

BEHAVIORAL RESPONSES BY DALL'S SHEEP TO OVERFLIGHTS BY FIXED-WING AIRCRAFT

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Abstract: Are behavioural responses by Dall's sheep (*Ovis dalli dalli*) exposed to overflights by a light fixed-wing aircraft consistent with economic models of antipredator behaviour? Agreeing with such models, the probability of active sheep fleeing and of bedded sheep un-bedding increased as aircraft approached more directly. Un-bedding probability was affected by the vertical and horizontal components of angle of approach, as indexed by the sheep's minimum distance from the aircraft's trajectory and relative elevation, respectively. Fleeing probability was affected only by the horizontal angle of approach, possibly because trials in which the aircraft was very high above sheep were few. When active sheep fled during overflights, the time they neither fed nor bedded increased as angle of approach decreased. Active sheep did not feed less or move more within 10 min after overflights than prior to disturbance. Almost all bedded sheep that interrupted resting bouts, however, were active for 44-100% of the post-overflight period, suggesting that the energetic costs of interrupting rumination were greater than those of decreased foraging and increased locomotion. Sheep would increase fitness if they learn that aircraft overflights are not a lethal threat and do not warrant costly antipredator responses, but there was no evidence of habituation. This study provides parameters for models predicting energetic and fitness costs incurred as a function of overflight rates, and logistic regression models of fleeing and un-bedding probability that could be used to create pilot guidelines to mitigate disturbance. Results support that fixed-wing aircraft are substantially less disturbing to sheep than helicopters.

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Human disturbance may create energetic costs to animals by displacing them from feeding sites, decreasing foraging time, interrupting resting bouts, and increasing movement (e.g. Stockwell et al. 1991; Côté 1996; Sutherland 1996; Gill et al. 1996; Maier et al. 1998; White et al. 1999). Theoretical models predict that if these costs occur at a high rate, disturbance could jeopardize the body condition, reproductive success (Bradshaw 1994, Gill et al. 1994, Luick et al. 1996, White et al. 1999) and population dynamics of wildlife (Gill et al. 1994, Sutherland 1996).

It is difficult to quantify empirically the reproductive consequences of motorized disturbance on ungulates. The few experimental studies that have attempted the task found that fitness decreased as disturbance rates increased (Yarmoloy et al. 1988, Harrington and Veitch 1992), which is consistent with theoretical predictions (e.g. Bradshaw 1994, Luick et al. 1996). These experimental studies, however, had small sample sizes and the generality of their conclusions is controversial. Correlational studies suggest that high rates of motorized disturbance could cause ungulate populations to decline (Joslin 1986, Maier

1996), but their study designs lacked the replicated control sites that could rigorously test disturbance effects (Underwood 1994). Thus, empirical studies have yet to make strong inferences on the functional relationship between motorized disturbance and the fitness and population dynamics of ungulates. Collectively, however, prior work does suggest that the potential effect of motorized disturbance on wildlife deserves further consideration. Concern for potential effects may be particularly relevant for mountain sheep (*Ovis* sp.), which habituate only partially to strong stimuli, such as helicopter overflights (Bleich et al. 1994).

A comparison of prior studies suggests that mountain sheep respond more strongly to helicopter overflights (Stockwell et al. 1991, Bleich et al. 1994, Frid 1999a) than to fixed-wing aircraft (Krausman and Hervert 1983, Bleich et al. 1994) and military jet overflights (Krausman et al. 1998). Fixed-wing aircraft, however, still may disturb sheep substantially. Krausman and Hervert (1983) found that sheep moved >100 m during 19% of observations when the plane flew directly towards sheep and circled them up to 10 times.

In this study I analyze responses by Dall's sheep (*O. dalli dalli*) to overflights by a light fixed-wing aircraft and relate results to sheep conservation. My framework is based on economic models of antipredator behavior predicting 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, Bulova 1994). It is based also on the hypothesis that animals respond similarly to human disturbance and predation risk (Gill et al. 1996, Sutherland 1996). To my knowledge, no other work on disturbance by fixed-wing aircraft has focused on Dall's sheep or considered most of the variables I analyzed.

My first prediction was that the probability of active sheep fleeing and of bedded sheep interrupting a resting bout would decrease as the minimum distance between sheep and the plane's trajectory increased, and as the plane's elevation relative to sheep became greater. The basis for this prediction is that minimum distance from the trajectory and relative elevation are geometrically correlated to the plane's three-dimensional angle of approach, with a shorter distance and lower relative elevation implying a smaller angle and a more direct approach (see Bulova 1994). Direct approaches might indicate that the predator has detected the prey and intends to capture it (reviews in Cooper 1997, 1998). Not surprisingly, prior studies found that the proportion of prey fleeing and their distance from the predator at which they began to flee increased when predators (as simulated by humans) approached more directly (Burger and Gochfeld 1981, 1990; Cooper 1997, 1998; see Bulova 1994 for an exception). Studies of mountain Caprinae disturbed by aircraft also provide a basis for this prediction; animals were less likely to flee as minimum distance from trajectory (Côté 1996; Frid 1999a) or as the aircraft's relative elevation became greater (Krausman and Hervert 1983). As an extension of this prediction, I expected that the time that sheep interrupted feeding or bedding would be inversely related to the plane's angle of approach (see Côté 1996).

