger groups can be expected to have greater FID and DM because the presence of a particularly wary animal is more likely in a larger group, and typically the movements of the most wary group member have a contagious effect on the rest of the group (e.g., in mule deer, *O. hemionus* spp.: Dasmann and Taber, 1956; Lingle and Wilson, 2001; Stankowich and Coss, 2007). Smaller groups can be expected to have greater FID and DM because of higher *per capita* risk due to a lack of the 'dilution effect.' This intraspecific variation when other major factors are controlled for indicates that effects of group size on flightiness may not be species-specific and their presence and direction might depend on the history of the population/subspecies (e.g., feral, domestic, or wild), season, the level of exposure to humans in a recreational context, ruggedness of the landscape, or some other social or environmental factor (e.g., feeding competition or reproductive/social status within the group).

Openness of habitat had a weak but consistent effect on ungulates' flight responses (Table 1: Habitat Type), which agrees with the results from other taxa (reviewed in Stankowich and Blumstein, 2005). When there is little cover or distance to refuge is great, risk is greater and animals flee at greater distances. Open areas may be optimal feeding or mating sites and voluntary withdrawal due to disturbance often involves movement to areas with more cover that may be smaller in area and/or less favorable for these activities (e.g., Batcheler, 1968; Dorrance et al., 1975; Swenson, 1982; Jeppesen, 1987; Kufeld et al., 1988). If alternative habitat is

not available, prey experience an increased cost of leaving their current habitat, which could influence migration or the probability of flight, and ultimately lead to an underestimation of the level of disturbance and stress (Gill et al., 2001). There is a tradeoff between the level of protective cover and perceptual constraints, prey may flee as soon as they detect a threat, and reduced flight distances in closed habitats also may be due to limited ability to detect a threat at longer distances. However, an economic approach to questions about flight behavior has been shown to be more parsimonious given the evidence from the literature (Ydenberg and Dill, 1986).

Reproductive status and sex in ungulates have large consistent effects on the decision to flee. In general, males are less wary than females, and this is especially true when they are guarding or competing for access to females (Table 1). Similarly, females are most wary when they are guarding newborn offspring or young, which are more vulnerable to predation. These effects appear to be consistent within species (e.g., caribou) and are unaffected by stimulus type or hunting status. While we know that hunting increases wariness in general (see discussion below), I found no study that measured the effect of sex-selected hunting (e.g., only males are hunted) on sex differences in seasonal wariness; one explanation for this lack of data is that males might be more secretive during hunting season, and therefore it would be difficult to get sufficient amounts of data to show an effect. Clearly flight behavior factors like sex and reproductive status may influence inter- and intraspecific vulnerability to hunting and other forms of harassment, and this inherent variation in flight response influences the degree to which species, populations, or particular demographic groups are susceptible to overexploitation by recreational or subsistence hunting (Fitzgibbon, 1998).

Animals assign different levels of risk to different types of predatory threat and disturbance. Loud noises (e.g., mine or military noises) that do not precede a true harassment event are equal or lesser in effect to a human approacher (Table 2: Anthropogenic Disturbance). In general, humans on foot are the most disturbing and are more evocative than humans on horseback, on bicycles, or in cars; this suggests that human disturbance on wildlife can be minimized with these latter types of interactions. When used in a harassing manner, airplanes and helicopters are equally as disturbing, and all studies using aircraft found that low-altitude flyovers were much more disturbing than high-altitude passes, causing rapid flight and distress in ungulate groups.

The appearance of a human on foot is more frequently associated with targeted harassment (e.g., hunting) than humans in vehicles; therefore they are treated as more threatening. Both humans and canids are disturbing to ungulates, but the flight response tends to be stronger towards humans (Table 2: Animals). This trend may be explained by the larger relative size difference between domestic dogs and the particular ungulate species studied: larger predators tend to be more evocative than smaller predators (Stankowich and Blumstein, 2005). Alternatively, the more effective hunting skills of humans over small dogs also may contribute to this effect. There is evidence (Miller et al., 2001; Taylor and Knight, 2003b) that humans off trails are perceived as more threaten-

ing than on trails (Table 2: Humans in Context). A human exposed on a trail is unlikely to be followed by a dangerous consequence (e.g., gunshot or chase), whereas when humans leave the trail, the likelihood that they intend to approach or harass the individual probably increases exponentially.

