HYPOTHESES AND PRELIMINARY EXPERIMENTAL DESIGNS FOR INVESTIGATING IMPACTS OF HELICOPTER DISTURBANCE ON DALL'S SHEEP

Alejandro Frid
Boreal Research Associates, Site 20, Comp. 357, RR 1, Whitehorse, YT,
Y1A 4Z6, Canada, email: afrid@yknet.yk.ca

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

November 1996

TABLE OF CONTENTS

LIST OF TABLES AND FIGURE

1. GENERAL INTRODUCTION

Aircraft disturbance of Dall's sheep (*Ovis dalli dalli*), mountain goats (*Oreamnos americanus*), woodland caribou (*Rangifer tarandus caribou*), and other wildlife is a growing concern in the Yukon for two reasons. First, the economy is largely dependent on mining, and most mineral exploration occurs in mountainous, roadless areas which require aircraft access. Such areas often contain the year-round ranges of sheep and goats, or the summer/rutting ranges of caribou. Second, an aircraft-based tourism industry (sight-seeing and access to remote areas for hiking or river trips) is rapidly growing and largely unregulated. Economic pressures to expand mining and tourism likely will lead to higher levels of disturbance in the near future. Wildlife managers should be concerned with this problem because aircraft disturbance could lead to population declines (Harrington & Veitch 1992; Bradshaw 1994; Sutherland 1996; Fig. 1).

The purpose of this report is to provide *a priori* hypotheses and preliminary experimental designs for investigating the impacts of helicopter disturbance on Dall's sheep. Hypotheses were developed from my preliminary work at Killermun Lake, southwest Yukon (Frid 1995, 1997a) and from published research on several ungulate taxa. The project focuses on helicopters because they are the aircraft most likely to be used by the mining industry, and because their impact is significantly greater than that of fixed-winged aircraft (Bleich et al. 1990; 1994), including jet fighters (Harrington & Veitch 1991). Although my focus excludes mountain goats (which are very susceptible to helicopter disturbance: Côté 1997) and caribou, the conservation of these ungulates and other wildlife must be addressed by future projects.

Disturbance of wildlife from aircraft and other human activities is analogous to an increase in predation risk (Berger et. al 1983; Sutherland 1996). While only predation causes direct mortality, both predation and disturbance affect population dynamics indirectly by altering an individual's investment in antipredator behaviour (Dehn 1994; FitzGibbon & Lazarus 1995; Sutherland 1996; Fig. 1). Antipredator behaviour often results in greater energetic costs; animals perceiving increased risk may seek safety by running and/or moving to a different location (e. g. Berger et al. 1983; Tyler 1991; Bleich et al. 1994; Bradshaw 1994; Chubbs et al. 1994; Frid 1995, 1997a) and, in the case of some Caprinae, by increasing use of steep terrain (e. g. Murie 1944; Côté 1997). An investment in antipredator behaviour also reduces foraging efficiency by increasing vigilance, and/or by forcing animals to forage in habitats where safety is greater but food is scarcer (review in Lima & Dill 1990). Increased energetic costs and reduced foraging efficiency could reduce the reproductive success of individuals and lead to population declines. The link between increased disturbance and reduced population productivity has already been documented by empirical studies of woodland caribou (Harrington & Veitch 1992; R. Florkiewicz pers. comm.). In essence, the effect of disturbance on individual behaviour can be a substantial part of what drives population dynamics (Bradshaw 1994; Sutherland 1996; Fig. 1).

Although there is an abundance of consultant reports assessing aircraft and/or industrial-related disturbance impacts on ungulates, most of these reports

Fig. 1. Conceptual model comparing the effects of helicopter disturbance and predation on individual behaviour and population dynamics. While only predation kills individuals directly, both helicopter disturbance and predation affect antipredator behaviour. An increase in antipredator behaviour results in reduced foraging efficiency and increased energetic costs, thereby affecting body condition and reducing reproductive success. Increased antipredator behaviour and direct predation interact to affect population dynamics.
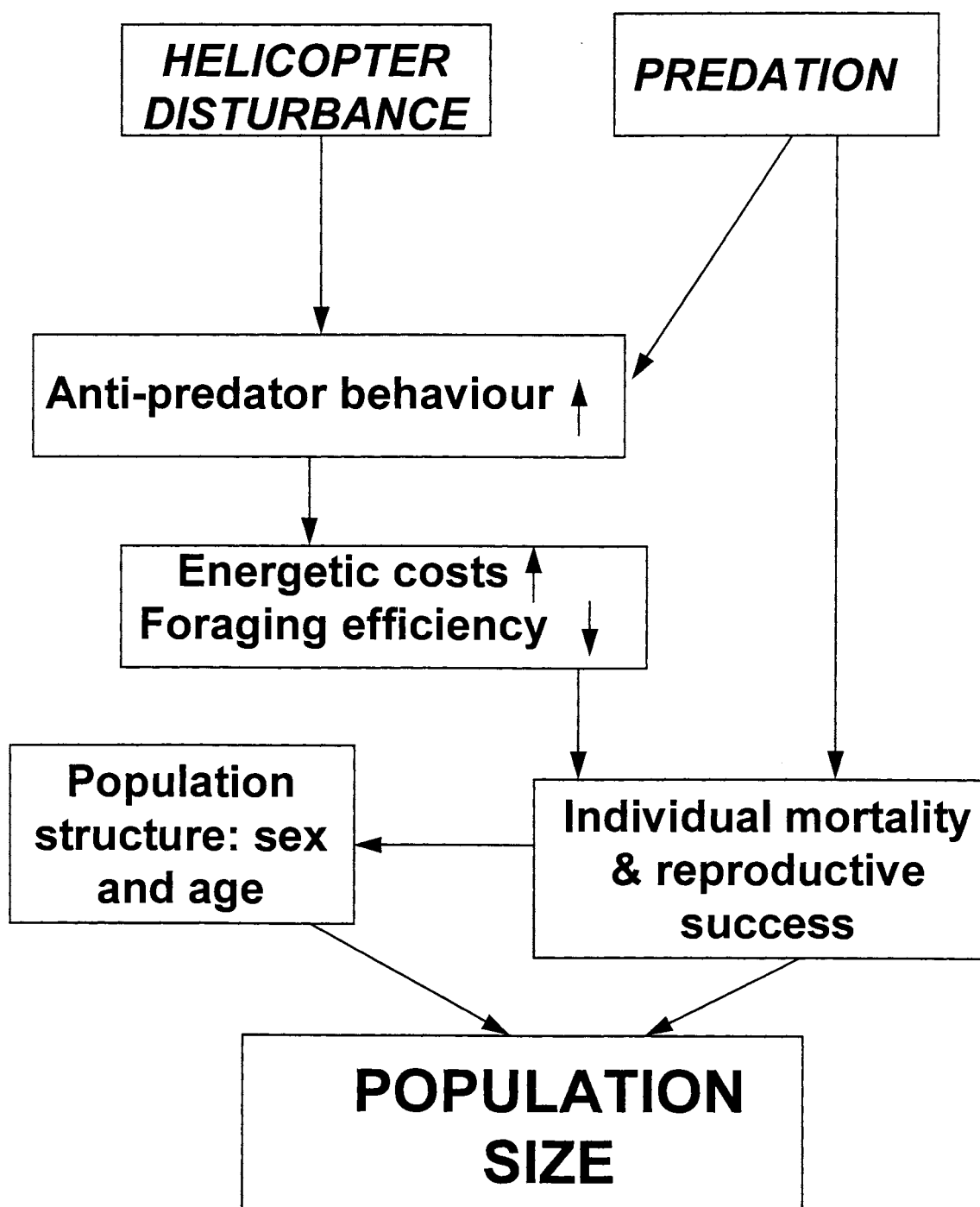
had poor experimental design and lacked *a priori* hypotheses. Thus, they do not provide reliable conclusions (critical review in Bradshaw 1994).