My second prediction was that sheep farther from rocky slopes would be more likely to flee or interrupt resting bouts than sheep near or on rocky slopes. The basis for this prediction is that rocky slopes are a refuge from cursorial predators for sheep (review in Frid 1997), and sheep may be more responsive to any threatening stimuli while far from refuge (see Ydenberg and Dill 1986, Dill and Houtman 1989, Bulova 1994, Kramer and Bonenfant 1997). While

it is unclear how the sheep's perception of risk from a simulated aerial predator (i.e. aircraft) relates to mountainous terrain (only lambs are preyed on by aerial predators, such as golden eagles (*Aquila chrysaetos*: Nette et al., 1986), the prediction is based also on observations of sheep farther from rocky slopes being much more likely to flee during helicopter overflights (Frid 1999a). Unfortunately, while collecting data for analyses presented here, sheep almost always were on or near rocky slopes, which contrasted sharply with my prior observations (Frid 1997, 1999a). Thus, the prediction was rejected while I was still in the field, and distance to rocky slopes was analyzed only as a statistical control.

Thirdly, I predicted that time spent foraging would be lower and time spent moving would be greater after than before overflights, and that bedded-sheep that interrupted resting bouts would spend less time bedded after overflights. The basis for this prediction is that after a predator encounter, prey may remain alert and not resume energy-gaining activities for some time after the predator is no longer visible, but potentially could return (review in Lima and Dill 1990). This prediction is based also on observations of mountain sheep foraging less efficiently, increasing movement, or spending less time bedded after helicopter overflights (Stockwell et al. 1991, Bleich et al. 1994, Frid 1999b).

Finally, I predicted that sheep would become more tolerant of direct approaches by the plane as cumulative weeks of 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 behaviour (see Burger and Gochfeld 1981, 1990).

METHODS

Study site and season

I collected data between 22 June and 15 July 1999, at Hoge Pass (ca. 61°19' N, 139°33' W), Kluane National Park Reserve, southwest Yukon Territory, Canada. The site is roadless and rugged. It consists of alpine habitats without shrubs or tree cover. Large meadows are found at the base of steep, rocky terrain and sheep predators (including grizzly bears [*Ursus arctos*] and wolves [*Canis lupus*]) are common. At least 200 sheep used the study area.

Hoge Pass is the same site where I studied helicopter disturbance of sheep during 1997 (Frid 1999a, 1999b). 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. The study area was overflowed multiple times per day by commercial jet planes travelling at very high elevations (several thousand meters above); it is plausible that such traffic may have made sheep less sensitive to experimental overflights that were far from sheep and/or high above them.

Animals sampled

Data presented are for adult females (two years or older). I intended to reduce potential sources of variability by sampling only females with young. Perhaps due to the cold wet spring that preceded fieldwork, however, there was a large proportion of barren females and sampling mothers only would have resulted in small sample sizes. Thus, 41% of 81 observations analyzed for immediate responses were of females without young. Preliminary analyses found no effect of reproductive status on responses to aircraft (contingency table analyses for proportion of active sheep fleeing: Pearson Chi-square = 0.072, DF = 1, N = 51, $P = 0.79$; for proportion of bedded sheep un-

bedding: Yates-corrected Chi-square = 0.001, DF = 1, N = 30, $P = 0.98$), and reproductive status is not considered further.

Sheep were not marked. To reduce the problem of individuals contributing more than one observation to the data set (Machlis et al. 1985), I considered observations to be independent only if they involved individuals from different groups during the same overflight. Sheep groups using the same area for several days were sometimes sampled during more than one overflight. I believe, however, that pseudoreplication of focal individuals was quite low because there were >200 sheep using the area and groups moved constantly, merging with other groups and splintering apart.

Experimental overflights

Sheep were exposed to 42 overflights by a single fixed-wing aircraft (Cessna 206). Analyses, however, include only 32 overflights because the GPS system failed to record trajectories during six overflights (see below), and because all focal animals were strongly affected by the plane circling during four overflights. The plane was stationed outside the study area and was called in via satellite phone to overfly sheep following an explicit trajectory. Depending on weather, there were 0-3 overflights per day, with ≥ 8 hours between overflights. (Poor visibility precluded overflights during four days.) Sheep were disturbed by two helicopter overflights related to camp logistics at the onset of the study, plus helicopter activity unrelated to our work during two days. Sheep were not sampled for ≥ 8 hours after a helicopter flew through the area.

Analyses consider only overflight trajectories in which the plane followed a straight path through the study area and did not circle over focal individuals. (Exceptions were two cases in which the plane circled after the initial response by

sheep, for which only fleeing probability was analyzed, and two cases in which the plane circled in line of sight of bedded sheep that did not un-bed.) Within the restrictions of pilot safety, weather, and topography, I reduced uncontrolled variability by designing trajectories that met the following criteria:

1. No substantial turns or changes in relative elevation within 3 km of the focal animal (see Cooper 1998). Two cases were excluded from analyses because the aircraft turned directly towards sheep within 1.5 km of them.
2. No topographic features that could block the line of sight between sheep and plane within 2 km of focal sheep (see Frid 1999a). One case was excluded from analyses because this requirement was not met.
3. Consistent aircraft speed (see Ydenberg and Dill 1986). Mean \pm SD ground speed was 197 ± 16 km/h (N = 38 overflights).

