EFFECTS OF AIRCRAFT DISTURBANCE ON BEHAVIOUR OF HARLEQUIN DUCKS (Histrionicus histrionicus)

ROBERT IAN GOUDIE

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by

© Robert Lee Goudie

A thesis submitted to the School of Graduate Studies
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Department of Biology, Faculty of Science
Memorial University of Newfoundland

May 2006

St. John's   Newfoundland

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Thesis abstract

I studied behaviour of Harlequin Ducks (*Histrionicus histrionicus*) at Fig River (53° 03' N, 63° 09' W) and Crooked River (54° 06', 60° 48' W) in Labrador in spring and summer of 1999 to 2002. Observations indicated that paired adults devoted modest proportions of time (30 to 40%) to foraging. This, and the lack of variation in time budgeted to feeding across time and space, indicated that Harlequin Ducks were not limited by food on their breeding habitat in Labrador.

Most pair bonds dissolved by early June indicating nest initiation by the females. All adult females that were examined following capture and/or followed by radio signal appeared to be reproductively active. Low annual productivity on the study areas appeared to be due to predation of nests, and I concluded that Harlequin Ducks breeding in Labrador may be limited by predators.

Noise is a significant stressor for animals, and the non-auditory effects of noise are considered whole body stress responses. In addition to overt responses, behavioural effects of noise on adult Harlequin Ducks were subtle and protracted. I interpreted this as evidence that a larger 'whole body' or physiological response was occurring. Animals challenged repeatedly develop high circulating levels of stress hormones in the bloodstream that can ultimately lower survival and inclusive fitness.

Alert responses by adult Harlequin Ducks in central Labrador occurred to noise (75 –

120 dBA) generated from low-level (30 – 100 m agl) military jet over-flights. Alert (startle) was generally < 1% of time budgets, and increased in a dose-response manner, accelerating above a threshold of approximately 80 dBA. Protracted effects included increased inactivity, and decreased time out of water. There was evidence of residual effects of increased agonistic behaviours up to 1 h and decreased courtship up to 1.5 h following over-flights by military jets. The protracted and residual effects have the potential to negatively affect time-activity budgets of individuals. Multivariate statistical analyses demonstrated the importance of considering behaviour holistically because the inclusive modeling of covariance among behaviours was superior to traditional univariate approaches. Important effects may easily be overlooked because of bias by researchers in defining 'behavioural responses' *a priori* (e.g. Startle or Alert) that are easily observed because effects can be subtle and protracted well beyond the actual disturbance.

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Waters Cycle *by Ian Goudie*

Bald eagles circle
As we ascend Fig Lake
Entering her riffles
To find Kapanunipi

Your rivers drain
The large lakes
That make your basin
The water flowing cycle

Birds of white water
Traveling your rapids
And returning to sea
That water goes full cycle

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Chapter 1. Introduction and Literature Review

1.0 Noise as disturbance

The study of the effects of noise disturbance on wildlife is a very broad subject ranging from impacts on physiology and/or behaviour of the individual animal, through to consequences of noise to populations, to alterations of the communities, landscapes and ecoregions. Noise is one of the most important stressors that humans and their devices have imposed upon the natural world (Nisbet 1977). Arguably, no areas of earth and few wildlife species have escaped the effects of humans on this planet. Effects of noise are any consequence of this anthropogenic disturbance, and are not necessarily biologically significant or negative (Bowles et al. 1991). Noise potentially affects many animals (Ryals et al. 1999, Manci et al. 1988, Fletcher and Busnel 1978) from humans (Kryter 1985, Fidell et al. 1991), bats (Hill 1970, Thomas 1995), ungulates (Curatolo and Murphy 1986, Cassirer et al. 1992, Harrington and Veitch 1991, 1992, Bradshaw et al. 1997,Cronin et al. 1998, Duchesne et al. 2000), and marine mammals (Richardson and Malme 1995, Frankel and Clark 2000), through birds (Saunders and Dooling 1975, Burger 1981, Dahlgren and Korschgen 1985, Ellis et al. 1991), reptiles (Jacobson and Lopez 1994, Johnson et al. 1996) fish (Scholik and Yan 2002) to insects (Frings and Frings 1959, Floren and Linsenmair 1999). Noise disturbance may cause stress in animals and this has physiological implications that have received attention in humans (Davies and Tune 1970, Kryter 1985) and wildlife (Wasser et al. 1997, Westman and Walters 1981, Siegel 1980, Selye 1976, Welch and Welch 1970)

Effects of noise on wildlife are arguably under-represented in the scientific literature. The effects of noise on wildlife have implications to individual animals and subsequently populations. In some cases, these may have inferred consequences to larger ecological units. I attempt to draw on important directions in the scientific literature toward our understanding of the consequences of noise disturbance on wildlife. Noise disturbance stimulates the auditory senses of wildlife, and effects originate from acoustical stimulation of the neuro-physiological system in animals (Welch and Welch 1970). Behavioural responses range from mild annoyance to panic and escape behaviour, and such responses are manifestations of stress. Excessive stimulation of the nervous system can amount to chronic stress, and this has implications for health, growth and reproductive fitness of animals (Fletcher 1980). I propose that individual responses to this type of human disturbance can be generalized through a physiological-behavioural model because behavioural response is linked to a physiological response (e.g. Thiessen and Shaw 1957). This review is therefore important before beginning to discuss the effects of aircraft noise on behaviour of the Harlequin Duck.

1.1 Definition of Terms

Considerable terminology is applied to the study of sound and noise, and behavioural response to disturbances. To facilitate comprehension, a set of definitions follows.

1.1.1 Response and Effects

Disturbance is any relatively discrete event in that disrupts individuals, ecosystems, community, or population structure and changes the distribution of resources, substrate availability, or the physical environment (White and Pickett 1985). Disturbances are responsible for a change in the state of a system, and systems that are not in equilibrium may be disturbed as readily as those that are (Hockin et al. 1992). Human disturbance relates to machines or even the activity of a single person. Individual disturbance is any stimulus that causes an animal to alter its behaviour, often by behaving alarmed and/or fleeing. Disturbances are not in and of themselves impacts.

Noise is defined as a sound of human origin that can significantly disturb animals (Bowles et al. 1991), that is, it may have deleterious effects on wildlife. Noise can be sudden or anticipatory. Noise is a significant stressor in animals, and the non-auditory effects of noise are considered whole body stress responses (Selye 1976). An animal's body can respond physiologically to sound stimulation even while the individual is asleep, under anesthesia, or after removal of its cerebral hemispheres (Welch and Welch 1970).

Effect (in this context) is any consequence of an anthropogenic disturbance. Effects are not necessarily negative or significant. An "effect" is any change in animals, and generally involves changes in behaviour (usually temporary) that locally affect the temporal and spatial distribution of the animal(s). Effects are easier to observe and quantify than are impacts. Impacts need to be assessed against a background of population level and limiting factors such as food availability, extent of habitat, and survival probabilities that determine the carrying capacity of a region.

Stimulus refers to the physical features or signals of the noise or other type of disturbance. This implies that the animal has some ability to perceive the output of the disturbance. Man-caused stimuli relate to visual, auditory or vibrational cues; such stimuli are rarely monitored and quantified in the field.

Response is a physiological, behavioural, and/or physical change that occurs in animals after exposure to a stimulus.

Startle response is an animal's reaction to unfamiliar stimuli, and allows it to respond rapidly to possible dangers. Although animals normally habituate to a particular kind of stimulus if not harmed, and sensitize when exposed to real dangers, ability to habituate rapid onset noise is limited. Learning allows the individual animal to distinguish harmless and dangerous kinds of disturbance.

Compensation for disturbance occurs when individuals or groups of animals alter their behaviour or habituate to human activities (e.g. Davidson and Rothwell 1993).

Aversion is a response by an animal or group of animals indicating perception of a stimulus as painful, stressful or frightening. Avoidance (particularly flight), defecation or urination immediately after exposure, and shivering, stress vocalization, prolonged increases in heart rate or catecholamine levels and shock are all considered to be evidence that a stimulus has produced an aversive response.

Stress is the nonspecific response of the body to any demand (Selye 1976). Stress is any physiological or behavioural response of an animal to an environmental challenge that results in some detriment. Chronic stress can lead to loss of immune function, decrease in body weight, psychological depression, loss of reproductive function, and abnormal thyroid function. Acute challenges elicit the "alarm" reaction, sometimes called the "fight or flight" response, in which catecholamines (epinephrine and norepinephrine) are released rapidly into the bloodstream, sometimes causing death from shock. The immediate physiological consequences of the release of catecholamines include changes in heart rate, lipid metabolism and gut function, and changes in attention. Reactions to acute stress may involve three stages, namely: alarm, resistance, and exhaustion. During the resistance phase some of the physiological functions return to normal whereas continuation of the stressful stimuli may result in animals reaching a stage of exhaustion during which the initial body changes recur (Selye 1976).

Animals challenged repeatedly over long periods develop high circulating levels of cortisol in the bloodstream, enlarged adrenals, and reduced thymus, spleen and lymph nodes. Elevated cortisol results in increased protein breakdown, increased blood sugars, electrolyte imbalance and increased vascular activity. Many other hormones are also affected leading to increased water retention, stimulated tissue repair, and decreased egg and sperm production (Selye 1976).

A Stressor is any stimulus that produces stress. Different stressors produce their own unique effects, and individual reactions to stress can vary considerably (the same amount of stressor may provoke different responses in two individuals of the same species, Selye 1976). Some animals or individuals may have a greater disposition to be impacted by a stressor than others, for example, individuals that have had previous exposure to a stressor may suffer more or less stress.

Acute exposure relates to the negative impacts resulting from the direct exposure to an intense harmful stimulus, for example, the loss of hearing (temporary or permanent) due to an unanticipated high noise level (e.g. explosion).

Chronic exposure is continual exposure to repeated sublethal disturbance stimuli resulting in cumulative physiological and behavioral effects in wildlife. For example, Dubovsky et al. (1996) demonstrated that juvenile black ducks (*Anas rubripes*) fledged at lower body mass and had lower survival rates than controls when exposed to an average of 70 military jet over-flights per day.

Habituation is the decline in response by an individual or group of animals to repeated exposure to disturbance stimuli. Often some lower level of response remains relative to the initial effect. Responses such as heart rate may habituate (Espmark and Langvatn 1985) or in some cases remain elevated beyond the 3 min monitoring time of studies (Weisenberger et al. 1996). Animals habituate poorly to high amplitude noise with rapid onset (Korn and Moyer 1966), and physiological effects are characterized by a rapid increase in heart rate and cardiac output, shutdown of the gut and other non-essential functions, and rapid mobilization of glucose reserves to supply the muscles (Hoffman and Searle 1968). Some responses, such as blood pressure, do not seem to habituate, and habituation to intermittent noise happens more slowly than to continuous noise (Informatics 1980).

Sensitization is the increasing magnitude of response to a disturbance stimulus and is the opposite of habituation. Disturbance from one source may also increase wariness and subsequent response to other sources of man-made disturbances (Bell and Owen 1990). Owens (1977) noted that with more frequent hunter disturbance waterfowl become more wary.

1.1.2 Acoustics

Background

Sound can occur in almost any medium but in the context of this research we are concerned with transmission through air. Sound results from a series of pressure fluctuations in the air that are detected by the ears of animals. The rate at which pressure fluctuations occur, i.e., the number of cycles per second, determines the frequency or pitch of the sound that is usually measured in Hertz (Hz). Many sounds contain a complex mixture of frequencies, and this frequency spectrum gives any sound its identifiable character. Hearing response is not equally sensitive at all frequencies. Similar to humans, the most sensitive range in birds is approximately 1 kHz to 4 kHz with sensitivity dropping off at lower and higher frequencies. For this reason, birds are more likely to respond to mid-frequency noise. Sound measures are given a frequency weighting in order to account for this, and the most widely accepted is A-weighting for humans and birds.

The frequency range generated by military fighter jets is in the order of 0.2 kHz to 4 kHz that is equivalent to 0.630 kHz to 4 kHz in the A-weighted scale. Hence noise from low-level military jets is perceived as predominantly mid-frequency, and completely overlaps the most sensitive hearing range of birds. The rate at which noise increases and decreases during fighter over-flights depends primarily upon its altitude above the ground (AGL), its speed and the lateral distance (slant distance) between the flight path and the point of observation. The presence of trees can increase the onset rate when aircraft are at low altitude. Onset rates can be very rapid (e.g. 67 dB/sec), and hence typical of impulse noise (Coles 1980). Startle effects at 30 m AGL extend to a 450 m radius (DND 1994).

The amplitude of sound, i.e., loudness, is determined by the amplitude of pressure fluctuations in the air, and these can vary by huge orders of magnitude, hence the logarithmic or decibel (dB) scale. Decibels use ratios to express any given value relative to an agreed upon reference value hence an increase in sound power from 1 watt to 10 watts represents the same decibel increase as does an increase from 10 watts to 100 watts.

Animals can be extraordinarily sensitive to sounds in some situations and quite insensitive to sounds in other circumstances (Larkin 1996). Animals respond to sound due to variation in air pressure. Measurements of sound must also take frequency (the number of cyclical variations in air pressure per second, Hz) into account as animal species differ in their ability to detect frequencies. "Loudness" is closely proportional to generated air pressure provided the animal's hearing is sensitive to the frequencies of the sound stimulus. For repetitive or continuous sound, a Sound Pressure Level (SPL, measured in decibels dB) is expressed as an average over a certain period of time of the ratio of the actual sound pressure to a reference sound pressure of 20 μPascal.

Birds possess a highly evolved auditory system and sensitive hearing, and vocal communication plays an important role in many species. The best hearing in birds is in the range of 1 to 4 kHz and there is a steep increase in the threshold up to 10 kHz that is the normal upper limit. In specialized species of birds the upper threshold approaches 20 kHz. Amplitudes of songs at average call frequencies range from - 15 to 50 dB SPL (where 0 dB = 20 μPascal), and at typical frequencies are 5 to 10 dB in most birds. Birds, such as owls, are unique with hearing sensitivity extending to about – 20 dB, and for example, in the pigeon hearing extends into the infrasound range down to 0.1 Hz. Similar to other mammals and humans, birds discriminate frequency differences and sound intensities. Because of the small head of most birds, sound attenuation between ears is small, and this is important for sound localization (Dooling 1982, 2000, Necker 2000). Sounds separated by a gap are recognized as separate if the gap exceeds 2 to 10 msec (Wilkerson and Howse 1975). Most birds are able to localize sound in the azimuth (horizontal plane) but not in elevation, an exception being owls that are able to localize sound both in the azimuth and in elevation with minimal localization error (Knudson 1980).

Weightings in decibels are applied to sound measurements and this scale is nonlinear (logarithmic) hence relatively small changes in decibels are large increases in the three-dimensional spatial volume of a sound, for example, a change of 3 decibels is equivalent to a doubling of the sound energy. To better approximate sound as perceived by the auditory system of a given animal, various filtering or weighting systems are used to modify the "flat" readings of sound measurement instruments. The most commonly used are A-weighting, approximating the human hearing thresholds. A-weighting has been generalized to birds (e.g. Brown 1990) but this is an over-generalization since hearing varies among bird species, and some researchers have developed species-specific weightings of noise metrics (e.g. Delaney et al. 1999).

Reported measurements of sound therefore must include reference to the weighting system applied, e.g., "dBA" for measurements made using A – weighting (Larkin 1996). Because weighting systems cut off ("roll off") certain (threshold) frequencies, it can generally be stated that A-weighting was intended to represent the loudness of sounds below 65 dBA, B-weighting for 65 to 85 dB, and C-weighting above 85 dB. For research purposes, the Sound Exposure Level (SEL) refers to a cumulative exposure to sound equivalent in energy to one second of sound at the stated level (Larson Davis Laboratories 1997).

Infrasound, audio frequencies and ultrasound are concepts of sound as determined by the human audiogram (airborne compression waves of frequencies roughly 20 Hz to 20,000 Hz). Compression waves of frequencies above about 20,000 Hz we call ultrasound; those below 20 Hz we call infrasound while those in between we can hear and we call them audio frequencies. Many songbirds (Dooling 1982) and terrestrial mammals (Fay 1988) have audiograms similar to those of humans; however many other species of animals do not, for example, frogs can hear frequencies from 10 – 4000 Hz whereas some insects hear sounds from 150 Hz up to 240,000 Hz. Many mammals smaller than humans have useful auditory sensitivity above 20,000 Hz., for example, dogs and cats up to 70,000 up to 100,000 Hz and bats up to 150,000 Hz. Such high frequency sounds attenuate very rapidly in air with distance from source. Marine mammals are sensitive to sounds; seals: 500 Hz to 45,000 Hz, porpoises, dolphins and toothed whales: 8,000 to 145,000 Hz (Richardson and Malme 1995).

1.1.3 Classes of noise

Noise can be broadly classified as: (i) continuous noise (ii) impulse noise (iii) impact noise, or (iv) wind noise. Continuous noise is seldom encountered by wildlife except when adjacent to human activities. Some animals, such as Harlequin Ducks, live in environments with higher background sound levels. The rapid onset of intense noise, i.e., sudden onset such as during a jet over-flight, may cause such noise to sound less loud than is indicated by its power spectrum, and to act as if it has effects at high audio frequencies disproportionate to their representation in its spectrum (Coles 1980 cited in Larkin 1996). Therefore rapid-onset impulse noise may be potentially more damaging than would be predicted strictly from its physical characteristics. Impulse noise and continuous noise differ both in their potential physical effects, namely hearing damage, and in their sensory-mediated physiological and behavioural effects (Roberto et al. 1985). Animals habituate poorly to high amplitude noise with rapid onset (Korn and Moyer 1966).

Wind noise represents an important source of background sound outdoors, and is generated from the movement of air across the surface of objects, such as through tree branches, and can be very loud (e.g. >80 dBA), and classifiable as noise. It is particularly a nuisance parameter when trying to measure anthropogenic sounds in the natural environment. Nevertheless, animals react to wind noise, and game species are notably more "wary" on windy days. Natural ambient noise from wind can presumably mask gradual increases of noise such as approaching aircraft or vehicles thereby converting gradual-onset sound into rapid-onset sound capable of startle (Harrington and Veitch 1991).

Acoustical environment of the study animals can have an important influence on habituation or sensitization, and outcomes may be non-intuitive (Larkin 1996). For example, animals may sensitize to rapid onset noise even in a situation of naturally high and continuous background sound levels (Davis 1974).

Masking is the inability to hear important sound cues from other animals because of the presence of other sounds. Masking of signals of significance may involve individuals having difficulty in finding mates, escaping predators, and communicating with conspecifics (Amoser and Ladich 2003). Masking of communication of marine mammals, notably baleen whales (Cetacea, family Balaenopteridae) is serious concern because of the need for long distance communication of individual whales, possibly through the emission of low frequencies (Myrberg 1980).

Hearing damage from loud noise is a result of physiological change to the auditory system, notably loss or damage to hair cells in the cochlea (Liberman and Bell 1979). Hearing loss or damage can be produced by brief exposure to very loud sound (McCauley et al. 2003) or by prolonged exposure to moderate levels of sound (Marler et al. 1973). Animals vary greatly in their sensitivities and susceptibilities to hearing loss (Fletcher and Busnel 1978). The frequency content of sound is very important because sounds of different spectra affect the auditory system differently; for example, high frequency tones tend to produce localized changes in the inner ear, whereas low frequency tones tend to produce changes throughout the length of the cochleae (Fletcher and Busnel 1978). Some mammals, such as rodents, are much more sensitive to noise damage than humans (Peterson 1980).

Temporary threshold shift manifests in a temporary elevation of the level of faintest audible sound and is often caused by brief exposure to moderate noise levels. This threshold usually returns to normal after a quiet recovery period (Nachtigall et al. 2003).

Permanent threshold shift results in permanent hearing loss or where lower levels of sound originally audible can no longer be heard, and are usually related to exposure to severe noise (Clark 1991).

Attenuation is progressive diminishing of sound levels attributed to interference from vegetation and topography. In the air, attenuation of sound is dominated by direct heating of air and water molecules by high frequency sounds, which is why low frequencies predominate over a distance.

Habituation is learned responses to disturbances by animals that are well adapted to deal with stimuli that are not associated with attacks, and they quickly learn to distinguish harmless from dangerous stimuli, an important adaptation for avoiding dangers without unnecessary energy expenditure (Bowles et al. 1991).

Intentional disturbance (to control pests) has received considerable study for such purposes as reducing damage to agricultural crops and reducing safety risks at airports (Blokpoel 1976, Burger and Gochfeld 1994). Some authors have demonstrated more effective deterrence when using human effigies (Boag and Lewin 1980).

1.2 Special cases of human noise

There are special cases of noise that have received focused scientific research mainly on humans that seemingly have implications to urban wildlife. These disturbances include such areas as tourism noise, urban noise, industrial noise, and military noise (Anderson et al.1996, Holthuijzen et al. 1990, Larkin 1996).

Hunting is a contentious area within public systems of resource management. Much effort is focused on the direct mortality impacts, with endless debate on density dependent compensation with natural mortality (Nichols et al. 1984). Yet there is little attention to its secondary effects that are possibly far greater (Owen 1972, Tuite et al. 1984, Madsen 1985,1994, Madsen and Fox 1995). Frederick et al. (1987) concluded that the direct effect of hunting (killing birds) was less important in reducing the population size of geese than the associated disturbance which led to early emigration. They noted that disturbance from hunting caused disruption of feeding patterns, reducing energy gains and hastening emigration. In Germany the density of waterfowl and coots was inversely related to hunting pressure (From Reicholf 1973 in Bell and Owen 1990). Increased tourism may result in considerable disturbance of tropical wildlife (Griffiths and Van Scheik 1993)

1.3 Effects on Individuals

1.3.1 Implications of Noise Disturbance

Noise and human presence have similar effects on wildlife, i.e., they interfere with the normal activities of wild animals or invoke stress in individual animals. In some cases, noise may have greater negative implications than human presence to wildlife because of the physical characteristics of the habitat, notably for fish and aquatic mammals. For example, noise travels faster and for much greater distances in water than in air and with less attenuation (Richardson and Malme 1980, Amoser and Ladich 2003). Underwater noise may interfere with locating mates in fish (Fine and Lenhart in Informatics 1980, Amoser and Ladich 2003) and marine mammals (Lesage et al. 1999), and/or cause hearing loss (McCauley et al. 2003). Noise can affect the behaviours of animals (Frankel and Clark

2000, Brown 2001) with subsequent negative effects, such as Spadefoot Toads (*Scaphiopus couchi*) emerging (expecting rain) when subjected to motorcycle noise (95 dBA) (Bondello and Brattstrom 1979). Simulated noise has been used as a management tool to alter migration routes of wildlife [such as Gray Whales in response to Killer Whale sounds (Cummings 1971)], evict bats (Hill 1970), and attract insects (Frings and Frings 1959).

1.3.2 How animals respond to disturbance

Animals can avoid noise disturbance, and this can involve abandonment of preferred habitat, change in home ranges, and/or altered migration patterns, and may result in a decrease in survival. In some cases wildlife may demonstrate no response or may habituate or adapt to noise disturbance. In certain cases, wildlife may be attracted to the disturbances such as vehicles and traffic (e.g. raptors and small mammals attracted to area of airport runways possibly because of availability of food, Informatics 1980).

When confronted with noise disturbance, an animal may: (i) choose a behavioural response, and/or it may evoke the (ii) autonomic and/or (iii) neuroendocrine systems (Figure 1). The responses of the latter systems result in changes in biological function, i.e., diverting the animals own resources from ongoing biological activities to new biological activities that may assist the animal in coping with the stressor (Moberg 1987). Reflexes may be weakened and learning responses decreased through chronic exposure to harmful noise levels.

