BEHAVIOURS INFLUENCING THE DISTRIBUTION OF GREAT BLUE HERONS (*ARDEA HERODIAS FANNINI*) IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA

by

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ABSTRACT

The Great Blue Heron (*Ardea herodias fannini*), a nonmigratory subspecies endemic to the Pacific Northwest of North America, is COSEWIC-listed in Canada as a species of 'special concern'. The Breeding Bird Survey (BBS), conducted since 1969, indicate an ongoing decline in numbers. Recent findings show that nest and colony abandonments are common, and are strongly associated with disturbance by bald eagles (*Haliaeetus leucocephalus*).

Vanishing bearings of herons departing foraging sites were strongly associated with colony locations, and led to the discovery of small, previously unknown colonies. A probabilistic model predicted that dispersed nesting offers increased nestling safety under high eagle depredation. Ideal free distributions accounting for colony locations as well as foraging-site size and quality best matched the observed distribution of foraging herons. These findings support the hypothesis that great blue herons have redistributed into smaller, more widely-scattered colonies as eagle numbers have recovered over recent decades.

ACKNOWLEDGEMENTS

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CHAPTER 1:
GENERAL INTRODUCTION

The Great Blue Heron (*Ardea herodias*) is a common wading bird found

throughout most of North America (Butler 1992). The non-migratory *fannini* subspecies

is located in the Pacific Northwest with large concentrations inhabiting the coastal

regions of Puget Sound, Washington and the Strait of Georgia, British Columbia (Butler

1992). Biologists are concerned with the sustainability of the Great Blue Heron

population of southwestern British Columbia (Vennesland and Butler 2004). As such,

the federal Committee on the Status of Endangered Species in Canada (COSEWIC 2004)

lists this population as a subspecies of "special concern". A designation of "special

concern" implies that this species "may become a threatened or endangered species

because of a combination of biological characteristics and identified threats" (COSEWIC

2004; p. 1). For example, human development in this area has severely fragmented the

forested landscape on which herons rely for breeding habitat (Vennesland and Butler

2004).

Recently, studies have shown that this population has the lowest reproductive

success of any subpopulation of Great Blue Herons in North America (Vennesland and

Butler 2004). An important component of this low reproductive success is the complete

abandonment of entire colonies during the breeding season resulting in zero reproductive

success. Though there is no measured historical background level of colony

abandonment for a sustainable population, Vennesland and Butler (2004) documented a

high frequency (42%) of colony abandonment during a single breeding season in this region. It has been suggested that the cause of these abandonments may be either or both of predation by Bald Eagles (*Haliaeetus leucocephalis*) or human disturbance (Simpson *et al.* 1987; Norman *et al.* 1989; Butler *et al.* 1995; Vennesland and Butler 2004). Abandonment from human disturbance has been suggested to have increased over the last couple of decades as the human population has increased in this (Vennesland and Butler 2004). However, Vennesland and Butler (2004) found that human disturbance was seldom the cause of colony abandonment. On the other hand, if eagles are the cause, then colony abandonment may only be a recent phenomenon as the population size of Bald Eagles increases from past persecution and the detrimental effects of pesticides (Buehler 2000; Elliott and Harris 2001).

Unpredictable disintegration followed by reestablishment of heron colonies, possibly at new locations on this rapidly changing coastal landscape, due to colony abandonment events leads to difficulties in planning conservation of this species. Indeed, past conservation practices of securing relatively small parcels of land supporting existing large heron colonies may be a risky venture given some such secured colonies have abandoned. An understanding of which biological mechanisms lead to the observed distribution of herons on the landscape is therefore an important factor in prescribing conservation actions. More generally, understanding how individuals are distributed across a landscape has long been a question that fascinates ecologists in general and is central to studies of the life history of colonial nesting species, including Great Blue Herons (e.g. Furness and Birkhead 1984; Gibbs *et al.* 1987; Gibbs 1991; Gibbs and Kinkel 1997; Brown and Brown 2002).

To allow effective conservation planning for this local subspecies of the Great Blue Heron, it is imperative to have knowledge about the current distribution of individuals across the landscape as well as to have an ability to estimate population size accurately. Censusing known colonies has historically been the method employed to estimate population size. However, frequent colony abandonments may lead to an underestimate of population size if new colonies are not located. To address this concern, Chapter 2 details a method for estimating the number of Great Blue Heron colonies. The method involves measuring the vanishing bearing of a heron leaving a foraging site en route to its nest to provision its nestlings. Analysis and interpretation of these vanishing bearing data for various foraging sites assists in determining how many colonies are potentially associated with a given foraging site. The identification of vanishing bearings that were consistent with known colonies was considered evidence that the methodology could work well for identifying undiscovered colonies. Thus, vanishing bearings inconsistent with known colonies were investigated for the presence of a previously undiscovered colony by progressively following herons along their vanishing bearing until a colony was located. Therefore, use of this methodology should improve population size estimates.

Chapters 3 and 4 address factors that may affect the distribution of an avian species across the landscape, such as food availability, intraspecific competition, predation danger, information sharing, and nest site availability. This thesis focuses on three of these factors (food availability, intraspecific competition, and predation danger) for potentially explaining the distribution of herons. Specifically, two questions are examined that relate to how the individuals of a population are distributed: (1) how does

an increase in predation danger affect the nesting distribution of herons? And (2) how might herons distribute themselves across a number of foraging sites differing in size, the amount of food available, and in the number of conspecific competitors?

In behavioural ecology, as in other scientific disciplines, there are two paradigms for advancing scientific understanding of the system under investigation. One is to undertake a controlled experiment where the factor of interest (e.g. predation danger) is manipulated and the response of the subject (e.g. heron) is recorded and tested against an appropriate null hypothesis. For the Great Blue Heron system, this experimental approach is impractical. This leaves the second method for addressing behavioural ecology questions: a modelling paradigm. Modelling allows putative hypotheses to be posed and challenged with observed data without experimentally manipulating a natural or laboratory system (Hilborn and Mangel 1997). Competing hypotheses are then formally evaluated for their rank and quality in explaining observed phenomena in the context of hypothesized mechanisms (Burnham and Anderson 2002).

As mentioned above with respect to Chapter 3, it has been speculated that predation from Bald Eagles is a likely cause of colony abandonment (Simpson *et al.* 1987; Norman *et al.* 1989; Butler *et al.* 1995; Vennesland and Butler 2004). This raises the question of how herons might alter their colonial nesting strategies in response to an increase in predation danger. However, there is very little theory or data in the literature on the costs and benefits of colonial nesting in terms of predator avoidance. In an effort to improve the understanding of anticipated responses of breeding herons to changes in predation danger from eagles, Chapter 3 describes a probabilistic model that formalizes a hypothesis investigating the trade-off between nesting in a large, conspicuous colony

with a potentially high dilution effect versus nesting in one of many small, cryptic colonies. The trade-off in reproductive success among colonies between ease of detection by a predator, and predation danger once detected, is evaluated for different eagle densities and different eagle attack rates. A key consideration questions if the dilution effect of being an individual in an easily found colony is more advantageous than being a more likely chosen prey but in a much more difficult to find colony.

Chapter 4 exploits the premise that variables that are accurate predictors of the number of individuals using a habitat are likely to be useful indicators for conservation planners. One such variable is foraging site size, and many studies have correlated Great Blue Heron colony size to the amount of nearby foraging area (Gibbs *et al.* 1987; Gibbs 1991; Gibbs and Kinkel 1997). However, these studies have assumed all foraging sites to be of equal quality and have simply used a correlative approach to infer that foraging site size and use are functionally related. This approach does not explicitly provide a mechanism for the observed distribution. In a more functional approach, Fretwell and Lucas (1969) propose a null model, termed the ideal free distribution (IFD), where individuals choose the foraging site that maximizes energy intake. Chapter 4 compares the observed distribution of herons across foraging sites to the distribution predicted by four competing IFD models, conditional on the observed distribution of herons within colonies. A game theoretic model (Maynard Smith 1982) was created to predict the IFD of herons by allowing each individual to choose a foraging site in an effort to maximize its payoff (the amount of food returned to its nest to provision the nestlings), dependent upon the foraging decisions made by other individuals in the population. This approach allowed competing hypotheses to be ranked to determine if differences in site quality, the

number of competitors, and the costs of travel between colonies and foraging sites were reliable predictors of the number of herons using each foraging site.

The three approaches outlined in this thesis designed to increase our understanding of the distribution of herons in a changing landscape, although independent, can be synthesized to improve conservation practices designed to sustain the Great Blue Heron. Therefore, Chapter 5 describes how vanishing bearings can be used to validate the predictions obtained from the models presented in Chapter 3 and Chapter 4 and how incorporation of knowledge of both nesting distribution and foraging site distribution can provide better intuition on how to best provide a landscape conducive to a sustainable heron population. Butler and Vennesland (2000) proposed a framework within which future research of wading bird populations should be conducted to deal with conservation problems such as increasing densities of predators and habitat change due to climate change. Chapter 5 articulates how this thesis provides a contribution within this framework.

CHAPTER 2:
USE OF VANISHING BEARINGS
FOR LOCATING WADING BIRD COLONIES

Introduction

Estimating population size and productivity of colonial breeding birds has been

the focus of many studies (e.g. Forbes *et al.* 1985, Kelly *et al.* 1993, Butler *et al.* 1995,

Parsons and McColpin 1995). However, knowing the location of colonies, which range

in size from a few to several hundred birds, is imperative in order to estimate these

parameters. Methods previously proposed and used to locate wading bird nesting

colonies are plagued with inefficiencies and biases. For example, Frederick *et al.* (1996)

describe an aerial and boat survey used to locate wading bird colonies, but these

methodologies were biased towards light-coloured birds, required searching all potential

nesting sites, and was conducted in the best possible conditions for aerial surveys. A less

labour intensive method that takes advantage of the behaviour of the birds and that can be

used in a wider variety of situations is evaluated here.

Past studies of wading birds have observed the flight direction of birds departing

from and arriving to a colony and/or roost in an effort to determine where these birds

were foraging (Siegfried 1971, Krebs 1974, Pratt, 1980, Bayer 1981, Erwin 1984, Dowd

and Flake 1985, Forbes 1986, van Vessem and Draulans 1987, Benoit *et al.* 1993,

Parsons and McColpin 1995, Wong *et al.* 1999, Custer and Galli 2002). In addition,

Krebs (1974) placed observers along the observed flight paths in order to confirm the

arrival of a bird at the foraging site. Using this logic, it should also be possible to observe

and follow the flight directions of wading birds returning to their colonies from foraging sites to locate a previously undiscovered colony.

This study describes the methodology used to determine the number and general location of cryptic colonies of Great Blue Herons (*Ardea herodias*) by analysis of the vanishing bearings observed from coastal and estuarine foraging sites in British Columbia. As well, an intensive search effort methodology used to find any undiscovered colony predicted by the vanishing bearing analysis is described. To establish the validity of this method, (1) all known colonies must be associated with vanishing bearings from one or more foraging sites and (2) all vanishing bearings from a site must be associated with a colony. A corollary of these conditions is that herons leaving estuaries in directions inconsistent with known colonies are flying to previously undiscovered colonies. This thesis examines the veracity of these conditions. Additionally, the utility of the frequency of observed vanishing bearings for estimating the size of unknown colonies is discussed.

Methods

Study Area

The study area was located in the Strait of Georgia, British Columbia (Figure 2-1). At the time of this study (April-June 2002 and 2003), there were approximately 1,000 pairs of Great Blue Herons foraging at the many estuarine and non-estuarine intertidal foraging sites that characterize this region. Most foraging sites are extensive, geographically discrete intertidal estuarine mudflats; consisting of eelgrass beds where up to 700 individual Great Blue Herons forage during most low tides. Estuaries range in

size from 18 ha to >7,500 ha (Ryder *et al.* 2004). Within the vicinity (<10 km) of most foraging sites are large tracts of forests of suitable nesting trees such as Red Alder (*Alnus rubra*), Douglas Fir (*Pseudotsuga menziesii*), and Western Hemlock (*Tsuga heterophylla*) (Butler *et al.* 1995).

Field Data

Observations of foraging herons were conducted along the coast of the Strait of Georgia between 30 April and 26 June in 2002 and 2003. This period coincides with the provisioning period of nestlings (Butler 1993). Sites visited in 2002 were Boundary Bay, the Chemainus River estuary, Cowichan Bay, Hornby Island, Maplewood and Port Moody in Burrard Inlet, the Nanaimo River estuary, the Puntledge River estuary, and portions of the Fraser River estuary at Roberts Bank and Sea Island. These, plus five other sites (Baynes Sound, the Capilano River estuary, the Englishman River estuary, Esquimalt Harbour, and the Sidney Island lagoon), were visited in 2003. Each site was visited for two to six days and vanishing bearings were recorded for approximately 2-3 hours preceding a low tide, as this is when most provisioning herons forage (Butler 1993, Matsunaga 2000) and the 2-3 hours following a low tide, depending upon the number of birds remaining on the foraging ground.

An observer was positioned in or along the periphery of a Great Blue Heron foraging site to record the vanishing bearings of birds seen departing the foraging site. A vanishing bearing is defined as the relatively straight-line direction a bird is observed flying as it returns to its colony. A key assumption was that in order to minimize energetic costs, a heron would, where geographically feasible, fly a direct route between its foraging site and its colony. Vanishing bearings were measured by determining the

compass bearing the bird flew (Figure 2-2). Compass bearings were recorded using GPS technology. Ideally, this compass bearing would be a true vanishing bearing as the heron disappeared on the horizon while heading directly away from the observer. However, not all herons departed directly away from the observer. Sometimes the observer had restricted (by geographical, safety, or private property constraints) access to ideal observation posts, while at other times proximity to the herons could cause unwanted disturbance. Consequently, many of the vanishing bearings obtained were affected by the parallax caused by oblique observation of heron flights (Figure 2-2).

The true bearing between a foraging site and known colonies could be calculated using trigonometry. Using the GPS coordinates of the foraging site and a known colony as vertices of a right triangle, and the line between the two as the hypotenuse, the angle of flight was calculated and converted to a compass bearing. Observed vanishing bearings were compared to these true bearings to determine if the herons were flying to known colonies.

Vanishing bearings inconsistent with known colonies were investigated to determine whether herons were flying to unknown colonies. Low intensity searches for colonies were conducted for about one hour following completion of daily observations on a foraging site. Searches were necessarily constrained to roadways because with little additional information extensive searches of private land were not feasible. Searches were limited to within ten kilometres of the foraging estuary as Butler *et al.* (1995) concluded heron colonies were located on average only 2.9 km from foraging sites in this region. When possible, local residents were queried about the whereabouts of any nearby colonies.

In 2004, a single foraging site (Cowichan Bay) was revisited and vanishing

bearings recorded over a five-day period. A large colony abandonment had occurred at

this site in 2001 and the locations of active colonies were unknown. After the vanishing

bearings had been determined, a high intensity ground search for colonies was

undertaken. One observer remained on the foraging site and communicated via cellular

phone with observers placed along the flight paths (cf. Krebs 1974) indicated by

vanishing bearings. The location of potential colonies was then narrowed down by

progressively following colony-bound herons.

Statistical Analysis

A modal analysis of the frequency distribution of vanishing bearings for each

foraging site was conducted to identify patterns in vanishing bearings for each site. A

maximum likelihood frequency analysis was conceived and designed specifically for

analysing these vanishing bearings and was coded in Microsoft Visual Basic® (B. D.

Smith pers. comm.). The analysis was based on the general methodology of Schnute and

Fournier (1980) that has provided a template for several specific frequency analysis

designs (e.g., see Smith and Botsford 1998). When conducting the modal analyses of

vanishing bearings, it was recognized that the modal clusters were generally separated to

an extent that they could be readily identified by this analytical technique (Figure 2-3).

Based on the variation in vanishing bearings that were measured (SE < 0.5), a confidence

interval of $\pm 10°$ was chosen to account for the effect of variable flight paths and parallax

to cause the observed vanishing bearing to differ from the true bearing between the

foraging site and colony. This range was then used as an estimate of the uncertainty in

observed vanishing bearing modes for predicting the location of unknown colonies. The

mean of each observed vanishing bearing mode was regressed against the true bearing

between a foraging site and a colony to determine how consistently the observed

vanishing bearings corresponded to the true bearing between a foraging site and a colony.

The frequency of observed vanishing bearings (measured in the units of vanishing

bearings per hour) consistent with known colonies was regressed against the size of

known colonies (Vennesland 2003; McClaren 2004) to determine if the frequency of

observed vanishing bearings could be used as a reliable predictor of the size of any

potential unknown colonies. Average vanishing bearing frequencies and known colony

sizes from 2002-2004, including colonies found during this study, were used in this

analysis.