I defined overflights as the time the plane was within 4 km of sheep while approaching and exiting the area. This 4-km threshold is based on the 75% quartile of the distance between animals and aircraft at which active sheep became vigilant towards the plane (3.8 km, N = 38 focal sheep). I divided time relative to overflights into three experimental periods:

1. *Pre-overflight*: 10 min prior to overflights.
2. *During overflight*: the time when the plane was ≤ 4 km of sheep, which had a mean \pm *sd* duration of 128 ± 23 seconds (range 55-186 s, N = 48 focal animal for which post-overflight behaviour was recorded).
3. *Post-overflight*: 10 min after overflights.

Recording behaviour and other sheep-related data

Two assistants and I observed focal individuals from the ground, from distances of >1 km and using spotting scopes. Only one focal individual per group was observed during a given overflight. Unless <3 groups were observable, we made three observations per overflight (1/observer). We obtained continuous behavioural records of focal individuals (Martin and Bateson 1993) using either a notebook computer programmed as an event recorder (ca. 1/3 of samples), or by speaking observations into tape recorders. In the latter case, tapes were transcribed into electronic files with the event recorder.

Focal animal samples began ≥ 10 min prior to overflights and continued for ≥ 10 min after the plane left the study area. Samples were shorter, however, if the plane arrived earlier than expected or if sheep went out of sight behind topography. Variability in sample duration may affect variability in the proportions of time focal animals spent on different behaviors during the sample (Frid unpublished data). Thus, for the pre- and post-overflight periods I reduced longer samples to 10 min, and excluded samples that were <9 min from analyses of behaviour in relation to experimental stage.

Recording aircraft trajectories and sheep locations

The pilot recorded aircraft trajectories with a Trimble Geo Explorer II GPS system, which was programmed to record one location per second. Trajectories recorded in the field were later corrected with data from a base station. Sheep locations were plotted shortly before beginning focal animal samples using compass bearings and 1:50,000 topographic maps.

After fieldwork, locations of focal sheep were transcribed into the GIS files containing the corresponding overflight

trajectory. Variables involving the sheep's location and/or timing of sheep behaviour in relation to the plane's position (see below) were measured using Pathfinder Office V.2 (Trimble Navigation Limited 1996). Because sheep locations were less precise than trajectory records (partly because active sheep may have moved during the pre-overflight period), values of horizontal spatial variables were rounded-off to the nearest tenth of a kilometer.

Variable definitions

I will refer to focal animals that were active and bedded when overflights began, respectively, as *active sheep* and *bedded sheep*. Variables requiring definitions and which represent responses to the approaching plane are as follows:

1. *Flee*: Binomial variable quantifying the proportion of active sheep that ran and/or walked ≥ 10 steps before stopping for ≥ 10 s to be vigilant or feed, vs. the proportion that moved 0-9 steps.
2. *Un-bed*: Binomial variable quantifying the proportion of bedded sheep that stood up to be vigilant and/or flee, vs. the proportion that remained bedded.
3. *Vigilance initiation distance*: Continuous variable measuring in km the distance from aircraft at which active sheep became vigilant towards the plane.
4. *Time not foraging or bedded*: Continuous variable that applies to active or bedded sheep that fled or un-bedded. It measures in seconds the time between the first overt response towards aircraft and when the focal animal bedded or began to feed continuously for ≥ 5 s, without interrupting either activity by walking and/or being vigilant for >1 min.

Independent variables are defined below. (Note that distributions of independent variables reported for bedded sheep do not

include cases excluded from analyses, as described under Data Analyses.)

1. *Minimum distance from trajectory*: Continuous variable measuring in km the length of the line from the sheep's pre-fleeing position to its perpendicular intersection with the projected forward trajectory of the plane. This variable is geometrically correlated with the plane's angle of approach, with a smaller value implying a smaller angle and a more direct approach (Bulova 1994). The range of minimum distance to trajectory was 0-3.7 km for active sheep (median = 0.3 km, 25% quartile = 0.2 km, 75% quartile = 0.8 km, N = 51 focal animal samples), and 0-2.9 km for bedded sheep (median = 0.4 km, 25% quartile = 0.1 km, 75% quartile = 0.7 km, N = 30).
2. *Relative elevation*: Continuous independent variable measuring the plane's elevation minus the sheep's elevation (m). Values are negative when the plane was below sheep. Relative elevation ranged between -210 m and 560 m for active sheep (median = 30 m, 25% quartile = -30 m, 75% quartile = 140 m, N = 51 focal animal samples), and from -60 m to 380 m for bedded sheep (median = 80 m, 25% quartile = 30 m, 75% quartile = 190 m, N = 30).
3. *Distance to rocky slopes*: Continuous independent variable measuring the pre-overflight distance (m) between focal sheep and steep (>30°) outcrops or scree slopes. Its range was 0-750 m for active sheep (median = 5 m, 25% quartile = 0 m, 75% quartile = 15 m, N = 51 focal animal samples) and 0-100 m for bedded sheep (median = 0 m, 25% quartile = 0 m, 75% quartile = 3 m, N = 30 focal animal samples).

