SHORT-TERM EFFECTS OF HELICOPTER OVERFLIGHTS ON ACTIVITY BUDGETS OF DALL'S SHEEP

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ABSTRACT

I assessed how helicopter disturbance disrupts activity budgets of Dall's sheep (*Ovis dalli dalli*) after overflights end. Overflights lasted <5 min, and were defined as the time the helicopter was in direct line of sight and within 4 km of sheep. Relative to the 15-min period preceding overflights, the mean proportion of bedded sheep was 48 % lower 6-10 min after overflights and, though not significantly, a third lower 11-20 min after overflights. Most sheep became vigilant during overflights, and 6-10 min afterwards the mean proportion of vigilant sheep was three times higher than prior to disturbance. Activity disruptions were short-term. Proportions of vigilant sheep returned to pre-disturbance levels 11-20 min after overflights, and 21-45 min after overflights the proportion of bedded animals was not significantly different from pre-disturbance levels. Furthermore, the mean proportion of sheep bedded during early afternoon did not differ between undisturbed groups and groups that were disturbed earlier that morning. Data represented sheep that moved in response to disturbance for a median distance of only 60 m. Thus, results indicate that even if the energetic costs of locomotion caused by disturbance are small or negligible, helicopter overflights can still disrupt energy assimilating activities. As determined by other studies, disruptions of bedding affect rumination, and increased vigilance reduces foraging efficiency. Short-term disruptions of activity budgets may not affect sheep productivity if disturbance rates are low, but potentially could lead to reduced reproductive success when disturbance rates are high, particularly in years of poor range quality.

INTRODUCTION

Several studies suggest that high rates of aircraft overflights and other forms of motorised disturbance potentially can affect the productivity of ungulates (Joslin 1986; Yarmoloy et al. 1988; Harrington & Veitch 1992; Bradshaw 1994; Maier 1996; but see Krausman et al. 1998 for an exception). Ungulate populations, however, can have large temporal variability in response to food supply and/or predation (Caughley & Gunn 1993; Ross et al. 1997). Empirical evidence linking disturbance with the reproductive success of individuals is hard to obtain and is quite limited (Yarmoloy et al. 1988; Harrington & Veitch 1992). Some studies found relationships between increasing rates of aircraft disturbance and population declines, but data were correlational and consisted of unreplicated time series (e. g. Joslin 1986; Maier 1996). As pointed out by Maier (1996), these data do not provide unequivocal evidence of cause and effect relationships.

In this study I focused on how disturbance disrupts activity budgets. There is recent evidence suggesting that activity disruptions (and increased heart rates) are not a conservation concern for bighorn sheep (*Ovis canadensis*) disturbed by low-flying military jets (Krausman et al. 1998). Studies of low-flying jet disturbance of caribou (*Rangifer tarandus*: Maier 1996; Maier et al. 1998), and of helicopter disturbance of mountain Caprinae (Stockwell et al. 1991; Bleich et al. 1994; Côté 1996), however, suggest that activity disruptions are one mechanism that potentially could reduce reproductive success when disturbance rates are high. This may be of particular concern during years of poor range quality (White 1983; Maier 1996; Maier et al. 1998).

Past studies found that aircraft disturbance affects activity budgets of ungulates in at least three ways. First, animals may become more vigilant and thus forage less efficiently (Stockwell et al. 1991; Côté 1996). Second, animals may interrupt resting bouts, thus increasing the number of resting bouts per day but decreasing their duration, and consequently spending more time active (Murphy et al. 1993; Maier 1996; Maier et al. 1998). Third, they may increase distances moved (Bleich et al. 1994; Maier et al. 1998). At least for caribou disturbed by low-flying jets, the extent to which activity budgets are disrupted depends on season (Murphy et al. 1993; Maier 1996; Maier et al. 1998).

My study focused on Dall's sheep (*O. dalli dalli*) exposed to helicopter overflights in the southwest Yukon. The effects of helicopter disturbance on mountain sheep (*O.* spp.) movements and vigilance are becoming better known (Krausman & Hervert 1983; Stockwell et al. 1991; Bleich et al. 1994; Frid 1998). I am unaware, however, of other analyses of disturbance effects on the bedding behaviour (resting bouts) of sheep. Disruptions of bedding are of conservation interest because they may affect rumination, and consequently reduce the efficiency of energy assimilation (review in Maier 1996).

Specifically, I assessed how helicopter disturbance disrupts activity budgets of Dall's sheep after overflights end. I predicted that the proportion of bedded animals would be lower and the proportion of vigilant, walking and feeding animals would be higher after overflights than prior to disturbance. I also expected that sheep activity would return to pre-disturbance levels some time after overflights, and estimated the minimum time required for this response. Finally, I assessed longer-term effects by comparing between recently disturbed and undisturbed groups the mean proportion of animals that were bedded during four-hour periods. My analyses is limited to animals that walked and/or ran away in response to disturbance for a median distance of only 60 m. Thus, it is useful for assessing how helicopter overflights disrupt energy assimilating activities when the energetic costs of locomotion caused by disturbance are small or negligible.

METHODS

Study site and season

Data were collected as part of a larger project on helicopter disturbance at Hoge Pass, Kluane National Park Reserve, southwest Yukon (ca. 61 °19' N, 139° 33' W). Observations were made 27-30 June (N = 3) and 28 July-8 August (N = 11), 1997. 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 various sheep predators (including grizzly bears: *Ursus arctos*) are common. At least 200 sheep used the study area. Further details can be found in Frid (1998).

General methods for experimental disturbance

Field work was based out of a field camp. The helicopter was stationed 75 km outside the study area. Sheep were exposed to overflights by a single helicopter (Bell 206B) flying at an air speed of 165 ± 31 km/h (mean ± SD), which was called in daily for the explicit purpose of experimental disturbance. I *a priori* designed helicopter trajectories, which I communicated to the pilot via radio.

