HABITAT SELECTION AND TIME OF BREEDING
IN THE GREAT BLUE HERON, (*ARDEA HERODIAS*)

By

ROBERT W. BUTLER
B.Sc., Simon Fraser University, 1976
M.Sc., Simon Fraser University, 1980

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Department of ___Zoology___

The University of British Columbia
Vancouver, Canada

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ABSTRACT

This thesis examines the causes and consequences of habitat selection and timing of breeding of the Great Blue Heron (*Ardea herodias*). My general hypothesis was that the duration of low tides and seasonal abundance of prey strongly influenced the location of colony-sites; timing of the breeding season; habitat shifts; and the use of space by foraging herons of different age- and sex-classes.

I studied Great Blue Herons along the Pacific coast of Canada for five breeding seasons and four winters. Breeding herons were studied at a colony of 85 to 100 pairs on Sidney Island near the town of Sidney, and periodic visits were made to about 40 other colonies around the Strait of Georgia, British Columbia. At Sidney, I studied the foraging behaviour, food availability, habitat use and reproductive success in detail. At other colonies, I recorded the reproductive success of herons, located their main feeding areas and searched for nests of a predator, the Bald Eagle. In the non-breeding season, I investigated the foraging behaviour, dispersion pattern and habitat shifts of juvenile and post-breeding adult herons in the Fraser River delta.

I hypothesized that heron colony-sites were located near food supplies or away from predators. Twenty-nine of 33 colony-sites were located within 6 km of their main feeding site. The number of heron pairs was slightly greater where eagles nested in high abundance than where eagle abundance was low, contrary to the hypothesis that breeding herons avoid areas with active eagle nests.

I hypothesized that herons began breeding in spring shortly after females acquired enough food energy to make eggs, or so chicks were in nests when food was most plentiful to their parents. Egg-laying began about 9 days after a

female's daily food intake crossed an energy threshold of 1715 kJ/day, whereas the peak availability of food energy to adults occurred about 35 days before the peak food demands of their chicks. Food intake rates by adults increased gradually in March and April with the increasing duration of low tides and the inshore movement of fishes. Adult food intake rates reached a peak in May when sea perch were most abundant, and diminished through June and July.

Most juvenile and adult female herons foraged on beaches from February to October and in marshlands and grasslands from November to January. Some males returned to territories along riverbanks in August and remained there until the start of the next breeding season in March.

I tested the hypothesis that herons leave foraging habitats in autumn when they can no longer catch enough food or when interference from conspecifics reduced foraging intake rates below a threshold required to maintain their energy balance. In October and November adults moved to marshlands and juveniles moved to grasslands when they could no longer maintain daily energy balance on beaches as a result of declining duration of low tides and food intake rates. Interference competition was too infrequent to explain habitat shifts by adult or juvenile herons in autumn.
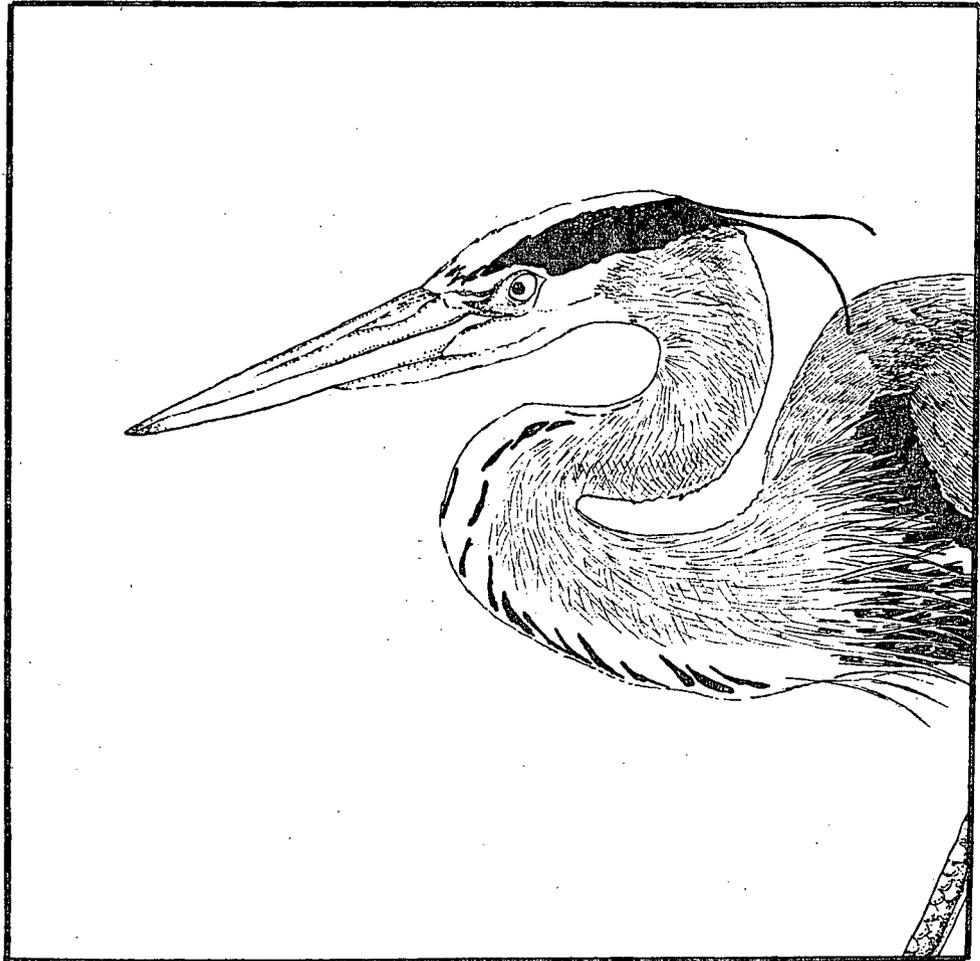
GREAT BLUE HERON (Ardea herodias)

Robert Butler

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CHAPTER ONE. INTRODUCTION

This study arose from my continuing interest in how animals adapt to coastal environments. I am particularly interested in animals that rely on the intertidal zone for foraging. The rhythm of oceanic tides pervades the lives of many birds using seashores by determining when they will feed, nest and migrate. The discovery of dioxin contamination of Great Blue Herons (*Ardea herodias*) and their prey in British Columbia (Elliott *et al.* 1989) provided a specific stimulus to begin this study.

The Theory of Habitat Selection

One of the most important decisions an animal makes in its lifetime is where it settles. This decision may involve a complex interplay between age, social status, sex, competitive ability, foraging skill, presence of predators and the suitability of the habitat (Catterall et al. 1989). It is well established that where animals settle affects their survival and reproductive success (e.g Krebs 1971, Whitham 1980, Alatalo *et al.* 1985). Individuals settling in good habitats are thereby rewarded by producing more offspring in subsequent generations.

Habitat selection theory has arisen in the past two decades to explain how individuals might settle sites. The 'ideal free distribution' assumes that individuals that are equally skilled and have complete information about the habitat should move freely to wherever fitness rewards are greatest, and thus should experience the same average rate of return (Fretwell and Lucas 1970, Fretwell 1972). Their 'ideal despotic' model posits that the best competitors limit settlement of inferior competitors to smaller sites in good

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habitat or to sites in poor habitat. This results in unequal rewards between individuals.

Brown (1969) proposed a similar explanation for different densities of birds in breeding habitats. According to his model, good habitats are filled to a critical density after which successively poorer habitats are occupied at lower densities. Non-breeding 'floaters' that roam between habitats or live secretively in territories (e.g. Smith 1978), eventually appear when populations are very dense.

