RESPONSES TO HELICOPTER DISTURBANCE BY DALL'S SHEEP: DETERMINANTS OF ESCAPE DECISIONS

Alejandro Frid, Boreal Research Associates, Site 20, Comp. 357, Whitehorse, YT, Y1A 4Z6, Canada,
Email: afrid@yknet.yk.ca

Prepared for the Yukon Fish and Wildlife Branch, Department of Renewable Resources,
Whitehorse, Yukon.

February 1998

ABSTRACT

I present data on escape decisions made by Dall's sheep (*Ovis dalli dalli*) disturbed by helicopters in the southwest Yukon, Canada. These data are important for conservation because animals escaping from human disturbance suffer energetic and other costs that can reduce fitness and cause population declines. I quantified the directness of the helicopter's approach from the perspective of the sheep's location by measuring the nearest distance between the sheep and helicopter, or least distance. Escape probability decreased as least distance became larger (i.e. as the helicopter's approach became less direct). The relationship, however, was strong only when sheep were inside or near steep rocky terrain (security cover), in small groups, or when groups had a large proportion of lambs. (Distance to security cover was the most important of these factors.) Otherwise, sheep always had a high probability of escape, regardless of least distance (within a 3-km range). Escape probability also decreased as the helicopter's elevation relative to the sheep became lower. The distance from the helicopter at which sheep initiated their escape increased as the sheep's distance to a ridge blocking view of the approaching helicopter (terrain block) became larger, and, though not significantly, as group size became greater. Sheep escaped farther if terrain blocks were closer, presumably because the sudden appearance of a helicopter was more startling. This relationship, however, weakened as the proportion of bedded animals in the group increased. Distance escaped increased also as group size and distance to security cover became larger, but not significantly. I provide logistic regression models of escape probability to determine setback distances and elevations for reducing helicopter disturbance of sheep. When available, data on the seasonal and/or diurnal altitudinal ranges and distances to security cover used by most members of a population should be incorporated into these models, but I provide also alternatives for when these data are lacking. Based on my logistic regression models I present *preliminary* guidelines for reducing helicopter disturbance of sheep in the Yukon. Future guidelines should be improved by considering not only escape costs, but also costs related to lost foraging time.

INTRODUCTION

The task of quantifying and mitigating the effects of human disturbance on wildlife has its theoretical foundation in behavioural ecology. Disturbance studies are directly derived from research on how animals reduce their risk of predation, and on the costs of antipredator behaviour to other life-history needs, such as feeding and reproducing (Berger et al. 1983; Stockwell 1991; Bradshaw 1994; Gill et al. 1996; Sutherland 1996). They are a good example of how basic science and wildlife management are closely related disciplines (see Sinclair 1991).

Disturbance from human activities affects wildlife by increasing the individual's investment in antipredator behaviour and physiological stress. The consequences include the energetic costs of escaping (Bleich et al. 1994; Bradshaw 1994; Côté 1996), lower foraging efficiency (Berger et. al 1983; Stockwell 1991), and higher heart and metabolic rates (MacArthur et al. 1982; Chabot et al. 1990; Chabot 1991). These mechanisms can deteriorate the body condition of individuals, leading to decreased reproductive success and population declines (Bradshaw 1994). In fact experimental studies of caribou (*Rangifer tarandus*: Harrington & Veitch 1992) and mule deer (*Odocoileus hemionus*: Yarmoloy et al. 1988), and an observational study of mountain goats (*Oreamnos americanus*: Joslin 1986) already provide strong support for this hypothesis. Disturbance also may cause mother-young separation, which decreases young survivorship (Côté & Beaudoin in press). Because disturbance can be a substantial force driving population (Gill et al. 1996; Sutherland 1996), and perhaps community dynamics (see Schmitz et al. 1997), understanding how it affects decisions made by individuals is essential for wildlife conservation.

Helicopter disturbance of Dall's sheep (*Ovis dalli dalli*) 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 sheep and goats, or the summer/rutting ranges of caribou. Second, a helicopter-based tourism industry (sightseeing and access to remote areas for hiking or river trips) is rapidly growing and largely unregulated (e. g. Hegmann 1995). Economic pressures to expand mining and tourism likely will lead to higher levels of disturbance in the near future. Similar concerns about helicopter or other motorised disturbance are common outside the Yukon (Berger et al. 1983; Harrington & Veitch 1991; Stockwell 1991; Tyler 1991; Bleich et al. 1994; Bradshaw 1994). Because helicopter use in roadless places supporting wildlife often is related to strong economic interests, banning helicopters from all areas would be unrealistic. Thus, wildlife conservation generally will depend on defining explicit setback distances and elevations that represent an acceptably low impact.

Here I present data on escape decisions by Dall's sheep disturbed by helicopters, and suggest mitigation measures derived from these analyses. Of the overt behaviours that can be quantified, escaping is the most energetically expensive (Bleich et al. 1994; Bradshaw 1994). Animals must interrupt maintenance activities, such as feeding or ruminating, to spend energy and time running and/or walking away from a perceived threat. In addition to these energetic costs, the post-escape location may have a higher risk from natural predators (e. g. sheep leaving a cliff when disturbed) or lower food density or quality, than the pre-escape location. Even when distances escaped are short (10-50 m), escaping represents other costs, as there almost always is a vigilant period before and after the escape (Frid unpublished data). Furthermore, escaping indicates a high level of excitement, which increases heart and metabolic rates, and a bighorn sheep (*O. canadensis*) study found heart rate responses to last 6.3 times longer than overt responses (MacArthur et al. 1982). Therefore, escape decisions might be the best measures for the short-term costs of disturbance, particularly because they are easier and cheaper to record than heart rate responses. I acknowledge, however, that focusing on escape decisions ignores the subtler, yet important consequences of reduced foraging efficiency (Berger et al. 1983; Stockwell et al. 1991).

During previous research I proposed and found empirical support for the Interactive Factors Hypothesis (Frid 1997), and I framed this study around it. With this hypothesis I postulate that animals make antipredator decisions by simultaneously considering multiple factors that affect overall risk. For example, I expected that sheep would feel more threatened as a helicopter's approach became more direct (as quantified by least distance: Fig. 1), but the magnitude of their response to this perceived threat would depend on other risk-related factors. Thus, when sheep are on a cliff, where predation risk is lower (Frid 1997), their probability of escape should decrease substantially as the helicopter's approach becomes less direct. Sheep far from cliffs and under high predation risk, however, might be more "edgy" and always have a high probability of escape, even if a helicopter's approach is very indirect. Other escape decisions also should be sensitive to the combined risk created by several factors.

More specifically, based on preliminary observations (Frid 1995), the literature (Tyler 1991; Harrington & Veitch 1991; Côté 1996; Frid 1997; Kramer & Bonenfant 1997), and insights gained during fieldwork, I asked the following questions:

1) Are escape decisions affected by the directness of the helicopter's approach (as quantified by the nearest distance between sheep and the helicopter: Fig. 1), the helicopter's relative elevation, and distances between sheep and the nearest terrain block obscuring the helicopter? Do these variables act independently (additively) or do they interact (multiplicatively) with each other?
2) Do variables related to the pre-disturbance condition of the sheep (group size, distance to security cover, proportion of lambs, and proportion of bedded animals) affect escape decisions? If so, do these variables interact (multiplicatively) with helicopter-related variables?

My results provide quantitative criteria for determining setback distances and elevations between sheep and helicopters. They could be used also to predict some of the energetic costs of disturbance and associated consequences to body condition and reproductive success (see Bradshaw 1994). My analyses, however, were based on limited sample sizes (N = 42 to 57). Management criteria derived from them will need to be updated as data sets and our knowledge increase. Still, as far as I am aware this work currently is the most in depth analyses of escape decisions by ungulates affected by helicopter disturbance.

METHODS

Study sites, seasons, disturbance histories, and animals

Fieldwork took place during 1997 in the southwest Yukon Territory, Canada. Most observations (86 %, N = 57) were made during late June, late July, and early August at Hoge Pass (ca. 61 °19' N, 139° 33' W), Kluane National Park Reserve (KNPR). Seven observations were made at Nines Creek (ca. 61° 11' N, 138° 50' W), Kluane Wildlife Sanctuary, during mid June and late July. One additional observation was made at Vulcan Creek (ca. 60° 55'N, 138° 29' W), KNPR, on 3 July. Preliminary data used for refining methods were collected at Vulcan creek during mid-June, but these were not reliable enough to be included in analyses. All sites contained large sheep populations of >200 animals (J. Carey unpublished data; Manfred Hoefs unpublished data; Frid unpublished data), were roadless, and harboured carnivores known to attack sheep, such as grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), coyotes (*Canis latrans*), and wolverine (*Gulo gulo*). More information on these sites can be found in Hegmann (1995).

Helicopter traffic at all sites occurs almost exclusively between May and September, but Vulcan Creek and Nines Creek had a more substantial disturbance history than Hoge Pass. At Vulcan Creek there were 5-30 sightseeing flights a week during the two previous summers (D. Hladun, personal communication). Due to mineral exploration within the Game Sanctuary, Nines Creek was disturbed by helicopters during approximately 25 days in 1994, 60 days in 1995, and 25 days in 1996 (K. Hattie personal communication). Sheep at Hoge Pass had been previously disturbed only infrequently by flights related to tourism or research (R. Breneman personal communication). Sample size limitations precluded me from analysing study site effects, and I pooled data for all sites. Given that 86 % of the data came from Hoge Pass, my study primarily represents sheep that were relatively unhabituated to long-term helicopter disturbance. Disturbance history differences, however, may have introduced unaccounted variation in 14 % of the data.

Like other polygynous ungulates in temperate or high latitudes, the adult sexes of Dall's sheep differ in their investments in antipredator behaviour. Males are greater risk takers, and spend most of the year segregated from females (Main et al 1996). Thus, there are *a priori* reasons to expect group composition to influence responses to disturbance. Sample size limitations, however, precluded analyses of these effects, and I pooled observations for female-young groups (68 %) and male groups (32 %). Group composition may have been a second source of unaccounted variation.

Plant phenology affects body condition (Klein 1965), and animals in poor condition may invest less in antipredator behaviour than animals in good condition (McNamara & Houston 1987). Given that I did not begin fieldwork until mid June, after plant green-up was already well advanced, I assume that the relationship between plant phenology and body condition was not a substantial source of unaccounted variation.

Field methods and Variables

Sheep were observed from the ground, from distances of >1km and using spotting scopes and/or binoculars. Observers vocally recorded continuous sampling of the behaviour of focal sheep groups (Martin & Bateson 1993) into tape recorders. One to four groups (1/observer) were observed simultaneously during disturbance events. Female-young groups tend to be large, and often it was not possible to accurately observe all group members at once. Due to this constraint, I quantified the timing of responses to disturbance based on the behaviour of ≥ 1 group members (most responses involved >50 % of the group, see Results). Variables are defined in Table 1 and Fig. 1.

At Hoge Pass and Vulcan Creek, I had radio communication with the helicopter pilot, and in almost all cases I designed *a priori* the helicopter trajectory. I planned routes to disturb as many sheep groups as there were observers, and to attempt sampling independent variables across their ranges (e. g. small and large groups, near and far flights, etc).

For almost all observations at Hoge Pass (92 %, N = 49), which made up 79 % of the data, the helicopter trajectory and its relation to the timing of sheep responses was recorded using a new method I devised. 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) during an overflight. An observer on the ground supplemented these data by mapping the helicopter trajectory (including elevations based on adjacent topography) on a 1:50, 000 map. Points required for analyses that were intermediate to GPS locations were later estimated from the helicopter's speed and climbing/dropping rates. These records later allowed reconstruction of the timing of sheep behaviour in relation to helicopter locations. Distances between sheep and helicopter were measured from the 1:50,000 maps using a ruler.

For all data at Nines Creek (where I had no radio communication with the pilot), four observations for which the helicopter GPS was unavailable at Hoge Pass, and the one observation at Vulcan Creek, the helicopter trajectory and its relation to the timing of sheep responses were recorded as follows. An observer picked *a priori* distinct points on 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. This observer also mapped the helicopter trajectory, including elevations based on adjacent topography. The taping of sheep behaviour and helicopter locations were synchronised in time, which later allowed for reconstruction of the timing of sheep behaviour in relation to helicopter locations. Points on the helicopter's trajectory that were not recorded in the field but that were required for analyses were later estimated using the helicopter's speed and climbing/dropping rates. At Hoge pass and Vulcan creek these were obtained from the pilot, and at Nines creek they were estimated from the time the helicopter took to travel between mapped locations.

In all cases, the disturbance was caused by a single helicopter (Bell 206B) flying at a mean ± SD air speed of 165 ± 31 km/h. The helicopter had a sling only in three observations collected simultaneously during the same disturbance event.

At all study sites, the sheep's distance to security cover and the distance the sheep escaped were estimated using 1:50,000 topographic maps and known points on the landscape if these distances were large (>100 m). For smaller distances, these estimates were made using the torso length of an adult sheep (representing approximately 1 m) as reference points. The distance between sheep and the nearest terrain block that would obscure the approaching helicopter (usually a ridge) was estimated from 1:50,000 maps. My estimate of distance to terrain block considered topography and helicopter elevations because ridges might have been visual blocks only when the helicopter was below a certain elevation.

Because groups were often large and spread out over a wide area, all distances were measured from the group's "centre of gravity". The latter is the imaginary balance point of the horizontal plane contained by the perimeter of the group, with the distribution of animals within that perimeter determining the weight of the plane.