During observations, the smallest distance between sheep and helicopter ranged from 0.2 to 2.1 km (median = 0.75 km), and the helicopter's elevation ranged from 120 m above to 180 m below sheep (median = 30 m above sheep). While other analyses determined that these two variables affect escape decisions (Frid 1998), sample sizes were inadequate to analyse how helicopter distance and elevation affect the extent to which overflights disrupt activity budgets.

Before, during and after overflights, my assistants and I observed sheep from the ground, from distances of >1km and using spotting scopes and/or binoculars. We simultaneously observed 1 to 2 focal groups (1/observer), and recorded behaviour (see below) into tape recorders.

For 11 of 14 disturbance observations, the helicopter trajectory and its relation to the timing of sheep responses was recorded as follows. Synchronised with the behavioural tape records and through a radio operated by observers on the ground, the pilot read into a tape recorder his GPS location (coded by a 3 digit number), speed, and elevation several times per minute (usually 2-3). An observer on the ground supplemented these data by mapping the helicopter trajectory on a 1:50,000 map. For the remaining three observations, an observer picked *a priori* distinct points in the landscape, and numbered them on the 1:50,000 map. When the helicopter flew over these points, he spoke the number identifying them into a tape recorder. For both recording methods, points on the helicopter trajectory that were not recorded in the field but that were required for analyses were later estimated using the helicopter's speed.

Defining overflights and related experimental stages

I defined overflights as the time the helicopter was within 4 km of the sheep while approaching and exiting the area. This 4-km threshold is based on data indicating that sheep may walk and/or run away when helicopters are as far as 3 km away (Frid 1998). I added one km (which can be flown in ca. 22 seconds at the average helicopter speed) to this maximum escape initiation distance because sheep usually become vigilant towards the helicopter prior to escaping. If ridges obscuring the line of sight between sheep and helicopters were present within 4 km of the sheep, I considered overflights to not begin and/or end until the helicopter was past (while approaching) and/or behind the ridge (while exiting). The rationale was that escape initiation distance is affected by the sheep's distance to these visual obstructions (Frid 1998).

During observations the helicopter flew through the area without landing and the mean ± SD duration of overflights was 2.83 ± 0.95 min. I excluded from analyses four observations in which the helicopter landed and kept its motor going for >10 min. I divided time relative to overflights into the following experimental stages:

1) *Pre1*: 60-16 min prior to overflights.
2) *Pre2*: ≤15 min prior to overflights.
3) *During*: the time during which overflights (as defined above) occurred.

4) *Post1*: ≤5 min after overflights.
5) *Post2*: 6-10 min after overflights.
6) *Post3*: 11-20 min after overflights.
7) *Post4*: 21-45 min after overflights.

Recording behaviour in relation to overflights

For experimental stages preceding and following overflights, instantaneous scan-sampling (Martin & Bateson 1993) was used to record the proportion of sheep in a group that were bedded, feeding (standing with head down to the ground), walking (with head above shoulder height), vigilant (standing with head above shoulder height) and running. Behaviours outside these categories were classified as "other", but these were rare and not analysed.

Inter-scan durations varied between experimental stage, depending on my *a priori* expectation of the rates of behavioural change during a particular stage (see below). Also, because I never knew exactly when the helicopter was going to appear and because sheep behaviour may have been affected before the helicopter entered my semi-arbitrarily defined 4-km threshold distance, inter-scan periods were shortest just before overflights. The latter allowed observers to continuously focus on sheep at the time of their first response to helicopters.

The inter-scan periods for each experimental stage were 15 min for *Pre1* (when there is no chance of the helicopter showing up), 3 min for the first 10 min of *Pre2* and 1-2 min (2 min for larger groups) for the last 5 min of *Pre2* (when overflights may begin suddenly), 1-2 min (2 min for larger groups) for *Post1* and *Post2* (when behaviour may change rapidly), 3 min for *Post3*, and 15 min for *Post4* (when behavioural changes are slowing down). Increasing inter-scan periods in relation to experimental stage was important to avoid observer fatigue, which could lead to inaccurate data. In spite of these pre-determined inter-scan intervals, sometimes logistics (pilot communications, animals disappearing behind topography, etc) resulted in inter-scan periods being longer than planned.

Sometimes part of a group was obscured by fog or topography, and sampling a low proportion of animals may not be representative of the whole group. In 92 % of scans (414 of 449), however, I recorded behaviour for ≥75 % of group members, suggesting that data represented groups reasonably well.

During overflights, behaviour changed quickly and could not be accurately represented by scan sampling. Thus, I quantified behaviour by estimating the maximum proportion of sheep simultaneously involved in antipredator-type behaviours (vigilance, walking, running), and the minimum proportion of sheep simultaneously involved in maintenance behaviours (feeding and bedding). Even though all animals may have been disturbed, the proportion of animals involved in a given antipredator-type behaviour may have not been recorded as 100 % if, for instance, some animals were vigilant while others were running.

Animals sampled during experimental disturbance

I present data only on groups that walked and/or ran for short distances during disturbance. I cannot present data on sheep that escaped large distances because these often crossed gullies and/or went over ridges, temporarily going out of sight. Of the groups analysed, 13 had maximum escape distance of ≤ 100 m, and one escaped for 300 m (median value of maximum distance escaped = 60 m).

I pooled observations of female-young groups (N = 10) and all-male groups (N = 4) to maximise sample sizes. There are *a priori* reasons to expect differences between mothers with young and other reproductive classes (Maier et al. 1998). In pooling reproductive classes I chose to gain statistical power at the cost of potential increases in unexplained variability.

To maximise sample size, I pooled observations of groups observed in the morning (start of observation between 0800 and 0900; N = 8) and afternoon (start of observation after 1300; N = 6). There are *a priori* reasons to expect activity budgets to be affected by time of day (e. g. Maier 1996) , but I justified pooling because graphical analyses suggested that trends in the proportion of bedded animals relative to overflights was similar for both periods of the day.