Results

In total, 23 vanishing bearing modes were identified at ten coastal foraging sites

of Great Blue Herons along the Strait of Georgia in 2002, while 29 modes were identified

at 15 foraging sites surveyed in 2003. In 2002, eleven colonies were known to exist at

the start of the breeding season and 15 were known in 2003. Because one colony foraged

at two separate estuaries in 2002, twelve modes were expected to be associated with

known colonies. Comparisons of the vanishing bearings consistent with a known colony

and the actual bearing between the foraging site and colony suggested a $\pm 10°$ range be

used to account for parallax (see Methods). The estimated vanishing bearings contained

75% (9 of 12) of the known colonies within this range in 2002 and 67% (10 of 15) in

2003 (Table 2-1). Regression of the estimated vanishing bearing means against the true

bearings shows a high correlation when an outlier was removed since a colony at Hornby

Island had abandoned at some point during the breeding season ($r^2 = 0.98$, Figure 2-4).

This high correlation suggests that measuring vanishing bearings accurately determines the direction that herons return to their colony. If the analysis is restricted to vanishing bearing modes with a sufficient sample size (N $\geq$5), then 73% (8 of 11) in 2002 and 87.5% (7 of 8) in 2003 of known colonies are contained within the estimated vanishing bearing ranges. Combining both years results in 79% (15 of 19) of known colonies being consistent with the estimated vanishing bearings. The estimated vanishing bearings suggest that there may have been eleven and 14 undiscovered colonies in 2002 and 2003, respectively. The number of modes inconsistent with known colonies suggests that potentially 48% of all colonies were undetected. Of these undiscovered colonies, two (seven and 42 nests) were found in 2002 while only one (35 nests) was found in 2003 using the low intensity search method.

A high intensity search was conducted in 2004 in an attempt to confirm that vanishing bearings that were known to be inconsistent with bearings between the foraging site and a known colony were associated with previously undiscovered colonies. Analysis of observed vanishing bearings identified three modes (Figure 2-5). Intensive searching along these vanishing bearings resulted in two colonies being confirmed, one to the south (57 nests) and one to the southeast (seven nests). These colonies were found within a couple of hours of beginning the search. A colony was not found along the third vanishing bearing (towards the northwest) after two days of searching, although the lack of a found colony does not necessarily prove that a colony did not exist. However, a heron was observed landing and successfully foraging at a secondary freshwater foraging site. As well, the vanishing bearing intersects a freshwater marsh that also may be used as an alternate foraging site.

The frequency of vanishing bearings and the size of known colonies was correlated (p=0.0005, r^2= 0.36, Figure 2-6), however, this relationship was driven by the large differences in colony size. Removal of the two largest colonies (>400 nests) weakened the correlation (p=0.0446, r^2= 0.15).

Discussion

The two conditions that need to be validated for the use of vanishing bearings as a methodology to estimate the number and location of heron colonies on the landscape have generally been satisfied. Fulfilling the first condition, most known colonies had vanishing bearings that accurately estimate the actual bearing between the colony and the foraging site. In the few cases where this condition was not fulfilled, the actual bearing is minimally outside of the predicted range (Figure 2-4). Only one known colony (Hornby Island) had no observed vanishing bearings associated with it although this colony abandoned at some point during the breeding season (McClaren 2004). The second condition, that vanishing bearings not consistent with known colonies predict a previously undiscovered colony, was fulfilled, as a total of five colonies were found over the course of three years. More specifically, the intensive search method in Cowichan Bay in 2004 confirmed two out of three vanishing bearing modes being associated with previously undiscovered colonies. However, the intensive search of vanishing bearings at Cowichan Bay also revealed that vanishing bearings might be observed when a heron travels from one foraging site to another foraging site.

The goal of this study was to investigate a method that had potential to be employed to more accurately estimate the heron population size in the Strait of Georgia. In both 2002 and 2003, when low intensity searches were conducted, the discovery of

three colonies using vanishing bearings accounted for 3.5-5% of the total estimated population each year (approximately 1,000 pairs along the coast). Vanishing bearings predicting nearly half of all colonies had not been discovered and an increase in population size estimates with only three new colonies being discovered suggests that investing in locating colonies can substantially improve estimates of population size.

Collecting information on vanishing bearings and locating colonies is efficient in its use of resources, requiring only optical equipment, cellular phones, and a GPS. During the provisioning season a sufficient number of vanishing bearings can be recorded over a single foraging period. The intensive search for colonies conducted in 2004 required only four observers for two days plus communications equipment. Benefits of this methodology for following birds include no need for aerial surveys, any capture or handling of the birds, and no use of radio-transmitters and their associated costs. However, it is recognized this study benefited from reliable cellular phone coverage and road access in a mixed suburban-rural landscape and readily identifiable and geographically discrete foraging sites.

Using the behaviour of birds to determine the location of a colony is advantageous over systematic aerial searches of an entire area of interest or flushing birds from potential nesting sites as described by Frederick *et al.* (1996). In areas with numerous potential colony locations such as this study area, a systematic search would be impractical because it would be difficult to perform the low level flying required due to geography (large hills) and human development. Furthermore, the dark colour of the birds and obscurity of nests in trees makes sighting difficult. The vegetation density and size of potential nesting sites prevent the use of vehicles from being used to flush birds

from cover. However, similar to this study, Frederick *et al.* (1996) do acknowledge the unique conditions available in their study.

Nevertheless, there are some caveats that need to be considered when implementing this methodology. There are two reasons for a vanishing bearing to not have the same bearing as a known colony: equipment error or observer measurement error due to parallax. Most standard errors of each identified mode were calculated to be quite small, suggesting that measurements were precise. The GPS unit used for measuring vanishing bearings was rated for $\pm 2°$, which would not account for the parallax discrepancies observed. However, observer bias due to parallax is a likely cause of the large confidence intervals required. Proper positioning of the observer either on the flight path or very near to where the birds depart from can reduce the amount of parallax considerably. Reducing parallax will lead to a more accurate estimate of the vanishing bearing, thus enabling an observer to be positioned in the best possible location along the flight path of the herons when intensive searches for colonies are conducted.

Predicting a colony to be located along an identified vanishing bearing when a colony may not exist is another consideration when using this methodology. Not verifying the existence of a predicted colony could lead to an overestimate of the number of colonies. Vanishing bearings that lead to other foraging sites instead of to a colony may cause these false positives. Thus, in adherence to condition 2, it is imperative for the investigator to either follow the vanishing bearings using the intensive search methodology or to be aware of other foraging sites within foraging range to minimize overestimating the number of colonies.

There are a number of factors that were not controlled in the methodology for determining if the frequency of vanishing bearings can be used as a predictor of colony size. Energy demands of the nestlings increase through the provisioning period (Bennett et al. 1995); therefore, adults should be expected to make more provisioning trips to meet these increased energy demands. Also, both parents are believed to forage during this time of year to effectively provision their nestlings such that more herons are observed foraging later in the breeding season (Butler 1995). Since not all foraging sites were visited at the same time of year, nor was each foraging site visited throughout the year, a seasonal effect of the frequency of vanishing bearings and changes in the number of individuals on the foraging site could not be statistically controlled. Other differences between foraging sites, such as the time required to complete a provisioning trip due to differences in the distance between the foraging site and a colony, or the observer's visibility of birds leaving the foraging site, can cause enough variation to decrease the predictive ability of vanishing bearings for estimating colony size. Erwin (1981) described a standardized approach of using a similar "flight-line count" and showed that even when standardizing as many variables as possible, the method performed poorly at predicting the size of an individual colony.

To conclude, this methodology is effective and efficient at quickly estimating the number, and determining the potential locations, of Great Blue Heron colonies, particularly small, cryptic colonies. This methodology can likely be employed in studies of most species of wading birds, along with other communally roosting or colonial nesting birds in all types of habitats.

Table 2-1:   Great Blue Heron vanishing bearings and number of herons observed using each
              vanishing bearing at foraging sites in the Strait of Georgia, 2002-2004. Fate refers to
              whether or not the observed vanishing bearing is associated with a known colony, had a
              new colony found, or had an unknown fate. Note that Boundary Bay and Roberts Bank
              likely shared a colony in 2002.

Foraging Site	Vanishing Bearing	Year	Herons Observed	Fate
Baynes Sound	297°	2003	20	Known Colony
Boundary Bay	42°	2003	5	Unknown
	97°	2003	7	Unknown
	73°	2002	13	Known Colony
	307°	2002-03	110	Known Colony
Capilano River	160°	2003	1	Known Colony
	58°	2003	4	Unknown
Chemainus River	122°	2002	3	Unknown
	160°	2002-03	323	Colony Found in 2002
	190°	2002-03	42	Unknown
Cowichan Bay	41°	2002	4	Colony Found
	110°	2002-04	14	Colony Found in 2004
	193°	2002-04	472	Colony Found in 2004
	298°	2003-04	13	Foraging Site Found in 2004
	319°	2002	30	Known Colony
Englishman River	118°	2003	1	Known Colony
	253°	2003	1	Known Colony
Esquimalt Harbour	2°	2003	2	Unknown
	102°	2003	5	Unknown
	283°	2003	15	Unknown
Hornby Island	261°	2002	52	Known Colony
	56°	2003	1	Unknown
Maplewood	4°	2003	4	Unknown
	116°	2002	5	Known Colony
	343°	2002	1	Unknown
Nanaimo River	150°	2002-03	50	Known Colony
	235°	2002	43	Unknown
	333°	2002-03	10	Known Colony
Port Moody	119°	2003	3	Unknown
	145°	2002	4	Unknown
	183°	2002	1	Unknown
Puntledge River	241°	2002	12	Unknown
	155°	2002-03	149	Known Colony
Roberts Bank	33°	2002-03	9	Known Colony
	52°	2002	7	Known Colony
	65°	2003	54	Colony Found
	136°	2002-03	832	Known Colony
Sea Island	38°	2002-03	13	Known Colony
Sidney Island	95°	2003	3	Unknown
	222°	2003	46	Known Colony
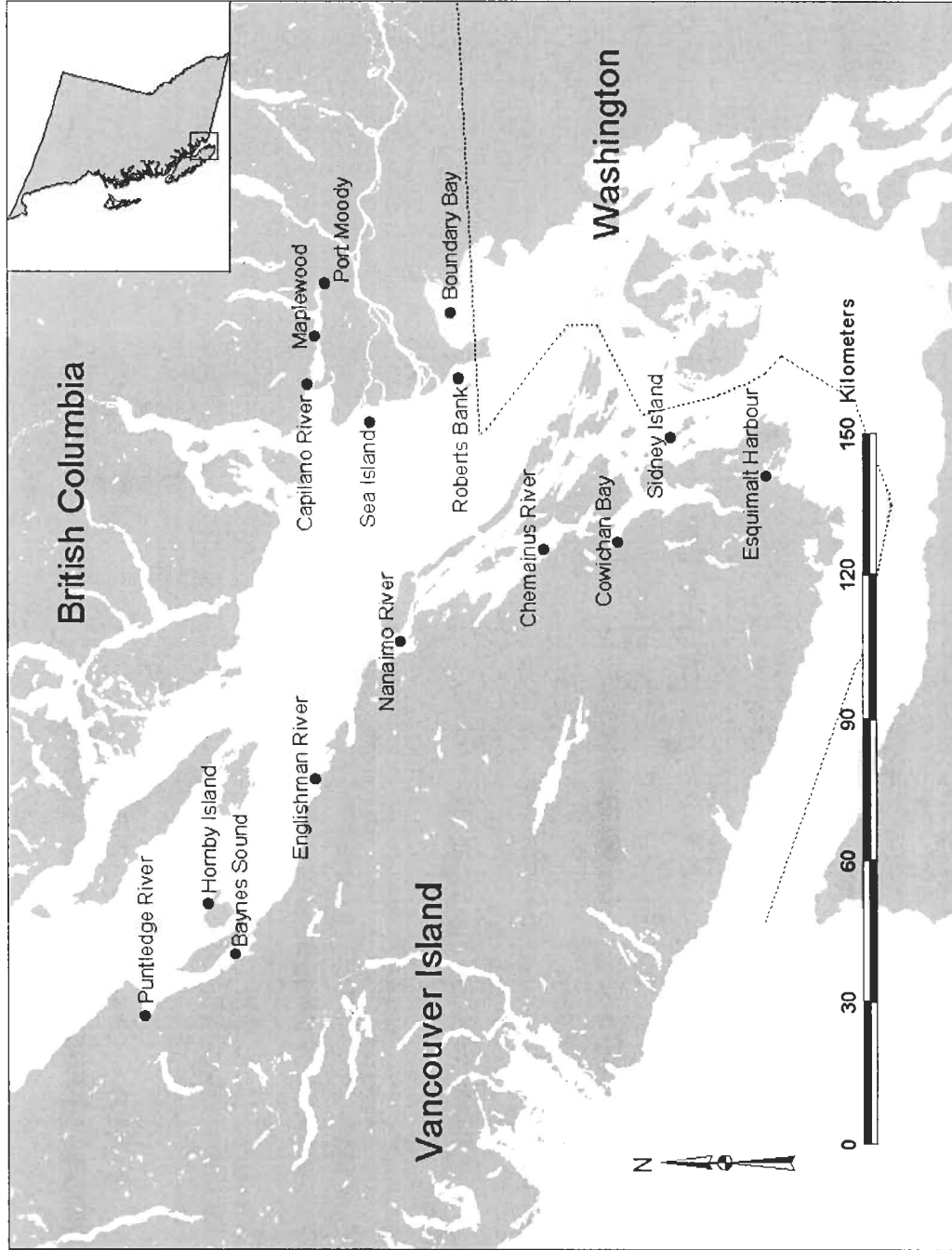
Figure 2-1: Map of the Strait of Georgia, southwestern British Columbia study site, showing location of Great Blue Heron foraging sites.