Hunting has wide, sweeping effects on all aspects of ungulate biology. Not surprisingly and in agreement with evidence from avian species (Fox and Madsen, 1997), ungulate populations that experience higher hunting activity are more wary than less habituated populations (Table 3: Hunting). But this effect was highly heterogeneous in ungulates ($I^2 = 93\%$). No effect of hunting status was found in white-tailed deer (*Odocoileus virginianus*: Grau and Grau, 1980), however the disturbance stimulus used in the study was an automobile and unless hunters shoot from automobiles, we would not expect population differences in how deer treat automobiles. Colman and colleagues (2001) attribute their lack of effect of hunting activity on flight responses of caribou to the populations becoming habituated to humans during non-hunting seasons due to high human recreation traffic. Therefore a temporary, seasonal burst of hunting activity in an area where human recreation is already allowed year-round may not have a significant negative impact on caribou survival.

When animals experience a disturbance frequently, they tend to become habituated to it, and the degree of habituation may vary among individuals in a population (Picton, 1999). Ungulates in areas with frequent contact with humans showed reduced flight responses compared to those in areas where human contact is rare, which is in agreement with studies of other taxa (Stankowich and Blumstein, 2005), including lizards (e.g., Labra and Leonard, 1999; Cooper et al., 2003) and birds (e.g., Cooke, 1980; Blumstein et al., 2003). While resource scarcity and lack of alternative sites to move to may explain some of this apparent “habituation” (Gill et al., 2001), the ubiquity of the effect across studies suggests that ungulates do habituate to humans in heavily populated areas. Two studies, however, found the opposite effect. If ungulates are completely naïve to humans, we can expect to them to treat humans as curiosities and not as threatening, much like predator naïve animals on islands (e.g., Galápagos Islands) show no fear of humans. Naïve prey probably learn quickly to recognize bipedal approachers as dangerous when they are associated with harassing or deadly consequences. Alternatively, isolation on islands, not fewer predators, may be responsible for this island effect (Blumstein and Daniel, 2005): island living may select against highly ‘reactive’ (Sih et al., 2004) individuals and this selection can impact anti-predator responses. This is the likely explanation for the results of Hone (1934), while the negative results of King and Workman (1986) were likely heavily influenced by greater hunting activity in the high human density site compared to the low density site.

It has long been recognized that learning plays a major role in the manner and degree to which ungulates respond to humans (Geist, 1971a). If animals associate human presence with food, they will be attracted to human settlements, but if they are hunted, stalked, or subjected to repeated harassment, they will flee from humans (e.g., sheep: *Ovis spp*; Dwyer, 2004). However, habituation to even low impact, nonconsumptive, human stressors (e.g., hiking and mountain

biking) may take many years or never occur at all (Fairbanks and Tullous, 2002). Nevertheless, animals in general show decreased flight responses in areas with larger human populations (Stankowich and Blumstein, 2005). Many ungulate populations become too habituated to human presence and encroach on human settlements. This “refuge effect” can have negative impacts on human settlements (reviewed in Kloppers et al., 2005), often attracting natural predators towards settlements or causing an outright loss of prey when predators will not enter settlements.

4.1. Interactions between factors and unresolved questions

All meta-analyses showed high levels of heterogeneity across studies in the size and direction of the effects. However, when animals pay attention to two or more factors simultaneously, these factors may not be additive in their effects on flight responses and responses may depend on the multiplicative or dynamic effects of multiple factors. For example, Frid (2003) found that the probability of Dall’s sheep (*Ovis dalli dalli*) fleeing from a helicopter was lower during indirect approaches, but this effect was more pronounced when sheep were on rocky slopes, which provide safety, than when sheep were farther from rocky slopes. Similarly, Frid (1997) showed that group size has a strong effect on vigilance in sheep when groups are far from the safety of cliffs, but there is little effect of group size on vigilance when groups are near cliffs. These interactions may mask or reduce the effect size of certain factors depending on the conditions under which animals were tested, and they are sorely lacking in the studies reviewed here (but see Cooper, unpublished manuscript for a review of factor interactions in lizard escape behavior). Potentially interesting interactions with management implications in ungulates and potential to contribute to the optimization framework in escape theory include: sex \times season (i.e., hunting vs. non-hunting), hunting effects \times recreation effects, group size \times season, group size \times distance to refuge or habitat type, directness of approach \times type of disturbance, and reproductive status or presence of calves \times distance to refuge or habitat type.

Human disturbances can be particularly detrimental during certain critical periods of an animal’s life or during the year when animals are in poor condition or more vulnerable to injury (e.g., pregnancy, calving, and fly season: Geist, 1971a,b; Kuss et al., 1990a; Phillips and Allredge, 2000). Beale and Monaghan (2004) showed that birds (turnstones: *Arenaria interpres*) in good condition (i.e., received food supplementation) flushed at greater distances, had increased scanning rates, and moved greater distances when flushed compared to birds that did not receive food supplementation. When animals are in poor condition, there is a greater cost of leaving a site where food is present, resulting in decreased flight distances. There also may be an interaction between food abundance in a site and body condition where animals in good condition always flee at greater distances regardless of food abundance, but animals in poor quality may be more sensitive to food abundance, fleeing at shorter distances when food is present. While it is known that ungulates in poor condition are targets of predators (Mech, 1970; Huggard, 1993; Gese and

Grothe, 1995; Mech et al., 1995; Gese, 1999; Husseman et al., 2003), they may also suffer disproportionately from human disturbance, but this has never been quantified formally. Therefore, when a population contains individuals in poor, malnourished condition, using distance metrics alone to quantify disturbance would be misleading and disturbance models must take into account both individual condition and resource abundance (Beale and Monaghan, 2004).