1.3.3 Compensatory behaviours

Animals may avoid sites when disturbance events are frequent but subsequently use such sites when less disturbed sites have been depleted of food (e.g. Owens 1977). Some animals may compensate for daytime disturbances by feeding at night (Owen and Williams 1976). Compensatory feeding may be constrained by the morphology of feeding apparatus or time-activity budgets (Goudie and Ankney 1986). Some animals are able to increase their feeding rate (e.g. Swennen et al. 1989), while other animals do not (e.g. Belanger and Bedard 1989).

1.3.4 Stress and other general physiological effects

The concept of noise as a stressor is basic to understanding its physiological effects on animals. Altered reproductive behaviour resulting from noise disturbance (e.g. Anderson et al. 1989, Holthuijzen et al. 1990) is a major area of concern due to possible effects on survival of populations or species (Informatics 1980). Ultimately, all response to noise disturbance is affected by physiological changes in individual animals.

While stress responses seem maladaptive, they actually perform important functions, such as reducing inflammation and speeding acclimation to environmental stressors (Bowles 1994). When an animal's capacity to adapt is exceeded, it experiences distress (pathological), evidenced by clinical systems of ill health, including such things as neurotic behaviour, reproductive failure, inhibition of growth, and/or disease. Depending on type and intensity of noise disturbance, the same adverse stimulus may affect either the whole body or mainly one part (Selye 1950, 1976) because stress involves a number of complex neuro-endocrine interactions (Moberg 1985).

1.3.5 Behavioural responses to noise disturbance

Individuals may react to noise disturbances by ceasing all activity ("freezing") (Gabrielsen et al. 1985), reducing feeding rates (e.g. Cramp and Simmons 1977), reducing food intake (e.g. Stockwell et al. 1991), ceasing feeding (e.g. Belanger and Bedard 1989) and/or diverting their attention to the source of disturbance (e.g. Brown 1990) or by moving to another area (Anderson et al. 1986, Colescott and Gillingham 1998, Bell and Owen 1990). Individuals affected by noise may demonstrate short term responses yet exhibit protracted residual effects also, such as: (i) becoming more aggressive, and (ii) decreasing courtship (Chapter 4), increasing self-comforting behaviours (e.g. preening), increasing vigilance, and becoming inactive (Chapter 5). Time/activity budgets could be affected by disturbance (Salter 1979, Murphy and Curatolo 1987, Maier et al. 2001). The lack of behavioural response to disturbances does not necessarily mean that animals are not stressed by stimuli because physiological changes may still occur even when no outward behavioural change is apparent (e.g. Conomy et al. 1998a but see Temple et al.

1996, Gill and Sutherland 2000, Jungius and Hirsch 1979).

It is generally accepted that wildlife respond to disturbance stimuli when some threshold level is reached or exceeded (Delaney et al. 1999). Response above such a threshold usually follows a logistic relationship (e.g. Brown 1990, Reijnen et al. 1995).

1.3.6 Lowering of breeding success

Many studies of the effects of human disturbance on breeding success of individuals show biologically significant results (Hockin et al. 1992). Sometimes real effects on the study animals are compounded by effects attributable to the presence of researchers (e.g. Gotmark 1992, Rodway and Montevecchi 1996). However, few studies have quantified reactions of animals or their young to disturbance and few have quantified the mechanisms by which reproductive success was affected (but see Anderson and Keith 1980, Flemming et al. 1988). Many studies rely on the perception of the observer of the potential disturbing effect rather than a measure of effects on individuals (Bell and Owen 1990). Such shortcomings can be improved when demonstrating the relationship between response in animals and to a measurable dose of disturbance (Bowles et al. 1991).

The main reasons postulated for lower breeding success in birds subjected to human disturbances are:

(i) nest abandonment (Anderson and Keith 1980).

(ii) increased predation of eggs and young (Titus and van Druff 1981)

(iii) direct destruction of nests (Burger 1991)

(iv) Deferment of breeding (Tremblay and Ellison 1979, Hobson and Hallinan 1981)

(v) Exposure of eggs (Hunt 1972)

(vi) Inhibiting effects on female maternal behaviour (broodiness) (Jeannoutot and Adams 1961)

(vii) Reduced feeding and brooding of young and increased mortality (Flemming et al. 1988)

(viii) Accidental collisions (Safina and Burger 1983, see also Blokpoel and Hatch 1976)

1.3.7 Predator impact

Humans and their noises may make animals, especially young, more vulnerable to predators (Swennen 1989). Birds can lose eggs and young to predators after being startled into flight (Rodway and Montevecchi 1996). Harrington and Veitch (1992) reported that caribou exposed to low-altitude over-flights by military jets in Labrador lost more calves (to wolves) than unexposed caribou. Individuals in groups may respond differently. For example, waterfowl flocks may be as sensitive as the most vigilant member of the group, so that larger flocks have a greater chance of responding than small flocks. Individuals also respond differently in different settings (Owens 1977).

1.3.8 Implications for energy budgets

Disturbance generally reduces feeding time and increases energetically costly behaviours, notably flying (Owens 1977, Belanger and Bedard 1989, 1990), and overall daily energy expenditure can increase significantly (e.g. 31% in White-Robinson 1982, 20% in Watmouth 1983). For example, energetic costs of flight are 10 to 12 times Basal Metabolic Rate (BMR), swimming 4 times BMR, comfort behaviour 2 times BMR, brooding 1.5 times BMR, and walking, hopping and running 3-5 times BMR (Paynter 1974). Such stress is thought to confer a survival cost to individuals, and increased mortality within populations (Miller 1994, Miller et al. 1994).

Effects of disturbance on behaviour may make certain feeding sites unprofitable. Disturbance may affect body condition, subsequent reproductive output, and/or parental care (Fernandez and Azkona 1993). Arctic nesting geese are known to rely heavily on nutrient reserves accumulated before nesting (Ankney 1984, Ankney and MacInnes 1978, Ebbinge 1989, Madsen 1994) therefore disturbance during migration may prevent birds from reaching optimal body condition.

1.3.9 Impacts on body condition and survival

A change in distribution has a number of possible consequences, including restriction of feeding opportunities (time and space), increased energetic costs of moving, and increased concentration of individuals which increases intraspecific competition and/or risk of disease. Such consequences may affect condition of individual animals (e.g. Dzubin 1984, Temple et al. 1996).

In Pink-footed Geese (*Anser brachyrhynchus*) in Denmark, staging individuals in undisturbed fields increased their body condition (as measured by Abdominal Profile Indices) whereas birds using disturbed fields did not. Of marked individuals re-sighted in the subsequent autumn, birds from the undisturbed sites were more successful at breeding (Madsen 1994).

1.3.10 Effects on family groups and pair bonds

Family groups may be less cohesive and suffer higher mortality when disturbed (Jones and Jones 1966, Bartlett 1987, Prevett and MacInnes 1980). Being in a family may confer survival advantages on young animals, and family breakup implies a cost in terms of future survival and productivity (Owen and Black 1989). Disturbance may affect pair bonds (Owen et al. 1988). Paired birds may out compete lone birds, and paired females may have access to the best feeding areas (Paulus 1984). Accumulated nutrients are important to breeding success (Krapu 1981). Therefore disturbance factors that affect the pair bond may influence future breeding success.

1.4 Effects on populations

1.4.1 Effects on vital rates

Changes in survival rates, emigration rates and/or breeding success of individuals affect populations. If disturbance has an effect on the local survival and/or fecundity of individuals then there is a consequential change in population size (Cayford 1993). Disturbances can reduce populations in certain geographic areas or zones of disturbance (Reijnen and Foppen 1994). The sizes of animal populations are determined by the availability of a limiting resource, usually food (Lack 1968), but carrying capacity over extensive areas is difficult to measure.

Disturbance may cause redistribution of wildlife. If animals are displaced from a site, their survival depends on the availability of alternate feeding sites. Displaced individual animals may suffer from mutual interference when forced to feed elsewhere under increased densities, thereby affecting food intake rate which affects carrying capacity leading to meta-population effects and subsequently population effects (Sutherland and Anderson 1993, Goss-Custard et al. 1995). Hill et al. (1997) presented a schematic model of the relationship between disturbance and habitat loss, food supply, intake rate, carrying capacity and importance to meta-populations that helped highlight the complexity of these relationships.

Effects of disturbance on wildlife are species specific (Reijnen et al. 1995, Amoser and Ladich 2003) and group specific (Dzubin 1984). Response of wildlife to disturbance may also vary depending on the environmental setting or abiotic conditions that the subjects are in (e.g. Cooke 1980, Schueck and Marzluff 1995). Some authors have hypothesized that species having the most difficulty meeting their energy requirements are most sensitive to disturbance (Bell and Owen 1990, Mayhew 1988).

1.4.2 Effects on density

Disturbance may lower carrying capacity of habitat for wildlife leading to lower densities in zones affected by disturbances (Madsen 1994, Reijnen and Foppen 1994). Alternatively, disturbance may result in wildlife feeding in poorer quality habitats, and feeding below the threshold rate required for survival sufficient to maintain populations over the longer term. This leads to increases in the proportion of birds dying or emigrating as population size increases, i.e., a density dependent effect (Goss-Custard et al. 1995, Gill et al. 1996).

1.4.3 Effects on reproductive output

Disturbance can lower reproductive performance of a population or segment of a population (Reijnen and Foppen 1994). For example, human disturbance at seabird colonies can cause mass loss of eggs and/or young affecting the reproductive output of the entire colony (Manuwal 1978).

1.4.4 Timing of disturbance

Disturbance is most likely to have an impact during the periods of the annual life cycle when food resources are depleted and birds have difficulty in meeting daily energy requirements (e.g. winter in Madsen 1994). Such periods probably occur when individuals need to build up nutrient reserves in advance of periods of high energetic demand. In migratory species, energy reserves are accumulated in the late summer-fall and/or early winter to "fuel" migration or in spring to 'fuel" breeding. Such reserves may be depleted but subsequently replenished (Ebbinge 1992, Owen et al. 1992, Owen and Cook 1977, Fox et al. 1992, Pienkowski et al.1984). If resources are not accumulated then reduced clutch sizes or even mortality occur (Goudie et al. 2000). Strong intraspecific competition can limit nutrient acquisition when resources are space limited (Teunissen et al. 1985, Ebbinge 1992).

1.4.5 Landscape effects

Disturbance can be equated to lessening of carrying capacity (Bell and Owen 1990), specifically, habitat loss that is reversible. Owen (1973) calculated that due to disturbance from hunting only half the potential usage by the geese of the Wildfowl Trust refuge at Slimbridge, England was being realized. Animals may distribute themselves more widely in the absence of disturbance (Gerdes and Reepmayer 1983 in Bell and Owen 1990, Mayhew

1985). Some animals may distribute themselves around the landscape in relation to disturbance, implying that birds are being prevented from exploiting areas they would otherwise favour (Jepsen 1983 in Bell and Owen 1990).

1.4.6 Effects on communities

Notwithstanding that disturbance may impact species differentially, it is intuitive that certain types of disturbance can impact biological communities. For example, Reijnen et al. (1995) determined that 26 of 43 species of songbirds showed reduced densities adjacent to noisy highways. It is generally accepted that reduced use of available habitat equates to habitat loss. In theory the impact is reversible.

1.5 Mitigation and management of effects

Wildlife may benefit greatly from the elimination of disturbance. For example, waders increased from 20,000 to 220,000 individuals on an islet that the birds could use at high tide in France following protection from hunting (Campredon 1979 in Bell and Owen 1990). Considerable attention has focused on the mitigation of potential negative effects of disturbance, including noise, on wildlife (e.g. Fyfe and Oldendorff 1976, Nimon and Stonehouse 1995, Rodgers and Smith 1995, Richardson and Miller 1997, Carney and

Sydeman 1999, 2000, Nisbet 2000). Such approaches as determining thresholds of response, such as distance to disturbance and/or noise levels, and discrimination of important explanatory variables are used to develop management recommendations that, if applied, should minimize human impacts (Grubb and King 1991).

Wildlife managers are especially concerned about:

1. Changes in health and survivorship;
2. Changes in fecundity and productivity;
3. Changes in distribution, habitat use and abundance;
4. Changes in the demographic composition of single populations;
5. Changes in species diversity

(after Bowles et al. 1991)

Managers seek to minimize human disturbance on wildlife. Management actions may be based on empirical data, especially where dose and response are known but this is rare, or, in many cases, may be based on subjective judgments. Bowles (1994) proposed a number of general approaches to help reduce important behavioural and physiological responses of wildlife to noise disturbance. These include (i) diverting noise sources away from wildlife, (ii) making noise predictable, (iii) eliminating disturbance if animals show a behavioural response, (iv) gradually habituate animals to noise, and (v) altering noise by combining with a masking noise. Bowles further elaborated on a series of recommendations from the Committee on Pain and Distress in Laboratory Animals of the

National Research Council of the United States aimed to minimize the potential for distress, including limiting cumulative exposure to noise by (i) limiting the frequency and duration of noise (ii) eliminating meaningful noise (iii) eliminating or reducing exposure to disturbing noise and (iv) proving safe cover in areas of noise exposure.

1.6 Theoretical and methodological considerations

1.6.1 Emergence of the Mobergian model

Moberg (1987) rationalized that scientists need to define and evaluate an animal's well-being, and that one approach is to determine if the animal is suffering from stress. If an animal is stressed, its well-being is threatened. A behavioural stressor is perceived by the animal as a threat to its well-being. The measurement of stress has been hampered by: (1) determining the best measure of stress, (2) the lack of a nonspecific response that characterizes all stressors, (3) inter-animal variability in the biological response to a stressor and (4) failure to establish which biological responses to stressors have a meaningful impact on an animal's well-being.

When confronted with a stressful situation an animal may: (1) choose a behavioural response or alter its biology by evoking the (2) autonomic and/or (3) neuroendocrine systems. The latter responses result in changes in biological functions, diverting physiological resources from ongoing biological activities to new ones that may assist the animal in coping with the stressor. These responses have been used as indicators of stress (Selye 1976), for example, stereotypic behaviour, or responses in the autonomic nervous system, such as increase in heart rate, or responses in the neuroendocrine system such as release of corticosteroiods. Unfortunately, no one biological response is characteristic of all types of stressors, despite earlier postulations of a nonspecific response indicator (Selye 1950), and inter-animal variability can be considerable.

The measurement of behavioural stress requires a variable(s) that accounts for the diverse patterns of biological responses resulting from different stressors and inter-animal variability. Such a response variable must have a meaningful impact on an animal's well-being (Moberg 1987). The response of animals to stressful events are composed of three major components: (1) recognition of a threat to homeostasis (central nervous system), (2) the stress response (behavioural, autonomic and/or neuroendocrine and (3) the consequences of stress (alleviation or amelioration of effects or no effect).

Regardless of its effectiveness in assisting an animal to cope with the stressor, the change in biological function accounts for the biological cost of the stress. It is this change in biological function that can threaten the animal's well-being by placing it into a pre-pathological state. When an animal enters a pathological state there is no question that its well-being has been jeopardized. Moberg (1987) proposed that the development of pre-pathological state is the best indicator of behavioural stress. In recent research there has been considerable focus on measuring 'stress hormones' such as cortisols (mammals) and corticosteroids (birds) as indicators that study animals which may be entering pre-pathological states (Wasser et al. 1997). Repeated activation of these physiological pathways leads to pathology.

1.6.2 Dose-response approach

A major weakness of the existing literature is its "all or none" view of impact (Bowles et al. 1991), and studies are sometimes conducted when noise levels of treatment areas do not differ from control areas or are likely below the threshold level at which responses are expected (e.g. Trimper et al. 1998, Grubb et al. 1998, Doresky et al. 2001). Many studies imply effects on behaviour of wildlife due to noise yet noise is never quantified (e.g. Andersen et al. 1996, Gibeau et al. 2002). In other cases the hypothesized effects are supported by correlations (Harrington and Veitch 1991, 1992; Reijnen and Fopper 1994, Reijnen et al. 1995), and these do not support cause and effect. Some studies have documented noise thresholds below which wildlife do not respond behaviourally (Burger 1991, Delaney et al. 1999).

The determinations of effects of noise disturbance on wildlife require an understanding of outcomes of exposure to stressors at the level of the individual. This predisposes many studies to be hampered by low sample size and statistical power. Often researchers do not assess the statistical power of their methodologies, and conclusions of no impact are better phrased in the context of inability to reject a null hypothesis (no impact) but with little inherent power to detect a significant result (e.g. Trimper et al. 1998).

More convincing evidence of a causal association occurs through demonstrating an increase in an adverse outcome (response) with a corresponding increase in the level of exposure (dose) (Brown 1990). Wildlife managers have not fully embraced the need for a dose-response approach (Brown 2001a). The result has often been failure to measure any impact but the immediate and obvious behavioural responses of naïve animals (Bowles et al. 1991). Animals generally respond behaviourally to disturbance at certain thresholds. Quantifying the disturbance (dose) is therefore very important.

Disturbances can be subjectively categorized on the basis of (a) their level, and (b) their frequency of occurrence identifying a gradient from passive, low-level disturbance at one end, to active high-level disturbance on the other end (Hockin et al. 1992). Moberg (1987) recommended using "outcome measures" to correlate with exposure to disturbance stressors, namely: (i) reproductive success, (ii) growth rate, (iii) incidence of disease, and/or (iii) changes in survival. Some authors have proposed an analysis of growth curves of fledging birds as a potential measure of the effects of environmental stressors, and effects may manifest themselves in young but not in adults (Dubovsky et al. 1996).

1.6.3 A multivariate approach

Many dependent and independent factors are inherent in quantifying effects of disturbance. The study of behaviour is complex, and researchers may not have *a priori* means of predicting which behaviours (response) track disturbances (dose). Furthermore, behavioural data are invariably intercorrelated, and multivariate analyses handle this well because they model covariance, and potentially permit researchers to synthesize complex relationships and reduce the dimensionality of datasets. Resulting multivariate variables can then be interpreted as sets or suites of behaviours. Classical multivariate discriminant analyses are sometimes not applicable because of threshold responses and the inclusion of nominal and interval data in addition to ratio-scaled predictor variables (Grubb and King 1991). These authors presented classification and regression tree (CART) models that are nonparametric dichotomous keys that hold considerable promise.

The univariate approach to assess impact between "disturbed" and "undisturbed" categories can logically be extended into the multivariate environment. Statistical models usually encompass response variable with categories (e.g. undisturbed and disturbed) in relation to ratio or rank variables, and are appropriate for the application of a Multivariate Analysis of Variance (MANOVA) which maximizes the ratio of among-group to within group variance in canonical scores. Subsequent to a statistically significant MANOVA, a Discriminant Analysis (DA) can be applied. It is logical to consider DA as an extension of MANOVA because overall we are interested in testing the null hypothesis that the groups do not differ, whereas in DA we are interested in describing the linear combinations of dependent variables that discriminates maximally among groups. In other words, MANOVA and DA correspond to the inferential and descriptive aspects of analyses in much the same way as the univariate ANOVA and subsequent multiple range tests because in the latter we seek to describe where the differences among groups lie (McGarigal et al. 2000).

1.6.4 Disturbance in an ecological context

Estimates of the potential effect of disturbance on behaviour of wildlife must be grounded in behavioural ecology. This framework predicts, for example, that responses to disturbances will decrease if the "costs" to an animal for not responding are not consequential, whereas responses will increase dramatically if there are substantial "costs" for not responding. Optimal foraging theory provides a useful framework for analyzing factors affecting habitat (patch) selection and exploitation (Cayford 1993).

Because animals often perceive humans as potential predators, researchers evaluate the trade-offs that animals face between disturbance rates and the amount of a given resource available between patches (Gill et al. 1996). A consequence of this approach is that researchers can estimate the amount of resource not utilized (Lima and Dill 1990), and the number of animals that may be sustained by these unexploited resources in the absence of disturbance (Gill et al. 1996).

Some authors have stressed the importance of conducting larger landscape-level experiments (Gutzwiller 1991, Madsen 1994). Disturbance can be regarded as equivalent to habitat loss (although its effects are reversible) in situations where human-induced disturbance results in animals abandoning a site. In some disturbance situations, individual animals forage sub-optimally (Prins and Ydenberg 1985). Wildlife densities rise as their habitats are lost. Whether or not this affects the local or global population depends on whether rates of emigration, mortality and reproduction are already or will become density dependent (Goss-Custard et al. 1994).

1.7 Discussion

Effects of noise disturbance on wildlife are pervasive across the animal kingdom, and reasonably well documented, yet the ability to quantify disturbances and especially responses (effects) remains somewhat elusive. High inter- and intraspecific variation in behavioural responses are the norm. Responding to disturbance involves the central nervous system, the autonomic nervous system and/or the neuroendocrine systems of individual animals. If animals cannot eliminate or reduce the effect of a disturbance stimulus through behaviour or habituate to it then physiological effects are manifested. These physiological changes have evolved to address short-term threats to an animal's well-being, such as an attack by a predator. Human disturbance, on the other hand, exposes wildlife to continuous or chronic disturbances that threaten the well-being of individuals. Such exposures result in pre-pathological, and ultimately, pathological effects on wildlife as vital physiological functions are altered to the longer-term detriment of individuals.

I suggest that the study of effects of noise on wildlife can be improved using an experimental dose-response approach by assessing the relationship of behaviour and/or pre-pathological outcome measures to noise levels. In Chapter 4, I use a Before-After-Control-Impact (BACI) study design to demonstrate impact of noise generated by military jets on behaviour of Harlequin Ducks breeding in central Labrador. This design controls for variation that might otherwise be attributed to variation in time or space (Green 1979). This approach employs univariate Two-way Analyses of Variance, and is an attempt to treat specific behaviours independently and provide succinct analyses. After statistical support for an effect of noise on behaviour has been detailed, I model magnitude of response against the recorded noise levels generated by military jets. The resultant dose-response curves are among the first in the scientific literature, and the first to demonstrate an effect of military jet over-flights on the environment of the Military Training Area of central Labrador.

In Chapter 3, I assess empirical support for the paradigm that productivity in Harlequin Ducks is limited by available epibenthic foods. This theory has important implications to foraging behaviour in Harlequin Ducks because food limitation may impose time constraints on foraging, and have implications on the interpretation of effects on time-activity budgets; specifically, if aircraft disturbance results in significantly less time allocated to feeding.

No behaviours can truly be considered in isolation of others because considerable co-variation exists among the suite of behaviours exhibited by wildlife. I argue that when assessing behavioural responses it is important to invoke a multivariate statistical approach in order to model this co-variation among behaviours. A potentially beneficial outcome is the quantitative assessment of "disturbance space" relative to "undisturbed space" in reduced dimensionality of cumbersome datasets. In Chapter 5, I use Multivariate Analysis of Variance (MANOVA), Multivariate Analysis of Covariance (MANCOVA), and subsequent Discriminant Analysis (DA) to model the suite of 16 behaviour categories in disturbed and undisturbed space. I incorporate data collected during over-flights by Military jets, helicopters and fixed wing floatplanes in order to assess the relative response of Harlequin Ducks to different aircraft types. The resultant canonical variables, as linear combinations of the original variables, are modeled against recorded noise levels in order to assess dose-response.

Moberg (1987) has provided the framework for assessing behavioural stress on animals. His hypothesis of identification of pre-pathological "states" as the best indicators of negative effects of disturbance (= stress) on well-being of individual animals warrants further application in the field of behavioural ecology. Such pre-pathological states are, as yet, poorly defined but initially should include some measure of behavioural response, such as Alert or Startle, because this indicates that a physiological response may be occurring. Consequences of behavioural and physiological responses to noise may affect reproductive success, body condition, growth rates and survival. All these potentially affected "states" are demographic components, and subsequently affect the longer-term conservation of species. My research linked these behavioural responses of individuals to levels of aircraft noise (dose), and are therefore likely to enlighten this evolving field of behavioural ecology.

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Chapter 2. CO-AUTHORSHIP STATEMENTS

I am the main and first author on all research papers included in this thesis. I designed, planned and executed the studies, and participated in the collection of the data. I performed all the statistical analyses and wrote the manuscripts. Dr. Ian L. Jones is a second author on two of these manuscripts, and he contributed to the elaboration of ideas, study plans, and made many editorial comments on earlier drafts of the manuscripts.