Independence between observations

There were repeated flights on numerous days, but such events are not independent of the first flight of the day (see von Ende 1993). Further, preliminary data suggested that sheep respond more strongly to the first disturbance event of the day than to subsequent flights (Frid 1995). The results I present in this report include only the first flight of the day to disturb the focal sheep group.

When >1 group were simultaneously observed during the same disturbance event, these groups were almost always several km apart or not in direct line of site of each other. There were very few observations in which two or more groups were in near view of each other, potentially violating the assumption of independence by one group responding to the other's behaviour rather than to the helicopter.

Sheep were not marked. To reduce the problem of groups contributing more than one observation to the data set (Machlis et. al 1985), I considered observations to be biologically independent only if they involved groups that could be temporarily distinguished by their position in the landscape or if they occurred on different days.

Model building and statistical analyses

I analysed effects of independent variables on escape decisions (defined in Table 1) with multiple regression models. My approach to model building, a task involving subjective intuition (Neter et al. 1983; Wilkinson et al. 1996), centred around my *a priori* prediction that escape responses are affected by interactions between sheep and helicopter variables. This approach was also limited by a the guideline that, due to statistical power and model saturation issues, the number of independent variables selected for model building should be no more than 1/6 of the sample size (Neter et al. 1983). Thus, I built models in three stages, with each stage reducing the model to its most significant form with backward stepping procedures (see details below). The first stage reduced one model testing the independent and interactive effects of all helicopter-related variables. The second reduced 3-4 models, one for each independent sheep-related variable (Table 1), testing interactions between each sheep variable and the helicopter variables in the reduced model of Stage 1. If additional variables were added to the model of Stage 1, during a third stage the variables of each reduced model from Stage 2 were tested with a single model, which I reduced to its most significant form. Because of limited sample size and potential interpretation difficulties, I did not consider three-way interactions.

The two exceptions to this approach were as follows. First, I excluded least distance from analysis of escape initiation distance because the latter can be only greater than or equal to least distance, and this constraint creates an artifact in which the relationship between these variables will always be strong and positive. This reduction in the number of variables allowed me to consider all sheep-related variables except proportion of lambs in a single model during the second stage of model building. (Proportion of lambs was analysed separately because all male groups had to be excluded from analyses of this variable.) Second, during the first stage of model building for analysis of distance escaped, no helicopter variables were significant. Thus, for Stage 2 I chose the helicopter variable that was significant for escape initiation distance, and intuitively decided to also include least distance.

For analyses of escape probability, I used logistic regression, and reduced models to their most significant form following the criteria described in Trexler & Travis (1993). Using JMP (SAS Institute 1996), I specified one subset of independent variables at the time, and compared Rho^2 values, whole model tests, lack of fit tests and effect-likelihood ratio tests between the models that included different variable subsets. Models could not become significant unless the lack of fit test had a Chi-square probability >0.05, and variables could not remain in the model unless the effect likelihood ratio probability was <0.05. Function plots were generated with the equation (see Trexler & Travis 1993):

$$\text{Escape probability} = 1-[(\text{EXP}(\alpha+\beta_1X_1+\beta_iX_i\ldots))/(1+(\text{EXP}(\alpha+\beta_1X_1+\beta_iX_i\ldots)))]$$

For analyses of escape initiation distance and distance escaped, I used linear regression models, which I reduced with backward stepping procedures (Neter et al. 1983; Wilkinson et al. 1996) using SYSTAT (SPSS 1996). Stepping was interactive, and independent variables were excluded from the model unless their P-values were <0.05.

To avoid collinearity problems in both logistic and linear regressions, variables could not remain in the model unless they had tolerance values >0.1 (Wilkinson et al. 1996). (Tolerance is 1 minus the multiple correlation between a predictor and the remaining predictors in the model.) These values were calculated for both regression types with SYSTAT (SPSS 1996). I also assessed correlations between independent sheep-related variables that were not in the same model, but that were tested during Stage 2 of model building. The only significant correlation was between group size and distance to cliffs (see Discussion).

I used arcsine square-root or logarithmic (base 10) transformations to normalise continuous variables (Zar 1984). The success of these transformations was confirmed with density function plots (SPSS 1996).

To check the assumptions of regression, I examined scatter plots of residuals and leverage, and probability plots of residuals (Neter et al. 1983;Wilkinson et al. 1996). Residuals and leverage values were calculated with LOGIT (Steinberg & Colla 1991) for logistic regression and SYSTAT for linear regression. There was 1 model (Model 1 of Table 3) in which one case had a high leverage value (0.53). I re-tested the same reduced model without the high leverage case and compared the result to the test using the entire data set. Excluding the high leverage case caused no changes in significance that would invalidate the model, and the Rho^2 value increased by 0.01. After examining the raw data and finding no errors, I kept the test using the entire data set.

RESULTS

Of 57 sheep groups exposed to helicopter disturbance, 75 % responded with at least some group members escaping. In the remaining groups, all sheep either became vigilant without escaping or did not respond overtly. Much of the variance in these escape decisions is explained by variables examined below.

When animals escaped, there usually was an initial run or walk, which I refer to as first escape, followed by a period of standing vigilant, and then more escape-vigilance sequences. Animals ran or alternated running and walking in 86 % of first escape responses, and walked during the remaining (N = 43). Escape almost always was preceded by at least some group members becoming vigilant towards the helicopter.

The first escape response usually involved most group members. It included >50 % or 100 % of the group, respectively, during 62% and 48 % of escapes (N = 42). Even if some sheep were not involved in the first escape response, most group members eventually escaped at some point during the disturbance event. The maximum percent of group members escaping was >50 % or 100 %, respectively, in 88 % and 76 % of observations (N = 42). It is noteworthy, however, that sometimes there was true split decision making within the group, with some group members escaping dramatically while others remained feeding or bedded, or only responded by becoming vigilant.

To escape or not escape

The probability that sheep would escape from a helicopter was affected strongly by the helicopter's least distance and its interactions with sheep-related variables. (Recall that least distance is a measure of the directness of the helicopter's approach from the perspective of the sheep's location, and is relevant even when escape initiation distance is greater than least distance: Fig. 1). The helicopter's relative elevation also had an effect (Tables 2-4).

Sheep were more likely to escape as least distance became smaller (as the helicopter's approach became more direct), but the strength of this relationship depended on the sheep's distance to security cover. The relationship was strong when sheep were inside or near security cover. When sheep were farther from cover, however, they had a high probability of escaping (e. g. ≥ 0.6 at 75 m from cover, Fig. 2a), regardless of least distance. In fact, a model considering the interaction between least distance and distance to security cover and the independent effects of the helicopter's relative elevation (see below) best predicted the probability of escape (Rho^2 = 0.64, Model 1 of Table 3, Fig. 2). These results suggest that, when sheep are under high predation risk because they are farther from security cover (see Frid 1997), they feel most threatened by the mere presence of a helicopter and, within a 3 km range, least distance has little influence on escape decisions. When they feel safer due to their proximity to security, however, sheep are more reluctant to escape.

Whether the sheep's decision to escape was affected by the helicopter's least distance also depended on group size (Model 2 of Table 3; Fig. 3). Sheep in very large groups always had a high probability of escape (e. g. ≥ 0.5 for groups with 40 sheep), regardless of least distance, whereas sheep in smaller groups became substantially less likely to escape as least distance became larger (Fig. 3a). Likely due to low statistical power (see Thomas & Juanes 1996), this interaction was excluded from a model that considered multiple sheep and helicopter variables (Table 4).

The effect of least distance on escape probability also depended on the proportion of lambs in the group (Model 4 of Table 3; Fig. 4; male groups excluded from analyses). For groups with a high proportion of lambs, the probability of escape decreased strongly as least distance became larger. Groups with a low proportion of lambs, however, always had a high probability of escape (e. g. ≥ 0.6 for groups with lamb proportion of 0.1), regardless of least distance (Fig. 4a). These results suggest an escape cost that is specific to mothers. In fact, lambs sometimes strayed behind the escaping group, possibly increasing their chance of separation from their mother. Because this analysis excluded male groups (thus lowering sample sizes), proportion of lambs could not be considered in a model that included multiple sheep variables (Stage 3 model, see Methods).

When the helicopter was far below them, sheep were substantially less likely to escape than when the helicopter was at their elevation or above. This effect was independent of other variables (Model 1 of Table 3; Fig. 5).

I found no significant effect of the sheep's distance to terrain block (defined in Table 1) and the proportion of bedded animals on escape probability (respectively, Table 1 of Model 3 and Table 3). The lack of effect from distance to terrain block was surprising, as the sudden appearance of a helicopter behind a nearby ridge seems more likely to startle sheep and cause them to panic. This variable and the proportion of bedded animals, however, did influence other escape decisions (see below).

Escape initiation distance

The distance at which sheep initiated their escape from helicopters ranged from 100 m to 3 km, and had a mean ± SD value of 1.04 ± 0.67 km (N = 42). Much of the variance (22 %) around this mean was explained by the animals' distance to terrain block.

Escape initiation distance increased as distance to terrain block became larger. This is a simple consequence of sheep not being able to see, and likely hear, the helicopter until it is past the terrain block (Tables 5, 6; Fig. 6).

I found no significant effects of the helicopter's relative elevation (Table 5) nor of sheep-related factors (Table 6). A descriptive plot, however, suggested that escape initiation distance increased as group size became greater (Fig. 6c). This effect was nearly significant (P = 0.07: Table 6), suggesting that the relationship is biologically important, but that larger sample sizes are needed to detect the smaller effect size (see Thomas & Juanes 1996). Indeed, we can expect larger groups to be able to detect potential threats from a greater distance (review in Roberts 1996).

Distance escaped

The distance sheep escaped from helicopters ranged from approximately 15 m to 2.2 km (mean ± SD = 253 ± 438 m, N = 43), and was affected by the interaction between the proportion of bedded animals and the sheep's distance to terrain block ($R^2 = 0.25$, Table 8). Surprisingly, the helicopter's least distance and relative elevation had no effect (Table 7).

Distance escaped decreased as distance to terrain block became larger. This may be because the sudden appearance of a helicopter behind a nearby terrain block is more threatening than when the helicopter can be seen approaching gradually. The relationship, however, was relatively strong only when the proportion of bedded animals was large, and weakened as this proportion decreased (Table 8; Fig. 7).

Although distance to security cover and group size were excluded from regression models, they were nearly significant (respectively, P = 0.05, 0.08: Table 9). Descriptive plots suggested that groups farther from cover escaped for larger distances (Fig. 8a). This is because, unless the helicopter was approaching from the same direction as security cover, sheep generally escaped towards cover. Plots also suggested that larger groups escaped farther than smaller ones (Fig 8b). These relationships likely are biologically important and larger samples are needed to detect their smaller effect sizes (see Thomas & Juanes 1996)

DISCUSSION

One of the main findings of my study is that, although factors related to the helicopter strongly influenced escape decisions made by sheep, these factors did not always act in isolation of the pre-disturbance condition of the animals. Attempts to mitigate disturbance, however, will be based primarily on the factors that can be controlled by pilots. Thus, before considering interactions and the conservation implications of my results in more detail, I will summarise the effect of helicopter variables as if they did act in isolation of sheep variables.

Least distance, which is a measure of the directness of the helicopter's approach from the perspective of the sheep's location (Fig. 1), was the most important helicopter variable. The smaller the least distance (i.e., the more direct the helicopter's approach), the greater the probability that sheep would escape. (This effect depended on sheep-related variables.) I found no effect of least distance on the distance sheep escaped.

The sheep's probability of escape decreased as relative elevation became lower. (This relationship was independent of sheep-related variables.) Likely there is an upper elevation threshold, however, above which escape probability would decrease. I could not test this prediction because my observations did not include overflights that were >1200 ft above the sheep. I found no effect of relative elevation on escape initiation distance and distance escaped.

The sheep's distance to a terrain block obscuring the helicopter's approach also affected escape decisions. The closer this block, the smaller the escape initiation distance because sheep cannot see (and likely hear) the helicopter until it is past this block. (This relationship was independent of other variables). Sheep escaped for greater distances if terrain blocks were nearby. (This relationship depended on the proportion of bedded animals.) Perhaps this response occurs because the sudden appearance of a helicopter from behind a nearby terrain block is more threatening than when sheep can see the helicopter approaching gradually. I found no effect of distance to terrain block on escape probability.

Interactions between multiple factors

There are important costs to escaping, such as increased energy consumption, giving up a profitable site (as determined by predator safety or food), or mother-young separation. Thus, it would be adaptive for escape decisions to simultaneously consider several risk criteria, and for animals not to escape unless multiple factors combine to push overall threat beyond a certain threshold. This is a re-statement of my Interactive Factors Hypothesis (Frid 1997).

Some results supported this hypothesis. Sheep inside or near security cover, where predation risk is lower (Frid 1997 and references cited within), became substantially less likely to escape as least distance increased. Sheep farther from cover, where predation risk is higher, always had a high probability of escape, regardless of least distance. Essentially, due to threats unrelated to the helicopter, animals far from security cover seem to be more "edgy", and are more easily disturbed. Meanwhile, animals inside or near security cover appear to feel safer from factors unrelated to the helicopter and can avoid the costs of escape, unless the perceived threat -- as affected by least distance -- becomes particularly large.