Published, conclusive studies on the impacts of aircraft disturbance on mountain sheep (*Ovis* sp.) are few. They are largely limited to desert bighorn sheep (*Ovis canadensis*: e.g. Krausman & Hervert 1983; Stockwell et. al. 1991; Bleich et al. 1994; Weisenberger et al. 1996) and, to my knowledge, substantial data sets on helicopter disturbance of Dall's sheep are non-existent. Given the lack of information, conclusions of disturbance studies on desert bighorns have been directly generalized for Dall's sheep (e.g. Hegmann 1995), which could be unwarranted. Furthermore, some frequently cited studies of bighorns took place were substantial aircraft disturbance had already been occurring for some time (e. g. Stockwell et. al. 1991), and sheep behaviour likely had already been altered prior to the study. Thus, conclusions from these studies cannot account for the full magnitude of disturbance effects, and may be inapplicable to populations without a long and intense history of disturbance. Also, several variables useful for quantifying disturbance impacts have been recorded only in very limited sample sizes for mountain sheep (see variables recorded by Frid 1995, 1997a).

Although the experimental designs I present here are preliminary, they provide a good foundation for building better designs and for seeking peer review. Fieldwork related to this project will have a small budget (J. Carey pers. comm.), thus I could not consider experiments based on known individuals with satellite or radio-collars. Such experiments have provided rigorous quantification of how disturbance affects energetic costs and habitat selection (e .g. Harrington & Veitch 1991;1992; Bleich et al. 1994; Bradshaw 1994), and should be considered in the future.

Testing the hypotheses developed in this report will have several immediate applications to conservation. For example, results will provide a basis for developing set-back distances (see Frid 1995, 1997a; Côté 1997) for populations that differ in their long-term disturbance histories, even if such populations have not been studied before. They will also assist in developing helicopter routes that minimize impact for specific populations (e. g. Frid 1995, 1997a).

Furthermore, tests of the hypotheses will have an experimental approach which, relative to the results of mensurative studies, will have greater predictive power about the consequences of disturbance and the efficacy of mitigative measures (Underwood 1994). By addressing how disturbance affects individual behaviour, most hypotheses presented here are in fact guides to acquiring empirical data needed to predict long-term population consequences of disturbance (see Fig. 1). Bradshaw (1994) provides a good example of such predictive mathematical models, and Sutherland (1996) synthesizes and expands the theory needed to develop these models. Some studies have already found empirical evidence that reproductive success of ungulates can decrease due to aircraft disturbance (e. g. Harrington & Veitch 1992; R. Florkiewicz pers. comm.). Many studies, however, will not be long enough to detect changes in reproductive success and population productivity. Thus, in

spite of their theoretical nature, mathematical models linking individual behaviour and population dynamics will -- as long as they are built on solid empirical data -- be important tools for the conservation of mountain sheep and other wildlife susceptible to harassment from helicopters.

2. DO IMMEDIATE RESPONSES TO DISTURBANCE WEAKEN DUE TO HABITUATION?: LITERATURE REVIEW AND HYPOTHESES

2.1 Introduction and literature review

Some studies have found that immediate responses by ungulates to motorized disturbance become weaker due to apparent habituation (e. g. Yarmoloy 1988; Tyler 1991; Frid 1995, 1997a; Weisenberger 1996). Still, a study with rigorous experimental design found that, in a population which already had a long history of helicopter disturbance, "(m)ountain sheep did not habituate or become sensitized to repeated helicopter flights" (Bleich et al. 1994:1). Moreover, "both sexes of mountain sheep moved dramatically as direct result of pernicious disturbance of helicopter surveys" (Bleich et al. 1994:5), which resulted in shifts between habitats and sometimes between mountain blocks.

This contrast between studies highlights the fact that there are huge gaps in our understanding of variables affecting habituation processes, including environmental and social factors, taxa, disturbance type, and time scale. Of these variables, I consider time scale to be particularly little understood, especially in relation to how long-term disturbance history affects the strength of immediate responses. In fact, in the published literature I found no convincing studies explicitly comparing immediate responses to disturbance by naive animals (those with very little or no disturbance history prior to the study) and veteran animals (those with a disturbance history of multiple, consecutive years). Understanding how disturbance history at different time scales affects immediate responses is important for predicting the long-term consequences of disturbance on population productivity. In order to point out knowledge gaps, below I critically review studies assessing habituation by ungulates to motorized disturbance.

2.1.1 Habituation at a long-term scale (multiple years)

Bleich et al. (1994) found no evidence of habituation. Immediate responses to helicopters were independent of the long-term disturbance history of individual bighorn sheep. Such histories were quantified with the "(t)otal number of helicopter surveys and capture episodes conducted in the study area from 1 April of the year of the study animal's birth up to, and including, the aerial surveys reported herein" (Bleich et al. 1994: Table 1). Bleich et al., however, assumed that study animals experiencing helicopters for the first time were behaving as naive animals. This assumption is flawed because sheep are "followers" (Geist 1971; Lent 1974), and a young sheep experiencing helicopters for the first time will not have a reaction of its own, but rather will respond as its mother does. Given that the population had been surveyed for many years prior to the study, it is likely that the mothers of all study animals already had a long history of

Table 1. Variables for quantifying impact of helicopter disturbance on Dall's sheep. The first 10 variables are measures of the strength of the immediate reaction to helicopters.

Variable	Definition
First reaction distance	Distance from helicopter at which sheep first reacted (either vigilance or escape).
Vigilance initiation distance	Distance from helicopter at which sheep first became vigilant. (A sub-component of *first reaction distance*.)
Escape initiation distance	Distance from helicopter at which sheep began escape. (A sub-component of *first reaction distance*.)
Escape	Binomial variable describing whether disturbed sheep moved from their pre-disturbance location to a new area. Usually an initial run is followed by walking; some nervous feeding sometimes occurs during the walk (Frid 1995, 1997a).
Escape distance	Distance sheep escaped before either bedding or feeding without traveling.
Escape run time	The time sheep spent running while escaping from the helicopter
Escape walk time	The time sheep spent walking while escaping from the helicopter
Total escape time	Escape run time plus escape walk time
Response time	Time between first reaction (either vigilance or escape) and resuming feeding without traveling or bedding
Feeding interruption time	For animals feeding prior to disturbance, time spent between first reaction and resuming feeding. (A sub-component of *response time*.)
Helicopter time	Time the helicopter was audible to observers (an index of how long the helicopter was in the area).
Least distance	Smallest distance between sheep and the helicopter, which may or may not be smaller than the *first reaction distance*.

disturbance at the onset of observations, and the data could not have detected habituation during the initial disturbance history of the population. In spite of this sampling gap, Bleich et al. (1994:1) have very strong evidence for their assertion that, even in a population with a long disturbance history, "mountain sheep respond dramatically to helicopter(s)". The possibility remains, however, that responses would have been even more dramatic if study animals *and* their mothers had not had prior experience with helicopters.

Berger et al. (1983) studied immediate responses to disturbance by female pronghorns (*Antilocapra americana*) at a roaded, heavily disturbed site (about 200 vehicles/week) and at a relatively undisturbed, but also roaded, site (traffic was about 15 vehicles/week). Traffic at the more disturbed site was, for at least six years up to the time of observation, "associated primarily with mining activities, construction, *and a limited one-week hunting season*" (Berger et al. 1983:204, my emphasis). At the relatively undisturbed site, "none (of the traffic) was associated with environmental exploitation" (Berger et al. 1983:204-5). Results showed the antithesis of habituation. Immediate responses to disturbance from vehicles and people on foot (as measured by escape effort, time for which feeding was interrupted, and frequencies of pilo-erection and clumping behaviour) were stronger for pronghorns from the heavily disturbed site than for pronghorns from the relatively undisturbed site. This study could have been a good test of the effects of disturbance history on immediate responses to disturbance, except that it is unclear whether responses at the more disturbed site were stronger because (a) cumulative disturbance from vehicles and people (non-hunters) was greater there, or (b) because pronghorns had learned to associate people and vehicles with hunting only at the more disturbed site, or (c) because of some interaction between hunting and cumulative disturbance from vehicles and non-hunters. Also, the authours pooled data on immediate responses to people on foot and to vehicles, which increases difficulties in separating effects of hunting and effects of motorized disturbance.