Infants likely do not recognise potential threats as readily as older conspecifics (FitzGibbon & Lazarus 1995), and I omitted lambs born that year from behavioural records. During scan sampling, however, lambs can be misidentified as older sheep, and in 8 % (37 out of 449) of scans the number of sheep for which I recorded behaviour exceed the number of non-lambs in the group, indicating that some lambs were mistakenly recorded as older sheep.

The groups I analysed had a median group size (not including lambs) of 9 (range 4-47). I excluded a group of two sheep from analyses because the behaviour of a single animal had a disproportionately high influence on my proportion-based data. Groups were defined as in Frid (1997).

Independence between observations

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

Analyses of experimental disturbance

I analysed the effect of time relative to overflights on the proportion of sheep in a group engaged in a given activity with multivariate repeated measures analyses of variance (von Ende 1993; Wilkinson et al. 1996). The exception was analyses of proportion of group members walking, which grossly violated the assumption of normally distributed residuals, and was analysed with a non-parametric Friedman test (Zar 1984). I used separate analyses for each response variable (vigilance, feeding, walking, and bedding), and did not consider results significant unless test statistics gave a probability that was lower than the Bonferroni corrected $\alpha = 0.05/4$. The multivariate statistic I report is Pillai Trace because this is the most robust one to violations of the homogeneity of covariance assumptions (Wilkinson et al. 1996). Other multivariate statistics (Wilk's Lambda and Hotelling-Lawlely Trace) yielded identical results.

Multiple comparisons were tested with orthogonal contrasts on dependent variables (C matrix procedure in SYSTAT: SPSS 1996), and were not considered significant unless test statistics had a probability that was lower than the Bonferroni-corrected $\alpha = 0.05$/number of contrasts tested for the given behaviour (von Ende 1993; Wilkinson et al. 1996). I examined with orthogonal polynomials the significance of trends in activity relative to the experimental stage. As recommended by von Ende (1993), I began by examining the quadratic polynomial and proceeded to examine lower order polynomials, stopping at the first significant one.

One group had missing data for the *Post3* experimental stage. Because multivariate analysis cannot handle missing values easily, I estimated these by regressing the proportion of sheep engaged in each behaviour against the 3 post-overflight experimental stages, which were coded as ordinal dummy variables (Scheiner 1993).

Data for the *Post4* period had only 9 observations and was excluded from multivariate analyses. It was used only in a non-parametric Wilcoxon signed-rank test (Zar 1984; SPSS 1996).

Diagnostic plots of residuals were checked to confirm that data did not seriously violate assumptions of parametric tests (Wilkinson et al. 1996). Proportions were arcsine-square root transformed (Zar 1984) for parametric analyses but untransformed data are presented in figures. Analyses were performed with SYSTAT 6.0 (SPSS 1996). In all tests, sheep groups were the units of analyses.

Comparison with undisturbed sheep

For analyses of longer term effects on activity budgets, I recorded every 15 min between 1100 and 1500 instantaneous scans of the behaviour of sheep that had not been influenced by overflights for at least 15 min. I then compared proportions of bedded animals between groups that had been disturbed that morning between 0930 and 1045 (treatment groups), and sheep that were undisturbed prior to 1500 (control groups). Control groups included four female-young groups and one male group. Treatment groups included five female-young groups and two male groups. Observations were made in a period of nine days (late July-early August) to avoid confounding effects of phenology.

RESULTS

Almost all animals that were bedded or feeding prior to disturbance interrupted these activities to be vigilant and/or run and walk during overflights. All group members ran and/or walked during eight observations (57 %), but 6-49 % of group members remained bedded during six observations (43 %). Helicopter disturbance affected activity budgets for at least 6-10 min after overflights ended (Figs. 1-5).

Effects on bedding and feeding

Most sheep that were bedded prior to disturbance did not re-bed and switched to feeding after overflights (Fig. 1: Pillai Trace statistic for proportion of bedded sheep = 0.85, $F_{5,9}$ = 10.23; P = 0.0017<0.05/4). Relative to the 15-min period preceding overflights, the mean proportion of animals bedded in a group was 63 % and 48 % lower, respectively, ≤5 min and 6-10 minutes after overflights (Fig. 1), but the difference between the two post-overflight periods was marginally non-significant (Table 1). The mean proportion of bedded animals was a third lower 11-20 min after overflights than during the last 15 min prior to overflights (Fig. 1), but not significantly (Table 1). The proportion of bedded sheep did not differ significantly between the last 15 min prior to overflights and 21-45 min after (Fig. 2: Z = -0.65, P = 0.51), even though the median proportion was much lower during the latter period.

Fig. 1 illustrates how most sheep that were bedded prior to overflights switched to feeding after being disturbed. The mean proportion of feeding sheep was 1.6 to 1.7 times higher after overflights than during the last 15 min prior to disturbance (Fig. 1), but differences were significant (Table 1). (Only the decrease in feeding animals during overflights is significant: Pillai Trace statistic = 0.76, $F_{5,9}$ = 5.84, P = 0.011< 0.05/4; Table 1).

Trends in Fig. 1 are significantly described by second degree polynomials (Bedding: $F_{1,13}$= 52.16, P =<0.001; Feeding: $F_{1,13}$= 11.60, P = 0.005), but variability is apparent by the large standard errors (Fig. 1). Exploratory analyses of variability in the proportion of bedded sheep (and by extension on feeding, which is largely the reciprocal of bedding) suggested that when >80 % of sheep were bedded within 15 min prior to disturbance, in five of seven observations the proportion of bedded animals decreased substantially during at least 20 min after overflights (Fig. 3a). However, when <80 % of animals were bedded during the last five min prior to disturbance (<60 % in six of seven observations), in five of seven observation the proportion of bedded animals increased or returned to similar levels during the first 20 min after overflights (Fig. 3b). More data are needed to investigate correlations between pre- and post-overflight activity.