Data analyses

I analyzed fleeing and un-bedding probabilities with logistic regression (Hosmer and Lemeshow 1989, Trexler and Travis 1993). I built preliminary multivariate models following procedures outlined by Hosmer and Lemeshow (1989), and then reduced these models to their most significant form with backwards stepping procedures. 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. If the reduced model was multivariate, I then tested for interactions with a second set of backwards stepping procedures (Hosmer and Lemeshow 1989). The independent variables considered were minimum distance from trajectory, relative elevation, and distance to rocky slopes.

I expected the effect of relative elevation to be an inverse U-shape function, with animals not responding at very low and very high elevations. Sample sizes, however, were marginal for following procedures necessary to detect a non-linear logit (Hosmer and Lemeshow, 1989). Thus, un-bedding probability was analyzed after eliminating the inverse U-shape effect by excluding three cases with relative elevations of < -60 m. (The three cases were excluded from all other analyses as well). Preliminary analyses for the inverse U-shape function (Hosmer and Lemeshow 1989) did not detect an effect of relative elevation on fleeing probability, and thus no cases with low relative elevations were deleted for analyses of this variable (see Results).

If the reduced model was multivariate, I assessed collinearity with condition indices (Wilkinson et al., 1996; Kleinbaum et al.,

1998). These were derived from eigenvalues calculated with factor analyses. Independent variables could not remain in the reduced model unless their condition indices were <15 (Wilkinson et al. 1996). 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). For the un-bed probability model, a case with an unusually large distance to rocky slopes had extreme leverage during a preliminary model, and data were reanalyzed after deleting the case.

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

$$P(Y) = 1 - \frac{1}{1 + (\text{EXP}(\alpha + \beta_1 X_1 + \beta_i X_i))}$$

where P (Y) is either the probability of fleeing or un-bedding, 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).

Time not foraging or bedded was analyzed with separate linear regression models for active and bedded sheep. The model for active sheep considered the same variables as for the logistic regression models and was reduced to its most significant form with backwards stepping procedures (Wilkinson et al. 1996, Kleinbaum et al. 1998). For bedded sheep, small sample sizes allowed the model to consider only one variable, which I chose to be minimum distance from trajectory. Log transformations (base 10) and standard diagnostic tests (plots of residuals and leverage) were used to ensure that regression assumptions were met (Zar 1984, Wilkinson et al. 1996, Kleinbaum et al. 1998). An outlier with high values for the dependent variable and for minimum distance from trajectory had large leverage during a preliminary model for active sheep, and data were reanalyzed after deleting the case.

Other statistical tests used are

commonplace and described in Zar (1984). Analyses were done using SYSTAT 8.0 (SPSS 1998). This program, however, provides neither 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

Probability of active sheep fleeing and distance fled

When focal sheep were active prior to overflights (N = 51), 37% fled and 63% did not. Sheep ran during 84% of fleeing events (16 of 19), including 5 cases in which the focal animal alternated running and walking, and walked during only 3 observations. When fleeing, sheep took a median of 28 steps (maximum = 173, 25% quartile = 13, 75% quartile = 40, N = 15; excluding 3 cases in which sheep ran out of sight behind topography and 1 case in which the plane circled sheep). After the initial flight, sheep usually stood vigilant and then walked a few steps before bedding or feeding (total steps taken before bedding or resuming feeding: maximum = 183, median = 31, 25% quartile = 14, 75% quartile = 63, N = 15; 4 cases excluded as above).

According to the reduced logistic regression model ($Rho^2 = 0.20$; Table 1), fleeing probability for active animals depended on minimum distance from trajectory. Fleeing probability was 0.5 when the plane flew directly towards sheep (i.e. minimum distance from trajectory was 0 km), but decreased steeply as minimum distance from trajectory increased to about 0.7 km. No animals fled when minimum distance from trajectory was >0.7 km (Fig. 1).

Univariate analyses during preliminary stages of model building (Hosmer and Lemeshow 1989) did not detect effects of relative elevation (Wald tests for the Box-

Table 1. Reduced logistic regression model estimating fleeing probability by active sheep.

Variable	Regression coefficient			Wald test	
	Estimate	Lower 95% confidence limit	Upper 95% confidence limit	T-ratio	P
Intercept	0.91	-0.13	2.14	1.57	0.11
minimum distance from trajectory	-3.26	-6.52	-1.07	-2.33	0.02

N = 51 focal animal samples, Log likelihood = -33.68, Chi-squared = 13.57, DF = 1, P < 0.001, Rho² = 0.20.

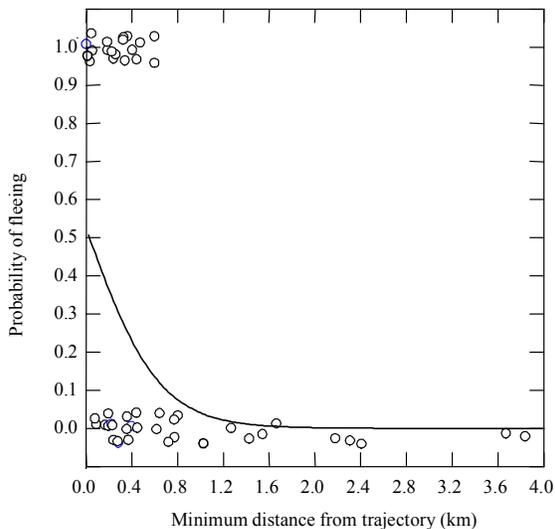


Fig. 1. Proportion of active sheep fleeing as a function of minimum distance from trajectory. The curve is the fleeing probability as estimated by the reduced logistic regression model of Table 1. Circles represent observed values and are jittered so that overlapping data points can be read.

