

**ASSOCIATIVE NESTING BEHAVIOUR BETWEEN
PACIFIC GREAT BLUE HERONS AND BALD EAGLES IN
THE PACIFIC NORTHWEST: TESTING THE PREDATOR
PROTECTION HYPOTHESIS**

by
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ABSTRACT

Pacific Northwest great blue herons (*Ardea herodias fannini*) appear to have modified nesting behaviour in response to the strong recent recovery of the bald eagle (*Haliaeetus leucocephalus*) population. Previously undescribed, herons now often nest in close association with some breeding eagles, even though eagles depredate heron nestlings, are implicated in the recent reproductive decline of herons, and may induce abandonment of heron breeding colonies. I tested the hypothesis that breeding herons gain protection from the territorial behaviour of eagles. Natural observations and simulated incursions showed that nesting eagles actively repel other eagles within at least 250m around the nest site, thereby establishing a relatively safe place for herons to nest. Surveys showed that 70% of heron nests and 19% of heron colonies were located within 200 metres of eagle nests with high reproductive success. These herons had greater reproductive success than those nesting far from eagle nests.

Keywords: heron, *Ardea herodias fannini*, eagle, *Haliaeetus leucocephalus*, predator protection, nesting association, colony, disturbance, territoriality, nest defence, predation, raptor, Pacific Northwest, Fraser River, habitat selection, Georgia Strait

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CHAPTER 1: GENERAL INTRODUCTION

Thesis Objectives

Within this thesis, I seek to describe and test a previously unidentified nesting association between the Pacific great blue heron (*Ardea herodias fannini*) and the bald eagle (*Haliaeetus leucocephalus*) in the Lower Fraser Valley of British Columbia. The primary goals of this research are to contribute to the theoretical body of knowledge in ecological and nesting association research and to provide information to aid heron conservation management.

Theoretical Background and Rationale

Exploring the causation of habitat selection, species coexistence and life history traits have long been a central theme in evolutionary ecology (Martin 1993). In birds, food availability has often been considered an important factor in determining the evolution of life history traits (Charnov and Krebs 1974, Martin 1995). The majority of theory across taxa however, considers variation in mortality as the driving force behind the evolution of life history traits (Martin 1995). Several authors think the importance of predation risk has been underestimated in determining avian life history pointing to evidence where predation of adults, chicks and eggs has been the main cause of reproductive failure (Ricklefs 1969, Martin and Li 1992, Forstmeier and Weiss 2004). Regardless of which of these processes is dominant in a given biological system,

it is clear that successful individuals must find enough food while avoiding mortality due to predation. Breeding strategies that minimize predation risk, while still allowing access to adequate levels of resources, likely lead to greater individual fitness and therefore, can be acted upon by natural selection (Lima and Dill 1990, Martin and Li 1992, Blanco and Tella 1997, Forstmeier and Wiess 2004).

A large suite of breeding strategies has been identified among avian taxa that allow sufficient access to resources while minimizing an individual's predation risk. One such strategy involves two or more individuals nesting in association to reduce one or both of their predation risk (Burger 1981, Haemig 2001, Quinn et al. 2003). These interactions are mediated in several ways, from simple predation dilution (Burger 1984) and increased vigilance (Blanco and Tella 1997) to collective nest defence (Fuchs 1977). A handful of studies have shown an association where a more timid species preferentially nests with a more aggressive species to benefit from its nest defence behaviour (Ueta 1994, Blanco and Tella 1997, Tremblay et al. 1997, Bogliani et al. 1999, Richardson and Bolen 1999, Quinn and Kokorev 2002, Quinn et al. 2003). That strategy and accompanying theory is referred to as the Predator Protection Hypothesis (Richardson and Bolen 1999). Species utilizing the predator protection strategy pay a cost due to aggression and/or predation from their host to avoid a greater cost due to predation elsewhere. For example, many species of ground-nesting Arctic geese preferentially nest in close association with predatory raptors such as the snowy owl (*Nyctea scandiaca*) and the peregrine falcon (*Falco*

peregrinus), despite occasionally being preyed upon or harassed by these aggressive hosts (Tremblay et al. 1997, Quinn et al. 2003). Those hosts defend their nest sites aggressively from the Arctic fox (*Alopex lagopus*), an effective predator of ground-nesting birds. Therefore, by paying a relatively small fitness cost to their host, these geese avoid a greater cost due to predation than exists elsewhere. A similar example as reported from central Italy where woodpigeons (*Columba palumbus*) nest with territorial hobby falcons (*F. subbuteo*). Both natural and artificial woodpigeon nests located far from hobby nests experience greater predation and reproductive failure than nests located closer to hobby falcons (Bogliani et al. 1999). Woodpigeons used this strategy despite making up 15% of the diet of hobby falcons (Bogliani et al. 1999).

The Predator Protection Hypothesis assumes that more timid species chooses to nest near the more aggressive species. However, an apparent association may occur between aggressive and timid species that use similar nesting substrates and foraging areas. One would expect this relationship to be magnified in cases where these habitats are of a rare or fragmented nature due to an absence of alternative nest sites. This hypothesis is often referred to as the Similar Habitat Selection Hypothesis (Orians and Wilson 1964, Quinn et al. 2003). Most species that have been identified as using the Predator Protection Strategy have been studied in relatively homogeneous environments. The Similar Habitat Selection Hypothesis has often been rejected in those cases simply due to there being many alternative nest sites of equal quality that are relatively free of the apparent host (Bogliani et al. 1992, 1999). The difference

between the Similar Habitat Selection Hypothesis and the Predator Protection Hypothesis is that an individual using the predator protection strategy must directly benefit from the association with its aggressive host (Quinn et al. 2003). Many methodologies can be used in building a case for the Predator Protection Hypothesis being in part responsible for an apparent nesting association between species, but to test it implicitly, a direct fitness benefit for the associate must be quantified.

Identifying that a given species' population trend, productivity and nest site selection are closely related to various key predators on the ecological landscape is not a new idea. However, theory directed toward understanding that key predators can create a refuge for prey species on that same landscape is in its infancy. Most predator protection nesting associations identified to date have resulted from studying biologically simple systems such as the Arctic tundra or in fairly uniform habitats containing several populations such as large tracts of woodlot (Bogliani et al. 1999, Quinn et al. 2003). In those simple habitats, identifying and directly measuring habitat choice and spatial relationships between species is much easier because there are relatively few other variables to consider. Most biological systems however are complex, consisting of a mosaic of habitats of differing quality and species composition. In those cases we must consider several other variables related to fitness such as the access to available forage, the competition among individuals, and the fragmented nature of the habitat. The next logical step in furthering predator protection theory is to identify and understand its importance in those more complex systems. I

examined a previously unidentified nesting association between the Pacific great blue heron and its primary predator, the bald eagle, in the Lower Fraser Valley. In doing so, I explored the next step in nest association research by applying the predator protection hypothesis to a biologically complex system.

Study System and Species

The Pacific great blue heron is a non-migratory, lowland subspecies only found in the coastal ecosystems of the Pacific Northwest of North America (Butler 1997). It nests from February to August and disperses locally for the non-breeding season. Herons in this region nest both individually and colonially with colony size varying from just a few to over 1000 nesting individuals (Butler 1992, Vennesland 2000, Kenyon 2007). It is generally believed that heron colony location and size are highly tied to the proximity and quality of aquatic foraging sites (Gibbs and Kinkel 1997). Urbanization and agricultural land use characterize the region and, therefore, the nesting habitat available to herons has decreased in amount and become more fragmented over the past several decades (Butler 1997). Currently, biologists are concerned because both the overall population size and the reproductive success of Pacific great blue herons possibly have shown a decline in the last 30 years (Vennesland 2000, Vennesland and Butler 2004). Due in part to this trend, the Pacific great blue heron has been declared a sub-species of special concern by the Committee On The Status of Endangered Wildlife in Canada (COSEWIC). This designation has made heron research and conservation a national priority in Canada.

Vennesland (2000) concluded that heron reproductive failure in the Pacific Northwest was highly correlated with and, therefore, related to the incursion of their colonial nesting sites by bald eagles. Bald eagles are considered the primary predator of herons in the region, being occasionally observed to depredate heron nests of eggs, chicks and sometimes adults (Norman et al. 1989, Vennesland and Butler 2004). Eagles nest along the shore and rivers of the region from about February to July. Large numbers of non-breeding adult and juvenile eagles are also present at this time. From August to October, most eagles depart the region for salmon spawning streams in Alaska and northern BC. Eagles return to the coastal rivers in November and December coinciding with salmon spawning and significant waterfowl migrations in the region. Bald eagle populations have been increasing in the Pacific Northwest over the last thirty years, having been released from previous lows mainly due to poisoning from pesticides, such as DDT, which were banned in the late 1960's (Gerrard and Bortolotti 1988, Buehler 2000, Elliott and Harris 2001). This trend is expected to continue and has heron biologists questioning the sustainability of the Pacific great blue heron on the current ecological landscape (Vennesland and Butler 2004).

An apparent paradox has recently arisen in which many heron colonies have located within 100 m of nesting pairs of eagles (Vennesland 2000). For example, in 2004 one of the largest heronries (> 400 pairs) in the region abandoned its nesting site in Point Roberts, USA after bald eagle incursions began (R. Butler, pers. comm.). Curiously, this colony relocated to a nearby

coastal site a few kilometres away at the English Bluffs in Tsawwassen inhabited by an active pair of nesting bald eagles. The herons have now taken up residency around and within the same tree as their primary predator. A large heron colony near Chilliwack has existed adjacent and even around a bald eagle territory since at least 1990 (J. Elliott pers. comm.).

Coastal bald eagles are predators feeding opportunistically on fish, birds, mammals and carrion throughout the year (Knight et al. 1990). During the breeding season bald eagles establish territories encompassing productive foraging grounds. Typically bald eagles defend these breeding territories from conspecific individuals, thereby limiting access to their mate and avoiding competition for resources (Gerrard and Bortolotti 1988, Mahaffy and Frenzel 1987, Stalmaster 1987, Buehler 2000). Herons nesting colonially with bald eagles may pay a lower cost due to predation by taking advantage of the territorial nature of their host. As posited in the Predator Protection Hypothesis, herons may choose to pay a relatively small cost to one nesting pair of eagles to avoid a greater risk due to predation from other territorial or non-breeding eagles. Alternatively, heron nesting habitat in the region where this association occurs may be fragmented or saturated with eagles to the point where a better alternative is not available and an apparent association results simply from similar habitat selection.

As eagle populations increase, it is possible that the predation danger experienced by the Pacific great blue heron will also increase. Understanding how the behaviour and subsequent habitat choice by herons will change as

predation danger increases is important in making population predictions and conservation decisions. Current heron conservation measures in the region include protecting tracts of habitat for herons and dedicating them as ecological reserves. We need to identify the habitat that is currently important to herons in the region and in the future. A recent study used theoretical ecological modelling techniques in predicting heron nest site selection on the coast of British Columbia (Kenyon 2005, Kenyon et al. 2007). The models predicted that the predator protection hypothesis may be a viable strategy used by coastal herons, however the author pointed to a lack of local ecological information related to bald eagle nesting ecology, territorial behaviour and their apparent nesting interactions with Pacific great blue herons in making further conclusions or developing more effective habitat selection models.

Several key assumptions and predictions can be described and examined in the interest of identifying the Predator Protection Hypothesis as a possible mechanism in explaining an apparent nesting association between the great blue heron and the bald eagle in the Pacific Northwest. In Chapter 2 of this thesis, I explore the reproductive success and population increase of bald eagles in the Lower Fraser River Basin to characterize factors that likely contribute to changes in decision-making among herons in this region related to predation risk. In Chapter 3, I examine the territorial nature of the bald eagle to understand the defence propensity of bald eagles. In Chapter 4, I examine the reproductive success of Pacific great blue herons in the Fraser River Valley and Delta in relation to their distance from nesting bald eagles and I describe an observational

case study to characterize the costs and benefits of heron-eagle nesting associations. In Chapter 5, I summarize and discuss the implications of my research.

I studied eagles and herons from February through June 2005 and February through June 2006. My study area was the Upper and Lower Fraser Valley between Hope and Delta, British Columbia (Figure 1-1). The area is characterized by fragmented woodlots along the Fraser River and is situated among rich farmlands and urbanized areas with estuarine and marine beaches and mudflats present where the Fraser River joins Georgia Strait in Delta. Bald eagles and great blue herons both rely on productive lowland and coastal aquatic habitats over much of their range (Gerard and Bortolotti 1988, Butler 1997, Butler et al. 2000). Great blue herons in the Fraser River Valley and Delta generally nest in close proximity to key aquatic foraging habitats such as tidal mudflats with eelgrass habitat such as that on Robert's Bank and Boundary Bay or productive stretches of the Fraser River and its tributaries. A recent diet study of bald eagles nesting on the coastline showed that fish comprised the greatest percentage of prey deliveries among studied nests (Elliott et al. 1998, Gill and Elliott 2003, Elliott et al. 2005). Bald eagles also rely on relatively large populations of resident and migratory waterfowl that are present because the Fraser River and Delta is a key stopover site and winter destination on the Pacific Flyway.

Bald eagles and herons differ greatly in their choice of substrate for nest building. Bald eagles nest in large mature or standing dead trees such as black

cottonwood (*Populus balsamifera trichocarpa*) or coastal Douglas-fir (*Pseudotsuga menziesii menziesii*) that are capable of supporting the massive weight of their nests while providing a suitable vantage point to survey their territory (Gerrard and Bortolotti 1988). These trees may or may not be part of a larger woodlot or undisturbed shoreline with many nests in the region in a single or standing row of trees between fields or on the edge of roadways and private properties. Herons in the region appear to be far less selective, nesting in many different live, vigorous shrubs and trees varying in height from a few meters or less to those similar in height selected by eagles. As with eagle nests, herons in the region nest in as little as a few standing trees, small patches of shrubs and cottonwoods, and large woodlots.