Dr. Greg J. Robertson and Dr. Edward H. Miller contributed valuable editorial comments on earlier drafts of all scientific manuscripts.

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Chapter 3. Feeding behavior of Harlequin Ducks *Histrionicus histrionicus* breeding in Central Labrador: a test of the food limitation hypothesis

3.1 Abstract

We quantified foraging behavior of Harlequin Ducks (Histrionicus histrionicus) in central Labrador in spring 1999 to 2002, to test predictions of the long-held paradigm that productivity of this species is limited by available epibenthic insect prey in streams used by breeding birds. Females without broods were observed early in the nesting cycle (> 70 % of the local population), and were ascertained to be failed nesters. These adult females without broods were indicative of what previous researchers had defined as "nonbreeders". Productivity of Harlequin Ducks breeding in central Labrador ranged annually with from 10.0% to 33.3% of females producing broods, compared to northern Newfoundland where it was higher (75.0% and 88.9%, in 1997 and 1998, respectively). In Labrador, females spent relatively low proportions of time feeding (mean: 0.369 of the ~17h of daylight, range: 0.354 ± 0.016 SE - 0.389 ± 0.025 SE), with little variability across years and similar to proportions of time spent feeding in northern Labrador (0.396) and insular Newfoundland (0.390 ± 0.051 SE). We suggest that females could have budgeted considerably more time to feeding if this had been necessary to meet their nutritional requirements. The lack of variation in time budgeted to feeding across space and time suggested that foraging behavior was not tracking a highly variable or limiting resource. Physical evidence of egg passage through the cloaca, and radio-telemetry of females indicated that all adult female Harlequin Ducks in our study area attempted

nesting each year. We found no support for the paradigm that females were constrained by lack of sufficient food on their breeding habitat and deferred breeding.

3.2 Introduction

Animals breeding in temperate environments exploit food resources that may be seasonally abundant (e.g. Fretwell 1972) yet food supply often limits reproductive success and survival of young and/or adults (Martin 1987). Lack (1968) proposed the food limitation paradigm for the K-selected life history patterns of seabirds, and suggested that these limits arise from the sparseness, patchiness and variability of food supply. Long-lived birds should accept few risks for the sake of a single breeding episode so that they may enhance future reproductive success (Ricklefs 1983). The low reproductive rates and long life spans of seabirds may reflect influences of environment and demographic consequences of interaction with the environment as part of their life history evolution (Ricklefs 1990).

Annual breeding propensity is thought to vary considerably in sea ducks (Goudie et al. 1994), and contribute to large fluctuations in annual productivity (Milne 1974, Coulson 1984, Goudie et al. 2000). Non-breeding in Harlequin Ducks has been defined as cases in which sexually mature birds migrate to and reside on natal rivers during the spring-summer period but do not breed (Bengtson and Ulfstrand 1971). Food limitation has been a plausible hypothesis explaining variability in breeding propensity and productivity in Harlequin Ducks because productivity and populations were weakly correlated with the quantity of epibenthic larval insect food available on the breeding streams in Iceland

(Bengtson 1972, Gardarsson and Einarsson 1994). This in contrast to DuBowy's (1988) assertion that no study had demonstrated a clear case where waterfowl populations were food-limited during the breeding season. Species are hypothesized to have an optimum time budget for environmental conditions, and selection should favor individuals whose time budgets are most favorably adapted (Verner 1965). Consequently, low levels of available food should limit the ability of individuals to budget sufficient time for feeding, which can be detected by field observations.

Failed breeding in birds due to predation, inclement weather and other factors is well known, yet in the early part of the twentieth century researchers proposed an hypothesis of periodic non-breeding among Arctic bird species, notably King Eiders (*Somateria spectabilis*), and Long-tailed Ducks (*Clangula hyemalis*; Bertram et al. 1934, Bird and Bird 1940). Some Arctic nesting species, such as the Snowy Owl (*Nyctea scandiaca*) are nomadic and eruptive which has resulted in considerable speculation that non-breeding is a common phenomenon linked to the cyclic nature of predominant prey species, namely lemmings: (*Dicrostonyx groenlandicus*, *Lemmus trimucronatus*) (Parmelee 1992). Some authors have noted a link between breeding propensity of Arctic-nesting bird species and lemming abundance (e.g. Summers and Underhill 1987, Underhill et al. 1993 - *Branta bernicla bernicla*; Quakenbush and Suydam 1999 - *Polysticta stelleri*; Blomqvist et al. 2002 - *Caladris canutus*, *C. ferruginea*, *B. b. bernicla*, *Anser albifrons*).

Direct behavioral and/or physiological evidence for facultative deferment or 'skipping' of breeding in some years is scarce. A physiological mechanism for such a phenomenon is an important consideration, and decisions to breed must occur weeks before the laying period because biosynthesis and egg formation may often occur before females can assess or benefit from increased food availability near the breeding site (Williams 1999). We believe more empirical research is required to definitively test the deferred breeding hypothesis. Based on this background, we tested predictions arising from the non-breeding hypothesis and supposed limitations imposed by available epibenthic food using data on behavior of Harlequin Ducks breeding in central Labrador, and elsewhere in North America. Specifically, these predictions were:

Prediction 1: Because productivity varies across sites, we expected to observe high variance in feeding behavior among sites in Labrador and Newfoundland.

Prediction 2: If adult females 'defer' or skip breeding, we expected pairs to remain intact on the breeding streams until such time as males depart for their marine molting sites. In other words, we did not expect to observe males unaccompanied by their mates, and/or paired females alone during the spring observation period if females were not breeding.

Prediction 3: If food limits breeding propensity by females, we expected that Harlequin Ducks should budget a high proportion of the day to feeding. In other words, a large proportion of the day should be budgeted to feeding activity in order to meet metabolic requirements for egg production.

Prediction 4: If food limits breeding propensity and hence productivity, we expected to see annual variability in proportions of time budgeted to feeding. Notably, higher proportions of the day should be budgeted to feeding during years when productivity, as indicated by hatched broods, is low because paired females have to increase time searching for epibenthic foods.

Prediction 5: "Non-breeding" females should not show evidence of egg passage in the form of physiological and physical changes of anatomy.

3.3 Methods

3.3.1 Behavior

From 1999 to 2002, we searched for apparently non-breeding adult female Harlequin Ducks on our study area at Fig River in central Labrador (53^0 03'N, 63 ^{0} 09'W) during the spring-summer period based on criteria used by Bengtson and Ulfstrand (1971). Behavior of Harlequin Ducks was quantified in spring (10 May -18 June) using an instantaneous focal sampling approach (Altmann 1974) linked to marked individuals. This was possible because Harlequin Ducks are philopatric to breeding sites (Robertson and Goudie 1999), and a large proportion of individuals on the study area were marked using field readable colored alphanumeric tarsal bands.

Behavior of Harlequin Ducks was characterized by bouts or states (e.g. Feeding and Resting, see Martin and Bateson 1986), and each of these bouts generally lasted less than 30 minutes. Focal birds were monitored for 30 minutes (or until lost from sight) using binoculars and/or (20X-60X) spotting scopes. Instantaneous behavioral classifications of focal birds were recorded every 15 seconds (every 60 seconds in 1999) using digital watches with countdown-return beeper functions) from a suite of 60 categories until 30 minutes had elapsed. We attempted to sample equally throughout the daylight period. In our analysis, we focused on the proportion of time spent feeding by paired female Harlequin Ducks. In order to maximize independence of behavioral data, a new bird was selected for observation or observers shifted locations to find other birds after each 30-minute watch was completed. In a few cases, two standardized watches were conducted in succession.

Instantaneous data recorded every 15 seconds were not statistically independent within each 30- minute watch. Therefore frequencies within behavioral categories were summed over each watch, and these summaries were converted to proportions which represented the primary unit for further analyzes, i.e., one data entry per behavioral watch of 30 minutes (Martin and Bateson 1986, Goudie and Ankney 1986).

3.3.2 Morphometrics and evidence of breeding

Adult Harlequin Ducks were captured by suspending 18 m x 3m mist nets across rivers, usually in early morning (0500-0800 h) when birds flew frequently. During high water, we erected mist nets in L-shaped patterns at the mouths of coves frequented by Harlequin Ducks. The birds were flushed into nets by concealed observers as birds fed along the inundated shorelines of these coves. After removal from mist nets, the Harlequin Ducks were placed in mesh bags, and shielded from visual stimuli by covering bags with a dark cloth. Birds were banded on the right tarsi using standard USFWS stainless steel bands, and marked on the left tarsi with a yellow plastic band bearing a 2-digit numeric-alpha code that could be deciphered through 15-60X spotting scopes when birds were roosting on rocks and ledges.

Bengtson and Ulfstrand (1971) inferred that all females without broods that were captured on their study area(s) in Iceland were adults (presumably based examination of the cloacae). They did not define any criteria for separating adult females from subadults or juveniles but it is assumed that the absence of a full or reduced bursa of Fabricus qualified individual females as adults (see Mather and Esler 1999). Individual birds were measured, and members of pairs were released together. Morphometrics were collected on captured birds, including: mass, length of: wing chord, 9th primary, tarsus, tail, culmen midline, and sternum. The following criteria (after Allen 1985) were indicative of recent egg laying: (i) splayed pelvic bones which easily allowed the passage of 2 fingers (~ 4 cm.) when moved over the lower abdomen (ii) the obvious presence of an egg in the oviduct, i.e., a hard bulge protruding in the lower abdomen (iii) a sunken lower abdomen indicating that an egg had recently been laid. As the egg matures in the abdomen and the shell is secreted, the egg can be detected as a hard bulge in the normally soft area of the abdomen. With egg passage, the pelvic bones that are normally "closed" across the abdomen to within about 1 cm of each other become splayed, and the abdomen displays a "sunken" appearance.

3.3.3 Productivity

Productivity, indexed as broods per adult female, was quantified annually from frequent searches of the study areas for broods, and linked to marked (or unmarked) females whenever possible. All broods were assumed to have been detected because our study areas were surveyed frequently and completely by field observers throughout the breeding season. Nevertheless, this measure underestimated nesting effort because females that failed during laying and incubation remained unknown. Therefore, to detect early nesting failure, sub-samples of females were captured prior to the laying period and fitted with radio transmitters in 2000 ($n = 4$) and 2001 ($n = 11$) attached by anchor sutures to the inter-scapular area of paired females (Pietz et al. 1995). From this it was possible to confirm that some females that subsequently appeared on the study area without broods had initiated or completed clutches. Radio-telemetry also helped us to assess the accuracy of the morphological indicators of egg passage noted above.

3.4 Results

3.4.1 Presence of Females without broods, productivity and pair bonds

By early to mid June of each year (by which time all females seen later with broods had to have laid), there were noticeable numbers (mean = 7.0 ± 2.71 SD, range 3 to 9) of marked adult females present without males or broods (Fig. 3.1). These represented "non-breeding" Harlequin Ducks as defined by Bengtson and Ulfstrand (1971).

Proportion of female Harlequin Ducks with broods was not detectably different among years at Fig River in central Labrador as in 1999, 5 of 15 females (0.33) produced young; in 2000, 3 of 12 females (0.25); in 2001, 6 of 17 females (0.35); and in 2002, 4 of 13 females (0.31) ($\chi^2 = 0.37$, $P = 0.95$). It was necessary to standardize productivity as the number of broods per marked female because it could not be assumed that unbanded females with broods in a given year were not present in previous years. These yielded somewhat different values as in 1999, 4 of 12 (0.333) females produced young; in 2000, 3 of 11 (0.273) females; in 2001, 2 of 10 (0.200) females; and in 2002: 4 of 12 females (0.333) that were also not significantly different ($\chi^2 = 0.63$, $P = 0.89$, Table 3.1). This was significantly lower than productivity documented for the Torrent River in northern Newfoundland: 1997: 6 broods from 8 females (0.75) [$\chi^2 = 6.28$, $P = 0.01$], 1998: 8 broods from 9 females (0.889) [$\chi^2 = 11.36$, $P = 0.0008$] (Goudie and Gilliland 2004, in press) but similar to productivity at Crooked River, Labrador (control site at 54^0 06'N, $60^0$48'W): 2000: 1 brood from 10 females (0.10) [$\chi^2 = 1.84$, $P = 0.17$], 2001: 3 broods from 17 females (0.176) [$\chi^2 = 0.81$, $P = 0.37$]. Young per female was lower in 2002 than in previous years at Fig Lake (Table 1, $\chi^2 = 7.31$; $P = 0.009$)

Overall across years, about 25% of pair bonds had dissolved by 31 May, a further 35% by 7 June, and most pair bonds were dissolved by 15 June (Fig. 3.2). This indicated that by early to mid spring period there were adult females present without mates.

3.4.2 Time budgeted to feeding

Paired female Harlequin Ducks at Fig River budgeted an average of 38.4% of the 17 hours of daylight to feeding, and we did not detect a diurnal pattern (Fig. 3.3 and 3.4). There were no annual or site differences in time budgeted to feeding by paired female Harlequin Ducks in central Labrador ($F_{4,\,1028} = 2.205$; $P = 0.067$) (Fig. 3.4), and feeding was strikingly similar in time/activity budgets calculated elsewhere in Newfoundland and Labrador (0.39 ± 0.051 SE for northern Newfoundland in Goudie and Gilliland 2004, in press; 0.396 for northern Labrador in Rodway 1998).

3.4.3 Morphological evidence of breeding

In the study areas in central Labrador, 6 females known to be laying and/or incubating eggs based on radio-telemetry that were examined during routine mark-recapture efforts corroborated the criteria defined as evidence of egg passage, i.e., splayed pelvic bones, sunken abdomen and/or mature egg present in oviduct.

In 1999, 2000 and 2001, 27 female Harlequin Ducks were captured in the spring-early summer period (15 May - 7 June). External examination of the lower abdomen of these individuals indicated that 25 had laid eggs. Females identified as subadults (n = 2 at Fig River, 1 at Crooked River), based on presence of a reduced bursa of Fabricus, did not have evidence of egg formation or passage (Table 3.2).

3.4.4 Evidence from radio-telemetry

Intact pair bonds were last observed for these females on 7 June 2000, and 24 May, 5 June, and 15 June 2001. In 2000, 3 of 4 radioed females disappeared from the general area of the outlet of Fig Lake where most banding and observations occurred but subsequently reappeared 2 to 3 weeks later without young. One of these apparently failed females had damage in the neck area (missing feathers and torn flesh) possibly indicating an encounter with a predator.

We hypothesized that nests may be depredated early in the nesting cycle because radioed females disappeared from the general area of the outlet of Fig Lake, and reappeared 2 to 3 weeks later, and remained there without broods until departure later in the summer. Therefore in 2001, we tracked females at Fig River soon after they were released with attached radio-transmitters. Of the 5 radioed females, 3 nests were located and 2 failed due to depredation of eggs most likely by mink (*Mustela vison*). Of the 2 remaining females, 1 was believed to have failed because it was previously triangulated at a potential nest site, and the other was 2 years old and may have not nested. The failed females, excluding the 2-year old, were subsequently regularly observed on the study area up to early July.

3.5 Discussion

There were relatively low proportions of the daytime budgeted to feeding by paired female Harlequin Ducks, i.e., 35% to 40%, in our study, and these were strikingly similar to findings at other locations in northern Labrador, Newfoundland and Alberta (30.0% in Robertson and Goudie 1999). Lower proportions of time spent feeding were presented for Alaska (21.1%) and Iceland (7.6% in Inglis et al. 1989). The findings were not consistent with the food-limiting hypothesis proposed by Bengtson (1972) because it would predict that proportions of time budgeted to feeding by adult female Harlequin Ducks should be variable, reflecting differences in food abundance among sites and across years. These findings were not consistent with the prevailing theory that the availability of epibenthic larval insects in rivers limited the ability of female Harlequin Ducks to acquire condition for nesting.

We suggest that individual Harlequin Ducks could have budgeted more time to feeding had it been necessary. For example, Harlequin Ducks averaged 68.9 % of the day feeding in winter (Goudie and Ankney 1986), and other species of sea ducks and waterfowl are capable of feeding for much greater proportions of the day (e.g. Long-tailed Duck *Clangula hyemalis*: 83.1% in Goudie and Ankney 1986, Pacific Brant *Branta bernicla* 84.4% cited in Goudie and Hearne 1997). Some species of birds are capable of increasing their ingestion rate under different regimes of food availability (Swennen et al. 1989). Our results underline the importance of testing prevailing paradigms with behavioral information because high proportions of time spent foraging are expected if food is scarce and hence limiting (Bengtson and Ulfstrand 1971, Inglis et al. 1989 Gardarsson and Einarsson 1994, Rodway 1998).

Collectively, the results did not support the hypothesis that productivity of Harlequin Ducks in central Labrador was limited by available food. All adult females attempted to nest. There was no direct evidence that any adult female skipped breeding in any of the 4 years. Adult females without broods that had been radioed on the study area had apparently failed due to depredation of nests, and were regularly observed in the post-pair period. Because nest failure often occurred relatively early in the nesting cycle, pair bonds were sometimes still intact or lone females were subsequently present without broods. There was no evidence of re-nesting despite, in some cases, the pair bonds still being intact when the original (partial) clutch was depredated.

Many studies of Harlequin Ducks reported observations of adult females without broods present well into the brooding season (Robertson and Goudie 1999). Coulson (1984) presented indirect evidence for extensive annual non-breeding in Common Eiders (*Somateria mollissima*) on the Farne Islands in Scotland (mean: 22.2 % of adult females, range 0 - 65.2 %). Individual-decision-based (facultative) non-breeding has become a paradigm in the sea duck literature, and it is speculated to b an important factor contributing to the K-selected life history pattern of these species (Goudie et al. 1994).

In wild birds, it is widely assumed that reproduction is both energetically and nutritionally expensive. There is often marked inter-individual variability in reproductive traits, and a few individuals repeatedly contribute most of the offspring to the population (Newton 1988, Williams 1999). Coulson (1984) speculated that Common Eiders reduce the risk of death caused by the stress of breeding by avoiding nesting in certain years, essentially a behavioral-physiological based system. Annual productivity of sea ducks such as Common Eiders and Harlequin Ducks varies considerably (Goudie et al. 2000, Robertson and Goudie 1999), and Milne (1974) speculated that a few "good" years over a decade or two were critical in stabilizing eider populations through time.

Bengtson (1972) proposed a food limitation hypothesis based on the coincidence of low productivity (described as frequency of non-breeding) with relatively low total standing crops of dipteran larvae in 1970 compared to 1969 (Bengtson and Ulfstrand 1971). However, closer inspection of those data indicated wide inter-year variance there were not statistically significant annual differences in availability of epibenthos. Bengtson

(1972) concluded that nest failure had little or no influence because 77 of 89 (87%) monitored nests in Iceland were successful over the 4 years of study. Hence he concluded that the presence of adult females without broods on the breeding streams must have, in part, represented birds that deferred breeding for that year. Since nests in his study were found by manual searching there was likely bias to specific locations such as mid-stream islands, and those samples may not have been representative.

It was apparent that annual productivity of Harlequin Ducks was low in central Labrador in 1999 to 2002, and the results of this study indicated that nest depredation was the proximate factor affecting breeding success of females. Other studies in Newfoundland and Labrador demonstrated different levels of productivity but very similar levels of foraging by paired females (Rodway 1998, Goudie and Gilliland 2004, in press). Cyclic predator-prey models have been described for many species in the north boreal zone (Boutin et al. 1995, Krebs et al. 2001). Increased productivity as a result of release from predation pressure during years of rodent abundance has been demonstrated for the Long-tailed Duck (*Clangula hyemalis*) (Pehrsson and Nystrom 1988), and could be important for Harlequin Ducks breeding in central Labrador because there were fewer young per female in 2002 when rodent populations were very low (pers. obs.).

A reciprocal model of population limitation contrasts sharply with the long-held food-limiting paradigm developed for Harlequin Ducks in Iceland (Bengtson and Ulfstrand 1971, Gardarsson and Einarsson 1994). Perhaps the situation in Labrador is unique yet the proportion of time spent feeding by females in Iceland (~ 7 % in Inglis et al. 1989) is not consistent with the food-limiting hypothesis. The methods used there likely underestimated actual time spent feeding because individuals that were underwater were likely missed during their scan sampling. Gardarsson and Einarsson (1994) presented 14 years of data on insects (Diptera) and productivity of Harlequin Ducks on river Laxá at Lake Myvatn that clearly appear cyclic which is consistent with the reciprocal model of predator-prey described above. Productivity in western North America also varies substantially (Robertson and Goudie 1999), and recent radio-telemetry work by Smith (2000) in Alberta confirmed that 15 of 17 radioed female Harlequin Ducks attempted nesting, and the remaining 2 may have failed nesting.

Evidence for deferred breeding or non-breeding in the context of a decision-based system on the breeding ground is still lacking. It is worth noting that support for non-breeding in Common Eiders presented by Coulson (1984) was based on inference from an uncatchable portion of the population that was not banded. This uncatchable component was assessed for band status when females flushed from nest sites on the colony. Our experience and others (S. Jamieson, pers. comm.) is that this technique is biased against detecting banded individuals because the tarsus is rapidly drawn under the flank feathers when birds flush. Without the unbanded component of uncatchable birds, the results presented in Coulson (1984) would not support the paradigm of deferred or non-breeding in Common Eiders. An alternative paradigm centered on an environmentally imposed cyclic variation in depredation is proposed to account for variation in annual productivity of Harlequin Ducks. Nevertheless, we do not rule out that this sea duck may defer breeding in some years by remaining in coastal habitats.

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Table 3.1. Numbers of adult Harlequin Ducks producing broods at Fig River, Labrador in 1999 – 2002.

YEAR	1999	2000	2001	2002
Females with broods	5	3	6	4
Marked Females with broods (proportion with broods)	4 (0.33)	3 (0.27)	2 (0.20)	3 (0.25)
Young per female	4.5	4.7	4.8	1.9
Total females present (No. marked)	15 (12)	12 (11)	17 (10)	13 (12)
Lone females (No. marked)	10 (8)	9 (8)	11 (8)	9 (9)

Table 3.2. Physical examination of captured adult female Harlequin Ducks for evidence of breeding at Fig River, Labrador, 1999-2001.

Date	No. Examined (No. with broods)	Open Pelvis and Dilated Cloacum	Sunken Abdomen	Egg in Oviduct	No Evidence of breeding	Subadults
Fig River						
18 May -9 Jun 99	9 (3)	7	1	1 (1)[1]		
3 – 7 Jun 00	4 (1)	2	1[2]	1		
20 – 25 May 01	5 (1)	2		2		1[3]
7 Jun 02	3	2	1			
Crooked River						
17-18 May 01	2	1				1[3]
30 May -1 Jun 01	4		1	1	2	
Total Spring 1999-2002	27 (5)	14	4	5	2	2[3]

[1] recapture of previously examined individual

[2] nest found

[3] 2-year old females with no evidence of breeding

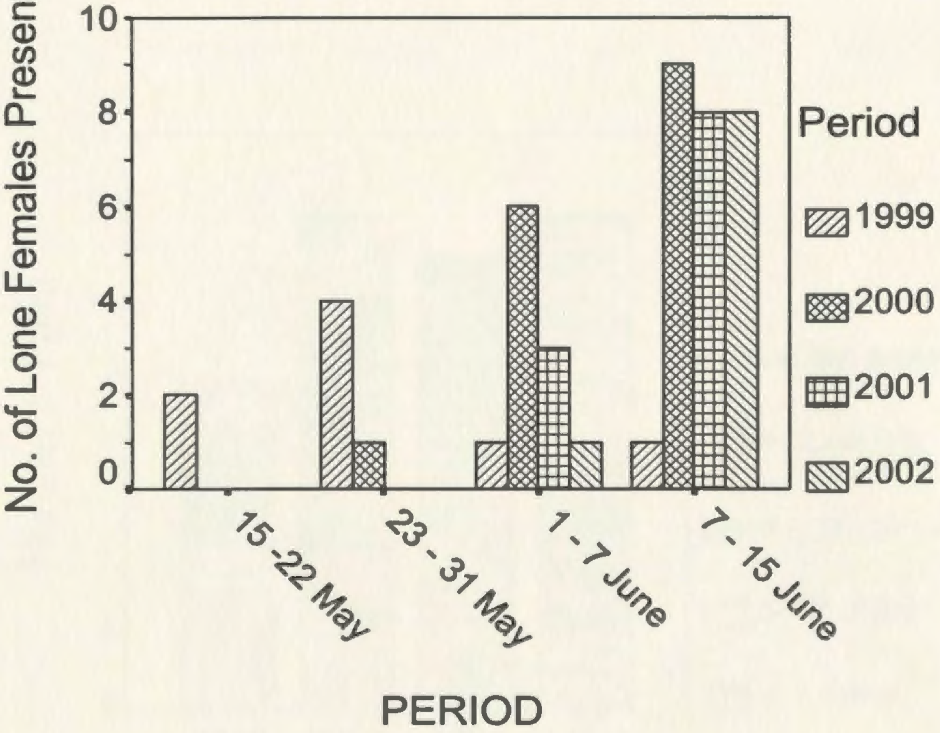


Figure 3.1. Number of lone female Harlequin Ducks observed at Fig River, Labrador, by observation period and year.

