

---

# Personality and Other Factors Mediating Ungulate Flight Initiation Distances

## Rob Found

Department of Biological Sciences, University of Alberta, Edmonton, Canada

### Email address:

[found@ualberta.ca](mailto:found@ualberta.ca)

### To cite this article:

Rob Found. Personality and Other Factors Mediating Ungulate Flight Initiation Distances. *Ecology and Evolutionary Biology*. Vol. 6, No. 4, 2021, pp. 125-135. doi: 10.11648/j.eeb.20210604.15

**Received:** November 14, 2021; **Accepted:** December 2, 2021; **Published:** December 24, 2021

---

**Abstract:** Flight response or initiation distances are important for wildlife management because these metrics can quantify changes in human-wildlife relationships such as tolerance and habituation, provide insight into the impacts of predator-prey interactions, and help mitigate human-wildlife conflicts by informing the prescription of minimum distances humans should maintain from wild animals. Despite the importance of flight response measurements, and the ubiquity of their measurement in active wildlife management programs, the relative importance of various environmental and behavioural factors influencing flight response in wild animals remains poorly understood. In this study I used results from 809 flight initiation distance trials on wild adult female elk, including marked individuals for whom I had previously quantified their personalities. These elk were parts of both highly and less habituated herds in the protected area of Banff National Park. Using linear models I identified "personality" and a correlate of wolf predation "risk" as the most important predictors of flight initiation distance. Boldness of personality type predicted lower flight distances, while recent exposure to predation risk increased flight distances, independent of personality. I used Monte Carlo simulations to demonstrate that the accuracy of mean flight response measures could be improved significantly with field methods controlling for personality and group-level risk variations, and that those controlling measures could be obtained using two easily observable correlates: position in herd (bold animals found on the perimeter) and herd clustering (herd structure tighter when currently or recently exposed to risk). I showed that fewer FID trials were necessary to obtain accurate means when these methods applied. Lastly, I showed how few FID trials were needed to obtain an accurate mean for any individual, due to the behavioural consistency of personality. These results showed that personality is the single most important factor influencing variation in ungulate flight initiation distance, followed by exposure to risk, and that both of these factors should be accounted for when collecting flight initiation data.

**Keywords:** Elk, Flight Response, Habituation, Personality, Predation Risk, Wildlife Management

---

## 1. Introduction

Wildlife typically respond to human approaches by moving away when humans get within a certain distance. This distance is referred to as the animal's flight initiation or flight response distance [1-3], where the "flight" may be literal (as in the case of birds), but in land animals can range from a gradual displacement at walking pace, to an outright run. This behaviour has been recorded in a diversity of taxa including birds [4] fish [5], reptiles [6], and mammals [7].

Flight initiation distances (FIDs) provide fundamental behavioural insights that can improve the management and conservation of wildlife [8]. First, mitigating human-wildlife conflict requires humans and wildlife be kept a safe distance

apart [9, 10]. Many jurisdictions will dictate a minimum distance humans should remain from large mammals, on the assumption that approaching closer than that would entail entering an animal's flight zone, and the resulting flight response could become an aggressive one [11, 12]. Secondly, since by definition entering an animal's flight zone results in disturbance to the animal, mandating minimum distances from animals is important for minimizing the disturbance humans cause to wildlife. This disturbance may not be overt, and can manifest itself in covert stress responses such as elevated heart rates [13, 14]. The importance of tourism in modern ecological and conservation programs means some degree of compromise with the common wildlife watcher's desire to approach wild animals, but approaching an animal

to the threshold of its FID has been shown to lead to desensitization and eventual habituation of wildlife [15]. Knowledge of population mean FID can therefore be important for establishing buffer zones [16]. For example Parks Canada in Banff National Park dictates that people should not approach bears, wolves, coyotes, or cougars closer than 100m, and should not approach elk, moose, bighorn sheep, or deer closer than 30m [17]. Monitoring trends in wildlife flight response distances can therefore also be used to monitor the impacts of human disturbance. For instance, reduced FID has been used as a way to quantify ungulate habituation [18], and animals with lower FID may be the only ones that can be successful in urban environments [19].

For wildlife, flight response distance is an optimality decision, where the animal has to decide whether the risk posed by the approaching human (in this case) outweighs the energetic costs of stopping its chosen behaviour and moving away [13, 20]. Interpreted this way, flight response distance is determined by the amount of risk the animal feels, regardless of whether that risk is correctly evaluated or not [21]. We certainly expect animals to have a longer FID when detectable risks are actually higher. We previously found that when elk FIDs were measured when there was local wolf activity that day or the previous day, FIDs were 15% greater than that individual's mean [22]. By the third day after local wolf activity, however, FID values had returned to within 1% of their individual means. It is therefore unsurprising that FIDs have been shown to be influenced by other factors implicated in the sensation of risk. Flight response distances have been shown to be influenced by the starting distance of the approach [9], the directness of the approach [23], time of day [24], reproductive state [25], the presence of cover [26], and group size [27]. At the same time, certain environmental conditions may not change the amount of risk an animal feels, but change the amount of risk an animal is willing to accept. For example, as snow depth increases it becomes harder for wild ungulates to forage, so they may be more reluctant to be displaced from areas where they have already expended energy uncovering forage buried under the snow.

The recent wealth of studies of animal personality has shown that there is consistent individual variation in how animal's respond to risk, but few studies have tested this explicitly with FID. Blumstein et al. [28] concluded that FID was a species-wide trait in shorebirds, independent of population-level habitat variability. Multiple studies, however, found reduced FID in urban birds compared to rural counterparts of the same species, and concluded that FID is selected for at the level of the sub-population, based on local habitat conditions [29, 30]. The first comprehensive study of flight response in ungulates was conducted on deer at the group level, on the assumption that they respond together, but this study questioned its own methods after realizing that there was instead significant individual variation in response [26]. Kloppers et al. [31] proposed that FID is a population wide trait in elk, where the entire group has similar FIDs based on local environmental, disturbance, and predation characteristics, but Found & St. Clair [22] later studied FID

in the same population, with a greater focus on individual behaviours, and found average individual FIDs were strongly correlated with a suite of 6 other personality characteristics. This conclusion ran counter to the findings of Petelle et al. [32], who found that individual variation in FIDs in marmots (*Marmota flaviventris*) were not part of a behavioural syndrome with the personality trait of docility, though this lack of correlation does not exclude the possibility that FID and not docility was the more dominant personality trait.

Because so many critical management and conservation decisions are made using quantified or estimated FID means for individuals, groups, or populations, it is equally important that those estimates are accurate and not biased by convenience sampling, over generalization, or ignorance of important sources of variation that affect FID.