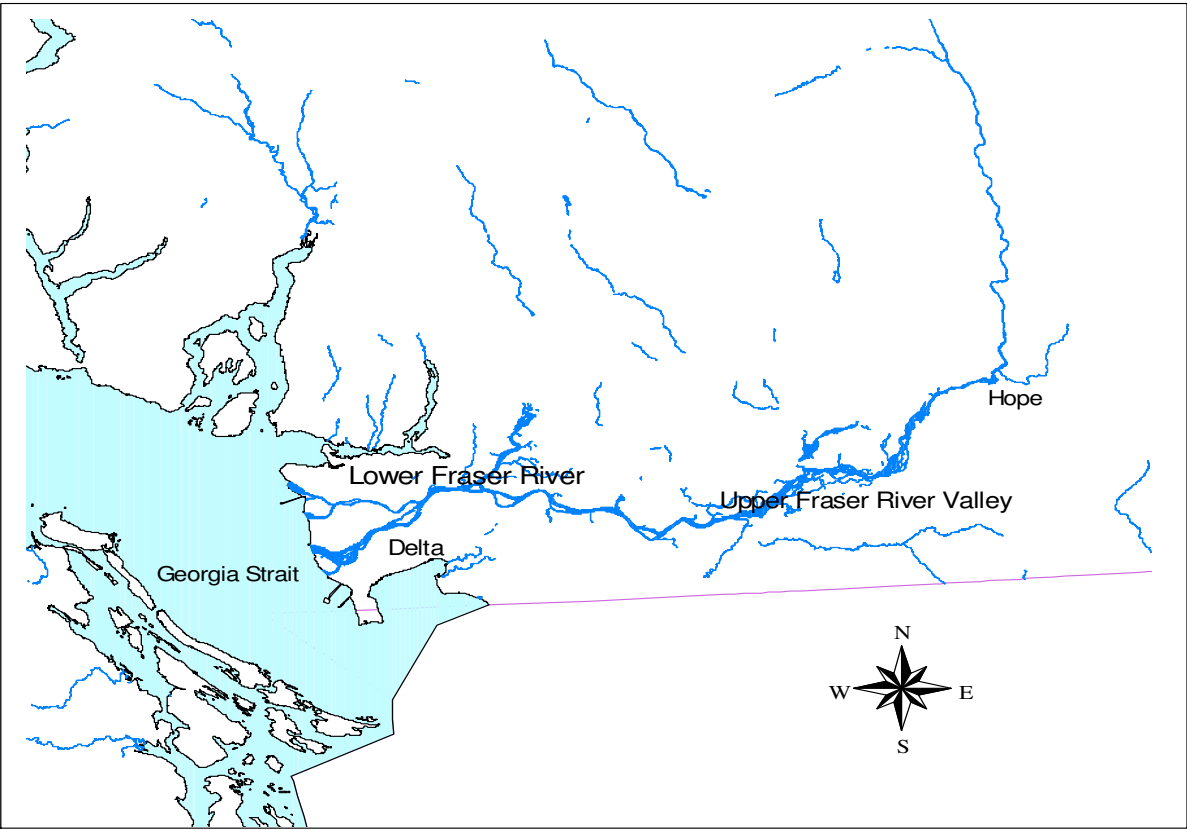


Figure 1-1: Upper and Lower Fraser River Valley in southwestern British Columbia.

CHAPTER 2: POPULATION GROWTH AND REPRODUCTIVE SUCCESS OF BALD EAGLES IN THE LOWER FRASER RIVER

Introduction

The bald eagle (*Haliaeetus leucocephalus*) is a major predator of the Pacific great blue heron (*Ardea herodias fannini*) in British Columbia and Washington (Norman et al. 1989, Vennesland 2000). Bald eagle abundance, distribution and reproductive success are thought to be important factors in determining great blue heron nesting strategies (Kenyon et al. 2007). In this chapter, I describe bald eagle population trends and reproductive success and their potential influence in great blue heron nest site selection and use of a predator protection strategy (Chapter 1).

Bald eagles and other raptors have increased through much of their range in North America following the ban of DDT and other pesticides in the late 1960's (Gerrard and Bortolotti 1988, Buehler 2000). Bald eagle population increases have been hypothesized to have resulted in increased abandonment and lower reproductive success among their prey species including the 'Pacific' great blue heron on the British Columbia coast (Vennesland and Butler 2004).

Hérons may respond to increased risk of predation from bald eagles by altering their nesting strategies (Kenyon et al. 2006). The Predator Protection Strategy (Chapter 1) posits that colonial-nesting Pacific great blue herons may

benefit from nesting with a breeding pair of territorial bald eagles providing the danger experienced directly from their host is lower than that which could be experienced by nesting elsewhere. As the local population of bald eagles increases, it is likely that the predation risk experienced by herons nesting in the region also increases. Therefore, an increase in the local bald eagle breeding population has the potential to increase the benefit of using the predator protection strategy among locally nesting Pacific great blue herons.

Food availability to nesting bald eagles may also influence the level of predation risk experienced by nesting herons. When food is scarce, eagles might resort to preying on herons but not without risk for bald eagles. Herons defend nests by using their beaks to jab at intruding eagles (Chapter 4). Eagles nesting in habitats with high prey availability may be less inclined to rely on herons as their primary food source. Food availability is an important factor in reproductive success of raptorial birds (Newton 1979, Gerard and Bortolotti 1988). By extension, great blue herons are therefore more likely to benefit from the predator protection strategy where a breeding pair of bald eagles experience high reproductive success.

In this chapter, I quantify the change in the number of nesting pairs of bald eagles over time and their reproductive success in the Fraser River Valley, British Columbia. I seek to characterize these factors related to bald eagle population ecology that may influence habitat selection and nesting strategies among Pacific great blue herons in the region.

Methods

Study Area and Species

The study was conducted in the Fraser River Valley in south-coastal British Columbia, Canada (Chapter 1). The study area was divided into the Upper Fraser Valley east of Aldergrove to the City of Hope and the Lower Fraser River from Langley to Georgia Strait (Figure 2-1). Bald eagle nest presence, activity and reproductive success were surveyed annually from 1987 through 2006 in the Upper Fraser Valley and 1994 to 2005 in the Lower Fraser Valley (J. Elliott, unpubl. data). General information on the study area and the biology of the bald eagle can be found in Chapter 1.

Bald Eagle Nesting Activity and Reproductive Success Surveys

I used historical data from helicopter surveys of nesting bald eagles conducted by Environment Canada (J. Elliott, unpubl. Data in collaboration with K. Stenerson of Kruger Forest Products) to quantify and monitor nest activity and reproductive success in both the Upper and Lower Fraser River Valleys. Those surveys involved a flight in a Bell 206 Jet Ranger helicopter during the incubation period (February-April) to search for nests in the study area and evaluate nesting activity, and a second flight during the final stages of chick rearing (June/ July) to evaluate nesting success. I participated in those flights in 2005 and 2006. We searched for nests and recorded breeding activity during the incubation period in early April before leaf-out. Once a nest was located, we confirmed the presence or absence of an incubating or attending adult bald eagle and recorded the position of the nest with a Global Positioning System (GPS). In the interest of

limiting disturbance at the nest, pilots were instructed to remain as high and at as great a horizontal distance from nests as possible while still allowing a view of the nest. If necessary, observers used binoculars to identify characteristics and activity at the nest. Nests were considered to be active if there was an adult in incubating position or if the nest was clearly tended and an adult was perched within 100 m. Nest searches consisted of flying stands of suitable trees within the study area such as those bordering agricultural properties, within woodlots and various water bodies following a similar route each year. The survey effort increased over time in the Upper Fraser Valley to include additional areas to that shown in Figure 2-1. To limit potential bias I have only considered the study area and nests indicated by John Elliott (pers. comm.) as occurring within the core study area that was flown consistently each year.

Data Analysis

Analysis of nest activity and reproductive success data was completed using JMP statistical software (Version 7). I totalled and plotted the number of active nests per year for the duration of the study and reproductive success for each region each year and tested for statistically significant trends using bivariate fit analysis.

Results

Active Nests

The number of active nests counted in the Upper Fraser Valley survey grew from a total of 10 active nests in 1987 to 36 in 2006, yielding an average

growth rate of 1.37 nests per year (Figure 2-2). In the Lower Fraser River there were 10 active nests in 1994 and 27 in 2005 for a total growth rate of 1.55 nests per year (Figure 2-3).

Reproductive Success

The average reproductive success measured as the number of fledging-aged chicks produced at active nests over the entire period of the study was 1.25 among 203 active Lower Fraser Valley nests and 1.31 at 420 active Upper Fraser Valley nests. For the purpose of this analysis, all nests within each year and between years were treated as independent samples. I plotted the reproductive success of actively breeding pairs in each of the two surveyed regions over the duration of the study, testing for significant changes through linear regression analysis. Bald eagles nesting in the Lower Fraser River did not show a significant linear trend ($P=0.8392$) in reproductive success over the duration of the study (Figure 2-4), while those nesting in the upper Fraser River experienced a significant ($P=0.0012$) decrease in reproductive success over the duration of the study (Figure 2-5). The total number of chicks produced in each region significantly increased (Figure 2-6 and 2-7).

Discussion

Analysis of historical data for the number of nesting pairs of bald eagles in the Upper and Lower Fraser Valley surveyed from 1987 and 1994, respectively, showed a significant increase in the number of nesting pairs over this period. These results concur with the overall trend in North America toward an increase

in the number of nesting bald eagles following the ban of widespread DDT use and the persecution of nesting bald eagles (Gerrard and Bortolotti 1988, Buehler 2000, Elliott and Harris 2001).

Counts of the number of nesting pairs were a by-product of surveys that were designed to evaluate reproductive success. There is a potential bias inherent within the survey design toward an increase in the number of nests as researchers return to existing nests each year, while also searching for and adding new nests. Habitat within the study area consists mainly of agricultural lands, fragmented urban habitats and linear strips of riparian forest along the Fraser River. Bias toward an overall increase in the number of nests is limited due to the nature of these habitats. Nests are readily located from the air within the study area leading to a high degree of confidence that nests present within the survey area are located each year. Considering bald eagles are the primary predator of Pacific great blue herons in the Fraser Valley, the increase in the number of breeding pairs of bald eagles likely resulted in more predation of great blue herons in the region. Eagle incursions and predation at heron nesting colonies were recorded infrequently during studies conducted at colonies in the 1980s (Norman et. al. 1989) and the early 1990's (R. Butler pers. comm.) while predation and incursions were 'common place' at some colonies during work conducted a decade later (Vennesland 2000). Should bias in determining the number of active nests be greater than is anticipated, it should does not affect my overall conclusion that the density of eagles and resulting risk for herons is greater now than in the recent past. Average reproductive success among bald

eagles in the Upper and Lower Fraser River Valley over the study period was greater than one chick per initiated nest (mean of 1.31 and 1.25, respectively). These values represent the upper range of average reproductive success recorded over time of bald eagles at occupied nests elsewhere in its range (Gerard and Bortolotti 1988, Gill and Elliott 2003, Jenkins and Jackman 2006). This relatively high reproductive success is likely attributable to the high availability of prey sources in the region combined with relatively stable weather conditions (Elliott et. al. 2006). The Fraser River Valley and Delta are major stopover sites on the Pacific Flyway for migrating birds and contains abundant freshwater and marine fish. These prey sources represent alternatives to Pacific great blue herons.

No significant trend in reproductive success was detected over the study period in the Lower Fraser Valley and a significant decline occurred in the Upper Fraser Valley eagle nests (Figs. 2-4 and 2-5). This result may suggest that optimal foraging habitats are occupied and additional eagles settling in the Upper Fraser Valley are occupying less than optimal habitats. As the number of breeding eagles increase within the bounds of the study area, a decrease in overall reproductive success may result as greater numbers of individuals competing for the available prey sources. This may be the case in the Upper Fraser Valley where suitable territories are tied to agricultural and forested areas along the Fraser River and other limited fish-bearing water bodies. Many suitable nesting trees are available throughout the Upper Fraser Valley, but their proximity to high quality food sources may be limited. While the reproductive

success in the Upper Fraser Valley has declined steadily, the rate of growth in the number of active nests remains relatively high and positive. This suggests that while optimal territories may be occupied, better alternatives may not be available elsewhere for young or immigrant eagles to initiate nest attempts.

In contrast, the Lower Fraser Valley has a higher degree of habitat fragmentation leading to fewer suitable nesting trees being available. Eagles are resorting to building nests in small trees and in some recent cases on transmission structures (I. Jones pers. observ.). Territorial competition for nest sites can be fierce and is magnified where suitable substrates are at a premium (Chapter 3). In addition, the core of the study area falls within proximity to marine, estuarine, freshwater and agricultural habitats that represent a higher diversity of available prey sources than that in the Upper Fraser Valley. Essentially, prey availability may be the largest factor limiting productivity in the Upper Fraser Valley study area while suitable nesting substrates may be the largest limiting factor to productivity in the Lower Fraser Valley. While differences in reproductive success trends may be explained by the above, overall both regions continue to experience increases in the number of nesting pairs where relative reproductive success values suggest abundant food availability.

A significant increase in the number of chicks fledged in each region likely results from the overall significant increase in the number of nesting pairs. It also suggests that neither habitat has reached saturation despite declining reproductive success over the study period in the Upper Fraser Valley.

Conclusions

In examining data collected during a long-term study of bald eagle reproductive success in the Upper and Lower Fraser Valley I was able to test two assumptions related to Pacific great blue herons potentially shifting to use the predator protection strategy in the region. First, the number of breeding pairs of bald eagles in the Upper and Lower Fraser Valley has increased significantly, thereby increasing the potential predation danger experienced by breeding Pacific great blue herons in the region. Although not quantified, it is likely that the number of non-breeding adult and juvenile bald eagles has also increased. Second, bald eagle reproductive success remains relatively high, likely indicating abundant food is present within occupied eagle territories.

Thus, Pacific great blue herons may benefit from altering their nesting strategy to nest in association with a single pair of territorial bald eagles, thereby counteracting the increased predation danger posed by non-territorial eagles. This strategy may be of greatest benefit where eagles experience high reproductive success because alternative food sources are abundant and the eagles do not rely on nesting herons and their chicks as a food source. The territorial behaviour of eagles is the topic of Chapter 3.

