

Caribou, military jets and noise: The interplay of behavioural ecology and evolutionary psychology

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Abstract: Whether a human activity is likely to have a negative impact on a species depends largely on how stimuli from that activity are interpreted and acted upon by individuals, within the context of their behavioural ecology. The interpretations and decisions made by individuals in response to these stimuli are largely governed by neural systems evolved by the species as adaptations to common and recurrent selective pressures. In this paper I will review previous findings concerning the responses of caribou to overflights by military jet aircraft in Labrador/Québec and Alaska, casting them in an evolutionary psychological framework. One prediction from such an exercise is that identical stimuli (noise from jet overflights) that elicit similar responses (short-distance avoidance) can have quite different population consequences for sedentary (woodland) and migratory (barren-ground) ecotypes. For a female woodland caribou, which shares her calving range with a resident predator population, an increase in movements following disturbance may significantly increase her calf's exposure to predators. Similar movements by a female barren-ground caribou, which has fewer predators to contend with, may have only a negligible impact on her calf's predation risk. Thus woodland caribou may be more vulnerable to negative impacts of military jet noise during calving periods, dependent on predator density.

Key words: activity budgets, calf survival, disturbance, jet aircraft, movements, population dynamics, predation, predation risk, *Rangifer tarandus*.

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Introduction

The potential negative impacts of human-generated noise on caribou have been of concern for a considerable time (*e.g.*, Calef *et al.*, 1976; Miller & Gunn, 1979). Studies on noise impacts have focused on a wide variety of sound sources, but one important source of noise for some caribou populations has been military training activity. For example, in both Alaska and Labrador, jet fighter aircraft are flown at altitudes as low as 30 m above ground level (agl), generating peak sound levels often well above the 90 dBA level generally considered to be the threshold above which potential negative effects are expected (Manci *et al.*, 1988). Several research programs focused on low-level flying have found short-term effects on behaviour and, in one case, possible negative impacts on calf survival (Harrington & Veitch, 1991; 1992; Maier *et al.* 1998), but at present we have no consensus about long-term impacts that

might be useful in assessing new or established activities or planning mitigation programs. For example, Davis *et al.* (1985) indicate there seems to be no obvious negative impacts on population dynamics despite decades of exposure to a variety of low-level training activities on the calving grounds of the Delta Herd in Alaska, whereas Harrington & Veitch (1992) suggest there may be strong negative impacts on calf survival for Red Wine Mountains caribou in Labrador. In an attempt to reconcile these apparent differences, this paper will review previous research on the impacts of jet fighter training on caribou within a framework informed by full consideration of the context within which potential noise disturbances are occurring. This context includes the consideration of the noise stimulus itself as well as both the animals' behavioural ecology and their evolutionary psychology. It will be shown that such a framework not only reconciles the disparate results

of previous research but also provides a profitable guide to our thinking about the spatial and temporal impacts of noise and other potentially disturbing stimuli.

When considering the potential impacts of noise, a clear distinction between short-term and long-term impacts should be kept in mind (Bowles *et al.*, 1993; Larkin, 1994). Short-term effects are those that occur coincident with the noise stimulus (*i.e.*, the behavioural and physiological reactions). These reactions are typically the focus of most of our studies of noise impacts, as short-term reactions provide us with quantifiable, objective data that can be directly related to various parameters of the stimulus. Thus, for example, a caribou may startle, or run, or cease feeding when a jet flies overhead, and then resume its previous activities 5 or 10 or 15 minutes later. However, from a population perspective, it may not matter that some or most caribou startle, or run or cease feeding when a jet flies over. What matters is whether these short-term responses translate into long-term effects: are caribou effected at the population level? If individual animals, in general, suffer no long-term negative impacts on their reproduction or survival, then the short-term impacts of a noise, no matter how dramatic, are ultimately inconsequential. After all, caribou react dramatically to their natural predators yet, on average, survive to reproduce.