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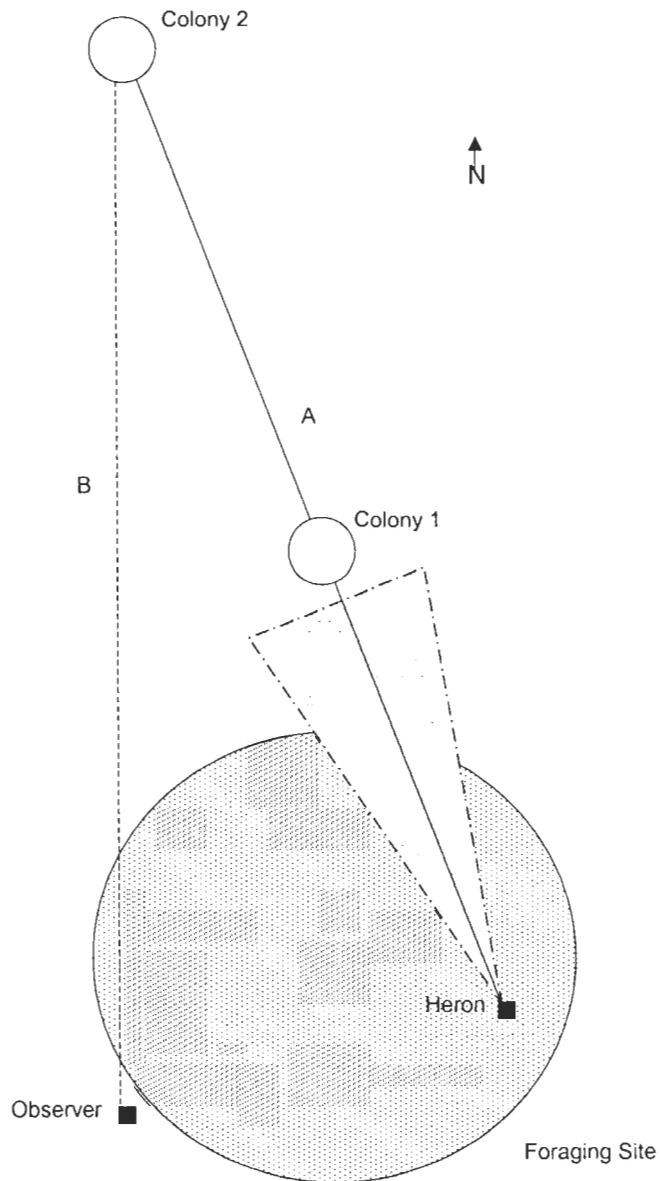
Figure 2-2: Diagram describing the vanishing bearing of a Great Blue Heron. When the heron leaves the foraging site, it follows a direct flight to its colony (line A). An observer determines this bearing by recording the compass bearing. However, due to parallax, when the observer loses sight of the heron as it leaves the foraging site, the measured vanishing bearing is subject to some measurement error. The hatched triangle contains the range of likely measured vanishing bearings, with the true vanishing bearing located within this range (line A). In situations where the colony is located near the foraging site (i.e. Colony 1), this parallax can lead to the true bearing between the colony and foraging site being inconsistent with the measured vanishing bearing. In situations where the heron can be observed for a long distance after it departs the foraging site en route to a distant colony (i.e. Colony 2), parallax is lessened as the line (line B) from the observer to the where the herons was last seen on the horizon begins to converge with the true vanishing bearing. The optimal position of the observer, in an effort to minimize parallax, would be directly along the heron's flight path.
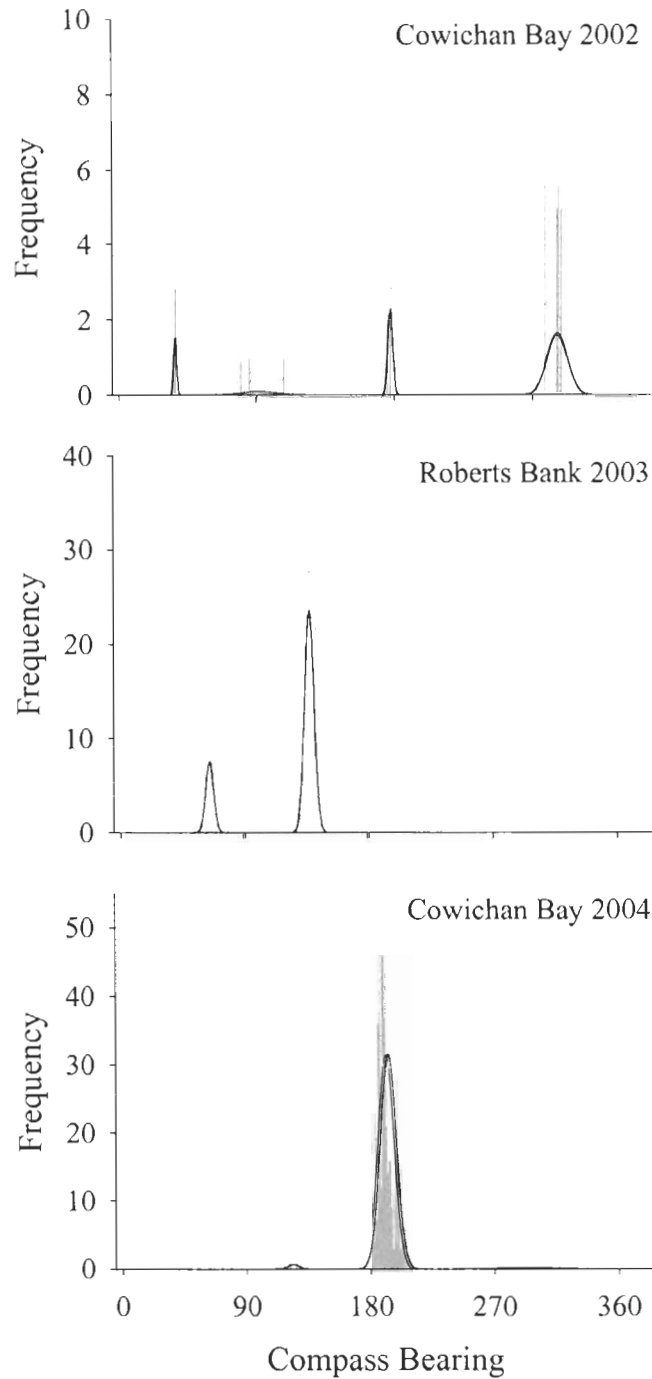
Figure 2-3: Examples of the observed frequency distributions of vanishing bearings of Great Blue Herons departing the foraging estuaries of Cowichan Bay (n=47) in 2002, Roberts Bank (n=257) in 2003, and Cowichan Bay (n=472) in 2004 (vertical bars). Modal analysis (curved lines following a normal distribution defined by its mean and standard deviation) identified four (Cowichan Bay 2002), two (Roberts Bank 2003), and three (Cowichan Bay 2004) clusters of vanishing bearings.
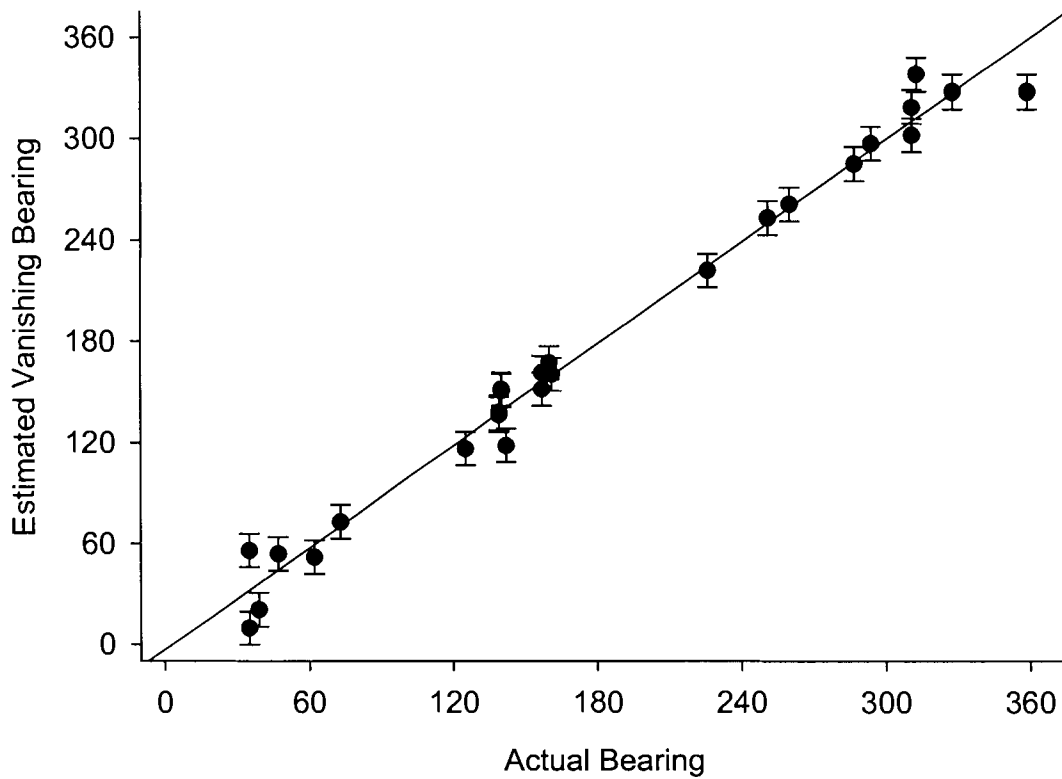
Figure 2-4: Correlation between the estimated mean vanishing bearing of departing Great Blue Herons and the actual bearing between a foraging site and a known colony. The high correlation ($r^2 = 0.98$) suggests a high degree of accuracy in being able to measure the actual vanishing bearing. Error bars are $\pm 10°$ to account for parallax and other sources of measurement error.
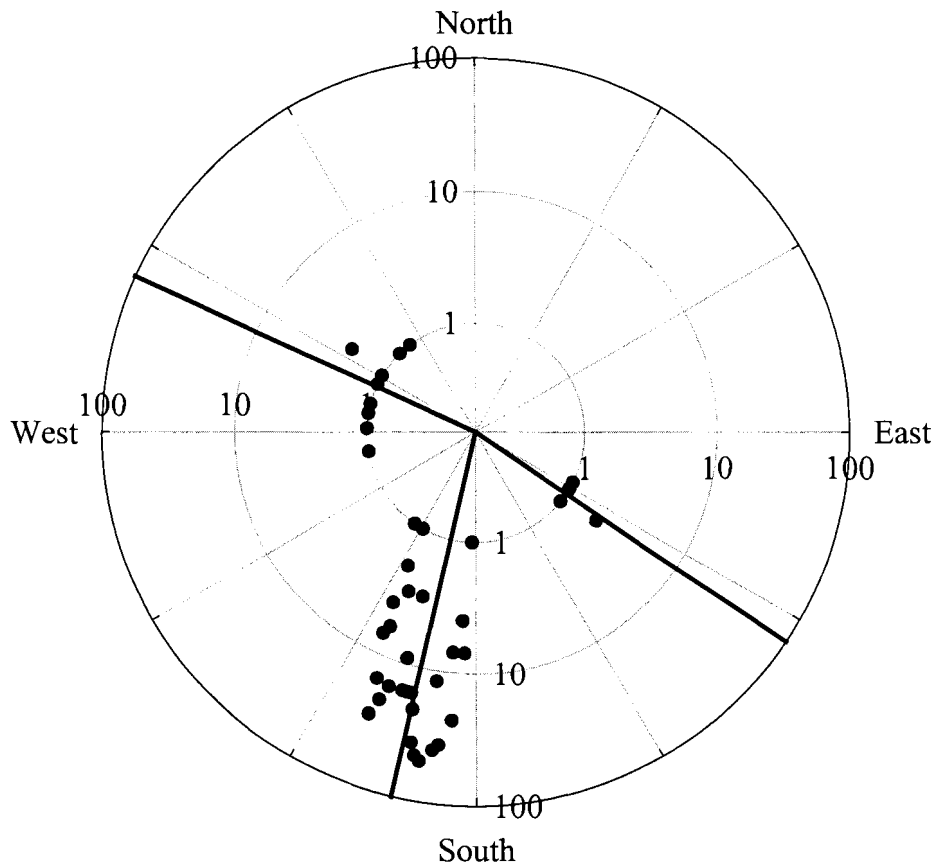
Figure 2-5: Vanishing bearing frequencies (N=472) for Great Blue Herons departing from the Cowichan Bay foraging site in 2004. Thick, dark lines indicate the mean flight direction for a particular mode. Confirmed colonies are associated with the south and southeast vanishing bearing modes.
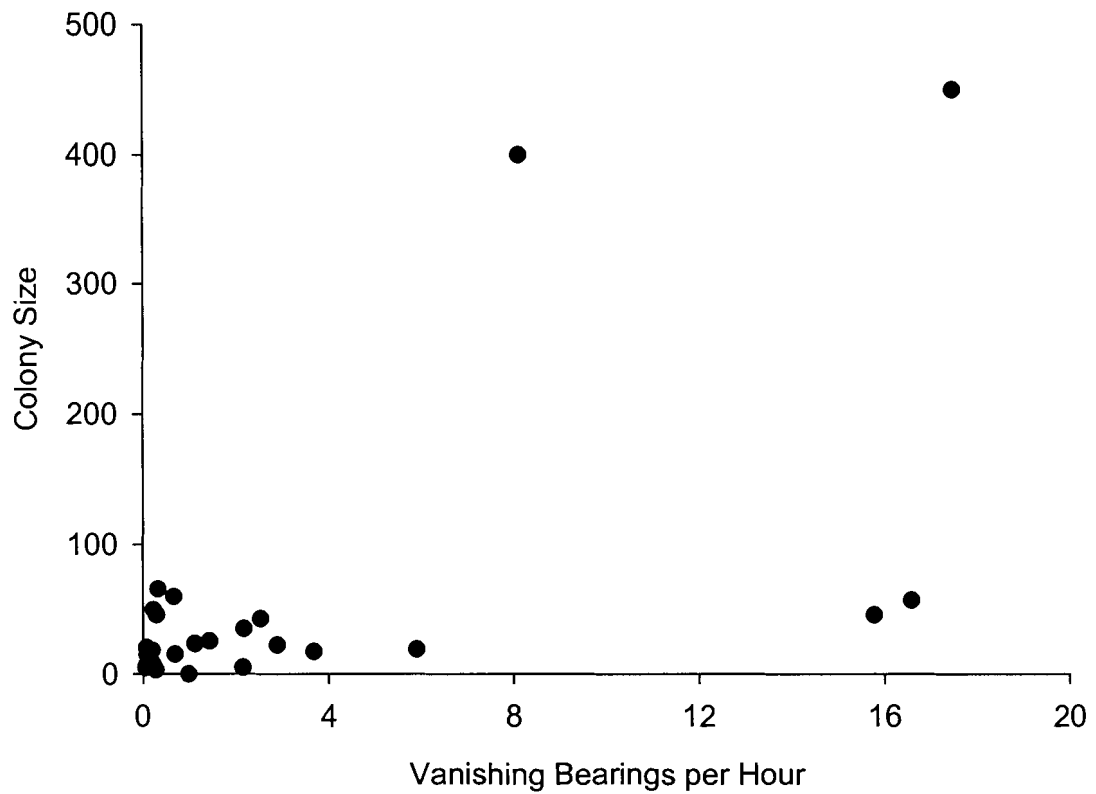
Figure 2-6: Relationship between the frequency of vanishing bearings of Great Blue Herons and size of the associated colony (from Vennesland 2003; McClaren 2004). Although this relationship is statistically significant (p=0.0005, r^2= 0.36), the ability of vanishing bearing frequencies to estimate colony size is compromised due to a variety of factors (see Discussion).

CHAPTER 3:
ALTERING THE DISTRIBUTION OF HERONS AMONG BREEDING COLONIES AS A STRATEGY TO MITIGATE PREDATION DANGER

Introduction

Predation theory argues that the threat of predation results in an optimal behaviour being adopted by an individual in its effort to minimize the probability of being killed by a predator (Lima and Dill 1990). As this threat of predation changes, the optimal behaviour may change as well. This response to changes in predation danger (sensu Lank and Ydenberg 2003) has been documented in many different systems in many different contexts (reviewed by Lima and Dill 1990). However, an individual's response to changes in predation danger has not been explicitly studied for understanding the variation observed in the distribution of breeding colonies of birds and the number of birds in those colonies.

Historically, predation has been considered as a selection pressure affecting the evolution of coloniality (Hamilton 1971; Wittenberger and Hunt 1985; Seigel-Causey and Kharitonov 1990; Danchin and Wagner 1997; but see Brown and Brown 1987). At the individual level, predation has been discussed as an important factor only for individuals located within a specific portion of a colony, such as the centre versus the perimeter (Brown and Brown 1987; Brown *et al.* 1990). In some instances, predation has been dismissed as a selective force due to few predatory events having been observed (e.g. van

Vessem and Draulans 1986; Brown and Brown 1987). However, this lack of predation events may be due to there being few predators on the landscape (Forbes 1989).

The same fitness costs and benefits of coloniality associated with predation act at both the evolutionary and ecological level. These benefits include a dilution effect and/or mobbing behaviour to decrease the probability of predation (Hamilton 1971; Turner and Pitcher 1986; Inman and Krebs 1987) while the costs include colonies becoming so large that they become conspicuous, thereby attracting predators and resulting in higher levels of predation (Wittenberger and Hunt 1985; Brown and Brown 2001). Turner and Pitcher (1986) argued that if the probability of a colony being detected by a predator increased proportionally with group size then there should be no advantage to group living. However, Inman and Krebs (1987) rebutted this argument saying that group living is not any less costly than solitary living if the probability of being detected by predators increases with group size. These costs and benefits set up a trade-off where the level of predation danger (as estimated by number of predators and/or attack rates) may influence the size and number of colonies within a population of colonial nesting birds.

A colonial nesting species which is undergoing an increasing level of predation compared to years past provides a suitable system for examination of this question. For example, the Pacific Great Blue Heron subspecies (*Ardea herodias fannini*) is endemic to southwestern British Columbia and breeds in colonies ranging in size from one to upwards of 400 pairs (Butler *et al.* 1995). Many studies have reported the Bald Eagle (*Haliaeetus leucocephalis*) as a significant predator of heron nestlings (Simpson *et al.* 1987; Forbes 1987, 1989; Norman *et al.* 1989; Butler 1992; Vennesland and Butler 2004). Vennesland and Butler (2004) have shown that incursions by Bald Eagles are the

likely reason for all herons in up to 42% of colonies to abandon breeding attempts in a single breeding season. Recently, the population of the Bald Eagle has been increasing (Figure 3-1) after a population decline in the 1970s due to pesticides and persecution (Buehler 2000; Elliott and Harris 2001). Butler and Vennesland (2000) hypothesised that herons may breed in a more dispersed pattern (i.e., a number of small colonies instead of a single large colony) as a response to this increasing predation danger. Understanding the mechanism leading to a change in nesting behaviour has important conservation implications as the Great Blue Heron is considered to be a species of "special concern" by COSEWIC (2004).

This study examines if benefits incurred from a dilution effect from nesting within a large colony can mitigate increases in predation danger on nestlings arising from an increase in predator populations despite the increased probability of detection of nesting within a large colony. A probabilistic model was created to predict the outcome of the interaction between these two opposing benefits. This model compares the expected annual reproductive success of herons nesting in various distributions of the number of colonies and colony sizes as the level of predation danger changes. Predation danger is altered through changes in the number of predators, the frequency of predatory attacks on nestlings, and the territorial behaviour of the predator. Differences in the reproductive success among different distributions of the number of colonies and colony sizes under differing levels of predation danger are discussed in terms of danger mitigation behaviour and implications for conservation.

Methods

The Model

Imagine a landscape where there is a single foraging site containing enough food for the entire breeding population of herons and their nestlings. Surrounding this foraging site are unlimited opportunities for nesting sites, all of equal and high quality. If a population of herons were to be placed on this landscape to breed, then, in the absence of nestling predation, they would be expected to fledge mE nestlings, where m is the proportion of a clutch of size E expected to survive to hatch. It is assumed that adult heron mortality during the breeding season is negligible.

The model determines the expected reproductive success of an individual breeding pair in a population consisting of N heron pairs for a given distribution of these pairs across $c = 1,2,...,C$ colonies. The reproductive success of the population is influenced by the characteristics of the herons, level of predation danger, length of time the nestlings are vulnerable to predation (t), and colony distribution and size (H_c). Pertinent characteristics of the herons include number of heron pairs (N) in the population and the expected number of eggs hatched (mE). The level of predation danger depends on the behaviour and number of non-territorial (P_{NT}) and territorial (P_T) eagles present, the daily attack rate of eagles upon heron nestlings (A), and the probability an eagle discovers a colony of some size s, ($p[F_s]$).