In contrast to Bleich et al. (1994) and Berger et al. (1983), Tyler (1991) found that reindeer (*R. t. platyrhynchus*) approached by a snowmobile had a stronger immediate response (ran earlier and farther) in a subpopulation that for several years had been exposed to heavier snowmobile traffic than in a subpopulation exposed to less traffic. (Hunting appears to not have been a confounding factor.) Even though Tyler (1991) provides a valuable comparison, the less disturbed subpopulation prior to the study already had a recent disturbance history; thus, we still do not know the full extent to which responses change with disturbance history. Also, Tyler (1991:90) points out that, "(t)here is no reason to assume that per capita supply of food in winter was the same in each area. Consequently it is not possible to say to what extent differences in response to a snowmobile between reindeer in the two areas were due to different levels of habituation or differences in nutritional status." Tyler's caveat, is supported by theoretical models predicting that nutritionally stressed animals will take greater risks in order to avoid starvation (McNamara & Houston 1987).

Long-term habituation is suggested by the following contrast between naive and veteran sheep. Dall's sheep at Killermun Lake, which had

experienced very little previous disturbance from helicopters, in 7 out of 10 occasions ran away when the helicopter was very far away, at an average horizontal distance of at least 1.3 km (mean of least distance for sheep that escaped in Table 1 of Frid 1995, 1997a). (The latter distance is an underestimate because I did not measure escape initiation distance [defined in Table 1] in that study.) In contrast, desert bighorns at Grand Canyon National Park, which for multiple consecutive years had been exposed to an estimated 15-42 thousand helicopter flights a year, became more vigilant during feeding but did not run away when helicopters were hovering only 250-450 m away (Stockwell et al. 1991). (Even though the Dall's sheep population was hunted and the bighorn sheep population was not, I doubt this would have been a confounding factor. Sheep would associate hunting with helicopters only if they were being shot from them, which is unlikely. Also, all of my observations were of females and juveniles, which cannot be legally hunted.) Although the difference in tendency to escape from faraway helicopters seems to provide evidence of long term habituation, the Dall's sheep data is quite limited, and the comparison may be confounded by differences between taxa and their environments. Thus, whether long-term habituation of immediate responses to helicopter disturbance actually occurs in Dall's sheep, remains to be tested. Also, why would the Grand Canyon population not run away from nearby helicopters, while those studied by Bleich et al. (1994) did, even after multiple years of helicopter disturbance? I suggest that the Grand Canyon bighorns represent a very extreme and unique case. (Where else are the same animals exposed to 15-42 thousand helicopter flight a year?). Therefore, generalizing the work of Stockwell et al. (1991) to populations with substantially lower exposure to helicopters, such as Kluane National Park Reserve (Hegmann 1995), is unwarranted. The observations of Bleich et al. (1994) likely are more representative of other sheep populations.

In addition to the above knowledge gaps, I was unable to find studies addressing whether long-term habituation is less likely to occur when there are lengthy interruptions between disturbance periods. This may well be the case in northern Canada, where helicopter flights related to mining exploration and outdoor recreation are concentrated during the summer months (which I will refer to as the "flying season"), and generally are rare for about 8 months of the year (heli-skiing flights currently being a rare exception).

2.1.2 Habituation at a mid-term scale (within the same year or season)

Some studies have found evidence of habituation of immediate responses to disturbance over a mid-term scale. For example, heart rates of captive bighorn sheep increased after exposure to noise from simulated jet aircraft, but this response was strongest and the frequency of alarm responses was greatest during the first 28-day experimental period than during subsequent experimental periods (Weisenberger et al. 1996). (Mule deer [*Odocoileus hemionus*] did not show the same pattern, but the authours suggest that this result was confounded by differences between the disturbance history of individuals.) Although Weisenberger et al. (1996) provide rigorous tests, their sample sizes are small (n

= 4 sheep) and observations involve captive-born animals that had already been handled extensively. Thus, it is unknown to what extent their observations can be generalized for free-ranging animals.

Yarmoloy et al. (1988) found that mule deer approached within 250 m by an all-terrain-vehicle ran away in 41 % of approaches during the first 2-week experimental period. The same individuals, however, ran away in only 11 % of approaches during the following experimental period. Although data collection was well designed and the study animals came from a naive population, the general application of the study could be limited by its sample sizes (n = 5 deer).

Nonetheless, both Yarmoloy et al. (1988) and Weisenberger et al. (1996) have strong results suggesting habituation of immediate responses to motorized disturbance in a mid-term scale. The findings of these studies, however, may not be applicable to helicopter disturbance, which appears to be even more harmful than jet-fighter disturbance (Harrington & Veitch 1991).

Yet even if immediate responses do weaken with habituation, some data from Weisenberger et al. (Tables 2, 3:1996) suggests that, at least in a mid-term scale, repeated disturbances can chronically affect heart rates of both mule deer and bighorns. Once disturbance had ceased, heart rates of captive mule deer and bighorn sheep were greater for 7-30 days after 28-day periods in which animals were exposed to simulated noise from jet aircraft, than 25-30 days prior to disturbance periods (Weisenberger et al. 1996: Tables 2, 3). Although the authours do not discuss this possibility, this data could in fact suggest the antithesis of habituation. If heart rates do become chronically elevated with repeated disturbance, there could also be chronic increases in metabolic rate and energy consumption (Chabot 1991), which perhaps could affect reproductive success.

2.1.3 Habituation in a short-term scale (within the same day)

My preliminary data on Dall's sheep suggested that habituation of immediate responses to helicopters can occur in a short-term scale. The strength of immediate responses to helicopters (as measured by response time, first reaction distance, and escape distance; see Table 1) was greater during the first helicopter flight of a day than during subsequent flights occurring on the same day (Figs 8 and 9; Frid 1995, 1997a). These observations, however, are based on a very limited sample (two sheep groups), and are useful only for generating hypotheses. It is interesting that, in his study of mountain goats (Côté (1997) found no difference in response by the same animals to the first and subsequent helicopter flights of the day.

2.1.4 Relative costs of immediate responses and foraging

Sub-section 2.2 presents hypotheses on how disturbance history at different time scales might affect immediate responses by sheep to helicopters. I must emphasize that these hypotheses focus on how disturbance *interrupts* maintenance activities (feeding and bedding), and creates additional energetic costs related to escaping from helicopters. They do not address how maintenance activities themselves are *altered* once resumed after disturbance,

which is the focus of the next two sections. Although some habituation may become apparent in immediate responses to helicopters, foraging efficiency could chronically decrease (see Berger et al. 1983, but see caveat in 2.1.1.) due to increased vigilance, and heart rates might chronically increase (see Tables 2 and 3 of Weisenberger et al. 1996) as cumulative disturbance becomes greater. Thus, even though sheep with greater frequencies of exposure to helicopters could have weaker escape reactions and interrupt maintenance activities for shorter periods, this level of habituation may not compensate for other, potentially greater costs of helicopter disturbance.

In response to motorized disturbance, why would animals habituate their immediate responses, yet increase the strength of vigilance responses? I suggest that animals frequently exposed to motorized disturbance cannot afford to fully stop maintenance activities and incur the energetic costs of escape every single time there is a disturbance event. They would simply starve all too quickly. However, if the disturbance to which they have tempered their escape response still is considered a potential threat, natural selection would favour increased vigilance for monitoring such potential threats. Indeed, less vigilant animals do have a greater probability of being preyed on (FitzGibbon 1989; Krause & Godin 1996). Thus, the more frequent the disturbance, the more sensitive vigilance has to be to keep up with the increased frequency of potential threats.

2.2 The Hypotheses
2.2.1 Controls for all predictions
In addition to the controls specified in the predictions themselves, tests described below should be controlled for or stratified by group size (Frid 1995, 1997a; but see Côté 1997), age-sex composition of group (Chubbs et al 1993, but see Bleich et al. 1994 and Côté 1997), distance to cliffs (although Bleich et al. 1990 found no effect of terrain type, see Foster and Rahs 1983), pre-disturbance behaviour (Harrington & Veitch 1991), and food quantity and quality, including phenological stage (see McNamara & Houston 1987 and Tyler 1991). Finally, some helicopter pilots claim that sheep respond to helicopters only when it is windy; thus wind strength is another factor to include in controls.