The ultimate goal in disturbance research is to characterize the long-term impacts of the noise, and this is precisely where our studies of noise effects often fall far short. When we collect data on noise impacts, we naturally focus on the most salient, reliably recorded reactions. These reactions are both explicit (*i.e.*, highly observable) and of short-duration. Typically, we measure responses over durations of seconds to minutes. Intervals any longer than a few minutes begin to obscure the relationship between cause and effect, as now other stimuli have occurred that may potentially influence the subject's behaviour. It becomes impossible to determine whether an overflight today may still have a lingering effect on the animal's behaviour a week or two down the road. Thus we are left to infer long-term impacts solely from the short-term reactions we observe, under the assumption that long-term impacts are merely the sum of the individual short-term responses we note (see caution by Bowles *et al.*, 1993). However, it is possible that the most important reactions to noise are too subtle for us to observe, as they are occurring within the animal's central nervous system with no immediate outside indication.

Evolutionary psychology

In order to understand the subtle, implicit reactions that might provide the link between short-term reactions and long-term effects, we have to "get inside the animal" psychologically. After all, the initial link between the noise stimulus and the animal's short-term response has long been the focus of experimental psychology. Psychology focused on the relationship between stimulus and response (S-R Psychology) in the first half of the last century, but since the 1960s, psychologists have broadened their consideration by focusing on the role that the organism itself plays in modulating the relationship between stimulus and response (S-O-R Psychology) (see Shultz & Schultz, 2000, for a review). Within the past 20 years, this consideration has been further developed by the subdiscipline of evolutionary psychology.

Evolutionary psychology posits that all species are endowed with a set of 'evolved psychological mechanisms' that guide an animal's responses to the stimuli it encounters (Buss, 1999). These mechanisms consist of nervous system modules that are sensitive to a particular subset of stimuli (*i.e.*, 'sign stimuli' or cues) and respond in specific ways when these stimuli are detected. An evolved psychological mechanism is proposed to consist of three components: 1) a recognition component, 2) an activation component, and 3) a decision component. The recognition component ignores the vast majority of incoming stimuli, responding only to a specific limited set of features. Once these features are recognized, an activation component triggers activity in a variety of other areas of the brain (*i.e.*, motor areas, association areas, memory areas, emotional/motivational areas), which have an evolved relationship to the recognized object or event. Neural activity in these areas is integrated with other information concerning both the individual and its environs and an appropriate course of action is selected (see Frid, 1997, for a related behavioural model).

This process can operate rapidly and the quicker a motor response is selected the more likely the process occurs unconsciously. Thus a 'predator detection mechanism' might evolve that is particularly sensitive to a subset of key stimuli that reliably have signaled the presence of a predator over evolutionary time. For example, a sudden, loud noise, over evolutionary time, has likely been associated with predators often enough for caribou to evolve a neural mechanism to categorize such sounds with other cues concerning predators (*i.e.*, sights or smells). Those caribou that possess such a mechanism are more likely to detect a predator, detect it earlier, and make the most appropriate behavioural response.

Thus two key characteristics of evolved psychological mechanisms are 1) their reliance of a limited set of indicators or cues and 2) their adaptation to past, not present, environments. This latter point is important when considering the potential impacts of human-generated noise, as the majority of potentially disturbing sounds are of recent origin, and thus we would not expect wildlife to have evolved mechanisms that would allow them to specifically cope with them. Rather, these evolutionarily-novel stimuli likely activate existing evolved psychological mechanisms and are therefore likely perceived as a member of an existing 'innate' category. Knowing how an animal categorizes the stimulus, and its typical responses to that category of stimuli, will suggest the form and degree of possible impact.

Jet fighter training and caribou

To put our analysis into action, I will briefly review the findings of two research programs, recasting the findings of these studies in an evolutionary psychological framework.

Alaska

The United States Air Force funded a study on the behavioural effects of low-level military jet training conducted at Eielson Air Force Base, Alaska, on barren-ground caribou (*Rangifer tarandus granti*) of the Delta Herd (Murphy *et al.*, 1993; Maier *et al.*, 1998). The training at Eielson Air Force Base involved low-level flights of A-10, F-15 and F-16 military jet aircraft. Sound level exposures were highest with the F-series jets. Although bombing, strafing and artillery fire have been part of the military training, they were not assessed in this study. Instrumented caribou (VHF collars with activity and noise monitors) were assigned to control and exposure groups, and exposure animals were targeted for low-level passes as low as 33 m agl and full power. Observers noted the caribou's distance to aircraft and monitored its activity budgets and instantaneous responses to the overflights. Observations were carried out in late-winter, post-calving and insect seasons.