The ideal free model explains the dispersion of some birds, insects, fish, amphibians and reptiles well (e.g. Have *et al.* 1984, Morse 1985, Pimm *et al.* 1985, and see review by Parker and Sutherland 1986). The ideal despotic and breeding territory models also explain different population densities in habitats that vary in quality (e.g. Krebs 1971, Fretwell 1972, Alatalo *et al.* 1985, Richner 1986), but only the latter model explains the presence of non-territorial floaters (e.g. Krebs 1971). All three models posit that individuals shift between habitats as the density of competitors changes.

Another view is that some animals switch between foraging habitats when food availability declines below some threshold level (Stephens and Krebs 1986). This view posits that the length of time a foraging animal resides in a habitat depends on its rate of prey capture (see review by Krebs *et al.* 1984, Dugan *et al.* 1988). The marginal value theorem (Charnov 1976) posits that animals move between food patches when their instantaneous rate of food intake reaches the average expected gain in the habitat. The optimal assessment policy posits that animals switch habitats when their net reward of residing in a foraging habitat returns to zero (McNamara 1982). This theory explains changes in habitat use by animals without invoking density-dependent interactions.

Gathering evidence that habitat shifts by birds are related to food availability has been hampered by the difficulty of following mobile animals from summer to winter habitats and by measuring the availability of their food. For example, Sullivan (1989, 1990) showed that the dispersion and survival of adult and immature Yellow-eyed Juncos (*Junco phaeonotus*) soon after the breeding season was positively related to their ability to acquire food.

The Timing of Breeding by Birds

Most birds breed during a season when food is relatively plentiful (Moreau 1950, Lack 1950). However, the mechanisms that determine precisely when birds begin to breed are less clear. Lack (1954, 1966) proposed that birds time their breeding seasons so that nestlings are present when food for the parents is most abundant. However, later studies showed that clutches laid on the average date were not, as predicted by Lack's (1954) hypothesis, always the most productive (Perrins 1965, Cave 1968, Perrins and Birkhead 1983).

An alternate explanation is that the amount of food available to the laying female determines when she will lay her eggs (Perrins 1965, 1970). Perrins' hypothesis predicts that females should begin to lay as soon as their foraging sites allow them to make eggs as well as maintain themselves. Many food addition studies with female birds early in the breeding season support Perrins' view (see reviews by Daan *et al.* 1988, Dijkstra *et al.* 1990).

Evidence that nestlings hatch after their parents' food supply peaks is mostly weak because of methodological problems in estimating the availability of food. Most studies have used measures of food abundance as an index of food availability (see Daan *et al.* 1988). Although this seems intuitively reasonable, the conclusions of these studies are equivocal. Daan *et al.* (1988) pieced together studies of 5 songbirds and 2 raptors to conclude that four

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species had nestlings at a time when their food supplies were increasing in abundance, and three while food abundance was waning.

A second methodological problem in relating food availability to the demands of the nestlings is establishing if and when a critical time occurs for the food-gathering parent. In some species, the peak demand for food occurs during the nestling stage (see review by Martin 1987) while in others it occurs after the young leave the nest (Weathers and Sullivan 1989, Sullivan 1989).

The Study Species

The ideal animal for studying habitat selection and time of breeding is a year-round resident that is highly visible, has recognizable age- and sex-classes whose reproductive performance can be documented, whose prey availability and food consumption can be measured, and is easy to catch and mark for life. The Great Blue Heron on the coast of British Columbia approximates this ideal. The species is sedentary and conspicuous on beaches, in marshlands and in neighbouring grasslands. Juveniles are easily distinguished from adults by plumage differences (Palmer 1962, Hancock and Kushlan 1984), and most adults can be sexed from a distance by estimates of culmen lengths (Butler *et al.* 1990). Most Great Blue Herons in British Columbia nest in colonies where their reproductive success can be readily documented (Simpson 1984, Butler 1989). Herons in British Columbia catch small fish on beaches near colony-sites (Krebs 1974, Simpson 1984) where prey populations and adult consumption can be estimated (Simpson 1984).

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Aims of the Thesis

In this thesis I describe seasonal changes in habitat use by different age- and sex-classes and test the 3 sets of alternative hypotheses that: (i) herons locate colony-sites near food supplies or away from predators (Chapter 3), (ii) foraging herons move between habitats in autumn because of interference from foraging conspecifics or are forced to move because of insufficient foraging time during tidal cycles (Chapter 4) and, (iii) female herons begin to lay eggs after a threshold of available energy for egg production has been passed or match the period of peak food demands of their chicks (Chapter 5). In Chapter 6, I examine the year-round relationships between habitat use, dispersal and foraging efficiency of age- and sex-classes.

CHAPTER TWO. STUDY SPECIES, STUDY AREA AND METHODS

STUDY SPECIES

Distribution – The Great Blue Heron is the largest and most widespread ardeid in North America (Hancock and Kushlan 1984). It breeds across the continent from the Arctic Circle in Alaska to Mexico and on the Galapagos Islands (American Ornithologists' Union 1983). The Great Blue Heron migrates from most of its northern range in winter except on the coasts of British Columbia and Alaska where it resides year-round.

Food – Great Blue Herons inhabit seashores, rivers and lakes where they wade in search of fish during day and night (Brandman 1976, Black and Collupy 1983). Great Blue Herons mostly hunt by standing in water where they wait for prey to pass within striking range ("Stand and wait" in Kushlan's (1976a) terminology) or "Walk Slowly" (Kushlan 1976a) until prey is encountered. I rarely saw the 28 other feeding techniques described by Kushlan (1976a). Most fish are caught between the finely serrated open upper and lower mandibles, and fish are immobilized by shaking. Large prey with dangerous spines are sometimes taken ashore where they are speared with the bill until the spines relax or break (Forbes 1982, pers. obs.). Great Blue Herons also eat mammals, insects, crustaceans, gastropods, amphibians, reptiles, birds and carrion (Kushlan 1978).

Breeding biology – The breeding biology of the Great Blue Heron has been documented across North America including Alberta (Vermeer 1969), Nova Scotia (McAloney 1973, Quinney and Smith 1979, Quinney 1983), Quebec (DesGranges and Laporte 1979, DesGranges *et al.* 1979), Oregon (Henny and Bethers 1971, Werschkul *et al.* 1977, English 1978, Blus *et al.* 1980), Washington (Calambokidi *et al.* 1985), Montana (Parker 1980), California (Pratt 1970, 1972 a,b, Brandman 1976, Pratt and Winkler 1985), and Florida (Powell 1983, Powell

and Powell 1986). In British Columbia, breeding Great Blue Herons have been studied near Pender Harbour on the Sechelt Peninsula (Kelsall and Simpson 1980, Simpson 1984, Simpson *et al*. 1987), and on the University of British Columbia Endowment Lands (now called Pacific Spirit Park) (Urhahn 1968, Paine 1972, Krebs 1974). The breeding biology of several coastal colonies were compared by Forbes *et al*. (1985a), and I have reviewed these and other colonies in more detail elsewhere (Butler 1989). I define a colony-site as the location where nesting herons gather, and a colony as the group of herons that gather there (Kushlan 1986).

Briefly, male Great Blue Herons on the coast of British Columbia return to their colony-sites near dusk in late February or early March. They settle on previous years' nests or in tree limbs which they defend against one another. When females arrive about a week later, the males vigorously display for their attention. Over the next few weeks females begin to arrive ever earlier in the afternoon until by late March or early April they remain near the colony-site all day.

Meyerriecks (1960) and Mock (1976) have described the displays of the Great Blue Heron in colony-sites elsewhere in North America. Great Blue Herons mate monogamously in each breeding attempt but apparently choose new mates each year (Simpson 1984).

In North America, Great Blue Herons nest on a variety of substrates including the ground, in bushes, on man-made structures and in trees (Palmer 1962). In British Columbia they nest in coniferous and deciduous trees (Butler 1989).