Effects on vigilance, walking and running

Sheep that interrupted maintenance activities were either vigilant or walking (Figs. 4, 5) and running during overflights. The mean proportion of vigilant sheep in a group 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. 4; Pillai Trace statistic = 0.90, $F_{5,9}$ = 15.98, P<0.001<0.05/4; Table 1).

Fig. 5 suggests that the median proportion of sheep walking increased substantially during overflights, was 4 times higher within 5 min after than within 60 min before overflights, and was similar to pre-disturbance levels within 6-10 min after overflights. These differences, however, were not significant (Friedman Test Statistic = 10.53; DF = 5, P = 0.06>0.05/4). The short effect of overflights on the proportion of walking sheep is not surprising, as my data represents animals that moved in response to disturbance for a median distance of only 60 m.

The maximum proportion of sheep in a group that ran simultaneously during overflights had a median value of 0.97 (N = 14, mean ± SD= 0.62 ± 0.46). Running was recorded rarely during the pre- and post-overflight stages and I did not analyse it further.

Comparison with undisturbed sheep

I found no difference (t = -0.43, DF = 10 , P= 0.67) in the mean proportion of sheep bedded during the afternoon (1100 to 1500) between undisturbed groups (mean ± SD of 15 min scans = 0.69 ± 0.12, N = 5 groups) and groups disturbed that morning (mean ± SD of 15 min scans = 0.70 ± 0.13, N = 7 groups).

DISCUSSION

Results indicate that even if the energetic costs of locomotion caused by disturbance are small or negligible, as was the case for most animals in my sample, helicopter overflights can still disrupt energy assimilating activities. Overflights lasting <5 min disrupted sheep behaviour for at least 6-10 min after the helicopter had left the area. Most notably, 6-10 min after overflights the mean proportion of bedded sheep was only half of the pre-disturbance proportion, and 11-20 min after overflights not all sheep that were bedded prior to disturbance had re-bedded. Also, 6-10 min after overflights the mean proportion of vigilant animals was three times higher than the pre-disturbance proportion. Côté (1996) observed similar effects of helicopter disturbance on the vigilance of mountain goats (*Oreamnos americanus*).

Disruptions of activity were short-term. The proportion of vigilant sheep returned to pre-disturbance levels 11-20 min after overflights, and the median proportion of bedded animals was not significantly different from pre-disturbance levels 21-45 min after overflights. Furthermore, I found no difference between the mean proportion of sheep bedded in the afternoon between undisturbed groups and groups disturbed earlier that morning.

The fact that sheep activities were most affected for only 6-10 min following overflights does not imply that helicopter overflights may have little consequence to sheep conservation. Increased vigilance reduces foraging time (Berger 1978; Stockwell et al. 1991; Frid 1997), and interruptions of rumination, which generally takes place when ungulates are bedded, decrease efficiency of energy assimilation (review in Maier 1996). While helicopter overflights likely are of little consequence when disturbance rates are low, a high rate of short interruptions of efficient foraging or digestion potentially could affect body weight and reproductive success (White 1983; Harrington & Veitch 1992; Bradshaw 1994; Maier 1996).

I must emphasise that my data represents only animals that were mildly disturbed. In 13 out of 14 observations, sheep walked and/or ran for ≤100 m in response to overflights. In the larger data set used to analyse escape decisions (Frid 1998), 35 % of groups (15 of 43) that walked and/or ran away from the first helicopter flight of the day moved for ≥200 m, and four of these groups moved 800-2200 m. Clearly, the activity budgets of these groups would be affected for longer periods of time than those of the groups I analysed. Unfortunately, when sheep move large distances they often go out of sight inside gullies or behind ridges, precluding data collection with my methods. Methods for remote recording of behaviour are required in such cases (see Maier et al. 1998).

I also emphasise that my analyses are only in relation to the first flight of the day. In their study of caribou disturbed by low-altitude jet aircraft, Maier et al. (1998) found that, during late winter but not during other seasons, the number of resting bouts increased but the mean duration of these bouts decreased as the number of repeated overflights occurring in a day became larger. Furthermore, an increase in time-averaged noise level decreased the daily amount of time caribou spent resting. The effect of repeated helicopter overflights (occurring the same day) on the activity budgets of sheep requires further investigation.

Implications for conservation

In a previous analysis of the same sheep population, I provided logistic regression models for predicting the probability that helicopter disturbance would cause sheep to escape, or walk and/or run away ≥ 10 m (Frid 1998). Even though distances escaped by sheep generally were much larger (median = 100 m), I argued that this short escape distance was a reasonable index of disturbance because it likely was associated with other costs, such as increased vigilance and other effects on heart rates and activity budgets (MacArthur et al. 1982; Berger et al. 1983; Stockwell et al. 1991; Maier et al. 1998). I suggested that my logistic regression models be used to create guidelines for setback distances between sheep and helicopters such that sheep would have a low probability of escaping.

In this study my data set was not large enough to relate helicopter variables to the extent that activity budgets are disrupted after overflights, and I cannot add more to my existing recommendations. However, this study supports my arguments for the application of my logistic regression models of escape probability (Frid 1998). Specifically, it provides evidence that helicopter disturbance affects sheep activity budgets for at least 6-10 min after helicopters leave the area, even when sheep escape for short distances. This activity budget disruption may not affect sheep productivity if disturbance rates are low, but potentially could reduce reproductive success when disturbance rates are large (Bradshaw 1994; Harrington & Veitch 1992), particularly in years when range quality is low (White 1983; Maier 1996; Maier et al. 1998).