The research program focused on three potential indicators of short-term impact: instantaneous reactions, changes in activity budgets, and changes in movement rates. About half the caribou overflown showed no overt behavioural responses to the overflights, with the remainder either becoming alert, standing up or moving (Murphy *et al.*, 1993). Differences between control and exposure animals were noted in the post-calving and insect periods, when exposed animals fed more, rested less and stood more often. Activity counts (mercury tip switches) from

collared animals indicated that exposed caribou spent more time active and less time resting during the post-calving and insect periods (Maier *et al.*, 1998). During the post-calving period, distance traveled during the 24-hour period following exposure (overflight) sessions was significantly greater (by about 50%) for females overflown than for females in the control group. Control animals moved somewhat farther on average during the winter and insect periods, although these differences were not significant (Murphy *et al.*, 1993; Maier *et al.*, 1998). The principal conclusions of this program were:

- 1) "Females with young calves may be less tolerant...and [their] reactions...suggest that caribou moved away from disturbed areas" (Murphy *et al.*, 1993: 485); and
- 2) "Overall, ...reactions to overflights were mild, but modifications of activity cycles and daily movements were evident" and "... responses were strongest when young calves were present... Therefore, we infer that females with young were more sensitive to aircraft disturbance" (Maier *et al.*, 1998).

Labrador

The Newfoundland Wildlife Division, with partial support from the Department of National Defense (Canada), funded a three-year study on the impacts of low-level jet fighter training conducted from Canadian Forces Base Goose Bay (Harrington & Veitch, 1991; 1992). Caribou (*Rangifer tarandus caribou*) belonging to two herds, the small (approx. 700) Red Wine Mountains herd of woodland ecotype and the larger (400 000+) George River herd of barren-ground ecotype. Short-term effects were measured through direct observations of caribou reactions to overflights during late-winter and through remotely gathered data on daily movements and daily activity levels (counts) collected via satellite radiotelemetry during the training season (April to October) (Harrington & Veitch, 1991). Long-term impacts were assessed by monitoring the survival of calves of selected, collared females whose daily level of exposure to low-level training activity was either manipulated or monitored throughout the low-level training period (Harrington & Veitch, 1992). As with the Alaska research program, the 10 collared females each season were split between control and exposure groups.

Visual observations indicated that caribou reacted with a strong startle response to the loudest overflights (*i.e.*, 30 m agl), with the severity of the startle response decreasing with greater distance from the jet's flight path or higher altitudes, and thus lesser noise levels (Harrington & Veitch, 1991). In gen-

eral, behavioural changes occurring during overflights followed an 'up one notch' pattern: resting caribou scrambled to the feet and sometimes lunged forward a few meters; standing caribou usually surged forward a number of meters but began to slow almost immediately; and caribou already walking broke into a run which lasted longer than the former two situations, but again the animals generally slowed and soon stopped as the jet receded in the distance. Except for the rare occasions where caribou spotted the jet during its approach, caribou did not react to the jet until it passed overhead. It is likely therefore that caribou usually did not detect the presence of the jet visually prior to the arrival of the sound of the jet. From our own experience of overflights in the field, unless the air was nearly calm, there was usually no forewarning of an overpass. It was only after the overpass that animals visually followed the receding jet as they slowed to a stop. Within the next minute or two, animals typically resumed their pre-flight behaviour.

Remotely collected data on movements and activity found few significant correlates of overflights (Harrington & Veitch, 1991). The 24-hour activity index was significantly related to a number of variables, including daily distance traveled and ambient temperature, and it also varied seasonally and individually. Daily distance traveled explained between 11-22% of variance in the daily activity index, suggesting that the activity index was a good indicator of movement by the caribou. However, the activity index was only correlated with level of exposure during one of three years, when it indicated a significant but marginal increase in activity level for some, but not all, of the most exposed animals. The measure of daily distance traveled was not particularly useful, as the error inherent in the Argos locations (± 1 km) represented about one third of the average distance moved during much of the study period. Thus exposure to low-level jet overflights, on a short-term basis, did not appear to cause a significant impact on overall activity level or distance traveled.