Herons in British Columbia lay eggs mostly in April (Butler 1989). Incubation duties are shared by the mated pair; males incubate mostly during the day and females at night (Paine 1972, Brandman 1976, Kaufmann and Cawley

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1986). Incubation lasts about 27 days (Vermeer 1969) and the eggs hatch asynchronously (Mock 1985). Clutch sizes average from five eggs in Alberta (Vermeer 1969) to fewer than three in Florida (Powell and Powell 1986). In coastal British Columbia the average clutch size is 4.1 eggs (Butler 1989). Nestlings are fed on fish caught near the colony-site during the day (Simpson 1984, pers. obs.). Sibling aggression results in the reduction in the size of some broods (Mock 1985). On average, about 2.5 young reach independence per successful nesting attempt in British Columbia (Forbes *et al*. 1985a, Butler 1989).

Non-breeding Season - Less is known about the Great Blue Heron outside its breeding season. Band recovery data indicate a southward movement of post-breeding herons in northern populations excluding coastal British Columbia and Washington (Henny 1972, Byrd 1978). Mortality estimates based on band recovery data show about three-quarters of the juveniles die before their first birthday (Henny 1972, Bayer 1981). Juvenile Great Blue Herons are less efficient foragers than adults after the close of the breeding season (Quinney and Smith 1980). Some post-breeding adults hold exclusive feeding territories (Bayer 1978).

Age-class Descriptions - Age-classes of the Great Blue Heron have been described by Bent (1963), Palmer (1962), and Hancock and Kushlan (1984), and by Millstein *et al*. (1970) for the Gray Heron (*A. cinerea*). The classes used in this thesis are defined below.

Chick: A heron between hatching and fledging is called a chick. This
          period lasts about two months, usually May and June;
Fledgling: Chicks are called fledglings from when they first leave the nest in
          late June or early July, until about two weeks later when no trace

of the neossoptile down remains. This 'down' is most apparent on the crown and on the face;

Juvenile: Fledglings become juveniles once they lose the neossoptile down in mid-July and remain in this class until the next breeding season which begins in March. They can be recognized in the field by a slate-grey crown, the absence of body plumes, and very short or no occipital plumes;

Yearling: Juveniles become yearlings about 11 months after hatching with the commencement of the adult breeding season in March. They remain in this age-class for twelve months. Yearlings can be distinguished by a small (c.3 cm) white crown patch, grey forehead and the presence of occipital plumes and by a chestnut-coloured bend of the wing. However, they lack the long adult body plumes, and some wing coverts are edged with brown like juvenile's;

Adult: Adults have a white crown, white or white flecked with grey forehead, and black post orbital stripes fusing at the posterior end into long plumes. Long plumes cascade over the back and splay out from the chest and belly most noticeably in the breeding season. The gray body plumage has no brown edging. In the breeding season, the bill approaches an orange-yellow hue (color 18, Smithe 1975).

STUDY AREA

I studied Great Blue Herons mostly in the Gulf Islands and in the Fraser River delta in the southwest corner of British Columbia, Canada. The maritime climate ensures a mild winter and cool summer, despite the high latitude (48-49°N). Infrequent visits were made to about 40 colonies around the Strait of Georgia and two areas were studied in detail.

Sidney Island - The breeding component of my study focused on a colony of 85 to 100 nesting pairs on Sidney Island, about 4 km east of the town of Sidney and 23 km ENE of Victoria, British Columbia. Sidney Island is one of a dozen large Canadian Gulf (San Juan) Islands that lie between Vancouver Island and the mainland of British Columbia.

Sidney Island is mostly covered in second growth Douglas Fir (*Pseudotsuga menziesii*) and mature *Arbutus menziesii*. The herons nested in Red Alder (*Alnus rubra*) trees. Littoral drift has created a lagoon (Fig. 2-1) (100 ha) in which most female herons fed each day. The first part of the lagoon exposed by falling tides is a saltmarsh community dominated by *Salicornia virginica* and *Distichlis spicata*. Herons used this marsh as a loafing site. Adjacent to the saltmarsh is a 60 ha mudflat that supports sea lettuce (*Ulva lactuca*) and sparse growth of eelgrass (*Zostera marina*). Some herons fed there before and after the tides exposed the most heavily used zone, which was dominated by a dense growth of eelgrass (40 ha).

Fraser River Delta - I studied herons during autumn and winter mostly in the Fraser River delta immediately south of Vancouver, British Columbia (Fig. 2-2). The Fraser is the largest estuary on the Pacific coast of Canada. A general description is given by Butler and Campbell (1987).
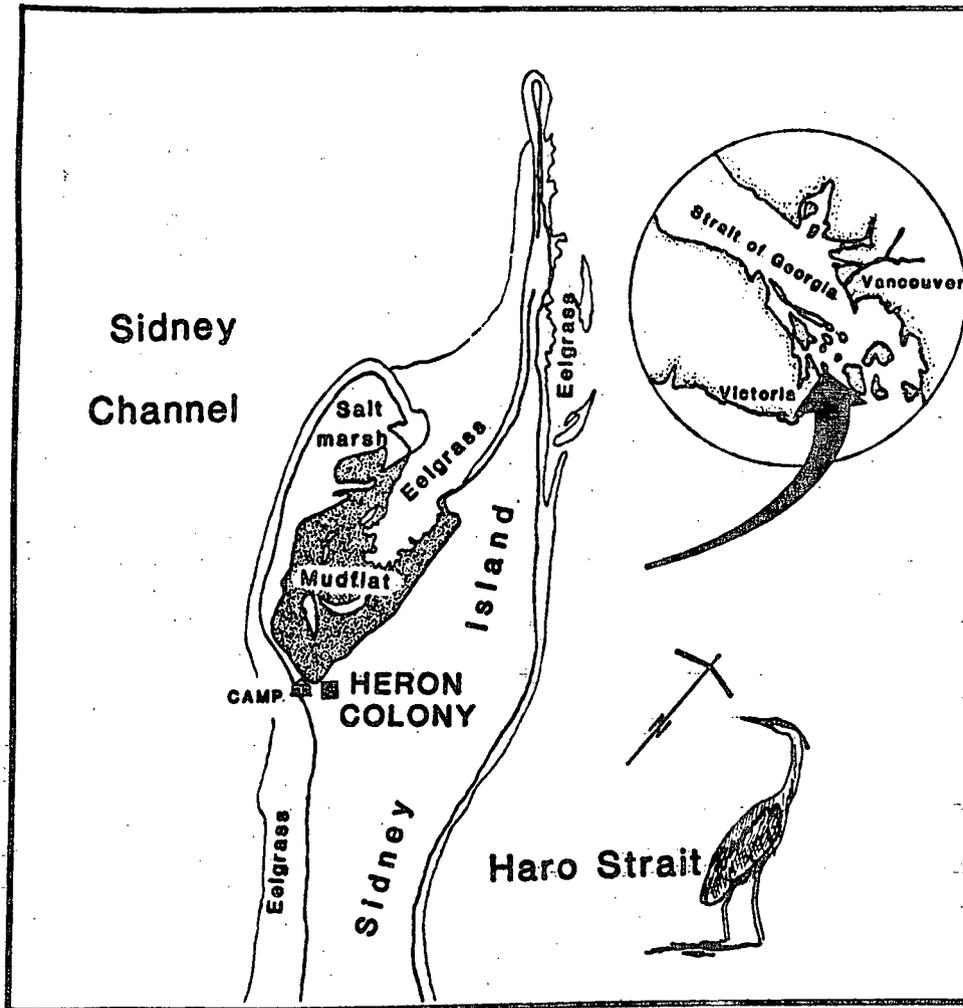
Figure 2-1. Location of the breeding colony-site and habitats used by herons on Sidney Island.
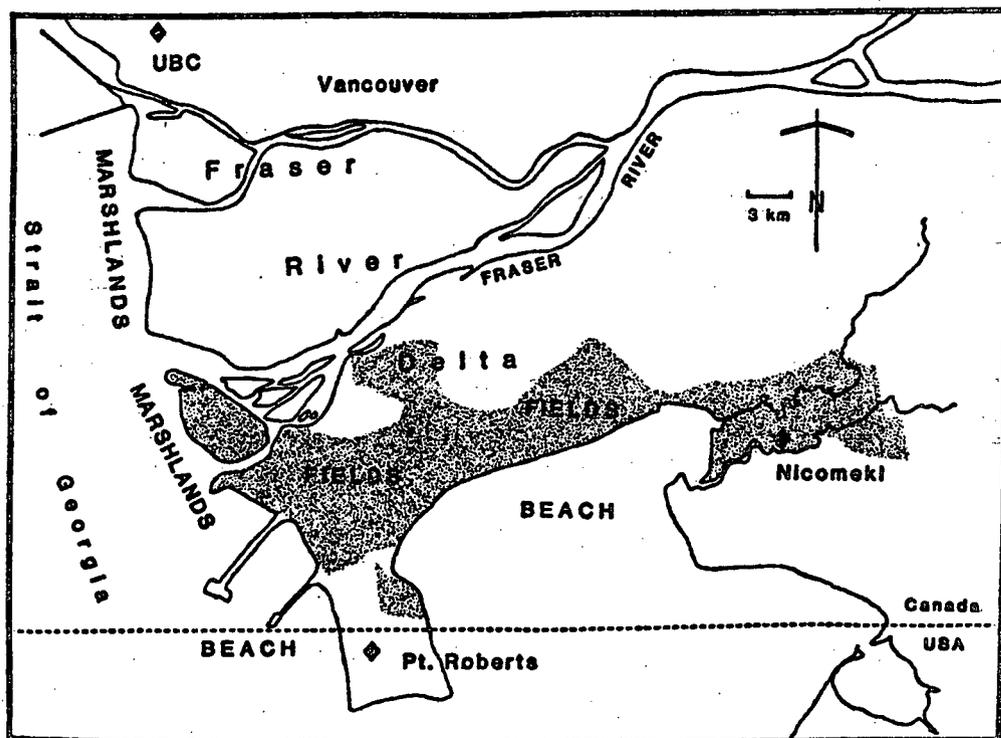
Figure 2-2. Location of habitats and three breeding colony-sites (diamond symbols) used by herons in the Fraser River delta.