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Table 1. Orthogonal contrasts between proportion of sheep in a group engaged in different activities during different experimental stages relative to the timing of overflights. These are multiple comparisons following multivariate analyses of variance for repeated measures. Only probabilities marked with an asterisk are significantly lower than the Bonferroni-corrected probability of 0.05 divided by the number of tests of contrasts for the given behaviour.

Behaviour	**Contrasts between time relative to overflights**						**$F_{1,13}$**	**P**
	Pre1	***Pre2***	***During***	***Post1***	***Post2***	***Post3***		
Bed	1	1	0	0	0	-2	2.91	0.11
	0	1	0	0	-1	0	8.63	0.012*
	0	0	0	-1	1	0	7.81	0.015
	0	0	-1	1	0	0	12.55	0.0036*
Feed	-3	-3	0	2	2	2	3.98	0.067
	1	1	-5	1	1	1	36.80	<0.001*
Vigilant	-1	-1	0	0	0	2	1.22	<0.29
	0	-2	0	1	1	0	8.0	0.014*
	0	0	2	-1	-1	0	36.29	<0.001*

FIGURE CAPTIONS

Fig. 1. Mean proportions of sheep in a group that were bedded or feeding as affected by time relative to overflights (N = 14 groups). Time periods with different letters (uppercase for bedded, lower case for feeding) have significantly different proportions of sheep engaged in the given behaviour (Table 1). Error bars represent standard errors of the mean.

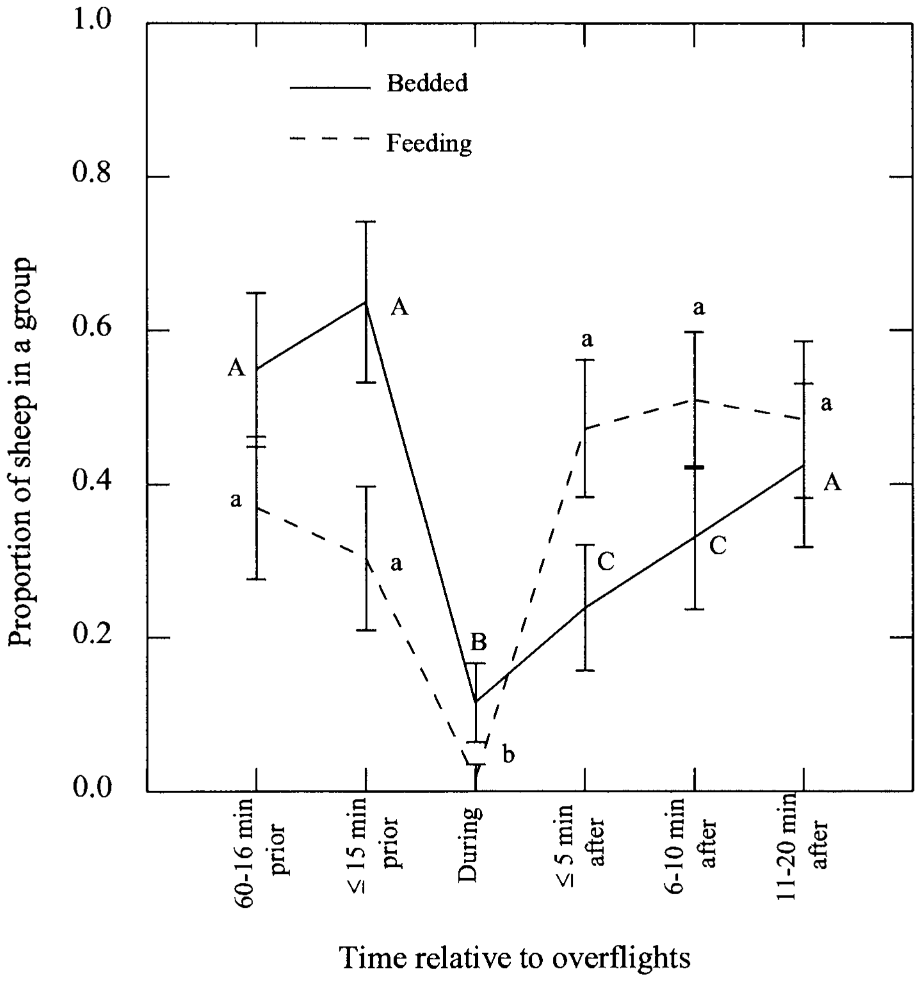
Fig. 2. Box plots of the proportion of bedded sheep in a group ≤15 prior and 21-45 min after overflights. Boxes encompass 25 % and 75 % quartiles, the central line within the box represents the median, and the whiskers encompass 90 % of the values (see Wilkinson et al. 1996).

Fig. 3. Proportion of bedded sheep as affected by time relative to overflights (experimental stages defined in Methods) for (a) groups in which the proportion of bedded animals was >0.8 within 15 min prior to disturbance (the Pre2 stage), and (b) groups in which the proportion of bedded animals was <0.8 within 15 min prior to disturbance. Each panel represents a different group. These are the same data summarised in Fig. 1.

Fig. 4. Mean proportion of vigilant sheep in a group as affected by time relative to overflights (N = 14 groups). Time periods with different letters have significantly different proportions of vigilant sheep (Table 1). Error bars represent standard errors of the mean.

Fig. 5. Box plots of the proportion of walking animals in a group as affected by time relative to overflights (N = 14 groups). Boxes encompass 25 % and 75 % quartiles, the central line within the box represents the median, and the whiskers encompass 90 % of the values. Values outside and far outside the whiskers are represented, respectively, by asterisks and circles (see Wilkinson et al. 1996).