In this paper I examined personality, risk, and other factors potentially influencing individual FID in wildlife, using a data set of 809 flight response distance trials of unmarked and individually identifiable elk. I did this in two ways. First, I used linear models to examine several environmental and behavioural variables to determine which were most important in predicting FID. I predicted that individual elk personality would be the most significant predictor of FID, followed in secondary importance by the degree of perceived predation risk at the time of the trial. I then took the most important variables and used Monte Carlo simulations to accomplish two things: a) examine the importance of accounting for individual variation (personality) and risk, and demonstrate the effect on accuracy and sampling volume when these two factors were accounted for within the FID methods; and b) show the importance of intra-individual variation. I showed how many individual FID trials must be performed on marked animals before the group's true FID is known to within a 90% confidence interval. I predicted that these simulations would show that FID field sampling methods that accounted for the most important variables influencing FID values would produce equally accurate and non-biased estimates of group mean FID with far fewer trials. In other words, I predicted the simulation results would show that for the same sampling effort, field methods that controlled for personality and variations in predation risk would produce mean FID estimates that were more accurate and less biased, or conversely could achieve the same accuracy with much less sampling effort, and thus more useful for wildlife management.

## 2. Methods

### 2.1 Study Area

Banff National Park (BNP) is a large protected areas within the Canadian Rocky Mountains. We conducted fieldwork in the Bow valley area of BNP from January-April of both 2010-2011 and 2011-2012. Habitat in the Bow valley consists mostly of coniferous trees such as lodgepole pine (*Pinus contorta*), spruce (*Picea spp.*), and fir (*Abies spp.*), as well as deciduous aspen (*Populus tremuloides*), interspersed

with native grasslands. Winter temperatures ranged from an average daytime high of 0°C, to an average overnight low of -13°C, with annual snowfall averaging 191.0 cm [33]. Our study area also encompassed the townsites of Banff, AB (51°10'41"N, 115°34'19"W, pop. 7000, elevation 1383 m). This area of high human disturbance created a predation refuge from surround habitat populated with the two year-round predators of elk; wolves (*Canis lupus*) and cougars (*Puma concolor*) [34-36]. This mix of disturbance zones also selects for a broad gradient of elk personalities and tactics, from those that habituate to humans and abandon migratory behaviour, to those that resist habituation and continue to migrate to and from higher elevations each year [37]. Excluding groups of elk comprised only by males, the total population of elk overwintering in the Bow Valley during this study was 200-250 each year, of which half were migratory [22]. At any one time during this study at least 40 of these adult female elk were marked with both VHF collars and individually numbering ear tags. These tags had numbers large enough to be visible to the naked eye, during video analysis, and on wildlife camera imagery.

## 2.2. Personality Assessments

I quantified elk personality for this study using behavioural data that were previously collected from this population for the purposes of quantifying personality [22]. Here I used non-metric dimensional scaling methods following Found & St. Clair [37], which reduced four separate recorded personality traits to a single personality gradient. These metrics include, social dominance, exploratory behaviour, vigilance behaviour, and spatial position within the herd. Social dominance was based on the results of 492 total dyadic dominance encounters, where displacement of one elk by another determined the winner of the encounter, and results of all encounters were used to create a dominance hierarchy. This ordinal score of social position was used as a continuous variable in the NMDS scaling. The variable for exploratory behaviour was the average score for individual responses toward 61 separate novel objects placed in wild habitat. As examples we used a brightly coloured bicycle, a stack of tires with metal pots hanging off it, skis sticking vertically out of the snow, and a large Canadian flag. Using automated cameras at each site, individual elk were assigned scores on a 1-4 scale: 1 = visited site and looked at object, 2 = approached object, 3 = investigated object to within a head length, 4 = physically interacted with the object. The metric for vigilance behaviour was determined 4-30 observation sessions per individual ( $\bar{x} = 21.3$ ), lasting 10-minutes each, where we recorded the proportion of time spent on vigilance behaviour versus other behaviours. These observation sessions were filmed, allowing us to use playback to differentiate vigilance postures (head up, alert eyes and ears) from non-vigilance behaviour where the animal might still have its head up (e.g. looking at conspecific). The variable for spatial position within the herd was based on on 4-20 observations per individual ( $\bar{x} = 11.1$ ) of individual positions relative to conspecifics. Positions scores were rank ordered

for "peripheral", "intermediate", and "interior". An elk was "peripheral" if it was on the edge of the group. An elk was considered "interior" if it was completely surrounded by other elk. Those not clearly belonging to either category were considered intermediate, and typically adopted positions in the middle rings of the generally circular herd structures. Elk in groups of three or fewer individuals were all considered peripheral, since no individual could be within the others in the group, and elk in groups of six or fewer individuals were considered peripheral or intermediate only. Using these criteria, we calculated a mean 'position' score for each individual that was not dependent on group size, with higher values indicating more peripheral positioning.

## 2.3. Flight Response Distance

Flight response distance (FID) trials were conducted over the winters of 2010-11 and 2011-12. Trials were conducted both inside and outside of human disturbed areas, in all weather conditions and habitat types. Starting distance has been shown to significantly influence FID in some datasets (Blumstein 2003). While starting distance was not strongly correlated with FID within my dataset ( $r = 0.26$ ) I attempted to standardize starting distances as much as possible in the field by starting my approaches to all elk when I was at least 75 m but no more than 110 m away. Standardizing starting distance further, such as starting each FID trial when exactly 100m away, was not possible or desirable for two reasons. First, high variation in sample-site habitat occasionally required different starting distances, such as when the presence of intervening trees did not allow uninterrupted lines-of-sight of more than 75m. In such an instance standardization of 100m would bias sampling towards open areas. Second, standardization to an exact value would bias sampling towards particular individuals. For example, standardizing to 75m would bias sampling towards elk on the perimeter of the herd, or otherwise most easy to access, as approaches of greater than 100m were sometimes necessary to sample individuals in the middle of groups of elk. Those elk are more likely to have shy-type personalities [22]. Standardizing starting distances to within a range should be considered a trade-off to reduce biases while minimizing the impact of variation in starting distance.

I approached elk only if I was visible to them, walking at a normal walking speed, which was not quantified but was estimated to range between 4-5 km/h, varying only slightly depending on terrain and snow depth. I used a laser range finder to record the distance at which the elk responded to my approach by moving at least 5 m. In addition to standardizing the starting distance, a single observer conducted all flight response trials in order to minimize the potential influence of speed, body size, or gait of an approaching human, changing only his clothing as a way to mitigate the influence of habituation on reducing FID values for the same individuals [37]. These trials and all other behavioural data collection were conducted under University of Alberta Ethics for Animal Use Protocol # 7121112.

I conducted multiple flight trials on each elk to account for

seasonal, spatial, and temporal variation, and allow the calculation of mean individual FID values, and a more representative value for the population FID mean. Marked elk were chosen for an FID trial based only on their identity and the desire to have an even sampling distribution across all elk. I did not choose targets based on their location relative to other elk or for the convenience of the observer. This ensured I was sampling elk regardless of whether they were alone, on the edge of groups, or in the middle of groups. I avoided conducting trials more than once / day on any elk, and avoided elk that were bedded, obviously sick or injured, physically interacting with another elk, or for which an escape response could be dangerous (e.g. running onto a roadway). No elk was exposed to more than one FID trial in a day, regardless of whether it was the target of the trial, or merely witnessed the trial of another elk in its group. In the few isolated cases where the target individual did not move when approached to within 1m, or moved toward the observer in response to the approach, I recorded its flight response as 0 m.

