FLEEING DECISIONS BY DALL'S SHEEP EXPOSED TO HELICOPTER OVERFLIGHTS

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Abstract: I asked whether Dall's sheep (*Ovis dalli dalli*) disturbed by helicopter overflights made fleeing decisions that were consistent with economic models of prey fleeing from predators. Agreeing with these models, fleeing probability decreased as the helicopter's approach became less direct, but the rate of decrease was greatest when sheep were on rocky slopes, which are a refuge from cursorial predators. Furthermore, sheep >20 m from rocky slopes always fled, even during indirect approaches, and distance fled increased with distance to rocky slopes. Approach directness affected fleeing probability only on a horizontal plane possibly because trials in which the helicopter was far above or below sheep were few. Contrary to predictions, flight initiation distance decreased with the horizontal component of approach directness. The latter, however, is geometrically correlated with the sheep's minimum horizontal distance from the helicopter trajectory, and flight initiation distance was largely determined by animals fleeing when the helicopter reached its nearest point to them. Flight initiation distance also increased with group size and distance to obstructive cover, suggesting lower perceptual constraints in groups of greater size or farther from obstructive cover. While sheep would increase fitness if they learn that aircraft overflights are not a lethal threat and do not warrant the energetic costs of antipredator behavior, I found no evidence of habituation. Results provide preliminary parameters for models predicting energetic and fitness costs incurred as a function of overflight rates. Guidelines to mitigate disturbance could be created using logistic regression models of fleeing probability predicting the minimum distance from trajectory (a geometric correlate of approach directness that is controllable by pilots) causing acceptably low disturbance rates.

Key words: approach directness, conservation biology, Dall's sheep, distance to refuge, fleeing decisions, group size, helicopter disturbance, obstructive cover, *Ovis dalli dalli*, predation risk

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Predation risk and human disturbance have similar effects on animal behavior. Both can limit access to resources (Gilliam and Fraser 1987, Cameron et al. 1992, Gill et al. 1996), cause greater vigilance (Stockwell et al. 1991, Frid, 1997), and elicit fleeing (Ydenberg and Dill 1986, Bleich et al. 1994, Côté 1996). These responses create energetic costs that may affect reproductive success. Thus, economic models of antipredator behavior predict that prey should maximize fitness by making optimal decisions that consider the trade-off between energetics and safety (e.g. Ydenberg and Dill 1986, Lima and Dill 1990).

Consistent with these models, prior studies have predicted and found that the probability of prey fleeing and their distance from the predator at which they begin to flee increase when predators (as simulated by humans) approach more directly (Burger and Gochfeld 1981, 1990; Cooper 1997, 1998; see Bulova 1994 for an exception). These responses might occur

because a direct approach indicates that the predator has detected the prey and intends to capture it (reviews in Cooper 1997, 1998). Flight initiation distance and distance fled from a predator have been predicted and found to increase as distance to refuge becomes greater. This response is attributed to risk of capture increasing with distance to refuge (Ydenberg and Dill 1986, Dill and Houtman 1989, Bulova, 1994, Kramer and Bonenfant 1997). The effect of group size on flight initiation distance is more difficult to predict because more sensory organs reduce perceptual constraints (i.e., larger groups might detect a predator when it is farther away), and group size therefore may be positively related to flight initiation distance. Larger groups, however, also dilute the individual's risk of predation, and flight initiation distance may be negatively related to group size (Ydenberg and Dill 1986, Dill and Ydenberg 1987). Not surprisingly, both positive and negative effects of group size have been observed (review in Ydenberg and Dill 1986).

Unlike prey facing predators, mountain Caprinae disturbed by helicopter overflights do not risk direct mortality. Still, these animals often behave as if helicopters were threatening by fleeing, increasing vigilance, and switching habitats (Stockwell et al. 1991, Bleich et al. 1994, Côté 1996). Thus, unless mountain Caprinae learn that helicopters are not a threat to life, they should treat the decision to flee from them as a trade-off between predation risk and energetics (see Ydenberg and Dill 1986). Prior research on helicopter disturbance, however, did not consider this hypothesis.

In this study I test whether fleeing responses by Dall's sheep (*Ovis dalli*

dalli) exposed to helicopter overflights are consistent with economic models and observations of prey fleeing from predators (e.g. Ydenberg and Dill 1986), and discuss the conservation implications of my results. I predicted that fleeing probability, flight initiation distance, and distance fled would decrease as the minimum distance between sheep and the helicopter's trajectory increased. The basis for this prediction is that minimum distance from trajectory is geometrically correlated to the plane's three-dimensional angle of approach, with a shorter distance implying a smaller angle and a more direct approach (Burger and Gochfeld 1981; 1990; Bulova 1994; Cooper 1997, 1998). I focused on the horizontal plane of approach directness because the helicopter's elevation relative to sheep had limited variability (see Methods). I controlled statistically, however, for the effect of relative elevation.

My second prediction was that fleeing probability, flight initiation distance, and distance fled would be directly related to distance from rocky slopes. Rocky slopes are a refuge from cursorial predators for sheep (Berger 1991; review in Frid 1997), and sheep may be less responsive to any threatening stimuli while near or on rocky slopes (see Ydenberg and Dill 1986, Dill and Houtman 1989, Bulova 1994, Kramer and Bonenfant 1997). Also, I expected that sheep not on rocky slopes would flee towards them.