The purpose of this model follows from its ability to express how herons may mitigate a given level of predation danger through their distribution of breeding pairs across colonies on the landscape, for specified values of N, A, E, m, C, H_c, P_{NT}, P_T,

t, and $p[F_s]$. Additionally, manipulating the degree of territorial behaviour of the eagles can also alter predation danger. Though the model can provide an estimate of the reproductive success for a pair of herons for a given set of parameter values, this is not the stated purpose of the model.

All model trials were executed using the fixed values of $N = 100$, $E = 4$, $m = 1$, $C = 20$, and $t = 50$, while values for P_{NT}, P_T, the vector of values of H_c, and the degree of territorial behaviour of the eagles were varied to simulate different levels of predation danger. Values for $p[F_s]$ were calculated by the following submodel:

$$[\text{Eq. 1}] \quad p[F_s] = \beta_0 \left(\frac{1 + e^{-\beta_1(N-\beta_2)}}{1 + e^{-\beta_1(H_c-\beta_2)}} \right)$$

where β_0 is the daily probability of finding a single large colony with N pairs of herons, and β_1 and β_2 are the coefficients determining the shape of the detectability relationship between $p[F_s]$ and colony size. A heron pair's reproductive success is highly sensitive to the parameters of this submodel. For example, this model could assign values of $p[F_s]$ to be equal for all colony sizes such that colony size becomes irrelevant with respect to being detected by a predator, though predation danger may still vary for individual nests in colonies of different sizes.

To compare the estimated reproductive success among distributions of colonies for a given level of predation danger, the model allowed heron pairs to nest according to one of a set of colony distributions. Mathematically, each member of this set of distributions is known as a partition of N. There are as many partitions of N as there are ways that the distribution of N heron pairs among the C colonies can be arranged.

Each unique partition ρ_j is indexed by $j = 1,2,...,W$ possible partitions. For $N = 100$,

the two extreme partitions are 100 colonies of one (1) pair each, or one (1) colony of 100

pairs, where the number of all possible partitions of $N = 100$ is the impractically large

number of $W = 190{,}569{,}292$. This numerical constraint was overcome by restricting

colony sizes to be a multiple of five; thereby resulting in 20 partitions, i.e., $\dfrac{N}{5}$, yielding a

more practical number of partitions of $W = 627$, and therefore a colony of five heron

pairs to be the smallest group possible (H_{min}). The model then compares the preferred

colony distribution across different levels of predation danger. The level of predation

danger is determined from the per capita daily number of attacks on nestling herons, A,

and the number and behaviour of eagles. Allowing the daily predation rate to change

reflects possible specialization of eagles on heron nestlings. Eagle behaviour ranges

along a gradient of territoriality with one extreme consisting of territorial eagles whose

territories cover the entire landscape, even if $P_T = 1$, therefore rendering non-territorial

eagles irrelevant (therefore $P_{NT} = 0$), to the opposite extreme where eagles are non-

territorial with each heron colony being susceptible to an attack from any and all eagles

($P_T = 0$ and $P_{NT} > 0$). A third scenario looked at a combination of territorial and non-

territorial behaviour where territorial eagles defend their own unique heron colony from

all other eagles while non-territorial eagles were allowed to search for and attack any and

all heron colonies not under protection from a territorial eagle. This scenario may be

considered analogous to a situation where breeding adult eagles hold a territory and a

population of non-territorial juvenile eagles are on the same landscape. For this scenario,

the model only used the value of P_{NT} equal to four (4) eagles since values of $P_{NT} > 4$

produced qualitative results very similar to when $P_{NT} = 4$. Values of $P_{NT} < 4$ produced

qualitative results that were between the results obtained when $P_{NT} = 4$ and results

obtained from when only territorial eagles occurred.

The eagles are allowed to search for heron colonies with a defined probability

$p[F_s]$ of finding a colony on any particular day. Once found, eagles randomly depredate

nestlings based on the attack rate A and the uniform probability of finding a surviving

nestling among the remaining active nests within that colony. When more than one

colony is available to an eagle, colonies are depredated sequentially. Specifically, once a

colony is found, the first nestling is lost to predation based on the probability that the

eagle selects any individual nest (n), which is simply $\dfrac{1}{H_c}$, where $R_c = mEH_c$ is the

reproductive success of the colony before any depredation, and R_n is the reproductive

success of nest n. After each predation event, the model updates reproductive success by

subtracting one nestling from both R_n and R_c. Each time a nest becomes completely

depredated ($R_n = 0$) the probability of finding an active nest is increased by the

cumulative number of nests with $R_n = 0$, i.e. to $\dfrac{1}{H_c - \sum\limits_{n=1}^{H_c} 1 \; if \; R_n = 0 \; else \; 0}$. There is no

preference for nests based on the number of surviving nestlings when $R_n > 0$. Each day,

eagles continue to take nestlings until the colony is completely depredated or they reach

their daily attack rate A. At the end of the breeding season of length t days, the

performance of each partition is measured in terms of the average reproductive success

per nest of the population (R_N) where:

$$[Eq. 2] \ \overline{R}_N = \frac{\sum_{n=1}^{N} R_n}{N}.$$

The Analysis

Each partition is ranked on a dispersion index ranging from a partition that is

termed 'clumped' (a single large colony) to 'dispersed' (20 small colonies) by increasing

the standard deviation of colony distribution, or partition (SD_ρ). A value for SD_ρ

measures the degree of dispersion of herons among colonies and is calculated from the

distribution of colony sizes across colony number where colonies are sequentially and

arbitrarily numbered from $i=1$ to C so that the mean (μ_ρ) is equal to:

$$[Eq. 3] \ \mu_\rho = \frac{\sum_{i=1}^{C} iH_c}{N}$$

and therefore the standard deviation is:

$$[Eq. 4] \ SD_\rho = \sqrt{\left(\frac{\sum_{i=1}^{C} i^2 H_c}{N} - \mu_\rho^2 \right)}.$$

Therefore, if all herons are in a single colony then $SD_\rho = 0$, whereas if herons are

dispersed evenly across all colonies then SD_ρ is maximized such that when $N = 100$ and

$C = 20$ then $SD_\rho = 5.766$. For a given set of parameter values (eagle number, attack

rate, etc.), the slope of the linear relationship between the average reproductive success

and the dispersion index is used as an index to describe the performance of clumped

versus dispersed nesting strategies for a given level of predation danger. A positive slope suggests that a dispersed nesting strategy is favoured whereas a negative slope suggests that a clumped nesting strategy is preferred. If the slope is zero there is no difference in reproductive success between any nesting strategies. Surface plots showing the value of the slope for each combination of eagle number and daily attack rate display the predicted preferred nesting strategies at differing levels of predation danger.

Models were run for each of the three eagle behaviours described above to evaluate two contrasting assumptions regarding the conspicuousness of heron colonies of different sizes. Due to an arbitrary manner of selecting parameter values for testing the effect of differential colony detectability, varying with colony size, it was critical to test if the difference in detectability of the different sized colonies influenced the results from the models. The first evaluation assumed that larger colonies are more conspicuous and therefore easier for predators to find (differential model). That is, parameter values for Eq. 1 were chosen to provide an obvious contrast in values for $p[F_s]$. Figure 3-2 exemplifies the type of relationship between colony size (s) and $p[F_s]$ investigated in this study. The second evaluation assumed there was no difference in detectability among colonies of different sizes (null model). This was accomplished by setting $p[F_s]$ to a constant for all C colonies for each of the three model scenarios above (Table 3-1). For all models, a matrix of values of eagle number and daily predation rate per eagle is used to define the varying levels and combinations of predation danger.

Results

Differential Model

The behaviour of the eagles has a large effect on the performance of the partitions of heron colonies. Under the "territorial eagles only" behaviour, Figure 3-3a shows that the number of eagles has little effect on the preferred nesting distribution. However, as the level of predation danger increases through an increase in the daily attack rate, A, the stronger the preference for a more dispersed nesting distribution. The switch from a clumped nesting distribution to a dispersed nesting distribution occurs as the dilution effect breaks down, causing nesting in large colonies to become a poor decision by the herons due to the conspicuousness of the colony to predators. Adding non-territorial eagles to the model predicts that increasing eagle numbers could lead to a more dispersed nesting distribution of herons (Figure 3-3b). As eagle numbers rise, there is a tendency for more dispersed nesting by herons. Consistent with the "territorial eagles only" behaviour, as the predation rate increases the more profitable nesting distribution is several small colonies. With few territorial eagles and low daily predation rates, the surface plot suggests a clumped nesting distribution is strongly preferred, possibly due to herons paying a small price to a territorial eagle in an attempt to avoid predation by the many non-territorial eagles. The "non-territorial eagles only" model (Figure 3-3c) also results in similar predictions about the preferred nesting distribution. A more dispersed nesting distribution is predicted to be preferred as predation danger is increased but only up to a point before it appears that the trend is reversed. This reversal is likely due to overall predation levels being so high that it reduces the reproductive success of the

herons to zero, creating the appearance of no nesting distribution being preferred. High

levels of predation are incompatible with sustainability of the heron population.

Null Model

Models where all colonies have an equal probability of being found, regardless of

size, suggest that the difference in colony detection is an important factor in determining

the performance of different colony distributions. There is little difference between the

"territorial eagles only" and "territorial and non-territorial eagles" models (Figures 3-3d

and 3-3e). In both cases, a clumped distribution of heron colonies seems to be favoured,

with the preference increasing at higher territorial eagle numbers. As the predation rate

increases, the preference approaches neutral due to reproductive success being close to

zero for all partitions, thereby resulting in a slope equal to zero. Figure 3-3f shows that

for the "non-territorial eagles only" behaviour, the predation levels are so high that the

reproductive success is very near zero, or at zero, for all combinations of eagle number

and predation rate.

Discussion

This model formalizes the hypothesis that altering the distribution of breeding

herons among colonies of different sizes is a possible strategy colonial nesters can use to

mitigate the effects of increasing predation danger. However, direct field tests of this

hypothesis are difficult to execute. Hogstad (1995) found a positive correlation between

the nesting distribution in fieldfares (*Turdus pilaris*) and the abundance of rodents. When

rodent numbers crashed, their main predator (mustelids) switched to preying on

fieldfares. This increase in danger is suggested to cause a shift in fieldfare nesting

distribution from colonial to solitary in years when the rodent population is low (Hogstad 1995). The presence of tawny owls (*Strix aluco*) in southern Sweden was correlated with smaller colonies of fieldfares when compared with northern Sweden where the owls were absent (Wiklund and Andersson 1994). Many studies have put forward correlations of predation danger with degree of colonial nesting. Clode (1993) claims that the nesting distributions of seabirds are correlated with predation danger where highly dangerous inshore habitats have seabird species that nest solitarily or in small colonies while those in less dangerous offshore habitats are more likely to nest in larger colonies, consistent with the model predictions. Most studies have attempted to determine only if the probability of predation is greater inside or outside a colony (e.g., Andersson and Wiklund 1978; Bellinato and Bogliani 1995) but few studies have varied or controlled for the degree of danger in the environment.

This model has proven useful as a technique for predicting the general trend in heron nesting distribution that is expected as predation danger changes. Since determination of the optimal nesting distribution of a population of herons for a given level of predation danger is not the aim of this model, then the problem of optimal group sizes being unstable (Sibly 1983) can be ignored. To clarify, each partition created in the model is likely to be unstable in terms of the distribution of individuals between colonies because an individual in a poorly performing colony within that partition could likely increase its probability of reproductive success by moving to another colony. Sibly (1983) predicts group sizes to be larger than the predicted optimal group size because individuals in small groups would increase their fitness by joining a group that is already at the optimal size, therefore, predictions of an optimal distribution of colony numbers

and sizes from this model would be ineffective. However, the prediction of group sizes being larger than optimal may dampen the effects of increased predation danger, predicting a more dispersed nesting distribution.

Although the model suggests that a more dispersed nesting distribution may be beneficial as the predation danger increases, other selection pressures may retard the degree to which predation danger is predicted to affect the nesting distribution. There have been a number of hypotheses put forward to explain the evolution of coloniality for reasons other than as a means to avoid predation. These include food-finding benefits (e.g. Ward and Zahavi 1973; Krebs 1974), hidden leks (Draulans 1988; Morton *et al.* 1990; Wagner 1993), and conspecific reproductive success (Danchin *et al.* 1998). Regardless of what the true biology is in the case of herons, this model has not investigated the trade-off between mitigating predation danger and these other selection pressures.

As shown by comparing two contrasting assumptions of colony detectability with respect to colony size, the assumption of large colonies being easier to find is key to the model's predictions. This assumption has been proposed in the literature (Wittenberger and Hunt 1985) but has not been adequately tested. Simpson *et al.* (1987) suggest that new heron colonies decrease in their profitability over time as predators begin to increasingly exploit the colony. The model predicts very little preference for small colonies if they were found at the same probability as large colonies compared to when colonies are found with increasing probability as colony size increases (see Figures 3-3a, b, d, and e) thus suggesting a strong pressure for herons to refrain from nesting in small colonies if all colonies were found with an equal probability regardless of colony size.

However, there exist many small colonies of herons thereby suggesting that there are differences in detectability between colonies of different size.

An intriguing outcome of the model is that it may in part be able to explain the variance in reproductive success of Great Blue Herons nesting in large versus small colonies as described by Butler *et al.* (1995). Butler *et al.* (1995) compared large colonies to small colonies throughout the Strait of Georgia, British Columbia and found they had similar mean reproductive success but the variance in reproductive success was largest for small colonies and smallest for large colonies. The logic of this model suggests that small colonies may be able to avoid predation by being cryptic to the predators, thereby resulting in a high reproductive success in the circumstance where they are not discovered before chicks fledge. However, if a small colony happens to be found, then an eagle predator could exert heavy predation on the few nests in that colony, causing reproductive success to be low. Large colonies would be found readily by an eagle predator but should be better able to withstand an attack rate equivalent to one executed on a small colony. Looking across a number of small colonies, the mean reproductive success could conceivably be similar to that of the large colonies but the variance would be high due to the "all-or-nothing" outcome of the colony's reproductive attempt. However, any differences in predation danger between colony locations was not accounted for by Butler *et al.* (1995), therefore it cannot be said with certainty that this hypothesis explains this phenomenon.

The predictions of this model can be used to aid in the conservation of colonial nesting species. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) considers the Pacific Great Blue Heron population in southwestern B.C. of

"Special Concern" (COSEWIC 2004) in part due to the frequent abandonment of breeding attempts by entire colonies (Vennesland and Butler 2004). Conservation measures include enacting and enforcing laws that protect heron colonies from human disturbance during the breeding season and protecting a few extant large colonies by purchasing the land on which they occur. This latter action implies a belief that these heron colonies are likely to persist at that location.

However, the model suggests that a more dispersed nesting distribution may be more likely to be optimal for herons if they are behaving to retain reproductive success as Bald Eagle numbers continue to recover. That is, the landscape may be becoming more dangerous for individual herons nesting in conspicuous large colonies as the danger from eagle predation increases. This contemporary practice of protecting individual colonies may therefore not be suitable in the future as herons may require a landscape containing many nesting options to allow for flexibility in their choice of location and size of their breeding colony to mitigate increasing predation danger. Future conservation initiatives would be more robust to uncertainties about their efficacy if they were to allow for this behaviour by protecting a number of potential colony sites (i.e., an entire landscape) instead of only the currently used sites. As raptor numbers rise in areas where they are currently depressed, alterations in colonial breeding behaviour can be anticipated as a possible response to this increase in predation danger.

Table 3-1: Parameter values for a differential model where larger colonies have a higher probability of being detected by a predator and a contrasting null model where all colonies have equal probability of being detected by a predator. Column subheadings "Territorial", "Territorial and Non-territorial", and "Non-territorial" refer to the behaviour of the eagles included in the model.

