Dall's sheep responses to overflights by helicopter and fixed-wing aircraft

Alejandro Frid

PO Box 10357, Whitehorse, YT, Canada Y1A 7A1

Abstract

High rates of behavioural disruption caused by human activities could jeopardize the body condition and reproductive success of wildlife. I exposed Dall's sheep (*Ovis dalli dalli*) of the Yukon Territory to experimental overflights by a fixed-wing aircraft and a helicopter. Aircraft approaches that were more direct (as determined by the aircraft's elevation and horizontal distance from sheep) were more likely to elicit fleeing or to disrupt resting. Latency to resume feeding or resting after fixed-wing overflights was longer during more direct approaches. During indirect approaches by helicopters, sheep far from rocky slopes were much more likely to flee than sheep on rocky slopes. Sheep did not flee while nearby helicopters flew along the opposite side of a ridge, presumably because the obstructive cover buffered disturbing stimuli. Results provide preliminary parameters for predicting energetic and fitness costs incurred as a function of overflight rates, and can help mitigate disturbance by guiding temporal and spatial restrictions to aircraft.
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1. Introduction

Ungulates may incur energetic costs when disturbed by aircraft overflights or other human activities. These costs may results from overt behavioural responses, including fleeing, habitat shifts, increased movement, and lower foraging and resting rates (e.g. Stockwell et al., 1991; Bleich et al., 1994; Côté, 1996; Bradshaw et al., 1997, 1998; Maier et al., 1998). More subtle responses, such as increased heart and metabolic rates (MacArthur et al., 1982) and disruptions of rumination (Maier, 1996), also may have energetic consequences.

While ungulates may suffer no substantial fitness costs when disturbance rates are low to moderate, some empirical studies suggest that high disturbance rates could reduce reproductive success and potentially impact populations (Joslin, 1986; Yarmoloy et al., 1988; Harrington and Veitch, 1992; Maier, 1996; Phillips and Aldredge, 2000). These empirical data, though often limited by sample sizes or by being correlational, are consistent with theoretical models predicting energy

costs affecting body condition and lower reproductive success of large mammals under high disturbance rates (Luick et al., 1996; Bradshaw et al., 1998; White et al., 1999). 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).

Aircraft disturbance of Dall's sheep and other wildlife is a growing concern in the Yukon Territory, Canada, for two reasons. First, the economy is largely dependent on mining, and most mineral exploration occurs in mountainous, roadless areas that require aircraft access (e.g. Frid, 1995). Such areas often contain the year-round ranges of Dall's sheep and mountain goats (*Oreamnos americanus*), or the summer and rutting ranges of caribou (*Rangifer tarandus*). Second, an aircraft-based tourism industry (sightseeing and access to remote areas for hiking or river trips) is rapidly growing and largely unregulated. Economic pressures to expand mining and tourism likely will lead to higher levels of disturbance in the near future. Similar concerns about aircraft disturbance are common outside the Yukon (e.g. Krausman and Hervert, 1983; Stockwell et al., 1991; Harrington and Veitch, 1992; Bleich et al., 1994),

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E-mail address: ilexp@yknet.yk.ca (A. Frid).

and extend to a diverse array of vertebrate taxa, including marine mammals (Born et al., 1999), raptors (Delaney et al., 1999), and waterfowl (Ward et al., 1999). Aircraft overflights often relate to economic activities and cannot be banned from all areas used by wildlife. Thus, mitigation measures often will depend on defining setback distances and elevations that represent acceptably low impacts.

In this paper I quantify behavioural responses by Dall's sheep exposed to experimental overflights by helicopter and fixed wing aircraft. To my knowledge, prior studies of aircraft disturbance have not focused on Dall's sheep nor considered several variables analysed here. Thus, while my data do not directly consider the reproductive costs of disturbance, they are an important step towards future work predicting which disturbance rates could impact population dynamics (see Gill et al., 1996, 2001; Luick et al., 1996; Bradshaw et al., 1998; Gill et al., 2000). Based on preliminary observations (Frid, 1995) and the literature, I asked the following questions:

1. Are behavioural responses affected by the directness of the aircraft's approach (as quantified by the aircraft's nearest distance and elevation relative to sheep)?
2. When topographic features block the line of sight between aircraft and sheep, can aircraft approach more closely without causing a disturbance?
3. Do reproductive status and other variables related to the pre-disturbance condition of sheep (e.g. group size, distance to rocky slopes) affect responses? If yes, do these variables act independently (additively), or do they interact (multiplicatively) with the directness of the aircraft's approach (see Frid, 1997)?
4. Do sheep become more tolerant of direct approaches by aircraft as cumulative weeks of overflights increase?

2. Study area

Fieldwork was done in the southwest Yukon Territory, Canada. Data on helicopter disturbance were collected between mid-June and early August 1997, primarily at Hoge Pass (ca. 61 °19′ N, 139° 33′ W), Kluane National Park Reserve (KNPR) (79% of fleeing responses); additional observations were made at Nines Creek (ca. 61° 11′ N, 138° 50′ W) and Vulcan Creek (ca. 60° 55′N, 138° 29′ W; 6 and 1 observations, respectively). All data on fixed-wing overflights were collected at Hoge Pass 22 June–15 July 1999. All fieldwork occurred after the season of births. Hoge Pass had large alpine meadows at the base of rocky terrain, but the

other sites were rockier. All areas contained > 200 sheep, were roadless, rugged, and harbored large carnivores, including grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*). Hunting, though legal for First Nations, is nil.

The main site was chosen because its observation conditions and abundant sheep allowed experimental manipulation of disturbance responses, and because it had little traffic by low-flying aircraft that was unrelated to the study. The latter occurs mainly between May and September, and averages about 25 flights per season for each aircraft type.

3. Methods

Experimental disturbance was approved by the agencies who commissioned and funded the study: the Fish and Wildlife Branch of the Yukon's Territorial Government, and Kluane National Park Reserve.