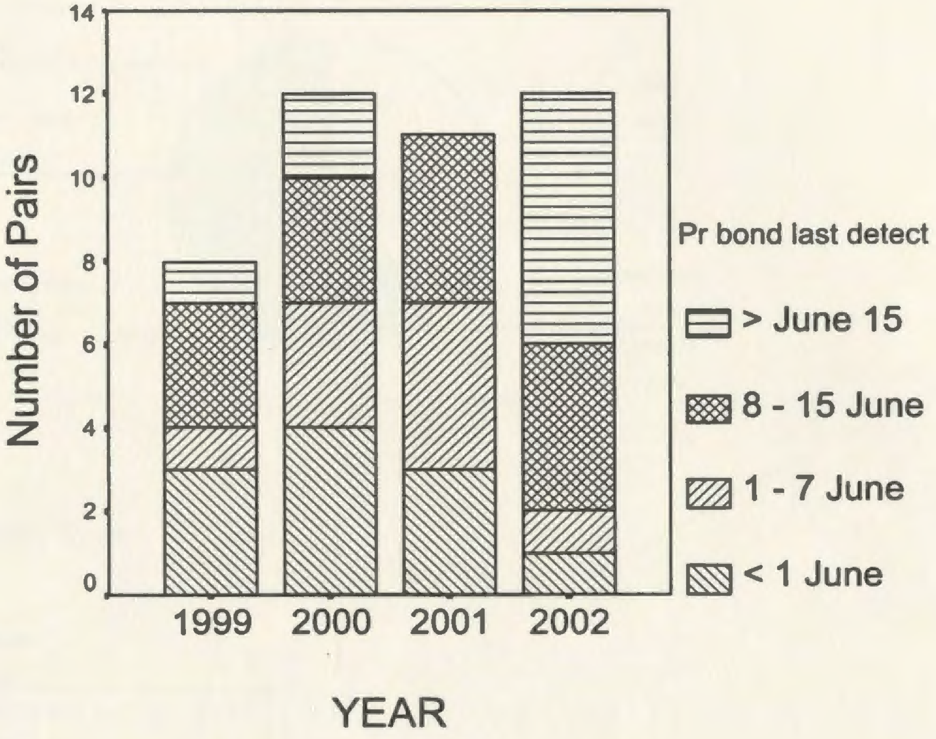
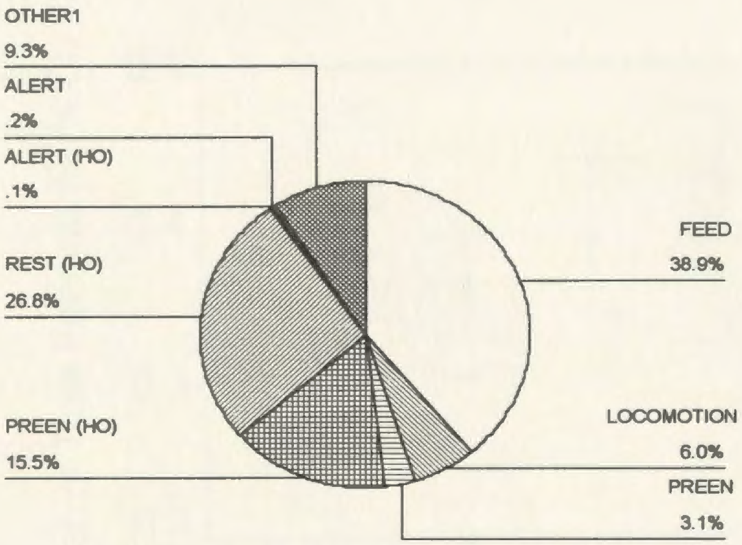


Figure 3.2. Period when pair bonds were last detected for Harlequin Ducks at Fig River, Labrador, 1999 to 2002.

Fig River



Crooked River

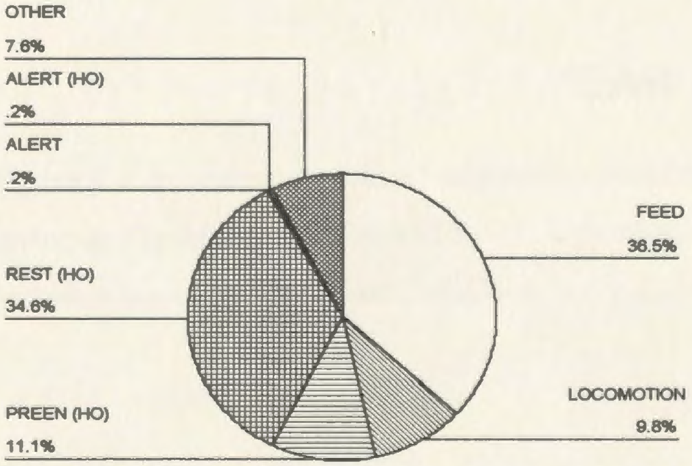


Figure 3.3. Behavior of adult female Harlequin Ducks at Fig River (n = 141) and Crooked River (n = 203), central Labrador, 2001. (HO) represents out of water; (see Table 4.1 for definitions).

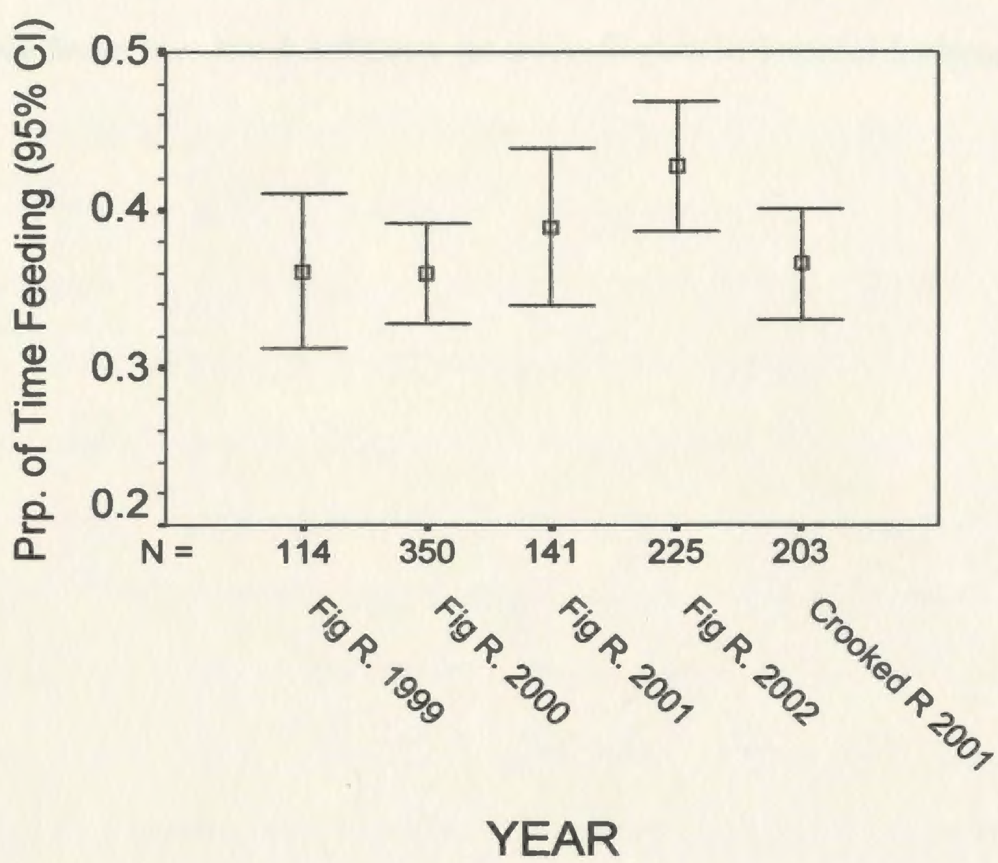


Figure 3.4. Proportion of time budgeted to feeding by adult female Harlequin Ducks in spring at Fig River and Crooked River, Labrador, 1999 to 2002. Differences across years and sites were not significant: ANOVA - $F_{4, 1028} = 2.205$; $P = 0.067$.

Chapter 4. Dose-response relationships of Harlequin Duck behaviour to noise from low-level military jet over-flights in central Labrador

4.1 Abstract

At Fig River, a tributary of the Lower Churchill River in central Labrador, we applied a Before-After-Control-Impact (BACI) study design to quantify effects of aircraft over-flights on behaviour of individual Harlequin Ducks (*Histrionicus histrionicus)* in the 130,000 km^2 Military Training Area of central Labrador. Noise generated from low-level passes (30 – 100m agl) by military jets was sudden in onset and high in amplitude (> 100 dBA), substantially above background sound levels both at Fig Lake outlet (40 – 50 dBA) and rapid sections of Fig River (60 – 70 dBA). Harlequin Ducks reacted to noise from military jets with Alert behaviour, showing a positive dose-response that intensified especially when noise exceeded 80 dBA. Residual effects, i.e., deviations from normal behaviour patterns after initial responses, were linked with decreased Courtship behaviour for up to 1.5 h after, and increased Agonistic behaviour for up to 1 h after military jet over-flights. Direct behavioural responses to military jet over-flights were of short duration and generally lasted less than 1 minute, and unlikely to affect critical behaviours, such as Feeding and Resting, in the overall time-activity budgets of breeding pairs. However, the presence of residual effects on behaviour implied whole body stress responses that were potentially more serious and require further study. A dose-response curve related to the noise of aircraft over-flights has not been reported previously in the scientific literature, but could be a valuable conservation tool for the detection and

mitigation of environmental impacts of aircraft and other noise.

4.2 Introduction

Noise is defined as anthropogenic sound that can significantly disturb animals (Bowles et al. 1991), and is often thought to be a biologically significant stressor on wildlife, yet our knowledge of noise as a form of ecological disturbance is limited (Brown 2001a). The non-auditory effects of noise are classified as whole-body stress responses (Selye 1976). An animal's body can respond physiologically to noise while the animal is asleep, under anesthesia, or even when the cerebral hemispheres are removed (Welch and Welch 1970). When confronted with noise disturbance, an animal may: (i) choose a behavioural response, and/or it may evoke the (ii) autonomic and/or (iii) neuroendocrine systems. The responses of the latter systems result in changes in biological function, i.e., diverting the animals own resources from ongoing biological activities to new biological activities that may assist the animal in coping with the stressor (Moberg 1987). Reflexes may be weakened, learning responses decreased, and reproduction impaired through chronic exposure to harmful noise levels (Welch and Welch 1970).

Ultimately, all responses to noise disturbance is affected by physiological change in individual animals. Through behaviour, an animal may avoid disturbance or habituate if the stimulus is not perceived to be harmful. Aircraft noise differs in properties with aircraft type, and birds respond differently to different aircraft types. Fixed wing and rotary blade types generate loud noise but are anticipatory in nature compared to military jets that are very loud and the associated noise is sudden onset (Grubb and Bowerman 1997). Sudden onset noise often elicits startle responses in wildlife that allow them to respond rapidly to possible dangers. The startle response is controlled and regulated by several neurophysiological processes (Bowles et al. 1991). Animals habituate poorly to high amplitude noise with rapid onset (Korn and Moyer 1966), and physiological effects are characterized by a rapid increase in heart rate and cardiac output, shutdown of the gut and other non-essential functions, and rapid mobilization of glucose reserves to supply the muscles (Hoffman and Searle 1968).

Few studies have quantified dose-response effects of noise on wildlife, and advancement of knowledge in this field has been hampered by a preponderance of small, disconnected, anecdotal or correlational studies as opposed to the use of controlled experiments (Larkin 1996). Comparability among studies is complicated by wide variations in the definition of disturbance, and variation in response among species (Ryals et al. 1999). Much of the existing literature adopts an "all or none" view of impact, or has used surrogate information, such as distance of study animals to disturbance source (van der Zande and Verstrael 1985), to evaluate noise events in the field (Brown 2001a).

There is likely to be wide variation in response by wildlife to the passage of aircraft depending on the noise level generated. Studies that quantify the natural acoustic background in natural environments are crucial to our understanding of the effect of noise on wildlife because they provide a baseline against which levels of intruding noise can be assessed (Brown 2001a). Causal association can most convincingly be established by demonstrating an increase in adverse outcome (response) with corresponding increases in level of exposures (dose) (Bowles 1994, Bowles et al. 1991). Quantification of dose – response is the preferred approach to mitigating negative impacts of noise on humans (Fidell et al. 1991). Our field studies aimed to quantify experimentally the dose-response relationship between military jet noise and avian behaviour.

Harlequin Ducks (*Histrionicus histrionicus*) are small sea ducks that inhabit fast-moving rivers and streams during the breeding season (Robertson and Goudie 1999), and their populations are sensitive to relatively small changes in adult survival (Goudie et al. 1994). The eastern North American population of Harlequin Ducks that breed throughout central Labrador was listed as *endangered* in 1990, and down-listed to *species of concern* in 2001 (Goudie 1991, Thomas and Robert 2001).

The Canadian Department of National Defence (DND) supports a low-level training program involving military jets in a Military Training Area (MTA) encompassing about 130,000 km^2 of central and southern Labrador. Following an Environmental Impact Statement (EIS), DND adopted a precautionary approach for mitigation of impacts on Harlequin Ducks in the MTA by providing exclusion zones around specific sites where the species was observed annually during single aerial surveys by helicopter (DND 1994). Scientific research has been supported through the establishment of the Institute for Environmental Monitoring and Research (IEMR) that has attempted to refine understanding of environmental impacts of low-level military jet over-flights. Management actions to mitigate potentially adverse impacts are to be adjusted based on such findings. More than 98% of the MTA receives on average of less than a single over-flight per day during May to September (Pigeon 2001). However, military jets frequently follow river valleys during low-level sorties (30-150m AGL) at speeds of 780 to 890 km/hr, generating loud noise exceeding 100 dBA (DND 1994).

Commencing in 1999, we initiated research on the effects of military jet noise on behaviour and demography of Harlequin Ducks breeding at Fig River (53° 03' N, 63° 09'W) in central Labrador near the geographic center of the MTA. In 2001, the study was expanded to include a control site at Crooked River (54° 06'N, 60° 48'W) near Nipisish Lake just outside the MTA. Our study addressed the following questions: 1) do noise levels generated by military jets exceed the background levels associated with the riparian habitats utilized by Harlequin Ducks at Fig River; 2) how do Harlequin Ducks respond behaviourally to low flying military jets; 3) is there a quantitative relationship between magnitude of behavioural response and the intensity of noise levels generated by military jet aircraft; and 4) generally, what are the likely conservation implications of low flying military jets to Harlequin Ducks breeding in the MTA.

4.3 Methods

4.3.1 General behaviour

We quantified behaviour of breeding pairs of Harlequin Ducks during mid May to mid June of 2001 and 2002. A focal-individual sampling approach (Altmann 1974) was applied, and linked to known individuals because most Harlequin Ducks at Fig River (treatment site, n=95) and Crooked River (control site, n=45) were individually marked with field-readable coloured plastic leg bands from 1999 to 2002.

Behaviour of Harlequin Ducks was characterized during bouts or states (e.g. Feeding and Resting; see Martin and Bateson 1986). For standardized watches, focal birds were monitored for 30 minutes (or until lost from sight) using binoculars and/or (20X-60X) spotting scopes. Instantaneous behavioural classifications of focal birds were recorded every 15 seconds, using digital watches with countdown-return beeper functions, from a suite of 16 general behavioural categories (Table 4.1). To minimize the chance that individuals were observed more than once, and to maximize the independence of our data, a new individually colour-marked bird was selected for observation or observers changed location to find new birds after each 30-minute observation period was completed. Our data were not pseudo-replicated. Since instantaneous data recorded every 15 seconds were not statistically independent within each 30-minute watch, frequencies of behavioural categories were summed over each watch, i.e., each behavioural watch contributed one data record as frequencies of recorded behaviours (Martin and Bateson 1986).

4.3.2 Undisturbed versus disturbed categories

Observation periods were classed as "disturbed" or "undisturbed". We considered the observation "disturbed" if focal birds were over-flown by a military jet at Fig River during the observation period. Concurrent data were collected at the control site at Crooked River, where no over-flights occurred, by communication between field crews via satellite telephones of expected Time On Target (TOT, see below). The observation periods at Fig River were classed as <30 min, 30–60 min, 60–90 min, and 90–120 min periods before and after military jet over-flights to assess potential residual effects on behaviour.

4.3.3 Military Jet over-flights

We scheduled some observation periods to coincide with expected times of military jets transits over the study area. In 2002, mock tank targets were airlifted and placed on peatlands within 300 m of the outlet of Fig Lake, and used for the tactical training of pilots. Staff at 5-Wing Goose Bay airport relayed time on target (TOT) of military jet over-flights to our field observers via satellite phone following the submission of daily flight plans by allied pilots.

The time of each aircraft transit over the study area was recorded and aircraft type was noted whenever possible. When the over-flying aircraft was visible, we noted the cardinal direction of transit, estimated altitude, and whether the aircraft transited over the Fig Lake outlet location where a digital time-logging Larson Davis Model 820 Sound Level Meter was deployed (see below). Our field crew relayed time of transiting of the study site by military jets to 5 Wing Goose Bay airport on a daily basis.

4.3.4 Sound and Noise Data

We measured sound and noise levels during observation periods. Sound meters were deployed within 2 m of the river edge in areas frequented by Harlequin Ducks under observation. A continuous digital time-logging Larson Davis Model 820 Sound Level Meter (LD820) (Larson Davis Laboratories 1997) was programmed and deployed at the outlet of Fig Lake in the area of maximal use by pairs of Harlequin Ducks. Collected sound data were A-weighted because this scale approximates the hearing sensitivity of most birds (Meyer 1986), and is the standard scale generally used to quantify aircraft noise in avian studies (Brown 1990).

For the analyses of dose-response we used the sound measure L*max* recorded every 60 seconds and as mean values every 30 minutes. L*max* was the maximum sound pressure level (as decibels–A-weighted) measured over the sampled period (in this case the jet over-flight event). To approximate the background level of sound on the study area, the metric L90 was chosen, and it represented the sound level exceeded 90% of the time (N. Stanton, personal communication 2000). Additionally, we compared L*max* of military jet over-flights with background levels at Fig Lake outlet and along sections of rapids and riffles further downstream. In addition to military jets, 'loud noise' events also included project- related aircraft and phenomena such as thunder or heavy rain.

Data were logged daily from 0500 to 2100 h to coincide with activity by Harlequin Ducks at the outlet of Fig Lake and to encompass over-flights by military aircraft. Behavioural data were also collected at other sites along Fig River and Fig Lake, and we recorded sound during those 30-minute watches using hand-held digital Larson Davis Model DSP80 Sound Level Meters (Larson Davis Laboratories 1997). These recorded L*max* (A-weighted) in decibels integrated over the 30-minute observation period.

We used the *Passby* function, a special exceedance event detector of the LD820 Sound Level Meter that measured the L*max* of the highest event to raise and lower ≥10 dB in Sound Pressure Level. It was used to capture single event noises (Larson Davis Laboratories 1997), and is preferred for measuring transient noise events (Pater 2001). L*max* was modeled against the behavioural response variables of the Harlequin Ducks in an effort to assess evidence for a dose-response relationship.

In addition to the noise levels measured, the date and time of L*max* and the duration of each event were recorded. The recorded maximum duration of the *passby* event was 64 or 128 seconds depending on whether a 0.5 or 1.0 second time history period was selected on the LD820 meter. Ten samples before and after the exceedance were stored up to a maximum of 255 samples with each sample period being 1/32 seconds; equivalent to 8 seconds before and after the over-flight event in our study. For the Fig River study, we set a time history period to 0.5 seconds triggered for events with a minimum duration of 3 seconds and exceedance threshold of 75 dBA.

4.3.5 Experimental design

Our study design applied a Before After Control Impact (BACI) statistical approach. This experimental design has controls in both space and time, and the General Linear Model for BACI is a two-way ANOVA with an area by time 2 X 2 factorial design whereby the evidence for impact effects is a significant interaction term (Green 1979). The treatment site and control site were concurrently studied in 2001 (before over-flights) and 2002 (during/after over-flights) (Fig.4.1).

The behavioural data collected every 15 sec during a 30-min watch were binomial in nature, (i.e., the birds either responded with a given behaviour or they did not). Therefore response was modeled using a binomial distribution with a logit link in the GENMOD procedure of program SAS (SAS Institute Inc. 1993). We used a case-control study that models the data as the odds ratio, and this is a method of association frequently used to assess the relative risk for rare diseases (Bowles et al. 1991, Agresti 1996). In this study, the odds ratio was the ratio of the odds of the behaviour occurring given exposure to a military jet over-flight to the odds of the behaviour occurring with no over-flight. Odds were defined as p/q where p = relative frequency of a given behaviour and $q = 1 - p$ or the relative frequency of not showing a given behaviour. Odds may be stated as the probability of engaging in a behaviour relative to the probability of not engaging in that behaviour (after Zar 1999). The data are presented graphically as proportions for more direct interpretation.

4.4 Results

4.4.1 Over-flights by military jets

From mid May to mid June 2001, only 4 military jet over-flights events were registered at the Fig Lake study area, so we used these data from this period as the Before component of the BACI design for the treatment site. The After component data were obtained during 19 May-18 June 2002, when a total of 94 low-level over-flights of the Fig River study site by military jets occurred. Approximately 66% of over-flights occurred in early to mid June and 33% occurred on 2 days. A total of 47 over-flights occurred in the 10:00–13:00 time window and 32 in the 15:00–17:00 period (Fig. 4.2). Over-flights at Fig River related predictably to takeoff times from the airfield at Goose Bay so regular contact with Military Command Centre (MCC) staff by satellite phone resulted in accurate forecasting of military jet over-flights. Simultaneous data collection was achieved at Crooked River (Control Site) in 2001 and 2002.

4.4.2 *Background sound and jet noise*

Noise generated by military jets was much higher than background sound levels near the outlet of Fig Lake (40–50 dBA) and along the rapids and riffles of Fig River (60–70 dBA) (Fig. 4.2). Noise events related to military jet over-flights were sudden onset and high in amplitude (L*max*, mean 91.4 dBA±11.7 SD; PEAK, mean 101.9 dBA±13.3 SD) but were brief (mean 6.1 sec±3.7 SD). The maximum PEAK noise level (A-weighted) registered during an over-flight by a military jet was 129.3 dBA (Fig. 4.3).