2.2.2 General hypothesis on habituation of immediate responses
In immediate response to helicopter disturbance, Dall's sheep generally interrupt maintenance activities (feeding or bedding) by either escaping (defined in Table 1) or standing vigilant. The strength of such immediate responses, however, weakens with increases in length and intensity of disturbance history. In other words, some level of habituation to disturbance can occur at different time scales.
Basis for hypothesis: Data of Yarmoloy et al. (1988); Stockwell et al. (1991); Tyler (1991); Frid (1995, 1997a); and Weisenberger et. al (1996).

2.2.3 Short-term habituation hypothesis (STH)

The strength of immediate responses to helicopter disturbance weakens as intensity of short-term disturbance history (cumulative disturbance in a day) increases. The magnitude of change in response strength, however, will be greater when intervals between disturbance events are shorter.

Basis for hypothesis: Preliminary data on immediate responses to multiple helicopter flights occurring the same day (Frid 1995, 1997a), and principle of interactions between risk factors (Frid 1997b).

Predictions

1) The strength of immediate responses to helicopters (Table 1) by individual sheep is greater during the first helicopter flight than during subsequent flights occurring on the same day.

2) The magnitude of change in response strength between the first and subsequent flights will be greater when the time interval between flights is shorter.

2.2.4 Mid-term habituation hypothesis (MTH)

The strength of immediate responses to helicopter disturbance weakens as length and intensity of mid-term disturbance history (cumulative disturbance over a flying season) increase. The magnitude of change in response strength, however, will be greater when intervals between disturbance events are shorter.

Basis for hypothesis: Data on habituation of immediate behavioural and cardiac responses to disturbances occurring within the same year (Yarmoloy et al. 1988; Weisenberger et. al 1996), and principle of interactions between risk factors (Frid 1997b).

Predictions

1) Within a period of similar plant phenology in a given flying season, immediate responses to helicopters by sheep (Table 1) are strongest early in that period, but such responses weaken as the cumulative number of days with helicopter flights increase. Given the potential for short-term habituation, tests of this prediction should use data from only the first helicopter flight of each day.

2) Within a period of similar plant phenology in a given flying season, the magnitude of change in response strength between early and later parts of that period will be greater when the number of days between helicopter flights is shorter.

3) If the strength of immediate responses to helicopters by sheep (Table 1) is greater during the first helicopter flight than during subsequent flights occurring on the same day (as predicted in the STH), then, within a period of similar plant phenology, the strength of this relationship should decrease as the number of helicopter flights during the flying season increases.

2.2.5 Long-term habituation hypothesis (LTH)

The strength of immediate responses to helicopter disturbance weakens as length and intensity of long-term disturbance history (cumulative disturbance over several years) increases. The above relationships, however, depend on whether years with disturbance are consecutive.

Basis for hypothesis: Contrasts in escape behaviour from helicopters between sheep with short (Frid 1995, 1997a) and long (Stockwell et al. 1991) disturbance histories, contrasts in escape behaviour between reindeer exposed to heavier snowmobile traffic and less disturbed reindeer (Tyler 1991), and principle of interactions between risk factors (Frid 1997b).

Additional controls for predictions

Given the potential for short-term and mid-term habituation, and for the effects of food variables, tests should be stratified for the first flight of the day, for the initial period of disturbance occurring in a flying season (e. g. first week), and by food distribution and quality and phenological stage of plants. Also, tests should be controlled for the intensity and extent of the flying season (e. g. seasons with 2 and 200 flights are not comparable).

Predictions

1) Immediate responses to helicopters (Table 1) are stronger for sheep in a population in its first year of disturbance (naive sheep), than for sheep in a population already disturbed for multiple, consecutive years (veteran sheep).

2) Within the same population, immediate responses to helicopters by sheep (Table 1) are greatest during the first year of disturbance, but weaken as the number of consecutive years with disturbance increases.

3) If disturbance does not occur on consecutive years, response strength remains constant between years.

4) If the strength of immediate responses to helicopters (Table 1) by sheep is greater during the first helicopter flight than during subsequent flights occurring on the same day (as predicted in the STH), then the strength of this relationship should decrease as the number of consecutive years with helicopter disturbance increases.

5) Differences between naive and veteran populations in strength of immediate responses to helicopters (Table 1) are directly related to differences between the populations in number of consecutive years of disturbance history.

3. HYPOTHESES ON DISTURBANCE EFFECTS ON FEEDING BEHAVIOUR

3.1. Introduction

Hypotheses in this section focus on how foraging efficiency within a habitat is altered once feeding is resumed after helicopter disturbance. They do not address whether disturbance causes habitat shifts that affect foraging, which will be addressed in a later section. Similarities between predation risk and disturbance provide the theoretical framework for hypotheses (Sutherland 1996; Fig. 1).

Again, I must emphasize that while some habituation can become apparent in the immediate response to helicopters, foraging efficiency could decrease chronically as cumulative disturbance increases (Berger et al. 1983). Thus, even though sheep with more frequent exposure to helicopters could interrupt maintenance activities for shorter periods, this level of habituation may not compensate for foraging costs caused by helicopter disturbance.

Vigilance, which in ungulates and other terrestrial vertebrates is recognized by the head-up position, is largely aimed at looking out for predators. This behaviour, however, is generally mutually exclusive with feeding (reviews in Elgar 1989 and Lima & Dill 1990; Illius & FitzGibbon 1994). While less vigilant individuals are more likely to be taken by a predator (FitzGibbon 1989; Krause & Godin 1996), individuals that are too vigilant will forage less efficiently. Thus, making decisions that optimize the trade-offs of vigilance and feeding has been a major evolutionary force shaping the behaviour of prey (reviews in Elgar 1989 and Lima & Dill 1990). As a result, vigilance responds to risk-related factors, such as group size, distance to refuge, and predator presence (review in Elgar 1989), as well as to their interactions (Frid 1997b). Helicopters appear to be perceived by sheep as a predator of sorts, and it makes sense to expect that helicopter disturbance decreases foraging efficiency by increasing vigilance. Such disturbance-related foraging costs could result in population declines (Sutherland 1996).

Below I present several hypotheses on how helicopter disturbance over different time scales could affect foraging behaviour. Throughout I treat disturbance history as a predation risk factor that interacts with other risk factors to affect vigilance (Frid 1997b).

3.2 The Hypotheses

3.2.1 Controls for all predictions

Vigilance is affected by a myriad factors related to predation risk, as well as by social factors unrelated to predation. As much as possible, tests described below should control for both kinds of factors, which are reviewed by Elgar (1989). Specific factors to control include group size, distance to cliffs, sex-reproductive class, distance to obstructive cover, position in group, wind strength, and food dispersion and quality (including phenological stage).

Unless otherwise specified in predictions, tests should use only data from the first helicopter flight of the day. They should also be controlled for or stratified by the number of days with helicopter activity within a given flying season.

Finally, tests should be controlled for or stratified by whether individuals escaped or just stood vigilant during immediate responses to helicopters. The choice between either responses may be a good predictor of how vigilant individuals will be once feeding is resumed. (See section 8.)

3.2.2 Helicopters as predators hypothesis (HPH)

Helicopters are perceived by sheep as predators, and they affect sheep foraging behaviour as predators would.

Basis for hypothesis: Theoretical models (Sutherland 1996), and empirical data on foraging bighorns exposed to helicopters (Stockwell et al. 1991) and on several taxa exposed to real or model predators (review in Elgar 1989).

Prediction
For paired samples of the same individual sheep, percent time spent vigilant is higher during the first foraging bout to follow a helicopter flight than during the last foraging bout prior to this flight.

3.2.3 Disturbance history - foraging hypothesis (DHFH)
The increase in vigilance during the foraging bout following a helicopter flight becomes greater as cumulative disturbance increases.

Basis for hypothesis: If disturbance history is a predation risk factor, its effect should be interactive rather than additive (Frid 1997b). Also Berger et al. (1983) found that, in the absence of disturbance, pronghorns with a long history of intense disturbance foraged less efficiently than animals with a less intense disturbance history (but see caveat in 2.1.1.).