To determine calf survival and its relation to low-level jet overflights, the presence of a calf at heel was determined once a month during the training season (from June – September/October), and again in December when satellite radiocollars were removed, from females of the Red Wine Mountains woodland herd (Harrington & Veitch, 1992). Calf survival was negatively correlated with a female's average level of exposure to overflights during the calving and immediate postcalving period. The fact that, despite the small and decreasing sample size (females were removed from the sample once their calves were lost), survival was significantly related to level of exposure

to low-level training suggests that the impact of overflights may have been quite large. These are the first data that suggest a long-term, population impact from low-level flight training.

Reconciliation

Davis *et al.* (1985) summarized data on the population demographics of the Delta Herd from 1950 through the early 1980s. Although military activity, including low-level flying by a variety of aircraft, has occurred throughout this period, Davis *et al.* could detect no sign that calving success or other measures of productivity were adversely affected. The population in the early 1950s probably numbered less than 1000 but by 1982, was estimated to be between 6500 and 7500. These findings, combined with those of Murphy *et al.* (1993) and Maier *et al.* (1998), suggest that despite the short-term impacts on activity or movements noted above, especially those seen during the post-calving period, no long-term negative impacts on population were evident. These findings can then be compared to those of Harrington and Veitch (1991; 1992), who found similar mild short-term impacts, yet did find a potential long-term impact on population through the decrease in survival of calves which, along with their mothers, were exposed to higher levels of overflight activity during the calving, immediate post-calving period (*i.e.*, the first 3-4 weeks after birth). Indeed, the Red Wine Mountains population has decreased from approximately 700 animals during the years of the study (1986-1988) to about 150 animals recently (1997) (Schaefer *et al.*, 1999), although no direct link to low-level training can be drawn.

When we first obtained our results on calf survival (Harrington & Veitch, 1992), we were quite surprised, as the short-term effects all seemed to indicate that, at worst, low-level overflights might temporarily alter behaviour and elevate overall activity, but not to such a degree that we would expect a negative impact on female or calf condition, let alone survival. When published in 1992, we did not have an explanation for this unexpected result. However, when our results are combined with those from Alaska, and we focus on the psychology of the animal, the following scenario emerges.

The 'evolved psychological mechanism' behind the various reactions of caribou to low-level jet overflight is that of predator detection and avoidance. This is hardly a surprising conclusion. Frid (1997; 1998) has recently developed an interactive model, based on predation risk, to describe the behavioural decisions made by Dall's sheep (*Ovis dalli dalli*) in response to helicopter disturbance. For caribou,

whether it is the noise of the jet that caribou first perceive, as is most likely in a forested setting, or its visual image during its approach, in either case the animal experiences a sound that rises in intensity from ambient levels to as high as 130 dB in under a second (Harrington & Veitch, 1991). On quiet days this increase could span 90 dB, and under average conditions probably exceeds 50 db. Most animals startle in response to a sudden loud noise, and this startle is associated with the body's 'fight or flight' system (Moller, 1978). All the various reactions observed during overflights suggest that the caribou are preparing to take rapid evasive action to a perceived threat. In some sense, this explanation seems quite obvious, as any animal that is vulnerable to predation must make an immediate response to any sudden-onset stimulus, whether auditory or visual. It must react in a reflexive manner first; a more 'leisurely' assessment can then follow.

However, it is important to keep in mind the three components of an evolved psychological mechanism. The first, recognition, occurs in this example in the split second that the animal is 'hit' with the sound. Recognition (of a sudden noise) triggers the activation stage, which involves, among others, the behavioural startle as well as the physiological changes in the autonomic system. There are likely other areas of the animal's nervous system that are also activated at this time, related to various antipredator tactics, but which may not show their effects until later. These may play an important role in the third stage, that of decision. In this case, among other options, the caribou may reassess its predation risk and decide to stay or leave over the next 24 hours.