Briefly, most of the 680 km^2 delta above high tide has been diked for agricultural, residential and industrial use. An extensive network of ditches and sloughs drains much of the delta. Vegetable crops are grown in fields in summer and fields either lie fallow or grow cold-hardy crops in winter. Outside the dikes, a 600 to 1000 m wide band of brackish marshland extends between the channels of the Fraser River (Fig. 2-2). From the western shore of Point Roberts east into Boundary Bay lie extensive sand and mud beaches over 4 km wide at their greatest width (Fig. 2-2). These beaches support flourishing beds of eelgrass (*Z. japonica* and *Z. marina*) (Fig. 2-2).

GENERAL METHODS

Great Blue Herons were studied year-round between 3 April 1986 and 31 August 1990. I studied herons for five breeding seasons, (3 April to 15 August 1986, 21 March to 24 September 1987, 21 February to 18 August 1988, 17 March to 15 August 1989, 1 April to 31 August 1990) on Sidney Island. Herons were watched at all times of the year in the Fraser River delta but most often from late summer to early spring (15 August to 15 March 1986-90).

Dispersion in the Breeding Season - Nesting colony-sites of Great Blue Herons reported by Forbes *et al.* (1985b) were visited by volunteers and me in 1987 and by A. Breault (pers. comm.) in 1988-89. Colony-sites unknown to Forbes *et al.* (1985b) were found by contacting naturalists and through public requests in local newspapers.

I examined how herons chose a site for their colony by comparing the relative importance of food supplies and the presence of predators, notably the Bald Eagle (*Haliaeetus leucocephalus*).

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Dispersion in the Non-breeding Season - The dispersion pattern of herons outside the breeding season was determined in two ways. Every two weeks 2 observers independently mapped all herons seen from a Cessna 185 aircraft flown above the beaches and marshlands of the entire Fraser River delta (Fig. 2-3). The maximum number of herons overall in each about 4 km segment of the route was considered as the best index of the number present. The airplane flew at an altitude of about 90 m and an airspeed of about 140 km/h. The flight coincided with the lowest mid-winter daytime tide (3 m) between 1 September 1986 and 31 March 1987 and 1 September 1987 and 30 April 1988. The flight path followed the tide line in one direction and the top of the beach in the opposite direction. This allowed both observers to record herons over the entire beach. The entire survey took about 70 minutes.

From 17 July 1987 to 31 March 1988 and from 5 July to 16 September 1988 I drove a 89.4 km route once a week that crossed the farmlands behind the dikes at Boundary Bay and the mouth of the Fraser River (Fig. 2-3). Two observers searched for herons in the ditches and fields on opposite sides of the road. Each heron was assigned an age using plumage characters (see Age-class Descriptions) and its location was noted on a map. Data from these road censuses were used to estimate habitat use and seasonal mortality of herons during the non-breeding season. Detailed methods are provided in following chapters.
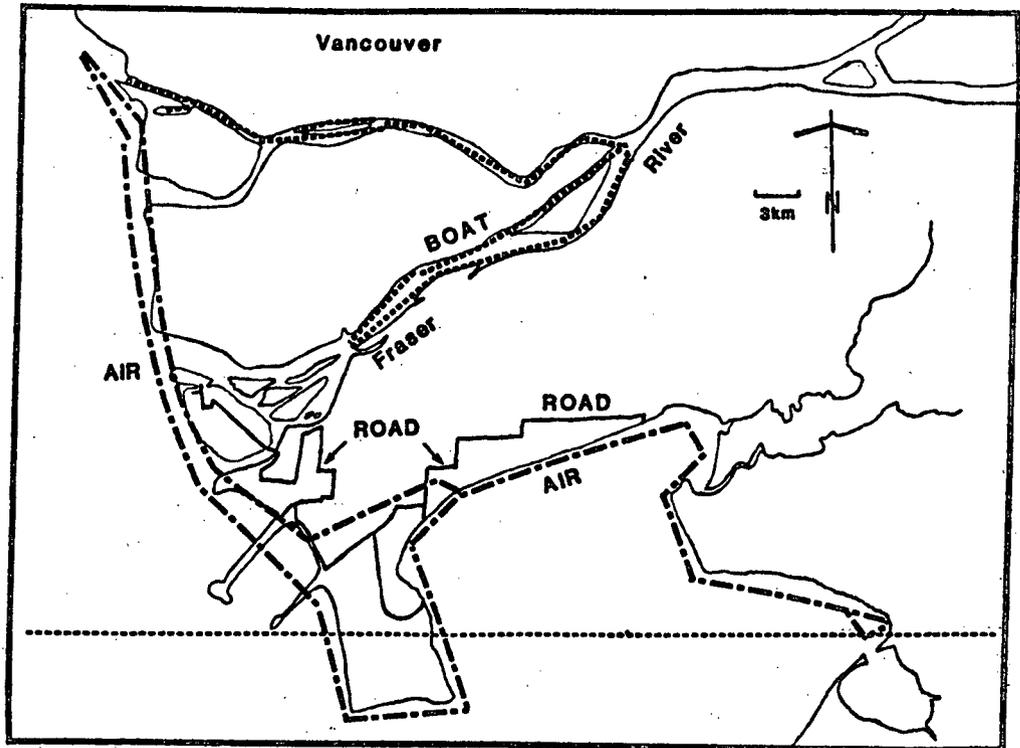
Figure 2-3.   Census routes followed to locate herons during the non-breeding season in the Fraser River delta.