I randomly selected 10 FID trial results for each marked elk, which allowed me to reduce biases from pseudoreplication, but maintain the sample size and individual replication necessary for further analyses. I calculated the known population mean as the average of all individual mean FID results. I also calculated individual mean FID values for the 32 elk individually marked with VHF collars and ear tags, for each of the two years of this study, and used standard error to quantify the intra-elk variation in FID values within any one year.

#### **2.4. Linear Models**

For the time of each FID trial I recorded several environmental or behavioural metrics as potential explanatory variables. Each of these variables is listed in Table 1, along with evaluative statistics for univariate candidate models containing each potential co-variable alone. Briefly described here are those variables included in the final model set (see Table 1). Ordinal day corresponds to the consecutive days of the study, and was included to determine if there were any habituation effects as individuals were exposed to multiple FID trials during the winter. Distance to cover may influence the sense of risk individuals may feel they are taking through exposure in open areas. Time of day was included because elk are crepuscular and more active near dawn and dusk, and also typically exposed to greater predation risk at those times. Elk use the Banff townsite as a refuge from predation because of its lower predation risk, so I included a binary variable to note whether they were in or outside of the established boundaries of this refuge (wolf activity maps available in [38]). Wind speed was included because of anecdotal observations that elk appeared less settled in windier conditions, and wind direction was included because that, in conjunction with the direct of approach by observer, would influence whether the elk detected the approach via scent. Lastly the structure and size of the herd were included as population variables that might also influence the sensation of risk felt by individual elk. I

also included a variable I used as a proxy for predator activity. Recent predator activity is known to increase an animal's fear response [39] including an increase in FID [22], regardless of whether or not the predator activity results in an actual predation event [40]. In my study area there were just three depredated elk in 2010, and none in 2011. For previous studies of this particular population of elk. [22, 38] I was able to quantify predator activity data post-hoc from snow-tracking surveys that were conducted each winter by Parks Canada in BNP, which recorded unique track detections of both wolves and cougars, along linear transects throughout the Bow Valley (methodology described in [36]). However, due to the minimal overlap of these transects with my FID trial locations, and the relative infrequency of these transects compared to the number of FID trials I conducted, there was no direct measure of predator activity available. However, both through that data and also from unpublished observational data, the overall sensitivity of the herd to human approaches was higher when there was recent predator activity [22]. Prior to each FID trial I classified this sensitivity on a 1-3 scale, where "1" described a group of elk with low sensitivity, and "3" described the most sensitive group of elk. I rated this sensitivity only when elk were not exposed to any visible external stimuli, so it was more likely their response was to a general sensation of risk. These data were collected before any other behavioural data were collected, so they could be collected from the greatest distance, using a spotting scope, and usually using a vehicle as a blind. At each observation session I conducted three scan samples of the entire group of elk, which I averaged to determine the average proportion of the herd that were exhibiting vigilance behaviour, compared to foraging, traveling, bedding, or social behaviours. Unlike during the focal sampling to determine individual vigilance for personality assessment (above), the need to scan sample the entire herd prevented me from assessing whether each elk had their heads up for vigilance behaviour, or for other social reasons, so vigilance behaviour in this context was determined only by whether an animal had its head up. On average approximately 6 % of the herd were expressing vigilance behaviours at any one time. If more than 6% of the herd was vigilant the sensitivity score would be recorded as either 2 or 3, but not 1. If less than 6% of the herd was vigilant its sensitivity score would be either 1 or 2, but not 3. The final scoring (1 versus 2, and 2 versus 3) was based on subjective assessment of herd structure (i.e. was the herd more tightly grouped than usual?), overall responsiveness to external stimuli (i.e. if a car drove by, or a raven flew above, or there was a distant crack of branches, did the elk seem to respond more quickly and strongly than usual?), and where elk seemed to be looking when their heads were up (i.e. were they looking towards innocuous stimuli such as roadways, trails, or other elk, or were they looking at the forest edges where predators would presumably be first spotted?). To reduce bias during these subjective assessments, all observations performed by the same single observer. tended to. I used this sensitivity metric as a proxy to quantify the

variable presence of "risk" associated with predator activity. Post-hoc I determined that this sensitivity scoring was significantly predicted by the presence of predators on that day or any of the previous two days, in that area ( $F_{1,43} = 4.45$ ,  $r = 0.31$ ,  $P = 0.041$ ).

Second, though I had collected comprehensive behavioural data enabling me to quantify elk personality [22, 37], I recognized that managers would require a more simple and efficient way to identify personality variation in wild animals that may or may not even be marked with tags or collars. In my previous studies I found that the spatial position an elk adopted within any group of elk was strongly correlated with its eventual personality classification (2010-11,  $F_{1,33} = 20.79$ ,  $r = 0.62$ ,  $P < 0.001$ ; 2011-12,  $F_{1,48} = 92.52$ ,  $r = 0.81$ ,  $P < 0.001$ ; data from [22]). Elk on the periphery of groups had bolder personalities, associated with greater risk taking, less responsiveness to stimuli, increased social dominance, and decreased vigilance. I classified each elk position from "1" (in the middle of the group, surrounded by other elk), to "3" (on the periphery of the herd), with "2" representing an intermediate scoring. I recorded each elk's position before I began each FID trial, and used this metric as a proxy for "personality" in the Monte Carlo simulations (below), but used the comprehensive personality value in the univariate modeling.

I used generalized linear mixed models (GLMM) to examine which factors were most important in predicting individual FID. I used "individual" as a random effect. I created a correlation matrix and where two variables were correlated  $r > 0.7$ , I selected the variable with the lower  $P$  value in univariate analysis [41]. Temperate and ordinal day were the only two variables correlated beyond  $r > 0.5$  (temperatures increased from January to April), and so I excluded "temperature" from model building. I built these models using purposeful selection of fixed effects [42], using  $P < 0.25$  for inclusion in the model,  $P < 0.10$  for retention, included all confounding variables (i.e. those influencing the parameters of any remaining variables by more than 20%) and then tested each ecologically-relevant, two-way interactions among variables. I tested each candidate model to determine if a linear or quadratic form improved the model fit, then used Akaike's Information Criterion to select the best-fitting model.

### 2.5. Monte Carlo Simulations

Following my hypothesis that "personality" and "predator risk" would be the two most important factors influencing variability in individual FID values in elk, I conducted Monte Carlo simulations to show the relative impact of accounting for these two variables when measuring FID. My objective was to determine how many FID trials a manager would have to conduct in order to determine a sample FID mean within an acceptable margin of error of the actual population FID mean. I calculated the known population mean using all FID trial results available to be drawn randomly for the Monte Carlo simulations. For the "Null" simulation I randomly drew 1-100 FID values from the 809 trial results, calculated the mean for each draw, and repeated each draw 100 times each.