I defined overflights as the time the aircraft was within 4 km of sheep while approaching and exiting the area, as sheep often became vigilant towards aircraft at that distance. The aircraft was stationed outside the study area and was called in via satellite phone or radio to overfly sheep following an explicit trajectory. Exceptions were helicopter overflights at Nines Creek and Vulcan Creek (a small proportion of data), where opportunistic observations were made on overflights related to industrial activities.

Analyses of helicopter disturbance are based on 25 overflights by a single helicopter (Bell 206B). There often were multiple helicopter overflights per day, but analyses consider only the first overflight of the day. Analyses of fixed-wing disturbance are based on 32 overflights by a single fixed-wing aircraft (Cessna-206). Depending on weather, there were 0–3 fixed-wing overflights per day, with ⩾8 h between overflights ('night' observations were possible in the nearly 24 h of summer daylight). If sheep were disturbed by one of the few overflights unrelated to my study, experimental overflights were cancelled for ⩾8 h. Several observers worked simultaneously, observing up to four sheep groups per overflight (1 per observer). Thus, sample sizes for most analyses exceed the number of overflights. 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 nor changes in elevation within 3 km of the focal animal (see Cooper, 1998). Exceptions were when aircraft circled in view of resting sheep which remained lying, or when aircraft circled after the sheep's initial response. In the latter case, only probabilities of rest interruption or of fleeing were analysed.

2. Avoidance of topographic features that could block line of sight within 2 km of sheep. This restriction applies only to fixed-wing overflights, as flight initiation distance in relation to obstructive cover is analysed for helicopter overflights.

3. Consistent aircraft speed (see Ydenberg and Dill, 1986). Mean ± SD ground speed and air speed, respectively, were 197 ± 16 km/h for the fixed-wing trials, and 165 ± 31 km/h for helicopter trials (ground speeds were unavailable for the latter).

3.1. Recording behaviour and related variables during helicopter trials

My assistants and I observed sheep from the ground, from distances of >1 km, using spotting scopes and/or binoculars. We simultaneously observed 1–4 focal groups (1/observer), and audio recorded continuous sampling of their behaviour (Martin and Bateson, 1993). Records started several minutes prior to overflights and continued until reactions ended. 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 behaviour of the first animal(s) to respond in the group (most responses involved >50% of the group).

For 14 focal groups, instantaneous scan-sampling (Martin and Bateson, 1993) was used to record the activity of sheep for 60 min before and 20 min after overflights. The inter-scan periods were 15 min for 60–16 min prior to overflights, 3 min for 15–5 min prior, 1–2 min (2 min for larger groups) for the 5 min before and after overflights, and 3 min for 11–20 min after. During overflights, responses were too fast for scan sampling, and instead we recorded the maximum and minimum proportions of sheep that were simultaneously involved, respectively, in antipredator-type behaviours (vigilance, walking, running) and maintenance behaviours (feeding and resting). Infants likely recognise potential threats less readily than older sheep and were excluded from observations.

3.2. Recording behaviour and related variables during fixed-wing trials

Two assistants and I observed focal individuals from the ground, from distances of >1 km and using spotting scopes. Unless <3 groups were observable, we made three observations per overflight (1/observer), but only 1 focal individual per group was observed. Data were collected for only adult females, which were ≥2 years old and identified from horn characteristics and relative body size (Geist, 1971). Continuous behavioural records of focal individuals were recorded using tape or computer event recorders. Observations began ≥10 min prior to overflights and continued for ≥10 min after unless sheep went out of view behind topography. For comparisons of activity before and after overflights, I reduced longer samples to 10 min, and excluded samples that were <9 min.

3.3. Recording aircraft trajectories and sheep locations during helicopter trials

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. 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 activated at the onset of observations. When the GPS was unavailable (11 observations), an observer picked a priori distinct points in the landscape, numbered them on a 1:50,000 topographic map, and tape recorded these numbers when the helicopter flew over the corresponding points.

Sheep locations were plotted shortly before beginning observations using compass bearings and 1:50,000 topographic maps. The helicopter's positions (each corresponding to a given second in the observation period) were transcribed onto the maps containing sheep locations. Distances (see later) were measured from maps based on the average center of the group. When distances were <100 m, however, estimates were based on torso lengths of adult sheep (ca. 1 m).

3.4. Recording aircraft trajectories and sheep locations during fixed-wing trials

The pilot recorded aircraft trajectories with a Trimble Geo Explorer II GPS system programmed to record 1 location per second. Data were corrected using a base station. Sheep locations were plotted shortly before observations using compass bearings and 1:50,000 topographic maps, and later transcribed into 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 were measured using Pathfinder Office V.2 (Trimble Navigation Limited, 1996) except distance to rocky slopes, which was estimated as for helicopter overflights.

3.5. Variable definitions

Dependent variables were:

Flee: The proportion of focal groups (helicopter data) or focal individuals (fixed-wing data) 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. A step was counted each time the sheep took a running stride or, if walking, each time a front leg touched the ground. During helicopter trials, fleeing responses usually involved all group members (see Results), but were recorded based on the behaviour of ⩾1 group member.

Distance fled: For the helicopter data it describes the maximum distance (m) moved by the average center of the group before ⩾90% of sheep resumed feeding or bedding (most group members resumed pre-disturbance activities synchronously). For fixed-wing data, the number of steps taken by focal sheep were counted as a proxy for distance fled.

Flight initiation distance: Horizontal distance (km) from the aircraft at which the focal animal (fixed wing data) or ⩾1 group member (helicopter data) began to flee.

Interrupt rest: Proportion of sheep resting prior to disturbance that, during fixed-wing overflights, stood up from their lying position to be vigilant or flee.

Latency to feed or rest: Time (seconds) between the focal animal's first overt response towards fixed-wing aircraft and when the focal animal resumed resting or feeding continuously for ⩾5 s, without interrupting either activity by walking and/or being vigilant for >1 min.

Independent variables are described below. Their ranges are reported in Table 1.