In addition to testing the above 2 predictions, I assessed the effect on fleeing decisions of group size and obstructive cover. Group size could be related to risk dilution and/or perceptual constraints, while obstructive cover is related to perceptual constraints only (Ydenberg and Dill 1986, Dill and Ydenberg 1987). I assessed also whether approach directness by the helicopter combined multiplicatively rather than additively (i.e., interacted) with group size and/or distance to rocky slopes to affect fleeing decisions. The rationale for analysing interactions was that

prior studies have found that the antipredator response by prey exposed to a given risk factor may depend on the level of risk created by other factors (e.g. Burger and Gochfeld 1981, 1990; Frid 1997; Kramer and Bonenfant 1997, Cooper 1998).

Finally, I predicted that sheep would become more tolerant of direct approaches by the helicopter as weeks of cumulative overflights increased. Predicting habituation is within the framework of economic models of predator avoidance because sheep would increase fitness if they learn that aircraft overflights are not a lethal threat and therefore do not warrant the energetic costs of antipredator behavior (see Burger and Gochfeld 1981, 1990).

METHODS
Study sites, animals, and season

I collected data between mid-June and early August, 1997, in the southwest Yukon Territory, Canada. I made 49 observations at Hoge Pass (ca. 61 °19' N, 139° 33' W), Kluane National Park Reserve (KNPR), 6 observations at Nines Creek (ca. 61° 11' N, 138° 50' W), Kluane Wildlife Sanctuary, and 1 observation at Vulcan Creek (ca. 60° 55'N, 138° 29' W), KNPR. All sites contained >200 sheep, were roadless, rugged, and harboured large carnivores.

At the principal study sites (Hoge Pass and Nines Creek), fixed wing and helicopter traffic occurs mainly between May and September, perhaps averaging 25 flights per season for each aircraft type (not including flights related to my studies), but precise records are lacking. I collected 88% of observations at Hoge Pass not because helicopters threatened sheep there, but because that site

provided excellent observation conditions.

I pooled observations of female-young groups (N = 38) and all-male groups (N = 18) to maximise sample sizes. In pooling reproductive classes, I chose to gain statistical power at the cost of potential increases in unexplained variability. I assessed, however, whether pooling the sexes was justified in analysis of fleeing probability (see Results.)

Experimental disturbance and recording behavior

Sheep were exposed to overflights by a single helicopter (Bell 206B) flying at a mean ± SD air speed of 165 ± 31 km/h. At Hoge Pass responses to disturbance were tested experimentally; I designed a priori and communicated to the pilot (via radio) the helicopter trajectory. At Nines Creek and Vulcan Creek, overflights were related mainly to mineral exploration and data were collected opportunistically.

My assistants and I observed sheep from the ground, from distances of >1 km and using spotting scopes and/or binoculars. We simultaneously observed 1-4 focal groups (1/observer), and recorded continuous sampling of their behavior (Martin and Bateson, 1993) into tape recorders. These records started several minutes prior to overflights and continued until animals stopped reacting. Female-young groups tend to be large, and often we could not observe all group members at once. Thus, I quantified the timing of responses based on the behavior of the first animal or animals to respond in the group (most responses involved >50% of the group, see Results).

Recording aircraft trajectories and sheep locations

In 45 of 49 observations at Hoge Pass (80% of data for all sites), the pilot obtained the helicopter's position in relation to time during the observation period using a GPS system. Specifically, he communicated his position and

speed via radio 2-3 times per minute to observers on the ground, who recorded data directly from the radio into a tape recorder which was activated at the onset of the observation period.

For all trials at Nines Creek, the 4 observations for which the helicopter GPS was unavailable at Hoge Pass, and the one observation at Vulcan Creek, the helicopter's position in relation to time during the observation period was recorded as follows. An observer picked a priori distinct points in the landscape, and numbered them on the 1:50,000 map. When the helicopter flew over these points, he spoke the number identifying them into a tape recorder which was activated at the onset of the observation.

Sheep locations were plotted shortly before beginning behavioral observations using compass bearings and 1:50,000 topographic maps. After field work, the helicopter's positions (each corresponding to a given second in the observation period) were transcribed onto the maps containing sheep locations. Spatial variables involving the sheep's location and/or timing of sheep behavior in relation to the helicopter's position were measured from these maps. Helicopter positions that were not obtained from the pilot that were needed for analyses were estimated from known positions and the helicopter's speed.

I used the 1:50,000 topographic maps and known points on the landscape to estimate the sheep's distances to rocky slopes and obstructive cover (defined below), and the distances fled. When distances were <100 m, however, estimates used torso lengths of adult sheep (representing approximately 1 m) as reference points.

Distances were measured from the "average" center of the group. In other words, when most group members were at a core area but there were also outlying group members, measurements were made from a point that was shifted from the center of the core towards outlying sheep. Within the limitations of visual estimates, this shift away from the center of the core was proportional to the number of outlying sheep.

Variable definitions

Variables were defined as follows:
1. *Flee:* Binomial dependant variable recorded only when sheep were not travelling prior to helicopter overflights. It describes whether sheep interrupted feeding or bedding (occasionally standing inactive) to run and/or walk (often alternately) ≥10 m in response to a helicopter flying <4 km away. Its value equalled one when sheep moved ≥10 m, and equalled zero when sheep moved <10 m.
2. *Flight initiation distance:* Continuous dependant variable measuring the distance from the helicopter at which ≥1 group member(s) (almost always >50%) began to flee. It applies only to observations in which flee equalled one.
3. *Distance fled:* Continuous dependant variable describing the maximum distance (m) ≥1 group member(s) (almost always >50%) fled before ≥ 90% of the group resumed feeding or bedding. It applies only to observations in which flee equalled one.
4. *Minimum distance from trajectory:* Continuous variable measuring in km the length of the horizontal line from the sheep's pre-fleeing position to its perpendicular intersection with the projected forward trajectory of the helicopter. This variable is geometrically correlated with the horizontal component of the helicopter's angle of approach, with a smaller value implying a smaller

angle and a more direct approach (see Bulova 1994). The range of minimum distance from trajectory was 0-2.4 km (median = 0.6 km, 25% quartile = 0.3 km, 75% quartile = 1.0 km, N = 56).