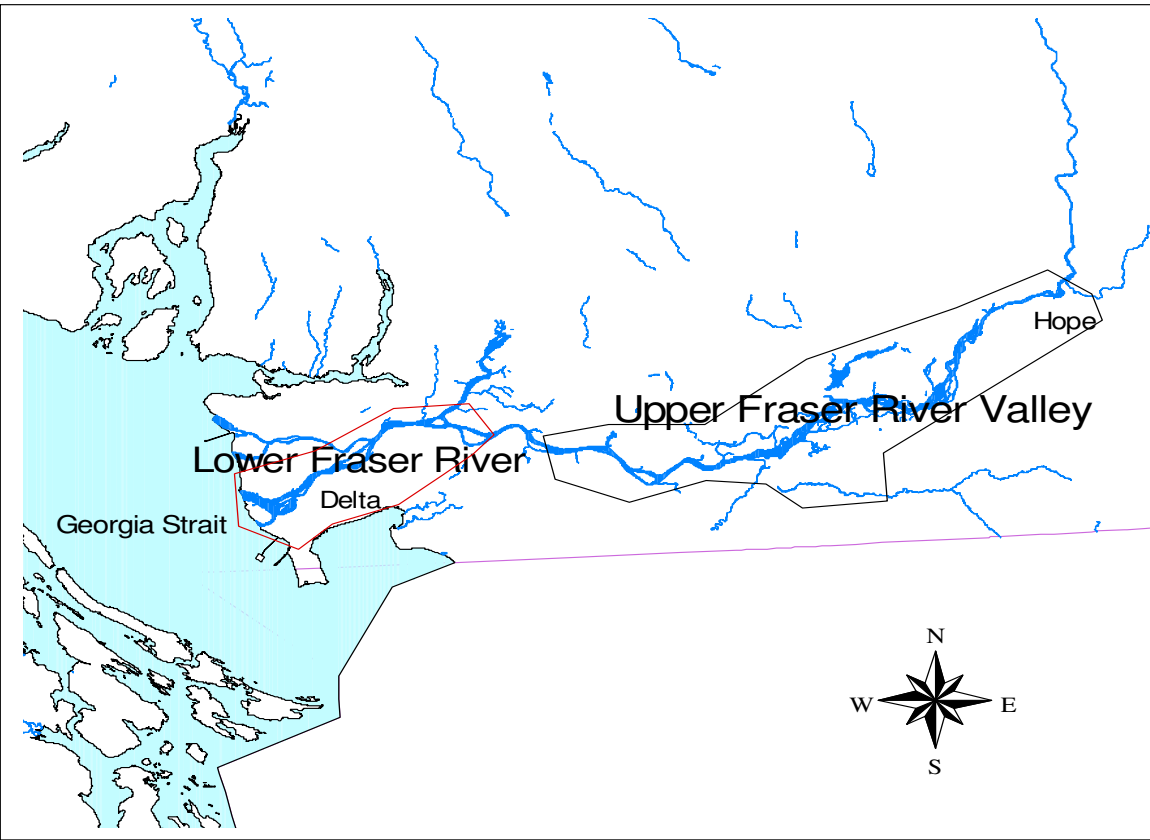


Figure 2-1: Surveyed area for bald eagles in the Upper and Lower Fraser Valley

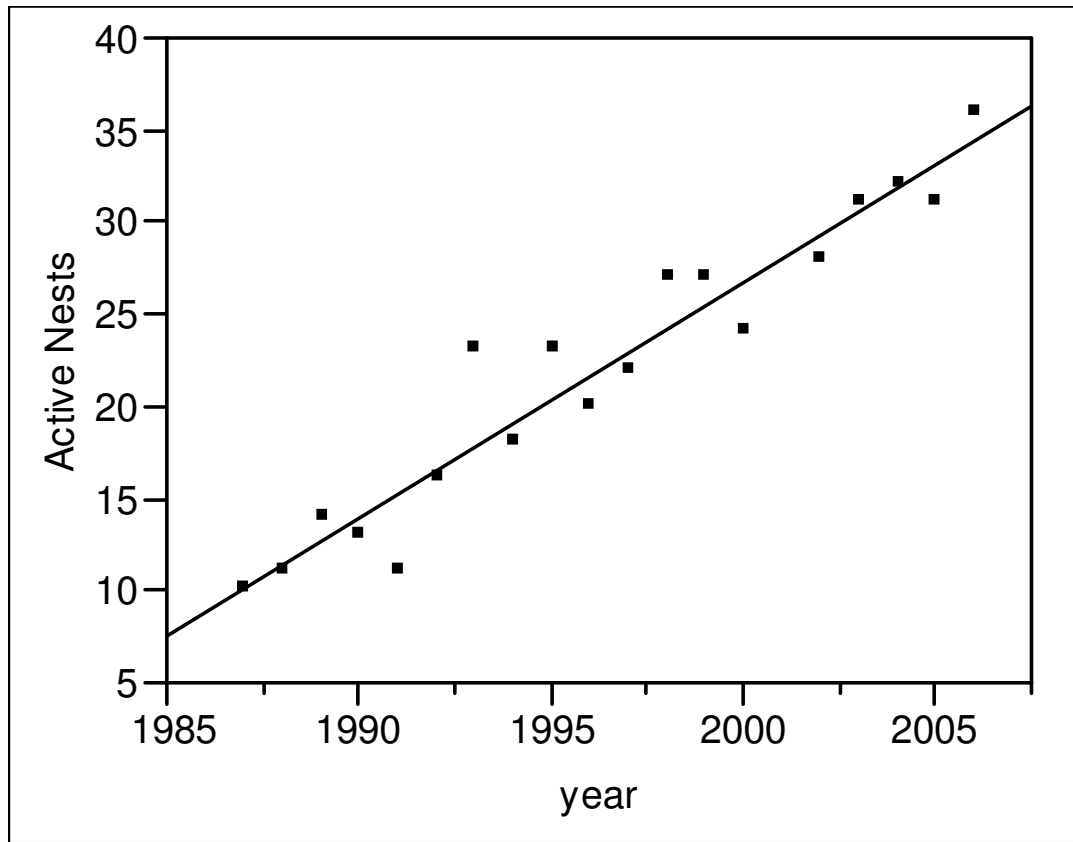


Figure 2-2: Change in the number of active nests surveyed in the Upper Fraser Valley from 1987-2006. The plot is a bivariate fit analysis of the total number of active nests observed (y axis) by the year that a given survey was conducted (x axis). The line represents the best linear fit through the data and is significant ($P < 0.0001$).

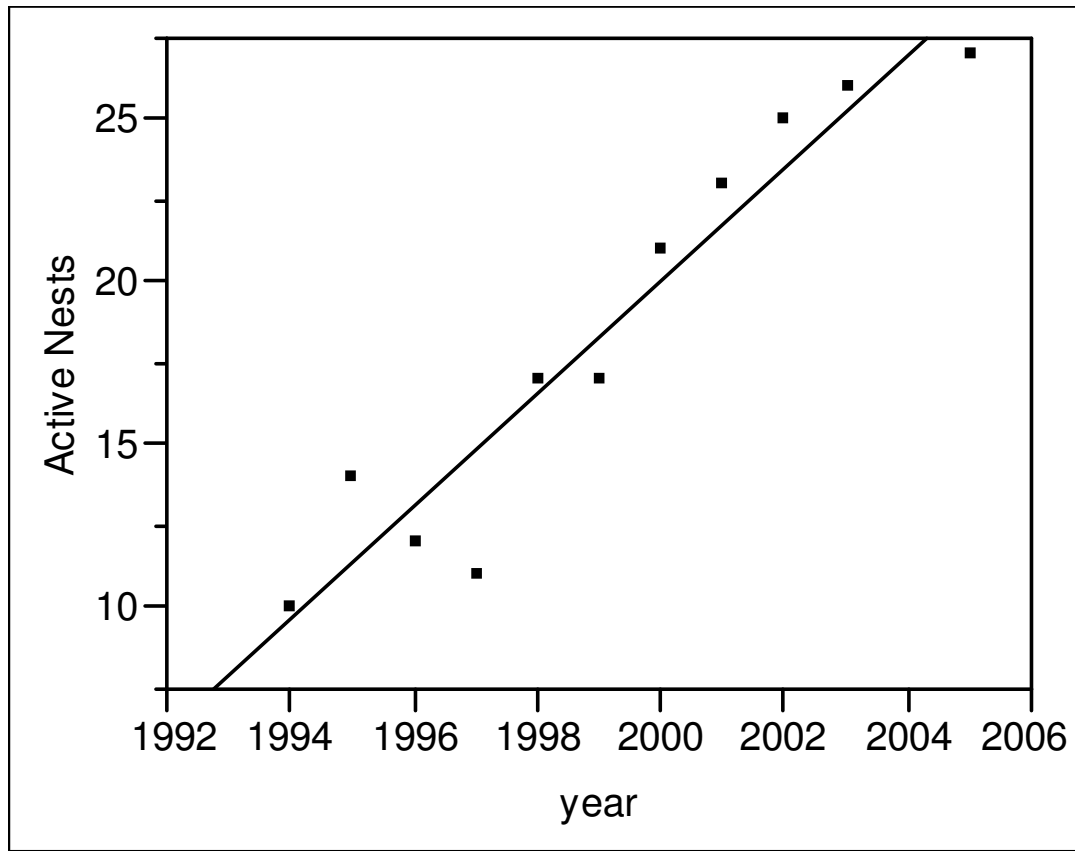


Figure 2-3: Change in the number of active nests surveyed in the Lower Fraser Valley between 1994 and 2006. The plot is a bivariate fit analysis of the total number of active nests observed (y axis) by the year that a given survey was conducted (x axis). The line represents the best linear fit through the data and is significant ($P < 0.0001$).

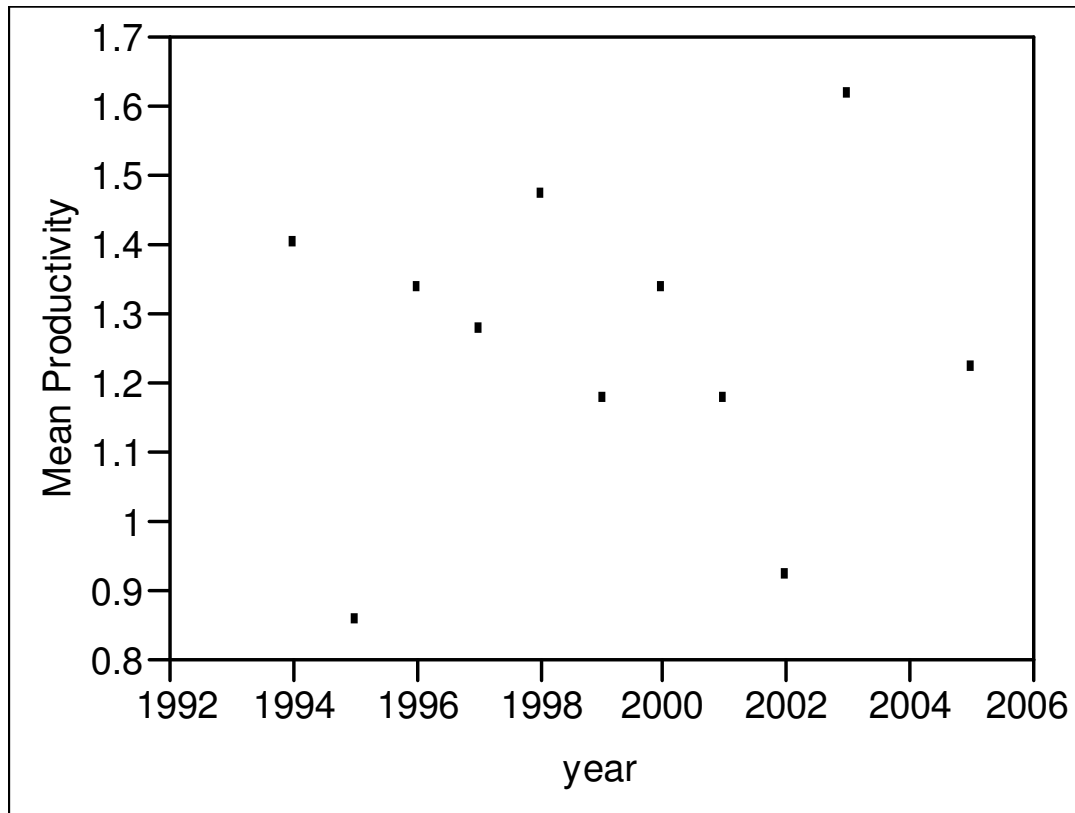


Figure 2-4: Change in the mean reproductive success (chicks fledged/ nest) in the Lower Fraser Valley over the duration of the study. The plot is a bivariate fit analysis of the mean productivity per active pair observed (y axis) by the year that a given survey was conducted (x axis). The best linear fit through the data was not significant ($P=0.8392$) and therefore is not shown.

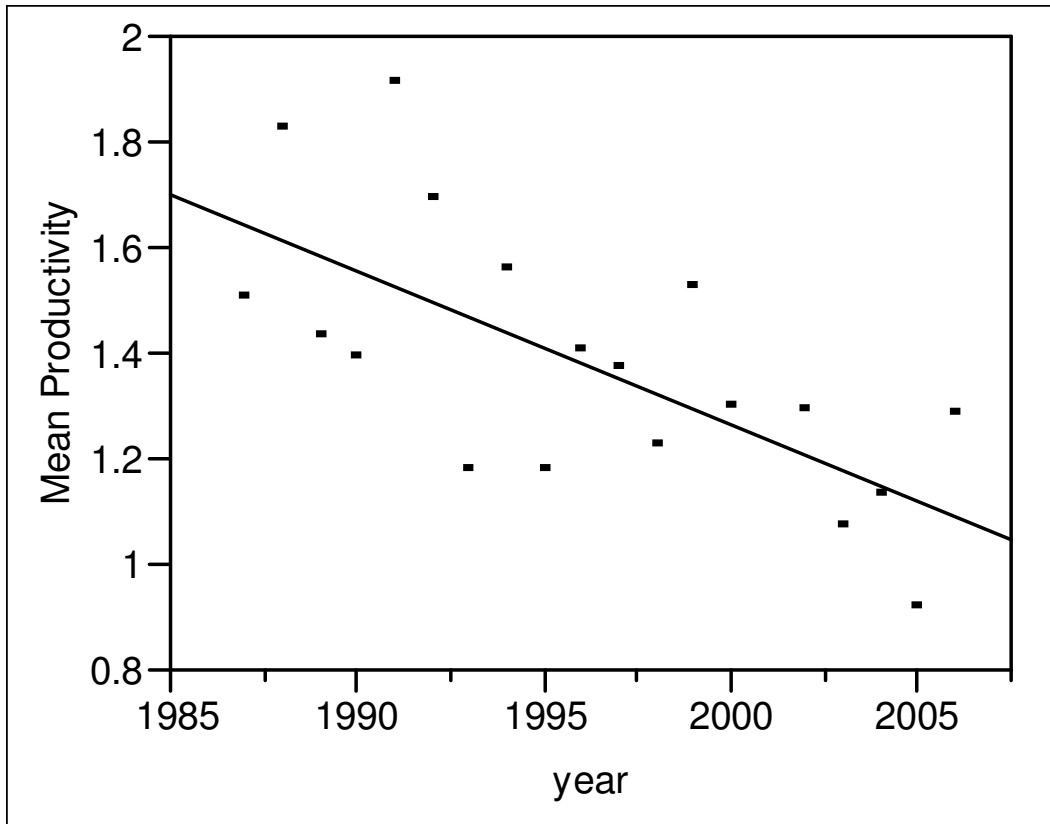


Figure 2-5: Change in the mean reproductive success (chicks fledged/ active nest) in the Upper Fraser Valley over the duration of the study. The plot is a bivariate fit analysis of the mean productivity per active pair observed (y axis) by the year that a given survey was conducted (x axis). The line represents the best linear fit through the data and is significant ($P=0.0012$).