Foraging - Feeding herons were watched on Sidney Island in spring and summer and in the Fraser River delta in summer and autumn through a 15-60x and a 20x spotting telescope. I opportunistically chose a feeding heron and an assistant recorded the time of the observations, the geographical location, the tide height (Department of Fisheries and Oceans 1986, 1987, 1988, 1989) and the age of the heron (juvenile or adult). Over the next ten minutes I recorded the time of each strike to the nearest second, the type of fish caught (e.g. gunnel, sculpin, etc.) and its estimated total length as a proportion of the culmen length of the heron (<1/4, 1/4-1/2, 1/2-3/4, 3/4-1, >1). A female Great Blue Heron in British Columbia has an average culmen length of 123.9 mm (S.E.=5.1, n=29, Simpson 1984) so these increments represent about 31 mm. Observer bias using this method was tested and accounted for during the analysis (see Chapter 5).

Prey populations in the lagoon on Sidney Island were sampled using a 2.4 x 18 m beach seine with a 6 mm mesh in April to July 1987-88 during the breeding season of the Great Blue Herons. Fish caught in seine hauls were identified using Hart's (1973) descriptions. The entire catch was emptied into buckets and counted later. Samples of the catch were weighed with Pesola spring balances, measured (total length) on a fish ruler and then released. These data were used to estimate the seasonal occurrence of major fish species and to produce length-weight regression equations. Detailed methods appear in Chapter 5.

In winter, herons in the Fraser River delta feed on voles, especially *Microtus townsendii*, caught in grasslands (Taitt and Krebs 1983). To assess daily and seasonal use of grasslands, I counted the number of herons on Alaksen National Wildlife Area fields on Westham Island, where large numbers of *M. townsendii* occur (Beacham 1980, Taitt *et al.* 1981, Taitt and Krebs

1983), from 13 November 1986 to 23 March 1987, and from 23 October 1987 to 12 February 1988.

Oceanic tides - Tides in the Strait of Georgia expose and cover the intertidal foraging sites of herons twice about every 25 h. The highest tide each day is followed about 8 h later by the lowest tide. An intermediate high and low tide complete the 25 h cycle. Within a year the lowest tides change gradually from midday in June to midnight in December. The maximum tidal amplitude is about 4.5 m. The number of minutes that low tides uncovered eelgrass beds (<1.7 m) each day at Sidney and the Fraser was derived from a computer model of predicted tides (A. Mau, pers. comm.).

Time of Breeding - Great Blue Herons throw hatched eggshells from their nests and the chicks begin calling soon after hatching (Brandman 1976; pers. obs.). Once the first chick was heard, I made nearly daily visits to gather shells in the colony. Two observers were used to reduce the total search time in the colony to about ten minutes. I used the date when the first shell was found below a nest as the date of hatching. On days when I was unable to visit the colony, I gathered eggshells the following day and assigned them a hatching date based on the amount of faeces splattered on them and on the freshness of the inner membranes.

Reproductive Success - In 1986 I counted the number of fledglings raised in nests at colony-sites: on Sidney Island, near the town of Crofton, in the University of British Columbia Endowment Lands, on Point Roberts (in Washington), and beside the Nicomekl River near Crescent Beach (Fig. 2-1). Volunteers gathered data on the number of nests used by herons and the number of chicks they produced at 23 other colony-sites on the British Columbia coast in 1987. In 1988-89, these and other colony-sites were visited by me and A. Breault (pers. comm.) to record nesting data.

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I numbered all nest trees at Sidney with a felt pen in March and early April 1987-90 before the eggs were laid. I later attached numbered aluminum plates to all trees with nests. Herons are often very sensitive to humans within sight or earshot of their nests early in the season (eg. Vos *et al.* 1985). To reduce this disturbance I restricted most colony visits in 1987 to within about 50 m of the edge of the colony until the eggs hatched. A black polyethylene plastic blind was built on the ground at the southeast corner of the colony in 1988 and 1989. Access was gained via a 100 m covered walkway beginning at the beach. This blind was used to observe herons at their nests and had no noticeable effect on the settlement or nesting success of herons.

About one month after hatching the surviving chicks were counted directly in easily observed nests, or when they became active during feedings at obscured nests. For many nests, two observers used vantage points on opposite sides of the nest and a count was made using binoculars. These counts were taken about once each week until the chicks became fledglings. Herons were considered to have used all nests that held eggs or chicks, or had hatched eggshells or feces on the ground below them.

Sex of Adult Herons - From 15 October 1988 to 30 April 1989 I drove to vantage points along the Fraser River and major roost and feeding sites to assign the age and sex to herons. I also opportunistically assigned the age and sex of other herons found in the delta over the same period. The sex was determined using the 'gradicule method' (Butler *et al.* 1990). This technique estimates culmen lengths against a gradicule scale mounted in the eye-piece of a telescope. The distance between the heron and the telescope is measured using a tape-measure, and the gradicule-scale measure is converted into actual beak lengths. The accuracy of this method depends on several factors including the angle of the culmen relative to the sight-line through the

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telescope and the distance between heron and observer. Nevertheless, the method allowed me to estimate the sex of about three-quarters of the herons within 65 m with 95% confidence. Records for the 25% of birds of unknown sex were discarded.

CHAPTER THREE. THE EFFECT OF PREDATORS AND FORAGING HABITAT ON

COLONY-SITE SPACING IN GREAT BLUE HERONS

In the next two chapters, I examine factors affecting how Great Blue Herons select habitats. In this chapter I focus on the relationship between the distribution of foraging habitat and presence of predators on the spacing of heron colony-sites.

Lack (1954, 1968) postulated that food availability was more important than predators in determining the location of most breeding colonies of birds. Several studies have shown that colonies are located near food supplies (see Perrins and Birkhead 1983, Kushlan 1976b, Gibbs *et al.* 1987) as predicted by Lack (1954, 1968). However, predators are often difficult to locate or their populations reduced so their impact on colony-site spacing is poorly understood. Predators cause colony-site abandonments in herons (Dusi and Dusi 1968, Simpson 1984) and might affect the spacing of their colony-sites.

The Great Blue Heron in British Columbia is suitable for exploring the relationship between food availability, distribution of predators and colony-site spacing because: (i) colony-sites can be located by following herons returning from feeding areas, (ii) the major predator in British Columbia is the Bald Eagle (*Haliaeetus leucocephalus*) (Vermeer *et al.* 1988, Norman *et al.* 1989) which nests in conspicuous places, and (iii) most female herons feed on intertidal beaches near the colony-sites during the breeding season (Chapter 4) and only females provision chicks under 3 weeks of age. The hypotheses I tested were that herons located colony-sites: (i) near food supplies or, alternately (ii) away from predators.

Predictions

Food supplies

(i)   More herons should breed near habitats with high prey availability than near habitats with low prey availability;

(ii)   Fledged brood-size should decline, and the number of deserted nests should increase, with distance between the food supply and the colony-site;

(iii) The number of breeding herons should be positively correlated with the area of foraging habitat;

Predators

(iv)   Fewer herons should breed in areas frequently used by eagles than areas infrequently used by eagles;

(v)   Fledged brood-sizes and the number of successful nesting pairs should be greater in colonies outside eagle territories than inside eagle territories.

METHODS

Great Blue Herons were studied at colony-sites around the Strait of Georgia, British Columbia (Fig. 3-1). General methods used to: estimate fledged brood-sizes, estimate the number of nests used at a colony-site, and locate colony-sites are given in Chapter 2.

Prey Availability

I assumed that shallow beaches with eelgrass (*Zostera marina*) beds, kelp (mostly *Nereocystis luetkeana* and *Laminaria* spp.) beds and marshes had high prey availability whereas other habitats had low prey availability. This assumption is discussed later. All eelgrass beds, kelp beds and marshes

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>10 ha in area in the Strait or Georgia were located from searches and published maps (Hutchinson 1982, Hutchinson *et al*. 1989).