Minimum distance from trajectory: Length (km) of the horizontal line from the sheep's pre-fleeing position to its perpendicular intersection with the projected forward trajectory of the aircraft. The variable is geometrically correlated with the aircraft's angle of approach; a smaller value implies a smaller angle and more direct approach (Bulova, 1994).

Relative elevation: The aircraft's elevation minus the sheep's elevation (m). The value is negative when the aircraft is below the sheep. This variable is geometrically correlated with the vertical component of the angle of approach, with a value closer to zero implying a more direct approach. Because sheep are on slopes, zero values can occur when the helicopter is flying at a given lateral distance from sheep.

Distance to rocky slopes: The pre-overflight distance (m) between focal sheep and steep (>30°) outcrops or scree slopes.

Group size: The number of non-lambs in a group. Young of the year were excluded because their behaviour likely depends on their mother's response. A 'group' contained sheep on the same aspect of the same slope, without cliffs or other obstructive cover blocking the line of sight between individuals.

Distance to obstructive cover: 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. It ranged from 0.3 to 6 km (median = 2.5 km, $N = 56$).

3.6. Analysis

Sheep were not marked. To reduce the problem of individuals contributing more than 1 observation to the data set (Machlis et al., 1985), I considered observations to be independent only if they occurred at least 8 h apart, or if they involved sheep from different groups that could be temporally distinguished from their position in the landscape. While some sheep may have been sampled more than once, I believe that pseudoreplication was low because there were >200 sheep using each area, and groups remained in one location for only a few days or less, often merging or dividing as they moved.

Analyses used SYSTAT 8.0 (SPSS 1998). Exceptions were diagnostics and confidence limits for logistic regression coefficients, which I obtained with LOGIT 2.0 (Steinberg and Colla, 1991) and JMP (SAS Institute Inc., 1996), respectively.

I analysed the probabilities of fleeing and interrupting rest 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 reduced these models to their most significant form with backwards stepping procedures. 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, for fixed-wing data the probability of interrupting rest was analysed after eliminating the inverse U-shape effect by

Table 1
Summary data for independent variables in relation to reproductive class and overflight type. Data are medians with ranges in parentheses

Reproductive class	Overflight type	Minimum distance from trajectory (km)	Relative elevation (m)	Distance to rocky slopes (m)	Group size
Adult male ($N = 18$ focal groups)	Helicopter	0.6 (0.1–1.5)	−45 (−210 to 365)	23 (0–200)	6.5 (1–30)
Female–young ($N = 38$ focal groups)	Helicopter	0.6 (0–2.4)	8 (−275 to 275)	20 (0–1200)	19 (2–64)
Mother ($N = 48$ focal individuals)	Fixed wing	0.4 (0–3.6)	54 (−213 to 564)	1.5 (0–250)	9 (1–97)
Adult female without young ($N = 33$ focal individuals)	Fixed wing	0.3 (0–3.7)	61 (−183 to 518)	0 (0–750)	5 (1–59)

excluding three cases with relative elevations of < -60 m. For helicopter data, a case with an unusually low relative elevation (-460 m, the next closest value was -270 m) had extreme leverage in a preliminary model, and data were reanalysed after deleting it. 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 model of interrupt rest probability, a case with an unusually large distance to rocky slopes had extreme leverage during a preliminary model, and data were reanalysed after deleting it. Function plots were generated with the equation:

$$P(Y) = 1 - \left[\frac{(\exp(\alpha + \beta_1 X_1 + \beta_i X_i))}{1 + \exp(\alpha + \beta_1 X_1 + \beta_i X_i)))} \right]$$

Where $P(Y)$ is either the probability of fleeing or interrupting rest, 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).

Distance fled, flight initiation distance, and latency to feed or rest were analysed with multiple linear regression. Models were reduced to their most significant form with backwards stepping procedures (Wilkinson et al., 1996; Kleinbaum et al., 1998).

Activity during multiple stages before and after helicopter overflights was compared with multivariate repeated measures analyses of variance. Post hoc multiple comparisons were tested with orthogonal contrasts (von Ende, 1993; Wilkinson et al., 1996). Standard transformations and diagnostic tests (plots of residuals and leverage) were used (Zar, 1984; Wilkinson et al., 1996; Kleinbaum et al., 1998).

4. Results

4.1. Reproductive status

As is common for sexually dimorphic ungulates in seasonal environments (Main et al., 1996), males were spatially segregated from groups of females with young. During helicopter trials, the proportion of groups fleeing during overflights did not differ significantly between female-young groups (74%, 28 of 38) and male groups (83%, 15 of 18) (Yates corrected $\chi^2 = 0.21$, df = 1, $P = 0.65$). Lack of difference was not confounded

by determinants of fleeing probability (see below); both group types did not differ significantly in minimum distance from trajectory (Mann–Whitney U-test statistic = 420.5, $P = 0.17$) nor distance to rocky slopes (Mann–Whitney U-test statistic = 351.0, $P = 0.87$) (Table 1). Given these results, I pooled observations of both group types for subsequent analyses.

During fixed-wing overflights, the proportion of active sheep fleeing during overflights did not differ significantly between mothers with young of year (39%, 12 of 31) and adult females without young (35%, 7 of 20)($\chi^2 = 0.072$, df = 1, $P = 0.79$). The proportion of resting sheep interrupting rest also did not differ significantly ($\chi^2 = 0.62$, df = 1, $P = 0.43$) between mothers (53%, 9 of 17) and adult females without young (39%, 5 of 13). Lack of difference was not confounded by determinants of responses (see later); minimum distance from trajectory distance (Mann–Whitney U-test statistic = 693.0, $P = 0.34$) and relative elevation (Mann–Whitney U-test statistic = 849.0, $P = 0.58$) did not differ significantly between reproductive classes (Table 1). Given these results, I pooled data from both classes for subsequent analyses.