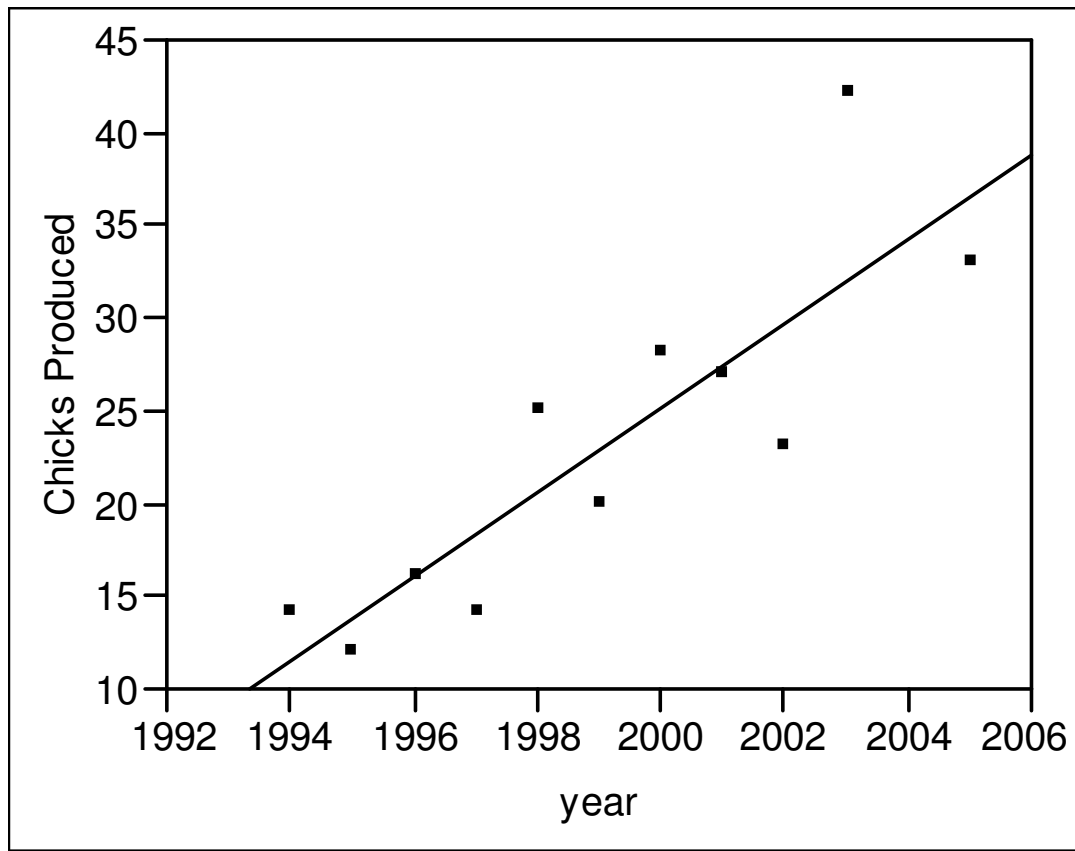


Figure 2-6: Change in the total number of chicks produced in the Lower Fraser Valley over the duration of the study. The plot is a bivariate fit analysis of the total number of chicks observed (y axis) by the year that a given survey was conducted (x axis). The line represents the best linear fit through the data and is significant ($P < 0.0007$).

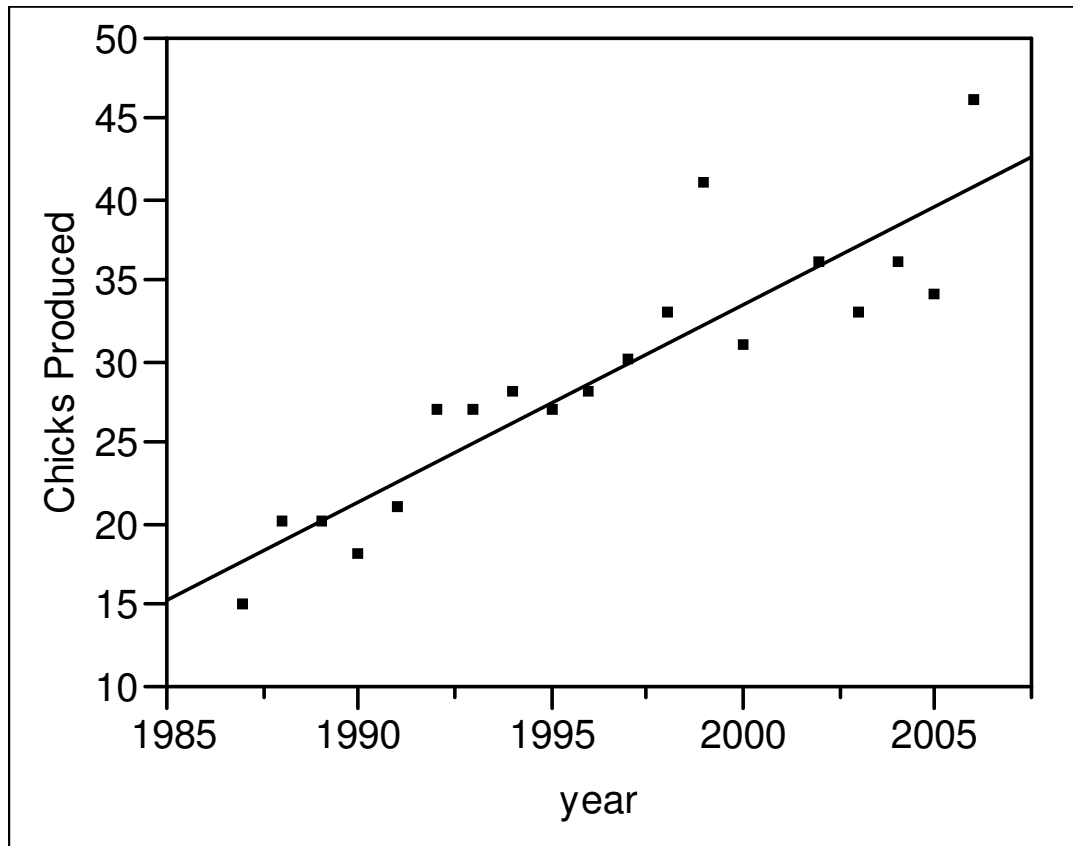


Figure 2-7: Change in the total number of chicks produced in the Upper Fraser Valley over the duration of the study. The plot is a bivariate fit analysis of the total number of chicks observed (y axis) by the year that a given survey was conducted (x axis). The line represents the best linear fit through the data and is significant ($P < 0.0001$).

CHAPTER 3: AN EXPERIMENTAL TEST OF BALD EAGLE NEST TERRITORIAL BEHAVIOUR IN SOUTHWESTERN BRITISH COLUMBIA

Introduction

The predator protection hypothesis (Chapter 1) posits that Pacific great blue herons (*Ardea herodias fannini*) nest in association with nesting bald eagles (*Haliaeetus leucocephalus*) whose territorial behaviour provide relative safety from other eagles. In this chapter, I combine results from an experiment with field observations to describe the territorial defence and size of bald eagle nest territories.

Most North American raptors, including bald eagles, are known to defend their nest sites from intra and inter-specific nest competitors during the breeding season (Newton 1979, Stalmaster 1987, Gerrard and Bortolotti 1988). Most of our understanding of bald eagle defence, however, is anecdotal (Mahaffy and Frenzel 1987). The few studies reported in the literature suggest that there are local and regional differences in the size of the defended area (Hancock 1970, Sherrod et al. 1976, Mahaffy and Frenzel 1987, Gerrard and Bortolotti 1988, Buehler 2000) and it is not clear what spatial range eagles defend. Eagles might defend feeding areas, nests sites, access to mates, or all three (Gerrard and Bortolotti 1988).

Bald eagles are generalist predators feeding on a variety of items including but not limited to fish, avian, small mammal, reptilian, invertebrate and carrion prey. The nature and availability of prey items in a given habitat likely determines whether raptors defend territories (Newton 1979). In habitats with high prey availability, raptors typically defend smaller territories than where food is less abundant. Some authors have speculated that bald eagles are likely to defend small territories or not at all in the Pacific Northwest as food is thought to be plentiful (Gerrard and Bortolotti 1988). One author speculated that eagles in the Pacific Northwest only defend a cone-shaped territory directly above the nest because the author did not observe defensive behaviour toward other eagles feeding on a seal carcass placed on the beach near the nest (Hancock 1970).

Bald eagles often nest in large trees that might be in short supply in some areas of the lower Fraser River Valley. Bald eagles invest a large amount of energy establishing a suitable nesting platform within a suitable nesting tree (Gerrard and Bortolotti 1988). Animals that invest heavily in obtaining a resource should spend considerable amount of effort in its defence if the cost of finding, procuring and building a new nest exceeds the cost of that defence. Where eagles are abundant, the availability of good breeding territories and nest sites capable of supporting a breeding pair diminish (Newton 1979, Gerrard and Bortolotti 1988). In these cases, many juveniles, sub-adults and unattached adults make up a large component of the non-breeding population heightening competition among individuals for access to prey and appropriate nesting sites. Nesting pairs on productive territories may reasonably have a higher propensity

to defend their nest site from other individuals than those with nests sites in poor territories.

In one of the few studies examining nest site and mate fidelity of bald eagles, Jenkins and Jackman (1993) reported high annual and inter-annual fidelity among both mates and nest sites. However, replacements of mates and pairs did occur in a few cases. In one case, an intruding female killed a nesting female and took her place in subsequent breeding seasons (Jenkins and Jackman 1993). This observation suggests that competition amongst conspecific individuals occurs and it can be intense. Georgia Strait and the Fraser River is used by all age classes of eagles including juveniles, sub-adults and unattached adults that likely pressure territorial holders for access to nest sites in current or subsequent seasons.

Male bald eagles also protect access to their mates by other male eagles (Gerrard and Bortolotti 1988). The occurrence of extra pair copulations (EPC's) in species of raptors previously thought to be monogamous was as high as 68% in one study (Mougeot 2004). Males combat these effects with frequent copulations and mate guarding. EPCs were more frequent among those species existing in densely populated areas than those that were dispersed. Considering that the region is used by all age classes including many unattached adult eagles, extra-pair copulations are likely a concern for territorial male eagles and may lead to a greater propensity to defend in the region. Therefore, it is not unreasonable to expect that eagles would defend differently against reproductively immature and mature eagles.

Defence propensity may fluctuate temporally through the breeding season. If defence toward adult eagles is driven by mate guarding, then the propensity to defend would likely subside after the fertile period of the female. Alternatively, if defence propensity toward adult eagles is driven by a requirement to protect the breeding site itself and/or subsequent mating opportunities, then defence would likely remain high throughout the breeding period. Defence may also fluctuate temporally with the demand for resources increasing as more energy is required with demands of the chicks and parental investment. In this case, one would expect the defence propensity toward juvenile eagles to increase as chick energy demands increase.

Many methodologies have been used to study raptor defence propensity. Often the inter-nest spacing between breeding pairs of the same species are used to define the defence boundaries between territories. This indirect measure of defence can be influenced by many other variables such as habitat suitability. Direct observations of aggressive behaviour toward other individuals by a nesting pair of raptors can also be used in gaining an understanding of the defence propensity of raptors. This methodology is anecdotal and often not sufficient to define defence boundaries. Eagles might use a suite of subtle cues between individuals to warn of possible intruders and become overtly aggressive only when these cues are ignored (Gerrard and Bortolotti 1988).

Few studies have measured the defence propensity of bald eagles directly or with the same methodology over time, making comparisons difficult to interpret. One exception is a study by Mahaffy and Frenzel (1987) who used

papier-mache models of an adult bald eagle to elicit territorial responses from nesting bald eagles. The authors tested the validity of this technique against responses elicited by a nesting pair toward a live captive eagle and a stuffed eagle and found no significant difference in defended distance between these treatments. The authors were able to obtain a direct measure of the average defended territory size defended from a decoy in Central Minnesota. Mahaffy and Frenzel (1987) gradually moved the decoy closer to the nest each successive day until a “call” response was noted. They assumed that a call was a response to a trespass within the defended distance. Most of the time in this study was spent recording a non-event and therefore, little information was extrapolated on the intensity of defence near and far from the nest. In addition, no control treatment was used so there was no measure of the background rate of calling at nests that were sampled or a clear definition of what constituted “defensive behaviour”.

The purpose of my study was to adapt methodologies pioneered by Mahaffy and Frenzel (1987) to directly measure the defence propensity of bald eagles in the Pacific Northwest. I used an experimental approach with artificial decoys which included controls to elicit territorial responses from nesting bald eagles. I also surveyed active nesting locations, recording observations of aggressive behaviour toward intruding individuals throughout the nesting season to complement my experimental results in measuring defence distance in eagles and to gain an understanding of the temporal fluctuation in nest defence. Measuring the distance and temporal nature at which eagles defend will assist in

predicting the distance and time constraints, identifying how herons may benefit from this territorial behaviour, and thus, test two key assumptions of the Predator Protection Hypothesis.

Methods

The study was conducted in the Upper and Lower Fraser River Valley in south-coastal British Columbia, Canada between 20 February and 7 July 2006. General information on the study area and the biology of the bald eagle can be found in Chapter 1.

Artificial Decoy Experiment

I directly measured bald eagle territorial defence by nesting pairs using an artificial decoy of an adult bald eagle in combination with audible eagle call playbacks. Twelve bald eagle nests in the Fraser River Valley and Delta were chosen from a pool of those surveyed annually for reproductive success over a 20-year period (See Chapter 2). I selected nests that had been consistently used by eagles over many years to reduce the chance that they would be abandoned. I surveyed each of these nests early in the breeding season during settlement, courtship and nest building to assess their suitability for conducting territorial observations and experiments. Nests were deemed suitable if they had an active pair of adult bald eagles attending the nest, were relatively accessible from the ground with adequate terrain and sight lines for experimentation, and where landowners allowed me to visit the nests.

Decoy Apparatus

I constructed decoys based on the dimensions of an adult female bald eagle measured from a prepared specimen in the Simon Fraser University Biological Museum. A fibreglass mold was taken from a decoy carved from high-density polyurethane foam. The mold allowed identical replicas to be poured quickly using two-part expanding polyurethane foam, in the event that decoys were destroyed during the experiment. A thin coating of fibreglass resin was applied to the surface of the decoy to seal it before sanding and painting with acrylic-based paints to resemble adult bald eagle plumage. A final coat of sealer was applied to waterproof the decoys. Decoys were affixed in a perched position to the top of a 3-meter long black PVC pole that could be broken down into sections for transport. In the field the pole was anchored to the ground using stabilizing twine and spikes and placed in a prominent position above ground vegetation visible to the nesting pair. A tubular drop curtain placed over the decoy was tripped remotely to reveal the decoy when the experiment commenced.

Call Playback

Call playback was conducted near the decoy to further mimic an intrusion by eagles near active nests using a 40-watt horn speaker, a 20-watt amplifier and a portable CD player. All but the speaker was concealed in a sealable plastic brown tote. A repeating loop of bald eagle calls was created using calls from a commercially published CD (Peterson 2005). This loop consisted of a “dead air” period before calls started so as not to elicit responses or draw attention to the

apparatus before I could return to my observation position. The calls ran for 20 seconds every five minutes with “dead air” between each calling bout for the duration that the decoy was presented.

Study Design

The experiment included decoy displays during the incubation period at 3 distances: <50, 100, and 200 m and a control treatment at <50 m. Control treatments consisted of a black block displayed in the same manner as decoy treatments with call playback apparatus set out but not activated. I conducted 9 controls, and 8 treatments for <50 m, 7 for 100 m and 7 for 200 m, respectively. The order and type of treatment were randomized for each nesting location with no nest receiving a duplicate treatment. The duration of each treatment was 1.5 hours. The number of resident eagles present, the behaviour of each individual during the experiment, and the time when each of these behaviours occurred was recorded. Presentations were conducted when one or two eagles were present at or near a nest. For the purposes of standardizing frequency of response between treatments, only the resident that responded with the greatest frequency and intensity during a presentation is reported.