Predictions
In the predictions below, PTV stands for percent time spent vigilant during the first foraging bout to follow a helicopter flight

1) For a given day, PTV increases as the cumulative number of helicopter flights becomes greater.
2) PTV increases as the cumulative number of days with helicopter flights during that flying season becomes greater.
3) PTV increases as the number of consecutive years sheep have been exposed to helicopters disturbance becomes greater.
4) The difference between PTV and percent time spent vigilant during the last foraging bout prior to disturbance (first flight of day) is greater for sheep in a population in its first year of disturbance (naive sheep), than for sheep in a population disturbed for multiple, consecutive years (veteran sheep).
5) Differences between naive and veteran populations in PTV are directly related to differences between the populations in number of consecutive years of disturbance history.
6) On days without helicopter flights, naive sheep are less vigilant while foraging than veteran sheep, and the difference in vigilance levels is directly related to differences between the populations in number of consecutive years of disturbance history.

4. STRESS HYPOTHESES

4.1 Introduction
Animals under stress suffer an increase in metabolic rate, and consequently an increase in energy consumption (Chabot 1991). The latter could affect physical condition and reproductive success.

Chronic stress symptoms may become greater as cumulative disturbance history increases. For example, once disturbance had ceased, heart rates of captive mule deer and bighorn sheep were greater for 7-30 days after 28-day periods in which animals were exposed to simulated noise from jet aircraft, than 25-30 days prior to disturbance periods (Weisenberger et al. 1996: Tables 2, 3).

In a study of Spanish ibex (*Capra pyrenaica*), Alados et al. (1996) found that fractal dimension of vigilance-feeding sequences can be used as an indicator of stress. Individuals stressed by parasites or pregnancy had simpler fractal dimensions of vigilance-feeding sequences than animals not under stress. (In other words, vigilance-feeding sequences were more predictable in stressed animals.) It is plausible that fractal dimension analysis could also reflect stress related to helicopter (Alados pers. comm.). Although heart-rates also are known to reflect disturbance-related stress in ungulates (e. g. MacArthur et al. 1982; Chabot 1991; Weisenberger et al. 1996), the advantage of using fractals is that stress can be assessed in free-ranging animals without capturing and handling them (Alados et al. 1996), and without using expensive heart-rate telemetry.

4.2 The Hypotheses

4.2.1 Controls for all predictions: Same as in hypotheses on disturbance effects on feeding behaviour.

4.2.2 Short-term stress hypothesis (SSH)

Short-term stress caused by helicopter disturbance does not end when immediate responses are over, but continues into the first foraging bout to follow the helicopter flight.

Basis for hypothesis: Data on cardiac (MacArthur et al. 1982; Weisenberger et al. 1996) and behavioural responses (Elgar 1989; Stockwell et al. 1991) to predators or disturbance.

Prediction

For paired samples of the same individual sheep, fractal dimension of vigilance-feeding sequences is simpler during the first foraging bout to follow a helicopter flight than during the last foraging bout prior to this flight.

4.2.3 Disturbance history - stress hypotheses (DHSH)

Chronic stress symptoms of foraging sheep increase as cumulative disturbance becomes greater.

Basis for hypothesis: Heart rate data of Weisenberger et al. (Tables 2, 3:1996), foraging behaviour data of Berger et al. (1983) (but see caveat in 2.1.1.), and principle of interactions between risk factors (Frid 1997b).

Predictions

In predictions listed below, FD stands for fractal dimension of vigilance-feeding sequences during the first foraging bout to follow a helicopter flight.

1) FD becomes simpler as the number of flights occurring that day increases.
2) FD becomes simpler as the number of days with helicopter flights during a given flying season increases.
3) FD becomes simpler as the cumulative number of consecutive years sheep have been exposed to helicopter disturbance increases.
4) FD is more complex for sheep in a population in its first year of disturbance (naive sheep), than for sheep in a population that already has been disturbed for multiple, consecutive years (veteran sheep).

5) Differences between naive and veteran populations in FD are directly related to differences between the populations in number of consecutive years of disturbance history.
6) On days without helicopter flights, naive sheep have a more complex fractal dimension of vigilance-feeding sequences than veteran sheep, and the difference in fractal dimension is directly related to differences between the populations in number of consecutive years of disturbance history.

5. HABITAT SHIFTS HYPOTHESES (HSH)

5.1 Introduction

Bleich et al. (1994) provide strong evidence for the hypothesis that helicopter disturbance causes mountain sheep to shift habitats. Similarly, adult female caribou (R. t. caribou) displaced by motorized disturbance related to clear-cut logging selected mature spruce forests and avoided more open habitats, whereas prior to disturbance they used all habitats in proportion to their availability (Chubbs et al. 1993). In addition to increasing energetic costs (e. g. Bradshaw 1994), such forced habitat shifts can keep animals from utilizing the best food patches, thereby reducing their foraging efficiency and ultimately causing population declines (Sutherland 1996). In this section, following the four studies cited above, I present predictions for the hypothesis that helicopter disturbance causes sheep to shift from preferred to marginal habitats.

5.2 Predictions

Predictions below address only short-term habitat shifts, but long-term shifts can also be expected (Sutherland 1996). Predictions should be controlled for group size (Frid 1995, 1997a), age-sex composition of group (Chubbs et al. 1993, but see Bleich et al. 1994), distance to cliffs at time of disturbance (Foster & Rahs 1983; but see Bleich et al. 1990), pre-disturbance behaviour (Harrington & Veitch 1991), plant phenology and other food variables (see discussion in Tyler 1991), long-term disturbance history, and whether during immediate responses individuals escaped or just stood vigilant. Tests should also be stratified for the first flight of the day and controlled for the number of days with helicopter flights that have occurred in the flying season.

   Predictions are as follows:
1) For paired samples of the same individuals, habitat type will differ before disturbance and after disturbed sheep resume maintenance activities.
2) Sheep will be found more frequently in preferred habitats (as determined by use vs availability analysis: Johnson 1980) just prior to disturbance than within 12 h periods following disturbance.
3) Sheep will be found less frequently in habitats that generally are avoided (as determined by use vs availability analysis: Johnson 1980) just prior to disturbance than within 12 h periods following disturbance.
4) Food quality and availability is lower in habitats used by sheep just prior to disturbance than within 12 h periods following disturbance.

5) Distance to cliffs and/or quality of nearest cliffs (as determined by their size, continuity, and steepness) differs between periods immediately preceding disturbance and 12 h periods following disturbance.

6. DYNAMITE VS SHOVEL HYPOTHESIS (DSH): SIMULTANEOUSLY USING MULTIPLE HELICOPTERS

6.1. Introduction

If a very intense period of helicopter flights must take place, it may be better to simultaneously use multiple helicopters and shorten disturbance time, than to extend disturbance time by using just one helicopter. For example, at Killermun Lake on 3 July, 1995; a helicopter moving the mining camp made over 40 passes (including return trips) over the lambing range. This extreme concentration of flights resulted in severe short-term damage. Prior to disturbance 107 adult females and juveniles, including 17 lambs (68 % of the known population), was on the lambing range. By the time the last helicopter flight was done, only about 19 sheep (12 % of the known population) remained on the lambing range while the rest had escaped into the summer range (Frid 1995). Given that only one helicopter flying repeatedly caused almost all animals to abandon the area, increasing the intensity of disturbance by simultaneously using multiple helicopter may have not worsened the damage. On the contrary, reducing disturbance time by using multiple helicopters may have been less harmful. Predictions of this Dynamite vs Shovel Hypothesis are outlined below.

6.2. Predictions

(Escape time, response time, and helicopter time are defined in Table 1.)
1) Escape time, response time, and the time sheep take to return to their pre-disturbance location are inversely related to helicopter time.
2) For equivalent periods of helicopter time, escape time, and the time sheep take to return to their pre-disturbance location are independent of the number of helicopters simultaneously flying.