4.2. Management implications

Blumstein and colleagues (Blumstein et al., 2005) suggest that in order to develop predictive models of how different avian species will respond to disturbances, managers need three things: (1) multiple indicators of disturbance, (2) identification of the degree of interspecific variability, and (3) life history, natural history, and other ecological correlates with the behavioral responses of interest. This study supports those recommendations and builds on them. From the data summarized here, several generalizations can be made in developing predictive models for ungulate responses to harassing stimuli. First, it is important to identify ways in which responses vary between sexes, between different stages of their reproductive cycle, and with individual body condition. Second, the impact of hunting activity (when seasonal) on ungulates may vary depending on the level of exposure to humans in a non-threatening recreational context (e.g., vehicles and hikers on trails). Third, it is necessary to examine the ways in which the population of concern differs in natural history and exposure to other sources of predation from other populations under consideration as predictive indicators for responses to disturbance. Fourth, when judging the impact of a disturbance and the level of habituation, it is important to consider the availability of alternative sites. Fifth, as shown by Frid (1997, 2003), distance to safety and habitat type may determine the impact of other factors (e.g., disturbance type, group size, presence of young) on response level.

The first step in visitor impact management of wildlife (Kuss et al., 1990b) is to review what is already known about the species and issues of interest. Management of wild ungulates requires reasonable knowledge of the total biology of the species, its behavioral adaptations, and its local history of human contact. Some studies reviewed here make specific recommendations for how to reduce behavioral reactions to human recreation and disturbance. For example, managers may restrict off trail movements of humans, prohibit dogs from critical areas, partition the landscape into recreation zones to allow certain human activities in some areas but ban them in others, and educate visitors about how their actions influence wildlife (Miller et al., 2001). The results of this review and meta-analysis suggest that information on behavioral responses to disturbance can be useful in the formation of predictive models of human impacts on wildlife.

The behavior of ungulates toward humans is likely to be the sum of the effects of all human activities (Jeppesen, 1987). While hunting has clear effects on flight responses in most species, nonconsumptive recreation may buffer these effects and seasonal hunting may not impose enough negative stimuli towards humans to override habituation (Colman

et al., 2001). Moreover, the negative impacts of hunting may be minimized further if ungulates that are not killed do not experience negative stimuli from hunters (i.e., hunters shoot and clean their take without being noticed by other ungulates). Several studies have shown that ungulates may not show behavioral differences in response to hunting if they also experience humans in a non-threatening context (Behrend and Lubeck, 1968; Grau and Grau, 1980; Kufeld et al., 1988). Therefore, ungulates that routinely encounter humans in non-threatening contexts to which they can habituate, may only suffer minimal impacts on their behavior towards humans if exposed to seasonal hunting.

Given the frequency of intraspecific variation in factor effects on flight behavior (e.g., Group Size, Time of Day), it is important to recognize that populations may differ in the way they respond to human disturbance. These differences might stem from variation in experience with humans (types of recreation, presence of hunting, history of exposure, etc.), availability of alternative habitats, population size, presence of other predators, and physical terrain. Therefore, whatever prior information is available on responses to anthropogenic disturbance from other populations of the focal species' must be discounted or adjusted for differences in natural history and ecology.

In summary, by examining the results of empirical research on flight responses of ungulates with reference to different types of environmental factors, harassment types, and exposure to hunting, I have identified key factors that reliably affect flight response and types of disturbance most likely to cause the greatest increase in stress. I suggest that interactions between multiple factors explain a significant amount of the heterogeneity across studies, and propose specific interactions to examine in future studies. From these results, I generated testable management predictions about flight responses that can help managers understand and regulate human recreation and disturbance in ways that can enhance wildlife fitness and human experiences.

Acknowledgement

I thank D. Blumstein, R. Coss, C.C. St. Clair, and 3 anonymous reviewers for providing comments on a previous version of this manuscript. T.S. was supported by the Darwin Postdoctoral Fellowship from the University of Massachusetts, Amherst.