Nests were allowed a cooling-off period of 5 days between successive treatments to minimize potential stress to the nesting pair. I also did not conduct decoy presentations when it was raining to minimize exposure of eggs to cool temperatures should incubating individuals respond by leaving the nest.

Natural Territorial Disturbance Observations

I watched 12 active bald eagle nests used in the above experiment, noting the behavioural responses of the nesting pair to other bald eagles and raptors near their nests. I estimated the nearest distance that intruders approached the nest horizontally and vertically using a laser range finder to approximate distances (Bushnell Yardage Pro). I also noted the species, the age class where applicable and the behaviour of the intruder at the time of incursions. I assigned intruding bald eagles into either adult or juvenile age classes based on their plumage characteristics (McCollough 1989). I considered an eagle to be a juvenile and not of breeding age if it had an absence of a completely white head and tail.

The behaviours by eagles were defined as follows: Vocalization - an eagle in the nest or perched in the nest tree utters a call; Hop Hover- an eagle in a nest or a perched eagle in a nest tree, lifts off the tree and hovers above the nest; Flight – an eagle attending the nest flies from the nest circling the nest or flying toward or over the intruder before returning to the nest; Talons – an eagle attending the nest flies over the decoy dropping its feet to display its talons; Stoop – an eagle attending the nest flies over the decoy and folds its wings dropping in elevation over the decoy. I assumed that this sequence of behaviours reflected increase agitation by the nesting pairs to the response.

All statistical analyses were completed using JMP statistical software (JMP Version 7).

Results

Artificial Decoy Experiment

During decoy and control presentations, bald eagles vocalized, hopped and hovered in flight 3-5 m above the nest, repeatedly circled the nest, flew directly toward the decoy and returned to the nest, flew directly over the decoy, dropped their talons displaying them over the decoy, and folded their wings to stoop over the decoy.

In total 167 individual behavioural events were recorded during decoy and control presentations at 12 nests. Of these 167 behavioural events, 55.7% were Vocalizations, 1.7% Hops and Hovers, 32.3% Flight responses, 6.5% Talon Displays and 3.6% Stoops (Figure 3-1). Resident eagles never physically contacted the decoy or control apparatus during the experiment.

During the 9 control presentations, resident eagles performed a single call and did not perform any other behaviours. Mean Calling during control presentations was significantly less frequent than during three treatment distances combined (Figure 3-2 and Table 1-1). A comparison of the frequency of responses at all nests is shown in Figure 3-3. There were no other significant differences among the mean response behaviour between treatments.

Eagles exhibited all 6 behavioural responses at 50 m, 5 responses at 100 m and 4 responses at 200 m (Figure 3-3). Calling was the most frequent response, Stopping only occurred with 50 m, and Hop Hover occurred at 50 and 100 m (Figure 3-3).

Natural Incursion Observations

Behaviours noted by resident pairs during incursions were similar to those displayed by resident eagles at decoy presentations. For the purposes of analysis, I ranked incursion events as inducing a response or not based on the presence or absence of any one of those “defensive” behaviours, as defined within the decoy experiment results above. Eagles responded to eagle intruders in 57.4% of the 298 intrusion events within 150 m vertical distance above their nests and 250 m horizontal distance from the nest. Contingency analysis using both a likelihood and Pearson test revealed significant differences among the response to the different classes of intruder ($P = <0.0001$). Adults responded more often toward other adults than toward immature eagles, and less often to other species. Resident bald eagles responded to intruding adult bald eagles in 75.0% ($n=79$), juvenile eagles in 50.7% ($n=219$) and non eagle intruders (red-tail hawks [*Buteo jamaicensis*], Northern harriers [*Circus cyaneus*] and turkey vultures [*Cathartes aura*]) in 17.1% ($n=117$) of the total respective intrusions recorded (Figure 3-4). When examining defence propensity toward each class of intruder by Julian date during the nesting season through logistic regression analysis, no significant trends were detected.

Eagles defend a three-dimensional air and ground space around their nests. I detected a significant and positive trend in defensive behaviours by resident eagles with horizontal ($P = 0.0405$) and vertical ($P = <0.0001$) distance from their nests (Figures 3-5 and 3-6). A downward deflection in response

occurs at about 800 m (Figure 3-5), suggesting that the territorial boundary is at least that far from a nest.

Discussion

My experimental results concur with Mahaffy and Frenzel's (1987) finding that bald eagles respond to artificial decoys in their territory. Further, by using a control treatment I was able to discern between background responses and defensive responses, thereby defining what can be considered a defensive response. Observations of these behaviours during actual intrusions in which residents effectively warned off intruders further strengthen my conclusions that those responses displayed toward the artificial stimuli were defensive behaviours.

During the experiment, resident bald eagles defended at significantly greater rates than control treatments and with statistically equal frequency among all other treatments (50, 100 and 200 m). My experimental results indicate that on average, bald eagles in the Fraser Valley defend their nest sites from other adult bald eagle intruders to at least 200 m from their nest site in horizontal distance.

The few references to bald eagle defence in coastal British Columbia indicated that defended distances were very small if they defended at all (Hancock 1970, Gerrard and Bortolotti 1988, Buehler 2000). My results showed clearly that eagles in the Fraser Valley defend an area around their nest. Analysis of natural incursion observations at active bald eagle nests indicates

that some bald eagles in the Fraser valley defend a territory from other eagles approximately 1000 m in horizontal distance and 250 m in vertical distance above their nests. These results are at odds with those reported by Hancock (1970) who reported that bald eagles in Coastal British Columbia defend an inverted cone directly above their nest and do not defend regions at horizontal distance from their nest. His conclusion arose from an experiment where a seal carcass was placed below an active bald eagle nest on the BC coast and other eagles were noted feeding on the carcass with no response from the resident pair. In that situation, the resident eagles might have been unable to chase off a large number of eagles. Gerard and Bortolotti (1988) hypothesized that bald eagles in the coastal region may not defend a territory from competitors or they might defend at a much reduced rate due to the vast food resources available in the region. My findings indicate that eagles studied in the region defended relatively large territory sizes similar to those reported by Mahaffy and Frenzel (1987) at inland nesting locations in Minnesota.

Resident eagles showed significant differences in response frequency toward adult eagle, juvenile eagle and non-eagle intruders. These results are consistent with predictions derived utilizing the theory of economic defense. Adult bald eagles represent a complete competitor to nesting residents because they likely compete for breeding sites, mates and food resources while resident eagles likely only compete for food resources with juvenile eagles. The extra level of defence devoted toward adult eagles over that shown toward juveniles likely reflects these differences. Therefore, it is likely that bald eagles protect

food resources in the region despite an abundance of prey. The low response to non-eagle intruders likely reflects the low level threat they pose to nesting bald eagles. Red-tailed hawks and turkey vultures occasionally eat herons (I. Jones Pers. Observ.) but rarely if ever eat eagle chicks. Therefore, the occasional defensive action by eagles likely reflects their view of hawks and vultures as food competitors.

The defence shown toward the age classes did not fluctuate with the progression of the breeding season. This result might occur if prey levels near the nest rose to compensate for the energy demands on adults to provision growing eaglets. I have no data to test this idea, but it seems unlikely that food became more numerous. Waterfowl populations in the region decline rather than increase during the eagles' breeding season (Butler and Campbell 1987). It is unlikely that the defence is mate guarding behaviour alone because the level of defence remained high long after the female's fertile period. The most parsimonious explanation is that bald eagles defend nests, although I cannot rule out that this behaviour may also be to reduce extra-pair copulation opportunities. Bald eagles compete for breeding sites and mates in order to have an opportunity to breed in subsequent years (Jenkins and Jackman 1993) and suitable nesting sites or the access to mates are limiting factors to local breeding populations of bald eagles in the region.

Conclusions

In addition to contributing to an improved methodology and new findings to the territorial literature for bald eagles, this study has satisfied two key

assumptions required in examining the predator protection hypothesis as a possible mechanism in explaining an apparent nesting association between the Pacific great blue heron and the bald eagle in the Pacific Northwest. First, I showed that bald eagles defend their nest sites against adult and juvenile bald eagles and to a lesser extent other raptorial predators for about 1 kilometre (km) around the nest. The propensity of this defence toward intruders, and therefore the benefit available to herons, declines with distance from the nest. Second, bald eagles continued this level of defence toward all intruders without fluctuation through the breeding season which coincidentally coincides with the heron breeding season in the region (Chapter 1).

In Chapter 4, I explore the hypothesis that territorial behaviour of resident nesting bald eagles in the Fraser River Valley and Delta forms a 1-km radius umbrella of predatory protection for nesting herons for the duration of their nesting season.

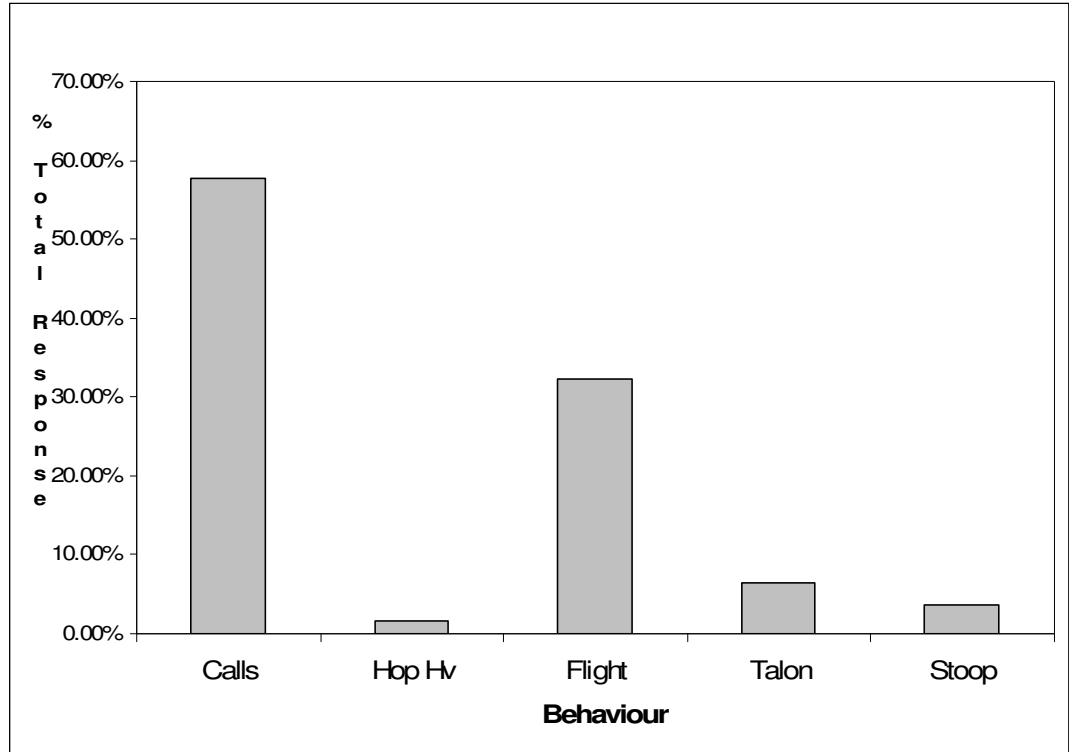


Figure 3-1: The frequency of the 167 responses by resident eagles recorded during all treatments in increasing rank order of assumed energetic expenditure by the nesting pair.

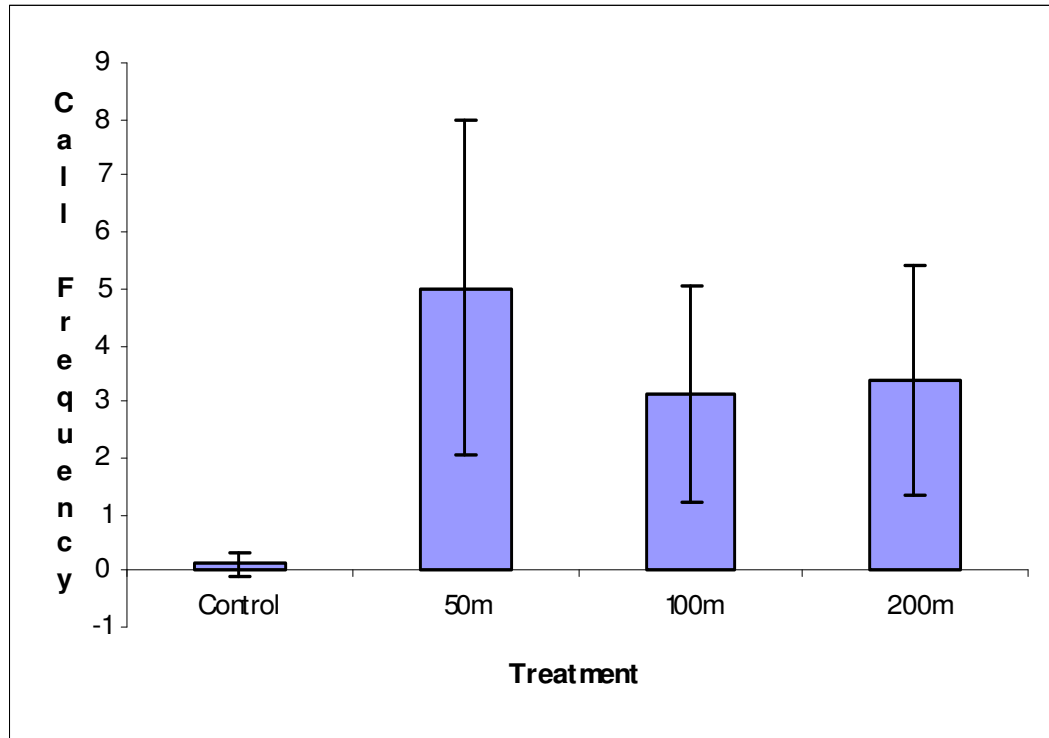


Figure 3-2: Mean territorial call frequency for each experimental treatment. Error bars are 95% confidence intervals.

Table 3-1: T-test results across all treatments for mean territorial calling frequency. Cross indicates the treatment that was crossed with the experimental treatment. CL stands for Confidence Limit. A P-Value of less than 0.05 indicates a significant result.