4.4.3 *Effects on behaviour*

There was a significant effect of military jet over-flights on behaviour. Ducks responded to over-flights by increasing the frequency of Alert behaviour (females: time X treatment: $X^2=38.79$, $P<0.0001$; males: time X treatment: $X^2=31.21$, $P<0.0001$; Fig. 4.4). Results of the BACI model for other behaviour categories were interpreted less readily, for example, there was a significant interaction term for Vigilant behaviour (females: $X^2=5.08$, $P=0.024$; males: $X^2=26.14$, $P<0.0001$) (Fig. 4.5) suggesting that paired female Harlequin Ducks increased Vigilance during over-flights by military jets. However the source of the significant time x treatment interaction for paired males was not clear because there was no difference between Before and After treatment at Fig River.

4.4.4 Dose-response relationships

There were highly significant dose -response relationships for the odds of being Alert to noise levels generated by military jets (females - slope (βi): $X^2 = 21.42$, $P < 0.0001$; males - βi: $X^2 = 13.25$, $P = 0.0003$), and the relationship was stronger for paired females than paired males, i.e., Deviance ratio: females = 25.1%, males = 16.7%, where the Deviance ratio = Deviance of Intercept – Deviance of L*max*) / Deviance of Intercept, after Agresti (1996) (Fig. 4.6).

4.4.5 Residual effects

Residual effects were defined as ongoing deviations from normal behaviour patterns that followed the initial response and persisted well after the passage of an aircraft. There was evidence indicating residual effects of noise generated by military jet on behaviours (Agonism - for paired females, $X^2=67.27$, df=6, $P<0.0001$; for paired males, $X^2=50.77$, df = 6, $P<0.0001$; Fig. 4.7) and Courtship - for paired females, $X^2=60.09$, df = 7, $P<0.0001$; for paired males, $X^2=57.05$, df = 7, $P<0.0001$; Fig. 4.8). The frequency of Agonistic behaviour was higher up to 1 h following over-flights, and the frequency of Courtship behaviour was reduced for up to 1.5 h following over-flights compared to levels of these behaviours exhibited prior to over-flights. We did not detect differences in other behaviours before, during or after over-flights.

4.5 Discussion

Harlequin Ducks increased Alert behaviour during military jet over-flights including Head-up orientation, and general Agitation and startle responses such as Flushing, and Panic Diving related to this sudden onset noise, and these responses increased in duration with increasing noise level. Due to the reflex nature of startle responses, habituation to such stimuli is not likely (Harrington and Veitch 1991). Our findings are the first experimentally demonstrated dose-response relationships of behaviour to noise levels generated by military jet over-flights.

Effects of military aircraft noise on wildlife have been reported for other species including; Mexican Spotted Owls *Strix occidentalis lucida* (Delaney et al.1999), Peregrine Falcons *Falco peregrinus* (Murphy et al. 2001), Ospreys *Pandion haliaetus* (Trimper et al. 1998), California Gnatcatcher *Polioptila californica* (Hunsaker II 2001) and caribou (*Rangifer tarandus*) (Maier et al. 2001, Jung and Jones 2001, Harrington and Veitch 1991, 1992). In general, behavioural responses by birds to aircraft noise are common, and some previous studies have documented noise thresholds below which responses were not detected (Burger 1981), and categories of noise levels and associated behaviour in relation to distance from disturbance stimuli as a surrogate to noise level (Grubb and Bowerman 1997). However, no studies have quantified response over a range of noise levels sufficient to define a dose-response curve in the wild (see Anderson 1988 for utilizing distance to disturbance).

Brown (2001a) noted that variable or manipulated noise stimuli provides the opportunity to define dose-response relationships for different species and the safe floor of noise exposure, yet few studies have designed experiments with a level of precision that can identify a threshold stimulus below which the target animal is unlikely to experience detrimental effects. Our results demonstrated that Alert responses by Harlequin Ducks intensified especially when noise levels exceeded about 80 dBA. A threshold in noise level for behavioural response is an important conservation tool (Pater 2001). Brown (1990) demonstrated that Startle and Escape behaviours in Crested Terns (*Sterna bergii*) intensified when simulated aircraft noise exceeded 85 dBA. Thiessen et al. (1957) demonstrated the threshold above which domestic fowl responded to loud noise ranged from 83 to 93 dB, and that there was close correspondence between behavioural response and increased heart rate. Bowles et al. (1991) concluded that noise begins to disturb birds at sound levels around 80 – 85 dB, and the threshold for flight is about 95 dB.

The Osprey is the only other bird species studied in the MTA (Trimper et al. 1998). Alert responses and posturing were reported to coincide with aircraft over-flights, although no quantitative results of these behaviours were presented and/or assessed for dose-response. The majority of military jet over-flight treatments for Osprey reported in that study were below 80 dBA (< 50 % exceeded 80 dBA, < 5% exceeded 90 dBA) because only 32% of 72 over-flights were within 1 km of 5 treatment nest sites under study. Noise at ground level is strongly affected by slant distance to and altitude of aircraft, terrain, ground cover, weather, and atmospheric attenuation (Pater 2001). Harrington and Veitch (1991) noted that the greatest impact of low-level flying jet aircraft was due to startle reactions caused by the loud and sudden noise of low, direct over-flights. Beyond 250 m from the jet's flight path, the mean sound pressure levels for jet overpasses were under 90 dB which is less aversive.

We considered that noise was likely to be the main stressor involved in any behavioural response to low-level military jet over-flights. Brown (2001b) carefully studied the behavioural effects of simulated aircraft noise versus optical stimuli on Crested Terns, and concluded that the acoustic component was far more important in generating behavioural responses than visual components. He detected responses to optical components that were of a much lower magnitude than acoustic stimuli. Kosin (1958) demonstrated effects of simulated airplane sounds on reproductive functions in male chickens. Ward et al. (2001) provided evidence that noise was the key factor in response by geese (*Branta bernicla, B. canadensis*) to aircraft disturbance in Alaska. In that study aircraft were visually detectable for considerable periods of time and at great distance.

On our study area in central Labrador, the military jet over-flights occurred at altitudes of 30 to 60m, and speeds of 780 to 890 kph. Because the backshore of our study area supported a mature Black Spruce (*Picea mariana*) – Balsam Fir (*Abies balsamea*) forest averaging 10 to15 m height, normally the jets had already passed invisibly before their presence was detected only by the delayed sound wave in their wake. Harrington and Veitch (1991) noted that caribou in forested habitats were unlikely to see jets, except briefly as they recede (for direct over-flight). Although we were unable to isolate optical from acoustical stimuli absolutely, it seemed unlikely that optical stimuli were important (see Brown 2001 and Ward et al. 2001) because at the high subsonic speeds evidenced, military jets often passed undetected by observers. Similarly, Harrington and Veitch (1991) considered noise the primary stressor in military jet over-flights because the aircraft were often not visible when caribou responded.

Adult Harlequin Ducks breeding at Fig River responded to noise generated from low-flying military jets. This was not surprising given that the noise was sudden onset with high intensity (>90 dBA), and substantially above background levels. In the context of time-activity budgets, Alert behaviours contributed a small fraction of the daily activity in undisturbed (~0.1%) (also see Rodway 1998) and disturbed (~1.0%) scenarios. Behaviour that consumed a significant portion of the time-activity budget included Feeding that averaged about 40% of the day. It appeared unlikely that a direct (Alert) response to military jets could jeopardize the ability of adult Harlequin Ducks to budget sufficient time to feeding unless the frequency of over-flights was considerably greater than the 94 registered in our study. There is ample flexibility in the time-activity budget for compensatory adjustments for important behaviour such as Feeding, and Harlequin Ducks, and other sea ducks can spend much higher proportions of the day feeding if necessary

(Goudie and Ankney 1986). Some species of birds can also increase the intensity of feeding (Swennen et al. 1989).

Because increased agonistic behaviour and decreased courtship lasted up to an hour or more following over-flights by military jets, the implications to time-activity budgets of adult Harlequin Ducks are potentially more serious than the demonstrated short-term immediate Alert responses. If behaviour changes following over-flights then some interference with feeding and resting could result. Increased aggression which has also been noted in domestic turkeys (Bradley et al. 1990 in Bowles et al. 1991) and Osprey (Poole 1981) subjected to aircraft disturbance, could have negative consequences to the long-term stability of pair bonds or site fidelity of the Harlequin Duck because birds may avoid sites of repeated over-flights (Platt 1977). Increased Aggression could also reduce time budgeted to Courtship.

Reduced courtship following over-flights by military jets is of concern because courtship serves important functions related to the maintenance of the strong pair bonds, and especially the continued fertilization of eggs that are laid every other day until the clutch is complete (about a 2 week period) (Robertson and Goudie 1999). Even as a 'rare' behaviour, courtship is critical to ensure eggs are fertilized, and it has been suggested that fertility can be compromised by noise-related stress (Kosin 1958).

Direct implications on time-activity budgets are only one potential effect of noise disturbance. The detection of residual effects (of jet noise) on behaviour raises the likelihood that a larger (physiological) effect had occurred (see Thiessen and Shaw 1957), and these residual changes in behaviour following military jet over-flights may be manifestations of these impacts. Alert and aggressive behaviours correlate with stress because they are aspects of the 'fight or flight' response that occurs with the activation of the neurophysiological system (Selye 1976). The immediate physiological consequences include changes in heart rate, lipid metabolism, gut function and changes in attention (Sen 1976).

Animals challenged repeatedly over long periods develop high circulating levels of cortisol in the blood stream, enlarged adrenal glands, and reduced thymus, spleen and lymph nodes. Chronic stress can lead to loss of immune function, decrease in body weight, depression, loss of reproductive function and abnormal thyroid function (Selye 1976). Bowles et al. (1991) noted that linkages between indices of stress, such as heart rate and circulating levels of cortisol, are more presumptive than real but concluded that there was little doubt that prolonged exposure to high noise levels can have physiological consequences, and startle responses have more serious consequences.

Effects of noise on wildlife cannot be generalized across taxa (Bowles 1994, Larkin 1996, Ryals et al. 1999, Pater 2001). Some waterfowl species may habituate to jet noise (e.g. Black Ducks *Anas rubripes*) whereas other species may sensitize (e.g. Wood Ducks *Aix sponsa*; Fleming et al. 1996). The acoustical context where the study animals live may be a very important factor, and affect whether animals habituate or sensitize to a noise stressor. When in an environment with "noisy" background levels, some species may sensitize to noise stressors to which they were otherwise habituated to under lower ambient background levels (Davis 1974). In other words, animals living in an environment with relatively loud background sound levels may ironically be at increased risk to the effects of additional anthropogenic noise. Because Harlequin Ducks live in a relatively noisy environment such scientific findings are important because military jets generate sudden onset noise that is loud, and could therefore cause harmful startle effects.

The frequency of over-flights by military jets at the Fig River study area in 2002 was considerably higher than that experienced across many of the watersheds occupied by Harlequin Ducks in the MTA. Potential for a high frequency of military jet over-flights coinciding with significant concentrations of Harlequin Ducks is currently limited in the MTA to only a few watersheds, most notably the Nauskapi-Red Wine Rivers (54°N 61°W) because of the heavy transiting use of these valleys for sorties to and from the northern portions of the MTA (see Trimper et al.1998).

Our study underlines the importance of maintaining specific buffer zones to reduce military jet disturbance on critical habitats for Harlequin Ducks in the MTA. Nevertheless, we concur with Brown (2001) that we lack an understanding of how proximate effects translate into demographic consequences for wildlife. Meanwhile, we recommend that as a precautionary approach, military aircraft over-flights over Labrador should be modified to reduce the noise exposure of river habitats used by Harlequin Ducks to below 80 dBA.

This could, for example, involve avoiding river valleys or defining minimum altitudes for over-flights that assure noise levels remain below this threshold.

4.6 Conclusions

Noise generated from low-level military jet over-flights was high in amplitude, and substantially above the ambient sound environment of the riparian habitat of the eastern Harlequin Duck in central Labrador. Individual birds responded to the sudden onset noise by exhibiting Alert behaviours, and these increased in a dose-response manner with increasing amplitude. Short-term effects on time-activity budgets were negligible as Alert behaviour constituted < 1% of the diurnal period. We detected residual effects of increased Agonistic and decreased Courtship behaviour up to 90 minutes after over-flights, and these indicated that a greater physiological response to military jet noise may have impacted these birds. Implications of residual effects are cause for concern, and potentially more detrimental than immediate responses.

The Alert and Aggressive responses documented are indicative of 'fight or flight' responses, and imply that Harlequin Ducks perceive loud military jet noise as a stressor. Chronic exposure to military jet noise could have negative consequences to individuals. We identified a threshold of response to noise in the area of 80 dBA, and consider that future mitigation actions could benefit from these findings to develop appropriate altitudinal and horizontal buffer zones for riparian habitats used by Harlequin Ducks in order to maintain noise levels below this level.

4.7 Acknowledgements

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4.9 Tables

Table 4.1. General categories used to summarize behaviours of Harlequin Ducks. Behaviours were segregated into on the water and out of the water (_ho).

Behaviour	Description
Agonism	Aggressive interactions among Harlequin Ducks including chasing and sometimes fighting with conspecifics.
Agonism_ho	Aggression while out of water
Courtship	All Courtship behaviour (on the water), e.g., inciting, prone, copulation
Feed	All aspects of obtaining food, including: dip, dive, submerged, pause, glean
Peer	Looking into water (may be associated with food seeking)
Locomotion	All types of movements, e.g., swim, scoot, fly, walk
Preen	Feather maintenance using the bill as well as flapping and shaking
Preen_ho	Preen while out of water
Inactive	Inactivity including resting, sleeping and head down
Inactive_ho	Inactivity while out of water
Social	Calls and head nods directed to conspecifics
Vigilant	Maintaining a look-out (vigil) usually while the mate feeds or sleeps
Vigilant_ho	Vigilance while out of water
Alert	Head stretched upward, body erect/tense, re-orientation, and agitated, often accompanied with locomotion. Includes startle responses such as splash dive and panic flush
Alert_ho	Alert while out of water

4.10 Figures

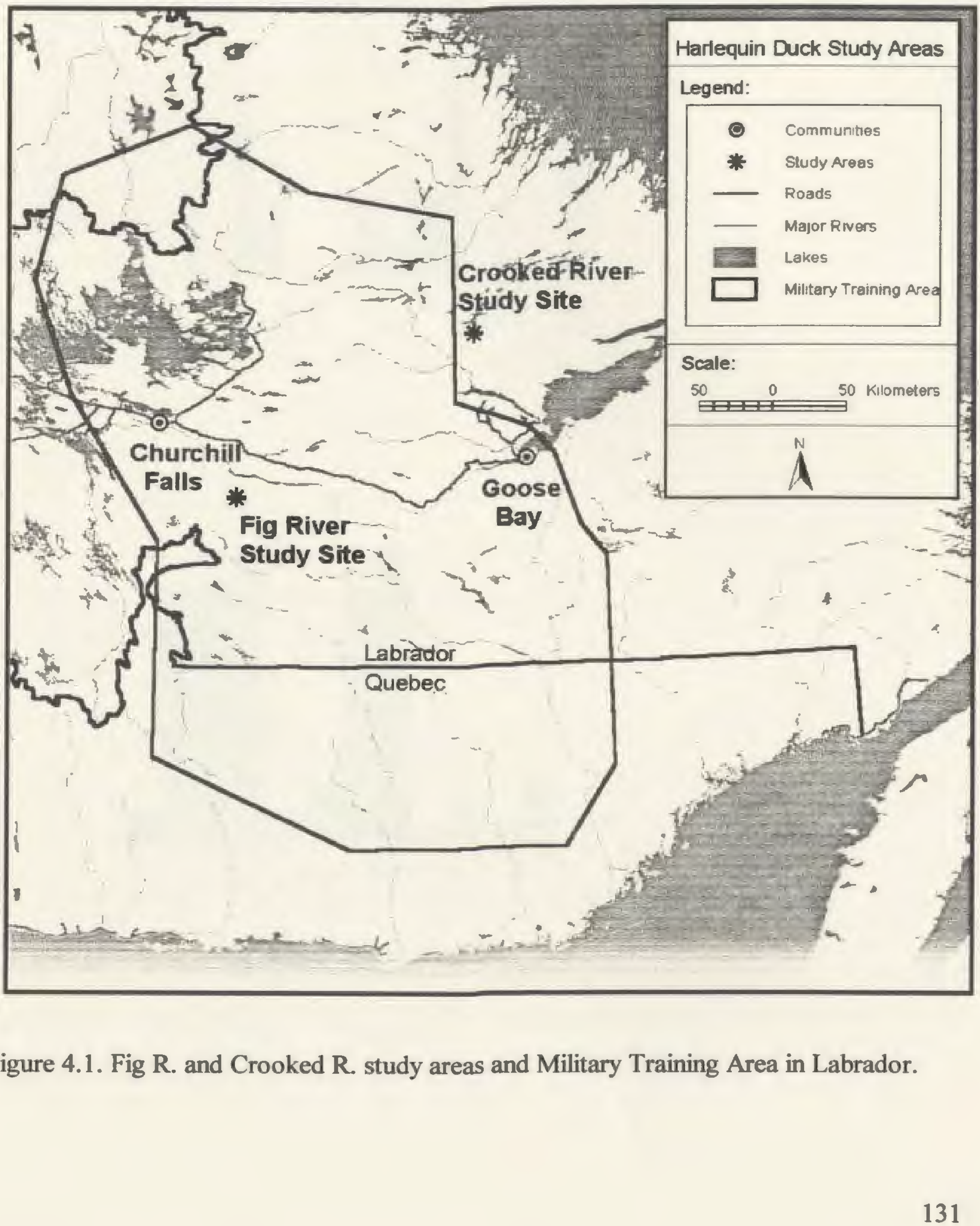


Figure 4.1. Fig R. and Crooked R. study areas and Military Training Area in Labrador.

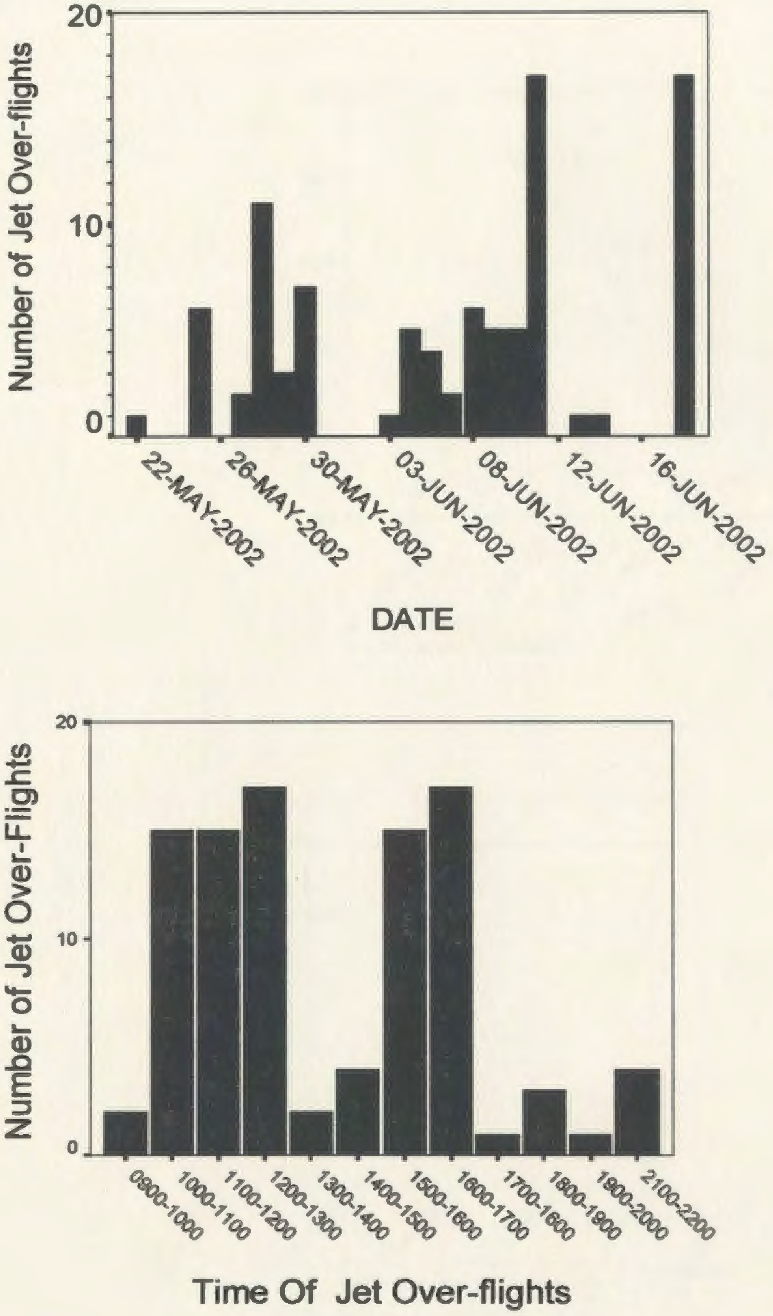


Figure 4.2. Dates (upper) and time periods (lower) of 94 military jet over-flights registered at Fig River, Labrador from 19 May – 18 June 2002.

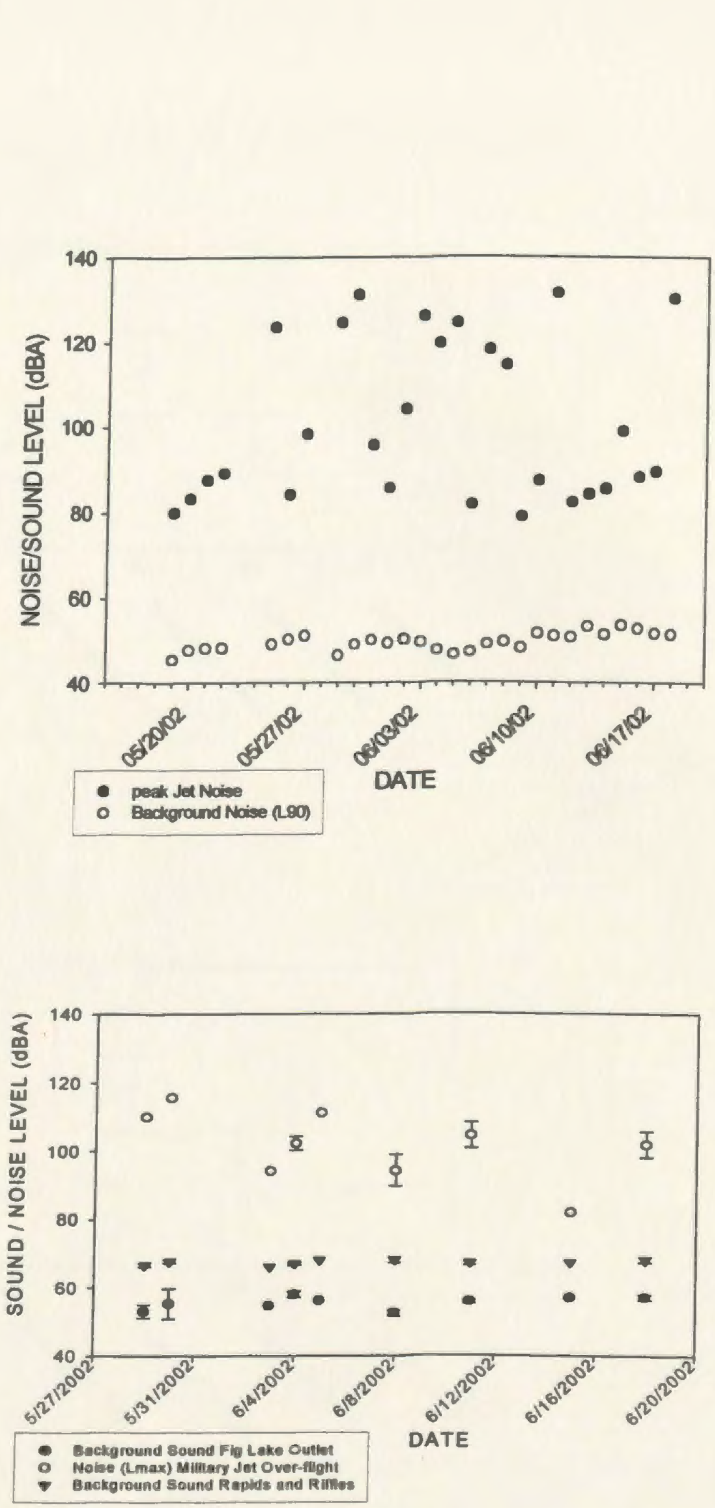
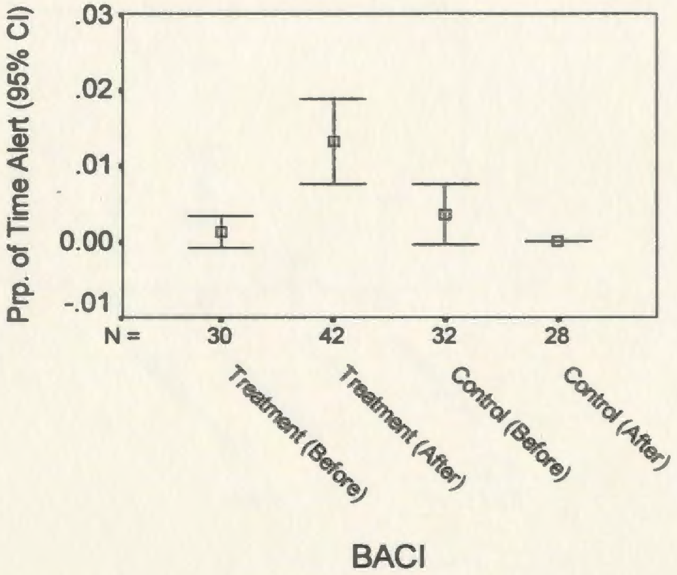


Figure 4.3. Peak noise levels registered during military jet over-flights and background sound levels near Fig Lake outlet (upper) and rapids and riffles on Fig River (lower), Labrador, 19 May – 18 June 2003.