REFERENCES

- Aastrup, P., 2000. Responses of West Greenland caribou to the approach of humans on foot. *Polar Research* 19, 83–90.
- Alados, C.L., Escos, J., 1988. Alarm calls and flight behaviour in Spanish ibex (*Capra pyrenaica*). *Biology of Behaviour* 13, 11–21.
- Altmann, M., 1958. The flight distance in free-ranging big game. *Journal of Wildlife Management* 22, 207–209.
- Andersen, R., Linnell, J.D.C., Langvatn, R., 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. *Biological Conservation* 77, 169–176.

- Batcheler, C.L., 1968. Compensatory response of artificially controlled mammal populations. *Proceedings of the New Zealand Ecological Society* 15, 25–30.
- Beale, C.M., Monaghan, P., 2004. Behavioural responses to human disturbance: a matter of choice? *Animal Behaviour* 68, 1065–1069.
- Behrend, D.F., Lubeck, R.A., 1968. Summer flight behavior of white-tailed deer in two Adirondack forests. *Journal of Wildlife Management* 32, 615–618.
- Bender, L.C., Beyer, D.E.J., Haufler, J.B., 1999. Effects of short-duration, high-intensity hunting on elk wariness in Michigan. *Wildlife Society Bulletin* 27, 441–445.
- Bergerud, A.T., 1974. The role of the environment in the aggregation, movement and disturbance behaviour of caribou, in: Bergerud, A.T. (Ed.), *The Behavior of Ungulates and its Relation to Management*. International Union for Conservation of Nature and Natural Resources (IUCN), Morges, Switzerland, pp. 552–584.
- Blumstein, D.T., 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management* 67, 852–857.
- Blumstein, D.T., Daniel, J.C., 2005. The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B* 272, 1663–1668.
- Blumstein, D.T., Anthony, L.L., Harcourt, R., Ross, G., 2003. Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation* 110, 97–100.
- Blumstein, D.T., Fernández-Juricic, E., Zollner, P.A., Garity, S.C., 2005. Inter-specific variation in avian responses to human disturbance. *Journal of Applied Ecology* 42, 943–953.
- Borkowski, J.J., White, P.J., Garrott, R.A., Davis, T., Hardy, A.R., Reinhart, D.J., 2006. Behavioral responses of bison and elk in Yellowstone to snowmobiles and snow coaches. *Ecological Applications* 16, 1911–1925.
- Boyle, S.A., Samson, F.B., 1985. Effects of nonconsumptive recreation on wildlife: a review. *Wildlife Society Bulletin* 13, 110–116.
- Calef, G.W., DeBock, E.A., Lortie, G.M., 1976. Reaction of barren-ground caribou to aircraft. *Arctic* 29, 201–212.
- Cassirer, E.F., Freddy, D.J., Ables, E.D., 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. *Wildlife Society Bulletin* 20, 375–381.
- Cederna, A., Lovari, S., 1985. The impact of tourism on chamois feeding activities in an area of the Abruzzo National Park, Italy. In: Cederna, A., Lovari, S. (Eds.), *The Biology and Management of Mountain Ungulates*. Croom Helm, London, pp. 216–225.
- Ciuti, S., Pipia, A., Ghiandai, F., Grignolio, S., Apollonio, M., 2008. The key role of lamb presence in affecting flight response in Sardinian mouflon (*Ovis orientalis musimon*). *Behavioural Processes* 77, 408–412.
- Cohen, J., 1988. *Statistical Power Analysis in the Behavioral Sciences*. Lawrence Earlbaum Associates, Hillsdale, NJ.
- Colman, J.E., Jacobsen, B.W., Reimers, E., 2001. Summer response distances of Svalbard reindeer *Rangifer tarandus platyrhynchus* to provocation by humans on foot. *Wildlife Biology* 7, 275–283.
- Cooke, A.S., 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biological Conservation* 18, 85–88.
- Cooper, W.E., Frederick, W.G., 2007. Optimal flight initiation distance. *Journal of Theoretical Biology* 244, 59–67.
- Cooper, W.E., Pérez-Mellado, V., Baird, T., Baird, T.A., Caldwell, J.P., Vitt, L.J., 2003. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. *Behavioral Ecology* 14, 288–293.
- Cooper, W.C., unpublished manuscript. Simultaneous risks and costs in escape and refuge use.
- Dasmann, R.F., Taber, R.D., 1956. Behavior of Columbian black-tailed deer with reference to population ecology. *Journal of Mammalogy* 37, 143–164.
- de Boer, H.Y., van Breukelen, L., Hootsmans, M.J.M., van Wieren, S.E., 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. *Wildlife Biology* 10, 35–41.
- Denniston, R.H., 1956. Ecology, behavior, and population dynamics of the Wyoming or Rocky Mountain moose, *Alces alces shirasi*. *Zoologica* 41, 105–118.
- Donadio, E., Buskirk, S.W., 2006. Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. *Biological Conservation* 127, 139–145.
- Dorrance, M.J., Savage, P.J., Huff, D.E., 1975. Effects of snowmobiles on white-tailed deer. *Journal of Wildlife Management* 39, 563–569.
- Duchesne, M., Cote, S.D., Barrette, C., 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. *Biological Conservation* 96, 311–317.
- Dwyer, C.M., 2004. How has the risk of predation shaped the behavioural responses of sheep to fear and distress? *Animal Welfare* 13, 269–281.
- Eckstein, R.G., O'Brien, T.F., Rongstad, O.J., Bollinger, J.G., 1979. Snowmobile effects on movements of white-tailed deer: a case-study. *Environmental Conservation* 6, 45–51.
- Fairbanks, W.S., Tullous, R., 2002. Distribution of pronghorn (*Antilocapra americana* Ord) on Antelope Island State Park, Utah, USA, before and after establishment of recreational trails. *Natural Areas Journal* 22, 277–282.
- Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environmental Conservation* 28, 263–269.
- Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2002. Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 80, 1212–1220.
- Festa-Bianchet, M., 2003. Exploitative wildlife management as a selective pressure for the life-history evolution of large mammals. In: Festa-Bianchet, M. (Ed.), *Animal Behavior and Wildlife Conservation*. Island Press, Washington, DC, pp. 191–207.
- Fiske, P., Rintamaki, P.T., Karvonen, E., 1998. Mating success in lekking males: a meta-analysis. *Behavioral Ecology* 9, 328–338.
- Fitzgibbon, C.D., 1998. The management of subsistence harvesting: behavioral ecology of hunters and their mammalian prey. In: Fitzgibbon, C.D. (Ed.), *Behavioral Ecology and Conservation Biology*. Oxford University Press, New York, pp. 449–473.
- Fox, A.D., Madsen, J., 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. *Journal of Applied Ecology* 34, 1–13.
- Frid, A., 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* 53, 799–808.
- Frid, A., 2003. Dall's sheep responses to overflights by helicopter and fixed-wing aircraft. *Biological Conservation* 110, 387–399.
- Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6, Online article #11: <http://www.consecol.org/vol16/iss11/art11>.
- Gabrielsen, G.W., Smith, E.N., 1995. Physiological responses of wildlife to disturbance. In: Gabrielsen, G.W., Smith, E.N. (Eds.), *Wildlife and Recreationists: Coexistence Through Management and Research*. Island Press, Washington, DC, pp. 95–107.