For the "Predation Risk" simulations I filtered the 809 trial results so that I used only those trials conducted when the herd sensitivity was scored a "1", meaning there was no presumed recent predator activity, and then repeated the simulation. For the "Personality" simulations I randomly drew from the 809 trial results, but ensured that I was drawing an equal number of trials during which the individual elk was in central, intermediate, and peripheral positions (position scores 1, 2, and 3). This simulates managers conducting FID trials with the awareness that elk of different personalities should be sampled, and using relative positions within the herd is a way to do this. I conducted a 4th simulation in which I controlled for both "Predation Risk" and "Personality", using both of the methods just described. For each of the four simulations I took the FID mean from each draw and compared it to the known population mean to calculate the % error, and graphed all results as response curves.

I also used the Monte Carlo simulations to also calculate how many FID trials would have to be conducted in order to correctly estimate the 95th percentile of the population FID, as for certain species or jurisdictions this threshold value may be of greater management interest [43]. I used the known population mean (from above) and known population standard deviation to calculate the known 95th percentile value, then used the simulations to determine how many trials were necessary to obtain estimates within 10%, 5%, and 1% percent error.

Lastly, I demonstrated the importance of personality in the measurement of FID with a different type of simulation in which the random draws were from known individual elk. The objective of this analysis was to determine how many FID trials one would have to conduct on each individual before the sample mean would approach the population mean of the 32 marked individuals. I conducted 100 simulations during which I randomly drew 1 FID result from each known elk, another 100 simulations during which I drew 2 FID results from each known elk, and so on, up to 8 FID results/elk (the most available for all 32 marked individuals). In each case I calculated the FID mean from the sample, which I compared to the FID mean of the entire FID data set on the marked elk.

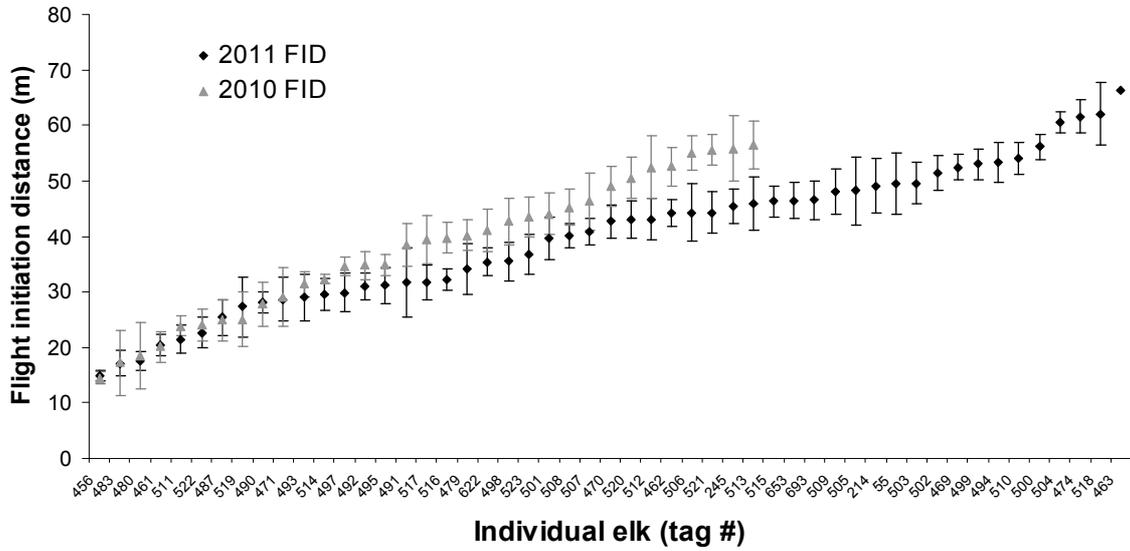
## 3. Results

### 3.1. Flight Response Distance

Over both study years I conducted a total of 992 FID trials, with 809 conducted on individually marked adult female elk, and 188 conducted on unmarked adult female elk (see Supplemental Materials, Data S1). These were conducted on 152 different days. Mean FID was significantly lower in marked elk ( $\bar{x} = 37.6\text{m}$ ,  $SE \pm 0.6\text{m}$ ) than in unmarked elk ( $45.4 \pm 1.1\text{m}$ ;  $t_{990} = 6.00$ ,  $P < 0.001$ ). In marked elk FID ranged from 0m (no displacement when within an arm's length of the elk) to 89.7m. In unmarked elk FID ranged from 3.4m to 90.8m. Mean individual FID values in 2010 (Figure 1) were

highly repeatable ( $R^2 = 0.72$ ) in the same individuals in 2011, so for this study pooled all FID from both years, in all

analyses. Group variance in FID ( $s^2 = 241.7$ ) was higher than mean intra-individual variance in FID ( $s^2 = 122.9$ ).



**Figure 1.** Individual mean flight response distances of individual elk in 2010 and 2011, from a single population of elk in Banff National Park, Canada. Error bars are standard errors. Data points with no SE are the mean values for unmarked/unknown elk.

**3.2. Linear Models**

Each collected variable was tested as a univariate model (Table 1). The strongest univariate models predicting FID were those with "personality" or "individual", though models with "herd size" and "ordinal day" were also statistically significant. Following model building, FID was best predicted by a linear model with the parameters "risk" (coefficient = 5.06, SE = 1.09,  $z_{832} = 4.66$ ,  $P < 0.001$ ) and

"personality" (coefficient = -5.01, SE = 0.97,  $z_{832} = -5.17$ ,  $P < 0.001$ ). Coefficients for this model showed that individual FID values increased when group sensitivity to risk was higher, and when individuals were found in more interior positions within the herd. Since those positions are correlated with increasing shyness of personality, this showed that FID is higher in shyer individuals ( $F_{1,48} = 50.4$ ,  $r = 0.72$ ,  $P < 0.001$ ). This model with both parameters outranked models with either risk or personality alone.

**Table 1.** Potential variables for selection of top model predicting individual elk flight initiation distance, and univariate model results for each variable.