Paired Females



Paired Males

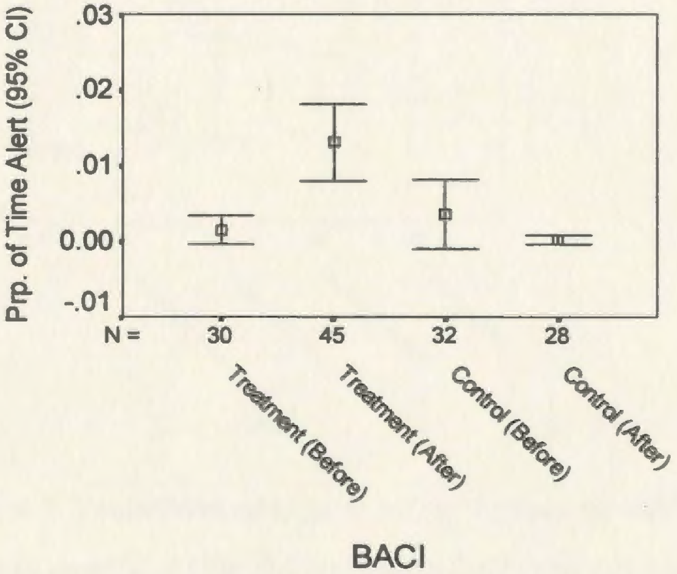
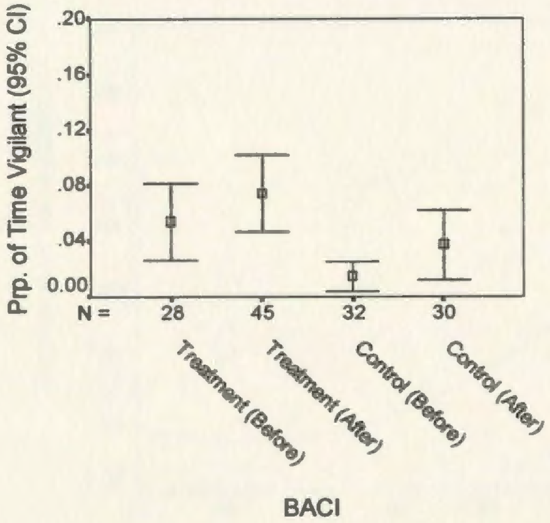


Figure 4.4. Proportion of time of being Alert by paired female and male Harlequin Ducks in treatment (Fig R.) and control (Crooked R.) locations before and after military jet overflights.

Paired Females.



Paired Males

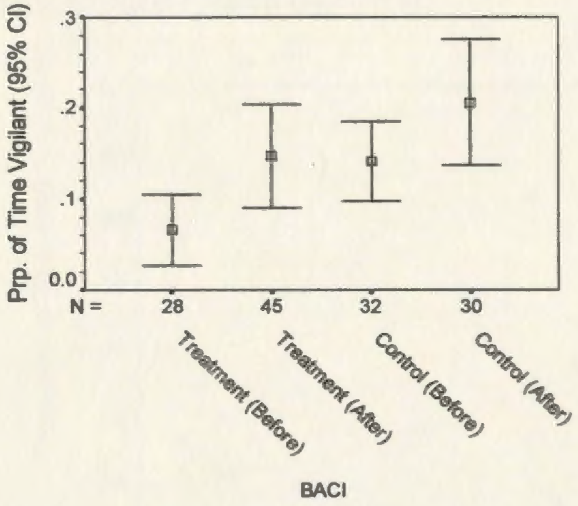
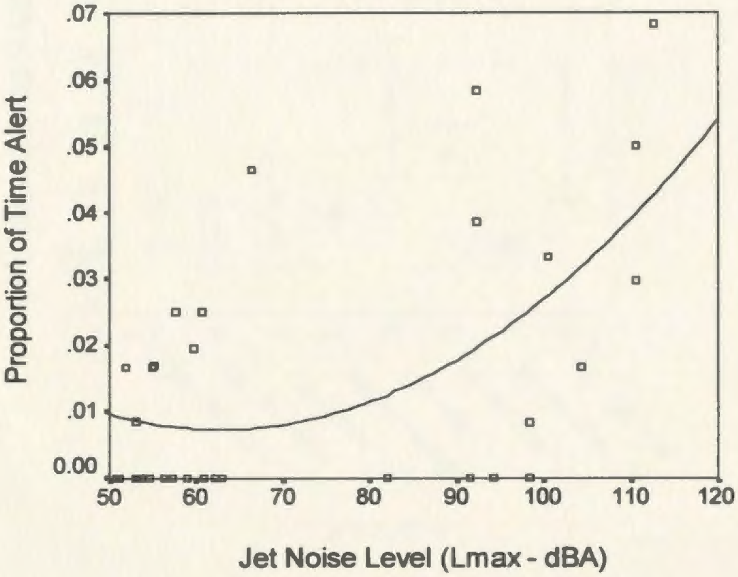


Figure 4.5. Proportion of time of being Vigilant by paired female and male Harlequin Ducks in treatment (Fig R.) and control (Crooked R.) locations before and after military jet over-flights.

Odds of Alert (paired female) = $e^{(-6.437 \pm 0.549 + 0.0287 \pm 0.0062\ \mathrm{Lmax})}$



Odds of Alert (paired male) = $e^{(-5.775 \pm 0.503 + 0.0215 \pm 0.0059\ \mathrm{Lmax})}$

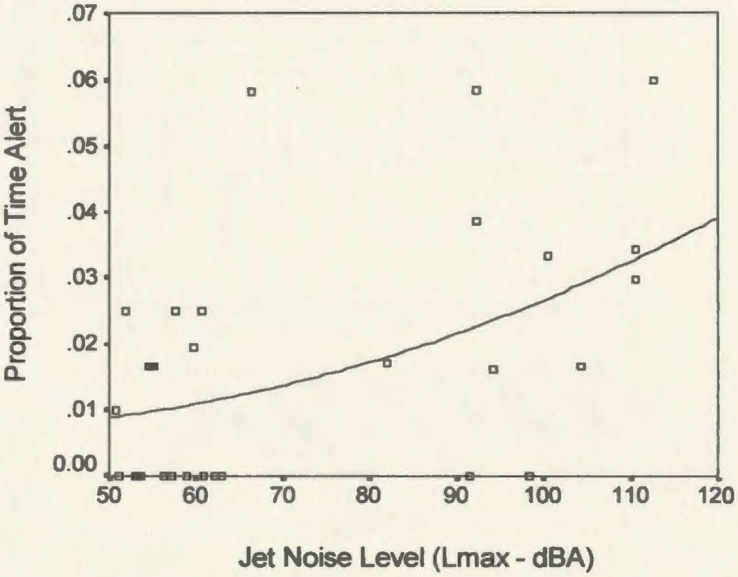
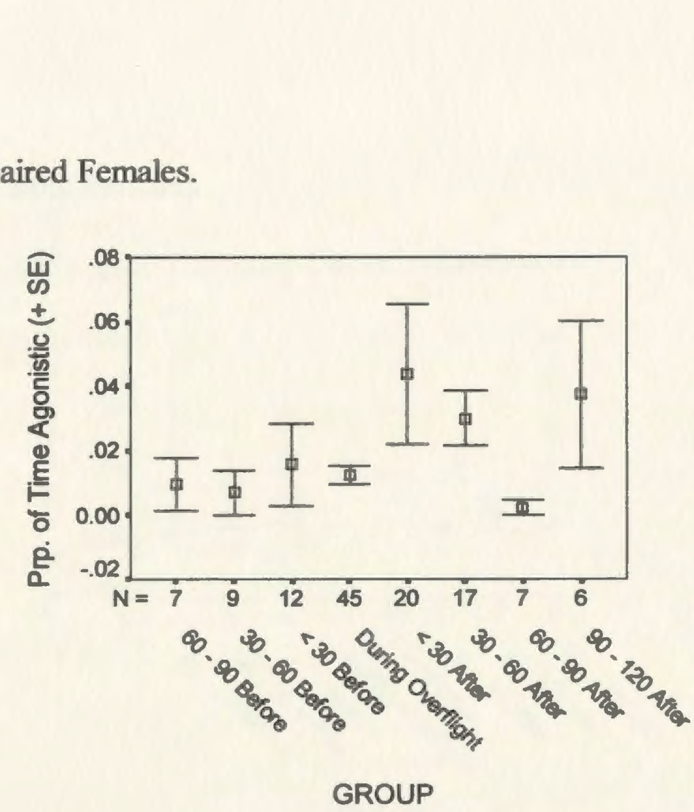


Figure 4.6. Proportion of time Alert versus noise level for paired female and male Harlequin Ducks at Fig River, central Labrador, 19 May -18 June 2002.

Paired Females.



Paired Males

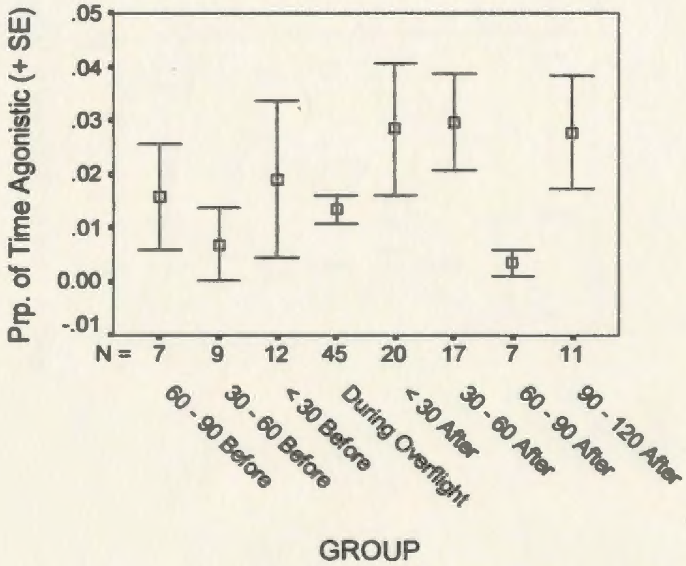
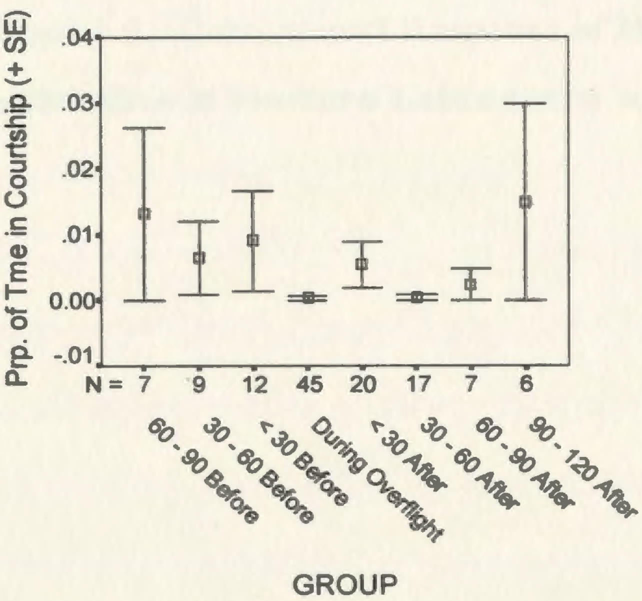


Figure 4.7. Time Agonistic for paired female and male Harlequin Ducks before, during and after over-flights by military jets at Fig River, central Labrador, 19 May -18 June 2002.

Paired Females.



Paired Males

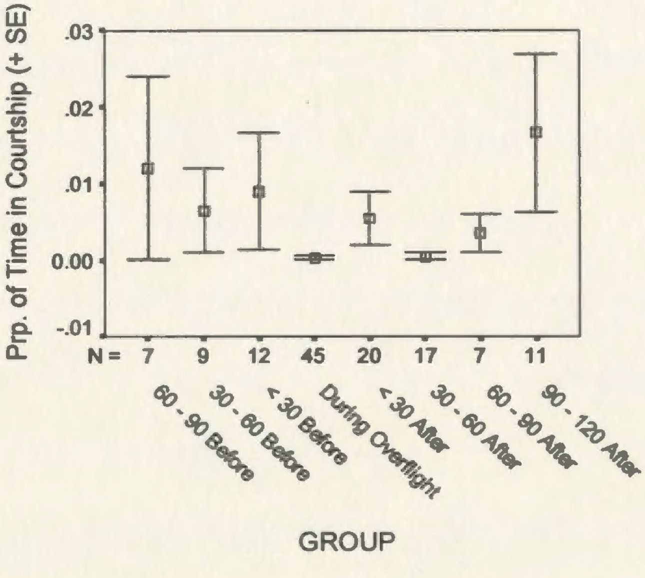


Figure 4.8. Time in Courtship for paired female and male Harlequin Ducks before, during and after over-flights by military jets at Fig River, Labrador, 19 May -18 June 2002.

Chapter 5. Behavioural Response of Harlequin Ducks to aircraft disturbance in southern Labrador: a multivariate approach

5.1 Abstract

The effects of low-level aircraft over-flights on behaviour of Harlequin Ducks (*Histrionicus histrionicus*) breeding in central Labrador were quantified during 2000 to 2002. A suite of 15 behavioural categories of paired males and females was modeled and a canonical variable representing Alert, Inactivity and decreased time out of water represented 73.1% of the variance in the data cluster, and provided marked separation of disturbed and undisturbed groups. Behavioural responses to military jets were 2 to 3 times stronger than to floatplanes, helicopters and military cargo planes, and the significant interaction of aircraft type and noise indicated that noise was the primary stressor affecting behaviour. We defined a quadratic response of Canonical Variable (CV1) to noise (Lmax - dBA) generated from aircraft during standardized 30-minute observation periods. The multivariate analyses indicated covariance in behavioural categories associated with disturbance that was not originally detected in univariate analyses, suggesting that this statistical approach provides a robust view of the birds' behavioural response to aircraft disturbance. The results of my study indicate significant effects of military jet over-flights on behaviours of Harlequin Ducks, emphasizing the need for studies directed towards population consequences of aircraft disturbance.

5.2 Introduction

Through behaviour, an animal may avoid a disturbance (e.g. fly away) or habituate if a stimulus is perceived as not harmful. Studies of responses of animals to aircraft have generally involved classifying observed behaviour into categories from no response to startle (Brown 1990). Typically in nature, patterns that we observe are driven by a number of interacting parameters that vary in time and space, hence the behaviour of an organism is affected simultaneously by many biotic (and abiotic) factors, and there is synergism and feedback among different kinds of responses to a stressor. This multiplicity and interaction make it difficult to analyze ecological systems especially in univariate statistical designs. Univariate methods are extremely powerful in situations where the response of a single variable is of sole interest (e.g. demonstration of dose-response) and other factors can be controlled.

In ecological research, it is more often the case that the question at hand can be answered only by considering a number of variables interacting simultaneously. Hence the emphasis is on sets of variables rather than individual variables (McGarigal et al. 2000). I considered that the noise resulting from aircraft over-flights in Labrador affects many different but partially correlated aspects of the behaviour of breeding Harlequin Ducks (*Histrionicus histrionicus*). Therefore it was necessary to consider how to combine these pieces of information, i.e., covariance, into a single "best" description of response through multivariate statistical analyses.

Noise is the primary stressor affecting wildlife during aircraft over-flights (Brown 1990, 2001b, Ward et al. 2001). For example, noise level resulting from helicopter over-flights increased with increasing distance from geese, and accounted for the observed flushing behaviour that initially seemed to be optically based (Ward et al. 2001). Causal association can most convincingly be established by demonstrating an increase in an adverse outcome (response) with corresponding increases in the level of exposure (dose; Bowles et al. 1991), and this has been demonstrated for Harlequin Ducks in relation to jet noise in Labrador (Goudie and Jones 2004, Chapter 4). Aircraft noise differs with aircraft type, consequently birds may respond differently to different aircraft types (Grubb and Bowerman 1997). Fixed wing and rotary blade aircraft types generate high amplitude noise but are anticipatory (i.e., have a gradual onset) in nature compared to noise from military jets that is very high in amplitude, and is sudden in onset. There is likely to be wide variation in response by wildlife to the passage of aircraft depending on the noise level generated. Much of the existing literature adopts an "all or none" view of impact (Brown 2001a), or has used surrogate information, such as distance of study animals to disturbance source (van der Zande and Verstrael 1985), to evaluate noise events in the field (Brown 2001a).

Sudden onset noise often elicits startle (overt) responses in wildlife that allow disturbed individuals to respond rapidly to possible dangers (Harrington and Veitch 1991).

The startle response is controlled and regulated by several neuro-physiological processes (Bowles et al. 1991). Resulting physiological effects may be characterized by a rapid increase in heart rate and cardiac output, shutdown of the gut and other non-essential functions, and rapid mobilization of glucose reserves to supply the muscles (Hoffman and Searle 1968). Ultimately, all responses to noise disturbance are affected by physiological changes in individual animals.

Animals habituate poorly to high amplitude noise with rapid onset (Korn and Moyer 1966). Habituation may be rapid for steady signals (e.g., constant sound of high amplitude), but relatively slow for intermittent ones (Bowles et al. 1991). Habituation to aircraft noise is species specific. For example, some waterfowl species may habituate to jet noise (e.g. Black Ducks *Anas rubripes*) whereas other species may sensitize (e.g., Wood Ducks *Aix sponsa*; Fleming et al. 1996), and comparability among studies is complicated by wide variations of response among species (Ryals et al. 1999).

I applied multivariate statistical analyses in order to incorporate the array of behaviour quantified for Harlequin Ducks breeding at Fig River in central Labrador. Behaviour was assessed in relation to categories of no disturbance and disturbance associated with aircraft over-flights. Behavioural responses to four types of aircraft, i.e., military jets, Transall (military cargo) planes, floatplanes, and helicopters were quantified and linked to associated noise data in order to test for an effect of aircraft type. These results represent the first reported multivariate integration of behavioural response with aircraft type and noise, and of behaviour in general.

5.3 Methods

5.3.1 Context and study area

The Canadian Department of National Defence (DND) supports a low-level training program involving military jets in a Military Training Area (MTA) encompassing about 130,000 km^2 of central and southern Labrador in eastern Canada. Following an Environmental Impact Statement (EIS), DND adopted a precautionary approach for mitigation of impacts on Harlequin Ducks in the MTA by providing exclusion zones around specific sites where the species was observed annually during single aerial surveys by helicopter (DND 1994). Scientific research has been supported through the establishment of the Institute for Environmental Monitoring and Research (IEMR) that has attempted to refine the understanding of environmental impacts of low-level military jet over-flights. Management actions to mitigate potentially adverse impacts are to be adjusted based on such findings. More than 98% of the MTA receives on average less than a single over-flight per day during May to September (Pigeon 2001). However, military jets frequently follow river valleys during low-level sorties (30-150m AGL) at speeds of 780 to 890 kph, and generate loud noise exceeding 100 dBA (DND 1994). Commencing in 1999, I initiated research on the effects of military jet noise on behaviour and demography of Harlequin Ducks breeding at Fig River (53° 03' N, 63° 09'W) in central Labrador near the geographic center of the MTA.

5.3.2 Behaviour

I quantified behaviour of breeding pairs of Harlequin Ducks during mid May to mid June of 2000, 2001 and 2002. A focal-individual sampling approach (Altmann 1974) was applied, and linked to known individuals because most Harlequin Ducks at Fig River (treatment site, n=95) were individually marked with field-readable coloured plastic leg bands during 1999 - 2002. Behaviour of Harlequin Ducks was characterized during bouts or states (e.g. Feeding and Resting; see Martin and Bateson 1986). For standardized watches, focal birds were monitored for 30 minutes (or until lost from sight) using binoculars and/or (20X-60X) spotting scopes. Instantaneous behavioural classifications of focal birds were recorded every 15 seconds, using digital watches with countdown-return beeper functions, from a suite of 16 general behavioural categories (Table 5.1).

To minimize the chance that individuals were observed more than once, and to maximize the independence of our data, a new individually colour-marked bird was selected for observation or observers changed location to find new birds after each 30-minute observation period was completed. I controlled for the variance associated with repeated watches of the same individuals in a nested design of the General Linear Model (disturbed or undisturbed groups were nested in known individuals). Because instantaneous data recorded every 15 seconds were not statistically independent within each 30-minute watch, frequencies of behavioural categories were summed over each watch and converted to proportions (each behavioural watch contributed one data record as the proportion of frequencies of the recorded behaviour).

Undisturbed versus disturbed categories: Observation periods were classed as "disturbed" or "undisturbed". I considered the observation "disturbed" if focal birds were over-flown by low-flying aircraft during the observation period. It was possible to anticipate some of the over-flights because of floatplanes and helicopters related to project support, and there was communication with the charter companies in Goose Bay. For military jets, Staff at 5-Wing Goose Bay airport relayed time on target (TOT) of military jet over-flights to our field observers via satellite phone following the submission of daily flight plans by allied pilots.

The time of each aircraft transit over the study area was recorded and aircraft type was noted whenever possible. When the over-flying aircraft was visible, the cardinal direction of transit was noted, altitude estimated, and whether the aircraft transited over the Fig Lake outlet location (53° 03' N, 63° 09' W) where a digital time-logging Larson Davis Model 820 Sound Level Meter was deployed. Behavioural watches of Harlequin Ducks were concentrated in the area of the outlet of Fig Lake because there was a relatively large concentration of breeding pairs there (10 or more pairs). Our field crew relayed time of transit at the study site by military jets to 5 Wing Goose Bay airport on a daily basis.

5.3.3 Sound and noise data

Sound and noise levels were measured during observation periods. Sound meters were deployed within 2 m of the river edge in areas frequented by Harlequin Ducks under observation. A continuous digital time-logging Larson Davis Model 820 Sound Level Meter (LD820) (Larson Davis Laboratories 1997) was programmed and deployed at the outlet of Fig Lake in the area of maximal use by pairs of Harlequin Ducks. Sound data were A-weighted because this scale approximates the hearing sensitivity of most birds (Meyer 1986), and is the standard scale generally used to quantify aircraft noise in avian studies (Brown 1990).