Symbol	Definition	Differential Model			Null Model		
		Territorial	Territorial and Non-territorial	Non-territorial	Territorial	Territorial and Non-territorial	Non-territorial
N	Pairs of herons	100	100	100	100	100	100
E	Clutch size	4	4	4	4	4	4
m	Clutch survival rate to hatch	1	1	1	1	1	1
C	Max # of colonies	20	20	20	20	20	20
H_{min}	Minimum colony size	5	5	5	5	5	5
t	Number of provisioning days	50	50	50	50	50	50
β_0	Probability of finding a colony of size N	0.15	0.15	0.10	0.10	0.10	0.10
β_1	Coefficient of rate of change in $p[F_s]$ with colony size	0.05	0.05	0.075	0	0	0
β_2	Colony size where $p[F_s]=0.5$	50	50	50	50	50	50

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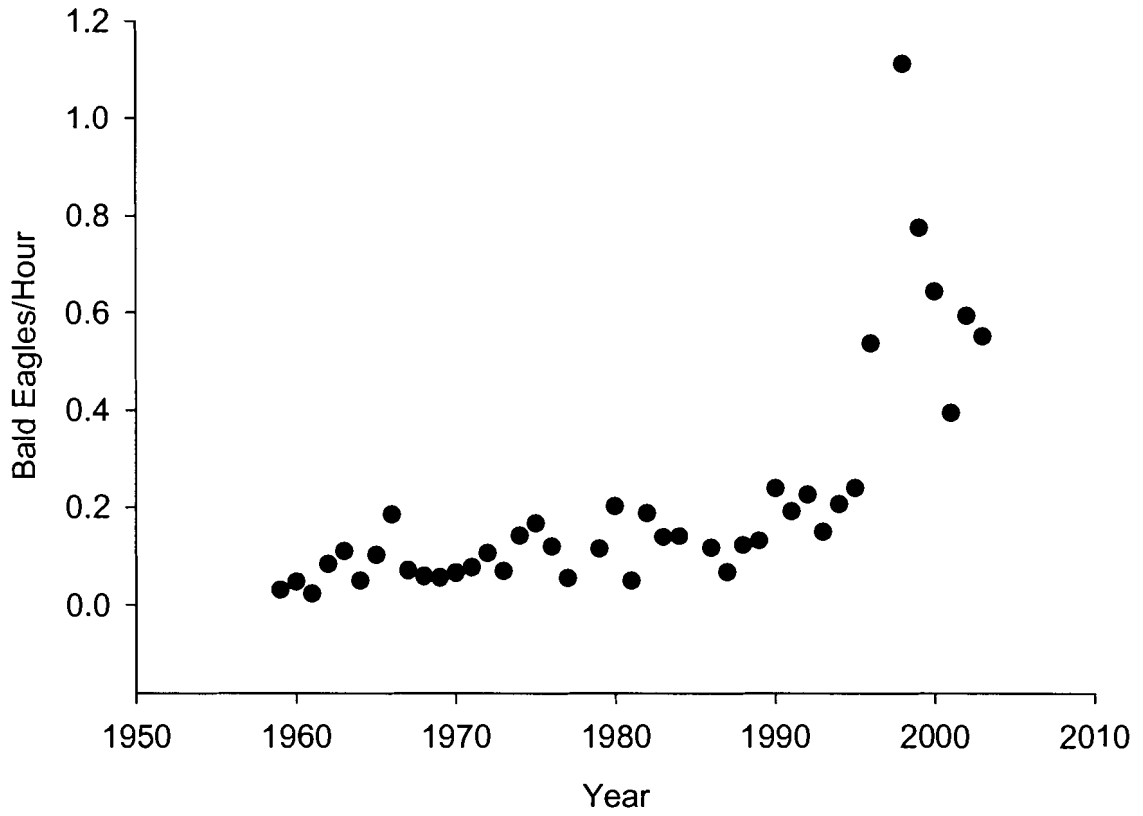
Figure 3-1:   Index of Bald Eagle abundance on Vancouver Island from 1959 to 2003. Data taken
from Christmas Bird Count (National Audubon Society 2002).
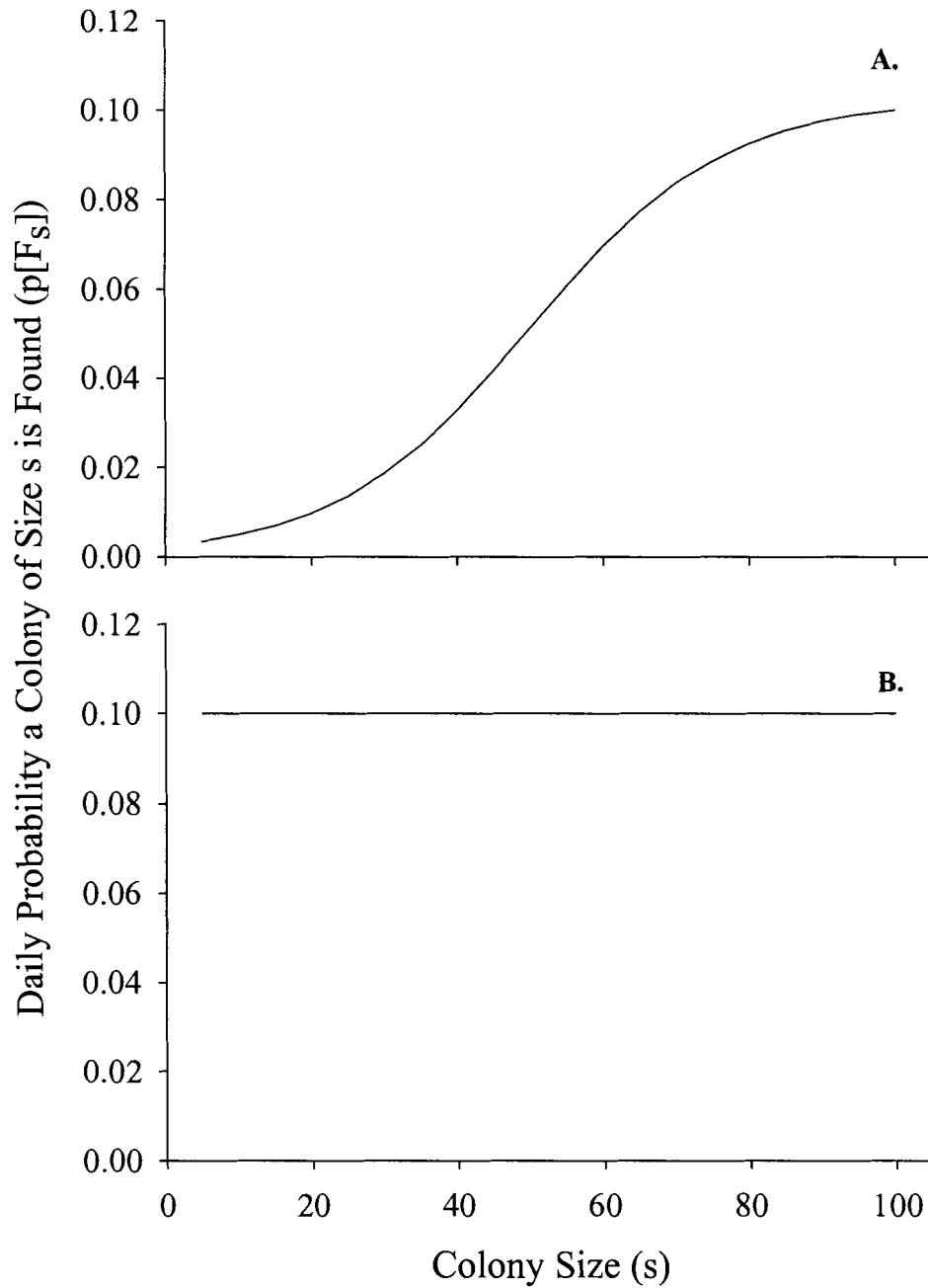
Figure 3-2: Two examples of the relationship between colony size, H_c, and the daily probability with which a colony of that size is found by a predator used in the model, $p[F_s]$.

Initial model runs used a relationship where large colonies are more likely to be discovered by an eagle (differential model; A.) while a contrasting model tested this assumption by using a relationship where all colonies have the same probability of being found (null model; B.).
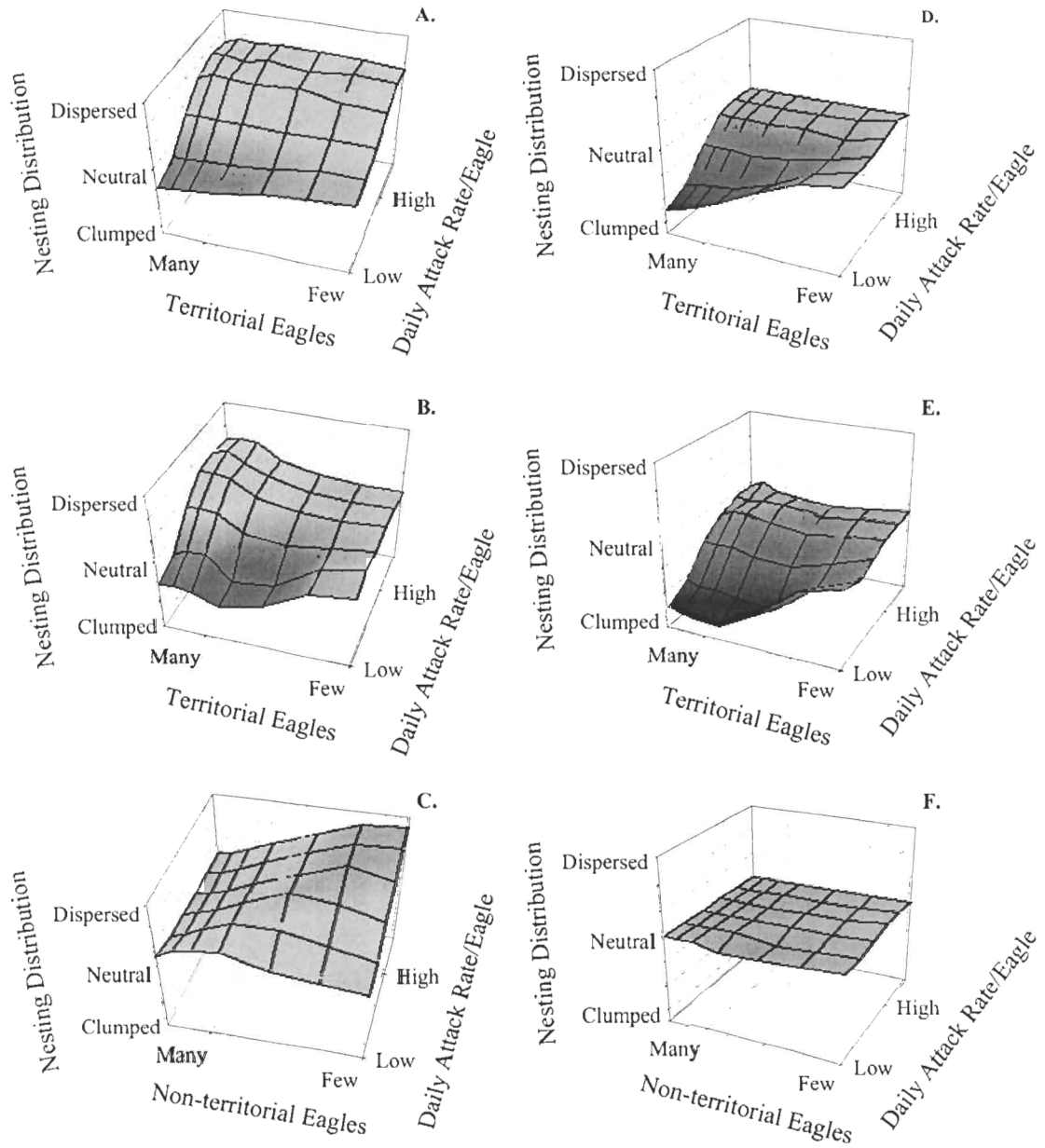
Figure 3-3: Changes in the reproductive success of the heron breeding population (Z-axis) as the level of predation danger changes. The level of predation danger is determined by both the number of territorial or non-territorial eagles (X-axis) and their attack rates (Y-axis). Graphs A-C (differential models) shows how the nesting distribution changes with predation danger for "territorial eagles only" (A), "territorial and non-territorial eagles" (B), and "non-territorial eagles only" (C), respectively. Graphs D-F (null models) have the same eagle behaviours as above, but all colonies have the same probability of being discovered by an eagle.

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CHAPTER 4:
EFFECTS OF FORAGING SITE SIZE AND QUALITY
ON THE DISTRIBUTION OF GREAT BLUE HERONS

Introduction

Determinants of avian colony sizes and their distribution have long been debated (Furness and Birkhead 1984; Gibbs *et al.* 1987; Cairns 1989; Gibbs 1991; Brown and Brown 2002; Brown *et al.* 2002; Ainley *et al.* 2003). It has been suggested that colonies are dispersed in a manner that decreases the level of competition between colonies for food while minimizing distance costs (Furness and Birkhead 1984; Griffin and Thomas 2000; Brown and Brown 2002; Ainley *et al.* 2003). It has also been argued that the amount of foraging area available near a colony is proportional to the size of the colony (Gibbs *et al.* 1987; Cairns 1989; Gibbs 1991; Gibbs and Kinkel 1997; Griffin and Thomas 2000; Brown *et al.* 2002). In addition, past studies have assumed all foraging areas to be of equal quality, differing only in size (Gibbs *et al.* 1987). Only a handful of studies have attempted to measure differences in quality (Brown *et al.* 2002; Ainley *et al.* 2003), with varying degrees of success.

Great Blue Herons (*Ardea herodias fannini*) foraging in marine habitats in the Lower Mainland region near Vancouver, British Columbia, Canada offer a good system to test if individuals are distributed across foraging sites in proportion to the size or quality of the foraging sites. Great Blue Herons nest in colonies ranging in size up to 400 pairs in this region (Butler *et al.* 1995). The location and size of colonies in relation to nearby foraging sites is known. The foraging sites typically are intertidal mudflats that

can be considered as discrete, isolated patches. Additionally, foraging site size was measured using GIS, foraging site quality was compared by estimating the abundance of food at each site, and the number of herons on each foraging site was determined during May and June as this was found to be the period of nestling provisioning (Butler 1993).

The purpose of this study was to create and test a conceptual model of heron foraging during their breeding season to evaluate competing hypotheses concerning the relationship between the location of colonies on the landscape and the foraging sites chosen by the provisioning herons associated with those colonies. The concept was to develop a spatially explicit model incorporating information on colony location and size (number of breeding herons), foraging site size, foraging site quality, intraspecific competition, and the distance a heron must travel from a colony to reach the foraging site. Then, by allowing individual herons to choose the foraging site that maximizes their individual payoff, hypotheses can be tested to judge the ability of this model for describing the number of herons observed on each foraging site.

A null model based on the ideal free distribution (IFD; Fretwell and Lucas 1969), was designed to predict the distribution of individuals across foraging sites as individuals trade-off their yield benefit of foraging at a site near their colony with the costs of intracolony and intercolony competition and travel, dependant upon what other individuals in the population have chosen to do. The assumptions of the IFD include individuals being free to move to any foraging site and perfect knowledge of the environment (Fretwell and Lucas 1969). Cressman *et al.* (2004) have shown that the IFD can be considered a game theoretic concept for a simple single species two-patch system. This study uses this game theoretic approach to determine the IFD of a population of

herons nesting in a landscape consisting of multiple colonies and foraging sites. The predicted distribution of herons is generated for a particular set of model parameters related to foraging yield and costs by placing herons from colonies of known size and location on foraging sites in a manner such that no individual can unilaterally move to another foraging site and improve its payoff, i.e., its foraging yield. This stable distribution of individuals across foraging sites is defined to be in Nash equilibrium (NE). Since an NE can exist for any set of parameters, a key purpose of the model is to (1) determine what set of parameter values generates a particular NE that best describes the observed distribution of herons on the foraging sites, and (2) then ask if these parameter values are biologically sensible. The attributes of the landscape incorporated into the model were estimated directly from field data. Data on colony location and size and foraging site size were taken from the literature. Distance between each foraging site and colony was determined to create a spatially explicit and accurate recreation of the landscape. Foraging site quality was estimated by using a beam trawl to estimate fish density at each foraging site.

A successful endorsement of this modelling approach confers credibility to model predictions that can guide conservation decisions. Conservation measures impacting either foraging areas or present and/or potential colony locations could be assessed using the modelling approach presented here.

The Model

Study Area

The Lower Mainland region of southwestern British Columbia is strongly influenced by the Fraser River estuary delta. The delta region of the mouth of the Fraser River provides excellent habitat for Great Blue Herons (Butler 1995). Herons forage on the large intertidal mudflats near the Fraser River and in nearby Burrard Inlet (Figure 4-1). These foraging sites vary from extremely small (18 ha) to very large (>3,000 ha) (Table 4-1) and also vary in the amount of eelgrass (*Zostera* spp.). In 2003, there were eight known colonies (McClaren 2004), mainly located near foraging sites (Figure 4-1) and ranging from nine to 400 pairs (Table 4-2).

Premise

Every heron associated with any breeding colony c acts independently of other herons by choosing a foraging site r that maximizes its individual payoff ($Y_{r,c}$) from available foraging sites R to provision its young. This premise implies that under an IFD, the distribution of herons across foraging sites results in a Nash Equilibrium (NE). An NE of herons distributed across foraging sites occurs when no heron from colony c foraging at foraging site r can improve $Y_{r,c}$ by choosing to forage at a different foraging site.

Goal

Under the assumption that an NE exists for the distribution of herons across all foraging sites, the goal is to solve for the combination(s) of parameter values for a, w, s

and *b* (see Definitions below) that produce the NE distribution that best describes the breeding season distribution of herons observed on the foraging sites.

Question

For statistically optimal parameter estimates for *a*, *w*, *s* and *b*, does the proposed model predict a distribution of herons on foraging sites that 'acceptably' approximates the observed distribution on those sites? 'Acceptability' is adjudicated by statistically evaluating the observed distribution of herons with respect to the predicted distribution of herons.

Null Hypothesis

The observed distribution of herons on the foraging sites along the coast of the Lower Mainland of British Columbia can be described as an NE distribution for the above conceptual-hypothetical model of individual payoff for biologically sensible values of the parameters *a*, *w*, *s* and *b*.