Distance between colonies and feeding sites

Most breeding herons feed at one major site near their colony-site (Chapter 4). Herons departing from 22 colony-sites were followed to their major feeding location when their nests held eggs and small chicks. The distance between the colony-site and centre of the feeding site was measured on 1:50,000 scale maps.

Distance between heron colonies and eagle nests

I assumed that the proximity of Bald Eagle nests was a good index of predation pressure at heron colonies. This assumption is discussed later. Eagle nests were found by ground (6 cases) and air searches (113 cases) (Vermeer *et al*. 1989) and by public request (74 cases). Bald Eagle feeding territories extend outwards for up to 3 km around their nests (Stalmaster 1987). Therefore, heron colony-sites >3 km from an eagle nest were assumed to be outside an eagle's territory and were considered to be 'far' from predators, whereas 'near' colony-site were located $\leq$3 km from an eagle nest and assumed to be within an eagle's territory.

Eagle-nest abundance

I assumed that eagles occurred in high abundance where 3 or more nesting territories were contiguous (i.e. nests were $\leq$6 km apart on average) and occurred in low abundance where their nesting territories were not contiguous (i.e. nests where >6 km apart on average).

RESULTS

Distance between colony-sites and feeding sites

Colony-sites were near feeding grounds; the average distance was 2.3 km (S.D.=1.3, N=22). Of 33 colony sites used in 1987-89, all but four small (5-40 pairs) colonies were near shallow beaches with kelp beds, eelgrass beds or marshes (Fig. 3-1). The feeding sites of these four colonies were unknown. However, all of them were within 2 km of the Strait of Georgia where lone herons foraged. Three apparently suitable feeding areas had no colonies nearby during this study but have been used in the past (Forbes *et al.* 1985b). The number of breeding pairs correlated positively and significantly with the area of the feeding sites used by each colony (Fig. 3-2). Brood size and nesting success were not significantly correlated with the flight distance between the colony-site and feeding area (Fig. 3-3), although brood sizes were weakly negatively correlated with flight distance as predicted.

These findings support the prediction that colonies are sited near feeding areas with abundant prey, and the number of breeding pairs is positively correlated with the area of foraging habitat. However, my results fail to support the prediction that reproductive success is related to the flight distance between colony-sites and feeding areas.

Predation

There was no support for the hypothesis that colony-sites were located far from eagle nests (Fig. 3-1). Four-hundred and ninety-seven herons nested in

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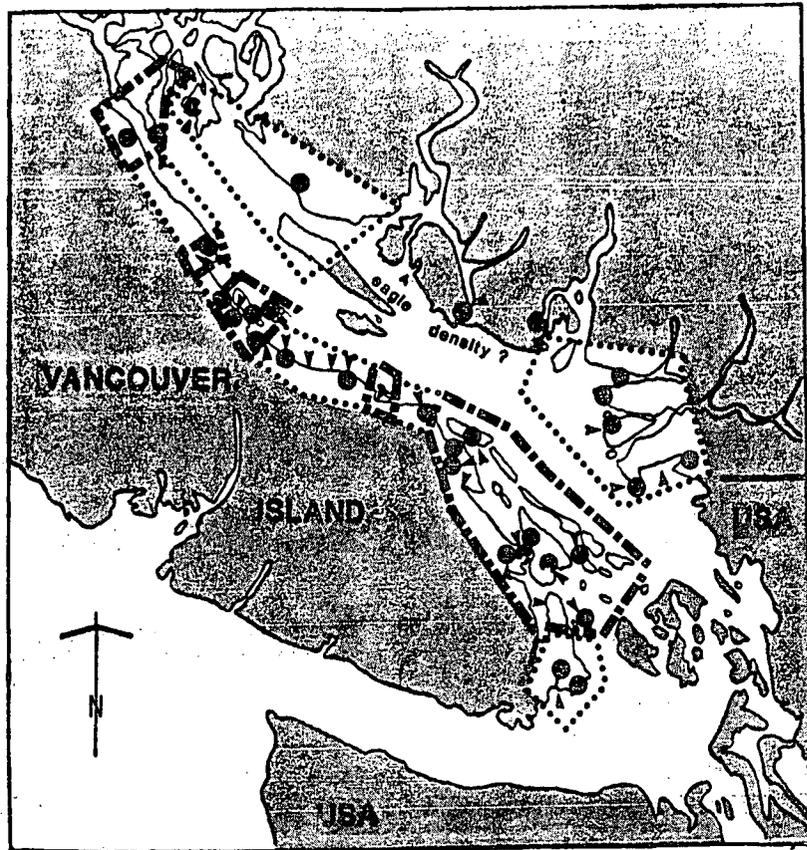
Figure 3-1. Location of Great Blue Heron colony-sites (closed circles), kelpbeds, eelgrass beds and marshes >10 ha (arrow) in relation to Bald Eagle nesting abundance. Dashed lines enclose areas where eagle nests averaged less than 6 km apart (high abundance) and dotted lines enclose areas where eagle nests averaged fewer than one every 6 km (low abundance).
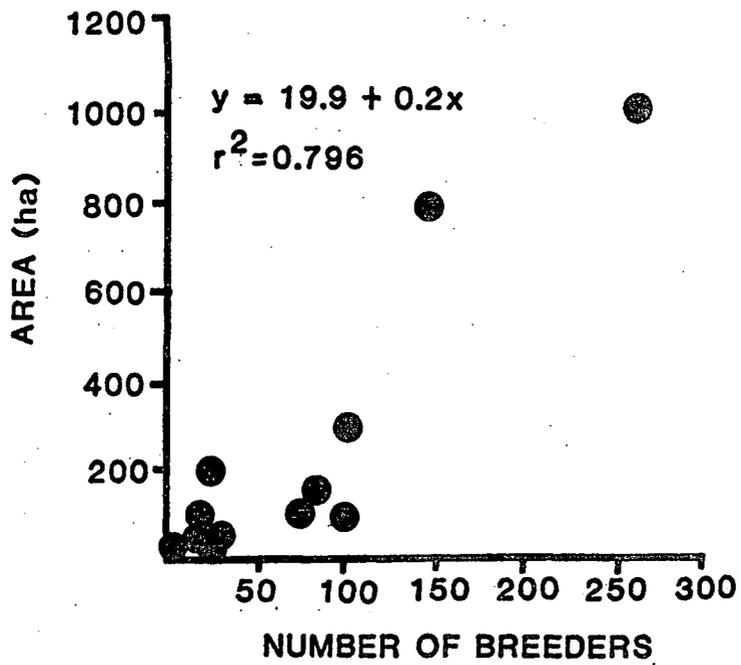
Figure 3-2. Numbers of breeding pairs of herons and the area of their foraging sites in 1988.
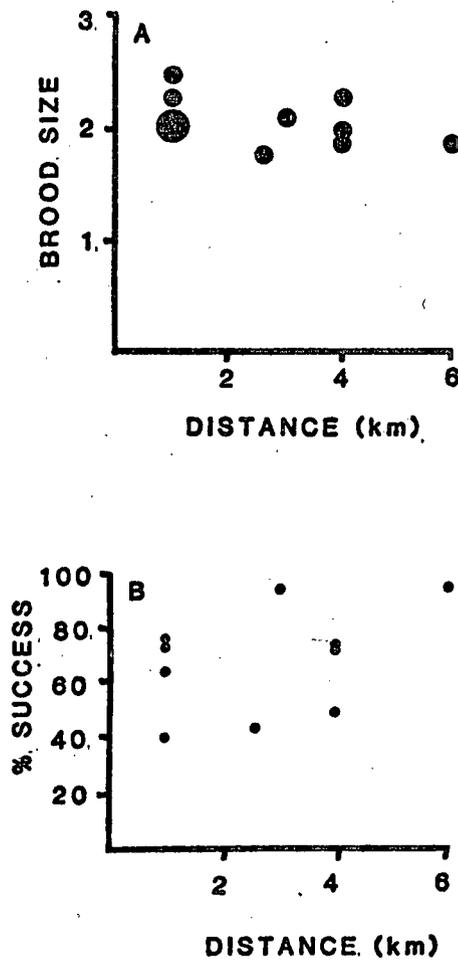
Figure 3-3. Mean brood size (A) and percentage of occupied nests that held one or more fledgling (B), in ten heron colony-sites versus distance to the major feeding site in 1988. Large dot in A = 2 colony-sites; all other dots represent 1 colony-site.