A related argument may explain why female groups with a large proportion of lambs were substantially less likely to escape as least distance became larger, but groups with a small proportion of lambs were not. Escaping from helicopters may cause mother-young separation, which decreases young survival (Côté & Beaudoin in press). Further, there is one documented case of a lamb straying behind a group escaping from a helicopter, and a golden eagle (*Aquila chrysaetos*) seizing the opportunity to kill the lamb (Nette et al. 1984). Thus, it may be adaptive for mothers to monitor threats but also to be particularly reluctant to escape unless the perceived threat (e.g. as affected by the directness of the helicopter's approach) becomes particularly large.

Contrary to the expectations of the Interactive Factors Hypothesis, sheep did not respond to interactions between helicopter variables. For example, I expected that the increase in escape probability due to decreasing least distance would be strong when the helicopter was at the sheep's level, but least distances would have little or no influence on escape probability when the helicopter was far below the animals. My analyses did not detect such interactions, and greater sample sizes and observations in the extreme ranges of independent variables are needed to assess these relationships further.

Least distance interacted with group size to affect escape probability. Smaller groups were substantially less likely to escape as least distance became smaller, but larger groups always had a high probability of escape, regardless of least distance. Given that predation risk decreases with increasing group size (review in Roberts 1996), this relationship is puzzling and appears not to support the Interactive Factors Hypothesis. Perhaps the group size effect is due to collective excitement increasing with group size. The observation that larger groups escaped farther than smaller ones, though not significantly, weakly supports this possibility. Alternatively (but not mutually exclusively) smaller groups might contain individuals that not only forego the safety of larger groups, but that are also greater risk takers in other ways.

A caveat in interpreting the effects of group size and distance to security cover on probability of escape (Figs. 2 and 3) is that group size is partially a function of distance to security cover (Fig. 9; see Warrick & Krausman 1987). This is not surprising. Predation risk increases with distance to security cover, and increasing group size reduces predation risk (see Frid 1997 and references cited within).

Further, meadows far from security cover generally have greater food abundance than rockier areas in or near security cover, and the upper limit of group size is constrained by food abundance (see Jarman 1974). Still, distance to security cover explained only 18 % of the variation in group size (Fig. 9). When assessing collinearity between group size, distance to security cover, and their interactions with least distance, all tolerance values were >0.1. This suggests that the effects of group size and distance to security cover on escape decisions are not confounded by collinearity (Wilkinson et al. 1996).

Groups with a high proportion of bedded animals escaped for smaller distances when distance to terrain block was greater. Groups with a low proportion of bedded animals, however, generally escaped farther and proximity to a terrain block did not affect the distance they escaped. The interaction between proportion of bedded animals and distance to terrain block might be unrelated to predation risk and requires further investigation.

Of course, sheep-related factors may also interact with each other. For example, distance to security cover may have a greater effect on escape decisions for smaller than for larger groups. My analyses did not address such interactions, and future work should consider them.

Implications for conservation

As discussed earlier, disturbance has energetic and other costs that can affect population dynamics (Joslin 1986; Harrington & Veitch 1992; Yarmoloy et al. 1988; Bradshaw 1994; Gill et al. 1996; Sutherland 1996). My results can be used to create guidelines that would reduce escape costs caused by helicopters. Guidelines would be preliminary because sample sizes were marginally adequate, and my analyses could not consider some important factors, including body condition as affected by plant phenology (Klein 1965; McNamara & Houston 1987), disturbance history (see Frid 1996), sex-composition of groups, and regional differences. Further, my analyses considered only escape decisions. They did not address subtler yet important costs of disturbance, such as decreased foraging efficiency (Berger et al. 1983; Stockwell et al. 1991) and increased heart rate (MacArthur et al. 1983). Thus, guidelines would have to be updated as data sets grow and as predictive models improve.

One simple way of reducing disturbance is to be aware that, as suggested by the relationship between escape initiation distance and distance to terrain block, sheep appear to not perceive a helicopter that is hidden by a ridge. Thus, when sheep distribution is well known, helicopter routes should be planned such that a ridge blocks the line of sight between the helicopter and where most animals are likely to be. I have successfully applied this approach in one situation (Frid 1995).

To create more specific guidelines, managers first must decide what is an acceptably low escape probability. The rigorous way of making this decision is to first estimate the energetic and foraging costs of the average disturbance event and the expected rate of helicopter flights in the area. These estimates can then be used to predict the maximum number of escape events per unit time that individuals can tolerate without suffering reduced fitness due to weight loss (see Bradshaw 1994). In the absence of rigorous models, managers may have to use professional judgement and temporarily guess an acceptably low escape probability (Fig. 10). The relative rate of helicopter flights in the area would be an important criterion for this guess. For example, guidelines for an area with 100 flights/month should be based on a much lower escape probability than for an area with 5 flights/month. (Although animals in the area of more frequent flights eventually may habituate to some degree, which could justify relaxing the guidelines, the common notion that animals readily habituate to disturbance sufficiently to eliminate concerns may be unsubstantiated. In one study, mountain goats were exposed to intense disturbance from seismic exploration that lasted eight years and peaked for four and the population declined throughout six years of data collection [Joslin 1986].)

Once managers decide on an acceptably low escape probability, logistic regression models should be used to determine set back distances and/or elevations for the helicopters. From my data I generated a choice of two models, depending on the knowledge available for a given population (Fig. 10).

Model 1 of Table 3 provides the best choice for populations in which distance to security cover is well studied, but otherwise will be impractical. This model explained the most variability (64 %) in the sheep's decision to escape, and illustrates how variability in distance to security cover has a dramatic effect on escape probability. For example, when a helicopter is at the same elevation as the sheep and at a least distance of 1 km, the chances of escape are <10 % for sheep inside security cover, but almost 100 % for sheep at 75 m from cover (Fig. 2a). I suggest that predictions of this model be based on distances to cover that are *no smaller* than the median + 1 quartile for the population (weighted by group size: see Jarman 1974), which would encompass where 75 % of the animals are likely to be found. As a margin of safety--

particularly for small, extinction-prone populations (see Berger 1990)--managers should consider making predictions based on greater distances to cover, such as the mean + 2 SD (weighted by group size) for the population, which would encompass where 97.5 % of the animals are likely to be found. Predictions should be adjusted according to seasonal and diurnal variation in distance to security cover. For example, if sheep are more likely to be far from cliffs during the afternoon, setback distances for helicopters would be larger in the afternoon than in the morning. Model 1 of Table 3 also accounts for how escape probability decreases as the helicopter's relative elevation becomes smaller. Thus, if the altitudinal range of sheep is known (Fig. 11), horizontal set back distances can be adjusted according to the helicopter's elevation (Fig. 12).

When data on distances to cliffs are lacking but the altitudinal range of animals is known or can be extrapolated from other studies, the model presented in Table 2 will be the best choice (Fig. 10). This model accounts only for least distance and relative elevation and, as exemplified in Fig. 12, likely is the most practical one to be used by managers. Even though this model explains only 28 % of the variability in escape decisions--less than half of the explanatory power of Model 1 of Table 3--basing guidelines on smaller escape probabilities can compensate for the poorer fit of the model. If there are no data on distances to cliffs and altitudinal ranges, I suggest being conservative and using the model of Table 2 to calculate setback distances based on a relative elevation of +1000 ft, and generalising this distance for all helicopter elevations.

I do not suggest that my logistic regression models are valid for all sheep populations, particularly outside of the Kluane Region of the Southwest Yukon. I do believe, however, that the approach I present here is of general application and could be used with data sets similar to mine.

Managers must be cognizant that helicopter routes that reduce disturbance on a particular sheep range could concentrate helicopters in areas that are important to nesting raptors, mountain goats or other wildlife. Thus, avoiding sheep-centrism and considering the conservation of other species should be a goal inherent to guidelines for helicopter use.

Future analyses should determine, for a wide range of disturbance rates, the maximum time per disturbance event that individuals can interrupt foraging without suffering reduced fitness. Logistic regressions could then be used to determine how different variables affect the probability of feeding interruptions exceeding these thresholds. Future guidelines for helicopter setback distances could then be improved by considering not only escape costs, but also costs related to lost foraging time. This would be particularly relevant for sheep groups with a high proportion of lambs, which I found to be more reluctant to escape but which may still interrupt feeding to monitor an approaching helicopter.

Preliminary **recommendations for reducing helicopter disturbance of Yukon populations**

1) If nothing is known about the population, use a setback distance of 3.5 km. (This distance is generalized for all relative elevations and, based on the model of Table 2, corresponds to an escape probability of 0.2 at a relative elevation of +1000 ft.)
2) When the altitudinal range where most sheep are likely to be found is known or can be extrapolated from the literature, determine setback distances and corresponding relative elevations using Table 10 based on an escape probability of 0.1 (but see point 4). These relative elevations then need to be converted to the actual elevations that pilots will refer to, as shown in Fig. 11. I suggest quantifying the elevation range used by most sheep with the median ± 1 quartile elevation for the population. Guidelines should be adjusted for seasonal and/or diurnal changes in the altitudinal distribution of sheep.
3) If good data on distances to cover are available, use Model 1 of Table 3 to generate guidelines that account for seasonal and/or diurnal variability in distance to escape terrain. See previous section for details.
4) Managers should use professional judgement to determine when escape probabilities that are higher or lower than those I recommend are justified. For example, if a population is of particular concern because of a high rate of disturbance and/or because it is small and extinction prone, follow the steps of Fig. 12 and recalculate set back distances based on lower escape probabilities to create more conservative guidelines.
5) When sheep distribution is well known, try to plan helicopter routes such that a ridge blocks the line of sight between the helicopter and where most animals are likely to be, as exemplified in Frid (1995).

6) A given route that reduces disturbance of sheep may place helicopters into areas that are important to goats, nesting raptors, or other wildlife. Thus, avoiding sheep-centrism and considering the conservation of other species should be a goal inherent to guidelines for helicopter use.
7) Be aware that my recommendations are based on marginally adequate sample sizes collected during one summer season in the Kluane Region (mainly Hoge Pass). Expect guidelines to change if research continues.

ACKNOWLEDGEMENTS

My project was a very satisfying experience of collaboration with many people. Thanks to the vision of Jean Carey, the Fish and Wildlife Branch of the Yukon's Department of Renewable Resources commissioned and funded the project. Manfred Hoefs obtained additional funds from the Yukon Fish and Wildlife Branch during the write-up stage. Kluane National Park Reserve, Trans North Helicopters, and Inco donated helicopter time and/or loaned equipment. Kathy Hattie, of Inco, greatly facilitated work at the Nines Creek Site. Ray Breneman and Terry Skjonsberg, of Kluane National Park Reserve, greatly facilitated work within the park. Pilot Doug Hladun, of Trans North Helicopters, constantly amazed me with his enthusiasm and ability to follow, with very short notice, complex trajectory instructions. The project would have not had the same success without his important contributions. My field assistant Marc Goudreau was a skillful helicopter behaviourist, and made life in the field never boring and a little bear-safer. I also thank the field volunteers, Gail Lotenberg, Jean Carey, Jennifer Staniforth, Marten Berkman, and Mike Dehn, for their work at Hoge Pass. Far from least, I thank Stuart Alexander for statistical advice and critical discussions, John Boulanger and Don Russell for discussions on the trigonometry of a helicopter trajectory, and Angela Milani for extracting raw data from maps. Stuart Alexander, Jean Carey, and Gail Lotenberg reviewed earlier drafts of this manuscript. Any flaws, of course, are my own.

Finally, I must acknowledge that to collect most of the data I present here, I chose to burn considerable amounts of fossil fuels for the sole purpose of experimentally harassing animals. I did not take this decision lightly. Experimental harassment was the quickest way of obtaining reliable knowledge that would actually tell us something about the nature of disturbance. I believe that my results have proved this approach to be well chosen, as also was the case for some of the best disturbance studies (Yarmoloy et al. 1988; Harrington & Veitch 1992; Bradshaw 1994). Still, I apologise to both future generations (for burning their fossil fuels) and the animals themselves, and can only hope that this work will actually contribute to wildlife conservation.

LITERATURE CITED

Berger, J., D. Daneke, J. Johnson, S. H. Berwick. 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. Biological Conservation 25: 193-208.

Berger. J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. Conservation Biology 4: 91-98.

Bleich, V. C., R. T. Bowyer, A. M. Pauli, M. C. Nicholson, & R. W. Anthes. 1994. Mountain sheep (*Ovis canadensis*) helicopter surveys: ramifications for the conservation of large mammals. Biological Conservation 70: 1-7.

Bradshaw, C. J. A. 1994. An assessment of the effects of petroleum exploration on woodland caribou (*Rangifer tarandus caribou*) in Northeastern Alberta. M. Sc. Thesis. University of Alberta.

Chabot, D. 1991. The use of heart rate telemetry in assessing the metabolic cost of disturbances. Trans. 56th N. A. Wildl. & Nat. Res. Conf.

Chabot, D., V. Geist, RH Johnston and RA MacArthur. 1990. Heart rate telemetry as a means of investigating duration of disturbance and bioenergetics in free-living ungulates. Telecomunication for health care: telemetry, teleradiology, and telemedicine 1355:126-131.

Côté, S. 1996. Mountain goat responses to helicopter disturbance. Wildl. Soc. Bull. (24:681-685).

Côté, S, & C. Beaudoin. In press. Grizzly bear attacks and nanny-kid separation in mountain goats. Mammalia.

FitzGibbon, C. D. & Lazarus, J. 1995. Anti-predator behaviour of Serengeti ungulates: individual differences and population consequences. Pages 274-296 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II: Dynamics, Management and Conservation of an Ecosystem. University of Chicago Press, Chicago and London.