Corollary

Non-rejection of the null hypothesis provides empirical support for the proposed model and allows interpretation of the model in the context of heron conservation. For example, the coefficient of distance costs (*w*), and realized yield ($Y_{r,c}$) can provide guidance concerning the benefit of proximity of heron colonies to foraging sites and yield, and the ranking of sites in terms of gross yield, respectively.

Definitions

c :　Index for a colony, $c = 1,...,C$

C : The total number of colonies

c_* : A particular colony

r : Index for foraging sites, $r = 1, ..., R$

R : The total number of foraging sites

r_* : A particular foraging site

$Y_{r,c}$: Individual payoff per heron (energy units per heron)

a : Maximum possible gross energy collected by a heron (energy units per heron, $a > 0$) in a defined time period t

v : Maximum realizable gross energy collected by a heron (energy units per heron) in a defined time period t

f_r : Total energy units available on foraging site r (not specific to any index) in a defined time period t

$\bar{f}_r$: Total energy units available on foraging site r (when using site size as an index) in a defined time period t

$\tilde{f}_r$: Total energy units available on foraging site r (when using fish density as an index) in a defined time period t

$D_{r,c}$: The straight-line distance between colony c and foraging site r

b : Instantaneous coefficient of attenuation of the time a heron spends foraging on a site due to time constraints such as flight time ($D_{r,c}^{-1}$, $b \geq 0$)

w : Instantaneous coefficient of attenuation of potential energy yield due to distance costs ($D_{r,c}^{-1}$, $w \geq 0$)

$h_{r,c}$: The number of herons from colony c predicted to be on foraging site r

$\breve{h}_{r,c}$: The number of herons from colony c predicted to be on foraging site r at a Nash Equilibrium

s : Scalar to assure that the total number of herons from all colonies C predicted to be on all foraging sites R equals the number of herons from all colonies C observed on all sites R (dimensionless, $0 \leq s \leq 1$)

$\hat{h}_r$: The predicted number of herons from all colonies foraging on site r

$\dot{h}_r$: The observed number of herons from all colonies foraging on site r; (note that there is no information as to which colonies heron s observed on foraging sites are from)

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h_c : The number of herons counted in colony c

t : Time period (day, week or season), but note that time is only an implicit consideration in this model

Foraging Model

The individual payoff Y_{r_*,c_*} of a heron from a particular colony c_* foraging on a

particular foraging site r_* is proposed to be a function of the total energy available on

foraging site r_*, f_{r_*}, discounted by the potential gain lost through competition with other

herons on foraging site r_*, $\hat{h}_{r_*}$, and the distance, D_{r_*,c_*}, travelled between the colony and

the foraging site. The predicted number of herons on foraging site r_*, $\hat{h}_{r_*}$, is defined by:

$$[\text{Eq. 1}] \quad \hat{h}_{r_*} = s \sum_{c=1}^{C} h_{r_*,c} e^{-bD_{r_*,c}},$$

where b discounts the potential number of herons foraging on a foraging site due to

herons' other time commitments, and s scales $\hat{h}_{r_*}$ to assure the number of herons from all

colonies C predicted to be on all foraging sites R equals the number of herons from all

colonies C observed on all foraging sites R. Distance costs can be conceptualised as the

potential yield an individual forgoes due to required travel time to and from the foraging

site. The model assumes that each heron chooses only one foraging site to exploit during

the breeding season and that there is an insignificant cost of making a choice to use a

different site. The model also proposes that a heron's individual payoff (Y'_{r_*,c_*}) is

diminished proportionally by the number of herons on foraging site r_*, i.e.,

$$[\text{Eq. 2}] \quad Y'_{r_*,c_*} = \frac{f_{r_*}}{\hat{h}_{r_*}},$$

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therefore this formulation can be considered a dynamic game since the yield is altered by the presence of conspecific competitors.

The value Y'_{r_*,c_*} is then constrained by a saturation curve to limit a heron's foraging gain (v) to the lesser of its maximum possible daily intake (a) or the total energy available on site r_*, (f_{r_*}) i.e.,

$$[Eq. 3] \quad v = \frac{af_{r_*}}{a + f_{r_*}},$$

such that the realized energy gain is defined by

$$[Eq. 4a] \quad Y_{r_*,c_*} = \frac{vY'_{r_*,c_*}}{v + Y'_{r_*,c_*}},$$

with the following limit,

$$[Eq. 4b] \quad \lim_{Y'_{r_*,c_*} \to 0} Y_{r_*,c_*} = Y'_{r_*,c_*},$$

when conspecific competition alone is considered, but is defined by

$$[Eq. 5a] \quad Y_{r_*,c_*} = \frac{vY'_{r_*,c_*}}{v + Y'_{r_*,c_*}} e^{-wD_{r_*,c_*}},$$

with the following limit,

$$[Eq. 5b] \quad \lim_{h_{r_*} \to 0} Y_{r_*,c_*} = ve^{-wD_{r_*,c_*}},$$

when distance costs of the foraging heron are also included.

Evaluating a Nash Equilibrium

To determine if an individual heron from any particular colony c_* on any particular foraging site r_* is maximizing its gross energy yield, the change in Y_{r_*,c_*} if a heron from colony c_* were to move from foraging site r_* to any new site must be evaluated. Representing the potential movement of a heron from colony c from one site, r', to another, r'', by $h_{r'>r'',c}$, gives

$$[\text{Eq. 6}] \quad \frac{dY_{r_*,c_*}}{dh_{r'>r'',c_*}} = Y_{r'',c_*} - Y_{r',c_*} + \frac{dY_{r'',c_*}}{dh_{r'>r'',c}},$$

where

$$[\text{Eq. 7a}] \quad \frac{dY_{r'',c_*}}{dh_{r'>r'',c}} = -\frac{\left(\dfrac{v^2 f_{r''} s e^{-(b+w)D_{r'',c_*}}}{\hat{h}_{r''}^2} \right)}{\left(v + \dfrac{f_{r''}}{\hat{h}_{r''}} \right)^2},$$

with the following limit,

$$[\text{Eq. 7b}] \quad \lim_{h_{r'} \to 0} \frac{dY_{r'',c_*}}{dh_{r'>r'',c}} = -\left(\frac{v^2 s e^{-(b+w)D_{r'',c_*}}}{f_{r''}} \right).$$

When $\dfrac{dY_{r_*,c_*}}{dh_{r'>r'',c_*}} \leq 0$ for all $r' = 1,\dots,R$ and all $r'' = 1,\dots,R$ with $r' \neq r''$, or $\dfrac{dY_{r_*,c_*}}{dh_{r'>r'',c_*}} > 0$ but $h_{r',c_*} = 0$, then no individual heron can improve its yield by unilaterally moving, therefore, the distribution of herons is in an NE.

Data

Four data sources pertaining to a subpopulation of herons associated with intertidal mudflats along the coast of the Strait of Georgia, near the Lower Mainland (greater Vancouver), British Columbia, were used to challenge the proposed foraging model: (1) counts of herons observed foraging at low tide ($\dot{h}_r$), $R = 8$, (2) counts of adult herons ($\tilde{h}_c$) in known breeding colonies, $C = 8$, (3) distances between each foraging site and each colony, and (4) estimates of the energy available to herons at low tide on all significant sites (f_r). The observed heron distribution was determined through ground-based surveys conducted at low tide throughout the herons' provisioning period in May and June of 2003. Maximum counts were used as the estimates for heron usage (Table 4-1). Heron counts in colonies were taken from data found in McClaren (2004) (Table 4-2). The distance between each foraging site and colony was calculated as the straight-line distance from the geographic positioning system (GPS) location of each point (Table 4-3). Two estimates of the energy available (f_r) on foraging sites were used. One estimate was the size of the intertidal mudflat (Table 4-1). All sizes except for Port Moody and Maplewood were taken from Ryder *et al.* (2004). The size of the Port Moody and Maplewood foraging sites was estimated from Canadian Hydrographic Service marine charts by determining the intertidal area using GIS data. The Boundary Bay foraging site was split into three separate foraging sites (Boundary Bay East, Boundary Bay Centre, and Boundary Bay West) while the Fraser River estuary was split into two separate foraging sites (Roberts Bank and Sea Island). Splitting these foraging sites was done to accommodate the exceptionally large size of these sites and to acknowledge the heterogeneity in available energy (fish abundance) found at each site. Some regions of

the Fraser River estuary were not considered as part of either the Roberts Bank or Sea Island foraging sites since this area was excluded from heron use surveys as preliminary data suggest that few herons used this area.

The second estimate of energy available (f_r) was a combination of foraging site size and quality estimated from fish density. In 2002 and 2003, a beam trawl was towed behind a herring skiff to sample the fish assemblage at key foraging sites. Trawls were conducted during the periods near low tide as this time is when herons most intensely forage (Butler 1993; Matsunaga 2000) and the sampling effort to capture estuarine fish is most effective. Herons rely heavily upon the fish assemblage characteristic of shallow coastal eelgrass beds (Butler 1993). The beam trawl was 2.13 m in width and 6.4 m in length with 0.6 cm mesh at the distal end. Trawls were conducted in 1.5-2 m of water for 50-100 m at approximately 2.5 km/h. Date, time, tidal height, and GPS coordinates were noted for each trawl, with GPS also being used to measure the length (m) of each trawl. All fish were identified, counted, and returned to the water. Trawls were conducted between July 4 and August 7, 2002 and July 12 and September 10, 2003. The most abundant fish species caught were shiner perch (*Cymatogaster aggregata*), three-spine stickleback (*Gasterosteus aculeatus*), several sculpin species (mainly staghorn sculpin (*Leptocottus armatus*)), bay pipefish (*Syngnathus griseolineatus*), crescent gunnel (*Pholis laeta*), saddleback gunnel (*P. ornata*), and penpoint gunnel (*Apodichthys flavidus*)).

Fish catch was converted to catch-per-unit-effort (CPUE, Ricker 1975) of shiner perch abundance to generate an index of available energy. Since compelling evidence for a ln-linear relationship between CPUE and tidal height was found, raw CPUE estimates for the above-mentioned species were used to calculate a CPUE correction factor to

account for the differences in tidal height when trawls were done. The relationship provided a value of P=0.12 (Figure 4-2), strong enough that it was judged important to be considered when calculating CPUE. Therefore, for each trawl at foraging sites included for this model, the CPUE corrected to a zero (0) tidal height using

$CPUE_0 = CPUE_A e^{0.351A}$ where A is tidal height in metres.

Most shiner perch caught were young-of-the-year (YOY) born ovoviviparously in late June or early July. The CPUE of the YOY is be expected to decline with time as individuals suffer mortality and/or become more mobile and thus more difficult to catch due to avoidance of the beam trawl or altering their habitat. For most sites, beam trawl samples were collected on only one occasion, however at Boundary Bay and Roberts Bank beam trawls were collected throughout the summer to measure changes in $CPUE_0$ over time due to changes in catchability (Ricker 1975). A strong trend was detected (Figure 4-3); therefore $CPUE_0$ for all trawls were further standardized to day 0 of the season (June 30) using the seasonal change in catchability estimated for the seasonal series of Roberts Bank trawls, such that $CPUE_{0,0} = CPUE_{0,t} e^{-0.047t}$ where t is the day of season the trawl was conducted. The average $CPUE_{0,0}$ was converted to an energy equivalent measure for each site by multiplying $CPUE_{0,0}$ by the size of the foraging site ($\tilde{f}_r$). No shiner perch were caught at Port Moody so a particularly conservative $CPUE_{0,0}$ based upon the abundance of non-shiner perch fish caught was used to estimate the energy available at this site. The Capilano River foraging site was never sampled so it was assigned a small value of $CPUE_{0,0}$ equivalent to Port Moody.

Model Implementation

The model was implemented using data from eight colonies ($C = 8$) of different sizes and eight foraging sites ($R = 8$) of different sizes and energy availability associated with the coast of the Lower Mainland of British Columbia. Geospatial colony inventory data were used to calculate the straight-line distance between each colony and foraging site to determine distance costs (Table 4-3).

To begin any single model run, and for any set of values for parameters a, w, s and b, all herons associated with all colonies were randomly assigned to a foraging site. This results in $R \times C$ initial values for $h_{r,c}$ which are almost certainly non-optimally distributed across those sites. Next, the values for $Y_{r,c}$ and $\dfrac{dY_{r,c}}{dh_{r'>r'',c}}$ are calculated for all $R \times (R-1) \times C$ possible decision choices. If any values for $\dfrac{dY_{r,c}}{dh_{r'>r'',c}}$ are found to be positive, meaning an energy gain would be obtained by moving, then a discrete fraction of a heron (Δh) is moved from heron subpopulation $h_{r',c}$ to $h_{r'',c}$. In practice, $\Delta h = 0.1$ proved to be a good balance between acceptable resolution and efficient computation. The choice of which heron fraction to be moved was based on which value of $\dfrac{dY_{r,c}}{dh_{r'>r'',c}}$ was largest. The processes of calculating $Y_{r,c}$ and $\dfrac{dY_{r,c}}{dh_{r'>r'',c}}$, then moving the herons receiving the most benefit from a decision to move, was repeated until all $\dfrac{dY_{r,c}}{dh_{r'>r'',c}} \leq 0$ or $h_{r',c} = 0$, at which point an NE of the distribution of herons was declared. Each NE

distribution of herons, $\breve{h}_{r,c}$, was statistically evaluated for its goodness-of-fit (GOF) to the observed distribution of herons, $\dot{h}_r$.

Statistical Evaluation

Solutions for the NE distribution of herons on foraging sites, $\breve{h}_{r,c}$ can be obtained for any combination of the values (hypotheses) for the four parameters a, w, s and b. However, the degrees of freedom of this model are at most two since values for s and b are determined directly from the data and the posed values for a and w. Specifically, s and b are solved to yield the following equality, given a and w,

$$(\text{Eq. 8}) \quad \sum_{r=1}^{R} \hat{h}_r = s \sum_{r=1}^{R} \sum_{c=1}^{C} \mathrm{h}_{r,c} e^{-bD_{r,c}} \, ,$$

where when $b>0$ then $s=1$ or when $b=0$ ($0<s<1$) hypothesizes that the amount of time a heron spends at a foraging site is not diminished by distance ($D_{r,c}$). Eq. 8 assures that the number of herons predicted to be foraging on all sites equals the number counted on those sites.

Overall, four models were run to test specific parametric hypotheses (Table 4-4), two for each of the two energy surrogate hypotheses, $\bar{f}_r$ and $\tilde{f}_r$. Within these two overarching hypotheses, tests to determine the impact of distance on the distribution of herons were conducted. The goal was to locate the set of estimated parameter values that minimized the discrepancy between the observed and predicted ($\breve{h}_{r,c}$) distributions of herons on the foraging sites ($\dot{h}_{r,c}$). This discrepancy is formally evaluated for its GOF using the deviance statistic L that evaluates the negative ln-likelihood of the observed

heron distribution, with respect to the predicted distribution, under the assumption of a multinomial error distribution,

$$
\text{(Eq. 9a)} \quad L = 2\sum_{r=1}^{R}\left(\dot{h}_r \times \ln\left[\frac{\dot{h}_r}{\sum_{c=1}^{C}\breve{h}_{r,c}}\right]; \; if \; \sum_{c=1}^{C}\breve{h}_{r,c} > 0 \; and \; \dot{h}_r > 0; \; else \; 0 \right),
$$

where

$$
\text{(Eq. 9b)} \quad \sum_{c=1}^{C}\dot{h}_r = \sum_{c=1}^{C}\sum_{r=1}^{R}\breve{h}_{r,c} \; .
$$

Eq. 9a is statistically equivalent to the more familiar G-statistic. Note that it is both biologically and mathematically (Eq. 9a) illogical to have $\dot{h}_{r,c} > 0$ when $\breve{h}_{r,c} > 0$. That is, if a foraging site is so poor ($f_r = 0$) that it is predicted that no fraction of a heron should be observed there then Eq. 9a also fails. For any value of $f_r > 0$ and values for $\Delta h_{r,c} \rightarrow 0$, Eq. 9a would never fail. However, the practicalities of this discrete model compel the use of a value for $\Delta h_{r,c} > 0$ resulting in the potential for imprecise values of $\breve{h}_{r,c}$ being rounded to zero (0). To defeat the singularity in Eq. 9 that can result from predicted values of $\breve{h}_{r,c} = 0$; Eq. 9a was modified as follows,

$$
\text{(Eq. 10a)} \quad L' = 2\sum_{r=1}^{R}\left(\dot{h}_r \times \ln\left[\frac{\dot{h}_r}{\sum_{c=1}^{C}\breve{h}'_{r,c}}\right]; \; \dot{h}_r > 0; \; else \; 0 \right),
$$

where

$$\text{(Eq. 10b)} \quad \breve{h}'_{r,c.} = \breve{h}_{r,c.} \left(\frac{\displaystyle\sum_{c=1}^{C} \sum_{r=1}^{R} \breve{h}_{r,c}}{\displaystyle\sum_{r=1}^{R} \left(0.5\Delta h + \sum_{c=1}^{C} \breve{h}_{r,c} \right)} \right) ,$$

thereby retaining

$$\text{(Eq. 10c)} \quad \sum_{c=1}^{C} \breve{h}_r = \sum_{c=1}^{C} \sum_{r=1}^{R} \breve{h}'_{r,c} .$$

This minor correction prevents a foraging site from having the predicted number of herons foraging there ever being less than $0.5\Delta h$. As $\Delta h \to 0$, this correction approaches zero (0). The best (i.e., maximum-likelihood) parameter estimates occur for that set of parameter values that minimize L'; i.e., at L'_{MIN}.