Variable	n <sup>a</sup>	ll <sup>b</sup>	coefficient	SE	z	P
ordinal day <sup>c</sup>	809	-3171.7	-0.392	0.013	-3.11	<0.01
distance to cover <sup>d</sup>	809	-3176.5	-0.001	0.013	-0.12	0.907
time during day <sup>e</sup>	809	-3172.6	0.275	0.535	0.52	0.606
in/out of refuge <sup>f</sup>	809	-3171.9	0.599	1.031	0.58	0.561
accumulated snow <sup>g</sup>	809	-3172.1	-0.374	0.206	-1.81	0.070
wind direction <sup>h</sup>	809	-3172.3	-0.376	0.228	-1.64	0.100
wind speed <sup>i</sup>	809	-3144.7	0.013	0.277	0.05	0.962
approach direction <sup>j</sup>	809	-3172.3	-0.380	0.752	-0.51	0.613
herd size <sup>k</sup>	809	-3174.2	0.026	0.012	2.20	0.028
herd tightness <sup>l</sup>	809	-3172.3	0.468	0.600	0.78	0.436
Risk <sup>m</sup>	779	-3038.2	2.787	0.889	3.14	<0.005
Personality <sup>n</sup>	809	-3126.1	-5.053	0.299	-16.88	<0.001

<sup>a</sup> Variables collected during 809 flight initiation distance trials. <sup>b</sup> Log likelihood. <sup>c</sup> Day since January 1 of that year. <sup>d</sup> Distance (m) to nearest forest dense enough to hide an elk. <sup>e</sup> Time of FID trial. <sup>f</sup> Binary indication of whether elk was within townsite boundaries or not at time of FID trial. <sup>g</sup> Total snow depth (cm) at time of FID trial. <sup>h</sup> Wind direction (coded 1-8 to represent compass directions). <sup>i</sup> Speed in km/h at time of FID trial. <sup>j</sup> Coded 1-3 to represent whether observer approached upwind, downwind, or side-wind of the target elk. <sup>k</sup> Number of elk in group containing target elk. <sup>l</sup> Relative measure (1-3) of how conglomerated herd is (i.e. how close individuals are to each other, on average). <sup>m</sup> Relative measure (1-3) of elk sensitivity to perceived predator risk, based on observations of risk-aversion behaviours (i.e. vigilance), as a proxy for relative variation in predatory risk at that time. <sup>n</sup> Continuous standardized variable (1 to -1) derived from NMDS analysis of 6 separate personality traits.

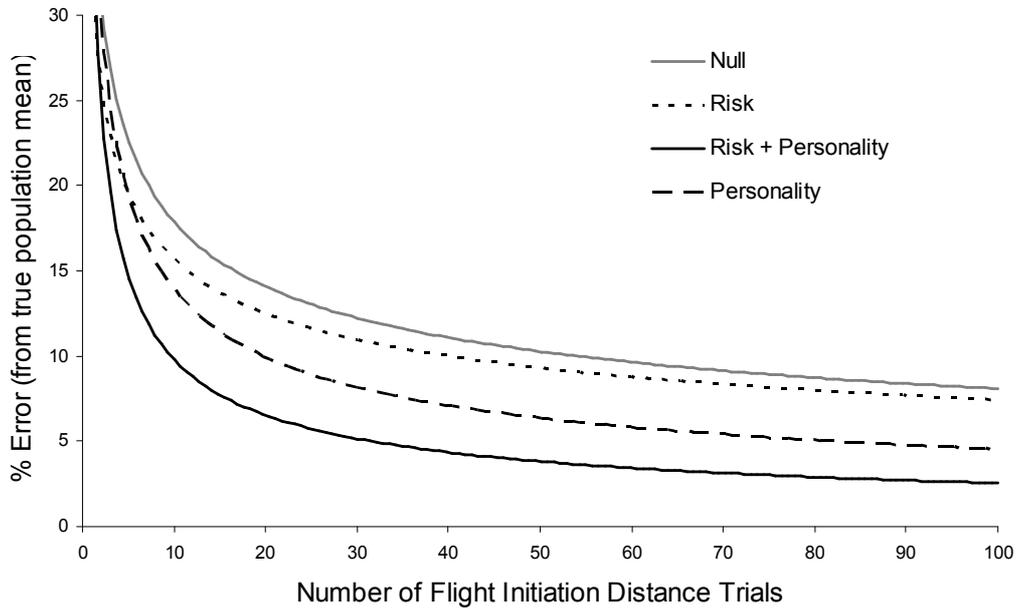
**3.3. Monte Carlo Simulations**

When simulated FID trials were conducted without controlling for risk or personality, 43 trials were necessary to

achieve an estimate of the mean group FID that was within 10% of the known mean (Table 2). Estimates were improved when FID trials were conducted during which risk was controlled for via measurement methods, requiring 23 trials

to achieve accuracy of 10%. When FID trials did not control for risk, but did control for personality, 10% accuracy could be achieved with 19 trials. Controlling for both personality

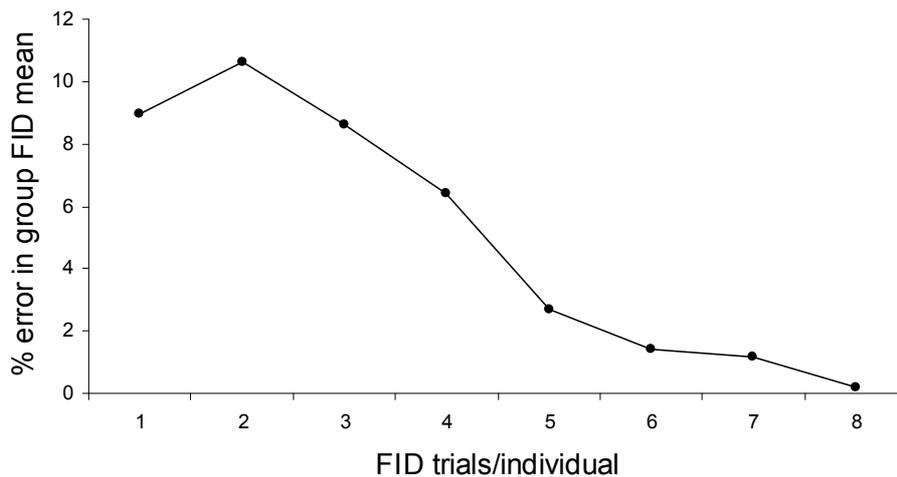
and risk improved estimates more than any other model (Figure 2). Controlling for both personality and risk required only 8 trials to achieve estimate accuracy of 10%.



**Figure 2.** Monte Carlo simulations of flight initiation distance trials where the methods control for variations in risk, personality, both risk and personality, or no controls (null). Y-axis shows percentage error from known population mean. 100 simulations of 1-100 trials were conducted using data from 992 real flight response distance trials on elk in Banff National Park, Canada, in 2010 and 2011.

The lowest errors in estimating the 95th percentile of FID in the population were achieved by controlling for personality alone, and required just 4 and 16 trials to achieve errors of less than 5% and 1%, respectively (Table 2, bottom). Simulations controlling for both personality and risk required 4 and 47 trials to achieve errors below 5% and 1%, respectively. Simulations controlling for risk alone did not

reduce errors to below 5%, with error rates stabilizing at approximately 6% after 100 simulations. Simulations in which neither personality nor risk were controlled for (null model) required 17 trials to to reduce error below 5%, but could not reduce error below 1%, stabilizing at approximately 4% (Table 2, bottom).



**Figure 3.** Number of flight response distance (FID) trials that need to be conducted on each individual elk in a group (X-axis) in order to achieve particular accuracy of group mean FID estimates. Group was composed of 32 marked adult female elk in Banff National Park, Canada.

Lastly, using a group of 32 know elk that had had their FID measured a sufficient amount of times, I found that each individual would only have to be sampled once in order to produce an estimate of the group mean within 10% of the

known mean value (Figure 3). Sampling each individual five times produced an estimate with just 2.72% error, which for this population represents about 1 meter between the observer and elk.