During most of the year, caribou likely respond to predators only for the duration of the imminent threat. Once the threat is removed (*e.g.*, the wolf moves on, another caribou falls victim, etc.), caribou should return to pre-disturbance activity. This follows as it is not advantageous for an animal to forego other important activity (*e.g.*, feeding, rutting) for a weak or former threat (see also Frid, 1997; 1998). In addition, it is likely not advantageous for the caribou to abandon its current habitat for another potentially safer one, as on average a caribou may not be able to reliably assess the level of predator risk in a local area as the distribution of predators is patchy and unpredictable.

Thus caribou quickly cease reacting and return to previous activity once they 'decide' the receding jet is no longer a threat. Responses to other aircraft (light aircraft or helicopters) tend to last longer than those to jets (Harrington & Veitch, 1991), if only because it takes longer for these other aircraft to overtake the caribou. As long as the aircraft contin-

ues to approach, suggesting the approach of a predator, the animals continue to flee. In our observations, caribou always darted quickly sideways as the helicopter passed over, as if avoiding the chase of a predator that has closed on them. As they did, they slowed dramatically and often stopped moving within a few seconds, though they continued to watch the aircraft as long as it was still in sight.

There is one period, however, when caribou are much more concerned with the presence of predators. During the calving period, female caribou are most sensitive to stimuli associated with threats, because their calves are particularly vulnerable during the first several weeks after birth (Bergerud, 1971; Adams *et al.*, 1995). Females with calves do not have an effective direct predator defense (Miller *et al.*, 1984), and thus must rely on indirect means to minimize predation risk. The most effective indirect defense appears to be avoidance of areas inhabited by predators: thus spacing away in barren-ground caribou and spacing out in woodland caribou (Bergerud, 1974; Miller *et al.*, 1984; Bergerud & Page, 1987; Bergerud *et al.*, 1990).

Our study of calf survival was conducted on a woodland caribou population. The 'space out' antipredation strategy was very apparent in this population. During March and April it was quite common to find a significant portion of the population on the Red Wine Mountains, where strong winter winds kept the alpine tundra vegetation assessable at a time when snow in the surrounding forested plateau reached 2-3 meters in depth (Brown & Theberge, 1990; Veitch, 1990). Groups of up to several dozen caribou were typical during the late-winter period on the mountains. During May, however, these groups broke up as females quickly dispersed onto the plateau. Although females sometimes left the mountains together, by the time they reached their calving sites a few days later they were usually alone. Their movements then became particularly restricted during the calving period, which likely represents both a concession to the lower mobility of the calf as well as a passive strategy to minimize contact with predators.

During the period of our study, populations of both wolves and black bears were relatively high (Veitch, 1990; Schaefer *et al.*, 1999). Even though caribou space out from one another, they remain in a habitat rich in predators. Thus the antipredator strategy does not reduce the average risk that a female or calf face from predators, but the restriction of movement at calving may reduce the likelihood of encounters during this critical period. In essence, caribou attempt to disappear within predator habitat long enough to see the calf through to a less vulner-

able age. Given a random search model, a predator has an increasing lower probability to encountering a cow/calf pair's sign (olfactory, visual or auditory) the more restricted the pair's movements become.

It is likely that females are predisposed to sit tight in a suitable area unless disturbed by a predator. Given the constrained movements of predators within territories or home range, it is likely that predators will return to areas where they have encountered prey or prey sign in the past. Thus a female that detects predator sign, or a predator itself, may be better off, on average, by moving to a new area, where she can attempt to 'disappear' once again. Stimuli that might be sufficient to generate such a home range shift could include visual, auditory or olfactory sign of predators. The loud noise of an overflight, as it triggers a startle response, may be classed in the same 'predator' category and thus, as Meier *et al.* (1998) found in Alaska, females experiencing a loud overflight may shift their home range.