5. *Relative elevation:* Continuous independent variable measuring the helicopter's elevation minus the sheep's elevation (m). The value is negative when the helicopter is below sheep. This variable is geometrically correlated with the vertical component of the helicopter's angle of approach, with a value closer to zero implying a more direct approach. Relative elevation ranged between 370 m and -270 m, but most helicopter trajectories were near the level of sheep (median = 0 m, 25% quartile = -60 m, 75% quartile = 40 m, N = 56).

6. *Distance to rocky slopes:* Continuous independent variable measuring the pre-overflight distance (m) between sheep and steep (>30°) rocky slopes. Its range was 0-1200 m. (median = 20 m, 25% quartile = 0 m, 75% quartile = 90 m, N = 56).

7. *Group size:* Continuous independent variable measuring the number of non-lambs in a group. I excluded young of the year from group size values because infant ungulates appear to recognize potential threats less readily than older conspecifics (FitzGibbon and Lazarus 1995), and their responses to risk likely are dependent on the responses of their mothers. I considered sheep to be in a group if they were on the same aspect of the same slope without cliffs or other obstructive cover blocking the line of sight between individuals (Frid 1997). Group sizes ranged from 1-64 (median = 14, 25% quartile = 6, 75% quartile = 25, N = 56).

8. *Distance to obstructive cover:* Continuous independent variable measuring the distance (km) between sheep and the nearest ridge blocking the line of sight between sheep and helicopter until the latter is past the ridge. Its range was 0.3 to 6 km (median = 2.5 km, 25% quartile = 1.5 km, 75% quartile = 3.5 km, N = 56).

Independence between observations

Multiple flights during the same day are not independent of each other, and here I present only data on the first flight of the day. Sheep were not marked. To reduce the problem of groups contributing more than 1 observation to the data set (Machlis et al. 1985), I considered observations to be independent only if they involved different groups that could be temporarily distinguished by their position in the landscape or if they occurred on different days. Because there were >200 sheep using each of the 3 study sites, and sheep groups moved constantly, merging with other groups and splintering apart, I believe that pseudoreplication was reasonably low.

Statistical analyses

I analysed fleeing probability with logistic regression (Hosmer and Lemeshow 1989, Trexler and Travis 1993). I built a preliminary multivariate model following procedures outlined by Hosmer and Lemeshow (1989). While readers should refer to Hosmer and Lemeshow (1989) for details, early stages of model building involved univariate tests for each independent variable. I then included in a preliminary multivariate model those variables whose univariate test statistics had probabilities of ≤0.25, and reduced the model with

backwards stepping procedures. Finally, I tested for the relevant interactions (see Introduction) with a second set of backwards stepping procedures (Hosmer and Lemeshow 1989). The independent variables considered were minimum distance from trajectory, relative elevation, distance to rocky slopes, and group size.

To avoid collinearity, independent variables could not remain in the reduced model unless their condition indices were <15 (Wilkinson et al. 1996, Kleinbaum et al. 1998). Scatter plots of residuals and leverage and probability plots of residuals were used to confirm that other regression assumptions were met (Hosmer and Lemeshow 1989, Steinberg and Colla 1991). A case with an unusually low relative elevation (-460 m, the next closest value was –270 m) had extreme leverage during a preliminary model, and data were reanalysed after deleting the case. (This case is not considered by any statistics.)

Function plots of logistic regression models were generated with the equation:

$$P(\text{Fleeing}) = 1 - [(EXP(\alpha + \beta_1 X_1 + \beta_i X_i))/(1 + (EXP(\alpha + \beta_1 X_1 + \beta_i X_i)))]$$

where α is the intercept, X_i is independent variable i, and β_i is the latter's regression coefficient (Hosmer and Lemeshow 1989, Trexler and Travis 1993).

For analyses of flight initiation distance and distance fled, I used linear regression models that were reduced to their most significant form with backwards stepping procedures (Wilkinson et al. 1996, Kleinbaum et al. 1998). This was done by first considering a preliminary model containing only main effects, and then a model containing variables that remained in the preliminary model plus their relevant second order interaction (see Introduction). Variables considered were the same as for analysis of fleeing probability, except that distance to obstructive cover was considered also for analysis of flight initiation distance. Log transformations (base 10) and standard diagnostic tests (condition indices, plots of residuals and leverage) were used to ensure that regression assumptions were met (Zar 1984. Wilkinson et al. 1996, Kleinbaum et al. 1998).

Other statistical tests used are common-place and described in Zar (1984). Analyses were done using SYSTAT 8.0 (SPSS 1998). This program, however, does not provide diagnostics nor confidence limits for logistic regression coefficients, which I obtained with LOGIT 2.0 (Steinberg and Colla 1991) and JMP (SAS Institute Inc. 1996), respectively.

RESULTS

Sheep groups fled during overflights in 43 of 56 observations (77%). During 13 observations (23%), all sheep in a group did not respond overtly or only became vigilant. Animals ran (sometimes combined with walking) in 37 of 43 fleeing events (86%), and walked during remaining events. In general, sheep first stared at the helicopter and then alternated movement with vigilance bouts.