Typically, maximum likelihood estimates for a and w were sought, with b being complementarily estimated using Eq. 8. The discrete structure of this model prohibited the effective use of gradient or direct search methods to efficiently find the pair of values for a and w that yielded L'_{MIN}. Therefore L' was evaluated for a two-dimensional matrix of trial values for a and w. Starting with an extreme range of possible values for a and w, successive searches focused on a smaller range of values for a and w, as the values for L' decreased and approached L'_{MIN}. Akaike's Information Criterion (AIC$_c$; Burnham and Anderson 2002) was calculated for each model to allow comparisons between hypotheses. The model with the lowest AIC$_c$ value was deemed to be the model best supported by the data, i.e., the "best approximating model".

Results

The AIC_c values for each of the four model runs are reported in Table 4-4. Site quality is consistently a better predictor of the number of herons foraging at a foraging site than the size of the foraging area alone. As well, the hypothesis that distance costs are an important factor in determining the distribution of individuals in a spatially explicit, multi-colony system is supported. When there are no distance costs, the model is completely insensitive to the value of a (Table 4-4).

However, no model accurately predicted the observed number of individual herons at each foraging site (Figure 4-4). The predicted distribution of the best model is highly different from the observed distribution (P<0.0001). This discrepancy between the observed and predicted suggested that any of (1) there being some cost or benefit involved in determining the distribution of individuals across foraging sites that the model does not consider or (2) the assumption that individuals are acting independently to maximize their net energy gain, given what all other individuals are doing, is incorrect, (3) the model concept or structure is flawed. Examining where individuals from each colony forage (Table 4-5) shows that only the Boundary Bay East and Roberts Bank foraging sites have individuals from more than one colony predicted to forage there. For example, modelled individuals from the Stanley Park colony are predicted to forage at the foraging site furthest away from their colony (Boundary Bay East). However, vanishing bearings recorded at this foraging site do not support this prediction (Chapter 2).

The model suggested that the distance between colonies and foraging sites has little affect on the amount of competition between individuals since $b = 0$. Parameter b determined the amount of time a heron has available to spend on a foraging site given its

travel commitments. When $b = 0$, the time available to forage was unaffected by the distance travelled and therefore become a redundant parameter.

Discussion

Cressman *et al.* (2004) have pointed out that a game theoretic approach to a single-species IFD is uncommon in the literature. They show that, in fact, this approach works well for determining the NE of the distribution of a single species in a simple two-patch environment regardless of the behaviour of the individuals and speculate that for this reason it is uninteresting in terms of its evolutionary significance and therefore absent from the literature. The model presented here is interesting despite the fact it is a single-species model because of the increased complexity of the landscape and the utility of the model in answering ecological questions by challenging it with observed field data. The model includes complexities such as many foraging sites, individuals being constrained to an assigned colony, and differential costs of travelling between each colony to each foraging site.

The model supports using foraging site quality to predict the numbers of individuals using a foraging site and that distance costs are an important factor in determining where individuals from a given colony choose to forage. As well, increasing the competition between individuals leads to a better prediction of the distribution of herons across foraging sites. This approach is an improvement over the correlational studies that did not take into account differences in site quality (Gibbs *et al.* 1987; Gibbs 1991; Gibbs and Kinkel 1997). However, the best model did not satisfactorily (in either a biological or statistical sense) predict the observed number of individuals at each foraging site. There are a couple of likely explanations for this dissatisfaction. First, factors not

included in the model, or improperly incorporated into the model structure, may be important in determining the distribution of individuals across foraging sites. One such factor may be predation danger at each foraging site. Dangerous sites are more costly for herons and therefore likely have fewer individuals than this model predicts. Secondly, the exponentially declining relationship describing distance costs may too heavily penalize relatively poor quality foraging sites near a colony.

A third factor contributing to model imprecision is the crude estimates of foraging site size and quality used. The beam trawl method of sampling has some systematic biases and limitations. It is likely that the highly vegetated foraging sites such as Roberts Bank and Boundary Bay East may not only make for better habitat for fish but may also allow fish to be caught more readily as the fish attempt to take refuge in the vegetation or do not see the beam trawl approaching, thus energy availability is potentially overestimated. At sparsely vegetated sites the fish may be able to better avoid the beam trawl either due to better visibility or lack of obstructions blocking their escape, thereby leading to an underestimate of energy availability. As well, the entire intertidal area was used as a measure of foraging site size. The foraging site size estimate needs to be considered as a crude estimate since only a portion of the intertidal area is available for a heron to forage in at any given time, depending upon the topography of the area. A more refined estimate of available area for foraging may enhance the predictive ability of the model.

The existence of colonies not included in this model may also hamper efforts to correctly predict the distribution of herons across foraging sites. The small size of the Nicomekl colony near the three Boundary Bay sites does not account for the large

number of herons observed feeding at these three sites. Additionally, the large distance herons from the Cliff Street and Stanley Park colonies were predicted to travel, suggest that there is potential for the Boundary Bay foraging sites to support more nesting pairs near Boundary Bay. The Nicomekl colony near the Boundary Bay East foraging site (8.2 km) was mostly abandoned in 2003, declining to 14 breeding pairs (McClaren 2004) from 65 breeding pairs the previous year (Vennesland 2003). A colony on the north side of Boundary Bay was predicted to exist based on vanishing bearing analysis (Chapter 2) but the actual size and location of this colony was not determined. If attributes of this colony were known then the likely location for these individuals to forage would be one of the three Boundary Bay foraging sites. It would then be likely that the competition would be greater at these three foraging sites, thereby making other, closer, foraging sites more profitable than Boundary Bay for individuals travelling from distant colonies such as Cliff Street and Stanley Park.

Imperfect estimates of foraging site usage by herons may account for a portion of the disagreements between the observed and predicted distribution of herons. Counts of herons across all foraging sites were not conducted simultaneously due to the impossibility of visiting all sites on the same day. Most maximum counts were observed in early June, as this time of year is when the tides are lowest and the energy demand of nestlings is the greatest (Butler 1993). These counts were conducted on a small enough temporal scale that any miscounting should have minimal effect on the outcome of the model.

The yield model presented here (Eq. 5a) is structured to estimate the parameter values that best predict the observed distribution of herons across foraging sites. These

estimates therefore need to be either directly measured, through observation or experimentation, or estimated from related field data in a conceptual model such as the one described here. The function used in calculating distance costs in this model results in a similar relationship between distance and associated costs to that estimated by Nemeth *et al.* (2005) where an exponential decrease in bird density was found as the distance from the colony increased. Direct measurement of the distance costs (measured as the time lost in acquiring yield) used in this model could improve the understanding of the relationship between distance between a colony and foraging site and yield. Model refinement could be achieved by following individually identified herons during a tidal cycle to measure, for example, the number of foraging trips made, and time spent foraging, for different colony-foraging site distances.

A result of the classic IFD models is that all individuals in a population receive the same reward, termed individual payoff in game theoretic models. In this model, the individual payoff is measured as the gross energy gain. Due to the constraint of individuals being assigned to a colony of a fixed location, individuals from different colonies pay different costs to travel to each foraging site. Differential travel costs may result in not all individuals receiving the same payoff. If the model predicts that this difference in payoff between individuals and the individual payoff is related to the individual's fitness, then one should ask why would the herons choose to place a colony at this particular location. One reason may be that the model is missing a cost or benefit, such as the probability of losing nestlings to predators at a given colony. Or, if the model is correctly predicting this difference in payoff, then it suggests that there is some difference in the competitive ability of individuals in terms of their choice of colony.

Simpson *et al.* (1987) found that herons that fed close to the colony had higher reproductive success than herons that fed further from the colony.

The results of this model are important for conservation purposes. This model allows for predictions to be made about the response herons may have to alterations in the quality of foraging sites. A decrease in the quality at one site may make another site relatively more profitable, resulting in a shift in the abundance of herons from the degraded site to the non-degraded site. Protection of colony locations should take into account the distance costs incurred by herons. Colony locations close to foraging sites should become a priority for conservation to minimize the distance costs.

Table 4-1: Description of attributes of foraging sites used by Great Blue Herons in the Lower Mainland region of British Columbia. Shiner Perch $CPUE_{0,0}$ is the tide and date corrected catch-per-unit-effort (CPUE) of the number of shiner perch caught per metre trawled. Note that the Capilano River foraging site was not sampled and no shiner perch were caught at Port Moody so conservative values for the estimated energy equivalents were chosen. Foraging site size for all but Maplewood and Port Moody were taken from Ryder *et al.* (2004). Maplewood and Port Moody sizes were estimated from marine charts using GIS.

Foraging Site	Number of Herons Observed	Foraging Site Size (ha)	Shiner Perch $CPUE_{0,0}$ (Shiner Perch/m)	Estimated Energy Equivalents (fish*m)
Roberts Bank	783	3732.8	10.026	37428.6
Boundary Bay East	163	2625.1	16.256	42672.0
Boundary Bay Centre	1	2143.1	0.768	1644.8
Boundary Bay West	2	2007.4	0.317	635.3
Sea Island	47	3962.4	0.015	59.9
Capilano River	7	18.5	N/A	0.3
Maplewood	38	87.0	0.024	2.1
Port Moody	10	93.3	0	1.4

Table 4-2:   Sizes, measured as the number of active nests, of Great Blue Heron colonies located in the Lower Mainland region of British Columbia in 2003 (from McClaren 2004).

Colony	Colony Size
Point Roberts	400
Tsawwassen Ferry	35
Terra Nova	9
Pacific Spirit Park	45
Stanley Park	21
Tilbury Island	15
Cliff Street	23
Nicomekl	14

Table 4-3: Distances between Great Blue Heron foraging sites and colonies in the Lower Mainland region of British Columbia, measured in kilometres.

Foraging Site	Colony							
	Point Roberts	Tsawwassen Ferry	Terra Nova	Pacific Spirit Park	Stanley Park	Tilbury Island	Cliff Street	Nicomekl
Roberts Bank	5.0	1.9	16.9	25.1	29.1	13.6	30.6	23.6
Boundary Bay East	14.0	15.4	27.8	34.0	35.1	16.5	29.2	8.2
Boundary Bay Centre	10.4	11.4	24.1	30.6	32.3	13.4	27.8	11.0
Boundary Bay West	7.8	7.7	20.2	27.1	29.3	10.5	26.5	14.3
Sea Island	22.3	18.7	3.7	9.7	15.6	15.4	24.4	33.2
Capilano River	36.2	32.9	16.7	9.2	3.4	21.9	13.9	36.5
Maplewood	34.0	31.1	18.7	14.3	8.9	18.4	5.2	29.7
Port Moody	35.9	34.0	27.9	26.1	21.6	21.3	8.0	23.5

Table 4-4: Best estimates of parameter values for model runs. The lower the value of AICc, the more likely this approximating model represents the underlying unknown true model. Values of parameter a denoted by a '-' indicate that virtually all values of a result in the same AICc value. Differences in the magnitude of parameter a and w between model 1 and model 3 can be explained by the different estimates of energy equivalents used. For models 1 and 2, the units of parameter a are fish*metre while in models 3 and 4 the units are ha. The units for both parameters b and w are km^{-1}. The value for parameter s is the same for all models at 0.935, representing the ratio of the number of herons counted on all foraging sites (1,051) to the number of herons in all colonies (1,124).

Model	Model Description	Parameter Values			AIC_c
		Maximum Energy Collected (a)	Coefficient of Time Attenuation (b)	Coefficient of Energy Attenuation (w)	
1	Site Quality Unequal, Distance Costs	25,500	0	0.31	140.4
2	Site Quality Unequal, No Distance Costs	-	0	0	1,596.1
3	Site Quality Equal, Distance Costs	0.10	0	0.01	430.2
4	Site Quality Equal, No Distance Costs	-	0	0	1,631.9

Table 4-5: Predicted distribution of Great Blue Herons from each colony across foraging sites from the best-fit model (Model 1).