Tidwell transformation [Hosmer and Lemeshow]: $t = 0.32$, $DF = 1$, $P = 0.75$). Distance from rocky slopes also did not enter the preliminary multivariate model (Wald test for univariate model: $t = 0.99$, $df = 1$, $p = 0.32$).

Probability of bedded sheep un-bedding

When focal sheep were bedded prior to overflights ($N = 30$), 53% remained bedded and 47% un-bedded. Of the latter, 57% (8 of 14) fled for 11-85 steps (median = 17, 25% quartile = 13, 75% quartile = 26, $N = 8$), while the remaining focal individuals

stood vigilant or took <10 steps. After the initial flight, sheep that fled tended to walk further before re-bedding or feeding (total steps taken before resuming maintenance activities: maximum = 95, median = 52, 25% quartile = 17, 75% quartile = 87, $N = 8$).

According to the reduced regression model (Rho² = 0.38; Table 2), the probability of un-bedding decreased as minimum distance from trajectory and relative elevation increased (Figs. 2, 3). The model estimated that when the plane was 80 m above sheep (the median relative elevation for observations of bedded animals) or at smaller relative elevations, un-bedding probability was very high (>0.8) if the plane flew directly towards the animals, and that un-bedded probability remained >0.2 when distances were <1 km (Fig. 2). Un-bedding probability, however, was much lower when the plane flew higher above sheep, even when minimum distance from trajectory was short. For example, at 190 m above sheep (the 75% quartile), the probability was ≈ 0.4 when the plane flew directly towards sheep, but decreased to <0.1 at minimum distances from trajectory >0.8 km (Fig. 2).

I found no effect of distance to rocky slopes. This variable did not enter the preliminary multivariate model (Univariate Wald test during preliminary model building [Hosmer and Lemeshow 1989]: $t = 0.88$, $df = 1$, $p = 0.38$).

Table 2. Reduced logistic regression model estimating un-bedding probability by bedded sheep.

Variable	Regression coefficient			Wald test	
	Estimate	Lower 95% confidence limit	Upper 95% confidence limit	T-ratio	P
Intercept	2.81	0.95	5.39	2.56	0.011
minimum distance from trajectory	-2.66	-5.91	-0.58	-1.97	0.049
relative elevation	-0.016	-0.031	-0.0057	-2.49	0.013

N = 30 focal animal samples, Log likelihood = -20.73, Chi-squared = 15.76, DF = 2, P < 0.001, Rho² = 0.38.

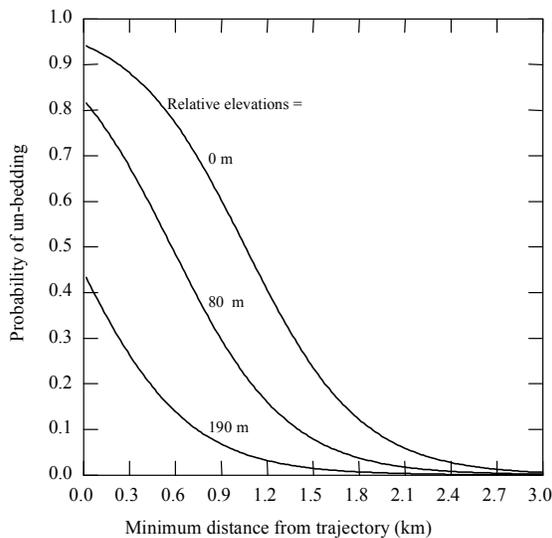


Fig. 2. Estimated probabilities of bedded sheep un-bedding as a function of minimum distance from trajectory and relative elevation. Curves were generated with parameters of the reduced logistic regression model of Table 2. Each curves represents, in descending order, a relative elevation of 0 m, 80 m (the median value), and 190 m (the 75% quartile).

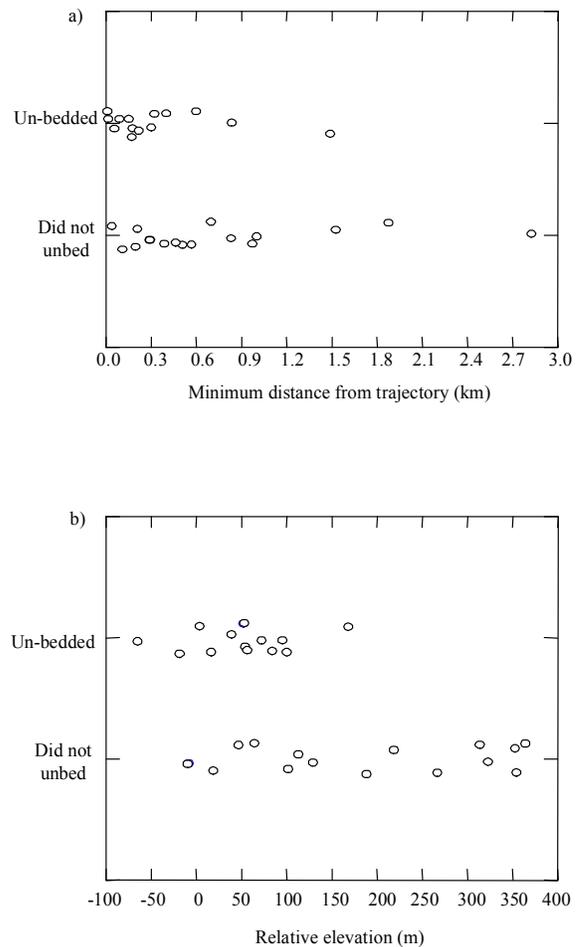


Fig. 3. Univariate scatterplots of the proportion of bedded sheep un-bedding in relation to (a) minimum distance from trajectory and (b) relative elevation. Figure is descriptive only because multivariate effects are not shown.