For the analyses of effects of noise on behaviour I used the sound measure L*max* recorded every 60 seconds. L*max* was the maximum sound pressure level (as decibels: A-weighted) measured over the sampled period (in this case the aircraft over-flight event). To approximate the background level of sound on the study area, the metric L90 was chosen, and it represented the sound level exceeded 90% of the time (N. Stanton, personal communication 2000). Goudie and Jones (2004, ms submitted) demonstrated that noise (L*max*) of military jet over-flights was much higher in amplitude than the background levels at Fig Lake outlet and along sections of rapids and riffles farther downstream. In addition to aircraft 'loud noise' events also included project- related activities such as chainsaw use and thunder or heavy rain storms.

Data were logged daily from 0500 to 2100 h to coincide with activity by Harlequin Ducks at the outlet of Fig Lake and to encompass over-flights by aircraft. Behavioural data were also collected at other sites along Fig River and Fig Lake, and sound was recorded during those 30-minute watches using hand-held digital Larson Davis Model DSP80 Sound Level Meters (Larson Davis Laboratories 1997). These recorded L*max* (A-weighted) in decibels integrated over the 30-minute observation period.

I used the *Passby* function, a special exceedance event detector of the LD820 Sound Level Meter that measured the L*max* of the highest event to raise and lower $\geq$10 dB in Sound Pressure Level. It was used to capture single event noises (Larson Davis Laboratories 1997), and is preferred for measuring transient noise events (Pater 2001). L*max* was modeled against the behavioural response variables of the Harlequin Ducks in an effort to assess evidence for an effect.

5.3.4 Statistical analyses

I was interested in the behaviour of paired male and female Harlequin Ducks that were disturbed by low-flying aircraft relative to behaviour without disturbance. I used the General Linear Model approach under GLM in SAS (SAS Institute Inc. 1999). Because known individuals were sampled many times over each year, I included a model term for the known individuals that was nested within disturbed and undisturbed categories for female and male Harlequin Ducks. This effectively controlled for variance associated with individuals, increased the degrees of freedom in the numerator and reduced the sum of squares in the error term thereby reducing the potential for a type 1 error.

My statistical models encompassed response variable with categories (undisturbed male and female, disturbed male and female) in relation to proportion of time spent in 15 defined behavioural categories (Table 5.1), and was therefore appropriate for the application of a Multivariate Analysis of Variance (MANOVA) which maximizes the ratio of among-group to within group variance in canonical scores. Subsequent to a statistically significant MANOVA, a Discriminant Analysis (DA) was applied. It is logical to consider DA as an extension of MANOVA because overall we were interested in testing the null hypothesis that the groups do not differ whereas in DA we are interested in describing the linear combinations of dependent variables that maximally discriminate among groups. In other words, MANOVA and DA correspond to the inferential and descriptive aspects of analyses much the same way as the univariate ANOVA and subsequent multiple range tests because in the latter we seek to describe where the differences among groups lie (McGarigal et al. 2000).

Significance of the MANOVA was assessed based on Wilks' Lambda, the likelihood ratio statistic that tests the null hypothesis that the group means are equal in the population. This statistic considers the differences among groups and the homogeneity within groups, and approaches 0 if any two groups are well separated or 1 if groups are essentially equal. In DA, each derived canonical variable is orthogonal (perpendicular) to the previous axis and describes progressively less information in the data set. Hence, in theory, there is no redundancy among canonical variables (CVs) and they are complementary in explaining differences among groups in the data cluster. The relative importance of each canonical variable in describing the multivariate data cluster was assessed by the relative magnitude of the eigenvalues because the greater the eigenvalue the greater the sample variation on that CV. This relative contribution is expressed as a proportion of the sum of the eigenvalues, and, known as the trace, this total equals the sum of the main diagonal of the secondary matrix used which in this case was the variance-covariance matrix.

Distribution of samples in multivariate space are derived by scoring the raw data using the canonical variable (vector), and the resulting discriminant scores represent the new multivariate data because they are derived from a linear combination of the original variables. By averaging the canonical scores within a particular group I derived the centroid for each group that is effectively from the composite mean of a number of initial variables. Distribution of centroids in multivariate space was assessed using 95% confidence ellipses or multi-way 95% confidence intervals.

I used a Multivariate Analysis of Covariance (MANCOVA) to model the influence of aircraft type (military jet, Transall cargo plane, floatplane, helicopter) and noise (Lmax) on behaviour of paired Harlequin Ducks at Fig River. I modeled the influence of noise as a quadratic term because the behavioural response Alert is nonlinear (Goudie and Jones, 2004 submitted). I was especially interested in the interaction term of aircraft and noise as a potential means to assess whether behavioural responses of Harlequin Ducks were independent of aircraft type.

5.4 Results

5.4.1 Effects of aircraft disturbance on behaviour

There were substantial differences in behaviour of undisturbed and disturbed (by aircraft) female (Wilks' Lambda = 0.060, $P < 0.0001$) and male Harlequin Ducks (Wilks' Lambda = 0.094, $P < 0.0001$) at Fig River, Labrador (Table 5.2). In the presence of aircraft, Alert, Inactivity, Comfort (preening) and Vigilance increased significantly, and out of water behaviour decreased (Fig. 5.1). I modeled disturbed and undisturbed females and males together using a discriminant analysis in order to highlight differences indicated in the ratio of among group variance-covariance matrices to within group variance-covariance matrices of the Multivariate Analysis of Variance (MANOVA: Wilks' Lambda = 0.0645, $P < 0.0001$).

Canonical variable 1 (CV1) accounted for 73.1% of the variance and represented Alert, inactivity (recorded as rest) and decreasing haul-out. CV2 accounted for 24.3% of the variance and represented increasing Vigilance and decreasing Feeding and Preening while CV3 accounted for 2.6% of the variance and represented increased Preening (Table 5.3). The CV1 provided maximum discrimination of the disturbed versus undisturbed cohorts, and I interpreted CV2 to be related to within-pair behaviour, particularly the role of increased vigilance by males in activities of pairs (Squires et al. 2004, ms submitted). In general, paired Harlequin Ducks that were exposed to aircraft over-flights exhibited Alert behaviour, became inactive, and spent less time out of water. Paired males spent more time vigilant and less time preening than paired females (Fig. 5.2 and 5.3).

5.4.2 Effects of aircraft type on behaviour

There were significant differences in behaviour of Harlequin Ducks and types of aircraft (MANOVA - Females: Wilks' Lambda = 0.0093, $P < 0.0001$; Males: Wilks' Lambda = 0.0135, $P < 0.0001$). These differences especially pertained to Comfort, Rest, Vigilant and Alert behaviour. In general, the behavioural effects of aircraft were most pronounced for military jets although in a few cases there were effects of similar magnitude for helicopter and especially a fixed-wing over-flight (Fig. 5.4a,b).

5.4.3 Effects of aircraft type and noise on behaviour

The MANCOVAs that incorporated aircraft type and noise (Lmax) were significant (females: Wilks' Lambda = 0.1038, $P < 0.0001$, males: Wilks' Lambda = 0.1010, $P < 0.0001$). However, the interaction terms of aircraft type and noise were significant for important behavioural categories that differed between disturbed and undisturbed groups (Table 5.4). This appeared because most aircraft noises of high amplitude were generated by military jets, but the sample sizes for other types of aircraft were relatively small (Fig. 5.5). A curvilinear relationship of canonical variable 1 with maximum noise level detected during standard 30-minute observation periods explained 43.1% of the overall variance in behaviour (Fig. 5.6).

5.5 Discussion

5.5.1 Effects of aircraft disturbance on behaviour

Harlequin Ducks at Fig River, Labrador responded to low flying aircraft by increasing Alert behaviour and becoming Inactive or immobile. Previously we showed that Alert response to noise generated from low-level military jets increased in a dose-response manner (Goudie and Jones 2004, ms submitted). The multivariate approach used here was more inclusive, and modeled covariance in Inactivity that was not originally detected in the univariate analyses that applied the Before-After-Control-Impact design. These findings are important because studies of effects of disturbance on behaviour may be biased to detecting overt responses. Once animals stop moving or commence feeding or normal locomotion, observers may perceive that the individuals have returned to "normal" behaviour (Harrington and Veitch 1991).

Detection of protracted or residual effects may be enhanced through a Before-During-After design (see Goudie and Jones 2004, ms submitted) but is evidenced best through a multivariate statistical design because it models covariance that is otherwise masked in univariate analyses. Harrington and Veitch (1991) noted that 5 to 10 minutes elapsed before behaviour of caribou returned to pre-disturbance levels, and that it was likely that heart rate remained elevated for several minutes following a jet overpass.

5.5.2 Effects of aircraft type and noise on behaviour

Noise generated from military jet over-flights can be very high in amplitude (e.g. up to 129 dBA; Goudie and Jones 2004, submitted, and up to 131 dB; Harrington and Veitch 1991). In general at Fig River, there were stronger behavioural responses by Harlequin Ducks demonstrated for military jet over-flights than other types (i.e., fixed-wing, helicopter or cargo plane). Nevertheless, under certain conditions, responses to the other types of aircraft were of similar magnitude. At Fig River, the noise generated from military jet over-flights was of higher amplitude than other aircraft. The significant interaction term of aircraft type and noise (Lmax) in the General Linear Model of effects on behaviour indicated that it was not possible to separate effects of aircraft type from generated noise.

Brown (1990, 2001b) and Ward et al. (2001) provided evidence that noise was the primary stressor in aircraft disturbance, and the fact that 43.1% of the variance in behaviour in paired Harlequin Ducks at Fig River, Labrador was explained by noise provides further support to this conclusion. Causal association can most convincingly be established by demonstrating an increase in an adverse outcome (response) with corresponding increases in the level of exposure (dose) (Bowles 1994, Bowles et al. 1991). Quantification of dose - response is the preferred approach to measuring and subsequently mitigating negative impacts of noise on humans through reduction of dose

(Fidell et al. 1991), and could be applied to reduce effects on Harlequin Ducks in the Military Training Area of Labrador (Goudie and Jones 2004, submitted).

At Fig River in Labrador, most over-flights by military jets that coincided with behavioural observations of Harlequin Ducks were under 100m above ground level (agl), and within 50m radius. It is possible that at such a low altitude the high amplitude noise masked any effect of aircraft type. Other authors had inferred that behavioural responses in some birds of prey vary by aircraft type beyond some threshold of distance. For example, Grubb and Bowerman (1997) argued that at distances to aircraft of less than 166 m there were no effects of aircraft type on behaviour of Bald Eagles (*Haliaeetus leucocephalus*) whereas stronger responses to helicopters versus military jets and light planes were documented beyond this distance. Although this finding may appear to support an effect of aircraft type, other researchers have demonstrated that noise generated from helicopters can increase with distance from the animals (Ward et al. 2001).

Harrington and Veitch (1991) detected overt responses of caribou (*Rangifer tarandus*) in 88% of 24 over-flights by military jets that were 30 m agl and within 50 m of animals, whereas responses were detected in only 38% of 16 times when over-flights were 300 m agl or greater than 75 m from animals. They concluded that initial response of caribou to a low-level jet aircraft was caused by the sound of the overpass, not the sight of the jet, and that beyond 250 m from the jet's flight path, the mean sound pressure level was under 90 dB which is less aversive to wild mammals (Manci et al. 1988). Nevertheless, they noted that caribou responded sooner to a helicopter and ran significantly longer and farther than in response to military jets, a possible consequence of slower air speed and greater visual detection. Additionally, helicopters actively pursue caribou (and investigate eyries in raptor research, see Trimper et al. 1998) especially for wildlife research, and animals may associate this aircraft with the threat posed by predators.

Behavioural responses to disturbance are selected from a complex intercorrelated repertoire. An increase or decrease in one behaviour results in a concomitant decrease or increase in other behaviours. A multivariate statistical approach highlights the covariance structure of the dataset that may contain more important and revealing information that is missed with univariate analyses. The multivariate approach used to quantify behaviour in relation to aircraft disturbance in my study indicated significant effects of aircraft noise on behaviour of Harlequin Ducks, and was more holistic in assessing effects than univariate approaches. These findings support the need for studies directed towards population consequences of aircraft disturbance.

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5.8 Tables

Table 5.1. General categories used to summarize behaviours of Harlequin Ducks. Behaviours were segregated into on the water and out of the water (_ho).

Behaviour	Description
Agonism	Aggressive interactions among Harlequin Ducks including chasing and sometimes fighting with conspecifics.
Agonism_ho	Aggression while out of water
Courtship	All Courtship behaviour (on the water), e.g., inciting, prone, copulation
Feed	All aspects of obtaining food, including: dip, dive, submerged, pause, glean
Peer	Looking into water (may be associated with food seeking)
Locomotion	All types of movements, e.g., swim, scoot, fly, walk
Preen	Feather maintenance using the bill as well as flapping and shaking
Preen_ho	Preen while out of water
Inactive	Inactivity including resting, sleeping and head down
Inactive_ho	Inactivity while out of water
Social	Calls and head nods directed to conspecifics
Vigilant	Maintaining a look-out (vigil) usually while the mate feeds or sleeps
Vigilant_ho	Vigilance while out of water
Alert	Head stretched upward, body erect/tense, re-orientation, and agitated, often accompanied with locomotion. Includes startle responses such as splash dive and panic flush
Alert_ho	Alert while out of water

Table 5.2. Univariate ANOVAs from the MANOVA[1] for undisturbed behaviour and disturbed by aircraft for paired adult Harlequin Ducks in Labrador.

Behaviour	ANOVA Female $F_{60, 843}$	Probability	ANOVA Male $F_{55, 850}$	Probability
Agonistic	1.38	0.032	1.39	0.036
Agonsitic_ho	1.03	0.411	1.59	0.005
Court	0.47	0.999	0.47	0.999
Feed	2.13	< 0.0001	2.35	< 0.0001
Locomotion	2.59	< 0.0001	2.90	< 0.0001
Comfort	9.77	< 0.0001	5.71	< 0.0001
Comfort_ho	2.37	< 0.0001	2.58	< 0.0001
Inactive	13.64	< 0.0001	13.52	< 0.0001
Inactive_ho	2.37	< 0.0001	2.12	< 0.0001
Vigilant	9.90	< 0.0001	2.15	< 0.0001
Vigilant_ho	2.15	< 0.0001	3.47	< 0.0001
Alert	5.54	< 0.0001	5.61	< 0.0001
Alert_ho	0.98	0.5234	1.53	0.0094

[1] Paired Female: Wilks' Lambda = 0.060, $P < 0.0001$

[1] Paired Male: Wilks' Lambda = 0.094, $P < 0.0001$

Table 5.3. Correlations between discriminating variables and standardized canonical functions.

Behaviour	CV1	CV2	CV3
Rest	**0.696**	- 0.127	- 0.196
Alert	**0.460**	- 0.079	- 0.171
Rest_ho	**- 0.274**	- 0.049	0.014
Vigilant_ho	0.260	**0.618**	- 0.276
Vigilant	- 0.148	**0.579**	0.310
Comfort_ho	- 0.251	**- 0.425**	- 0.200
Feed	- 0.011	**- 0.145**	- 0.001
Agonistic	0.053	**0.120**	- 0.055
Comfort	0.451	- 0.197	**0.745**
Locomotion	0.027	- 0.013	**0.034**
% Variance	73.1	24.3	2.6

Note: bold - indicates largest absolute correlation between each variable and discriminant function.

Table 5.4. Univariate ANCOVAs of the MANCOVA[1] for undisturbed behaviour and disturbed by aircraft for paired adult Harlequin Ducks versus aircraft type and noise in Labrador.

Paired Females

Behaviour	Noise (Lmax)	Probability	Aircraft Type	Probability	(Noise x type)	Probability
	$F_{1, 286}$		$F_{32, 286}$		$F_{32, 286}$	
Feed	0.14	P = 0.705	0.86	0.695	0.90	0.625
Preen	0.68	P = 0.410	1.52	0.040	1.33	0.118
Preen_ho	0.001	P = 0.946	1.95	0.0023	1.88	0.004
Inactive*	0.04	P = 0.840	6.72	< 0.0001	6.87	< 0.0001
Inactive_ho	0.09	P = 0.765	0.50	0.990	0.51	0.987
Vigilant	1.47	P = 0.227	0.86	0.691	0.87	0.675
Vigilant_ho	0.00	P = 0.981	0.53	0.985	0.54	0.982
Alert*	3.82	P = 0.052	1.98	0.002	1.91	0.003
Alert_ho	0.01	P = 0.939	1.72	0.012	1.39	0.086

[1] Paired females: Wilks' Lambda = 0.1038, P < 0.0001

(Table 5.4 cont.)

Paired Males

Behaviour	Noise (Lmax)	Probability	Aircraft Type	Probability	(Noise x type)	Probability
	$F_{1,295}$		$F_{30,295}$		$F_{30,295}$	
Feed	0.03	0.859	0.82	0.741	0.85	0.694
Preen	0.12	0.725	0.203	0.002	1.83	0.006
Preen_ho	0.17	0.684	1.45	0.066	1.44	0.070
Inactive*	0.01	0.915	5.39	0.0001	5.49	0.0001
Inactive_ho	0.08	0.783	0.51	0.986	0.53	0.980
Vigilant	0.00	0.961	1.12	0.305	0.96	0.528
Vigilant_ho	0.03	0.863	1.53	0.041	1.62	0.250
Alert*	6.87	0.009	3.08	< 0.0001	3.01	< 0.0001
Alert_ho	0.06	0.804	3.11	< 0.0001	2.53	< 0.0001

[1] Paired males: Wilks' Lambda = 0.1010, $P < 0.0001$

Note: * indicates significant behavioural category in CV1 for discriminating disturbed from undisturbed groups.

GLM Model Statement: Behaviour = Group (who) + noise^2 + type + noise^2 X type

5.9 Figures

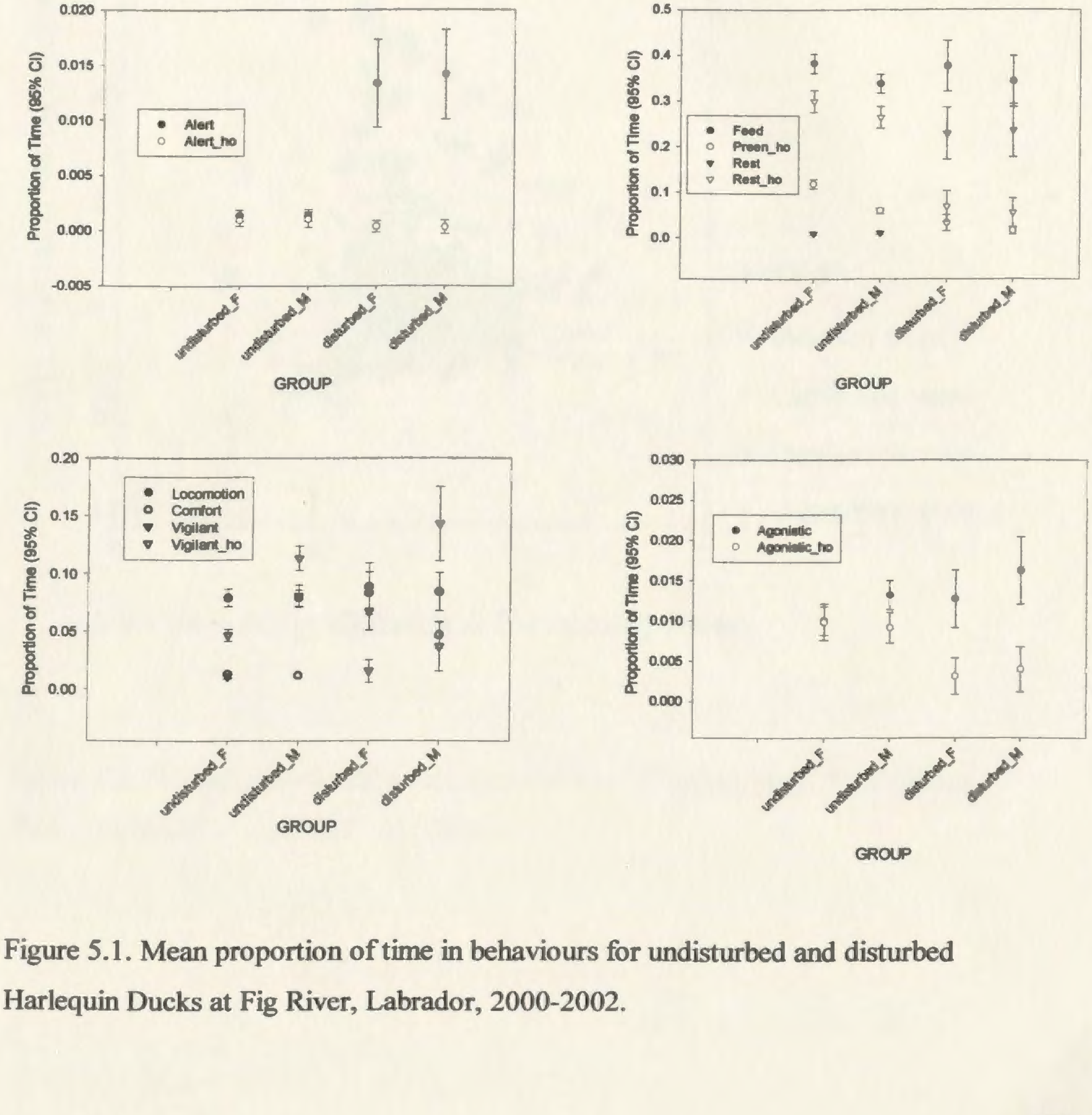


Figure 5.1. Mean proportion of time in behaviours for undisturbed and disturbed Harlequin Ducks at Fig River, Labrador, 2000-2002.

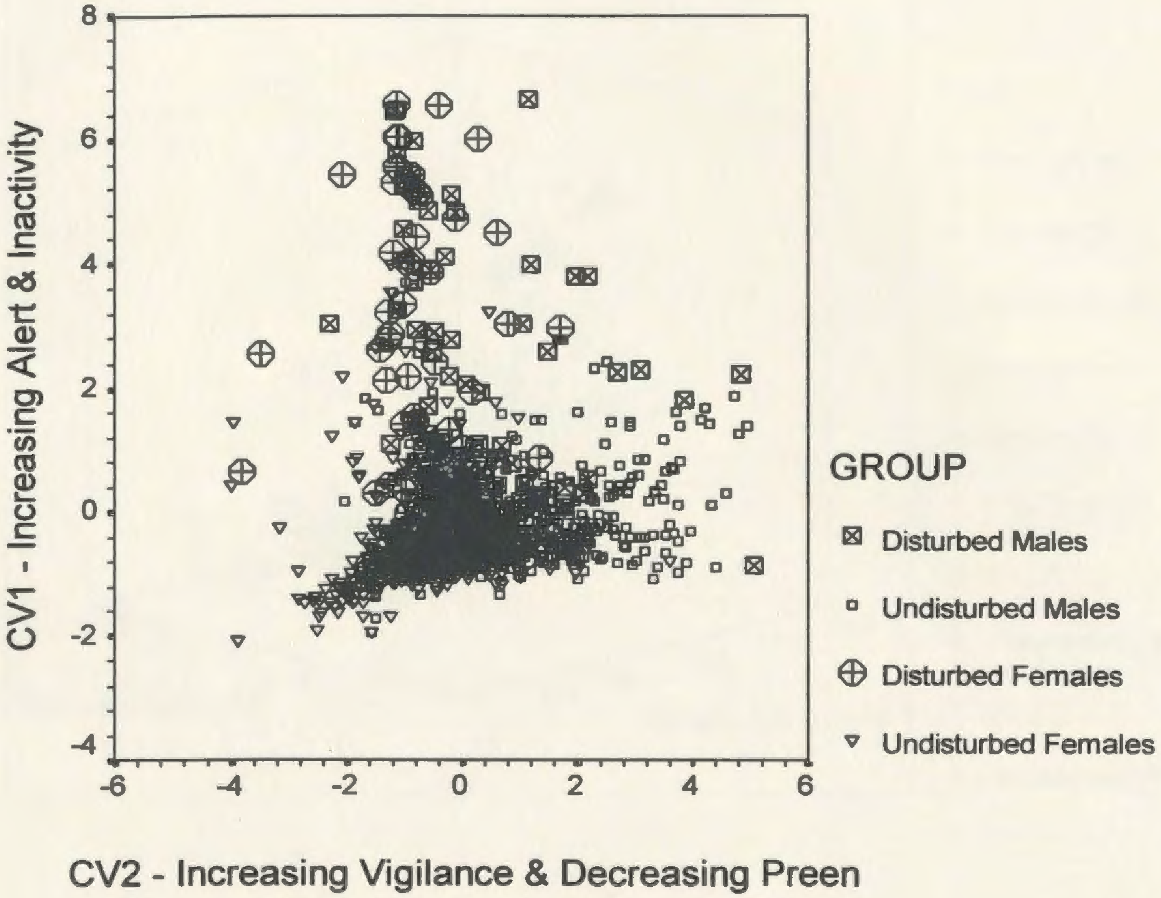


Figure 5.2. Plot of discriminant scores for behaviour of undisturbed and disturbed Harlequin Ducks at Fig River, Labrador.