**Table 2.** Results of 100 Monte Carlo simulations of 1-100 flight initiation distance (FID) trials estimating the known population mean (top) and 95th percentile of population FIDs (bottom). Models vary by whether "risk," "personality," both, or neither are controlled for with the methods. Models are evaluated using the percentage error from the known population mean or known 95th percentile. Simulations and known means and standard deviations are from 809 flight response trials conducted on wild elk in Banff National Park, Canada.

Model	# FID Trials Required to Estimate Population FID Mean		
	20% Error	10% Error	5% Error
null <sup>a</sup>	7	43	>100
risk <sup>b</sup>	4	23	>100
personality <sup>c</sup>	4	19	83
personality + risk	3	8	37

Model	# FID Trials Required to Estimate 95th Percentile of FID		
	10% Error	5% Error	1% Error
null <sup>a</sup>	3	17	>100
risk <sup>b</sup>	4	>100	>100
personality <sup>c</sup>	2	4	16
personality + risk	2	4	47

<sup>a</sup> Targets for FID trials are chosen randomly. <sup>b</sup> FID trials not conducted if there are signs of group-wide stress, as this is a correlate with current or recent predation risk. <sup>c</sup> Groups are sampled non-randomly to ensure individuals from all parts of the group are sampled, as this is a known correlate with personality.

## 4. Discussion

The two main predictors of flight response distance in elk were individual personality and ambient risk. Robust (within 5% error) estimates of the mean population FID required three times as many FID trials when not controlling for either factor. If management objectives could be achieved with estimate errors within 20%, such an estimate could be achieved with just three FID trials if both personality and risk were controlled for. Both of these factors could be controlled for with simple modifications to the methods of measuring flight response distances in the field, and without using individually marked individuals, because the central versus peripheral positions elk adopt within the herd structure is strongly correlated with complete and more comprehensively measured personality types [22], and a metric of herd-wide sensitivity was correlated with recent predator activity. Personality was the single most important factor predicting ungulate FID. Controlling for personality was also the most important factor in reducing errors in estimating the 95th percentile of FID across the population. For these estimates accounting for risk resulted in higher errors than when it was not accounted for.

It may not be appropriate to completely disentangle personality and predation risk, because the metric of FID is determined partly by innate temperament (*sensu* [44]) as well as by ongoing experience [45]. Both of these are likely especially sensitive to the risk of predation, which can vary both spatially and temporally. For elk, even indirect encounters with wolves can affect behaviour for up to several days [39]. Recent wolf activity is not necessarily evident in flight response [31], but my previous study of the elk population in Banff determined that wolf presence increased individual elk flight response distance only on the same day or the day after wolves were detected [22]. Predation risk in general may also have been demonstrably less important than personality partly because wolves are typically active around prey only every 10-14 days [46], so the impact of risk may be strong, but sporadic.

Individual state, such as nutritional status and body condition, may also have sporadic influence on the amount of risk an animal may be willing to take. A review by Moran et al. [47] found poor nutritional condition promoted high-risk behaviours. In the context of elk FID we might speculate whether elk with the lowest average FID might be in poorer condition, though in the Banff herd those animals were also socially dominant, which allowed them to easily displace more submissive animals from the prime habitat patches. Analysis of individual body condition of elk in this study, using camera imagery, did not reveal any marked variation in body condition of the study elk, so I could not determine its influence on FID. Regardless, unlike predation and nutritional status, which are expected to vary over the short and long term, personality is an omnipresent influence on elk.

My proxy for predation risk was a metric of herd-wide sensitivity was potentially confounded by the fact that this behaviour is a group-based response, and not an entirely individual one. Some animals may not feel the same sense of risk as others, but coalesce into a tighter group structure simply because others are doing so. Herd size was also a predictor of increasing FID, and this is likely related to herd coalescence. I previously found that shy animals preferred being closer to conspecifics than bold animals did, which demonstrates a link between individual behaviour and group structure, but while bold animals always showed a preference for being on the periphery of the herd, when the group was most sensitive this periphery was certainly closer to the shy elk on the inside of the group [38]. Though other studies have found FID is lower in larger groups [26], I found group size did not influence FID.

Previous studies have found that FID is associated with consistent individual behavioural variation (i.e. personality) in animals such as horses (*Equus caballus*; [23], marmots (*Marmot flaviventris*; [23], corvids [48] and flatfish (*Paralichthys olivaceus*; [49]. Flight responses should therefore vary more within a population than with an individual. I found this to be the case, to the extent that because individual FID varied so little, few replications were

needed to determine individual FID means, and to calculate group-wide mean FID values using individual FID values. Just five replications per individual were enough to determine the "true" FID mean for any animal, within 1 meter. Accomplishing this requires observations of multiple, individually-marked animals, which is not unusual for highly managed populations for which FID information is required. My previous work showed that mean individual FID values have low year-to-year variation, and once adulthood is reached, mean FID does not vary with age [22]. This suggests that the "true" FID mean for an individual is unlikely to vary throughout its lifetime without significant and sustained changes to the risks and rewards experienced by those individuals [37].

One important reason to measure FID may also represent a potential confound with repeated measures of FID. Habituation to stimulus likely reduces FID when the same individual is approached repeatedly [50], [51]. In a previous study I found that the mean FID declined over 40% in a group of elk subjected to just 6 days of habituation treatments, which consisted only of approaching individual elk up to the threshold of their FID [15]. However, the degree of habituation to FID also varied significantly depending on the personality of the elk, with bold animals habituating more quickly. In this study I found that ordinal day was correlated with decreasing FID, and as this was not explained by weather covariates, it is presumably the result of moderate habituation to repeated FID measures throughout the winter. In a previous study of the influence of aversive conditioning on FID I found that independent of aversive conditioning FID declined slightly over time, suggesting a slight habituation effect to the FID measures themselves [52]. Similar results were found with repeated FID measures of wolves in another study [53]. FID may also be lower when the stimulus is more predictable in time and space [26]. A study of convict cichlids (*Amatitlania nigrofasciata*) found that gradual desensitization to increasing risk was driven mostly by adaptive learning about that risk, as opposed to "sensory habituation" [54]. I conducted nearly 1000 FID trials over two years, on the same herd of 200-250 animals, so my approaches likely did become predictable over time, and allowed adaptive learning. It is also important to recognize that it is likely that many FID measures of herding animals must be conducted within sight of other individuals, so the social learning by individuals witnessing FID trials may have reduced FID than if each elk had been tested in isolation. Evidence of social transmission specifically of habituation responses to humans has recently been recorded in chimpanzees (*Pan troglodytes*) [55].