4.2. Fleeing responses during helicopter trials

Sheep groups fled during helicopter overflights in 43 of 56 observations (77%). During 13 observations (23%), no sheep in a group responded overtly except by becoming 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. Most group members fled synchronously. The initial run or walk away from the helicopter included $> 50\%$ or 100% of the group, respectively, during 62 and 48% of fleeing events. Even when some sheep delayed flight relative to other group members, all sheep eventually fled in 76% of fleeing events.

According to the reduced logistic regression model (Table 2; $rho^2 = 0.66$), the probability of fleeing depended on the multiplicative 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 from rocky slopes always fled, regardless of minimum distance from trajectory (within a 2-km range). A descriptive plot corroborated the model (Fig. 1; Table 2).

Group size was excluded from the reduced model, possibly because of limited statistical power. A univariate

Table 2
Reduced logistic regression model estimating fleeing probability during helicopter overflights

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 X 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

$N = 56$, Log likelihood $= -30.34$, $\chi^2 = 40.05$, df $= 2$, $P < 0.001$, $rho^2 = 0.66$.
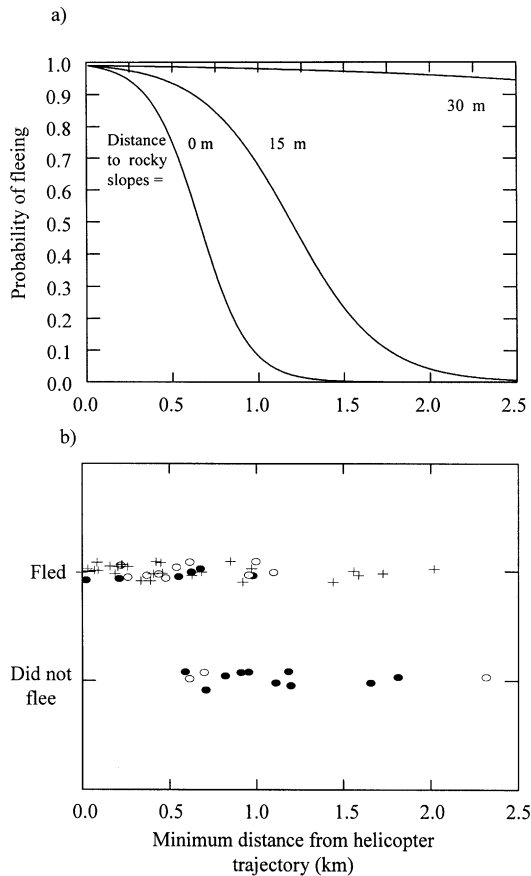
Fig. 1. (a) Estimated fleeing probabilities during helicopter overflights as a function of the interaction between minimum distance from trajectory and distance to rocky slopes; curves were generated with the reduced logistic regression model of Table 2. The latter provides values for 95% confidence limits around estimates. (b) Scatterplot corroborating estimates of Fig. 1a; dark circles = sheep on rocky slopes, open circles = sheep 5–20 m from rocky slopes (median = 20 m), crosses = sheep 25–1200 m from rocky slopes (median = 100 m). Points are jittered so that overlapping data can be read (i.e. there is no *y*-axis variability within response type).

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; $\chi^2 = 5.87$; $P = 0.016$; $rho^2 = 0.10$).

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): $t_1 = 1.055$, $P = 0.29$]. 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).

Samples sizes were inadequate for sorting the above analyses by pre-disturbance activity. The proportion of groups fleeing, however, did not differ significantly (Yates corrected $\chi^2 = 0.49$, df $= 1$, $P = 0.48$) between groups in which all sheep were resting (67%, 10 of 15) and groups in which 5–100% of sheep were active (81%, 29 of 36; four groups had missing values).

Distance fled ranged from 15 m to 1.5 km, and had a median of 100 m ($N = 43$). According to the reduced regression model, it increased as distance to rocky slopes became greater ($y = 1.66 + 0.23x$:$F_{1, 41} = 4.40$, $P = 0.04$). Sheep tended to run towards rocky slopes. The helicopter, however, often approached from the direction opposite from rocky slopes and I cannot discern whether sheep fled away from aircraft rather than towards rocky slopes. The relationship, however, was weak ($r^2 = 0.10$) because sheep that, prior to disturbance, were on or away from rocky slopes, respectively, often fled during very direct approaches or kept fleeing after reaching this terrain. Minimum distance from trajectory, relative elevation, and group size were excluded from the reduced model.

Flight initiation distance ranged from 100 m to 3 km, and had a median value of 0.9 km [$N = 42$ (1 observation had missing data)]. When overflights were very direct (minimum distance from trajectory $\leqslant 0.5$ km, and relative elevation > -100 and < 100 m), flight initiation distance increased with distance to obstructive cover (Fig. 2: $r^2 = 0.60$, $F_{1, 17} = 25.18$, $P < 0.001$), but group size and distance to rocky slopes were excluded from the reduced regression model. Low sample sizes precluded equivalent analyses for indirect overflights.

4.3. Fleeing responses during fixed-wing overflights

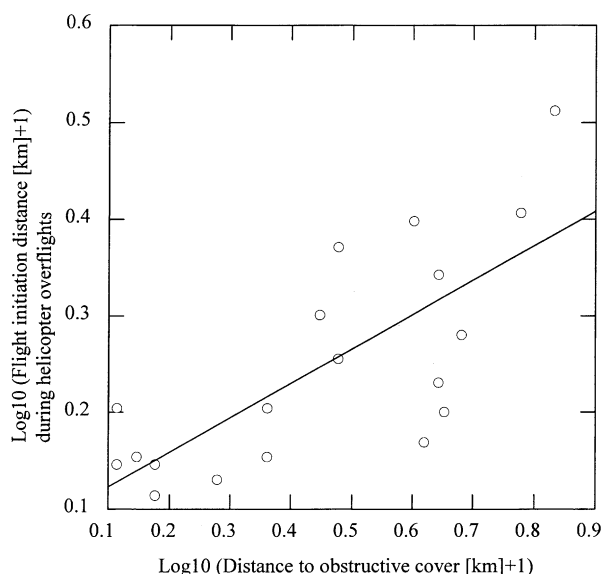When focal sheep were active prior to overflights ($N = 51$), 37% fled and 63% did not. Sheep ran during