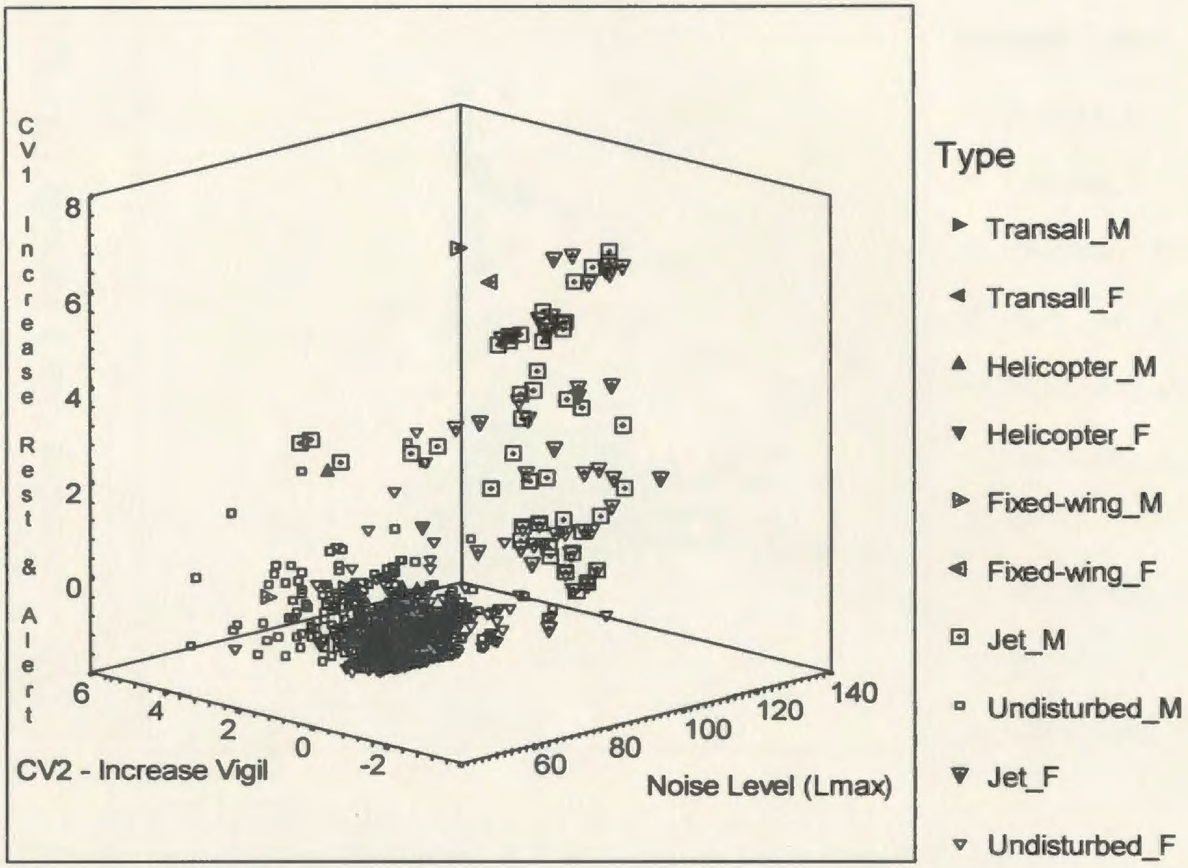


Figure 5.3. Three dimensional plot along CV1, CV2, and noise level using discriminant scores for behaviour of disturbed and undisturbed paired female (_F) and male (_M) Harlequin Ducks at Fig River, Labrador.

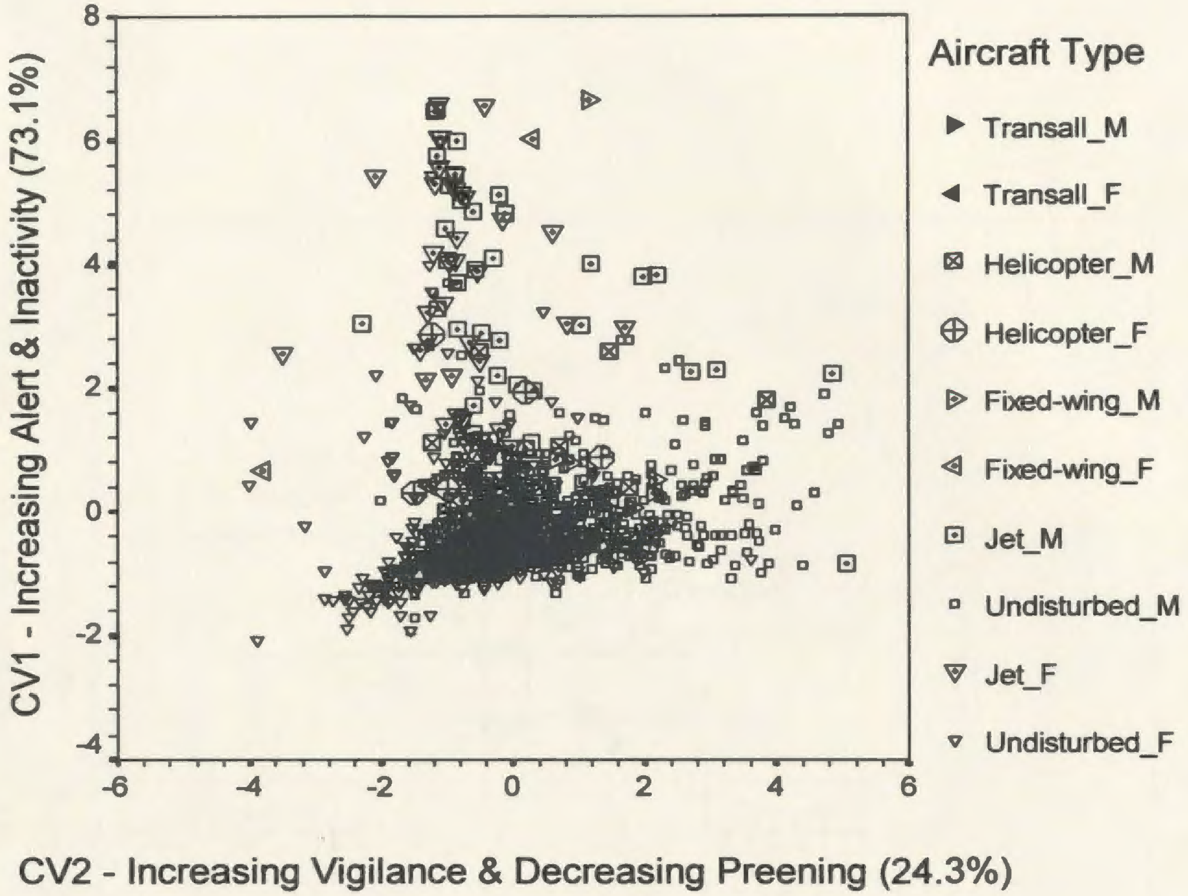


Figure 5.4a. Plot of discriminant scores for behaviour of undisturbed and disturbed paired female (_F) and male (_M) Harlequin Ducks at Fig River, Labrador in relation to aircraft type.

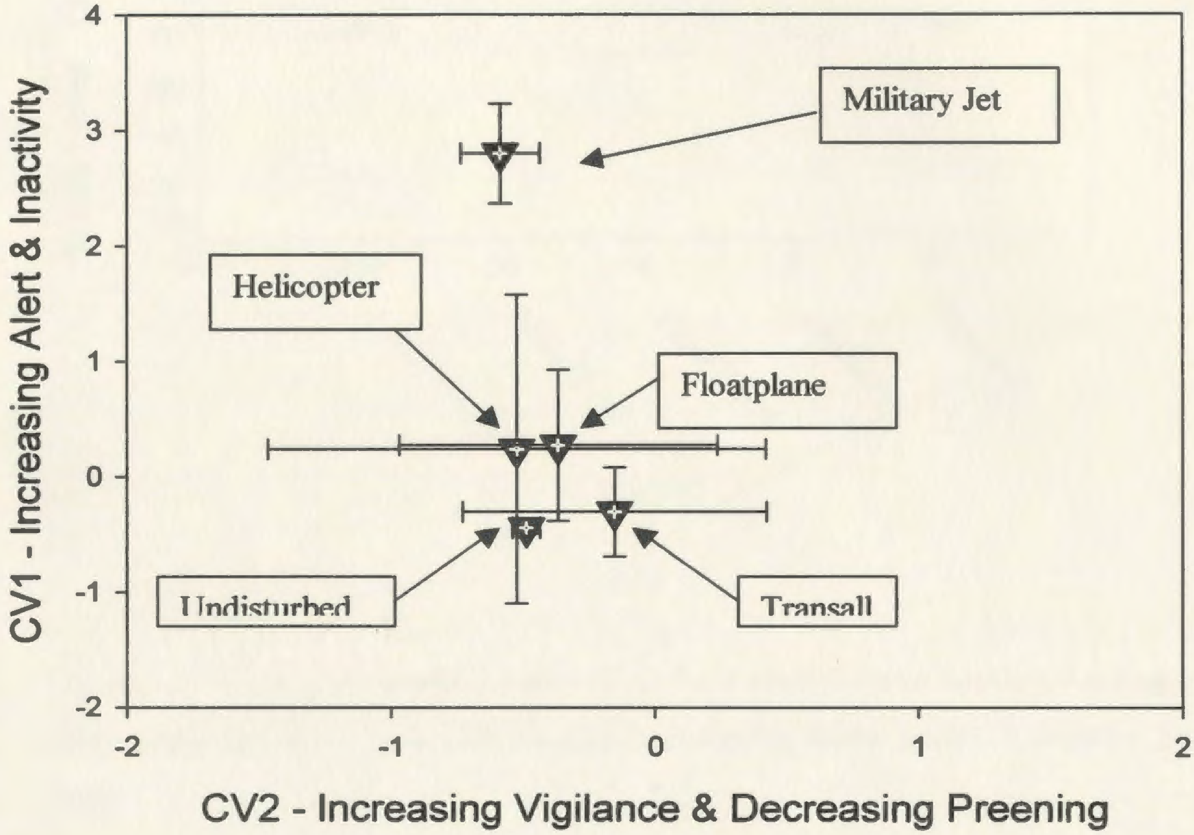


Figure 5.4b. Centroids and 95% confidence intervals for discriminant scores for behaviour of paired Harlequin Ducks at Fig River, Labrador in relation to aircraft type.

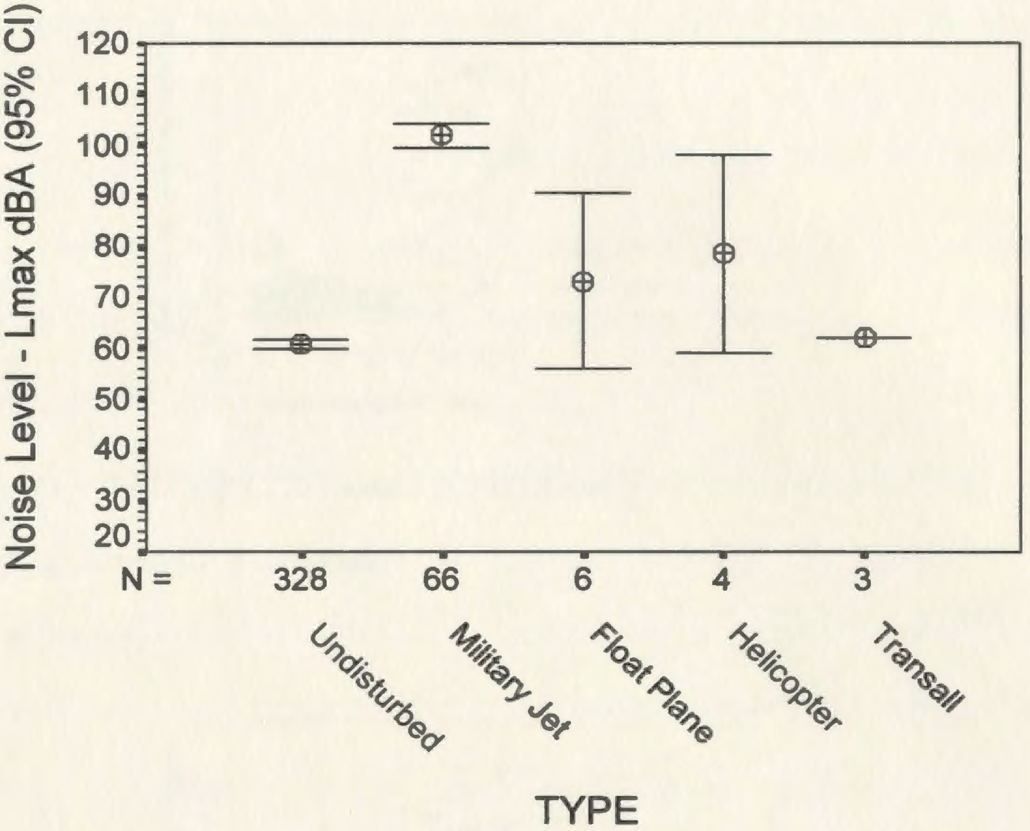
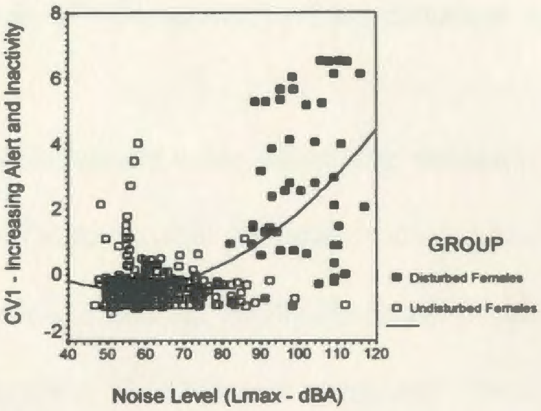


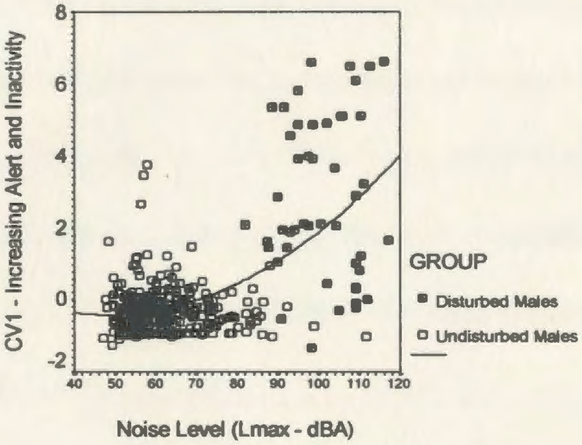
Figure 5.5. Mean noise levels (Lmax –dBA) for 4 aircraft types measured during behavioural watches of paired Harlequin Ducks at Fig River, central Labrador, 2000-2002.



$CV1 = 2.915 - 0.1225\ Lmax + 0.0011\ Lmax^2$

$F_{2,405} = 157.50, P < 0.00001$

$R^2 = 0.4375$



$CV1 = 1.618 - 0.084\ Lmax + 0.0009\ Lmax^2$

$F_{2,406} = 137.99, P < 0.00001$

$R^2 = 0.4047$

Figure 5.6. Relationship of Canonical Variable 1 to maximum noise level (Lmax) detected during standard observation of Harlequin Ducks at Fig River, Labrador.

Chapter 6. Summary, Conclusions and Recommendations

This thesis reports some of the first research on the effects of aircraft noise on behaviour of waterfowl in the wild. Noise generated from low-level military jets was of high amplitude (L*max* up to120 dBA) and substantially above the background levels of lake outlets (40 – 50 dBA) and rapids and riffles (60 – 70 dBA). My findings represent the first demonstrated dose-response relationship achieved by linking observed behaviours of adult Harlequin Ducks with levels of noise quantified before, during and after low-level military jet over-flights. Noise was interpreted as the primary stressor, and overt responses to aircraft over-flights involved Alert (startle) behaviour that increased to about 1% of time-activity budgets relative to undisturbed behaviour that averaged 0.1%. There were protracted effects on behaviour following initial overt responses related to increased inactivity and reduced time out of water. A residual effect was demonstrated for increased aggressive and decreased courtship behaviours lasting up to 1.0 h and 1.5 h following low-level military jet over-flights.

Implications of these findings to Harlequin Ducks are difficult to interpret directly and require further research. Protracted and residual effects are potentially more serious because (i) repeated exposure to noise from military jets clearly could negatively affect time-activity by reducing time budgeted to essential behaviours such as feeding, feather maintenance, and courtship, and (ii) these effects indicate that a whole body or physiological effect took place, and such responses have the potential to decrease survival and productivity. Negative effects on survival and productivity can result in effects at the population level. I was unable to test for effects of military jet noise on survival of adult Harlequin Ducks because of project termination by the IEMR. My applications of multivariate statistical analyses to behaviour are among the first to be applied to studies of effects of disturbance on wildlife. Because behaviours are often strongly correlated, and exhibit considerable covariance, I conclude that univariate statistical approaches have limited applications, and recommend the more holistic approach encompassed in multivariate designs. Univariate tests, such as the two-way ANOVA used in the Before-After-Control-Impact design, are convenient in demonstrating effects but I would recommend subsequent exploration of the dataset in a multivariate environment.

I concluded that studies attempting to assess effects of disturbance on behaviour of wildlife may be of limited value if the emphasis is on the detection of observable overt responses because the protracted and residual effects can only be detected through statistical analyses. Specifically, researchers often measure duration of impact as the time lapse between disturbance stimuli and return to behaviours evident prior to disturbance. Clearly, my results suggest that disturbance effects can also include alterations to these assumed "undisturbed" behaviours. Additionally, the application of multivariate statistics was more effective than univariate analyses at modeling behaviour because of the covariance or synergistic relationship among behaviours.

Information arising from my studies of breeding ecology of Harlequin Ducks (*Histrionicus histrionicus*) in central Labrador indicated that aerial surveys to quantify populations have not been exhaustive within the Military Training Area (MTA) of Labrador. Overall, a significant proportion of the population of Harlequin Ducks breeding in the MTA occurs high in watersheds where there is a high frequency of lakes and ponds, and many watersheds have not been fully surveyed. Aerial helicopter surveys underestimate true numbers by 40% to 50%, hence many rivers supporting only 1 or 2 pairs go undetected. Discrepancies related to brood inventories are much higher.

On average, breeding success of Harlequin Ducks in the MTA is low (e.g. averaging ~ 30%) but all adult females attempt to nest each year. There is little or no staging of Harlequin Ducks on the upper reaches of watersheds where they attempt to nest, and adult females are highly philopatric to specific river reaches in consecutive years. This in combination with a low probability of detection on the single spring surveys undertaken by DND in the past indicates that a new method for designating rivers as "supporting breeding" is required.

Based on my research findings, a precautionary management approach is recommended. Specific recommendations for the conservation and management of Harlequin Ducks are as follows:

Issue 1. Detection and inventory of adult Harlequin Ducks in the MTA.

i. Aerial surveys in the MTA for Harlequin Ducks be modified to encompass the upper reaches of watersheds, especially where review of topographical maps indicate a high frequency of lakes/ponds and rivers/streams.

ii. Rivers, such as Metchin River or Shoal River, be designated as *Rivers supporting Harlequin Ducks*, and not surveyed annually unless as a subsample for assessing population trend. By taking this approach, annual resources could be better focused on measuring within season error in detection and/or exploring new watersheds.
iii. Aerial surveys on rivers should be repeated at least once within the spring season in order to increase the power of detection of breeding pairs.

Issues 2 & 3. Resighting of marked Harlequin Ducks on multi-year study areas and Breeding Propensity

i. An avoidance program be implemented on a watershed basis by initially designating rivers as supporting or not supporting Harlequin Ducks. Further refinement of exploited reaches may be possible for rivers such as Fig River where ground studies have been able to demonstrate reaches used, or possibly for DND studies where telemetry work may have provided insight into distribution and movement of females.
ii. Avoidance polygons should be expanded, and realistically should encompass a buffer of 5 to 10 km up-stream and down-stream of observations.
iii. Replicated aerial surveys within years and telemetry results be used to refine knowledge of river reaches used by Harlequin Ducks.

Issues 4 & 5. The need for a precautionary approach and Avoidance Criteria

i. Rivers supporting pairs of Harlequin Ducks be designated as "breeding areas".
ii. Aerial brood surveys be abandoned except in situations requiring detailed monitoring, and then should be accompanied by ground truthing.

iii. Telemetry efforts aimed to establish if Harlequin Ducks breed along specific rivers in the MTA be abandoned.
iv. Resources be pooled in order to repeat spring surveys, and reduce the probability of not detecting mated pairs.

Recommendations following from scientific studies include:

i. An avoidance program for Harlequin Ducks in the MTA be continued, and modified as indicated in Recommendations 1.1 to 1.3.
ii. An above ground level criterion be implemented for transiting of a river system used by Harlequin Ducks when this is unavoidable. This level to be set such that average noise from military jets at ground level is < 85 dBA.
iii. For river reaches used by Harlequin Ducks, flight paths of low-level military jets cross at an oblique angle.
iv. Priority avoidance should be implemented on systems such as the Naskaupi River – Red Wine River where relatively high densities of Harlequin Ducks coincide with frequent low-level military jet sorties. Reaches of these specific river valleys are preferentially transited by allied pilots, and interestingly no successful breeding has been documented by effects monitoring surveys.

Harlequin Ducks are long-lived with low annual productivity resulting in populations being very sensitive to small changes (3 – 5%) in adult survival rates. Productivity of Harlequin Ducks on my study in central Labrador was low, and I demonstrated that all adult females were reproductively active. Nest success was apparently limited by depredation, and I found no support for the paradigm that non-breeding was influenced by limited food availability. There was no direct evidence that any adult female skipped breeding in any of the 4 years of my study. I conclud that more empirical research is required to test the deferred breeding hypothesis definitively in sea ducks.

There remains the need to assess the effects of noise from military jet over-flights on vital demographic rates of Harlequin Ducks. This would have been possible for adult birds in 2003 and/or 2004 within the application of my research program because of the relatively large samples of marked individuals (~ n = 100 at Fig River) but the Institute for Environmental Monitoring and Research discontinued the studies (2003) or did not propose sufficient funding to complete fieldwork at the treatment (Fig River and Control (Crooked River) sites (2004). Ultimately, future research should attempt to test for effects of military jet noise on survival of juvenile birds because other studies have suggested that the effects on vital rates may be most pronounced in this cohort of the population.