Most group members escaped in relative synchrony. The initial run or walk away from the helicopter included >50% or 100% of the group, respectively, during 62% and 48% of fleeing events (N = 42 [one observation had missing data]). Even when sheep delayed flight relative to other group members, all sheep fled in 76% of fleeing events (N = 42, one case had missing data).

To flee or not flee

According to the reduced logistic regression model (Table 1; Rho^2 = 0.66), the probability of sheep fleeing depended on the multiplicative

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effect of minimum distance from trajectory and distance to rocky slopes. (A preliminary model considering only the additive effects of these factors, explained 5 % less of the variability in the data and had coefficients with larger standard errors than the model with the interaction.) Fleeing probability decreased as minimum distance from trajectory increased, but did so at a higher rate when sheep were on rocky slopes than when sheep were 5-20 m from rocky slopes. Furthermore, sheep farther than 20 m of rocky slopes always fled, regardless of minimum distance from trajectory (within a 2.0 km range) (Fig. 1; Table 1). Although admittedly there were few observations for non-fleeing sheep that were 5-20 m from rock slopes, a descriptive plot corroborated the trends estimated by the logistic regression model (Fig. 2).
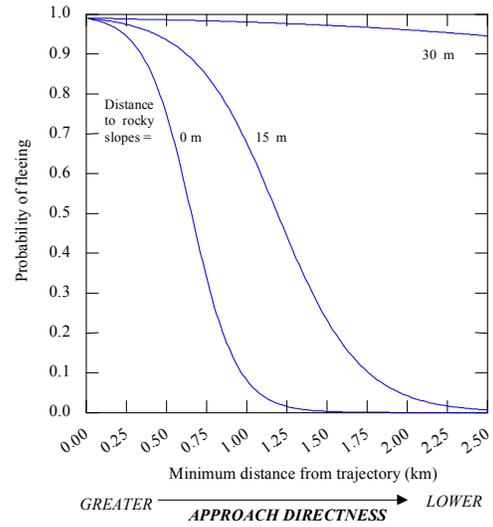

Fig. 1. Estimated fleeing probabilities as a function of the interaction between minimum distance from trajectory and distance to rocky slopes. Curves were generated with parameters of the reduced logistic regression model of Table 1 ($Rho^2 = 0.66$).

Table 1. Reduced logistic regression model estimating fleeing probability

Variable	Regression coefficient			Wald test	
	Estimate	Lower 95% confidence limit	Upper 95% confidence limit	T-ratio	P
Intercept	4.61	2.10	9.26	2.63	0.009
minimum distance from trajectory * distance to rocky slopes	0.21	0.09	0.42	2.70	0.007
minimum distance from trajectory	-7.04	-14.10	-3.41	-2.74	0.006

Log likelihood =-30.34, Chi-squared = 40.05, DF = 2, N = 56, $P<0.001$, $Rho^2 = 0.66$, N = 43 groups that fled, 13 that did not flee.
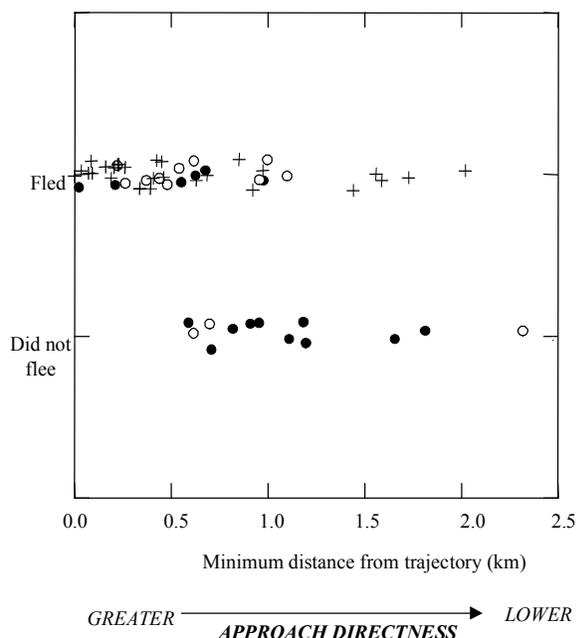
Fig. 2. Scatterplot of flee vs. no flee responses, as affected by the interaction between minimum distance from trajectory and distance to refuge. Dark circles represent sheep on rocky slopes, open circles represent sheep 5-20 m from rocky slopes (median = 20 m), crosses represent sheep 25-1200 m from rocky slopes (median = 100 m). Points are jittered so that overlapping data can be read. Figure is descriptive only because distance to rocky slopes was analysed as a continuous variable in the logistic regression (see Table 1, Fig. 1).

Group size was excluded from the reduced model, possibly because of limited statistical power. A univariate model of fleeing probability fitted during the first stage of model building, however, suggested that larger groups were more likely to flee than smaller groups (-log likelihood ratio = 30.34; Chi square = 5.87; P = 0.016; Rho^2 = 0.10).

I found no significant effect of the helicopter's relative elevation. This variable did not enter the preliminary multivariate model (Univariate Wald test during early model building stage [Hosmer and Lemeshow 1989]: t = 1.055, DF =1, P = 0.29). Descriptive plots indicated that the lack of effect was not because of an inverse

U-shaped function (i.e., sheep not fleeing at very high and very low relative elevations, but fleeing at intermediate elevations), which would not be detected by a logit assuming linearity (Hosmer and Lemeshow 1989).