Shifting a home range in response to predator sign is like any signal/noise problem (Table 1). A female that remains in her original range faces a low risk of losing her calf if she has not been detected by a predator. Once a predator has detected her, her risk to losing her calf increases. For females in the latter situation, movement to another area may reduce that risk, likely to a level intermediate between the two classes of risk faced on her original range. This interme-

diated level of risk is based on the simple idea that predator risk is a function, firstly, of a predator's ability to detect a prey. As wolves and bears likely use olfactory sign left by caribou, any extra movement by a female increases the area within which a predator may encounter her sign. This sign may be detectable for days to several weeks. In addition, visual and auditory sign occurring during the move also add, briefly, to her level of risk. Assuming a simple linear model, if a female increases the distance moved during one day by 50% (Maier *et al.*, 1998), she may increase the risk of predation by the same degree.

If a female has perfect knowledge of predator distribution, she can make appropriate decisions to keep her risk as low as possible. However, given less than perfect knowledge, a female may fail to detect a local predator, or a female may mistake a benign stimulus (*i.e.*, jet overflight noise) for a predator. Thus noise becomes a signal to the female and her avoidance movements increase. This increase in movements increases her calf's risk.

The scenario developed above holds for any female caribou, whether woodland or barren-ground. What differs between the two is the relative level of risk for the same absolute distance moved. The 'space away' strategy of a barren-ground female has already taken her to a region of low predator density. Within this region, any increase in her movements will increase

the risk of encountering a predator.

However, if the risk is low to begin with, increased movements may still fail to bring a female/calf pair in contact with a predator. Thus the short-term increase in movements found by Maier *et al.* (1998) for migratory Delta caribou may not result in a long-term demographic impact on the herd, given a low density of predators on the calving range. For sedentary caribou, on the other hand, increased movements may turn a moderate risk into a high risk, resulting in a significant long-term population impact.

However, not all sedentary populations may suffer the same long-term consequences, as predator density and hence predation risk is the deciding factor. For populations like the Red Wine Mountains caribou that face relatively high numbers of predators, unnecessary anti-predator movements triggered by false alarms to jet overflights may significantly elevate calf mortality. On the other hand, if local

Table 1. Signal/noise decision matrix for a female caribou exposed to stimuli during the calving season that may or may not represent a predator or other real threat. It is assumed that the female is minimizing predation risk for her calf by restricting her movements as much as possible. When detecting a potential predator, she avoids the area, shifting her activity to an adjacent area. The movement to the new area exposes her to unknown predation risk there, as well as temporarily enlarging the area within which a predator might detect her and her calf. These factors increase predation risk for a false alarm (*i.e.*, treating an aircraft disturbance as a threat) but decrease it for a hit (*i.e.*, avoiding an actual predator).

Actual stimulus	FEMALE'S CLASSIFICATION OF STIMULUS	
	Predator	Not predator
Predator	HIT – female avoids area and increases calf's survival	MISS – female ignores stimulus and decreases calf's survival
Not predator	FALSE ALARM – female avoids area and decreases calf's survival	CORRECT REJECTION – calf's survival unchanged

predator densities are low, then false alarms resulting in excessive movements likely would have no long-term consequences.

Summary

This paper has developed a scenario to understand the behavioural dynamics behind the potential for long-term impacts caused by human-generated noise. By first trying to understand how an animal likely perceives and categorizes the noise stimulus, we can then determine how an animal is likely to respond to that particular type of stimulus. Next, we can place the animal's likely response within the context of its behavioural ecology. Thus by combining the internal 'evolutionary psychology' of the animal with its external 'behavioural ecology,' we can begin to build predictive behavioural models that will allow us to make predictions about the long-term demographic consequences of noise disturbance. As the specific model developed here indicates, the same behavioural responses in two different populations may have quite different long-term consequences. Indeed, the same divergence of consequence can occur within the same population if, in this case, there is a significant change in predator density over time.

Thus the most important impacts of noise on caribou should not be expected to be direct and immediate. Rather, they are likely to involve indirect and secondary consequences stemming from innate behavioural responses to the noise that happen to put some portion of the population at greater risk to other factors. It is these other factors that directly affect the long-term demography of the population. These factors may operate well after the initiating noise stimuli are past and forgotten, at least by human researchers, making it difficult to make the link between noise and demographic response.

Finally, it must be emphasized that, although field data may be consistent with the scenario developed in this paper, the link between low-level jet fighter training and caribou population dynamics remains to be demonstrated. This paper provides only an hypothesis that can, and should, be tested in the field.

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