Frid, A. 1995. Dall's sheep of the Killermun Lake region: ecological and behavioural data in relation to mineral exploration. Yukon Fish and Wildlife consultant report TRC-95-2.

Frid, A. 1996. Hypotheses and preliminary experimental designs for investigating impacts of helicopter disturbance on Dall's sheep. Report to the Yukon Fish and Wildlife Branch.

Frid, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. Anim. Behav: 53:799-808.

Gill, J. A., W. J. Sutherland, & A. R. Watkinson. 1996. A method to quantify the effects of human disturbance on animal populations. Journal of Applied Ecology 33: 786-792.

Harrington, F. H., & A. M. Veitch. 1991. Short-term impacts of low-level jet fighter training on caribou in Labrador. Arctic 44:318-327.

Harrington, F. H., & A. M. Veitch. 1992. Calving success of woodland caribout exposed to low-level jet fighter overflights. Arctic 45:213-218.

Heggman, G. 1995. A cumulative effects assessment of proposed projects in Kluane National Park Reserve, Yukon Territory. Report to Kluane National Park Reserve, Haines Junction, Yukon.

Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. Behaviour 48:215-267.

Joslin, G. 1986. Mountain goat population changes in relation to energy exploration along Montana's Rocky Mountain Front. Proceedings fifth biennial symposium of northern wild sheep and goat council, pp 253-271.

Klein, D. R. 1965. Ecology of deer range in Alaska. Ecological Monographs 35:259-284.

Kramer, D. L., and M. Bonenfant. 1997. Direction of predator approach and the decision to flee to a refuge. Animal Behaviour 54:289-295.

MacArthur, R. A., V. Geist, & R. H. Johnston. 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. J. Wildl. Manage. 46:351-358.

Machlis, L, PWD Dodd, & JC Fentress. 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Z. Tierpsychol 68:201-214.

Main, M. B., F. W. Weckerly, & VC Bleich. 1996. Sexual segregation in ungulates: new directions for research. Journal of Mammalogy 77:449-461.

Martin, P. & P. Bateson. 1993. Measuring behaviour: an introductory guide. Cambridge University Press.

McNamara, J. M., & A. I. Houston. 1987. Starvation and predation as factors limiting population size. Ecology 68:1515-19.

Nette, T, D. Burles, & M. Hoefs. 1984. Observations of golden eagle predation on Dall sheep lambs. Can. Field Nat. 98:252-254.

Netter, J., W. Wasserman, & M. H. Kutner. 1989. Applied Regression Models. Irwin. Inc.

Roberts, G. 1996. Why individual vigilance declines as group size increases. Anim. Behav. 51:1077-1086.

SAS Institute Inc. 1995. JMP version 3.1. SAS Institute Inc., Cary, NC. USA..

Schmitz, O. J., A. P. Beckerman, & Kathleen M. O' Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology. 78:1388-1399.

Sinclair, A. R. E. 1991. Science and the practice of wildlife management. Journal of Wildlife Management 55:767-773.

SPSS. 1996. SYSTAT 6.0 for Windows. SPSS Inc.

Steinberg, D. & P. Colla. 1991. Logistic regression: A supplementary module for SYSTAT and SYGRAPH. SYSTAT Inc.

Stockwell, C. A., G. C.Bateman, & J. Berger.1991. Conflicts in National Parks: a case study of helicopters and bighorn sheep time budgets at the Grand Canyon. Biol. Conserv. 56: 317-328.

Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press.

Thomas, L. & F. Juanes. 1996. The importance of statistical power analysis: and example from *Animal Behaviour*. Animal Behaviour 52:856-859.

Trexler, J. C. & J. Travis. 1993. Nontraditional regression analyses. Ecology. 74:1629-1637.

Tyler, N. J. C. Short term behavioural responses of Svalbard reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. Biological Conservation. 56: 179-194.

von Ende, C. N. 1993. Repeated measures analysis: growth and other time dependent measures. Pages 113-137 in S. M. Scheiner & J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman & Hall.

Warrick, G. D., & P. R. Krausman. 1987. Foraging behavior of female mountain sheep in western Arizona. Journal of Wildlife Management 51:99-104.

Wilkinson, L., G. Blank, C. & Gruber. 1996. Desktop data analysis with SYSTAT. Prentice Hall.

Yarmoloy, C., M. Bayer, & V. Geist. 1988. Behavior responses and reproduction of mule deer, *Odocoileus hemionus*, does following experimental harassment with an all-terrain vehicle. Can. Field Nat. 102:425-429.

Table 1. Variable definitions.

Variable	**Definition**
	Dependent variables
Escape	Binomial variable describing whether ≥ 1 group members (almost always >50 %) disturbed by a helicopter moved ≥10 m (usually much farther) from their pre-disturbance location. In most cases there was an initial run or walk, followed by a period of standing vigilant, and then more escape-vigilance sequences. Often a small proportion of group members initiated the escape, and the rest of the group did not escape until later, if at all.
Escape initiation distance	Continuous variable describing the distance (km) from the helicopter at which ≥ 1 group members (almost always >50 %) began to escape.
Distance escaped	Continuous variable describing the maximum distance (m) ≥ 1 group members (almost always >50 %) escaped before ≥ 90 % of the group returned to feeding or bedding.
	Helicopter-related independent variables (all continuous)
Least distance	The smallest distance (km) between sheep and the helicopter. Because this distance is determined by an angle between the helicopter's trajectory and the sheep's location (Fig. 1), it should be interpreted as a measure of the directness of the helicopter's approach from the perspective of the sheep's location. Using an angle, rather than least distance, to measure the directness of a helicopter's approach may have eased the reader's interpretation of my results. I chose least distance, however, because ultimately it is the variable that helicopter pilots will be able to control and which will determine setback distances for reducing disturbance.
Relative elevation	The helicopter's elevation minus the sheep's elevation (ft). The value is negative when the helicopter is below the sheep.
Distance to terrain block	Distance (km) between the sheep and the nearest terrain feature (usually a ridge) that would obscure the helicopter until the helicopter is past that feature.
	Sheep-related independent variables(all continuous)
Distance to security cover	The pre-disturbance distance (m) between sheep and steep terrain (>30° degrees slope) with rocky outcrops or scree and talus forming its predominant ground cover. This distance equals zero when animals are inside security cover.
Group size	The number of non-lambs in a group. I excluded young of the year from group size values because infant ungulates appear to recognise potential threats less readily than older conspecifics (FitzGibbon & Lazarus 1995), and their responses to risk likely are dependent on the responses of their mothers. Thus, excluding young of year from group size values was an important consideration for pooling data from male and female-young groups. I used the same rationale for *proportion bedded* (see below). Group boundaries were defined as in Frid (1997).
Proportion of lambs	The proportion of lambs in a group; male groups were excluded from analyses.
Proportion bedded	Proportion of non-lambs in a group that was bedded just prior to disturbance.

Table 2. Reduced logistic regression model estimating the effect of helicopter variables on probability of escape (Stage 1 of model building, see Methods). Independent variables were transformed as Log_{10} (x+1). Because subset models with different combinations of variables were specified one at the time, there are several sets of non-significant statistics for each variable excluded from the reduced model, which are not presented for brevity.

Variables tested	**Variable included in model?**	**Effect likelihood ratio test of variables included (DF = 1)**			**Whole model test (N = 57)**				
		Estimate ± SE	χ^2	***P***	***-log-likelihood***	χ^2	***DF***	***P***	***Rho***^{2}
Whole model test					22.89	17.78	2	<0.001	0.28
Intercept	yes	-3.74 ± 1.04							
Least distance	yes	9.68 ± 3.32	11.08	<0.001					
Relative elevation	yes	-0.40 ± 0.18	5.92	0.02					
Distance. to terrain block	no								
Least dist. * relative elevation	no								
Least distance * distance to terrain block	no								

Table 3. Reduced logistic regression models estimating the effect of helicopter variables and their interaction with each sheep variable. (Stage 2 of model building, see Methods.) Distances, elevations, and group size were transformed as Log_{10} (x+1). Proportions were arcsine square root transformed. Because subset models with different combinations of variables were specified one at the time, there are several sets of non-significant statistics for each variable excluded from the reduced model, which are not presented for brevity.

Variables tested and sample sizes for each model	**Variable included in model?**	**Effect likelihood ratio test of variables included (DF = 1)**			**Whole model test**				
		Estimate ± SE	χ^2	***P***	***-log-likelihood***	χ^2	***DF***	***P***	***Rho***^{2}
Model 1 (N = 57)									
Whole model					11.51	40.54	3	<0.001	0.64
Intercept	yes	-7.00 ± 2.45							
Relative elevation	yes	-0.63 ± 0.31	5.99	0.01					
Least distance	yes	29.60 ± 9.56	29.81	<0.001					
Dist. to security cover * least dist.	yes	-9.89 ± 3.13	22.75	<0.001					
Distance to security cover	no								
Dist. to security cover * relative elevation	no								
Model 2 (N = 57)									
Whole model					20.21	23.14	2	<0.001	0.36
Intercept	yes	-4.85 ± 1.35							
Least distance	yes	29.00 ± 8.10	20.69	<0.001					
Group size * least distance	yes	-13.04 ± 4.43	11.27	<0.001					
Group size * relative elevation	no								
Group size	no								
Relative elevation	no								

Table 3, continued.

Variables tested and sample sizes for each model	**Variable included in model?**	**Effect likelihood ratio test of variables included (DF = 1)**			**Whole model test**				
		Estimate ± SE	χ^2	***P***	***-log-likelihood***	χ^2	***DF***	***P***	***Rho***^{2}
Model 3 (N = 52)									
Whole model					23.10	12.29	1	<0.001	0.21
Intercept	yes	-3.63 ± 0.99							
Least distance	yes	10.33 ± 3.49	12.29	<0.001					
Relative elevation	no								
Proportion bedded	no								
Proportion bedded * least distance	no								
Proportion bedded * relative elevation	no								
Model 4 (N = 39)					17.47	11.46	1	<0.001	0.25
Whole model									
Intercept	yes	-3.59 ± 1.12							
Proportion of lambs * least distance	yes	17.62 ± 6.50	11.46	<0.001					
Least distance	no								
Proportion of lambs	no								
Relative elevation	no								
Relative elevation * proportion of lambs	no								

Table 4. Reduced logistic regression model testing the effect of multiple sheep and helicopter variables on the probability that sheep would escape from helicopters. (Stage 3 of model building; see Methods). Independent variables were transformed as $\mathrm{Log}_{10}(x+1)$.

Model tested	**Variable included?**	**Effect likelihood ratio test of variables included (DF = 1)**			**Whole model test (N = 57)**				
		Estimate ± SEE	χ^2	***P***	***-log-likelihood***	χ^2	***DF***	***P***	***Rho***^{2}
Whole model					20.48	40.97	4	<0.001	0.65
Intercept	yes	-7.21							
Least distance	yes	34.32 ± 12.68	14.36	<0.001					
Relative elevation	yes	-0.59 ± 0.32	4.63	0.03					
Dist. to security cover * least dist.	yes	-9.24 ± 3.27	15.40	<0.001					
Group size* least distance	no	-4.18 ± 6.43	0.43	0.51					

Table 5. Reduced linear regression model estimating the effect of helicopter variables on escape initiation distance. (Stage 1 of model building, see Methods). Independent variables were transformed as $\mathrm{Log}_{10}(x+1)$.

Variable	**P**	**Included in reduced model?**	**Regression coefficient ± standard error**	**ANOVA SUMMARY FOR REDUCED MODEL**				
Intercept	0.01	yes	0.13 ± 0.050	***F***	***DF***	***P***	***R***^{2}	***SEE***
Distance to terrain block (DTB)	0.002	yes	0.30 ± 0.091	11.33	1,40	0.002	0.22	0.12
Relative elevation (RE)	0.13	no						
RE * DTB	0.16	no						

Table 6. Reduced linear regression model testing the effects of interactions between sheep and helicopter variables on escape initiation distance (Stage 2 of model building, see Methods). Distances and group sizes were transformed as Log_{10} (x+1), and proportions were arcsine square root transformed.

Variables	**P**	**Included in reduced model?**	**Regression coefficient ± standard error**	**ANOVA SUMMARY FOR REDUCED MODEL**				
				F	***DF***	***P***	R^2	***SEE***
Model 1 ***(N = 42)***				11.33	1, 40	0.002	0.22	0.12
Intercept	0.01	yes	0.13 ± 0.050					
Distance to terrain block (DTB)	0.002	yes	0.30 ± 0.091					
Group size	0.07	no						
Group size * DTB	0.1	no						
Distance to security cover (DSC)	0.3	no						
DSC * DTB	0.3	no						
Proportion bedded (PB)	0.2	no						
PB * DTB	0.3	no						
Model 2 ***(N = 28)***				4.74	1, 26	0.04	0.15	0.12
Intercept	0.02	yes	0.17 ± 0.071					
DTB	0.04	yes	0.27 ± 0.13					
Proportion of lambs (PL)	0.6	no						
PL * DTB	0.4	no						

Table 7. Helicopter variables excluded from reduced linear regression model estimating distance escaped. (Stage 1 of model building, see Methods). No variables remained in the model (N = 43).

Variable	**T (DF = 2)**	**P**
Distance to terrain block (TB)	1.67	0.2
Least distance (LD)	0.073	0.8
Relative elevation (ELEV)	1.54	0.2
LD * TB	0.41	0.52
LD * ELEV	1.48	0.2

Table 8. Reduced linear regression model estimating effects of interactions between proportion bedded and helicopter variables on distance escaped (Stage 2 of model building, see Methods). Proportion bedded was arcsine square root transformed, and remaining independent variables were transformed as Log_{10} (x+1).