- Gander, H., Ingold, P., 1997. Reactions of male alpine chamois *Rupicapra r. rupicapra* to hikers, joggers and mountainbikers. *Biological Conservation* 79, 107–109.
- Geist, V., 1971a. A behavioural approach to the management of wild ungulates. In: Duffey, E., Watt, A.S. (Eds.), *The Scientific Management of Animal and Plant Communities for Conservation*. The 11th Symposium of the British Ecological Society, University of East Anglia, Norwich. Blackwell Scientific Publications, Oxford, pp. 413–424.
- Geist, V., 1971b. Is big game harassment harmful? *Oilweek* 22, 12–13.
- Geist, V., 1978. Behavior. In: Geist, V. (Ed.), *Big Game of North America, Ecology and Management*. Stackpole Books, Harrisburg, Pennsylvania, pp. 283–296.
- Gese, E.M., 1999. Threat of predation: do ungulates behave aggressively towards different members of a coyote pack? *Canadian Journal of Zoology* 77, 499–503.
- Gese, E.M., Grothe, S., 1995. Analysis of coyote predation on deer and elk during Winter in Yellowstone National Park, Wyoming. *American Midland Naturalist* 133, 36–43.
- Gill, J.A., Sutherland, W.J., 2000. Predicting the consequences of human disturbance on behavioural decisions. In: Gill, J.A., Sutherland, W.J. (Eds.), *Behaviour and Conservation*. Cambridge University Press, Cambridge, pp. 51–64.
- Gill, J.A., Sutherland, W.J., Watkinson, A.R., 1996. A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology* 33, 786–792.
- Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation* 97, 265–268.
- Grau, G.A., Grau, B.L., 1980. Effects of hunting on hunter effort and white-tailed deer behavior. *Ohio Journal of Science* 80, 150–156.
- Gray, D.R., 1973. Winter research on the muskox (*Ovibos moschatus wardi*) on Bathurst Island, 1970–71. *Arctic Circular* 21, 158–163.
- Gurevitch, J., Hedges, L.V., 1999. Statistical issues in ecological meta-analyses. *Ecology* 80, 1142–1149.
- Halloran, A.F., 1943. Management of deer and cattle on the Arkansas National Wildlife Refuge, Texas. *Journal of Wildlife Management* 7, 203–216.
- Hamr, J., 1988. Disturbance behavior of chamois in an alpine tourist area of Austria. *Mountain Research and Development* 8, 65–73.
- Hansen, I., Christiansen, F., Hansen, H.S., Braastad, B., Bakken, M., 2001. Variation in behavioural responses of ewes towards predator-related stimuli. *Applied Animal Behaviour Science* 70, 227–237.
- Hicks, L.L., Elder, J.M., 1979. Human disturbance of Sierra Nevada bighorn sheep. *Journal of Wildlife Management* 43, 909–915.
- Higgins, J.P.T., Thompson, S.G., Deeks, J.J., Altman, D.G., 2003. Measuring inconsistency in meta-analyses. *British Medical Journal* 327, 557–560.
- Hone, E., 1934. The present status of the muskox in Arctic North America and Greenland. *Special Publications of the American Committee for International Wildlife Protection* No. 5, 1–87.
- Horejsi, B.L., 1981. Behavioral response of barren ground caribou to a moving vehicle. *Arctic* 34, 180–185.
- Huggard, D.J., 1993. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. *Canadian Journal of Zoology* 71, 140–147.
- Hunter, J.E., Schmidt, F.L., 1990. *Methods of Meta-Analysis: Correcting Error and Bias in Research Findings*. Sage Publications, Newbury Park, CA.
- Hunter, J.E., Schmidt, F.L., Jackson, G.B., 1982. *Meta-Analysis: Cumulating Research Findings Across Studies*. Sage Publications, Beverly Hills, CA.
- Husseman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R., Quigley, H., 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* 101, 591–601.