7. HYPOTHESIS ON BLOCKED STIMULI (HBS)

7.1 Introduction

Côté (1997) found that the extent to which mountain goats were disturbed depended on the distance between the animals and the helicopter. Such responses, however, were independent of whether the helicopter was in line of sight with the animals. In contrast, Tyler (1991: 185) found that "reindeer that had an unbroken view of the approaching snowmobile tended to bolt at a greater distance than groups that had a restricted view". Similarly, at Killermun Lake when a helicopter and a group of seven Dall's sheep were separated by a ridge, the sheep showed no response when the helicopter approached within 2.5 km,

which is only slightly longer than the mean distance (2.2 km) at which all sheep groups showed a response to helicopters. Also, 3 out of 9 groups were disturbed when helicopters were at this distance (Frid 1995, 1997a). Thus, although it may not be the case for mountain goats, whether sheep respond to a helicopter could depend on the interaction of distance to stimuli and whether the stimuli is in line of sight. If this hypothesis is not disproved, it could provide the basis for designing helicopter routes that minimize impacts on the animals, as I did at Killermun lake (Frid 1995).

7.2. Prediction
When a helicopter is away from sheep at a distance equivalent to the average first response distance (defined in Table 1) for that population, sheep will not respond if the helicopter is blocked out of sight by a ridge. Sheep, however, will respond if a helicopter at the equivalent distance is in direct line of sight.

8. TESTING FOR SOCIAL AND BEHAVIOURAL FACTORS THAT AFFECT INDIVIDUAL VARIATION IN RESPONSES TO DISTURBANCE (VAR)

8.1 Introduction
There is evidence that, at least in some ungulate taxa, social factors such as group size (Frid 1995, 1997a; but see Côté 1997), and behavioural factors such as pre-disturbance activity (Harrington & Veitch 1991, but see Côté 1997) affect immediate responses to aircraft disturbance. Furthermore, individuals of the same species, age-sex class, and population could differ in their degree of risk taking (see Martin & Kraemer 1987). In this section I develop predictions regarding these factors, and assess some behavioural correlates of "cool" (greater risk takers) and "wary" (more conservative) individuals. In the future, tests of these predictions could help improve sampling design thereby reducing variability in the data.

8.2. Predictions
1) The probability that sheep will escape from helicopters increases with group size (Frid 1995, 1997a: Fig. 7).
2) Within the same population, first reaction distance, escape distance, and total escape time (Table 1) are greater for individuals that were walking prior to helicopter disturbance than for individuals feeding/standing or lying prior to such disturbance (Harrington & Veitch 1991).
3) Within the same population, individuals which escaped in immediate response to helicopters will be more vigilant during the first foraging bout following disturbance than individuals whose immediate response to disturbance was to stand vigilant.
4) Within the same population and during the first foraging bout following disturbance, individuals who escaped during disturbance will have a simpler fractal dimension of vigilance-feeding sequences than individuals whose immediate response to disturbance was to stand vigilant.

9. REPRODUCTIVE SUCCESS HYPOTHESIS

9.1 Introduction

Disturbance can decrease reproductive success of individuals by affecting foraging efficiency and habitat use (Sutherland 1996), and by increasing energetic costs of the mother (e. g. Bradshaw 1994), thereby affecting the amount of milk available to the young (Ely & Peterson 1941, cited in Harrington & Veitch 1992). Indeed, empirical studies of woodland caribou have found support for the hypothesis that aircraft disturbance lowers reproductive success (Harrington & Veitch 1992; R. Florkwiewicz pers. comm.). In this section I present a prediction of this hypotheses.

9.2 Predictions

Within the same year, mother-young ratios are lower in a population subject to intense helicopter disturbance, than in an undisturbed population without a recent history of disturbance. Also, the difference in mother young ratios is directly related to differences between the populations in number of consecutive years of disturbance history. (The asymmetric ANOVA analyses [Underwood 1994] used in the design [Table 2] minimizes potentially confounding effects of differences between populations in food supply, plant phenology, weather, and predation.)

10. GENERAL FIELD METHODS

10.1 Food variables and phenological data

Food dispersion and quality could be indexed, respectively, by the mean number of steps taken between food patches, and by how frequently an animal moves between food patches (Berger 1983). These indices, however, need to be tested with comparisons to actual food measurements. Sampling design for the latter has yet to be determined.

I have emphasized the importance of plant phenology throughout the hypothesis. Although sampling design for phenology has yet to be specified, examples are found in Murray & Miller (1982).

10.2. Distances between sheep and helicopters

Sheep locations on a topographic map can be estimated by using marks on the landscape, either natural (e. g. specific bluffs) or artificial (e. g. flagging), as reference points. The horizontal distance between the helicopter and the sheep can be estimated with GPS readings taken by the pilot. In the absence of GPS readings, horizontal distance between helicopter and animals can be estimated with a topographic map and using known landscape features as reference points.

10.3. Behavioural data

10.3.1. Immediate responses

Immediate responses can be recorded by two observers working simultaneously as described in Frid (1995). The units of observation are the reactions of ≥ 50 percent of animals in a group. (Disturbance events are usually too fast and action packed to allow observations of unmarked focal individuals.) Replicates of sheep groups are independent only if they occur (a) on different days, (b) the same day but on different aspects of the mountain (such that sheep sampled second would not have been exposed to disturbance from the first trial (see BSH), or (c) when separate groups on the same side of the mountain respond to the same helicopter, but such groups are not within direct line of sight of each other (which would rule out the possibility that groups are responding to the behaviour of other groups, rather than to the helicopter).

10.3.2. Feeding behaviour

Methods for sampling vigilance and other components of feeding behaviour are detailed in Frid (1997b). In that paper I also discuss the statistical consequences of not having marked individuals, and the assumption of low pseudo-replication when unmarked individuals come from a large pool of animals. In order to satisfy requirements for sampling fractal dimension of vigilance-feeding sequences, sampling length should be standardized at 30 min (Alados et al. 1996; C. L. Alados pers. comm.).

10.4. Estimating minimum sample sizes from preliminary data

The short duration of this contract did not allow me to use my data from Killermun Lake and other populations (Frid 1995, 1997a, 1997b) to estimate sample sizes required for obtaining desired levels of precision. Such calculations should be made before fieldwork.

11. PRELIMINARY EXPERIMENTAL DESIGNS

11.1 Introduction

Properly designing experiments prior to data collection is one of the most crucial factors determining the usefulness of a research project. The preliminary designs of Table 2 provide a basis which, after subject to peer review, can be used to build more rigorous designs, following as much as possible principles outlined by Underwood (1994).

As specified earlier, experimental designs are limited by the funds available. The elegant but expensive experiments of Harrington & Veitch (1991, 1992); Bleich et al. (1994); and Bradshaw (1994) are currently not feasible. These studies had very large budgets for radio and satellite-collars, and for sampling from aircraft. Nonetheless, very valuable information can be collected from the ground and without access to marked individuals (e. g. Tyler 1991; Frid 1995, 1997a; Côté 1997), and experiments described in Table 2 were designed accordingly.

Admittedly, carrying out all of the experiments proposed by Table 2 would be overly ambitious. Once the research budget is specified, research priorities will be selected from Table 2.

11.2 Study sites and replication in space

Given that natural variation in behaviour and demography creates a constellation of confounding factors, replication in space is important for detecting true effects of disturbance (Underwood 1994). The logistical difficulties of juggling several study sites can, to some degree, be solved with asymmetrical sampling designs (Underwood 1994). Lack of replication in space, which could be the default situation for this study, does not preclude experiments from being useful, but does diminish their reliability.

Four distinct, but relatively adjacent populations should be studied. One population should consist of "veteran" sheep with a known and ongoing history of multiple, consecutive years of helicopter disturbance (VET population). The other 3 populations should consist of "naive" sheep, which have been exposed to very little or no helicopter disturbance, ideally during the last 10 years (most of the lifetime of the average Dall's sheep). At the very least, naive populations should have had negligible helicopter disturbance over the last two years. Two of the naive populations will remain undisturbed and act as controls (CONT populations). The third naive population will be experimentally disturbed (NEXP populations). Though likely unrealistic, having 2 NEXP, 2 VET, and 2 CONT sites would be very desirable for spatial replication.

Ideally, all sites should fulfill the following conditions:
1) Long-term demographic data is available (very useful, but not essential).
2) Long-term data on rates of helicopter (by season and year) is available.
3) Ecological conditions, including food distribution and densities of main predators (mainly wolves and coyotes) are similar at all sites.
4) Sites are roadless and have similar history of fixed-winged aircraft activity.