Fig. 2. Flight initiation distance during helicopter overflights in relation to the sheep's distance to obstructive cover. Regression line for log-transformed data is generated with the equation $y = 0.13 + 0.053x$ ($r^2 = 0.60$, see text).
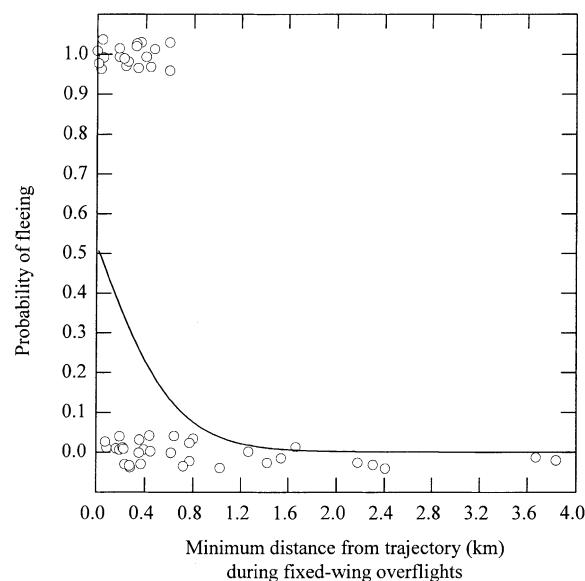

Fig. 3. Proportion of active sheep fleeing during fixed-wing overflights as a function of minimum distance from trajectory. The curve is the fleeing probability as estimated by the reduced logistic regression model of Table 3. The latter provides values for 95% confidence limits around estimates. Circles represent observed values and are jittered so that overlapping data points can be read (i.e. there is no y-axis variability within response type).

84% of fleeing events (16 of 19), including five cases in which the focal animal alternated running and walking, and walked during only three observations. According to the reduced logistic regression model ($rho^2 = 0.20$; Table 3), 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. 3). Univariate analyses during preliminary stages of model building did not detect effects of relative elevation [Wald tests for the Box–Tidwell transformation (Hosmer and Lemeshow, 1989): $t_1 = 0.32$, $P = 0.75$]. Distance from rocky slopes and group size also did not enter the preliminary multivariate model (Wald tests for univariate model, respectively, $t_1 = 0.99$, $P = 0.32$; $t_1 = -0.82$, $P = 0.42$).

When fleeing, sheep took a median of 28 steps (maximum = 173, $N = 15$; excluding three cases when sheep ran out of view behind topography and one case in which the plane circled sheep), most of which were running

strides. After the initial flight, sheep usually stood vigilant and then walked a few steps before bedding or feeding (total steps taken: median = 31, maximum = 183). Flight initiation distance for active sheep ranged from 0.2 to 4.6 km, and had a median of 1.2 km ($N = 19$). Small sample sizes precluded analyses of distance fled and flight initiation distance.

4.4. Interrupting rest: fixed-wing overflights

When focal sheep were resting prior to fixed-wing overflights ($N = 30$), 53% remained lying and 47% interrupted resting. Of the latter, 57% (8 of 14) fled 11–85 steps (median = 17), while the remaining focal individuals stood vigilant or took < 10 steps. After the initial flight, sheep tended to walk further before resuming resting or feeding (total steps taken: median = 52, maximum = 95).

According to the reduced regression model ($rho^2 = 0.38$; Table 4), the probability of interrupting

Table 3
Reduced logistic regression model estimating fleeing probability by active sheep during fixed-wing overflights

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 $= -33.68$, $\chi^2 = 13.57$, df $= 1$, $P < 0.001$, $rho^2 = 0.20$.

Table 4
Reduced logistic regression model estimating probability of resting sheep interrupting rest during fixed-wing overflights

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 $= -20.73$, $\chi^2 = 15.76$, df $= 2$, $P < 0.001$, $rho^2 = 0.38$.

rest decreased as minimum distance from trajectory and relative elevation increased (Figs. 4, 5). The model estimated that when the aircraft was 80 m above sheep (the median relative elevation) or at smaller relative elevations, the probability of interrupting rest was very high (>0.8) if the plane approached directly, and that probability remained >0.2 when minimum distances from trajectory were <1 km (Fig. 4). The probability of interrupting rest, 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 about 0.4 when the plane flew directly towards sheep, but decreased to <0.1 at minimum distances from trajectory >0.8 km (Fig. 4). Rocky slopes and group size did not enter the preliminary multivariate model (Univariate Wald tests, respectively: $t_1 = 0.88$, $P = 0.38$; $t_1 = -0.12$, $P = 0.91$).

The horizontal distance from the plane at which sheep interrupted rest (the equivalent of flight initiation distance for active sheep) ranged from 0.4 to 6.1 km, and had a median value of 1.6 km ($N = 14$). Low sample sizes precluded further analysis.
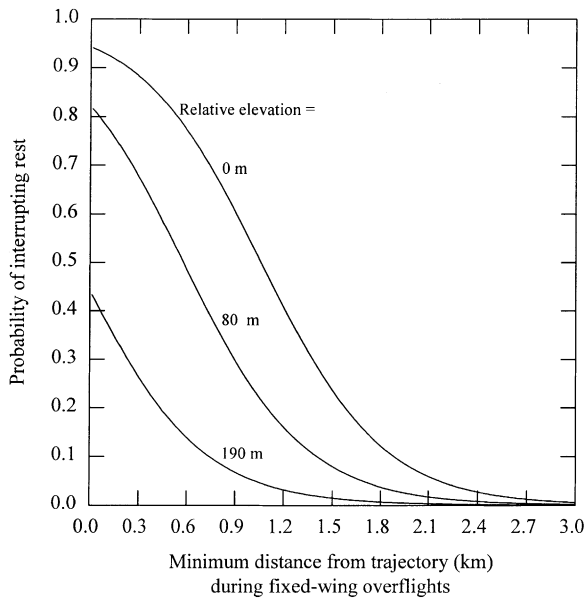