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19 colonies in areas where eagles occurred in high abundance, and 515 herons nested in 13 colonies in low abundance eagle areas. More importantly, the proportion of colony-site abandonments was actually slightly lower in high-abundance eagle areas than in low abundance areas (Table 3-1). At one site in Victoria, a pair of eagles nested in the colony-site and a second pair nested less than 1 km away. These eagles regularly attacked the herons in 1988, 1989 and 1990. The colony abandoned its eggs in 1990. Eagles attacked the Sidney colony in all 5 years of this study. The colony abandoned the site twice during the egg stage in 1989 and once in 1990. At least 3 adult herons were killed by eagles in the colony in 1989 and 5 in 1990. In 1989, many herons were seen on nearby islands where few had been seen in 1987-88 so I presume the herons did not attempt to nest a third time. In 1990, the Sidney herons abandoned after one attempt and renested about 6 km away on Vancouver Island. Eagles also attacked herons in 7 of 21 other colony-sites in 1988 and in 9 of 23 colony-sites in 1989.

Although eagles sometimes cause abandonments of entire colony-sites, there is no evidence that the proximity of nesting eagles affected the average reproductive success in heron colonies that raised fledgling-aged chicks. The mean brood size was nearly identical in colonies near and far from eagle nests (Table 3-2). More importantly, the mean percentage of successful nesting pairs was nearly identical in colonies near and far from nesting eagles (Table 3-2).

Table 3-1. Number of successful and failed heron colony-sites where eagles nested in high (nests ≤ 6 km apart) and low (nests > 6 km apart) abundance in 1987-89.

Eagle-nest abundance	Success	Fail
High	23	5
Low	17	6

Table 3-2. Percentage of successful (>1 fledgling) nesting pairs and mean brood sizes of colony-sites that produced fledglings near (<3 km) and far (>3 km) from an occupied Bald Eagle nest in 1989.

	Near			Far		
	Mean	SD	N	Mean	SD	N
Percent success	81.1	11.9	12	85.1	13.7	7
Brood size	2.6	0.4	12	2.6	0.4	7

DISCUSSION

Validity of assumptions

This analysis was based on two key assumptions. First, I assumed that prey availability was greater on beaches with kelp beds, eelgrass beds and marshes than on beaches without these habitats. This assumption is supported by several distribution studies of prey species eaten by herons in the Strait of Georgia (see Hughes 1985, Gordon and Levings 1984, Hay et al. 1989).

I feel less confident with the assumption that Bald Eagle nesting abundance was a good measure of predation pressure in heron colonies. First, my analysis of heron nesting success might have been more sensitive if I had used more than 2 categories of eagle nest abundance. Second, raccoons (Procyon lotor), Red-tailed Hawks (Buteo jamaicensis), and Turkey Vultures (Cathartes aura) also occasionally prey upon heron eggs and chicks in British Columbia (Simpson et al. 1987, A. Breault, pers. comm., pers. obs.) but I did not measure their impact. Most importantly, the proximity of nesting eagles might be a poor measure of predator pressure. For example, the 1990 abandonment at Sidney occurred after an immature-plumaged eagle killed an adult heron in the colony although a pair of eagles nested less than 1 km away. Thus, the number of attacks on herons by eagles might be unrelated to the proximity of occupied eyries. On 9-10 April 1987 when female herons were laying or incubating eggs in most colony-sites, over one-third (293 out of 797) of the eagles counted from aircraft in the Southern Gulf Islands were immature-plumaged birds. Moreover, the abundance of eagles in this part of British Columbia might be so great that herons can not avoid them. There was slightly more than one eagle per km of coastline on average (797 eagles along 750 km of shoreline) in the southern Gulf Islands in 1987 (data in Vermeer et al. 1989).

Food and Predators as Determinants of Colony Location

Several studies have shown that wading birds (Kushlan 1976b, Custer and Osborne 1978) including herons (Fasola and Barbieri 1977, Gibbs *et al.* 1987, Simpson *et al.* 1987) nest near productive foraging areas but my study is the first to my knowledge that shows that the distribution of heron colony-sites is unrelated to the density of breeding eagles.

Many heron colony-sites were located near eagle nests presumably because both species have similar habitat needs. Eagles in British Columbia eat a wide assortment of prey (mostly vertebrates) caught along seacoasts of which herons are of minor consequence (Vermeer *et al.* 1989). Heron colony-sites are located near foraging habitats (Fig. 3-1) with an abundance of small fish (Hughes 1985, Hay *et al.* 1989, Chapter 5). These biologically productive habitats also attract the prey species taken by eagles.

Gibbs *et al.* (1987) suggested that the spacing of heron colony-sites in Maine resulted from dispersers settling outside the foraging range of other colony-sites where they would get full access to unexploited resources. According to their model, new colonies would settle at the edges of the foraging ranges of neighbouring colonies once the best sites were full. Eventually, colony-sites would become evenly-spaced along the coast.

This model assumes that herons deplete food supplies near their colony-sites (Gibbs *et al.* 1987). If herons deplete local food supplies then spacing should be a function of colony size since large colonies require more food than small ones. However, colony-sites were evenly spaced in their study even though the number of breeding pairs ranged from 4 to 252 herons.

I agree with Gibbs *et al.* (1987) that food supply determines the spacing of colony-sites but I doubt that herons in general deplete their food supplies to a measureable extent. Herons in my study foraged mostly near the colony-

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site (Chapter 4) and had insufficient time during low tides to deplete their food supplies markedly (Chapter 5).

Flight Distance and Reproductive Success

Adult herons must increase their provisioning rates to raise large broods to fledging age (Sullivan 1988). Thus, adults should increase their foraging time and/or reduce their own energy requirements by decreasing travel time between the colony-site and foraging area (Orians and Pearson 1979, Bryant and Turner 1982). Therefore, it makes intuitive sense for herons to nest as close as possible to food supplies.

All colony-sites were located too close to food supplies to reveal any differences in their average fledged brood sizes. However, the power of the statistical tests to detect a significant difference here is low because of small sample sizes of colony-sites distant from feeding grounds.

Moreover, herons should avoid poorer sites if better ones are available near food supplies. It is unclear how far herons would have to nest from their feeding sites before differences in reproductive success should be detectable. Herons carry large amounts of food each trip and make few trips to feed young. Marion (1989) reported individual Gray Herons feeding up to 38 km from colony-sites in France but he did not relate flight distances to reproductive success. Simpson (1984) showed that Great Blue Herons feeding near a colony-site on the British Columbia coast had higher reproductive success than distant-feeding birds, but he did not know how far distant-feeders travelled (pers. comm.). Moreover, local-feeding herons supplemented their diet by making regular trips to tanks holding live herring (*Clupea harengus*) in Simpson's (1984) study.

I conclude that average nesting success in colonies is unrelated to the distance to the feeding site over the distances I measured.

SUMMARY

1) Great Blue Heron colony-sites (n=22) in the Strait of Georgia were located within 6 km of major foraging areas.