My results showed how management approaches may be biasing data collection. I found that the mean FID of marked individuals was lower than that of unmarked individuals. Because in previous work I showed that age did not influence FID, the likely reason for this FID bias is the capture process itself. Because all elk were captured using ground-based darting, animals could only be individually marked if they could be approached to within 30m. This unwittingly biased

our study population towards those animals least responsive to human approaches. Similar biases may result with other capture methods, since, for instance, aerial net-gunning tends to target animals on the periphery of groups, which in elk are positions that tend to be adopted by the animals with the boldest personalities. Biases should be expected with other capture methods, and with other species having their own personality based behavioural tendencies. Collecting FID data that encompasses the fuller range of individual variation in FID within a wildlife population is critical when determining management FID thresholds designed to protect those populations, as overestimations may lead to selection against behavioural diversity. Understanding the most important influences on individual flight response distances in animals will increase the utility of FID as a management tool for monitoring and mitigating habituation behaviour and the negative influences of humans on animal behaviour.

The theoretical underpinnings of these simulations can be usefully applied to other wildlife, and not just ungulates. The differences in FID found within single elk herds would be even more pronounced when compared to other ungulate species that may have larger or small body sizes relative to humans and other predators, or may be solitary rather than gregarious, since such taxonomic differences are already known to influence predator behaviour, and thus risk to the ungulates (eg. by wolves; [57]). However, those FID factors common across elk personalities may be conserved behaviours common to other species, and so the results of this study may have application to the management of other species involved in human-wildlife conflicts, such as bears (*Ursus* spp.), birds, and primates. Since personality traits are often quantified along an axis of bold-shy [58], boldness versus shyness is likely to influence FID decisions similarly across taxa.

## 5. Conclusions

There are a number of management implications for this study. First, for effective managing wildlife whose behaviour is influenced by human disturbance (e.g. prone to habituation) it is important to reduce bias and obtain accurate flight response measures [56]. Management on a population-level scale may require managers to estimate the 95th percentile of FID for a population [43], but such group-based values will be inaccurate unless measurement methods account for inherent variability in FID resulting from personality and ambient predation risk. I showed two simple proxies that successfully improved estimates while simultaneously reducing the labour required to take FID measures. These can be added to other standardization methods for reducing bias in FID, such as using a consistent starting position for the approach [9], or even the angle of approach [23].

Secondly, I showed that intra-individual variation in FID is so low that managers should expect changes in FID to be a reflection of larger changes due to changes in predation or management. For example, I used changes in mean individual FID to quantifying increasing ungulate fear in response to a long-term aversive conditioning regimen [37],

and in a separate population used changes in mean FID to quantifying a loss of fear due to habituation [15]. While much wildlife management continues to be conducted at the scale of population or group, there is growing recognition of the importance of managing also on the level of the individual. Use of population means, such as 95<sup>th</sup> percentile of FID, may incline managers to regard animals outside the 95<sup>th</sup> percentile as outliers, or anomalies, when in fact it is animals on the extreme ends that may require the most management. Management to address habituation behaviour is therefore going to be more effective if managers specifically target bold personality types, and at the same time will be more ethical because they will avoid intensive management of non-target individuals. The present study using Monte Carlo simulations to illustrate the importance of sampling volume and sampling strategies on obtaining such useful mean FID measures for individuals.

## 6. Supplemental Materials

Data S1. Raw data from flight initiation distance (flight response distance) trials on wild elk (*Cervus canadensis*) in Banff National Park, Alberta, Canada, during the winters of 2010 and 2011. A single observer approached elk targeting using their unique eartag numbers, recording the distance at which that elk was displaced by at least 5m. In/Out code refers to whether trial took place within or outside of the townsite area. Start or end “blockers” refers to the number of non-target elk that may have been between the observer and the target elk before or after the trial. All distances are in meters. All trials were conducted by the same observer, to reduce trial bias, but changing clothing in order to reduce habituation effects.

## References

- [1] Hediger H. 1934. Zur Biologie und Psychologie der Flucht bei Tieren. *Biologisches Zentralblatt* 54: 21-40.
- [2] Stankowich T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation* 141: 2159-2173.
- [3] Moller AP. 2014. Life history, predation and flight initiation distance in a migratory bird. *Journal of Evolutionary Biology* 27: 1105-1113.
- [4] Moller A. 2015. Birds. In W. Cooper, Jr & D. Blumstein (Eds.), *Escaping From Predators: An Integrative View of Escape Decisions* (pp. 88-112). Cambridge: Cambridge University Press. doi: 10.1017/CBO9781107447189.005.
- [5] Anchieta J, Nunes CC, Costa Y, Blumstein DT, Leduc A, Dorea AC, Benevides LJ, Sampaio CLS and Barros F. 2018. Global trends on reef fishes' ecology of fear: Flight initiation distance for conservation. *Marine Environmental Research* 136: 153-157.
- [6] Cooper W. 2015. Reptiles. In W. Cooper, Jr & D. Blumstein (Eds.), *Escaping From Predators: An Integrative View of Escape Decisions* (pp. 113-151). Cambridge: Cambridge University Press. doi: 10.1017/CBO9781107447189.006.
- [7] Stankowich T, Blumstein DT. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society B* 272: 2627-2634.
- [8] Blumstein, D. T. (2000). Understanding antipredator behavior for conservation. *The Open Country*, 1 (2), 37-44.
- [9] Blumstein, D. T. (2003). Flight initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management*, 67, 852-857.
- [10] Knight J. 2009. Making wildlife viewable: habituation and attraction. *Journal of Human-Animal Studies* 17: 167-184.
- [11] Galbreath DM, Ichinose T, Furutani T, Yan W, Higuchi H. 2014. Urbanization and its implications for avian aggression: a case study of urban black kites (*Milvus migrans*) along Sagami Bay in Japan. *Landscape Ecology* 29: 169-178.
- [12] Conover M. 2002. *Resolving human-wildlife conflicts: the science of wildlife damage management*. Lewis Publishers.
- [13] MacArthur RA, Geist V, Johnston RH. 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. *Journal of Wildlife Management* 46: 351-358.
- [14] Ditmer MA, Vincent JB, Werden LK, Tanner JC, Laske TG, Iazzo PA, Garshelis DL, Fieberg JR. 2015. Bears show a physiological but limited behavioral response to unmanned aerial vehicles. *Current Biology* 25: 2278-2283.
- [15] Found, R. 2019. Personality influences habituation behaviour in ungulates. *Journal of Ethology* 37: 47-58.
- [16] Rodgers Jr. JA, Smith HT. 1997. Buffer zone disturbances to protect foraging and loafing waterbirds from human disturbance in Florida. *Wildlife Society Bulletin* 25: 139-145.
- [17] Parks Canada. <https://www.pc.gc.ca/en/pn-np/ab/banff/visit/avance-ahead/regs/espace-space>. Accessed December 10, 2018.
- [18] Stankowich T, Coss RG. 2006. Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behavioral Ecology*, doi: 10.1093/beheco/arl086.
- [19] Møller AP. 2008. Flight distance of urban birds, predation and selection for urban life. *Behavioral Ecology & Sociobiology* 63: 63-75.
- [20] Geist V, Stemp RE, Johnston RH. 1985. Heart-rate telemetry of bighorn sheep as a means to investigate disturbances. In: Bayfield, N. G., Barrow, G. C. (Eds.), *The Ecological Impacts of Outdoor Recreation on Mountain Areas in Europe and North America*, Recreational Ecology Research Group Report, no. 9, Wye College, Wye, pp. 92-99.
- [21] Lind J, Cresswell W. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, doi: 10.1093/beheco/ari075.
- [22] Found R, St. Clair CC. 2016. Behavioural syndromes predict loss of migration in wild elk. *Animal Behaviour* 115: 35-46.
- [23] Birke L, Hockenhull J, Creighton E, Pinno L, Mee J, Mills D. 2011. Horses' responses to variation in human approach. *Applied Animal Behaviour Science* 134: 56-63.
- [24] Delaney DK, Gurb TB, Seibr P, Pater LL, Reiser MH. 1999. Effects of helicopter noise on Mexican spotted owls. *Journal of Wildlife Management* 63: 60-76.