Fig. 4. Estimated probabilities of resting sheep interrupting resting during fixed-wing overflights, as a function of minimum distance from trajectory and relative elevation. Curves were generated with parameters of the reduced logistic regression model of Table 4. The latter provides values for 95% confidence limits around estimates. Each curve represents, in descending order, a relative elevation of 0 m, 80 m (the median), and 190 m (the 75% quartile).
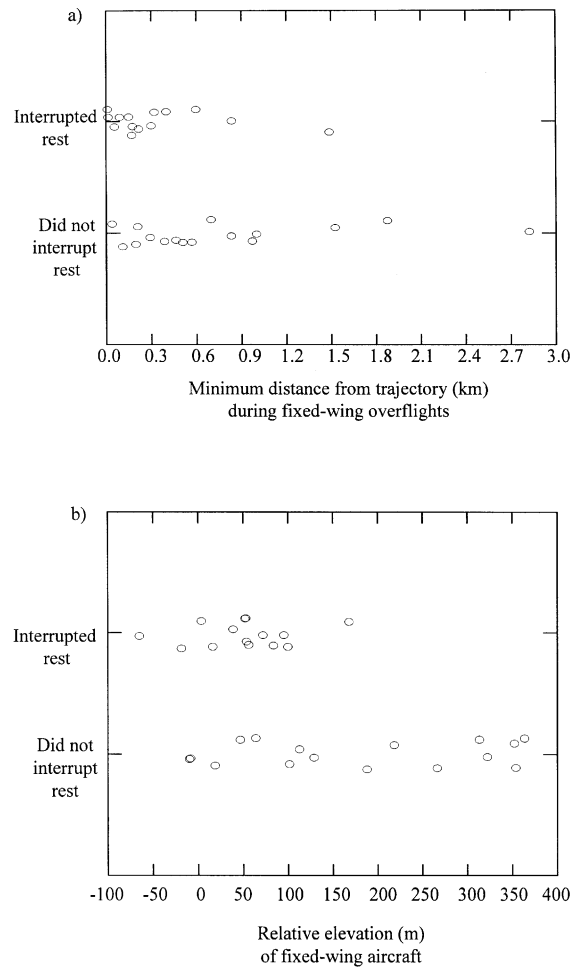
Fig. 5. Univariate scatterplots of the proportion of resting sheep interrupting rest during fixed-wing overflights in relation to (a) minimum distance from trajectory and (b) relative elevation. Points are jittered so that overlapping data can be read (i.e. there is no y-axis variability within response type).

4.5. Latency to feeding or resting: fixed-wing overflights

Active sheep that responded overtly (either stood vigilant or fled) took a median of 31 seconds to resume feeding or resting (range 2–149 s; $N = 37$; excluding three sheep that ran out of sight behind topography and two cases when the plane circled focal animals). According to the reduced regression model, latency to feeding or resting decreased as minimum distance from trajectory increased (Fig. 6: $F_{1, 35} = 10.55$, $P = 0.007$, $r^2 = 0.19$). Relative elevation, group size and distance to rocky slopes were excluded from the model.

Sheep that interrupted resting during overflights took a median of 86 seconds to begin feeding or resume resting (range = 16–370 s; $N = 14$), which was almost 3 times longer than for active sheep that responded overtly (Mann–Whitney U-statistic = 82, two-tailed $P < 0.001$). Low sample sizes precluded further analyses for resting sheep.

4.6. Activity by disturbed sheep before and after overflights

During helicopter overflights, sheep with strong fleeing responses moved out of view behind topography, precluding observations. Thus, comparisons are limited to groups that fled relatively small distances (median = 60 m, $N = 14$). Sheep that had been resting prior to overflights tended to not resume resting and switched to feeding after they stopped fleeing. In contrast, sheep that had been feeding tended to resume feeding shortly after settling down. Thus, the mean proportions of

sheep feeding and resting in a group increased and decreased, respectively, after overflights (resting: Pillai Trace statistic = 0.85, $F_{5, 9} = 10.23$; $P = 0.002$; feeding: Pillai Trace statistic = 0.76, $F_{5, 9} = 5.84$; $P = 0.01$). The proportion of sheep resting 6–10 min after overflights was about half of that prior to disturbance (Fig. 7a; Table 5). The mean proportion of vigilant sheep was three times higher 6–10 min after overflights than during the last 15 min preceding disturbance, but decreased to pre-disturbance levels 11–20 min after overflights (Fig. 7b; Pillai Trace statistic = 0.90, $F_{5, 9} = 15.98$, $P < 0.001$; Table 5). Proportions of sheep walking or running before and after overflights are not presented, as only sheep with mild fleeing responses could be sampled.

During fixed-wing overflights, for sheep that rested throughout the pre-overflight period but interrupted rest during overflights ($N = 6$), the median proportions of time spent resting, feeding, vigilant, and walking after
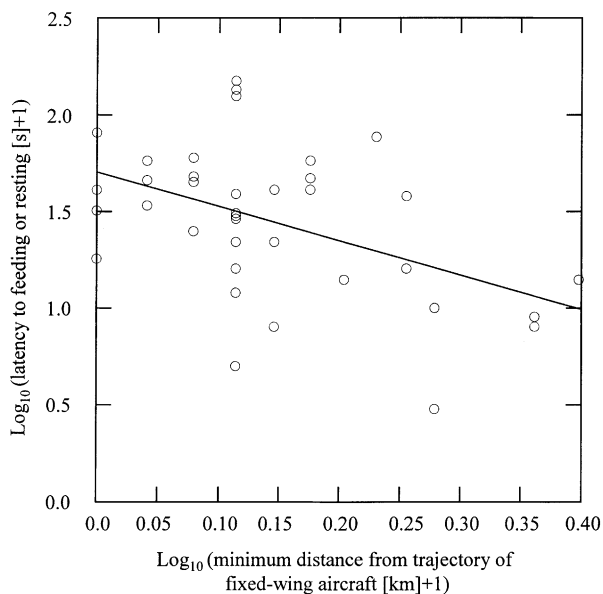