Variable	**P**	**Included in reduced model?**	**Regression coefficient ± standard error**	**ANOVA SUMMARY FOR REDUCED MODEL**				
Intercept		yes	2.34 ± 0.13	***F***	***DF***	***P***	R^2	***SEE***
Proportion bedded * distance to terrain block	0.001	yes	-8.00 ± 0.23	12.10	1, 37	0.001	0.25	0.52
Least distance	0.9	no						
Proportion bedded	0.9	no						
Distance to terrain block	0.7	no						
Proportion bedded * least distance	0.11	no						

Table 9. Sheep and helicopter variables excluded from reduced linear regression models testing for effects of distance to security cover and group size on distance escaped. (Stage 2 of model building, see Methods). No variables remained in the models.

Variable	T (DF =2)	P
Model 1 (N = 43)		
Distance to terrain block (TB)	1.67	0.2
Least distance (LD)	0.07	0.8
Distance to security cover (DS)	4.07	0.05
DS*TB	0.64	0.4
DS*LD	0.85	0.4
Model 2 (N = 43)		
Distance to terrain block	1.67	0.2
Least distance	0.07	0.8
Group size (GS)	3.14	0.08
GS*TB	0.0026	1.0
GS*LD	0.12	0.7

Table 10. Setback distances and elevations to be used as *preliminary* guidelines for the Yukon. Elevations were categorised according to criteria provided by Fig. 12. For each escape probability and elevation category, setback distances were estimated with the logistic regression model of Table 2. I suggest basing guidelines on an escape probability of 0.1. For comparison, the table also provides setback distances based on a probability of 0.2. Managers will need professional judgement to decide whether escape probabilities greater or lower than 0.1 are warranted (see Discussion and Fig. 10). See Fig. 11 for examples of how to translate relative elevations to actual elevations that pilots will refer to.

Escape probability	Relative Elevation (ft)	Setback distance (km)
0.1	< -500	2.1
0.2	< -500	1.6
0.1	≥ -500 and < 0	3.1
0.2	≥ -500 and < 0	2.4
0.1	≥0 and ≤ 1000	4.5
0.2	≥0 and ≤ 1000	3.5

Figure captions

Fig. 1. Trigonometry of a helicopter trajectory. The smallest distance between the sheep group (filled circle) and the helicopter trajectory (arrow), or least distance, determines the angle formed by the line of distance *x* and the helicopter trajectory. If *x* is held constant, this angle is smaller when least distance is (a) small than when least distance is (b) large. Because this angle and least distance are interchangeable measures, least distance should be interpreted as a measure of the directness of the helicopter's approach from the perspective of the sheep's location. Using an angle to measure the directness of a helicopter's approach may have eased the reader's interpretation of my results, but I chose to use least distance because ultimately it is the variable that helicopter pilots will be able to control and which will determine setback distances for reducing disturbance.

Fig. 2. Effect of the interaction of least distance and the sheep's distance to security cover on escape probability. The family of curves in Fig. 2a was generated with parameters of Model 1 of Table 3, with relative elevation held constant at 0. Sheep groups at distances to security cover of 75 m (the mean distance), 20 m (the median distance), and 0 m (inside security cover), are represented, respectively, by the short-dashed line, the solid line, and the long-dashed line. Fig. 2b is an example of the relationship described by this family of curves. Solid circles represent sheep inside security cover or within 10 m of it, and open circles represent sheep >10 m from cover. Data points are jittered so that overlapping points can be read. Because I had to categorise continuous three-dimensional data to show it in two dimensions, this example is only for descriptive purposes and statistically significant trends are in Fig. 2a.

Fig. 3. Effect of the interaction of least distance and the sheep's group size (lambs excluded) on escape probability. The family of curves in Fig. 3a was generated with parameters in Model 2 of Table 3. The long-dashed line, the solid line, and the short-dashed line represent groups with sizes of 40, 18 (the mean group size), and 2, respectively. Fig. 3b is an example of the relationship described by this family of curves. Dark circles represent groups with ≤ 20 sheep, and light circles represent groups with >20 animals. Data points are jittered so that overlapping points can be read. Because I had to categorise continuous three-dimensional data to show it in two dimensions, this example is only for descriptive purposes and statistically significant trends are in Fig. 3a.

Fig. 4. Effect of the interaction of least distance and the proportion of lambs in the group (male groups excluded) on escape probability. The family of curves in Fig. 4a was generated with parameters in Model 4 of Table 3. Groups with proportions of lambs of 0.1, 0.3 (the mean proportion), and 0.5, are represented, respectively, by the long-dashed line, the solid line, and the short-dashed line. Fig 4b is an example of the relationship described by this family of curves. Dark circles represent groups with a proportion of lambs ≥ 0.3, and lighter circles representing groups with a proportion of lambs <0.3. Data points are jittered so that overlapping points can be read. Because I had to categorise continuous three-dimensional data to show it in two dimensions, this example is only for descriptive purposes and statistically significant trends are in Fig. 4a.

Fig. 5. Effect of the helicopter's relative elevation on the decision to escape. See Table 2 and Model 1 of Table 3 for logistic regression parameters. Data points are jittered so that overlapping points can be read.

Fig. 6. Relationships between independent variables and escape initiation distance. Distance to terrain block (a) was included in the reduced linear regression model (Table 5). Group size (b) was excluded from the reduced model but was nearly significant (Table 6).

Fig. 7. Distance escaped in relation to the interaction between distance to terrain block and proportion of bedded animals. The family of lines in Fig. 7a was generated with parameters of Table 7. Fig 7b is an example of the relationship described by this family of lines. Dark and light circles represent, respectively, groups with proportion bedded ≥ 0.5 and <0.5. Because I had to categorise continuous three-dimensional data to show it in two dimensions, this example is only for descriptive purposes and statistically significant trends are in Fig. 7a.

Fig. 8. Descriptive plots of distance escaped in relation to (a) distance to security cover and (b) group size. Both variables were excluded from regression models estimating distance escaped but were nearly significant (Table 9).

Fig. 9. Effect of distance to security cover on group size ($y = 0.93+0.17 + x$; $R^2 = 0.18$, $N = 57$, $F_{1,55} = 11.79$, $P = 0.001$). Data points are jittered so that overlapping points at distance to cover = 0 can be read.

Fig. 10. Recommended decision making process for managers using logistic regression models of escape probability to generate setback distances that reduce helicopter disturbance of sheep.

Fig. 11. Example of how to apply knowledge of the sheep's' altitudinal distribution in the design of guidelines for helicopters. Relative elevations are based on the range where most animals are likely to be, and are converted to actual elevations that helicopter pilots can refer to. For each of these elevations there is a corresponding setback distance, as exemplified in Fig. 12.

Fig. 12. Example of setback distances and elevations generated with the logistic regression model of Table 2. Solid lines represent distances and elevations based on escape probabilities of 0.1, and dashed lines are based on escape probabilities of 0.2. I suggest grouping elevations into categories encompassed by the vertical dot lines (including the right y-axes), and using the setback distance that corresponds to the upper range of each elevation category. For example, for an escape probability of 0.2, a setback distance of 3.5 km corresponds to the elevation category of ≥ 0 and ≤ 1000 ft.

Fig. 1

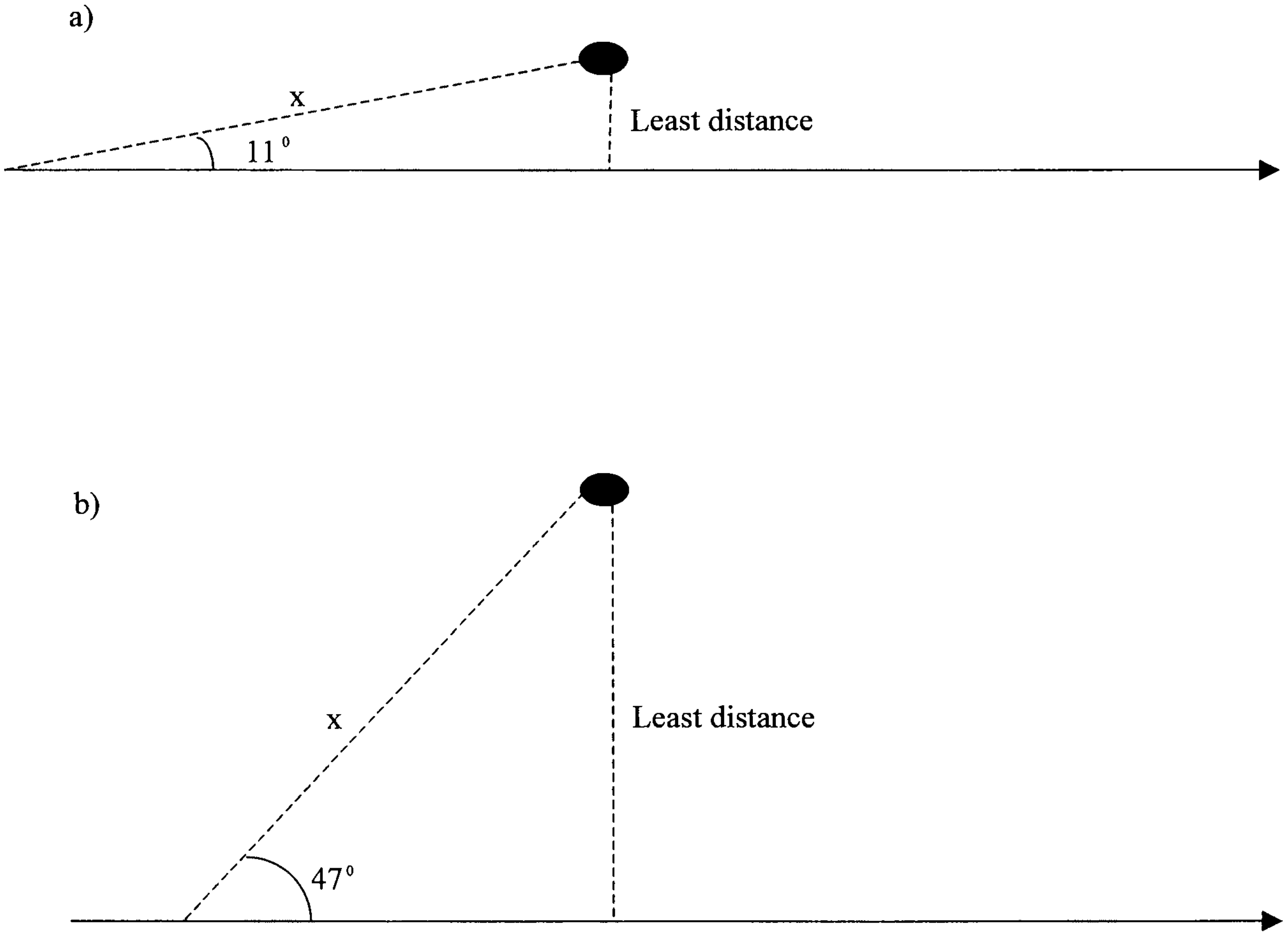


Fig. 2

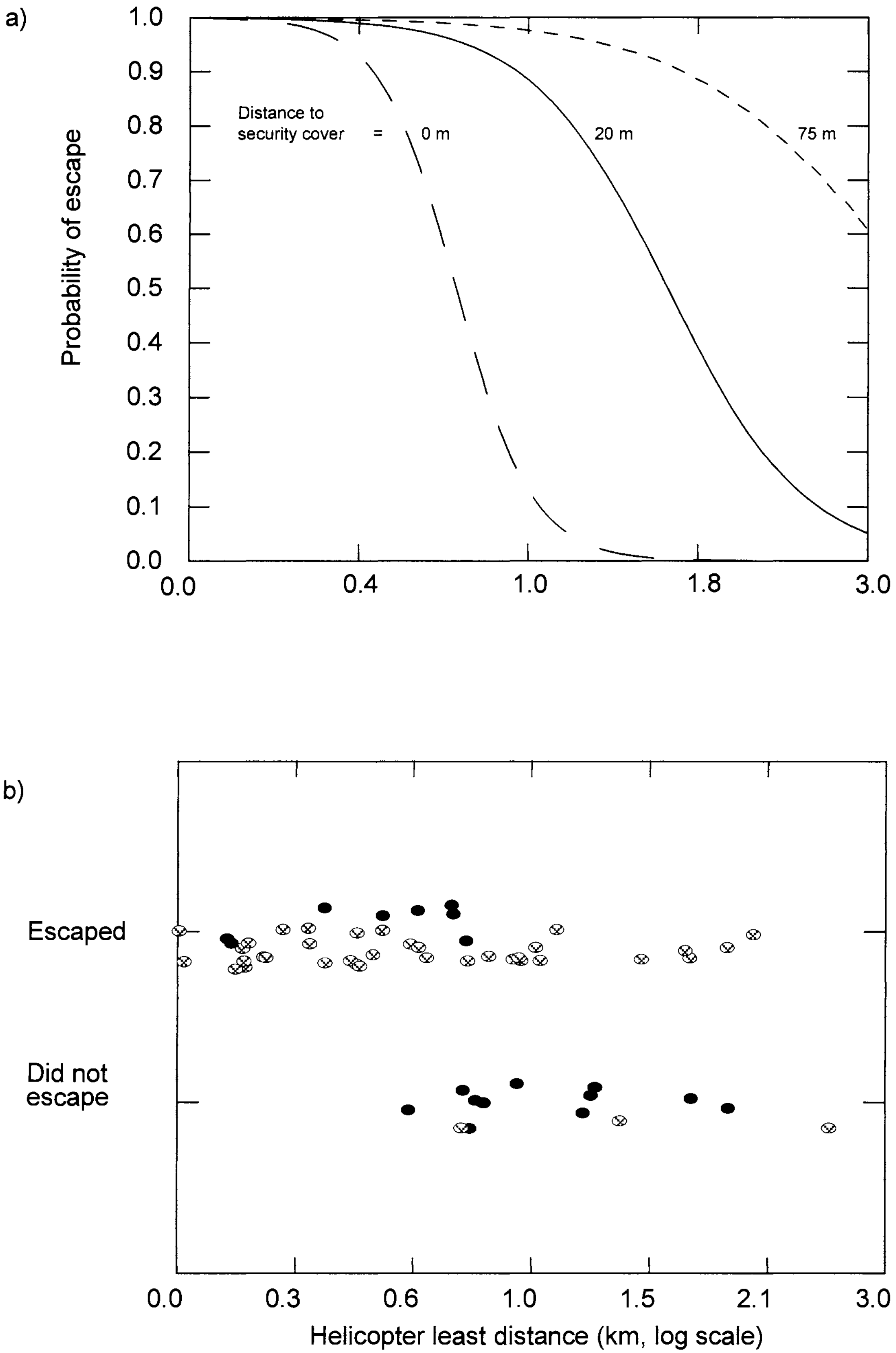

a)
Probability of escape
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Distance to
security cover =
0 m
20 m
75 m
0.0
0.4
1.0
1.8
3.0
b)
Escaped
Did not
escape
0.0
0.3
0.6
1.0
1.5
2.1
3.0
Helicopter least distance (km, log scale)