Pooling the sexes for analyses appeared to be justified. When I tested the reduced model using only data on female-young groups, coefficients changed little and the overall model was significant (Log-likelihood ratio = -21.59, Chi-square = 31.33, DF = 2, P <0.001, N = 27 groups that fled, 10 groups that did not flee; 1 case with large leverage was excluded from analyses). Wald tests for independent variables, however, were marginally not significant (P = 0.067, 0.072) because of the reduced sample size and power.

Flight initiation distance

Flight initiation distance ranged from 100 m to 3 km, and had a median value of 0.9 km (25% quartile = 0.5 km, 75 % quartile = 1.5 km, N = 42 [one observation had missing data]). According to the reduced linear regression model (Table 2; R^2 = 0.59), flight initiation distance increased as minimum distance from trajectory became greater and decreased as relative elevation increased (Fig. 3). Flight initiation distance also increased as group size and distance to obstructive cover became greater (Fig. 4).

Distance fled

Distance fled ranged from 15 m to 1.5 km, and had a median value of 100 m (25% quartile = 30 m, 75% quartile = 200 m, N = 43). Sheep tended to run towards rocky slopes and, according to the reduced regression model (F = 4.40, DF = 1,41, P = 0.042), distance fled increased as distance to rocky slopes became greater (Fig. 5). The relationship, however, was weak (R^2 = 0.10) because sheep on rocky slopes fled during

very direct approaches, and because sheep that were not on rocky slopes prior to overflights often kept fleeing after reaching these slopes (Fig. 5).

Fleeing responses in relation to weeks of cumulative overflights

This analyses is limited to observations made at Hoge Pass, which was the only site were I collected data over several weeks. There was 25-day gap in observations between Week 1 (26 June-1 July) and Weeks 2-3 (respectively, 25-31 July and 2-8 August).

The proportion of sheep fleeing was lowest during the first week of overflights but there was no difference between the second and third week (Fig. 6, Yates corrected Chi-square = 7.18, DF = 2, P = 0.03). This observation was not confounded by minimum distance from trajectory nor distance to rocky slopes (Fig. 6), which on average did not differ between weeks of observation (ANOVA on log-transformed data for minimum distance from trajectory: $F = 1.22$, DF = 2,46, P = 0.30; for distance to rocky slopes: $F = 0.18$, DF = 2,46, P = 0.84).

Table 2. Reduced linear regression model estimating flight initiation distance.

Variable	Regression coefficient ± standard error	Standardized coefficient	Condition index	t-value	P
Intercept	0.0 ± 0.056			0.003	1
group size	0.10 ± 0.042	0.2.8	1.94	2.37	0.02
minimum trajectory dist.	0.52 ± 0.12	0.48	4.18	4.25	<0.001
dist. to obstructive cover	0.032 ± 0.01	0.37	4.45	3.33	0.002
relative elevation	-0.024 ± 0.009	-0.31	10.26	-2.68	0.01

$F = 13.51$; DF = 4,37, P<0.001, $R^2 = 0.59$. Variables were log transformed except for distance to obstructive cover.
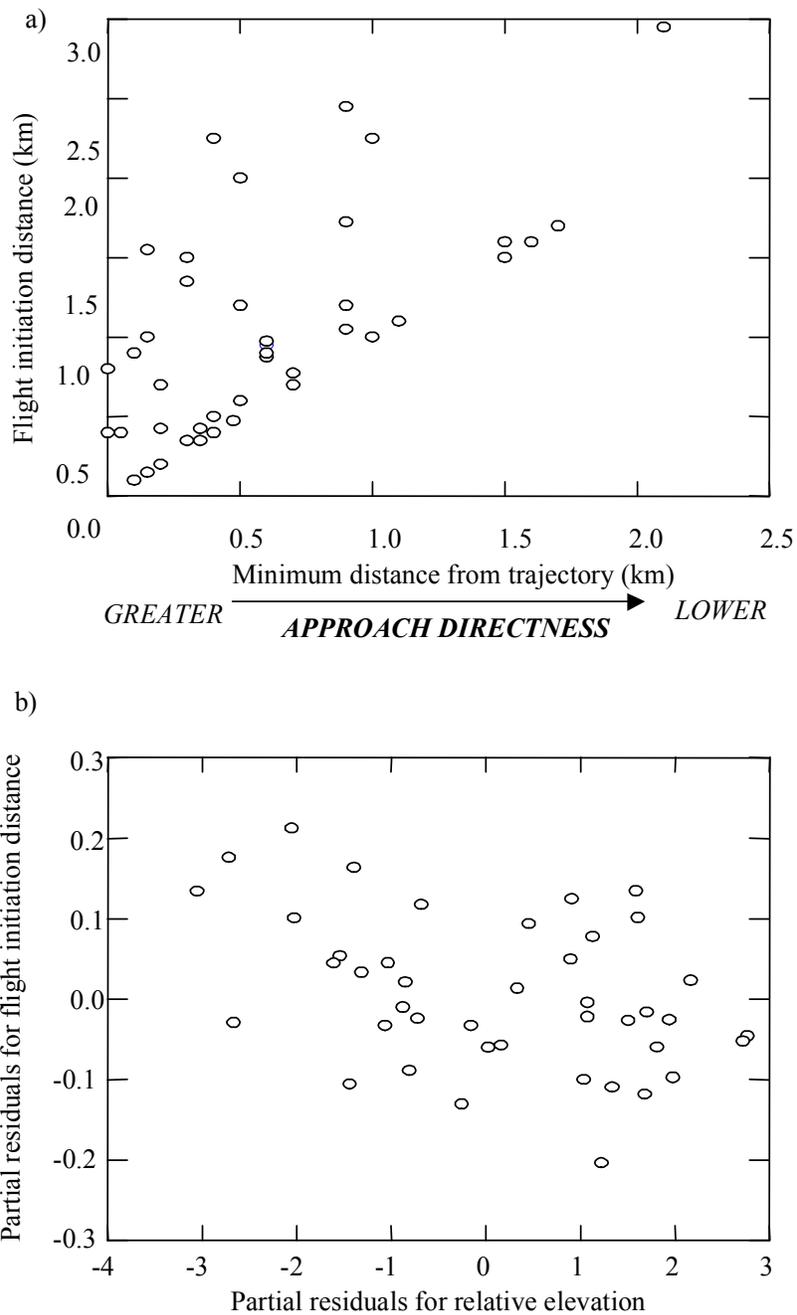
a)