Time not feeding or bedded

Active sheep that showed an overt response towards the plane (either stood vigilant or fled) took a median of 31 seconds to bed or resume feeding (25% quartile = 14 s, 75% quartile = 46 s, range 2-149 s, N = 37; excluding 3 cases in which sheep ran out of sight behind topography and 2 cases in which then plane circled focal animals). According to the reduced regression model, the time to return to energy-gaining activities decreased as minimum distance from trajectory increased (Fig. 4: $F = 10.55$, $DF = 1,35$, $P = 0.007$, $R^2 = 0.19$). Relative elevation and distance to rocky slopes were excluded from the model.

Bedded sheep that un-bedded during overflights took a median of 86 seconds to begin to either forage or to re-bed (range = 16-370 s; 25% quartile = 67 s, 75% quartile = 124 s, N = 14), which was almost 3 times longer than for active sheep that showed a response (Mann Whitney U-statistic = 82, $P < 0.001$). The time to begin feeding or to re-bed did not depend on minimum distance from trajectory (simple linear regression: $t = -0.016$, $DF = 1$, $P = 0.99$).

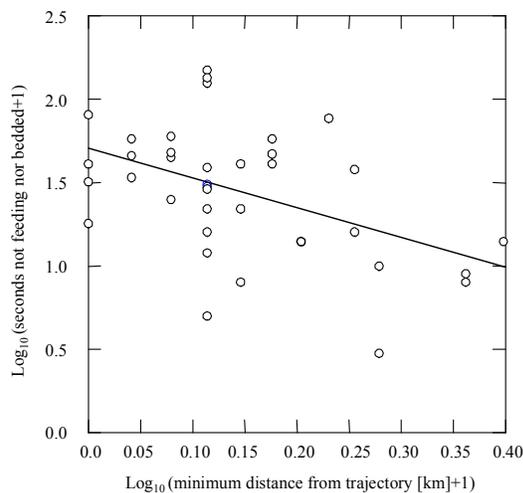


Fig. 4. Time not feeding or bedded by active sheep in relation to minimum distance from trajectory. Regression line is generated with the equation $y = 1.69 - 1.69x$ ($R^2 = 0.19$, see text).

Behaviour and time relative to overflights: foraging animals

Analyses described in this section are for active sheep. Because I was interested in the potential effect of overflights on energy-gaining activities, sheep which foraged for <50% of the pre-overflight period (who were travelling or engaged in social activities) were excluded from analyses.

Three of 8 focal individuals which fled during overflights bedded for 69% (1 sheep) or 91-100% (2 sheep) of the post-overflight period. In contrast, sheep that did not flee (N = 14) did not bed after overflights, except for 1 individual which bedded for the last 16 seconds of the post-overflight period.

For those individuals which did not bed during most or all of the post-overflight period, there was no substantial difference in time spent foraging before and after overflights (Fig. 5a), regardless of whether they fled or not (Wilcoxon signed rank test for sheep that fled: $Z = 0.31$, $P = 0.75$, $N = 5$; for sheep that did not flee $Z = 0.47$, $P = 0.64$, $N = 14$). There was also no difference in time spent moving during the pre- and post-overflight periods for these same animals (Fig. 5b: Wilcoxon signed rank test for sheep that fled: $Z = -0.41$, $P = 0.67$; for sheep that did not flee: $Z = -0.40$, $P = 0.68$).

Behaviour and time relative to overflight: animals that un-bedded

In the 7 samples of bedded sheep that un-bedded in response to the plane, 6 sheep were active for 44-100% of the post-overflight period. Specifically, the time spent bedded during the post-overflight period was 96% for 1 sheep, 48-56% for 2 sheep, and 0% for 4 sheep. Sheep which were active for at least 44% of the post-overflight period (N = 5) spent more time foraging (median = 45%) than vigilant (median = 8%) or walking (median proportion = 12%).