Fig. 3

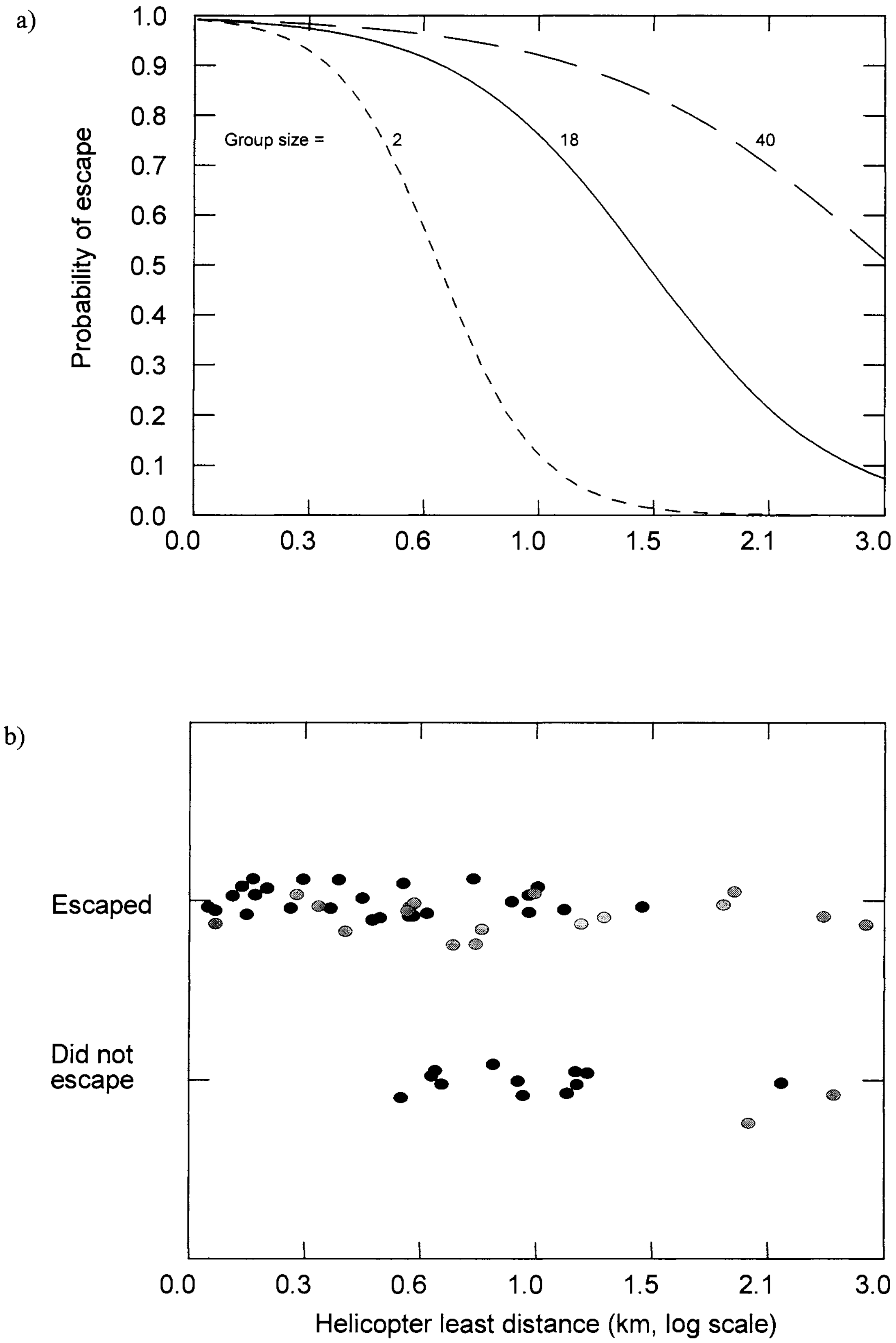

a)
Probability of escape
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Group size =
2
18
40
0.0
0.3
0.6
1.0
1.5
2.1
3.0
b)
Escaped
Did not escape
0.0
0.3
0.6
1.0
1.5
2.1
3.0
Helicopter least distance (km, log scale)

Fig. 4

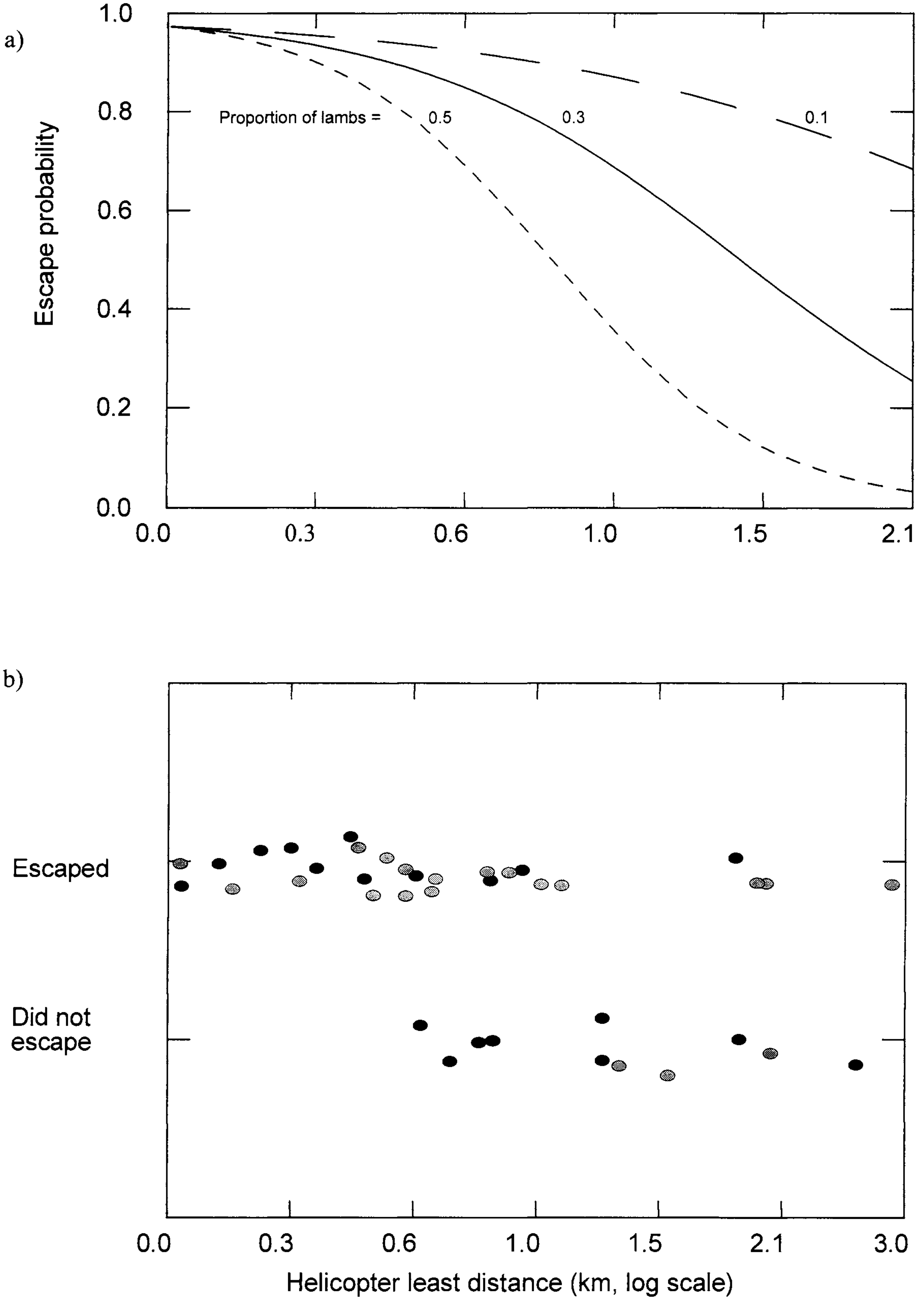
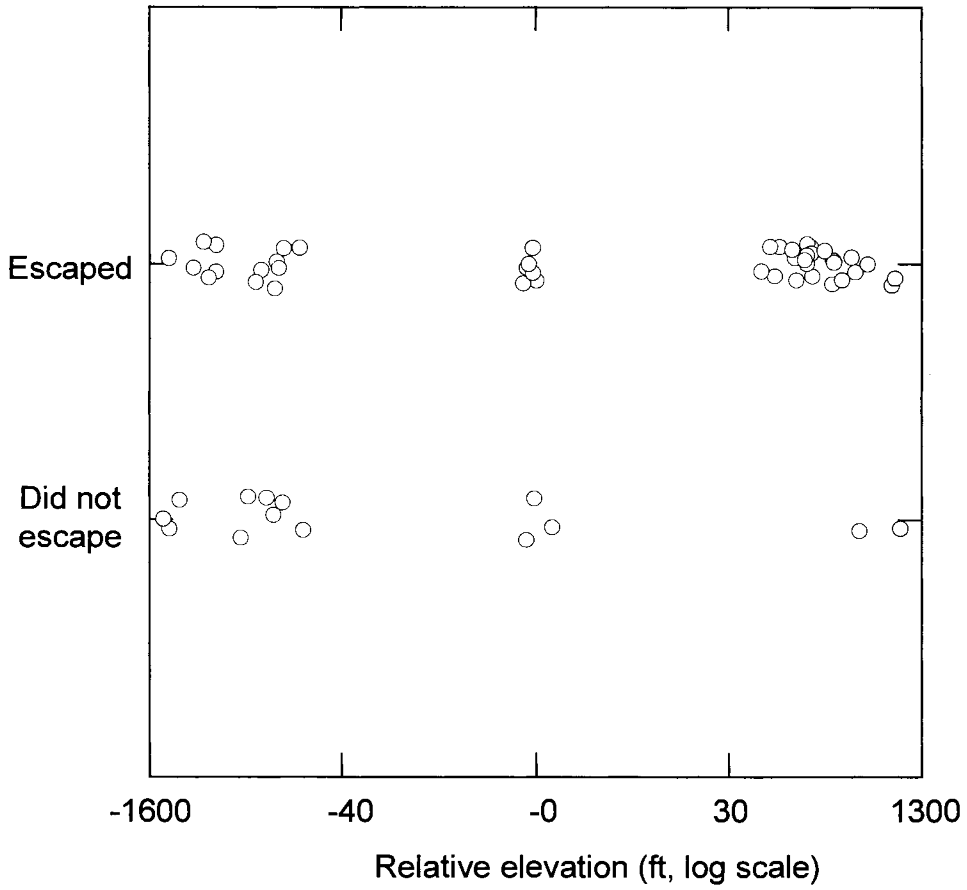

a)
1.0
0.8
0.6
0.4
0.2
0.0
Escape probability
Proportion of lambs =
0.5
0.3
0.1
0.0
0.3
0.6
1.0
1.5
2.1
b)
Escaped
Did not escape
0.0
0.3
0.6
1.0
1.5
2.1
3.0
Helicopter least distance (km, log scale)

Fig. 5



Escaped
Did not escape
-1600
-40
-0
30
1300
Relative elevation (ft, log scale)