Fig. 3. Relationship between flight initiation distance and (a) minimum distance from trajectory and (b) relative elevation. The scatterplot involving minimum distance from trajectory is only descriptive because it does not account for the effects of group size, relative elevation and distance to obstructive cover. The scatterplot for relative elevation is based on partial residuals because the effect was not strong enough to be shown without adjusting for the effect of other variables (see Wilkinson et al. 1996).
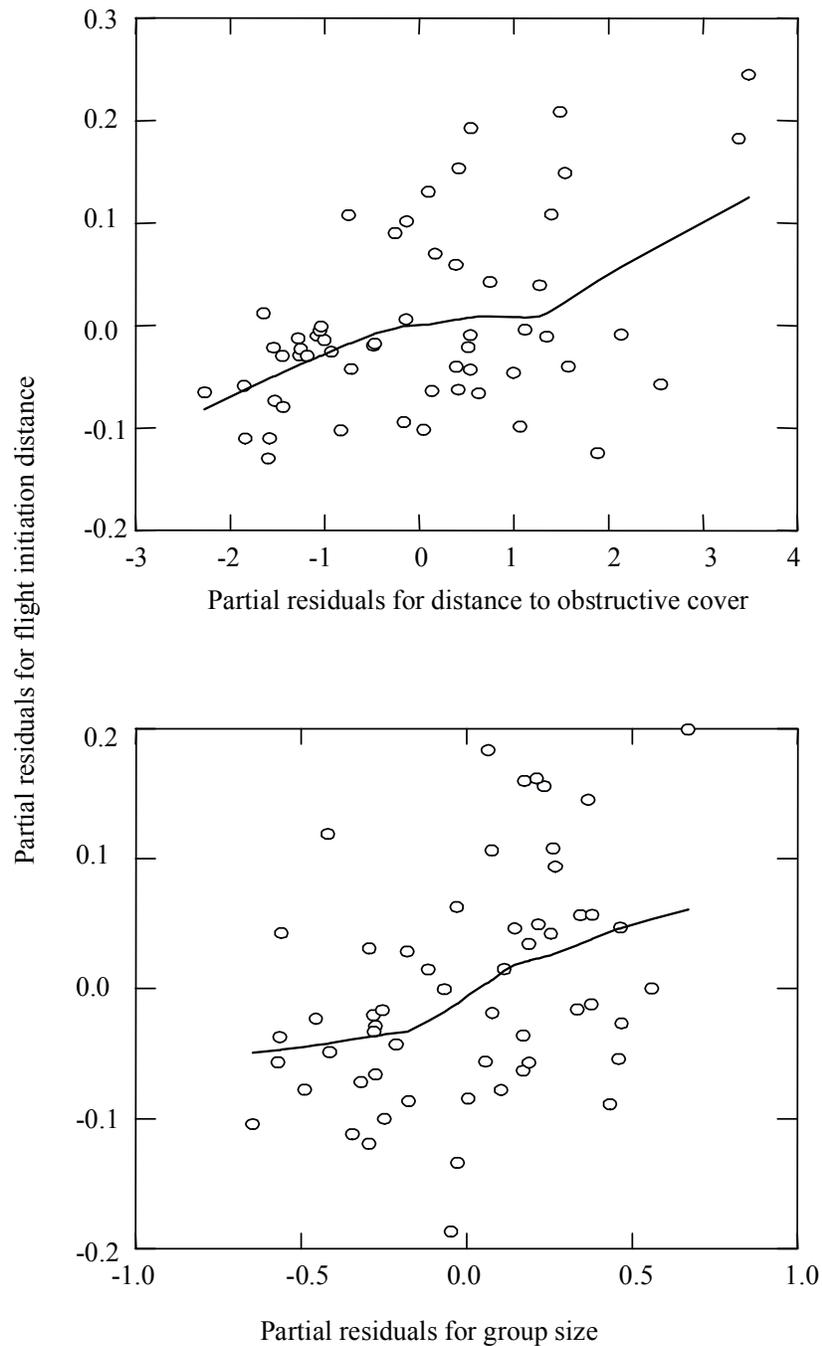
Fig. 4. Plots of partial residuals illustrating the effects of (a) distance to obstructive cover, and (b) group size on flight initiation distance. Partial residuals were used instead of actual data because trends were not strong enough to be shown without controlling for the influence of other factors affecting flight initiation distance (see Table 2). Trend lines are drawn with LOWESS smoothing at tension = 0.8 (Wilkinson et al. 1996), and are descriptive only. See Table 2 for the reduced regression model.
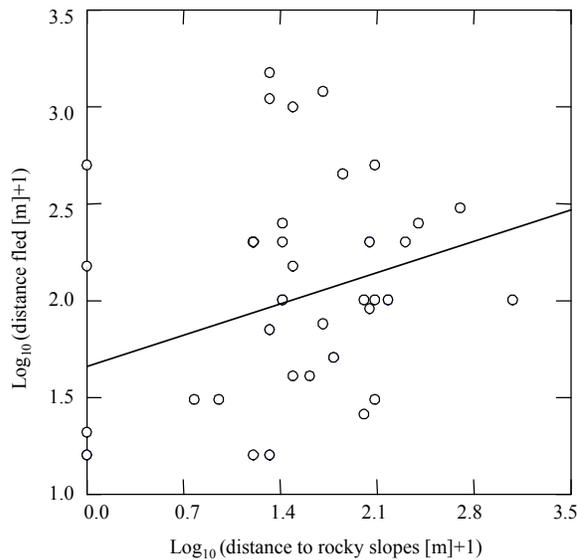
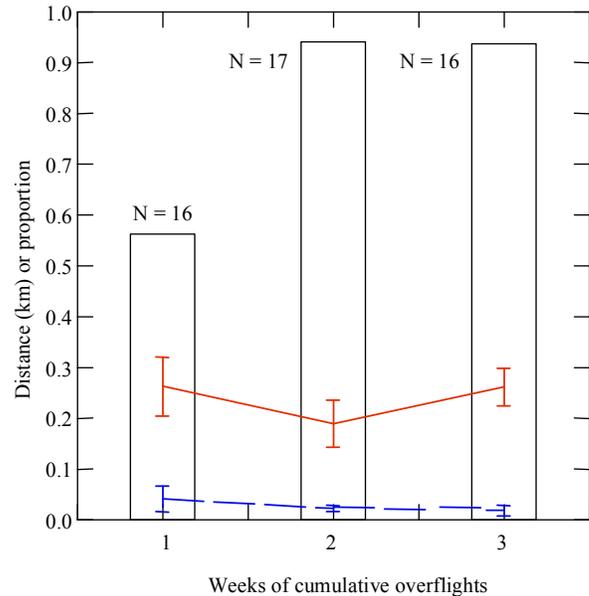Fig. 5. Distance fled in relation to distance from rocky slopes ($y = 1.66 + 0.23x$, $R^2 = 0.10$).