Fig. 6. Latency to feeding or resting by active sheep during fixed-wing overflights in relation to minimum distance from trajectory. Regression line for log-transformed data is generated with the equation $y = 1.69 - 1.69x$ ($r^2 = 0.19$, see text).
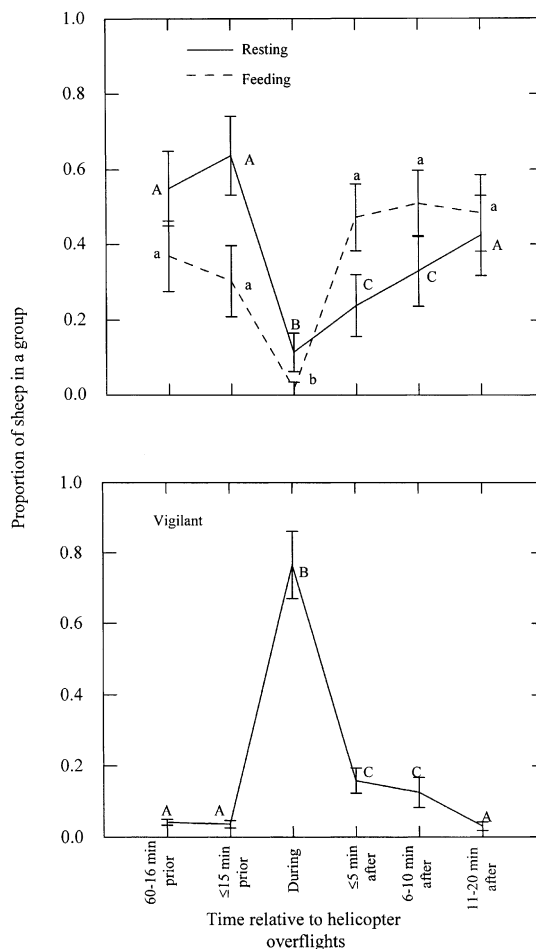

Fig. 7. Mean proportions of sheep in a group that were (a) resting, feeding, or (b) vigilant as affected by time relative to helicopter overflights ($N = 14$ groups). Time periods with different letters (uppercase for resting, lower case for feeding in Fig. 7a) have significantly different proportions of sheep engaged in the given behaviour (Table 5). Error bars represent standard errors of the mean. While figure shows untransformed data, analysis used arcsine square-root transformations.

Table 5
Orthogonal contrasts between proportion of sheep in a group engaged in different activities relative to the timing of helicopter overflights

Behaviour	Orthogonal contrast for time (min) relative to overflights						$F_{1, 13}$	P
	Before		During	After				
	60–16	$\geqslant 5$		$\leqslant 5$	6–10	11–20		
Rest	1	1	0	0	0	−2	2.91	0.1
	0	1	0	0	−1	0	8.63	0.01*
	0	0	0	−1	1	0	7.81	0.02
	0	0	−1	1	0	0	12.55	0.004*
Feed	−3	−3	0	2	2	2	3.98	0.07
	1	1	−5	1	1	1	36.80	<0.001*
Vigilant	−1	−1	0	0	0	2	1.22	<0.3
	0	−2	0	1	1	0	8.0	0.01*
	0	0	2	−1	−1	0	36.29	<0.001*

These are multiple comparisons following multivariate analyses of variance for repeated measures. Probabilities marked with an asterisk are significantly lower than the Bonferroni-corrected probability of 0.05 divided by the number of contrasts tested).

overflights were, respectively, 24, 57, 6, 10%. Thus, as in the case of helicopter trials, there was a tendency to not resume resting immediately after overflights. After fleeing, sheep which had been foraging during $\geqslant 50\%$ of the pre-overflight period ($N = 8$) either lay down for 69–100% of the post-overflight period (three sheep) or resumed feeding (five sheep). For the latter sheep, there was no significant difference in the median proportion of time spent foraging before (77%) and after overflights (80%) (two-tailed Wilcoxon signed rank test: $Z = 1.21$, $P = 0.23$).

4.7. Fleeing responses in relation to cumulative weeks of overflights

For helicopter trials, analysis is limited to Hoge Pass, the only site where data covered several weeks. There was a 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 groups fleeing was lowest during Week 1 (56%, 9 of 16), but there was no difference between the second (94%, 16 of 17) and third weeks (94%, 15 of 16) (Yates corrected $\chi^2 = 7.18$, df = 2, $P = 0.03$). Minimum distance from trajectory and distance to rocky slopes did not confound results, as they did not differ significantly between weeks (ANOVA for minimum distance from trajectory: $F_{2, 46} = 1.22$, $P = 0.30$; for distance to rocky slopes: $F_{2,46} = 0.18$, $P = 0.84$).

For fixed-wing trials, analysis is limited to minimum distances from trajectory that were $\leqslant 0.5$ km (weekly median = 0.3 km; weeks 3 and 4 were pooled). There was no significant difference ($\chi^2 = 0.65$, df = 2, $P = 0.72$) in the proportion of active sheep fleeing during the first week (50%, 4 of 8), second week (46.2%, 6 of 13) and weeks 3–4 (44.4%, 8 of 13).

5. Discussion

Fleeing probability in response to both aircraft types was inversely related to the aircrafts' angle of approach. These results are consistent with responses to aircraft overflights by mountain sheep (Krausman and Hervert, 1983), mountain goats (Côté, 1996), raptors (Delaney et al., 1999), waterfowl (Ward et al., 1999), and ringed seals (*Phoca hispida*: Born et al., 1999).