Ecological conditions will inevitably differ between sites, but the differences can be controlled statistically. Also, Underwood (1994:4) points out that when using spatial replication in asymmetrical ANOVA's (see Table 2), "there is no need to attempt to choose places with identical characteristics or abundances of the population. Not only is this impractical, it is unnecessary." Only some tests in Table 2, however, have true spatial replication.

11.3 Experimental Harassment

11.3.1 Who will do it?

At NEXP and VET sites, experimental harassment of animals likely will be done in collaboration with mining and/or heli-sightseeing companies who already were planning on using helicopters in the area. By collaborating in the project, such companies would be agreeing to modify their schedules and routes to meet sampling designs. If no such companies are available to cooperate with the project, hiring helicopter time for the sole purpose of experimental harassment should be considered.

11.3.2 How to do it

Whether a disturbance stimuli approaches the target animal directly or obliquely may affect the response strength of the animal (Tyler 1991). Thus, except for tests of the Blocked Stimuli Hypothesis, helicopters involved in experiments will approach sheep directly. (This type of harassment likely is more extreme than in typical flights, which would probably go past sheep obliquely. Thus, guidelines arising from this experiments likely will err on the conservative side.)

During experimental trials, sheep should be approached to the distance equivalent to the average first response distance (Table 1) for the population. (In the absence of data specific to the population, this distance can be calculated from Frid 1995, 1997a.) Once the helicopter approaches sheep at this distance, it turns around 180 degrees and leaves the area (at least hides behind a ridge or lands and turns engine off). Without this recording rule, predictions VAR-1, VAR-2, and VAR-3 (Table 2) would be untestable.

11.4 When to Sample

The timing of sampling will be determined by two conditions. The first is when collaborating mining and/or heli-sightseeing companies are going to be flying. The second depends on when plant phenology (which is also related to the timing of lambing: Rachlow & Bowyer 1994) is less likely to confound comparisons between sites. In other words, except for the asymmetrical ANOVA designs in Table 2, data used for comparing sites should be collected during similar periods of plant phenology. Unless data is collected when there is no plant growth (e. g. late winter) or when plants have senesced (e. g. fall), data collection could entail repeated, back-to-back, short field trips (4-7 days) to the 4 sites. Once collaborating mining and/or heli-sightseeing companies are identified, their planned flying schedules should be used to create a time table of data collection specific to each prediction.

Table 2. Preliminary experimental designs. Abbreviations for hypotheses are defined in Table 3. NEXP, VET, and CONT, are respectively, naive-experimental, veteran, and control sites (see section 11.2).

Hypothesis-prediction	Preliminary experimental design
STH-1	Design is a repeated measures factorial ANOVA (e. g. Hicks 1982). Experimental trials consist of helicopters directly approaching same sheep group several times ($\geq$ 3) in the same day at 25 min intervals between disturbance events. (Twenty five min was the mean interval between first and second flights for the two samples in Frid 1995 [Figs 8 and 9], and likely long enough for the average response time to be over). Two experimental sites are used, but of differences in disturbance history (1 NEXP, 1 VET), there is no true replication in space. Dependent variables are immediate responses (Table 1) during each flight. Independent variables include number of flights that have occurred on that day up to and including the observation, number of disturbance days that have occurred in that flying season up to and including the observation, site (i. e. long-term disturbance history), and interactions between these factors. Factors listed in sub-section 2.2.1 are controlled either by including them in the ANOVA or by stratifying the sampling.
STH-2	The design is as in STH-1, except that additional trials are done for different time intervals between flights. Treatments consist of trials with either 5, 10, 30, 60 or 120 min intervals between flights. The ANOVA would require additional independent variable terms for time interval and its interactions.
MTH-1	Design is a repeated measures factorial ANOVA (e. g. Hicks 1982). Experimental trials begin with the first helicopter activity of the flying season, and consist of helicopters directly approaching sheep during first flight of day. Trials occur during consecutive days within a period of similar plant phenology. Two experimental sites are used, but because of differences in disturbance history (1 NEXP, 1 VET), there is no true replication in space. Dependent variables are immediate responses (Table 1) during each trial. Independent variables include number of disturbance days that have occurred that flying season up to and including the observation, site (i. e. long-term disturbance history), and interactions between factors.
MTH-2	The design is as in MTH-1, except that in an additional NEXP site disturbance occurs every 5 days rather than on consecutive days. Also, the ANOVA requires additional independent variable terms

for time interval between disturbance days and the interactions of this factor. The requirement for an additional site likely precludes testing this prediction.

MTH-3   Statistical analysis is yet to be determined. The idea is to assess the interactive effect of cumulative number of disturbance days in a season on strength of the relationship described in the STH.

LTH-1   This is a factorial ANOVA design (e. g. Hicks 1982) comparing responses by animals in sites with different disturbance histories. Experimental trials consist of helicopters directly approaching sheep during the first flight of each day. Two experimental sites are used, but because of differences in disturbance history (1 NEXP, 1 VET), there is no true replication in space. Dependent variables are immediate responses (see Table 1) during each trial. Independent variables include site (i. e. disturbance history), number of disturbance days that have occurred that flying season up to and including the observation, and interactions between factors.

LTH-2   Design is a repeated measures factorial ANOVA (e. g. Hicks 1982), with observations made over several years. Experimental trials consist of helicopters directly approaching sheep during the first flight of each day. Two experimental sites are used, but because of differences in disturbance history (1 NEXP, 1 VET), there is no true replication in space. Dependent variables are immediate responses (Table 1) during each trial. Independent variables include number of years with disturbance which have occurred up to and including the observation, number of disturbance days that have occurred that flying season up to and including the observation, site, and interactions between factors. Factors listed in sub-section 2.2.1 are controlled either by including them in the ANOVA or by stratifying the sampling.

LTH-3   The design is as in MTH-1, except that at an additional NEXP site experimental disturbance occurs only every second year. Also, the ANOVA requires additional independent variables terms for disturbance continuity (consecutive years vs alternate years) and the interactions of this factor. The requirement for an additional site likely precludes testing this prediction.

LTH-4   Design is yet to be determined. The idea is to assess the interactive effect of cumulative number of disturbance years on strength of the relationship described in the STH.

LTH-5   To be determined.

HPH	Design is an asymmetrical ANOVA with Before and After measures for control (2 CONT) and impact (1 NEXP, 1 VET) sites (Underwood 1994). Even though only CONT sites have true replication in space, this is adequate (Underwood 1994). For impact animals, % time spent vigilant while feeding first is sampled before disturbance. At the end of sample, the same individuals are directly approached by a helicopter until harassment causes them to interrupt feeding. When immediate responses are over and the same individuals resume foraging, vigilance is re-sampled. At CONT sites, vigilance while feeding is sampled for the same individuals before and after a period equivalent to the average response time of NEXP sheep (could be estimated from 1995, 1997a). Factors listed in sub-section 3.2.1 are controlled either by including them in the ANOVA or by stratifying the sampling.
DHFH-1, 2, 3	Designs for DHFH 1, 2, and 3 are, respectively, as in STH-1, MTH-1, and LTH-3, except that the independent variable is % time spent vigilant during the first foraging bout to follow helicopter disturbance. Factors listed in sub-section 3.2.1 are controlled either by including them in the ANOVA's or by stratifying the sampling.
DHFH-4	Design is as in HPH, except that additional independent variables include the long-term disturbance history of impact animals (NEXP vs VET) and its interactions.
DHFH-5	To be determined.
DHFH-6	Design is a multiple regression model comparing between the 2 CONT and the VET sites % time spent vigilant while feeding during days without helicopter disturbance. The independent variable of most interest is disturbance history, which is entered as a dummy variable. Multiple regression would statistically control for variables listed in sub-section 3.2.1.
STSH	Design is as in HPH, except that the dependent variable is fractal dimension of vigilance feeding sequences (Alados et al. 1996).
DHSH-1, 2, 3, 4, 5, 6	Design is as in DHFH predictions with corresponding numbers.
HSH	Testing predictions of this hypothesis requires radio-collaring individuals and locating them from the air, or at the very least having individuals marked with coloured neck-bands. Budget

restrictions currently preclude using such techniques (J. Carey pers. comm.), and I have postponed designing the details of related experiments. Experimental designs would follow the asymmetrical ANOVA models of Underwood (1994).