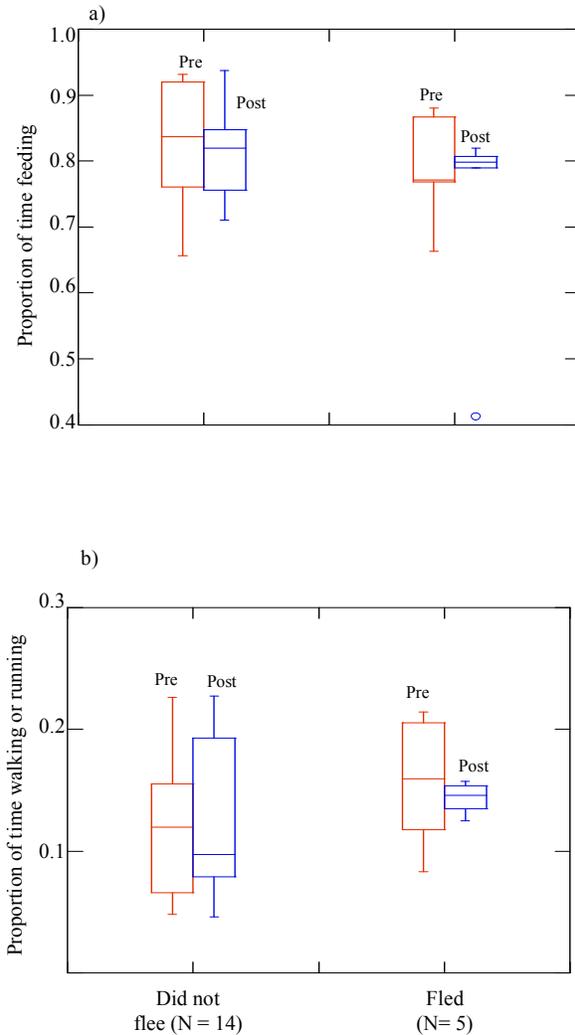


Fig. 5. Box plots of the proportion of time (a) feeding and (b) walking/running by active sheep during the 10-min periods that preceded and followed overflights. (These periods are marked on the figure as “pre” and “post” respectively.) Three sheep that were active before disturbance but which bedded almost immediately after overflights are excluded.) Boxes encompass 25% and 75% quartiles, the central line within the box represents the median, and the whiskers encompass 90% of the values. The circle in Fig. 5a represents a value outside the whiskers (see Wilkinson et al. 1996).

Fleeing responses to direct approaches in relation to cumulative weeks of overflights

Analyses presented here are limited to minimum trajectory distances of <0.6 km, which had a median value of 0.3 km during each week of the study (weeks 3 and 4 were pooled). There was no substantial difference in the proportion of active sheep fleeing during the 4 weeks of cumulative overflights (Fig. 6: Pearson Chi-square = 0.65, DF = 2, P = 0.72).

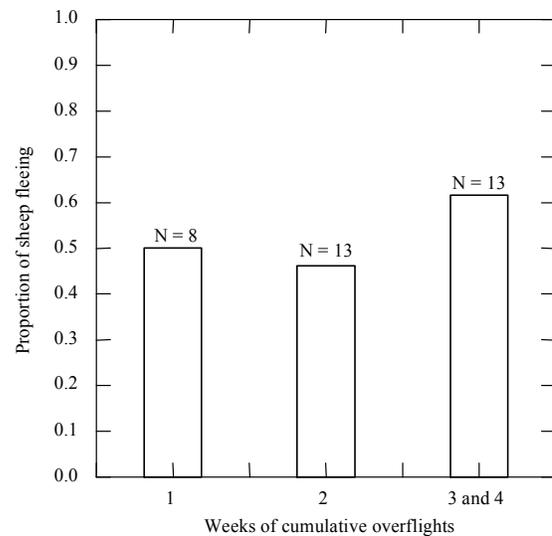


Fig. 6. Proportion of active sheep fleeing in relation to weeks of cumulative overflights. Data are shown only for overflights in which minimum distance from trajectory was <0.6 km (weekly median = 0.3 km).

DISCUSSION

Results supported the prediction that the probability of active sheep fleeing and of bedded sheep un-bedding would increase as the plane’s angle of approach became more direct. These results are consistent with observations of mountain Caprinae exposed to helicopter overflights (Côté 1996, Frid 1999a) and bighorn sheep (*O. canadensis*) disturbed by fixed-wing aircraft (Krausman and Hervert 1983), and with tests of economic models of prey fleeing from predators (Burger and Gochfeld 1981, 1990;

Cooper 1997, 1998; see Bulova 1994 for an exception). Angle of approach affected un-bedding probability in both a horizontal and vertical plane, as indexed by minimum distance from trajectory and relative elevation, respectively. There was no significant statistical interaction between these two variables, however, indicating that within the range of distances and elevations analyzed the vertical and horizontal components of angle of approach affected un-bedding probability independently. Relative elevations below -60 m were not considered by the model of un-bedding probability because of limited sample sizes at that part of the distribution. Observations of very low relative elevation are difficult to obtain at my study area because the complex topography would jeopardize pilot safety; future work at a site with safer flying conditions should test the hypothesis that the effect of relative elevation is an inverse U-shape function, with animals not interrupting resting bouts at very high and very low relative elevations. (Preliminary analyses which were marginally not significant suggested that was the case.) For fleeing probability, I detected an effect of angle of approach only in a 2-dimensional plane, possibly because sample sizes of very high relative elevations were inadequate (they were smaller than for the un-bedding probability model).

The prediction that the time that disturbed sheep did not feed or bed would increase as approach directness becomes greater was supported for active sheep, and results agreed with observations of mountain goats (*Oreamnos americanus*) disturbed by helicopters (Côté 1996). It is also consistent with studies testing the hypothesis that prey respond more strongly to predators approaching more directly (Burger and Gochfeld 1981, 1990; Cooper 1997, 1998.) (The prediction was not supported for bedded sheep, but sample sizes were low.)

As in the case of fleeing probability, only the horizontal component of angle of approach had an effect, possibly because of the limited distribution of relative elevations.