Fig. 6. Proportion of sheep groups fleeing (bars) in relation to weeks of cumulative overflights at Hoge Pass. Solid line is the weekly mean of minimum distance from trajectory, and broken line is the weekly mean of distance to rocky slopes. Error bars are standard errors of the mean.

DISCUSSION

Results generally were consistent with the hypothesis that sheep would treat the decision to flee from helicopters as a trade-off between energetics and predation risk (see Ydenberg and Dill 1986). They also confirm that while these trade-offs are important, flight initiation distance is partially a function of perceptual constraints (Burger and Gochfeld 1981, Ydenberg and Dill 1986, Dill and Ydenberg 1987).

Data supported the predictions that the probability of sheep fleeing would be inversely related to the helicopter's angle of approach (as indexed by minimum distance from trajectory) and directly related to distance from rocky slopes. The effect of these 2 factors, however, was multiplicative. Fleeing probability decreased at a faster rate for sheep on rocky slopes than for sheep 5-

20 m from these slopes, and sheep >20 m from rocky slopes always fled, even if the helicopter approached very indirectly. (These relationships were not an artifact of my definition of fleeing - sheep moving ≥10 m - because rocky slopes did not create a boundary limiting how far sheep fled; see Results for distance fled.) The main effect of approach directness is consistent with observations of mountain goats (*Oreamnos americanus*) exposed to helicopter overflights (Côté 1996), and with tests of economic models of prey fleeing from predators (Burger and Gochfeld 1981, 1990; Cooper 1997, 1998). I detected an effect of angle of approach only in a 2-dimensional plane probably because sample sizes of very low and very high relative elevations were insufficient to test for the vertical component of approach directness. The main

effect of distance from rocky slopes is consistent with economic models of prey fleeing from predators in which prey near a refuge have a lower "cost of remaining" (i.e., they are more likely to reach the refuge before the predator reaches them), and thus may avoid energetic costs of fleeing that do not contribute substantially to safety (Ydenberg and Dill 1986). Admittedly, it is unclear why rocky slopes affect responses by adult sheep to a simulated aerial predator (i.e., helicopter). Rocky slopes are a refuge for adult sheep from cursorial predators, such as wolves (*Canis lupus*) and coyotes (*C. latrans*) (Berger 1991; review in Frid 1997), and only lambs are preyed on by aerial predators such as golden eagles (*Aquila chrysaetos*: Nette et al. 1986). While distance to rocky slopes affected fleeing probability, it did not affect flight initiation distance. Group size was excluded from the multivariate model of fleeing probability possibly because of limited statistical power; larger sample sizes are needed to investigate its effect.

My observation that distance to rocky slopes and approach directness had a multiplicative effect on fleeing is consistent also with prior studies which found that the antipredator responses by prey exposed to a given risk factor may depend on the level of risk created by other factors. For example, Kramer and Bonenfant's (1997) woodchuck (*Marmota monax*) study, found that the relationship between distance to refuge and flight initiation distance was steeper when a person simulating a predator approached, relative to the woodchuck's position, from the opposite side of a refuge (and thus the woodchuck had to run towards the person to reach the refuge) than when the person approached from the same side of the refuge. Other examples can be found in Burger and Gochfeld (1981, 1990) and Cooper (1997, 1998). Multiplicative effects may be important not only for fleeing

decisions, but also for other types of antipredator behavior. For example, I found that individual vigilance decreased as group size became greater in Dall's sheep, but did so at lower rates as distance to rocky slopes decreased (Frid 1997). Antipredator behavior may not always depend on multiplicative effects, however, as was the case for flight initiation distance and distance fled in my study. Further theoretical work is needed to predict a priori when multiplicative effects should be expected.