- [25] Bauwens D, Thoen C. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology* 50: 733–743.
- [26] Recarte JM, Vincent JP, Hewison AJM. 1998. Flight response of park fallow deer to the human observer. *Behavioural Processes* 44: 65-72.
- [27] Burger J, Gochfeld M. 1990. Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): Variation as a function of human exposure. *Journal of Comparative Psychology* 104: 388-394.
- [28] Blumstein, D. T., Anthony, L. L., Harcourt, R. & Ross, G. (2002). Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation*, 110, 97-100.
- [29] Møller AP. 2010. Interspecific variation in fear responses predicts urbanization in birds. *Behavioral Ecology* 21:365–371.
- [30] Díaz M, Møller AP, Flensted-Jensen E, Grim T, Ibáñez-Álamo JD, Jokimäki J, Markó G, Tryjanowski P. 2013. The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS One*. 8:e64634.
- [31] Kloppers, E. L., St. Clair, C. C. & Hurd, T. E. 2005. Predator-resembling aversive conditioning for managing habituated wildlife. *Ecology and Society* 10: 31.
- [32] Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A. & Blumstein, D. T. Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour* 86: 1147-1154.
- [33] Environment Canada. 2021. Historical weather for Banff CS, Alberta. [https://climate.weather.gc.ca/climate\\_data/daily\\_data\\_e.html?StationID=27378](https://climate.weather.gc.ca/climate_data/daily_data_e.html?StationID=27378). Site accessed January 3, 2021.
- [34] Paquet, P. C., Wierzchowski, J. & Callaghan, C. 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7: 74-120.
- [35] Goldberg, J. F., Hebblewhite, M. & Bardsley, J. 2014. Consequences of a Refuge for the Predator-Prey Dynamics of a Wolf-Elk System in Banff National Park, Alberta, Canada. *PLoS One* 9.
- [36] Ham, S. 2010. Wildlife corridors around developed areas in Banff National Park. Progress report for Parks Canada Warden Service. Winter 2009/2010.
- [37] Found R, St. Clair CC. 2017. Ambidextrous ungulates have more flexible behaviour, bolder personalities and migrate less. *Royal Society Open Science* 4: 160958. DOI: 10.1098/rsos.160958.
- [38] Found R. 2015. Ecological implications of personality in elk. PhD Thesis. University of Alberta. Edmonton, Alberta, Canada.
- [39] Creel S, Winnie Jr. JA, Christianson D, Liley S. 2008. Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour* 76: 1139-1146.
- [40] Liley S, Creel S. 2007. What best explains vigilance in elk: characteristics of prey, predators, or the environment? *Behavioral Ecology* 19: 245-254.
- [41] Tabachnick, B. G., & Fidell, L. S. (1996). *Using Multivariate Statistics* (3rd ed.). New York: Harper Collins.
- [42] Hosmer, D. W. & Lemeshow, S. 2000. *Applied logistic regression*. Wiley, New York, USA.
- [43] Guay, P.-J., van Dongen, W. F. D., Robinson, R. W., Blumstein, D. T. & Weston, M. A. 2016. AvianBuffer: An interactive tool for characterizing and managing wildlife fear responses. *Ambio* 45: 841-851.
- [44] Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82: 291-318.
- [45] Sih, A., Bell, A., & Johnson, J. C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* 19: 372-378.
- [46] Weaver JL. 1994. Ecology of wolf predation amidst high ungulate diversity in Jasper National Parks, Alberta. Thesis. University of Montana, Missoula, Montana, USA.
- [47] Moran NP, Sanchez-Tojar A., Schielzeth H, Reinhold K. 2020. Poor nutritional condition promotes high-risk behaviours: a systematic review and meta-analysis. *Biological Reviews* 96: 269-288. DOI: 10.1111/brv.12655.
- [48] Gravolin, I., Key, M. & Lill, A. 2014. Boldness of urban Australian magpies and local traffic volume. *Avian Biology Research* 7. DOI: 10.3184/175815514X14151981691872.
- [49] Rupia E. J., Binnin, S. A., Roche, D. G. & Lu, W. 2016. Fight-flight or freeze-hide? Personality and metabolic phenotype mediate physiological defense responses in flatfish. *Journal of Animal Ecology* 85: 927-937.
- [50] Bejder L, Samuels A, Whitehead H, Finn H, Allen S. 2009. Impact assessment research: use and misuse of habituation, sensitization and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series* 395: 177-185.
- [51] Domjan M. 2010. *The Principles of Learning and Behavior*. Sixth Edition. Thomson Wadsworth, Belmont, CA, USA.
- [52] Found, R., & St. Clair, C. C. 2018. Personality Influences Wildlife Responses to Aversive Conditioning. *Journal of Wildlife Management* 82: 747-755.
- [53] Wam HK, Eldegard K, Hjeljord O. 2014. Minor habituation to repeated experimental approaches in Scandinavian wolves. *European Journal of Wildlife Research* 60: 839-842.
- [54] Ferrari MCO, Elvidge CK, Jackson CD, Chivers DP, Brown GE. 2010. The responses of prey fish to temporal variation in predation risk: sensory habituation or risk assessment? *Behavioural Ecology*: doi: 10.1093/beheco/arq023.
- [55] Samuni L, Mundry R, Terkel, J, Zuberbuhler K, Hobaiter C. 2014. Socially learned habituation to human observers in wild chimpanzees. *Animal Cognition*, 17: 997-1005.
- [56] Malo JE, Acebes P, Traba J. 2011. Measuring ungulate tolerance to human with flight distance: a reliable visitor management tool? *Biological Conservation* 20: 3477-3488.
- [57] Mech LD, Peterson RO. 2003. Wolf-prey relations. In: Mech, L. D, Boitani, L. (eds), *Wolves: behaviour, ecology and conservation*. The University of Chicago Press, Chicago, USA, pp. 131-157.
- [58] Carter AJ, Feeney WE, Marshall HH, Cowlshaw G, Heinsohn R. 2013. Animal personality: what are behavioural ecologists measuring? *Biological Reviews* 88: 465-475.