Treatment distance (m)	Cross	Difference	Lower CL	Upper CL	P-Value
50	C	4.8889	2.0084	7.7694	0.0016
200	C	3.2639	0.3833	6.144433	0.0277
100	C	3.0139	0.1333	5.894433	0.0409
50	100	1.8750	-1.0890	4.8391	0.2060
50	200	1.6250	-1.3390	4.5890	0.2714
200	100	0.2500	-2.7140	3.2140	0.8642

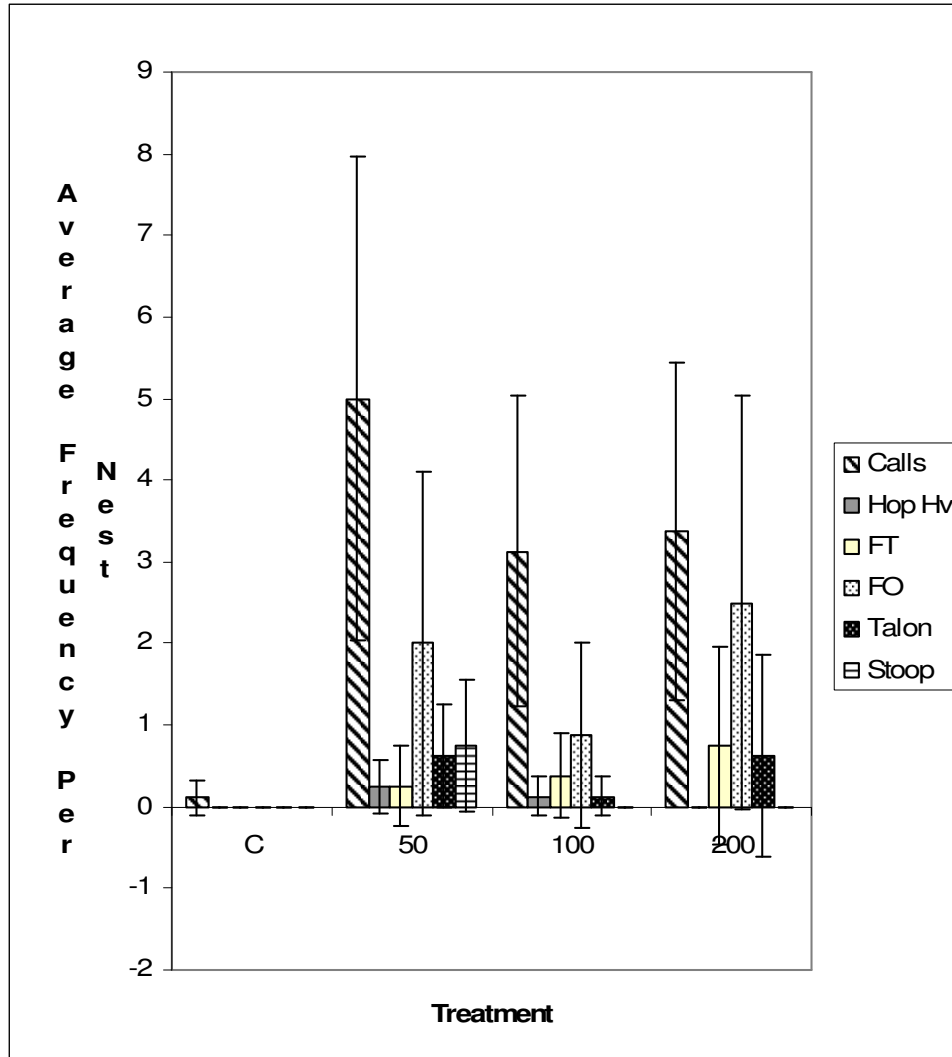


Figure 3-3: A comparison of the mean frequency of behaviours that resident eagles performed during each treatment. Hop Hv = Hop and Hover above the nest, FT = Fly toward the decoy and return, FO = Fly directly over the decoy, Talon = Perform a talon display over the decoy and Stoop = Eagles folded wings and rapidly lost elevation over the decoy. Error bars are 95% confidence intervals.



Figure 3-4: Contingency analysis for the presence or absence of defensive behaviour toward intruders. The y axis represents the frequency of defence expressed in percentage and categorical values are read by examining the area they occupy on the vertical scale. A = Adult Bald Eagle, J = Juvenile Bald Eagle and N = A Non Eagle Intruder. Y = Yes a response was recorded (blue) and N= No Response was recorded (red). Both a Likelihood and Pearson Test indicate significant differences in the response between these classes of intruder ($P = <.0001$).

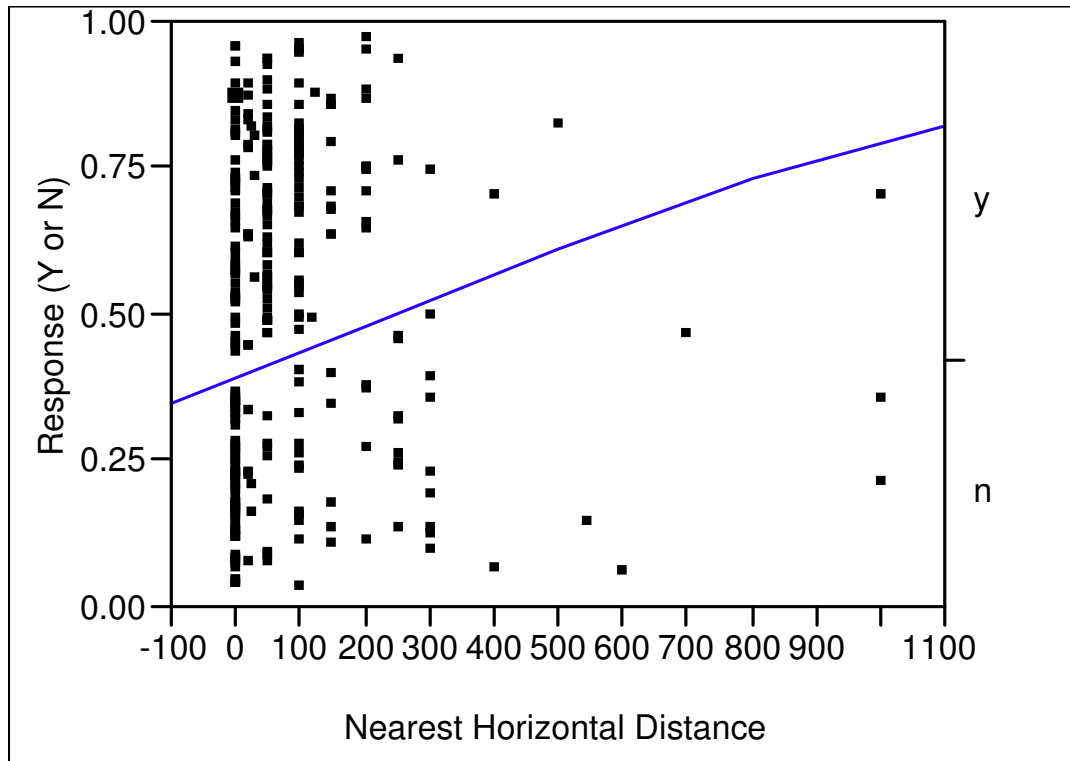


Figure 3-5: Logistic fit of response toward all eagle intruders with horizontal distance. The x axis represents the nearest horizontal distance that an intruder approached a resident nest. The y axis represents the frequency of defensive responses and is read by measuring the distance from the trend line to the appropriate axis. The expected frequency of a yes response is read by measuring the distance between the trend-line and 1.00. Individual data points are randomly jittered for each distance showing the total number of data points represented. A whole model Chi-square test indicates a significant result (P= 0.0405).

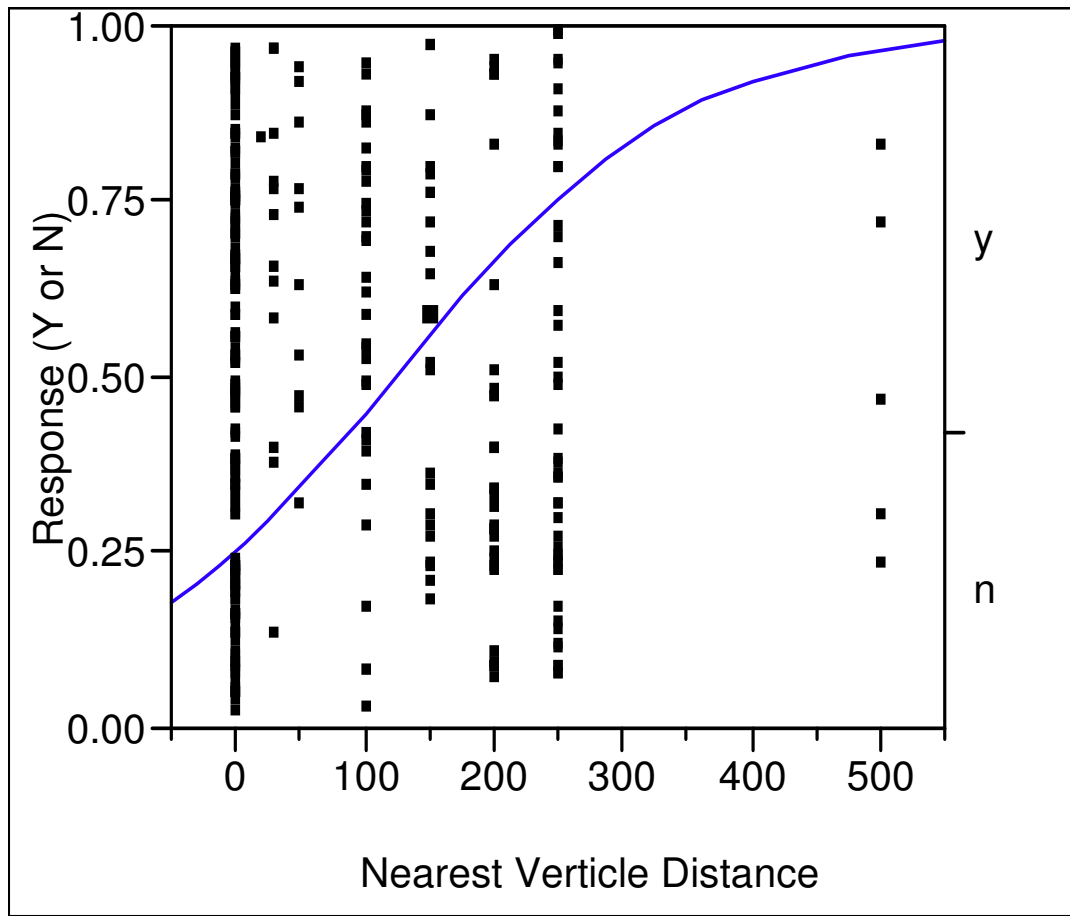


Figure 3-6: Logistic fit of response toward all eagle intruders with vertical distance. The x axis represents the nearest vertical distance in meters that an intruder approached a resident nest. The y axis represents the frequency of defensive responses and is read by measuring the distance from the trend line to the appropriate axis. The expected frequency of a yes response is therefore read by measuring the distance between the trend-line and 1.00. Individual data points are randomly jittered for each distance showing the total number of data points represented. A whole model Chi-square test indicates a significant result ($P = <0.0001$).

CHAPTER 4: HERON REPRODUCTIVE SUCCESS, COLONY SIZE AND NESTING LOCATION IN RELATION TO NESTING BALD EAGLES IN THE FRASER VALLEY AND DELTA IN BRITISH COLUMBIA

Introduction

Pacific great blue heron (*Ardea herodias fannini*) nest site selection is thought to be driven by factors influencing their reproductive success including predation by bald eagles (*Haliaeetus leucocephalus*) (Vennesland and Butler 2004, Kenyon et al. 2007). In this chapter, I examine reproductive success of herons in relation to their distance from active bald eagle nests to characterize the costs and benefits experienced by herons nesting in potential association with bald eagles in the Fraser River Valley and Delta.

The highest concentration of great blue herons in British Columbia nest in Georgia Strait and the Fraser River Valley (Butler 1997, Vennesland and Butler 2004). Generally, heron nest site selection and reproductive success is thought to be driven by several factors including proximity to high-quality aquatic foraging sites, the availability of suitable nesting substrate, colony size and proximity to human disturbance (Gibbs and Kinkel 1997; Vennesland and Butler 2004, Kenyon et al. 2007). Several studies have suggested that reproductive success may be related to incursions and predation by bald eagles sometimes causing colony abandonment (Norman et. al 1989, Vennesland and Butler 2004). Considering heron reproductive success in the region was suggested to be

significantly and negatively correlated with the frequency of eagle incursions (Vennesland and Butler 2004), one might predict that herons should seek to avoid nesting in proximity to eagles. Interestingly, herons have been noted to nest within 100 m from active bald eagle nests (Vennesland 2000). In 2004, a heronry located in Point Roberts, WA U.S.A was abandoned apparently following frequent eagle incursion (R. Butler pers. comm.). That colony subsequently relocated to a nearby coastal site a few kilometres away at the English Bluffs in Tsawwassen inhabited by an active pair of nesting bald eagles. The Tsawwassen Heronry at English Bluff is currently the largest colony in British Columbia with greater than 400 nesting pairs.

The Predator Protection Hypothesis (Chapter 1) posits that Pacific great blue herons nest in association with nesting bald eagles whose territorial behaviour provide relative safety from other eagles. A central prediction of the Predator Protection Hypothesis is that individuals using this strategy experience greater reproductive success than could be achieved elsewhere. In this Chapter, I examine both reproductive success and colony size of heronries related to their proximity to active bald eagle nests. I also report summary statistics from an observational case study at the Tsawwassen Heronry on the English Bluffs that recently re-located to nest in proximity to an active bald eagle nest. By examining the conditions and reproductive costs and benefits experienced by herons nesting in close proximity to bald eagles, I test central predictions of the Predator Protection Hypothesis.

Methods

Study Area Species and Colony Sites

The study was conducted in the Lower Fraser River Valley, Delta and Georgia Strait Basin in south-coastal British Columbia, Canada between 6 May and 29 June 2005, and 18 April and 24 June 2006 at a total of 15 great blue heron colonies (Figure 4-1). Colony locations were obtained from an inventory of known colonies (Vennesland 2000; Vennesland and Butler 2004) and information provided by Ministry of Environment and Canadian Wildlife Service. Fifteen colonies were visited in 2005 and 2006. I also documented interactions between a nesting pair of bald eagles and herons nesting together at the Tsawwassen Heronry located at English Bluff adjacent to the BC Ferry Causeway (Lat: 49°01'34", Long: 123°06'04") in 2006.

General information on the study area and the biology of the great blue herons and bald eagles can be found in Chapter 1.

Heron Reproductive Success Surveys

Reproductive success surveys were conducted using standardized protocols developed by the Heron Working Group adapted from methodologies used by Vennesland in 1998 and 1999 to determine the reproductive success of colonies (Vennesland 2000; Vennesland and Butler 2004). Heron colonies were visited between 1 and 3 times during the nesting season to count the number of nests, determine if they were active, count the number of associated adults and young, and determine the age of young. A nest attempt was considered to have

been initiated if an incubating heron was present. The number of young were counted from a vantage point beneath the nest using a telescope or binoculars.

Nesting productivity was estimated by observing samples of initiated nests that were each mapped and followed through the nesting season. Only the final result of each nest was used and therefore a failure was not recorded where a pair successfully re-nested. Sample sizes varied at each colony site depending on the size of colonies and the ease of viewing nests. All nests were sampled at small colonies (<50), but a sample of at least 30% of the total number of nests were taken at large colonies. Leaves on trees in the colonies obscured some nests in subsequent visits, usually precluding the use of all nests as samples. An initiated nest was one where incubation was observed. Nestlings were considered to have fledged when they perched on branches near the nest or when they were about 8 weeks old (Moul et al. 2001). Steps to minimize disturbance at nesting colonies specified in the protocol were followed closely and I am confident that these measures were sufficient to have no measurable impact on productivity of herons. Colonies were approached quietly to a vantage point outside of the radius of the colony to the point at which any heron responded by calling (about 10 to 100 m). No difference was seen in the behaviour of herons near and far from the vantage point and herons went about their normal nesting activities while observers were present.