Fig. 1



Bedded
Feeding
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of sheep in a group
A
A
a
a
B
b
a
C
a
C
a
A
60-16 min prior
≤ 15 min prior
During
≤ 5 min after
6-10 min after
11-20 min after
Time relative to overflights

Fig. 3b

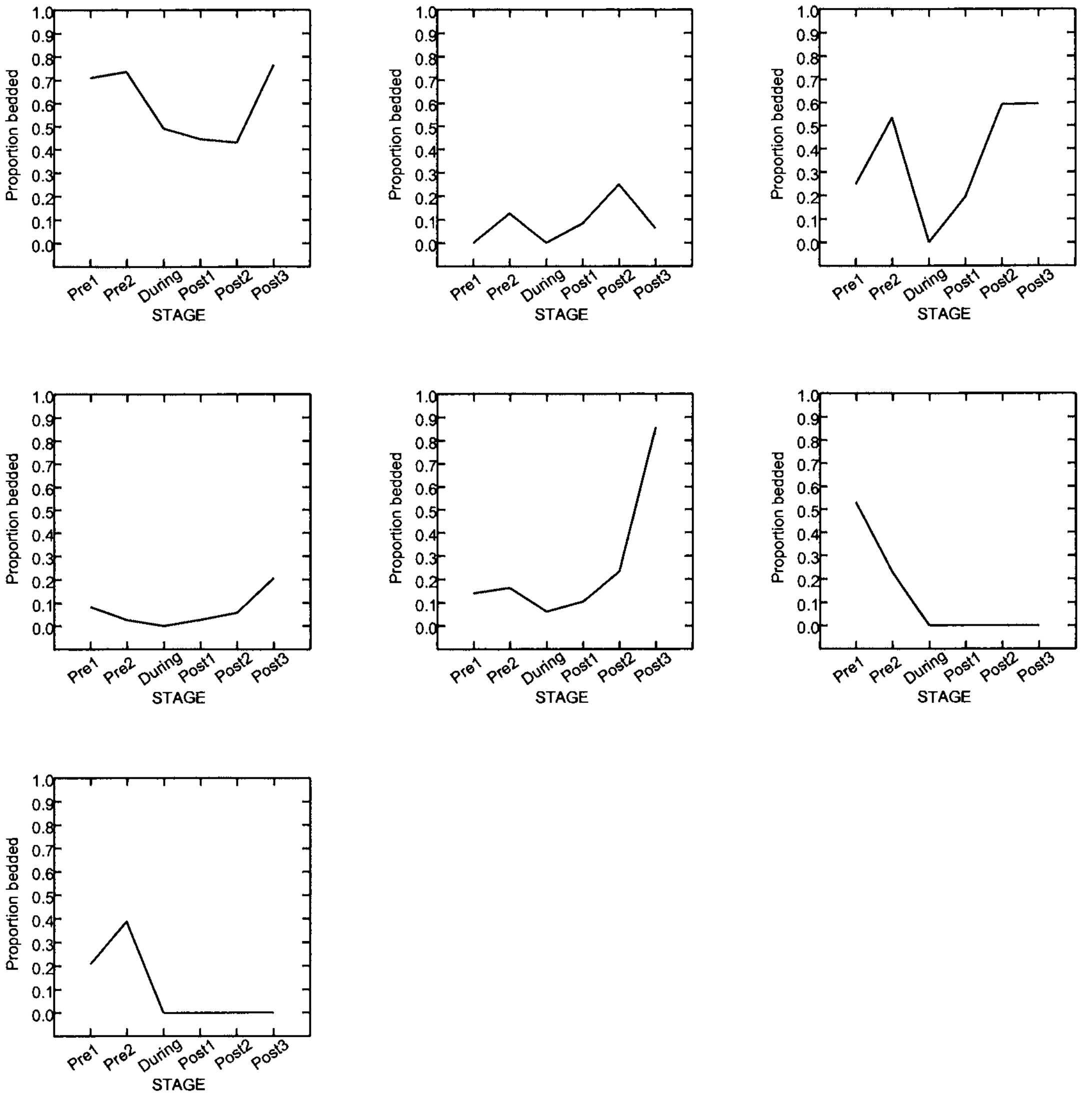

Proportion bedded
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Pre1
Pre2
During
Post1
Post2
Post3
STAGE