- Jeppesen, J.L., 1987. Impact of human disturbance on home range movements and activity of red deer *Cervus elaphus* in a Danish environment. *Danish Review of Game Biology* 13, 1–38.
- Kearnton, C., 1929. *In the Land of the Lion*. National Travel Club, London. pp. 298.
- Kilgo, J.C., Labisky, R.F., Fritzen, D.E., 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. *Conservation Biology* 12, 1359–1364.
- Kilgour, R.J., Melville, G.J., Greenwood, P.L., 2006. Individual differences in the reaction of beef cattle to situations involving social isolation, close proximity of humans, restraint and novelty. *Applied Animal Behaviour Science* 99, 21–40.
- King, M.N., Workman, G.W., 1986. Responses of desert bighorn sheep to human harassment: management implications. *Transactions of the North American Wildlife and Natural Resources Conference* 51, 74–85.
- Klein, D.R., 1974. The reaction of some northern mammals to aircraft disturbance. In: Klein, D.R. (Ed.), *XIth International Congress of Game Biologists*. National Swedish Environmental Protection Board. National Swedish Environmental Protection Board, Stockholm, pp. 377–383.
- Kloppers, E.L., St. Clair, C.C., Hurd, T.E., 2005. Predator-resembling aversive conditioning for managing habituated wildlife. *Ecology and Society* 10, Online article #3, <http://www.ecologyandsociety.org/vol10/iss11/art31/>.
- Knight, R.L., Cole, D.N., 1995. Wildlife responses to recreationists. In: Knight, R.L., Cole, D.N. (Eds.), *Wildlife and Recreationists: Coexistence Through Management and Research*. Island Press, Washington, DC, pp. 51–69.
- Knight, R.L., Gutzwiller, K.J. (Eds.), 1995. *Wildlife and Recreationists: Coexistence Through Management and Research*. Island Press, Washington DC, p. 372.
- Knight, R.L., Temple, S.A., 1995. Wildlife and recreationists: coexistence through management. In: Knight, R.L., Temple, S.A. (Eds.), *Wildlife and Recreationists: Coexistence Through Management and Research*. Island Press, Washington, DC, pp. 327–333.
- Kucera, E., 1976. Deer flushing distance as related to observers mode of travel. *Wildlife Society Bulletin* 4, 128–129.
- Kuck, L., Hompland, G.L., Merrill, E.H., 1985. Elk calf response to simulated mine disturbance in Southeast Idaho. *Journal of Wildlife Management* 49, 751–757.
- Kufeld, R.C., Bowden, D.C., Schrupp, D.L., 1988. Influence of hunting on movements of female mule deer. *Journal of Range Management* 41, 70–72.
- Kuss, F.R., Graefe, A.R., Vaske, J.J., 1990a. *Visitor Impact Management: A Review of Research*. National Parks and Conservation Association, Washington, DC. pp. 256.
- Kuss, F.R., Graefe, A.R., Vaske, J.J., 1990b. *Visitor Impact Management: The Planning Framework*. National Parks and Conservation Association, Washington, DC. pp. 256.
- Labra, A., Leonard, R., 1999. Intraspecific variation in antipredator responses of three species of lizards (*Liolaemus*): possible effects of human presence. *Journal of Herpetology* 33, 441–448.
- Lagory, K.E., 1987. The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. *Animal Behaviour* 35, 20–25.
- Lingle, S., Wilson, W.F., 2001. Detection and avoidance of predators in white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*). *Ethology* 107, 125–147.
- MacArthur, R.A., Geist, V., Johnston, R.H., 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. *Journal of Wildlife Management* 46, 351–358.
- Mahoney, S.P., Mawhinney, K., McCarthy, C., Anions, D., Taylor, S., 2001. Caribou reactions to provocation by snowmachines in Newfoundland. *Rangifer* 21, 35–43.