In contrast to my prediction and the results of other studies (Burger and Gochfeld 1980, 1991; but see Bulova 1994), flight initiation distance increased as the horizontal component of approach directness decreased. While the mechanisms are unclear, this observation likely is related to the geometric correlation between approach directness and minimum distance from trajectory and, as Fig. 3 indicates, to most sheep fleeing when the helicopter reached its nearest horizontal distance to them (i.e., when the point in the trajectory was at 90 degrees from the sheep's position).

Flight initiation distance increased with group size, suggesting that the effect of more sensory organs was stronger than the risk-dilution effect (Ydenberg and Dill 1986, Dill and Ydenberg 1987). In other words, results suggest that as group size increases the probability that a given individual will see a far away helicopter and begin to flee becomes greater, and sheep unaware of the helicopter flee because of cues taken from conspecifics. Flight initiation distance increased also with distance to obstructive cover, which is consistent with findings of other studies suggesting that flight initiation distance is affected by perceptual constraints (Burger and Gochfeld 1981; review in Ydenberg and Dill 1986).

As predicted, sheep tended to flee towards rocky slopes, and distance fled increased as distance to rocky slopes became

greater. Although the relationship was weak, largely because sheep kept fleeing after reaching rocky slopes, it is consistent with the expectation that fleeing should be done such that it decreases risk of capture (Ydenberg and Dill 1986). The decision to flee towards rocky slopes, however, may be confounded by the aircraft almost always approaching from a gap in mountainous topography and from the direction opposite from rocky slopes; thus, I cannot disprove the possibility that sheep were merely fleeing away from aircraft and rocky slopes happened to be in that direction. It is interesting that while approach directness strongly affected fleeing probability, it did not affect distance fled. This results rejects my prediction and contrasts with prior research (Bulova 1994).

I did not find evidence of habituation. At Hoge Pass sheep fled during each week of cumulative observation, with the lowest proportion (63%) occurring during the first week. While data did not support the hypothesis that animals should habituate to non-lethal human disturbance, thus avoiding unnecessary investments in antipredator behavior (Burger and Gochfeld 1981, 1990), my study may have been too short for a proper test. Multi-year research on helicopter disturbance, however, concluded also that bighorn sheep (*O. canadensis*) did not habituate substantially to overflights (Bleich et al. 1994).

Conservation implications

Ungulate populations may be highly variable in size due to predation (Ross et al. 1997) and forage availability (Caughley and Gunn 1993). Thus, rigorous quantification of the effects of helicopter disturbance on population dynamics requires multi-year studies of radio-collared individuals exposed to experimentally determined disturbance

rates. Such expensive projects rarely will be an option, and my study was no exception.

Experimental studies of the consequences of disturbance on ungulate fitness are limited to mule deer (*Odocoileus hemionus*) disturbed by an all-terrain vehicle (Yarmoloy et al. 1988), and caribou (*Rangifer tarandus*) disturbed by low elevation jet flights (Harrington and Veitch 1992). These studies found that individual fitness decreased with increased disturbance rates (Yarmoloy et al. 1988, Harrington and Veitch 1992), but are based on few study animals and the generality of results is controversial. Nonetheless, their results are consistent with theoretical models of caribou disturbed by seismic exploration (Bradshaw 1994) and military jet overflights (Luick et al. 1996), and with correlational evidence of a caribou population decreasing as rates of military jet overflights increased (Maier 1996).

As suggested by the above studies, whether fleeing responses and other disruptions of activity budgets caused by helicopter disturbance actually affect the body condition and, consequently, reproductive success, of Dall's sheep, likely depends on the rate of overflights. The potential impact is a legitimate concern, as sheep exposed to long-term helicopter disturbance have not been found to habituate substantially (Bleich et al. 1994).

Results provide a first step towards predicting and, if necessary, mitigating the fitness and population consequences of helicopter disturbance on Dall's sheep. The current application of my results, however, is limited because (1) they are based on one population during one season, (2) do not necessarily address all of the relevant factors affecting fleeing decisions, and (3) do not provide evidence that disturbance actually affects fitness. However, the results do provide preliminary parameters for models predicting energetic costs incurred as a

function of fleeing rate, distance fled, and time lost from rumination and foraging. Such models could determine which disturbance rates sheep can incur without suffering fitness costs. Once this prediction is made for a given population, logistic regression models of fleeing probability, similar to the one I present here, could be used to predict the minimum distances from trajectory that would result in an acceptably low disturbance rate. (Wildlife managers using my logistic regression model should heed confidence intervals [Table 1]). While angle of approach is the biologically relevant variable affecting fleeing probability, minimum distance from trajectory is geometrically correlated to the horizontal component of this angle, is controllable by pilots, and thus would be the focus of pilot guidelines to reduce disturbance of sheep. Models of fleeing probability could also account for seasonal and/or diurnal variability in the sheep's distance to rocky slopes (see Fig. 1), and pilot guidelines could be adjusted accordingly. While my study was not designed to explicitly test for effects of the vertical component of approach directness—the helicopter's relative elevation—future work should address whether horizontal setback distances for pilots can be relaxed when helicopters are very high above or very far below sheep ranges.

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