Fig. 3a

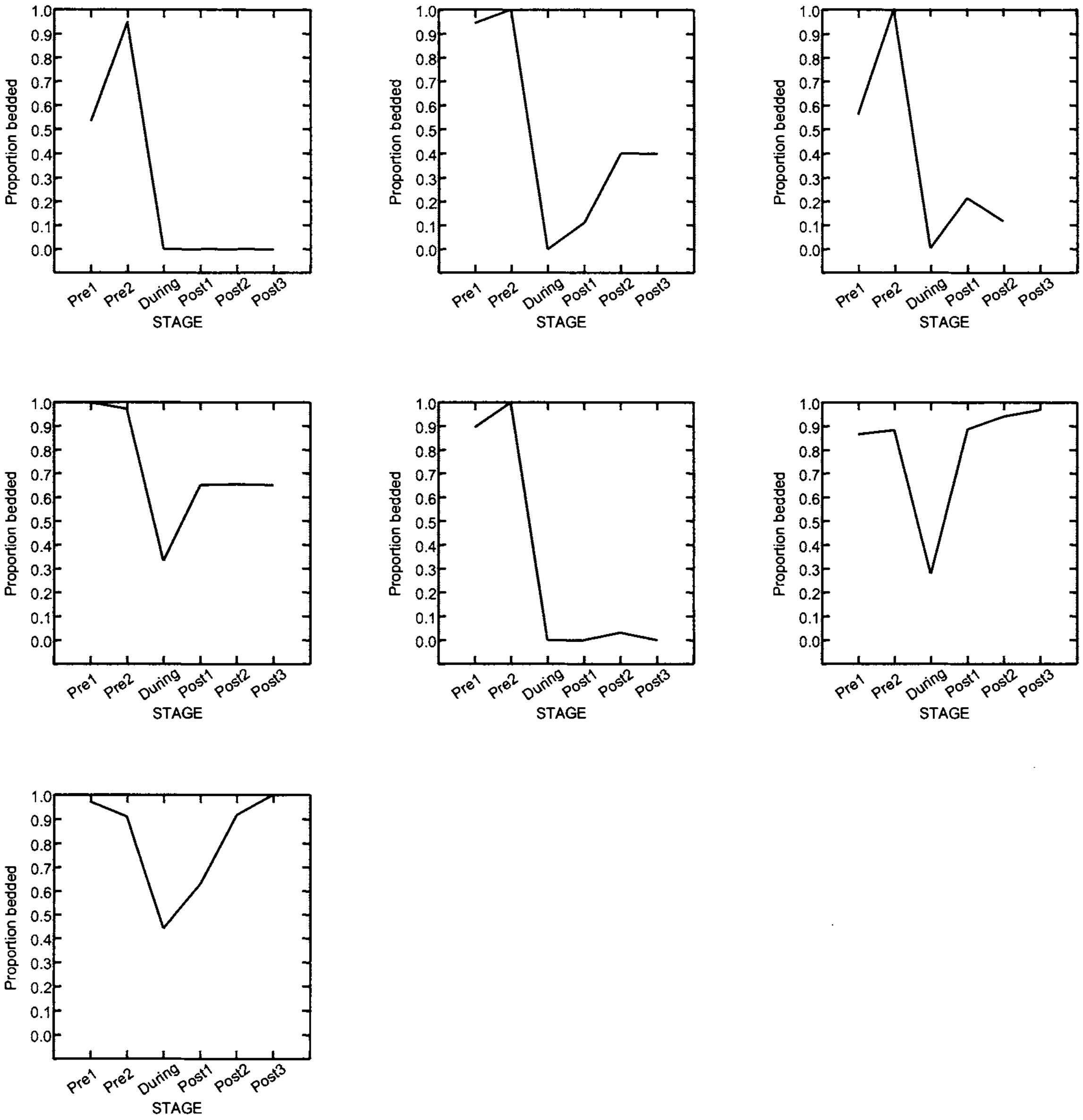

Proportion bedded
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Pre1
Pre2
During
Post1
Post2
Post3
STAGE

Fig. 4

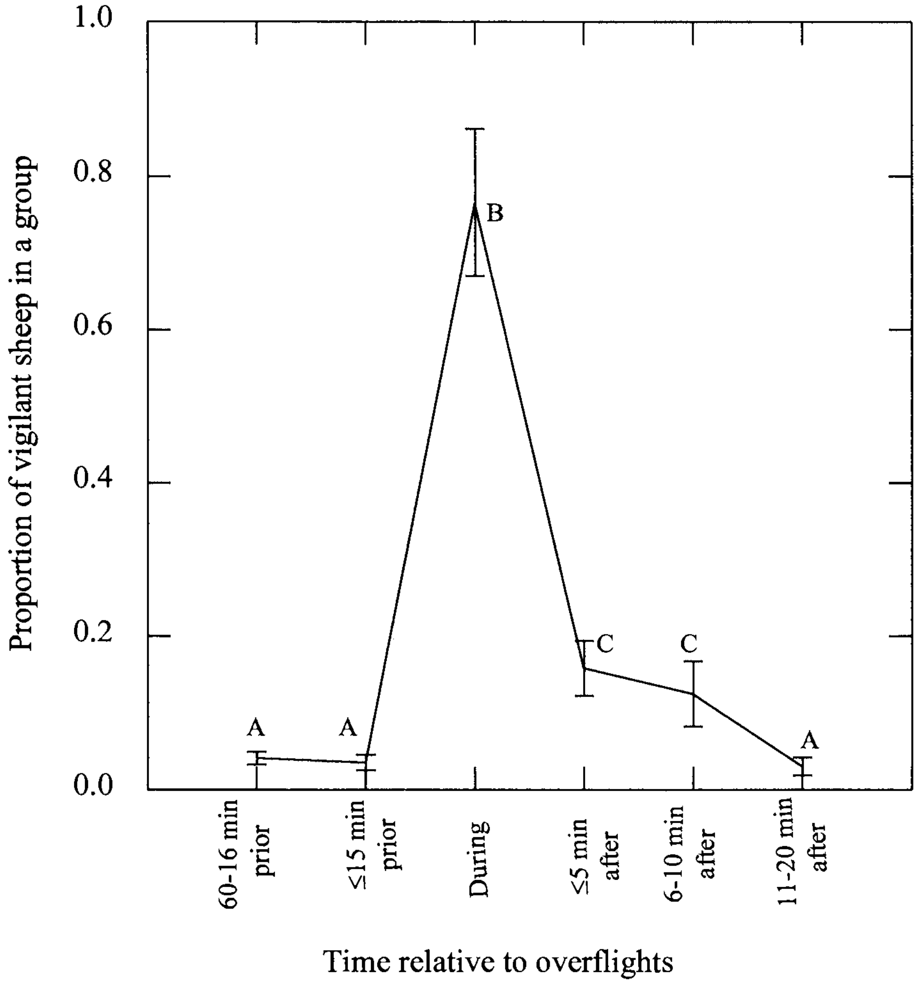

1.0
0.8
0.6
0.4
0.2
0.0
Proportion of vigilant sheep in a group
A
A
B
C
C
A
60-16 min prior
≤15 min prior
During
≤5 min after
6-10 min after
11-20 min after
Time relative to overflights