DSH-1   Experimental trials consist of helicopters flying parallel to mountain side, and hovering in line of site of sheep at a distance equivalent to 50 % of the average first response distance (Table 1) for the population. Treatments consist of helicopter times of 3, 10, 15, 20 min. Two experimental sites are used but, because of differences in disturbance history (1 NEXP, 1 VET), there is no true replication in space. Dependent variables are response time, total escape time and the time sheep take to return to their pre-disturbance location. Independent variables include helicopter time (Table 1), site (i. e. disturbance history), and their interactions. Analysis is a Multiple General Linear Model (either multiple regression with interactions or a factorial ANOVA.) Factors listed in sub-section 2.2.1 are controlled either by including them in the model or by stratifying the sampling.

DSH-2   Design is as in DSH-1, except helicopter time is fixed at 10 minutes and additional trials are done in which the number of helicopters varies between 1, 2, or 3. In analysis, the independent variable term for helicopter time is substituted with number of helicopter simultaneously flying.

BSH   Design is a repeated measures factorial ANOVA (e. g. Hicks 1982). Two experimental sites are used but, because of disturbance history differences (1 NEXP, 1 VET), there is no true replication in space. Experimental trials consist of helicopter first approaching sheep from behind a ridge at a distance equivalent to 50 % of average first response distance for the population and hovering for 5 min (which would be sufficient for eliciting responses when helicopter is in direct line of sight). Afterwards the helicopter flies around the ridge and approaches the sheep in full line of sight to a distance equivalent to 50 % of average first response distance for the population, hovering for 5 min, and then turning 180 degrees and leaving the area. Dependent variables are immediate responses (Table 1). Independent variables include visibility (helicopter in line of site or behind ridge), site, and the interaction of these variables. Factors listed in sub-section 2.2.1 are controlled either by including them in the ANOVA or by stratifying the sampling.

VAR-1   This is a logistic regression model with escape (see Table 1) as the dependent variable. Two experimental sites are used but,

because of disturbance history differences (1 NEXP, 1 VET), there is no true replication in space. Experimental trials consists of helicopter directly approaching sheep during the first flight of the day. Independent variables are group size, site, and the interaction of these factors.

VAR-2   Experimental trial consists of helicopter directly approaching sheep. Two experimental sites are used, but these sites differ in disturbance history (1 NEXP, 1 VET). The relationship within individuals between strength of immediate responses (Table 1) and pre-disturbance behaviour (feed, stand, or bed) is assessed with a correlation matrix for each site.

VAR-3   Design is as in VAR-2, except that variables in the correlation matrix are escape (Table 1) and % time vigilant during the first foraging bout after disturbance.

VAR-4   Design is as in VAR-2, except that variables in the correlation matrix are escape (Table 1) and fractal dimension of vigilance-feeding sequences during the first foraging bout after disturbance.

RSH   Design is an asymmetrical ANOVA with Before and After measures for control (2 CONT) and impact (1 NEXP, 1 VET) sites (Underwood 1994). Even though only CONT sites have true replication in space, this is adequate (Underwood 1994). Dependent variable is mother-young ratios during equivalent periods of spring and/or summer. "Before" disturbance ratios could be obtained from historical data. Analysis includes a term for disturbance history (NEXP vs VET).

Table 3. Definitions for abbreviations used for hypotheses in Table 2.

Abbreviation	Definition
STH	Short-term habituation hypothesis
MTH	Mid-term habituation hypothesis
LTH	Long-term habituation hypothesis
HPH	Helicopters as predators hypothesis
DHFH	Disturbance history - foraging hypothesis
STSH	Short-term stress hypothesis
DHSH	Disturbance history - stress hypothesis
HSH	Habitat shifts hypothesis
DSH	Dynamite vs shovel hypothesis
BSH	Blocked stimuli hypothesis
VAR	Predictions on social and behavioural factors that affect individual variation in responses to disturbance
RSH	Reproductive success hypothesis

12. LITERATURE CITED

Alados, C. L., J. M. Escos, & J. M. Emlen. 1996. Fractal structure of sequential behaviour patterns: an indicator of stress. Anim. Behav. 51: 437-433.

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. Biol. Conserv. 25: 193-208.

Bleich, V. C., R. T. Bowyer, A. M. Pauli, R. L. Vernoy, & R. W. Anthes. 1990. Responsees of mountain sheep to helicopter surveys. Calif. Fish and Game 76:197-204.

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.

Chubbs, T. E., L. B. Keith, S. P. Mahoney, & M. J. McGrath. 1994. Responses of woodland caribou (*Rangifer tarandus caribou*) to clear-cutting in east-central Newfoundland. Can. J. Zool. 71:487-493.

Côté, S. 1997. Mountain goat responses to helicopter disturbance. Wildl. Soc. Bull. (In press).

Dehn, M. 1994. Optimal reproduction under predation risk: consequences for life history and population dynamics in microtine rodents. Ph. D. Thesis. Simon Fraser University.

Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol. Rev., 64, 13-33.

FitzGibbon, C. D. 1989. A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. Anim. Behav. 37: 508-510.

FitzGibbon, C. D. & Lazarus, J. 1995. Anti-predator behaviour of Serengeti ungulates: individual differences and population consequences. In: Serengeti II: Research, Management and Conservation of an Ecosystem. (Ed. by A. R. E. Sinclair & P. Arcese), pp. 274-296, Chicago: University of Chicago Press.

Frid, A. 1995. Dall's sheep of the Killermun Lake region: ecological and behavioural data in relatio to mineral exploration. Yukon Fish and Wildlife consultant report TRC-95-2. (Available from Jean Carey, sheep and goat biologist, Department of Renewable Resources, Whitehorse, Yukon. email jcarey@yknet.yk.ca).

Frid, A. 1997a. Responses to helicopter disturbance by Dall' sheep: preliminary data from the southwest Yukon. IUCN Caprinae Specialist Group Newsletter. (In press).

Frid, A. 1997b. Vigilance by female Dall's sheep: interactions between predaton risk factors. Anim. Behav. (In press).

Foster, B. R., & E. Y. Rahs. 1983. Mountain goat response to hydroelectric exploration in northwestern British Columbia. Environ. Manage. 7:189-197

Geist, V. 1971. Mountain Sheep: A study in Behavior and Evolution. Chicago: Univ. of Chicago Press.

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.

Hicks, C. R. 1982. Fundamental concepts in the design of experiments. Saunders College Publishing.

Ilius, A. W. & FitzGibbon, C. 1994. Costs of vigilance in foraging ungulates. Anim. Behav., 47, 481-484.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Krause, J. & J. G. J. Godin. 1996. Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. Behav. Ecol. 7: 264-271.

Krausman, P. R., & J. J. Hervert. 1983. Mountain sheep responses to aerial surveys. Wildl. Soc. Bull. 11:372-375.

Lent, P. C. 1974. Mother-infant relationships in ungulates. Pages 14-53 in V. Geist and F. Walther. The behavior of ungulates and its relation to management, Vol. 1. IUCN. Morges.

Lima, S. L. & Dill, L.M.1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619-640.

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

Martin, P., & H. C. Kramer. 1987. Individual differences in behaviuor and their statistical consequences. Anim. Behav. 35:1366-1375.

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

Murie, A. 1944. The Wolves of Mount McKinley. U.S. Department of Interior, National Parks Service Fauna Series 5.

Murray, C., & P. C. Miller. 1982. Phenological observations of major plant growth forms and species in montane and Eriophorum vaginatum tussock tundra in central Alaska. Holarct. Ecol. 5:109-116.

Rachlow, J. L., & R. T. Bowyer. 1994. Variability in maternal behavior by Dall's Sheep: environmental tracking or adaptive strategy? J. Mamm. 75:328-337.

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.

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

Underwood, A. J. 1994. On beyond BACI: Sampling designs that might reliably detect environmental disturbances. Ecological Applications 4:3-15.

Weisenberger, M. E., P. R. Krausman, M. C. Wallace, D. W. De Young, & O. E. Maughan. 1996. Effects of simulated jet aircraft noise on heart rate and behavior of desert ungulates. J. Wildl. Manage. 60:52-61.

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.

13. ACKNOWLEDGMENTS