The location of bald eagle nests in proximity to heron colonies was determined during surveys in 2005 and 2006 (Chapter 2), and from information provided by B.C. Ministry of Environment and Canadian Wildlife Service

biologists. In addition, searches were conducted within 500 m of each colony site prior to leaf-out.

Tsawwassen Heronry Observational Case Study

An observational case study was conducted at the Tsawwassen Heronry at English Bluff between 27 March and 29 June 2006. Observations of resident eagle defence behaviour against other bald eagles and raptors in proximity to their nest (Chapter 3), incursions causing disturbance of nesting herons, or the depredation of heron nests were recorded by an observer from a central vantage point 100 m from the colony. Observation periods varied in length and were rotated through available daylight hours spread throughout the survey period with each observation period lasting between 2 and 8 hours.

A disturbance of the colony was defined as any adverse behavioural response from more than one heron when an antagonist was present (Vennesland 2000, Vennesland 2004). A predatory disturbance was recorded if a predator was noted entering the colony and attempting to depredate an adult or nestling heron or heron eggs. Typically herons responded to predatory raptors by alarm-calling, challenging the intruder through posture or kicking or jabbing at predators, or flushing them from their nest (as described in Vennesland 2000). De-predation was recorded when a predator was observed to remove a chick from a heron nest.

In total 130 hours were spent observing the Tsawwassen Heronry at English Bluffs during the 2006 breeding season. I was able to discern the

resident pair of nesting bald eagles from other intruding eagles in the territory through distinctive features in their plumage and their high degree of fidelity to the nest site.

Results

Heron Reproductive Success Surveys

Active bald eagle nests were noted within 200 m of 3 colonies in 2005 and 2 colonies in 2006. The reproductive success of colonies close (i.e., < 200 m) to an active eagle nest and therefore inside the eagle territory (Chapter 2) was compared to colonies far from eagle nests (i.e., > 200 m from the colony). All nests were assumed to be independent samples. Reproductive success of those heron nests close to active nesting bald eagles was significantly higher than that heron nests far from active eagle nests in both 2005 and 2006 (Figures 4-2 and 4-3). Respective mean reproductive success of nests surveyed far from an active eagle nest was 1.04 (95% confidence = 0.25) and 0.93 (95% confidence = 0.14) fledglings per initiated nest in 2005 and 2006, while nests near an active eagle nest in 2005 and 2006 was 1.75 (95% confidence = 0.15) and 1.81 (95% confidence = 0.15).

In 2005, the Chilliwack Heronry had an active bald eagle nest within 200 meters of the colony through the duration of the heron breeding period. In 2006, the eagle nest failed after the herons had laid eggs when it was blown out of the tree by strong winds. The pair of bald eagles periodically rebuilt the nest and defended the territory but were absent for long periods. This event became a

natural removal experiment in successive years comparing reproductive success with and without an actively nesting bald eagle. These results were also compared to the average for all other colonies in each respective year to account for changes in reproductive success that could potentially be related to other factors such as differences in overall food availability between years. Mean reproductive success at the Chilliwack Heronry was 1.62 (95% Confidence = 0.33) fledglings per active nest in 2005 when eagles were present and 1.11 (95% Confidence = 0.23) in 2006 when eagles were absent (Figure 4-4). The reproductive success experienced by all other colonies went from 1.53 (95% Confidence = 0.15) fledglings per active nest in 2005 to 1.4 (95% Confidence = 0.12) in 2006 (Figure 4-4). Comparisons within and between years for reproductive success at the Chilliwack Heronry and all other colonies were not significantly different.

In total, 1165 nests were counted within 15 colonies surveyed that ranged in size from 3 nests to 400 nests. Of those nests, 70.8% (n=825) were in the three largest colonies and associated with long-term eagle nests within 200 meters of the colonies (Figure 4-5). These colonies are all 2 to 4 times larger than the largest colony without an active eagle nest within 200 m. Clearly, the majority of surveyed herons nest near eagles.

Observational Case Study at the Tsawwassen Heronry

A pair of bald eagles nested in the colony throughout the heron breeding season and raised two eaglets. Heron nests ranged from approximately 0 to 100 horizontal meters from the nest (some heron nests were built on the same nest

tree as the eagle nest). All herons nested at a lower elevation in the trees than the eagles. A total of 192 incursions by other bald eagles occurred during the 130 hours of observation (1.47 incursions/h) and ranged in intensity from over flights to attacks on adult herons and landing on heron nests. The resident pair of eagles responded territorially to 75% of all incursions by other bald eagles. Resident eagles responded to all attempts to attack herons or depredate nests in the colony by other eagles by physically chasing and hitting other individuals that did not leave the area immediately following calls or flight displays. These behaviours were identical to those I observed during my experimental test of territorial defence (Chapter 3). I did not observe herons depredated by non-resident eagles at the Tsawwassen Heronry at English Bluff.

Resident bald eagles made 8 attempts to depredate herons and succeeded on 4 occasions. Depredation of chicks by resident eagles occurred 0.03 times per hour of observation. In 7 of the 8 attempts, adult herons attempted to defend their chicks by kicking and pecking at the incurring resident eagle. On two occasions, a heron successfully defended the chicks by pecking the incurring eagle until it dropped off the lip of the nest. In total resident eagle incursions occurred 0.06 times per hour of observation. Other low-level overflights by resident bald eagles including circling over the colony in proximity to their nest; transiting to and from their nest site and perching in trees above the colony rarely induced a response among nesting herons within the colony.

Discussion

In examining reproductive success among herons nesting near and far from active eagle nests, I was able to test a central prediction of the Predator Protection Hypothesis to explain nest site or colony site selection by great blue herons. This prediction states that individual herons using nesting near eagles should experience higher fitness through increased reproductive success than could be achieved elsewhere (Quinn et al. 2003). My results indicated that herons nesting within 200 meters of active bald eagle nests experienced significantly higher reproductive success than those nesting greater than 200 meters from active bald eagle nests in both 2005 and 2006. In addition, reproductive success declined, although not significantly, following a natural temporary removal of a bald eagle nest at the Chilliwack Heronry for a single nesting season. While the eagle nest failed the eagles continued periodically defend their territory while building their new nest. This reduced level of vigilance and periodic presence in the territory likely limited the complete effect that would have been experienced had the eagles been completely removed.

Almost three out of four herons within the examined study area nested in colonies located within 200 m of an active bald eagle nest. Further, those colonies were at least twice as large as the next largest colony located far from an active eagle nest. A colony effect was not considered nor was a potential regional effect among colonies located in the Upper and Lower Fraser Valley in testing for significance among reproductive success. Birds nesting colonially often benefit from predation dilution, collective nest defence and increased

vigilance (Fuchs 1977, Burger 1984; Blanco and Tella 1997). If herons nest in large colonies, a predator avoidance benefit is likely received through a dilution effect during any one predation event. In addition, herons use a distinctive alarm call when predators approach the colony and therefore incur a benefit from increased vigilance. However, herons do not collectively defend nest sites from predatory attack (Vennesland 2000). It has been argued that a benefit of coloniality is reduced if large colonies are more conspicuous to predators (Kenyon 2005). It follows that those birds nesting individually or in small colonies would therefore be less conspicuous and likely experience fewer predatory attacks than those birds nesting in large colonies as a group. My results suggest that large noisy colonies can benefit when an eagle guardian nests nearby.

Benefits from colonial nesting and the Predator Protection Hypothesis should not be viewed as mutually exclusive. A large colony nesting in proximity to a territorial pair of eagles may be able to manipulate the number of predators that have access to their colony. This would diminish the costs associated with large colonies being more conspicuous to predators. Individual or small colony nesters are unlikely to adopt a predator protection strategy because being found by even one formidable predator would likely lead to breeding failure. Therefore, large colony sizes are a logical solution where herons choose to nest with bald eagles to benefit from their territorial protection. Not all eagle nest sites are ideal for herons. Essential is that the eagles nest in a rich feeding area that keeps them well fed without solely resorting to herons.

Resident bald eagles at the Tsawwassen Heronry at English Bluff aggressively defended their nest site and the surrounding heron colony from intrusion by other eagles. This degree of defence was sufficient to completely inhibit depredation of herons, eggs and nestlings during 192 incursions into the territory observed by other bald eagles. In fact, disturbance and alarm-calling by nesting great blue herons often alerted the resident bald eagles to the presence of other eagles before they appeared to notice intruders. This potentially benefits both species by allowing for more efficient defence of the territory from other eagles due to an increase in vigilance by the group. Herons appeared to pay little cost through increases in agitated behaviour and flushing due to movement and passive overflights by the resident bald eagle as might be expected based on heron behaviour recorded in previous studies (Vennesland and Butler 2004). Herons appeared to discern between intruding and resident eagles.

Depredation of herons by resident eagles at the Tsawwassen Heronry at English Bluff occurred at a rate of 0.03 chicks per hour. Depredation events were not observed during the incubation period. Heron chicks typically fledge after a 60-day rearing period. Assuming heron chicks are consistently vulnerable to depredation throughout the rearing period, that all chick rearing occurs simultaneously at the colony over a single 60-day rearing period, and that all depredation of chicks occurs over daylight periods that average 16 hours over the rearing period, these rates would result in a total projected number of $(60d \times 16h/0.03 \text{ chicks/h}) = 29$ chicks being depredated at the Tsawwassen Heronry at English Bluff during a single breeding season by resident bald eagles.

Considering a total of 1600 eggs are potentially laid at the heronry each year this cost seems negligible in comparison to the complete avoidance of depredation experienced by herons during the observational period despite an incursion rate by non-resident eagles of 1.47 per hour. The Tsawwassen Heronry at English Bluff was among the most productive colonies surveyed in the region in both 2005 and 2006.

Conclusions

Within this chapter I have tested three key predictions of the Predator Protection Hypothesis as a possible explanation for an apparent nesting association between the Pacific great blue heron and the bald eagle in the Pacific Northwest. First, great blue herons choosing to nest with bald eagles experienced higher reproductive success than colonies not associated with nearby nesting eagles. Second, when eagles temporarily gave up on nesting, reproductive success at a nearby colony declined. Third, herons nesting in close proximity to active bald eagle nests inhabit large colonies, further diluting potential costs paid to their aggressive hosts while minimizing the number of other bald eagle predators that may find their nesting location because it is more conspicuous. Additionally, my observational case study of the Tsawwassen Heronry at English Bluff indicated that herons benefited from territorial defence by bald eagles while paying minimal cost due to aggressive and predatory behaviour to resident bald eagles nesting at the site.

Thus, great blue herons in the Fraser River Valley and Delta may choose to nest with resident nesting bald eagles to take advantage of the eagle's

territorial behaviour to gain relative safety from other eagles. The conditions required for this association to take place are an abundance of food to keep the eagles well-fed and to support a large number of herons.

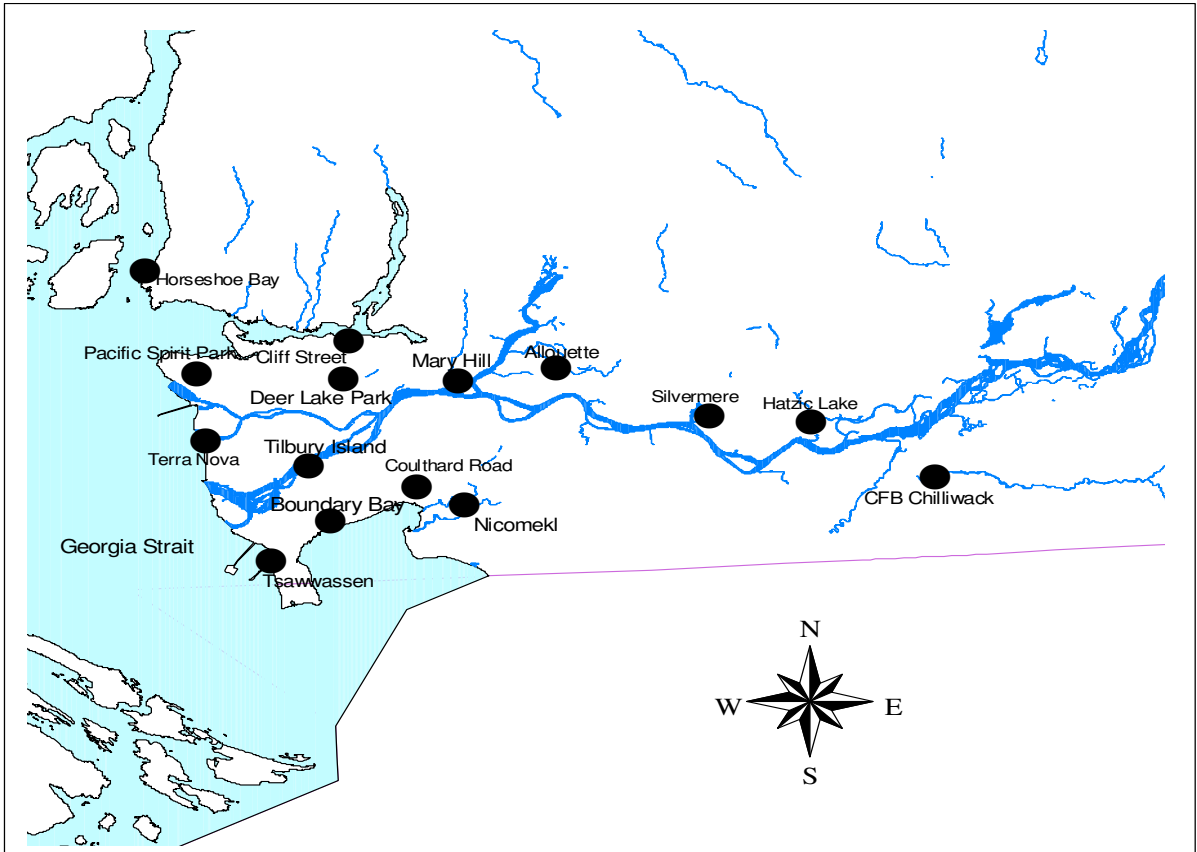


Figure 4-1: Location of surveyed Pacific great blue heron colonies in the Fraser River Valley and Georgia Strait Basin.