Fig. 6

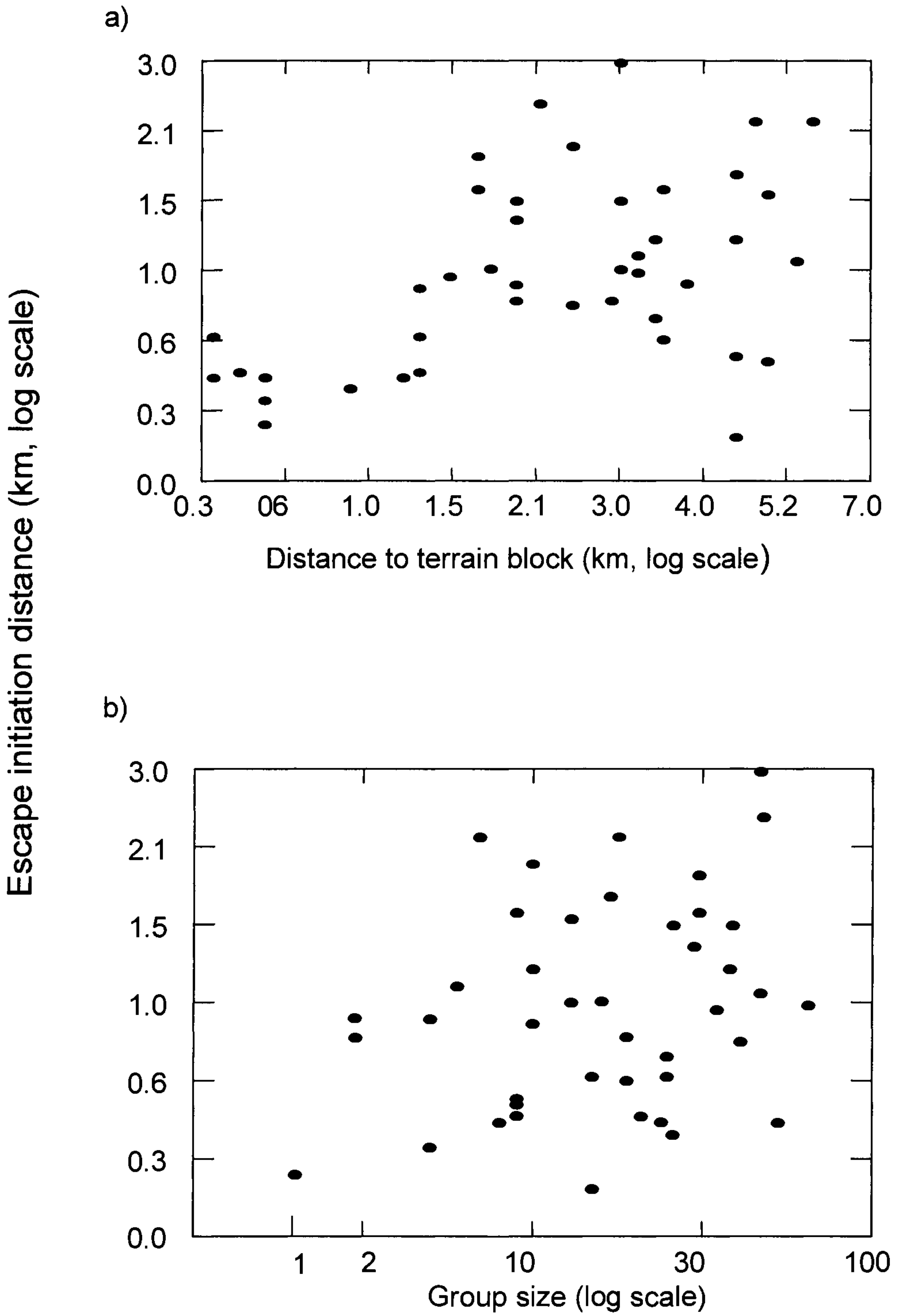

a)
Escape initiation distance (km, log scale)
3.0
2.1
1.5
1.0
0.6
0.3
0.0
0.3
06
1.0
1.5
2.1
3.0
4.0
5.2
7.0
Distance to terrain block (km, log scale)
b)
3.0
2.1
1.5
1.0
0.6
0.3
0.0
1
2
10
30
100
Group size (log scale)

Fig. 7

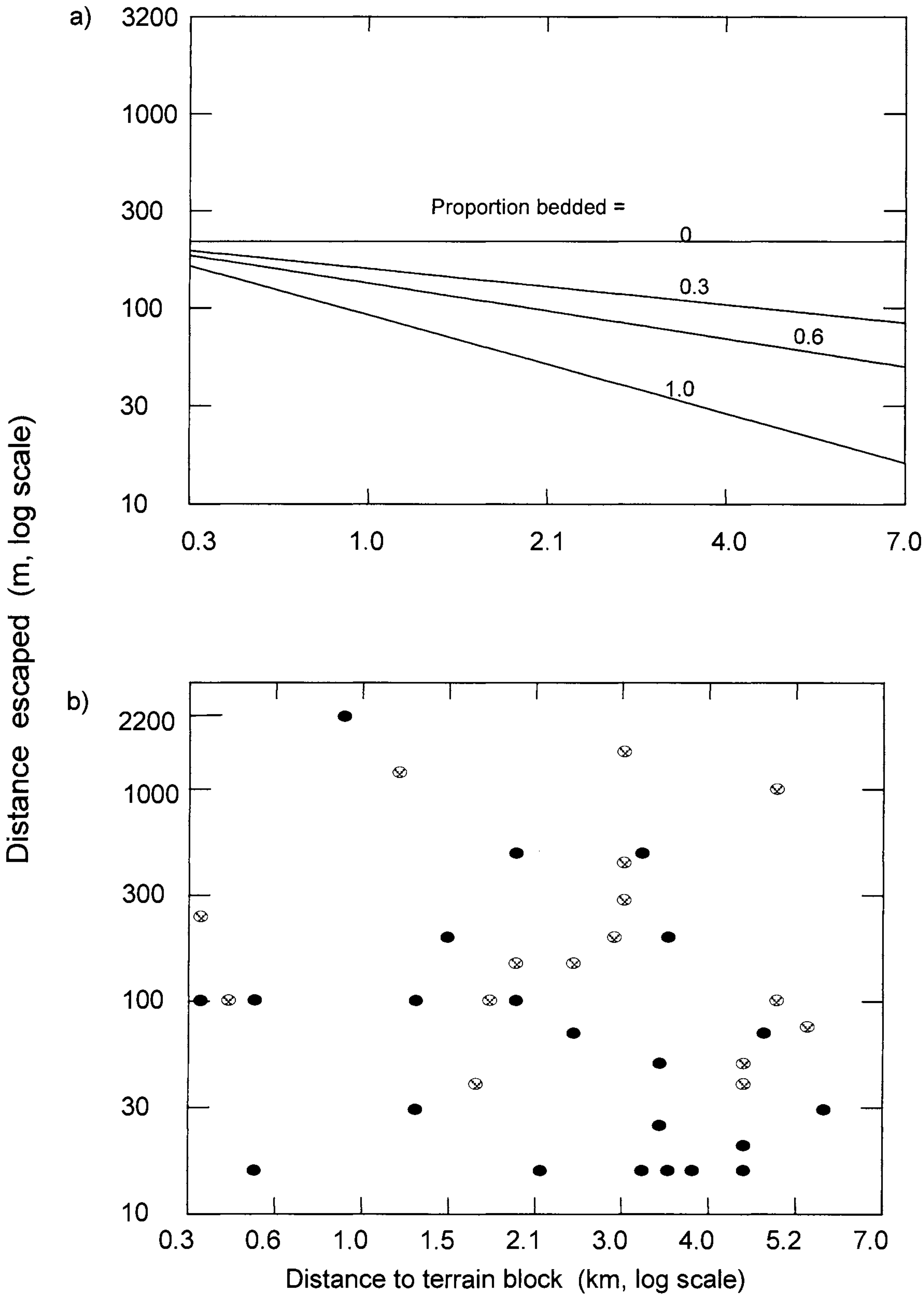

a)
3200
1000
300
100
30
10
Proportion bedded =
0
0.3
0.6
1.0
0.3
1.0
2.1
4.0
7.0
Distance escaped (m, log scale)
b)
2200
1000
300
100
30
10
0.3
0.6
1.0
1.5
2.1
3.0
4.0
5.2
7.0
Distance to terrain block (km, log scale)

Fig. 8

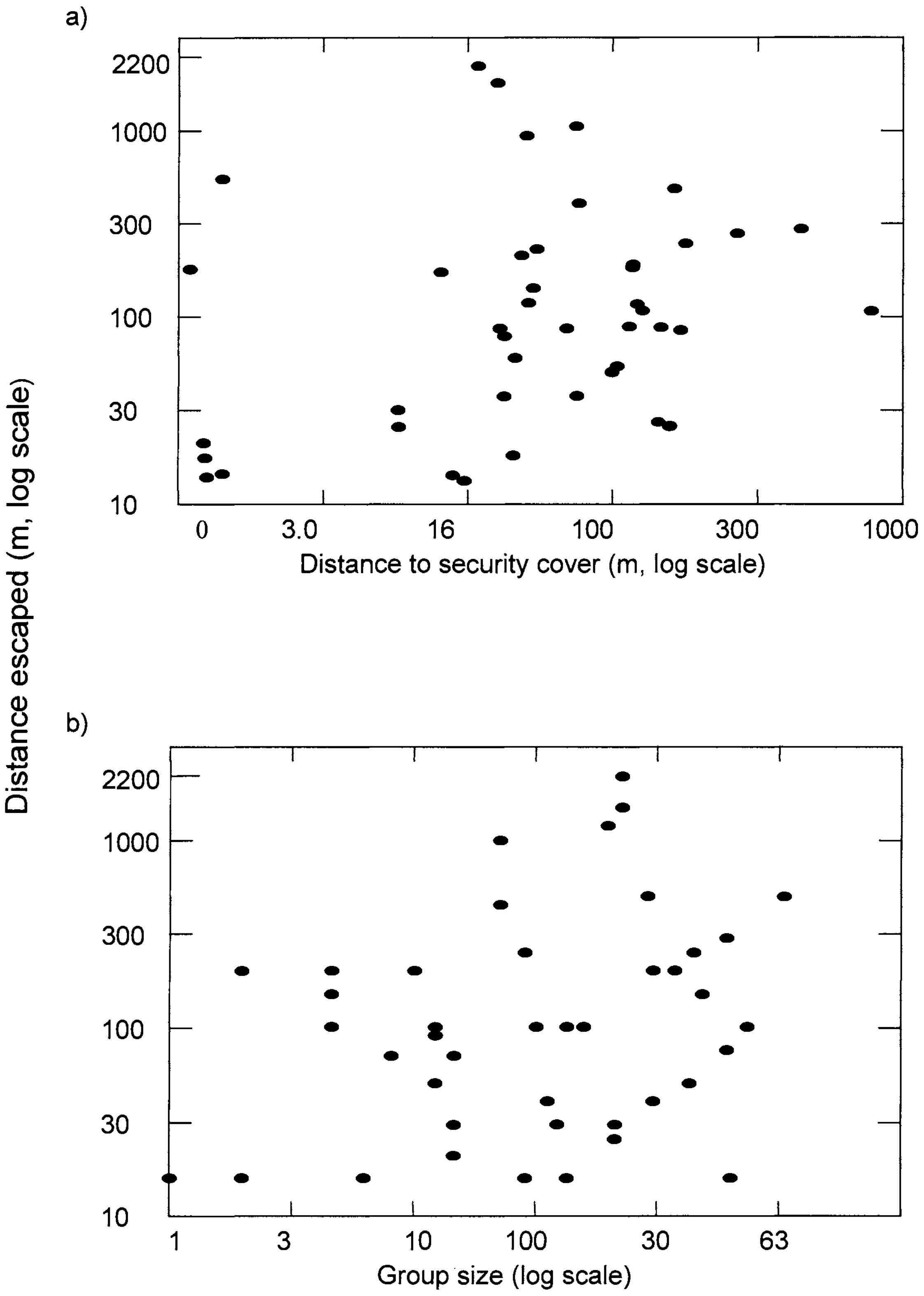

a)
2200
1000
300
100
30
10
0
3.0
16
100
300
1000
Distance to security cover (m, log scale)
Distance escaped (m, log scale)
b)
2200
1000
300
100
30
10
1
3
10
100
30
63
Group size (log scale)

Fig. 9

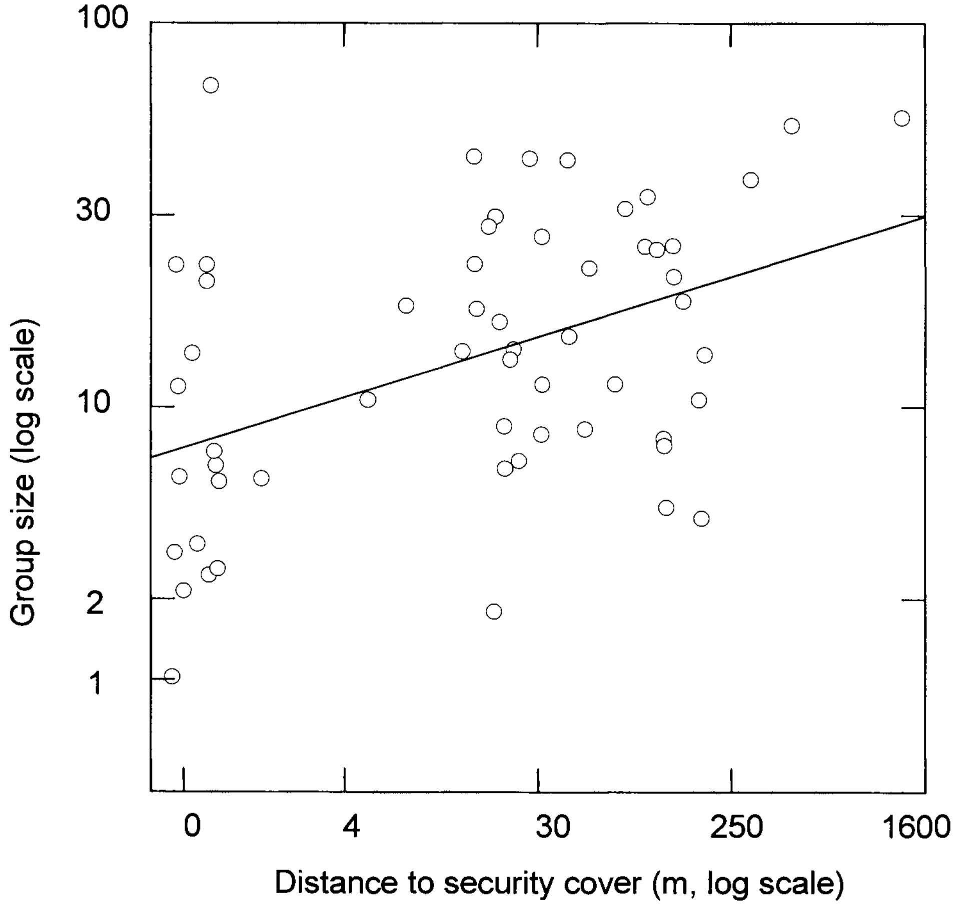

100
30
10
2
1
Group size (log scale)
0
4
30
250
1600
Distance to security cover (m, log scale)