- Manor, R., Saltz, D., 2005. Effects of human disturbance on use of space and flight distance of mountain gazelles. *Journal of Wildlife Management* 69, 1683–1690.
- Martinetto, K., Cugnasse, J.M., 2001. Reaction distance in Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) in the presence of hikers with a dog on the Caroux plateau (Hérault, France). *Revue D Ecologie-La Terre Et La Vie* 56, 231–242.
- Matson, T.K., Goldizen, A.W., Putland, D.A., 2005. Factors affecting the vigilance and flight behaviour of impalas. *South African Journal of Wildlife Research* 35, 1–11.
- McCourt, K.H., Feist, J.D., Doll, D., Russell, J.J., 1974. Disturbance studies of caribou and other mammals in the Yukon and Alaska, 1972. Canadian Arctic Gas Study Limited, Biological Report Series 5, 1–246.
- McCullough, D.R., 1969. *The Tule Elk: Its History, Behavior, and Ecology*, University of California Publications in Zoology. University of California Press, Berkeley. pp. 209.
- McLaren, M.A., Green, J.E., 1985. The reactions of muskoxen to snowmobile harassment. *Arctic* 38, 188–193.
- McMillan, J.F., 1954. Some observations on moose in Yellowstone Park. *American Midland Naturalist* 52, 392–399.
- Mech, D.L., 1970. *The Wolf: The Ecology and Behavior of an Endangered Species*. The Natural History Press, Garden City, NY. pp. 384.
- Mech, L.D., Meier, T.J., Burch, J.W., 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. In: Mech, L.D., Meier, T.J., Burch, J.W. (Eds.), *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute, University of Alberta, Edmonton, pp. 231–243.
- Miller, F.L., Gunn, A., 1979. Responses of Peary caribou and muskoxen to helicopter harassment. *Canadian Wildlife Service Occasional Paper No. 40*, 1–90.
- Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. *Wildlife Society Bulletin* 29, 124–132.
- Miller, K.A., Garner, J.P., Mench, J.A., 2006. Is fearfulness a trait that can be measured with behavioural tests? A validation of four fear tests for Japanese quail. *Animal Behaviour* 71, 1323–1334.
- Møller, A.P., Saino, N., 2004. Immune response and survival. *Oikos* 104, 299–304.
- Nellemann, C., Jordhøy, P., Stoen, O.G., Strand, O., 2000. Cumulative impacts of tourist resorts on wild reindeer (*Rangifer tarandus tarandus*) during winter. *Arctic* 53, 9–17.
- Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., 2001. Winter distribution of wild reindeer in relation to power lines, roads and resorts. *Biological Conservation* 101, 351–360.
- Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., Newton, A., 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. *Biological Conservation* 113, 307–317.
- Olliff, T., Legg, K., Kaeding, B. (Eds.), 1999. *Effects of winter recreation on wildlife of the Greater Yellowstone Area: a literature review and assessment*. Report to the Greater Yellowstone Coordinating Committee. Yellowstone National Park, WY, pp. 315.
- Orwin, R.G., 1983. A fail-safe N for effect size in meta-analysis. *Journal of Educational Statistics* 8, 157–159.
- Osenberg, C.W., Sarnelle, O., Cooper, S.D., Holt, R.D., 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* 80, 1105–1117.
- Papouchis, C.M., Singer, F.J., Sloan, W.B., 2001. Responses of desert bighorn sheep to increased human recreation. *Journal of Wildlife Management* 65, 573–582.
- Phillips, G.E., Alldrege, A.W., 2000. Reproductive success of elk following disturbance by humans during calving season. *Journal of Wildlife Management* 64, 521–530.
- Picton, H.D., 1999. Energetic cost of wildlife displacement by winter recreationists. In: Olliff, T., Legg, K., Kaeding, B. (Eds.), *Effects of winter recreation on wildlife of the Greater Yellowstone Area: a literature review and assessment*. Report to the Greater Yellowstone Coordinating Committee. Yellowstone National Park, Wyoming, pp. 135–144.
- Pomerantz, G.A., Decker, D.J., Goff, G.R., Purdy, K.G., 1988. Assessing impact of recreation on wildlife: a classification scheme. *Wildlife Society Bulletin* 16, 58–62.
- Recarte, J.M., Vincent, J.P., Hewison, A.J.M., 1998. Flight responses of park fallow deer to the human observer. *Behavioural Processes* 44, 65–72.
- Reimers, E., Colman, J.E., 2006. Reindeer and caribou (*Rangifer tarandus*) response towards human activities. *Rangifer* 26, 55–71.
- Reimers, E., Eftestøl, S., Colman, J.E., 2003. Behavior responses of wild reindeer to direct provocation by a snowmobile or skier. *Journal of Wildlife Management* 67, 747–754.
- Reimers, E., Miller, F.L., Eftestøl, S., Colman, J.E., Dahle, B., 2006. Flight by feral reindeer *Rangifer tarandus tarandus* in response to a directly approaching human on foot or on skis. *Wildlife Biology* 12, 403–413.
- Reimers, E., Dahle, B., Eftestøl, S., Colman, J.E., Gaare, E., 2007. Effects of a power line on migration and range use of wild reindeer. *Biological Conservation* 134, 484–494.
- Richens, V.B., Lavigne, G.R., 1978. Response of white-tailed deer to snowmobiles and snowmobile trails in Maine. *Canadian Field-Naturalist* 92, 334–344.
- Rosenthal, R., 1984. *Meta-Analytic Procedures for Social Research*, first ed. Sage Publications, Newbury Park, CA.
- Rosenthal, R., 1991. *Meta-Analytic Procedures for Social Research*, second ed. Russell Sage Foundation, New York, NY.
- Roussel, S., Hemsworth, P.H., Leruste, H., White, C., Duvaux-Ponter, C., Nowak, R., Boissy, A., 2006. Repeated transport and isolation during pregnancy in ewes: effects on the reactivity to humans and to their offspring after lambing. *Applied Animal Behaviour Science* 97, 172–189.
- Rowe-Rowe, D.T., 1974. Flight behavior and flight distance of blesbok. *Zeitschrift für Tierpsychologie* 34, 208–211.
- Schultz, R.D., Bailey, J.A., 1978. Responses of national park elk to human activity. *Journal of Wildlife Management* 42, 91–100.
- Seegerstrom, S.C., Miller, G.E., 2004. Psychological stress and the human immune system: a meta-analytic study of 30 years of inquiry. *Psychological Bulletin* 130, 601–630.
- Sih, A., Bell, A., Johnson, J.C., 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* 19, 372–378.
- Skarin, A., Danell, Ö., Bergström, R., Moen, J., 2004. Insect avoidance may override human disturbances in reindeer habitat selection. *Rangifer* 24, 95–103.
- Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society B* 272, 2627–2634.
- Stankowich, T., Coss, R.G., 2006. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behavioral Ecology* 17, 246–254.
- Stankowich, T., Coss, R.G., 2007. Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behavioral Ecology* 18, 358–367.
- Swenson, J.E., 1982. Effects of hunting on habitat use by mule deer on mixed-grass prairie in Montana. *Wildlife Society Bulletin* 10, 115–120.
- Tarlow, E.M., Blumstein, D.T., 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science* 102, 429–451.
- Taylor, A.R., Knight, R.L., 2003a. Behavioral responses of wildlife to human activity: terminology and methods. *Wildlife Society Bulletin* 31, 1263–1271.
- Taylor, A.R., Knight, R.L., 2003b. Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications* 13, 951–963.