Contrary to my prediction, I found no effect of distance to rocky slopes on any response variable. These results contrast sharply with my observations of helicopter disturbance of the same sheep population during 1997, when I found that the effect of minimum distance from trajectory on fleeing probability depended on the sheep's distance to rocky slopes. Fleeing probability decreased as minimum distance from trajectory increased, but did so at a higher rate for sheep that were on or near rocky slopes than for sheep farther from rocky slopes (Frid 1999a). While the lack of effect of rocky slopes in relation to fixed-wing overflights could reflect inherent differences between aircraft types, that possibility cannot be evaluated by my study because distance to rocky slopes was significantly smaller (Mann-Whitney U test statistic = 1394.5, $P < 0.001$) for the focal individuals observed in this study (median = 1 m, 25% quartile = 0 m, 75% quartile = 10 m, $N = 81$ focal animals) than for the focal groups observed during the helicopter disturbance study (median = 20 m, 25% quartile = 0 m, 75% quartile = 93 m, $N = 56$ focal groups).

My prediction that bedded sheep which interrupted resting bouts during overflights would spend less time bedded after overflights was supported; only 1 of 7 sheep re-bedded for the post-overflight period, and only 2 additional sheep re-bedded for >1% of this period. Disruptions of bedding activity could affect rumination and energy assimilation (review in Maier 1996), and thus are a conservation concern. Results were consistent with my observation that when sheep were disturbed by helicopters, on average, 6-10 min after overflights the

mean proportion of bedded sheep in a group was half of the pre-disturbance proportion and, though not significantly, 11-20 min after overflights the mean proportion of bedded sheep was two thirds of the pre-disturbance proportion (Frid 1999b). They are consistent also with studies testing the hypothesis that prey remain alert after a predator encounter because of the possibility of further attack (review in Lima and Dill 1990).

My prediction that sheep would feed less efficiently and move more after overflights than prior to them was not supported for active sheep. After overflights, some individuals bedded while others fed for a proportion of time that was similar to that of the pre-overflight period and to that of sheep that did not flee. These results suggest that each disturbance event caused a low energetic cost to active sheep. (It is interesting that several active sheep that fled bedded after disturbance; I observed a similar pattern during the helicopter disturbance study [Frid 1999b]).

I did not find evidence of habituation; when minimum distance from trajectory was <0.6 km, $\geq 46\%$ of active sheep fled during each week of cumulative observation, with the highest proportion (62%) occurring during the last 2 weeks of the study. While data did not support the hypothesis that animals should habituate to non-lethal human disturbance, thus avoiding unnecessary investments in antipredator behaviour (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 did not habituate substantially to overflights (Bleich et al. 1994). Thus, the potential effect of aircraft disturbance on sheep conservation remains a concern.

Conservation implications

While behavioural responses tended to be short-term, rigorously designed experiments (see Underwood 1994) and/or energetic models (see Bradshaw 1994; Luick et al. 1996; White 1999) have yet to determine whether a high-rate of fixed wing overflights can affect the reproductive success and population dynamics of mountain sheep. An energetic model was beyond the scope of this paper, yet my results provide some parameters (e.g. steps taken and time lost from foraging and rumination) needed for that model.

Once the disturbance rates which affect fitness are estimated theoretically, models of fleeing and un-bedding probability as a function of minimum trajectory distance and relative elevation could be used to generate restrictions on aircraft trajectories and maintain disturbance within acceptable levels. I suggest that these restrictions be based on un-bedding rather than fleeing probability. While active animals tended to resume foraging shortly after the plane left the area, most sheep that un-bedded during overflights did not re-bed afterwards. This was the case also during my study of helicopter disturbance (Frid 1999a). Furthermore, sheep that un-bedded tended to take almost 3 times longer than active sheep that fled to begin to feed or to re-bed. The potential consequences of disturbance could be more substantial in terms of lost rumination time rather than in terms of lost foraging time and locomotion costs (see Maier 1996). As illustrated by Fig. 2, the model of un-bedding probability also allows restrictions on minimum trajectory distance to be relaxed when the plane is flying high above sheep.

The logistic regression models I present here should be used with caution. They explain only 20-38% of the variability in responses, and confidence limits (Tables 1, 2) should be heeded. Also, models are

restricted to sheep under the conditions that I observed them in: during the weather and plant phenology of the particular field season, near rocky slopes, etc. Spatial and temporal replication are needed to increase the generality of my models.

I must emphasize also that my data do not quantify responses in relation to overflights in which the plane circled over sheep. These types of trajectories are much more disturbing to sheep (Frid unpublished data) and should be addressed by future work.

My findings were consistent with other work suggesting that fixed-wing aircraft was less disturbing to sheep than helicopters (Bleich et al. 1994). For example, when minimum distance from trajectory was <0.6 km, 100% of sheep (N = 25) fled during helicopter overflights, regardless of whether sheep were on rocky slopes (thus less likely to flee) (Frid 1999a). In contrast, during fixed-wing overflights in which minimum distance from trajectory was <0.6 km, only 53% of 34 active sheep fled and only 58% of 19 bedded sheep un-bedded. Thus, I suggest that wildlife managers should encourage commercial operations (mining, tourism, etc) occurring in roadless sheep ranges to use fixed-wing aircraft rather than helicopters whenever landing requirements allow.

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