Fig. 10

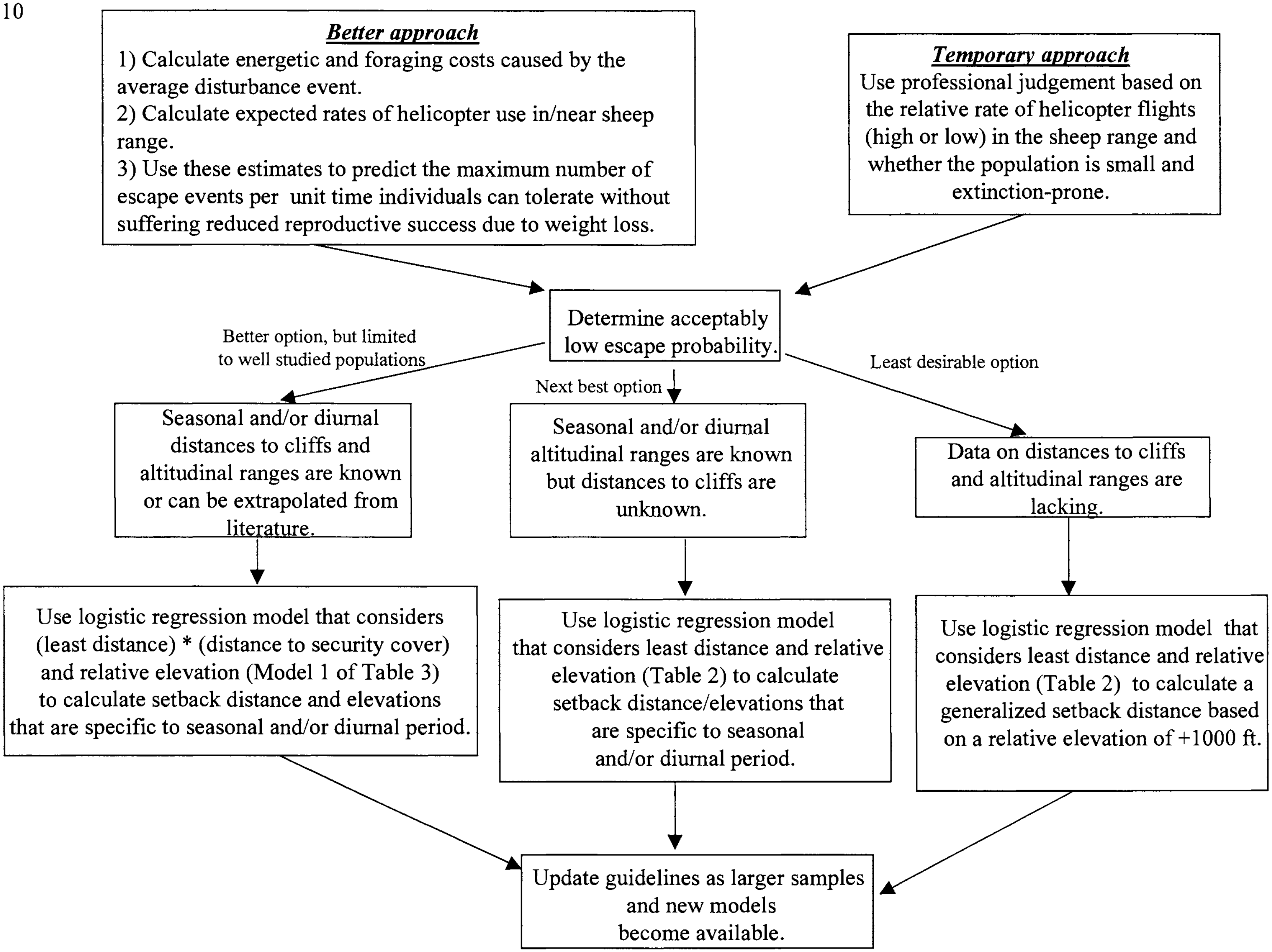

Better approach
1) Calculate energetic and foraging costs caused by the average disturbance event.
2) Calculate expected rates of helicopter use in/near sheep range.
3) Use these estimates to predict the maximum number of escape events per unit time individuals can tolerate without suffering reduced reproductive success due to weight loss.
Temporary approach
Use professional judgement based on the relative rate of helicopter flights (high or low) in the sheep range and whether the population is small and extinction-prone.
Determine acceptably low escape probability.
Better option, but limited to well studied populations
Next best option
Least desirable option
Seasonal and/or diurnal distances to cliffs and altitudinal ranges are known or can be extrapolated from literature.
Seasonal and/or diurnal altitudinal ranges are known but distances to cliffs are unknown.
Data on distances to cliffs and altitudinal ranges are lacking.
Use logistic regression model that considers (least distance) * (distance to security cover) and relative elevation (Model 1 of Table 3) to calculate setback distance and elevations that are specific to seasonal and/or diurnal period.
Use logistic regression model that considers least distance and relative elevation (Table 2) to calculate setback distance/elevations that are specific to seasonal and/or diurnal period.
Use logistic regression model that considers least distance and relative elevation (Table 2) to calculate a generalized setback distance based on a relative elevation of +1000 ft.
Update guidelines as larger samples and new models become available.

Fig. 11

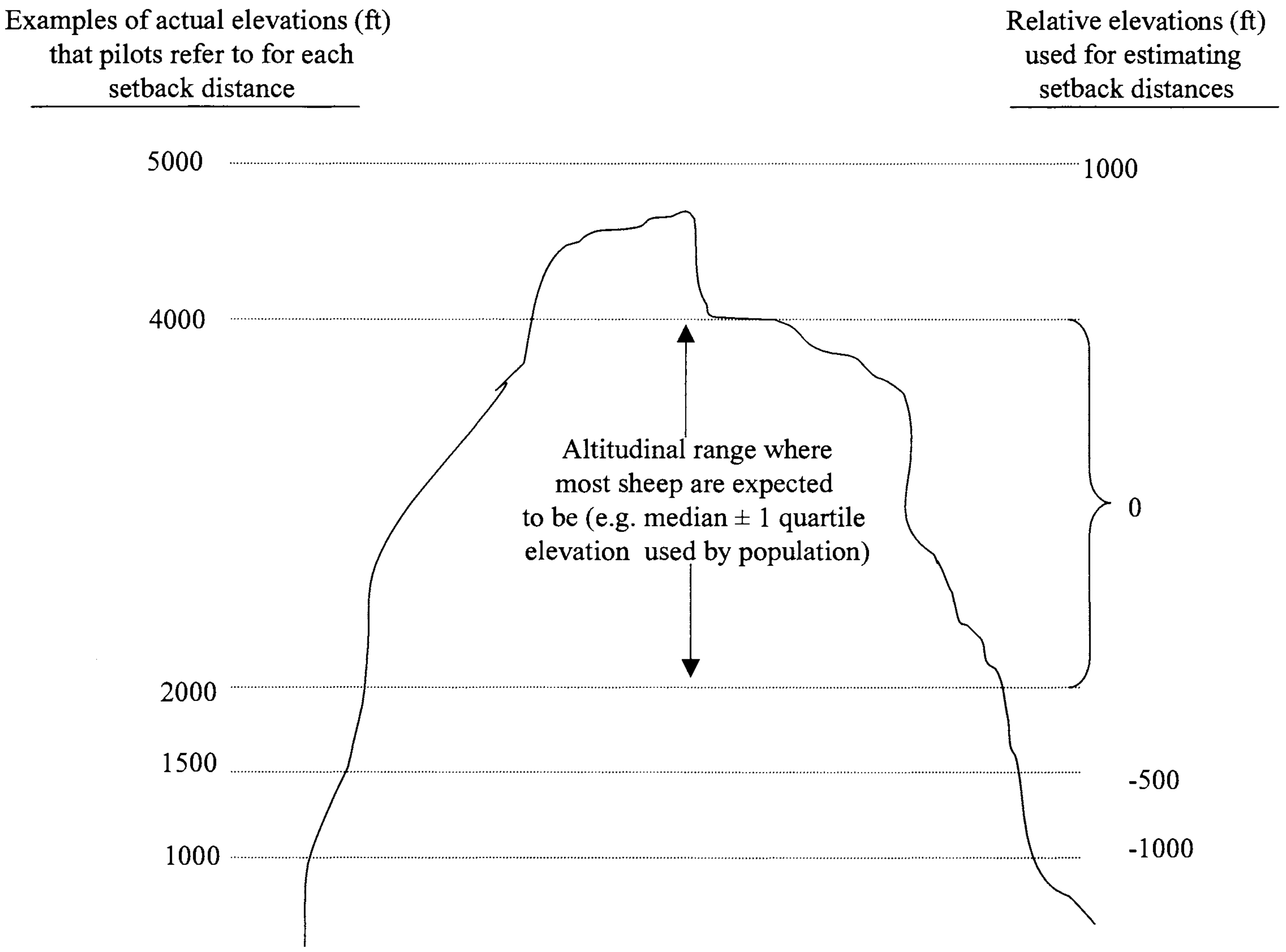
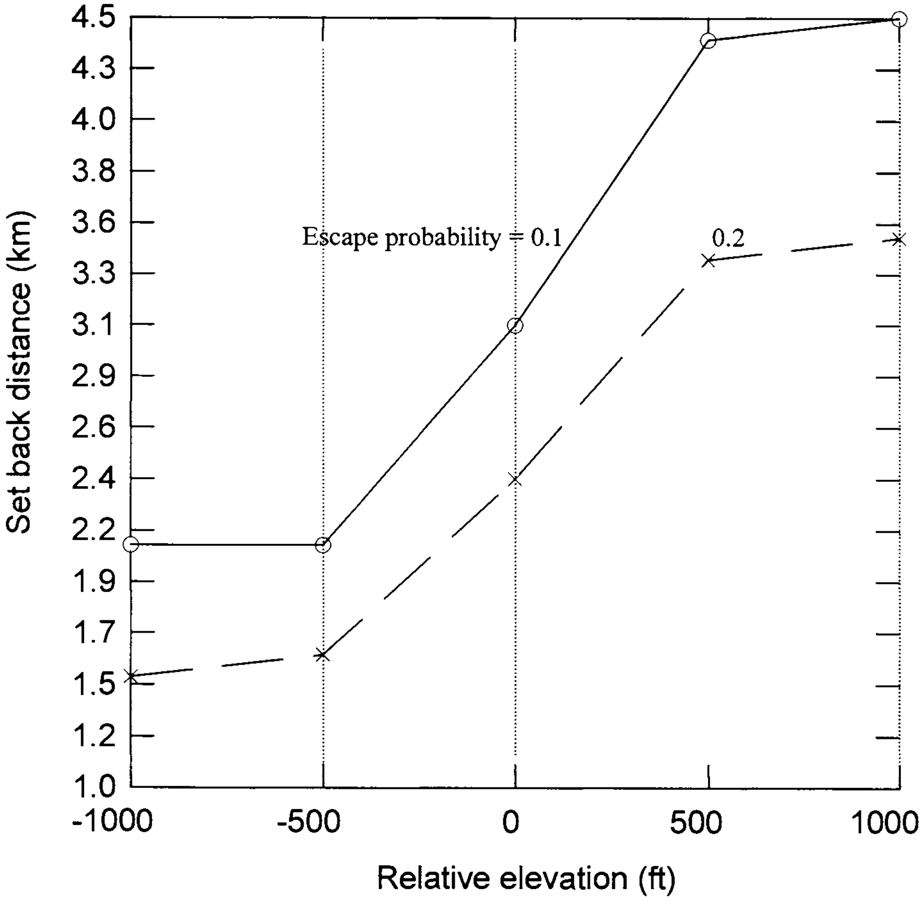

Examples of actual elevations (ft) that pilots refer to for each setback distance
Relative elevations (ft) used for estimating setback distances
5000
1000
4000
0
Altitudinal range where most sheep are expected to be (e.g. median ± 1 quartile elevation used by population)
2000
1500
-500
1000
-1000

Fig. 12



4.5
4.3
4.0
3.8
3.6
3.3
3.1
2.9
2.6
2.4
2.2
1.9
1.7
1.5
1.2
1.0
Set back distance (km)
-1000
-500
0
500
1000
Relative elevation (ft)
Escape probability = 0.1
0.2