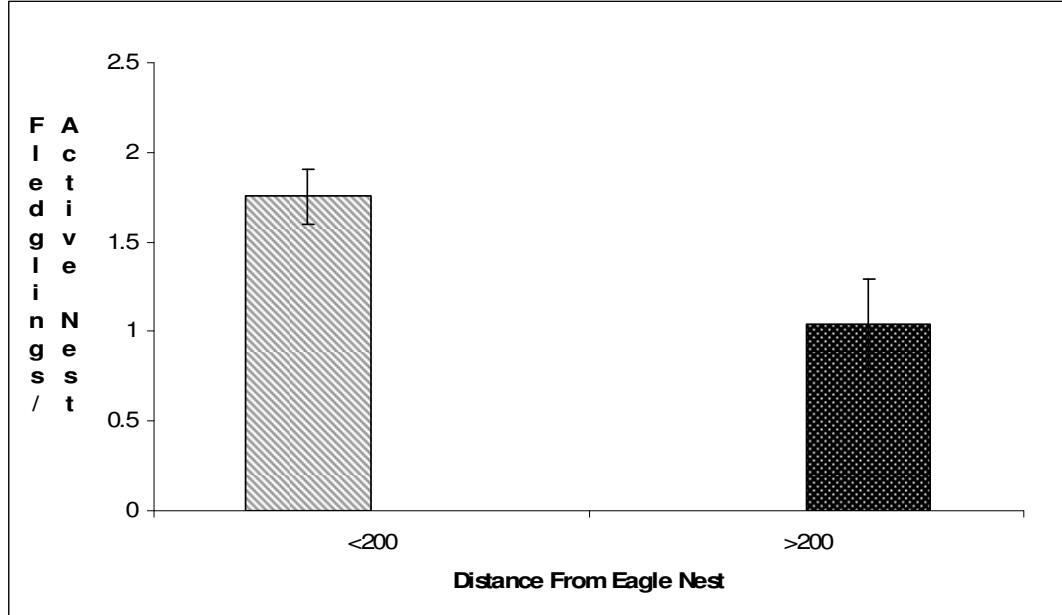


Figure 4-2: 2005 Mean reproductive success measured as the number of fledglings per active nest related to the distance in m from the nearest active bald eagle nest. N=78 heron nests >200 m from an active eagle nest and n=206 heron nests <200 m from an active eagle nest. Error bars are 95% confidence intervals.

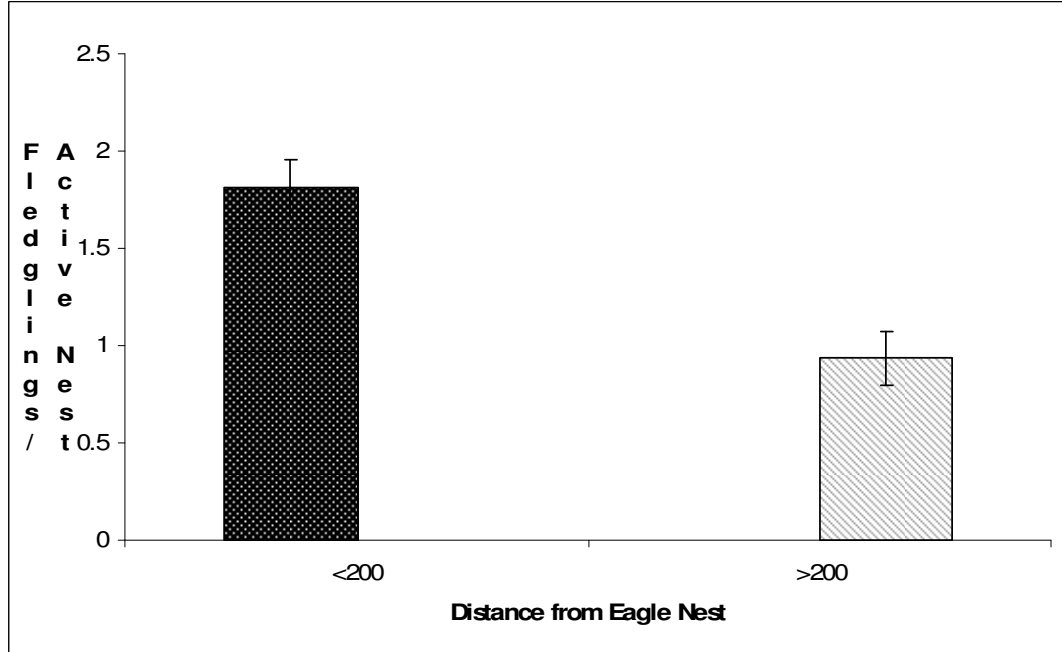


Figure 4-3: 2006 Mean reproductive success measured as the number of fledglings per active nest related to the distance in m from the nearest active bald eagle nest. n=232 heron nests >200 m from an active eagle nest and n=199 heron nests <200 m from an active eagle nest. Error bars represent 95% confidence intervals.

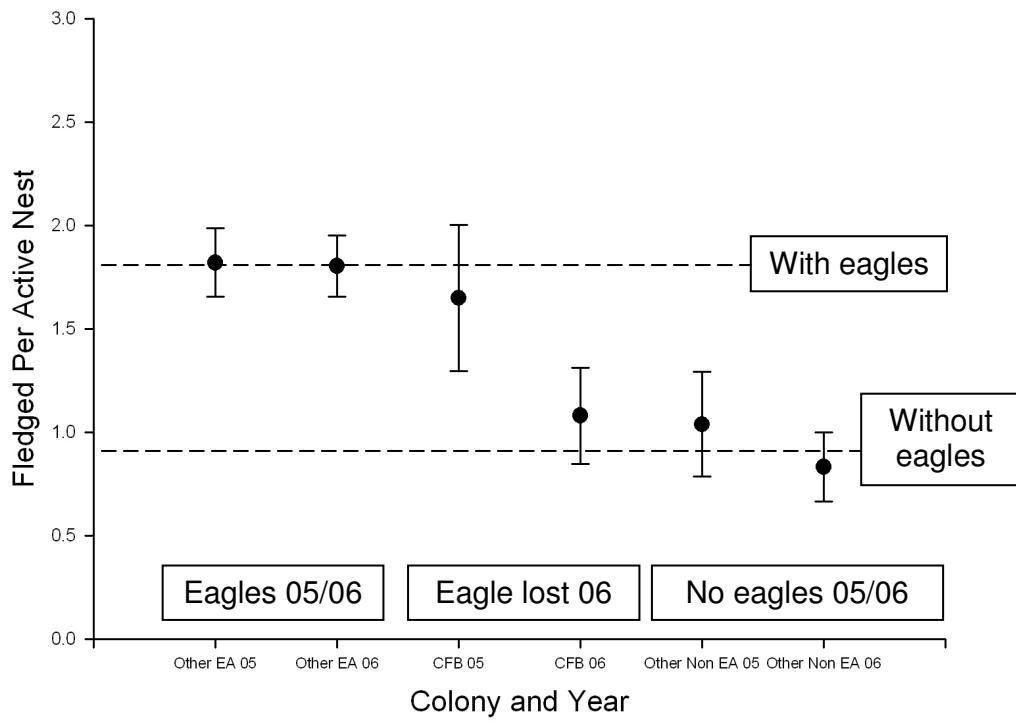


Figure 4-4: A comparison of the mean reproductive success at the Chilliwack Heronry measured as the number of fledglings per active nest to that measured for other colonies with active eagle nests within 200 meters and all other surveyed colonies in 2005 and 2006. An actively breeding pair of bald eagles was present in 2005 whereas the eagle nest failed in 2006 after being blown out of the tree in proximity to the Chilliwack Heronry. The pair of bald eagles worked on another nest in the area but did not re-nest during the 2006 breeding season at the Chilliwack Heronry. Error bars represent 95% confidence intervals.

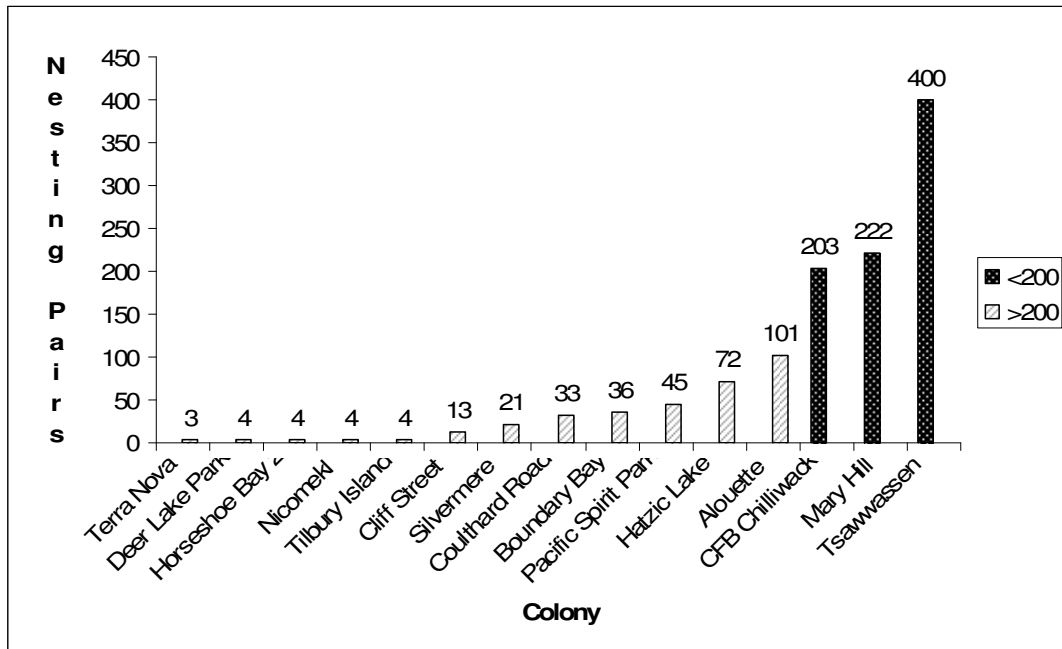


Figure 4-5: Colony size related to the nearest distance to an established eagle nest in 2005 and 2006.

CHAPTER 5: SUMMARY AND FUTURE DIRECTIONS

Thesis Summary

This thesis examined several key assumptions and predictions in the interest of investigating the Predator Protection Hypothesis as a possible mechanism in explaining an apparent nesting association between the Pacific great blue heron (*Ardea herodias fannini*) and the bald eagle (*Haliaeetus leucocephalus*) in the Pacific Northwest.

In Chapter 2, I examined data collected during a long-term study of bald eagle reproductive success in the Upper and Lower Fraser Valley to test two assumptions related to changes in predation risk experienced by Pacific great blue herons. First, the number of breeding pairs of bald eagles in the Upper and Lower Fraser Valley have increased significantly, thereby increasing the predation danger experienced by breeding Pacific great blue herons in the region. Second, bald eagle reproductive success remained relatively high through the study period, likely indicating abundant food within occupied territories. The above conditions create an environment where a shift toward the Predator Protection Strategy by herons is more likely. Breeding herons within the region may benefit from altering their nesting strategy to nest in association with a single pair of reproductively successful bald eagles to take advantage of their territorial behaviour to counteract increases in predation danger

experienced by herons. As the eagles are reproductively successful, they are less likely to rely on nearby nesting herons and their chicks as a food source.

In Chapter 3, I satisfied two additional and necessary assumptions for bald eagles to serve as a potential host for great blue herons through combining results from both experimental and field observation studies to describe the propensity for bald eagles to defend their nest sites in the Upper and Lower Fraser Valley. First, I showed that bald eagles defend their nest sites from adult and juvenile bald eagles and to a lesser extent other raptorial predators for about 1 km around the nest. The propensity of this defence toward intruders and therefore, the benefit available to herons, declines with distance from the nest. Second, bald eagles continued this level of defence toward all intruders without fluctuation through their breeding season which coincidentally coincides with the heron breeding season in the region. In addition to confirming that many great blue herons nesting in proximity to nesting bald eagles likely benefit from reduced predation risk experienced by non-host eagles, the above territorial study also contributes an improved methodology and adds previously undescribed new findings to the literature for bald eagle territorial behaviours.

Finally, in Chapter 4 I present my results for reproductive success of Pacific great blue herons in the Fraser River Valley and Delta in relation to their distance from nesting bald eagles. I also present and discuss an observational case study to characterize the costs and benefits of heron-eagle nesting associations. In doing so, I tested 3 key predictions and provide additional descriptive evidence of the Predator Protection Hypothesis as a possible

explanation for an apparent nesting association between the Pacific great blue heron and the bald eagle in the Pacific Northwest. First, great blue herons choosing to nest with bald eagles experienced higher reproductive success than colonies not associated with nearby nesting eagles. Second, when eagles temporarily gave up on nesting, subsequent reproductive success at a nearby colony declined. Third, herons nesting in close proximity to active bald eagle nests inhabited large colonies, further diluting potential costs paid to their aggressive hosts. Additionally, my case study of the Tsawwassen Heronry at English Bluff Colony indicated that herons benefited from territorial defence by bald eagles while paying minimal cost due to aggressive and predatory behaviour from resident bald eagles nesting at the site.

My findings provide evidence in support of the Predator Protection Hypothesis as a possible mechanism in explaining apparent associative nesting behaviour observed between the Pacific great blue heron and the bald eagle in the Lower Fraser Valley.

Conservation Implications and Future Research

Butler and Vennesland (2000) stated that climate change leading to changes in available foraging habitat and recent changes in predator abundance are factors that will be prominent for consideration when promoting and advocating wading bird conservation in the 21st century (Kenyon 2005). Raptor numbers are rebounding from persecution and pesticides in certain regions across North America (Bueller 2000, Butler and Vennesland 2000, Elliott and Harris 2001, Vennesland and Butler 2004) that are likely to lead to changes in

the distribution and breeding strategies of their avian prey species (Kenyon et al. 2007). The Pacific great blue heron is designated as a Species of Special Concern in Canada making heron research and conservation a B.C. priority (Kenyon 2005). This designation has resulted in part due to evidence for declines in overall population size and reproductive success related to habitat fragmentation, increased predatory and human disturbance of colonial nesting sites and predation.

Kenyon (2005) worked within the framework suggested by Butler and Vennesland (2000) to develop and test a set of theoretical models predicting optimal Pacific great blue heron colony site selection based on habitat variables present in the Georgia Basin. Kenyon stated that future research should focus on testing the predictions and assumptions the habitat selection model was based, in particular pointing to a lack of knowledge of bald eagle territoriality and how it might contribute to potential interactions among bald eagles and great blue herons. By measuring and describing territoriality among bald eagles in the region and describing and testing assumptions and predictions of the Predator Protection Hypothesis as a possible mechanism in explaining recently observed nest site selection among herons, my thesis has filled key gaps in knowledge required to revise and further test the predictive habitat models developed by Kenyon et al. (2007).

It is becoming increasingly apparent that future conservation strategies for herons in the Pacific Northwest should focus on both preserving current breeding sites while maintaining a variety of alternate nesting opportunities within suitable

distances of long-term foraging sites. Herons have demonstrated they possess a large toolbox of breeding strategies that they readily implement within and between breeding seasons in response to the changing habitat and predation risk variables. Future research should be focused toward implementing those findings of this thesis within refined predictive habitat selection models pioneered by Kenyon et al. (2007). Additionally, bald eagle nesting distribution and population fluctuations are also variables in determining heron habitat selection and therefore, developing and testing predictive bald eagle population and habitat selection models will be necessary to inform predictive habitat selection models for herons.

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