	Colony							
Foraging Site	Point Roberts	Tsawwassen Ferry	Terra Nova	Pacific Spirit Park	Stanley Park	Tilbury Island	Cliff Street	Nicomekl
Roberts Bank	748	66	17	0	0	0	0	0
Boundary Bay East	0	0	0	0	13	11	42	26
Boundary Bay Centre	0	0	0	0	0	9	0	0
Boundary Bay West	0	0	0	0	0	8	0	0
Sea Island	0	0	0	84	0	0	0	0
Capilano River	0	0	0	0	11	0	0	0
Maplewood	0	0	0	0	15	0	0	0
Port Moody	0	0	0	0	0	0	1	0
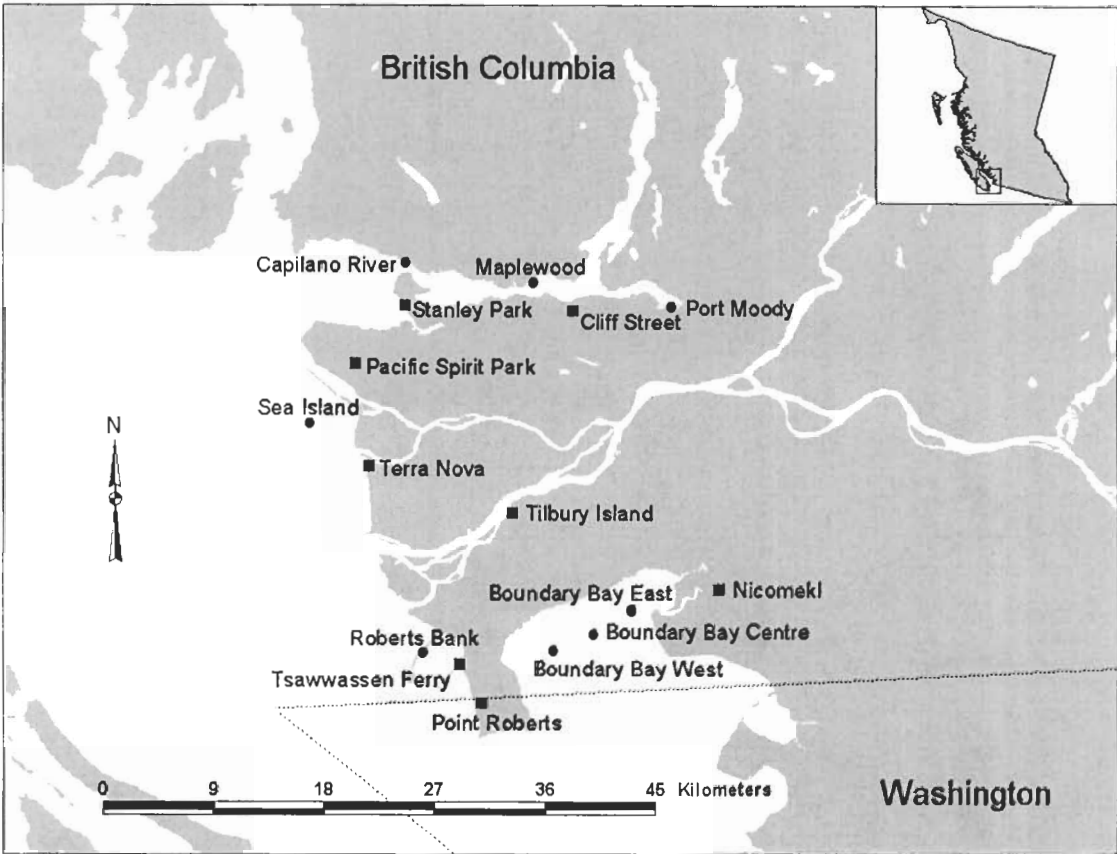
Figure 4-1: Location of discrete Great Blue Heron foraging areas (circles) and colonies (squares) in the Lower Mainland region of British Columbia.
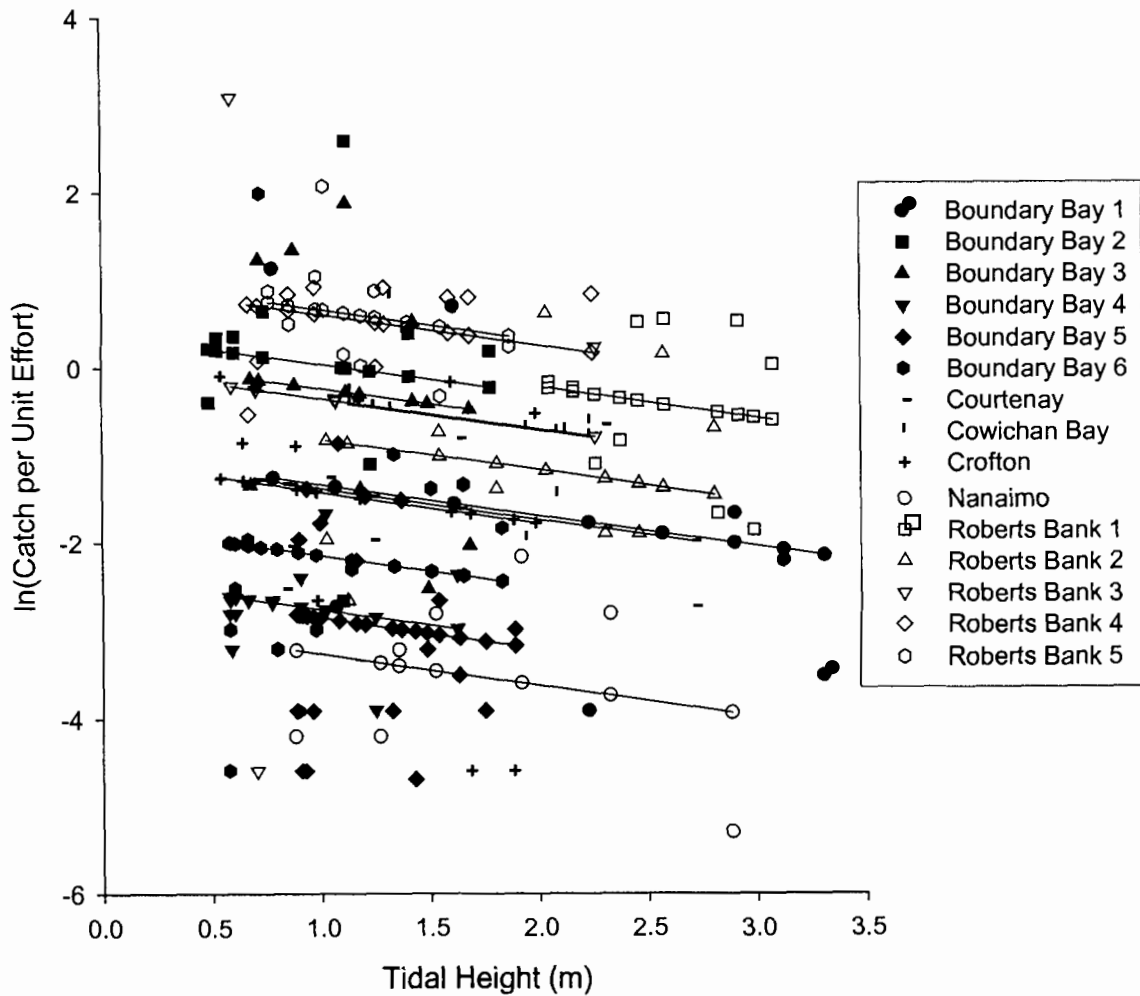
Figure 4-2: The effect of tidal height on the catch per unit effort (CPUE) of fish sampled with a beam trawl at a number of foraging sites within and near the study site as determined by analysis of covariance. This relationship produced a value of P=0.12 which was considered sufficient to correct all trawls to a standard tidal height of 0 metres using the slope of this relationship, i.e., $CPUE_0 = CPUE_A e^{0.351A}$ where A is tidal height in metres. Line plots show the predicted CPUE for each site while scatter plots represents the actual CPUE from each beam trawl sample. Multiple Boundary Bay and Roberts Bank samples represent different days that sampling occurred.
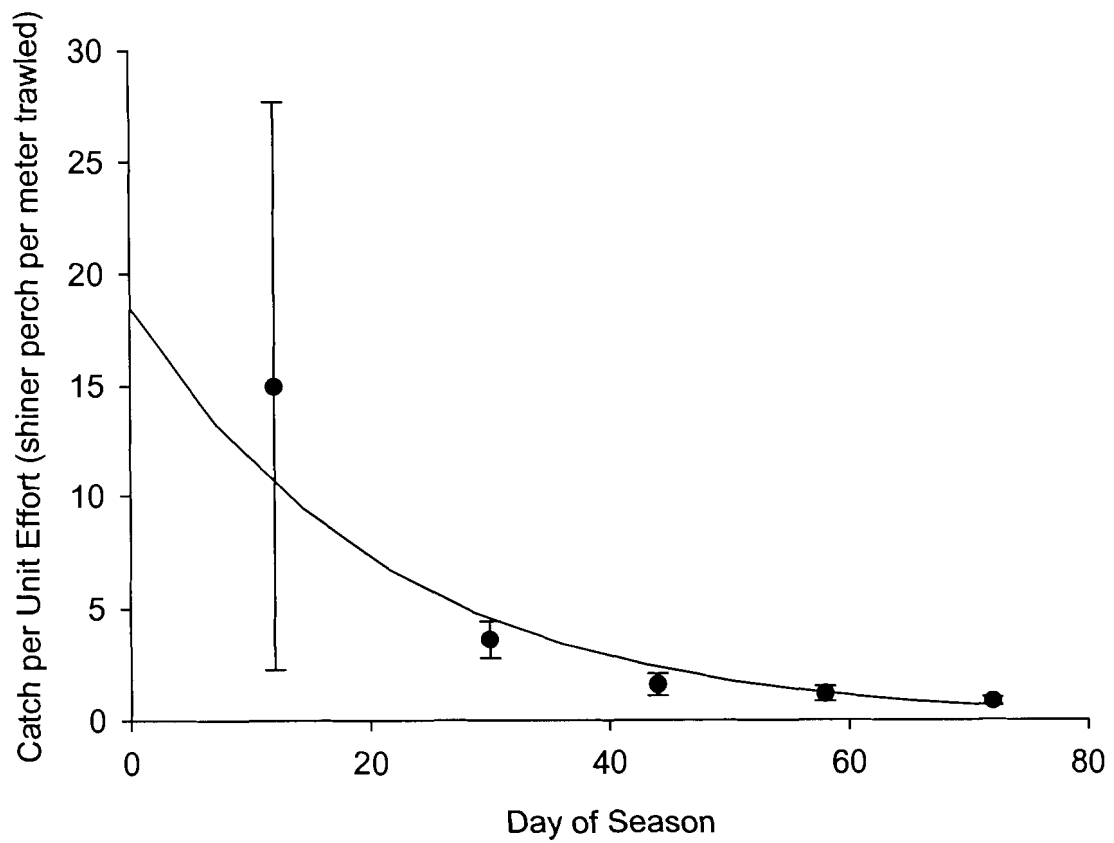
Figure 4-3: Decrease in catchability of shiner perch at the Roberts Bank foraging site through the summer of 2003. Error bars are one standard error. The $CPUE_{0,0}$ was estimated by solving the relationship, $CPUE_{0,0} = CPUE_{0,t} e^{-0.047t}$, for the maximum likelihood parameter estimates assuming a ln-normal error distribution and using the plotted data. Day 0 corresponds to June 30, 2003.
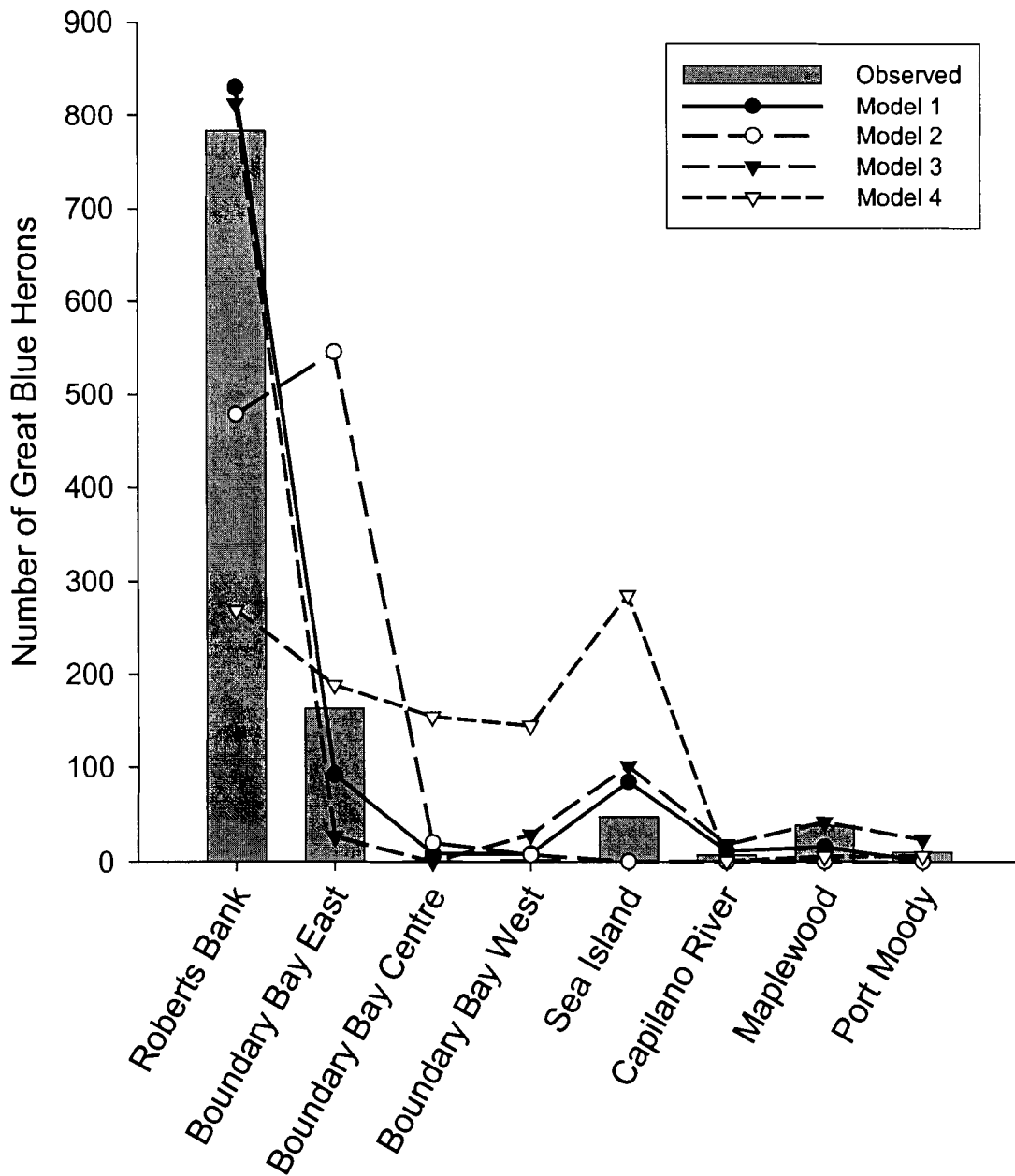
Figure 4-4: Comparisons of predicted distributions (lines) of Great Blue Herons across foraging sites against the observed distribution (bars). Model numbers correspond to the models described in Table 4-4. Using AICc, the "best approximating model" predicting the observed distribution is model 1.

CHAPTER 5:
FINAL THOUGHTS AND FUTURE DIRECTIONS

Thesis Summary

This thesis documents three approaches designed to improve the knowledge of the mechanisms for assessing and understanding the observed distribution of Great Blue Herons in the Strait of Georgia, B.C. First, exploiting knowledge of the behaviour of an individual by observing its vanishing bearing as it leaves a foraging site en route to a breeding colony has not previously been described (Chapter 2). This thesis validates this methodology for locating colonies of Great Blue Herons. Improvements in population size estimates from locating new colonies for Strait of Georgia Great Blue Herons should follow from diligent application of this methodology. The experimental use of this method to locate new colonies improved current population size estimates by up to 5% (Chapter 2). One key advantage of the use of vanishing bearings over previous methodologies described to locate wading bird colonies is that it requires a minimal financial investment in terms of labour and equipment costs.

Second, Chapter 3 formalizes a hypothesis regarding the trade-off between nesting in many small colonies versus nesting in a single large colony to minimize predation danger. To date, the risks of predation with respect to colony size to colonial nesting species have been only superficially described in the literature (e.g. Wittenberger and Hunt 1985; Butler and Vennesland 2000). The probabilistic modelling approach employed in this thesis allowed predictions of this hypothesis to be posed by generating a

range of reproductive success outcomes that vary according to the level of predation danger from territorial and non-territorial eagles, as mitigated by the distribution and detectability of herons among variously-sized breeding colonies. This thesis has provided a strong theoretical framework for field tests of this hypothesis.

Third, a game theoretic approach to predicting the ideal free distribution (IFD; Fretwell and Lucas 1969) of a single species has only recently been formally examined (Cressman *et al.* 2004). Cressman *et al.* (2004) showed that this approach is valid for predicting the IFD of a single species in a simple two-patch habitat. This thesis expands this approach by predicting the IFD of a population of Great Blue Herons that has a complex spatial structure due to its colonial nesting strategy. This predicted IFD was evaluated against observations of foraging activity. The payoff function for this IFD model was the quantity of food a provisioning heron could return to its nestlings. The incorporation of distance costs for travel between colonies and foraging sites in addition to competition between individuals for access to energy at the foraging sites resulted in interesting predictions. Although the model imperfectly predicts the observed distribution of foraging herons on this landscape, this information is still of value since the model does suggest that site quality is a better estimator of the number of individuals using a foraging site than is foraging site size.

The use of vanishing bearings was shown to be a useful tool for to locate colonies and improve population size estimates (Chapter 2). However, it also can be used to support or refute predictions made by the models presented in Chapters 3 and 4. Although not a direct test of the predictions made by the hypothesis presented in Chapter 3, the observed vanishing bearings do show that it is common for there to be more than

one colony associated with a single foraging site. Multiple colonies associated with a single foraging site is consistent with the model prediction that herons using a given foraging site may achieve higher reproductive success if they alter their nesting strategy to a more dispersed nesting strategy (i.e. many small colonies) as predation danger from Bald Eagles increases. In Chapter 4, the IFD predicted some individuals travel over 30 km from a colony to a foraging site. Vanishing bearings observed at this foraging site suggest that this prediction of a lengthy commute, which perhaps bypasses other more proximate foraging sites, is likely inaccurate. Individuals were not observed departing this foraging site in a direction consistent with either of the two colonies predicted by the model to have individuals foraging at this site. As noted in Chapter 4, there is reason to invest in refining either or both of the model structure or data input for the IFD model presented.

Conservation Implications and Future Research

Butler and Vennesland (2000) propose that climate change leading to changes in the amount of suitable foraging habitat, and changes in predator abundance, are factors that will be prominent for consideration when promoting and advocating wading bird conservation in the 21st century. They suggest that future research should work within this framework to improve conservation measures of wading birds. This thesis works within this framework and moves forward with this premise. Chapter 3 explicitly proposes a strong theoretical framework within which to test the effects predation danger may have on the distribution of a wading bird population. Although not explicitly dealing with changes in habitat quality, the IFD model approach detailed in Chapter 4 has potential to be a tool researchers can use to predict changes in the distribution of

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individuals due to loss, or a decline in quality, of foraging habitat caused by climate change.

Implications of the model results for conservation of Great Blue Herons were discussed in both Chapter 3 and 4. Chapter 3 discussed the need to conserve a landscape suitable to accommodate the predicted breeding colony distribution of herons as they respond to an increase in predation danger. This landscape should include multiple potential colony locations to allow herons to exercise their predicted optimal behaviour, given variation in predation danger. For example, if the predation danger is high, either through many eagles being present or a high attack rate per eagle, the model predicts herons should choose to nest in a more dispersed manner (many small colonies). Therefore a contiguous forested landscape with many potential colony locations will allow herons to behave in this manner to minimize the probability of detection by potential eagle predators.

One of the results of the IFD model presented in Chapter 4 was that distance costs were an important factor in determining which foraging site a heron should choose. This result, combined with the predictions made from the model in Chapter 3, can enhance the ability of habitat managers to promote to partners and stakeholders the need to provide a landscape that is conducive to the survival of this local subspecies population of Great Blue Herons. The model predicts herons to need multiple potential colony locations, but also the location of these potential nesting sites is important since the distance between a foraging site and colony will impact the profitability of that potential colony location for reproduction.

As much as this thesis furthers the understanding of the distribution of Great Blue Herons, it raises many new questions and forms the basis for future research. Testing the predictions made by the model in Chapter 3 should be a priority. Specifically, assumptions concerning the territoriality of Bald Eagles are an important aspect of the model. Determining to what extent eagles are territorial will allow further tests of the model predictions to be conducted. Direct tests of this model will be difficult to do with this heron population since the eagle population is believed to be already at a large size resulting in high predation danger. Direct tests need to include either the manipulation of perceived predation danger or alterations to the number of herons breeding within an area. Observations of alterations in nesting strategy of other wading bird populations, where predator numbers are only beginning to increase, may be a better system in which to test these predictions. It is also interesting and evocative to ask if the IFD model (Chapter 4) can be used in reverse to predict the size and/or location of colonies. An extension of this model would be to use the IFD approach to predict both the distribution of individuals on the foraging sites and the number, size, and location of colonies as a tool to identify high priority landscapes for conservation. Ideally, the two behavioural models presented in this thesis could be combined to make more accurate predictions of heron distributions, which could be evaluated against observed data. Model evaluations would require an ongoing investment in high quality data collection with regard to adult heron provisioning behaviours, reproductive success, quality of foraging sites, colony choice, abandonment and relocation strategies, land use projections, etc, in order for this approach to become a reality.

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