Sheep farther from rocky slopes were more sensitive to helicopter overflights. As minimum distance from trajectory became smaller, 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 $\geqslant 10$ m—because rocky slopes did not create a boundary limiting how far sheep fled. Paralleling my observations, mountain sheep are more likely to flee from coyotes when away from rocky slopes (Bleich, 1999), which are a refuge from coyotes and other cursorial predators such as wolves (Murie, 1944). Distance to rocky slopes—a condition affecting natural predation risk (Frid, 1997; Bleich, 1999)—apparently influenced how sheep perceive risk from the generalised stimuli of a large object approaching rapidly (see Dill, 1974; Frid and Dill, 2002).

While approach directness strongly affected fleeing probability, it did not affect distance fled during helicopter overflights. Approach directness, however, did affect the latency to resume feeding or resting by active sheep that fled during fixed-wing overflights. This result agrees with observations of mountain goats disturbed by helicopters (Côté, 1996). As in the case of fleeing probability, only the horizontal component of angle of approach had an effect.

In contrast to helicopter trials, there were no effects of rocky slopes on responses to fixed-wing aircraft. While lack of effect could reflect differences inherent to aircraft types, I cannot evaluate that possibility. Distance to rocky slopes was significantly smaller (Mann–Whitney U test statistic = 1394.5, 2-tailed $P < 0.001$) during 1999, the year of fixed-wing trials (median = 1 m, 25% quartile = 0 m, 75% quartile = 10 m, $N = 81$ focal animals) than during 1997, the year of helicopter trials (median = 20 m, 25% quartile = 0 m, 75% quartile = 93 m, $N = 56$ focal groups).

When topographic features blocked the line of sight between helicopter and sheep, the sheep's flight initiation distance was shorter when this topography was closer because sheep could not detect the aircraft until it had broken out of cover. This result reflects a constraint on early detection rather than a decision to withhold fleeing (Ydenberg and Dill, 1986), and is consistent with other disturbance studies (Steidl and Anthony, 1996).

The fixed-wing aircraft's angle of approach affected the probability that resting sheep would stand up to be vigilant and/or flee. Ungulates ruminate while resting, which is essential for energy assimilation (review in Maier, 1996). Angle of approach was significant 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 variables, indicating that the vertical and horizontal components of angle of approach acted independently. The caveat is that relative elevations below −60 m were not considered by analyses.

The main shift of activity after overflights was a tendency for sheep that had been resting to feed rather than resume resting, and for sheep that had been feeding to resume foraging relatively soon. However, animals that responded very strongly and fled out of view could not be included in analyses, and these sheep may have spent more time vigilant after disturbance. Also, analyses of activity budgets do not consider whether the quality of feeding sites may be poorer after fleeing, especially for sheep that fled from lush meadows to rocky slopes.

For both types of overflights, the proportion of sheep fleeing did not decrease with the number of cumulative weeks of disturbance. The caveat is that field studies may have been too short (3–4 weeks) for a proper test. Multi-year research on helicopter disturbance, however, concluded that bighorn sheep did not habituate (Bleich et al., 1994) and concerns for potential effects of intense, long-term disturbance on body condition and reproductive success are warranted (see Joslin, 1986; Maier, 1996; Bradshaw et al., 1998).

6. Conservation implications

Rate of direct approaches likely is the key variable that could determine whether aircraft disturbances occurring over long time scales affect reproductive success (see Harrington and Veitch, 1992, Luick et al., 1996, Bradshaw et al., 1998). My data on behavioural responses provide a useful first step and some parameters (e.g. distance fled and time lost from foraging and rumination) for predicting the rate of direct approaches that might affect fitness. Once these rates are estimated, models on the probabilities of interrupting rest and fleeing could be used to generate restrictions on aircraft trajectories that limit disturbance to acceptable levels. While angle of approach is the biologically relevant variable (Burger and Gochfeld, 1981; Cooper, 1997), minimum distances from trajectory and relative elevations are the correlated variables that pilots can control. Aircraft restrictions can take the form of either setback distances and elevations that eliminate direct approaches, or of limiting the maximum rate of direct approaches.

For fixed-wing overflights, I suggest that setback distances be based on the probability of interrupting rest rather than on fleeing probability. Rest interruption occurred at greater minimum distances from trajectory than fleeing (contrast Figs. 3 and 4). Furthermore, while limited data suggest that active animals resume foraging shortly after overflights, most sheep that interrupted rest did not resume rest within 10 min after overflights, and took longer to end vigilance or fleeing than animals that had been active prior to disturbance. Disturbance costs could be more substantial in terms of lost rumination time rather than foraging and locomotion costs (Maier, 1996; Maier et al., 1998). The model estimating probability of interrupting rest also allows restrictions on minimum distance from trajectory to be relaxed for aircraft flying high above sheep (Fig. 4). For helicopter overflights, models of fleeing probability could account for seasonal and/or diurnal variability in the sheep's distance to rocky slopes (Fig. 1a). Such variability may be predictable (see Fox et al., 1992), and pilot guidelines could be adjusted accordingly. The effects of obstructive cover on flight initiation distance suggests that a simple way to avoid disturbance is to design flying pathways which use ridges to block the line of sight between aircraft and areas of high sheep density. A caveat is that my logistic regression models may be specific to my study conditions, and confidence limits around parameter estimates (Tables 2–4) should be heeded. Also, the effects of relative elevation need to be assessed beyond the limited range that I examined. Future work should consider situations in which overflights circle over sheep, which are much more disturbing than single passes (Frid, unpublished data).

Results were consistent with prior work suggesting that fixed-wing aircraft are less disturbing than helicopters (Bleich et al., 1994, Born et al., 1999, Ward et al., 1999). When minimum distance from trajectory was ≤0.5 km, all 25 groups of sheep fled during helicopter overflights, but only 53–58% of 53 focal sheep fled or interrupted rest during fixed-wing overflights. Conservation agencies should encourage commercial operations (e.g. mining and tourism) in roadless sheep ranges to use fixed-wing aircraft rather than helicopters when landing requirements allow.

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