- Thomson, B.R., 1972. Reindeer disturbance. *Deer* 2, 882–883.
- Tyler, N.J.C., 1991. Short-term behavioral responses of Svalbard reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. *Biological Conservation* 56, 179–194.
- Vistnes, I., Nellemann, C., Jordhøy, P., Strand, O., 2001. Wild reindeer: impacts of progressive infrastructure development on distribution and range use. *Polar Biology* 24, 531–537.
- Vistnes, I., Nellemann, C., Jordhøy, P., Strand, O., 2004. Effects of infrastructure on migration and range use of wild reindeer. *Journal of Wildlife Management* 68, 101–108.
- Walther, F.R., 1969. Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour* 34, 184–219.
- Ward, A.L.W., Cupal, J.J., 1979. Telemetered heart rate of three elk as affected by activity and human disturbance. In: Ward, A.L.W., Cupal, J.J. (Eds.), *Proceedings of the Symposium on Dispersed Recreation and Natural Resource Management: A Focus on Issues, Opportunities and Priorities*. Utah State University, Logan, UT, pp. 47–55.
- Whittaker, D., Knight, R.L., 1998. Understanding wildlife responses to humans. *Wildlife Society Bulletin* 26, 312–317.
- Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. *Advances in the Study of Behavior* 16, 229–249.