Fig. 5

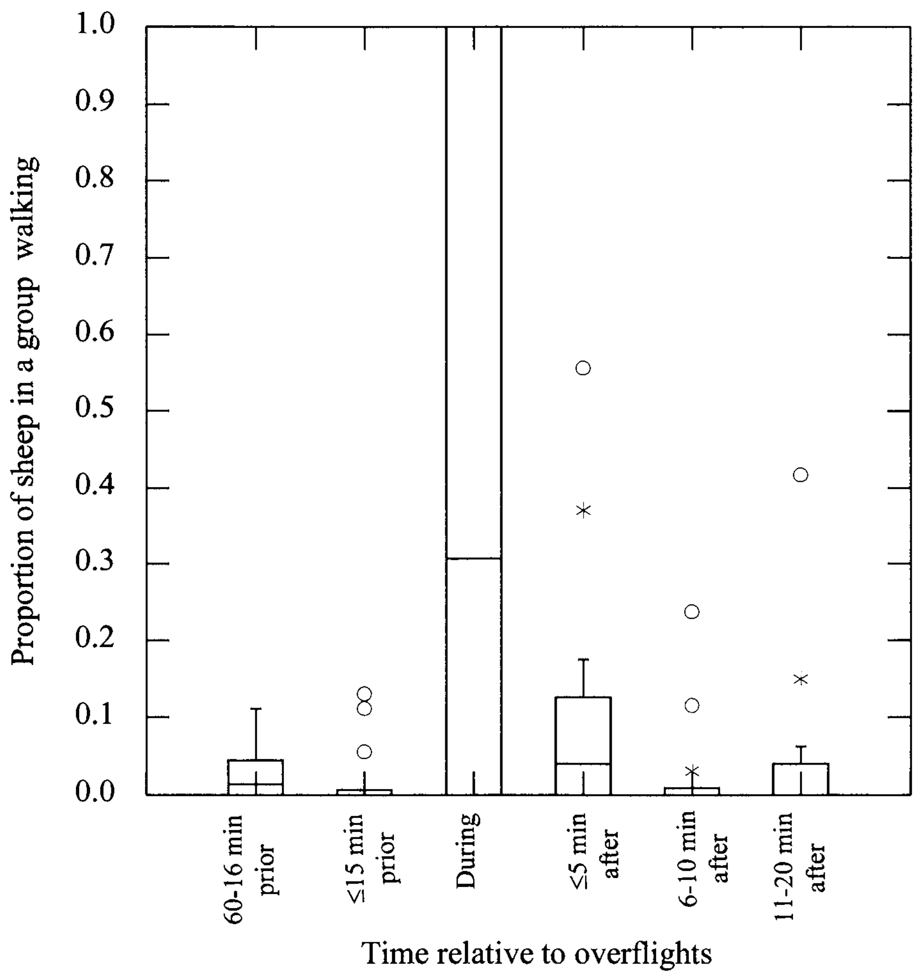
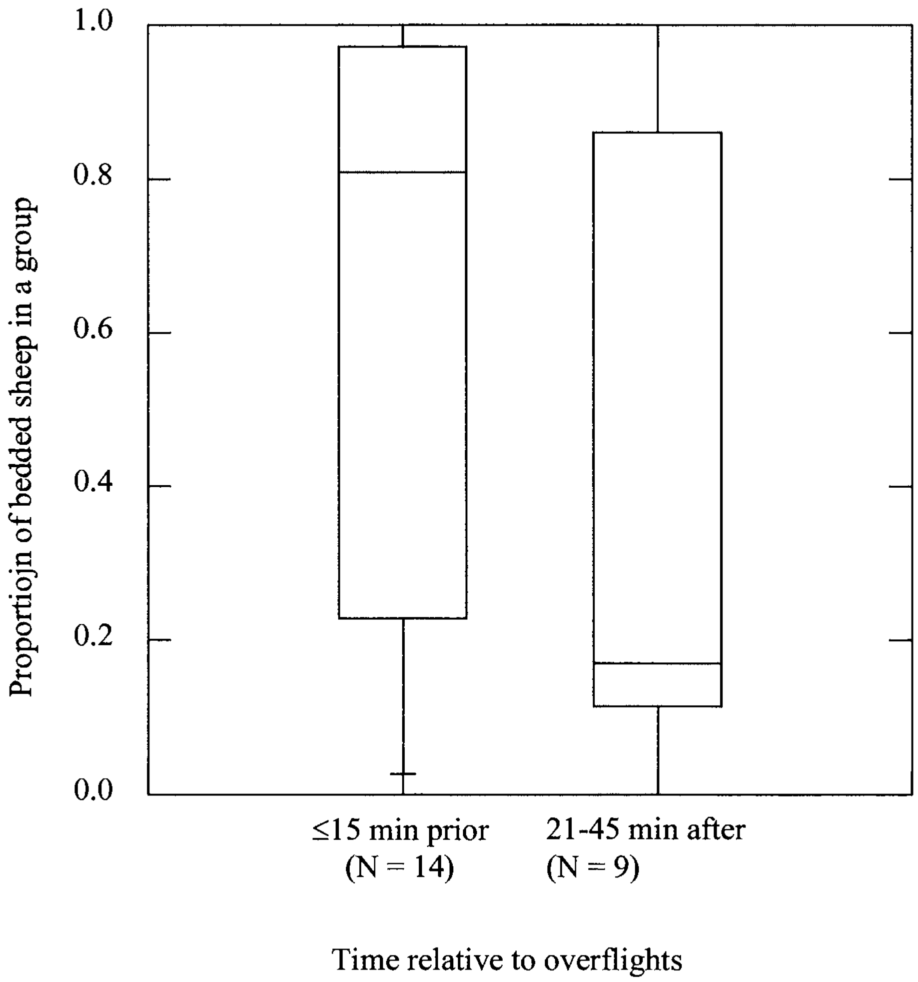

Proportion of sheep in a group walking
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
60-16 min prior
≤15 min prior
During
≤5 min after
6-10 min after
11-20 min after
Time relative to overflights

Fig. 2


1.0
0.8
0.6
0.4
0.2
0.0
Proportiojn of bedded sheep in a group
≤15 min prior
(N = 14)
21-45 min after
(N = 9)
Time relative to overflights