2) The number of breeding pairs, reproductive success, or number of abandonments of heron colony-sites were similar in low and high density eagle-nesting areas. Predictions from the hypothesis that predators affect the location of heron colony-sites were not supported but more direct evidence of effects of predators, including Bald Eagles, is required to test the hypothesis further.

3) The spacing of heron colony-sites in British Columbia is best explained by the distribution of shallow beaches with kelp beds, eelgrass beds and marshes where most herons foraged in summer.

CHAPTER FOUR. SEASONAL PATTERNS OF HABITAT USE BY FORAGING GREAT BLUE HERONS

In the previous chapter I showed that the spacing of heron colony-sites was explained by the distribution of food supplies. In this chapter, I describe the habitat use by foraging herons and relate seasonal shifts in this distribution to intraspecific competition and food availability.

One view of habitat selection posits that as the density of foragers increases, the best competitors establish exclusive feeding territories or dominate weaker individuals who then move to marginal habitats (Fretwell and Lucas 1970, Fretwell 1972, Sutherland and Parker 1985, Chapter 1). Another view posits that an individual's foraging skill mostly determines where it will forage, independently of the density of competitors (Stephens and Krebs 1986, Chapter 1).

Tests of the foraging competition and food availability hypotheses have been hampered by difficulties in tracking mobile animals between habitats through the year. This is particularly important since foraging skills (see review by Burger 1988) and competitive skills (Partridge and Green 1985, Goss-Custard and dit Durell 1987a,b) improve with age in many animals.

Great Blue Herons in British Columbia lend themselves well to studies of foraging habitat selection because: (1) they feed year-round in open habitats where interactions can be observed and food ingestion rates can be estimated (Chapter 5), (2) some defend feeding territories (Brandman 1976, Bayer 1978) while others feed alone or in groups (Krebs 1974, Kushlan 1978), and (3) juveniles are less proficient at foraging than adults (Quinney and Smith 1980).

The aim of this chapter is to relate the dispersion of age- and sex-classes of herons across habitats to the presence of intraspecific competitors and availability of foraging time. First, I describe the year-round use of

habitats by heron age- and sex-classes. Next, I compare the hypotheses that foraging herons move between habitats in autumn because of: (i) interference from foraging conspecifics (Sutherland and Parker 1985), or (ii) insufficient foraging time (Sullivan 1990) during low tide. Finally, I discuss how the foraging skill of juvenile and adult herons affects their survival.

Predictions

Intraspecific foraging competition

(i) Juvenile herons should depart from foraging habitats when interference from adults reduces energy ingestion rates below the daily energy maintenance requirement;

(ii) Feeding territories should be defended by adult males because they are larger and heavier (Simpson 1984) than adult females and juveniles, and thus better able to exclude other age- and sex-classes.

Foraging time and foraging success

(i) Herons should leave foraging habitats when there is too little time per tide cycle to catch enough food there to meet their daily energy maintenance requirement (McNamara 1982);

(ii) Juveniles are less proficient foragers and should therefore vacate foraging habitats before adults in autumn.

STUDY AREA AND METHODS

Great Blue Herons were studied mostly on Sidney Island during the breeding season and in the Fraser River delta during the non-breeding season. I describe the study areas and general methods in Chapter 2, and also describe there how I: i) estimated tide heights, diets and foraging rates, ii) determined use of foraging habitats by breeding adults, iii) counted herons in marshlands, on beaches, in grasslands, and along rivers, and iv) assigned age and sex to herons. I estimate the energy in heron prey and the daily energy maintenance needs of herons in Chapter 5.

Habitat use of Age- and Sex-classes

Breeding season dispersion – The directions of all incoming and outgoing foraging flights by breeding adults from the Sidney colony-site were recorded from dawn to dusk during 19 low tides and 17 high tides on 16 days at 3 times in the season. I observed birds on 4 days when most nests held eggs (12 April-4 May) and 4 days when nests held small chicks (10-31 May). When nests held large chicks (16 June-10 July), I recorded flights during five low tides and one high tide. Bearings of major flight directions off the island were drawn on a map and destinations visited about once every two weeks to search for feeding herons. Arrival and departure directions at these sites confirmed that the herons came from Sidney Island.

Non-breeding season dispersion – I censused herons in potential habitats from an airplane, car and boat. These covered all heron habitats although census efforts were uneven. I consider these habitats were most important to herons but it remains open that some herons might have been overlooked in other habitats.

Herons feed on beaches, in marshlands and grasslands and along river banks in the Fraser River delta. Herons were plotted on maps during aerial censuses of the Fraser River delta beaches and marshlands (Fig. 2-3) between September 1986 and February 1987. Nearest-neighbour distances were later measured from these maps. A 300 m buffer zone was drawn around the census areas to reduce edge-effect bias (Krebs 1989). An index of aggregation and tests of significance for its deviation from randomness were derived for marsh and beach habitats (pp. 126-129 in Krebs 1989).

Habitat Selection

Intraspecific foraging competition

Interference - I used interference, including territorial behaviour, as an indicator of intraspecific competition for food and foraging sites. I noted the frequency and duration of chases, displays and fights of foraging herons on beaches in the 1987 and 1988 breeding season at Sidney and from 1 August- 3 November 1987-89 in the Fraser River delta (see Chapter 2). The effect of this interference was quantified by estimating the reduction in Metabolized Energy (ME, see Chapter 5) to a foraging heron resulting from interactions.

Territoriality - The smallest territory defended by 32 herons on the Oregon coast was about 200 m long (Bayer 1978) and about 300 m in my study area (6 cases). I assumed that other feeding territories existed in my study area if: (i) single herons repeatedly used a site avoided by neighbouring herons (4 cases), (ii) a heron I disturbed returned to the same site and avoided areas used by other herons (3 cases), or (iii) a total of 200 m or more of continuous unoccupied habitat extended on one or both sides of a solitary heron (25 cases).

Habitats and the locations of herons along the banks of the Fraser River (Fig. 2-3) were mapped from a boat on 10 January 1990. Habitat segments less than 200 m long were eliminated from the analysis because they were unlikely to be large enough to hold a heron territory (see Bayer 1978).

Relative availability of foraging time

Relative availability of foraging time is the proportion of the total available time required by adult and juvenile herons to meet their daily maintenance energy needs on beaches and in grasslands in the non-breeding season. I assumed that adult and juveniles required the same amount of maintenance energy because they have similar body masses.

Beaches - I estimated the relative availability of foraging time to herons foraging on beaches in September-November using the formula:

$$F_1 = \frac{[(I_d \cdot T_d) + (I_n \cdot T_n)]}{M} \times 100$$

where F_t is the percentage of the low tide foraging period required by a heron to meet its daily maintenance energy in each 24 h period, M is the amount of energy (kJ) required by herons for daily energy maintenance, I_d and I_n are the respective ingestion rates during day and night, and T_d and T_n are the respective number of minutes of low tides available for foraging during day and night. Each of these terms in the equation is now explained in detail.

Maintenance energy (M) - I estimated the amount of energy needed for maintenance (=1560 kJ) using methods outlined in Chapter 5. I assumed that adult and juvenile herons had similar energy maintenance needs because they have similar body masses.

Ingestion rates (I) - Ingestion rate is the amount of energy (kJ) consumed per minute of foraging by an adult and juvenile heron. It was estimated by

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multiplying foraging rates of adult and juvenile herons (see below) by the average amount of energy in their respective diets (see Methods in Chapter 5).

Foraging rates of adult and juvenile herons on beaches on the Fraser River delta were estimated on 33 days between 1 August and 3 November 1987-89. The mean capture rate during high tides at Sidney in May-June was 3.6 times faster during the day ($\bar{x}$=2.6 mins/fish, S.E.=0.3, N=81) than at night ($\bar{x}$=9.4 mins./fish, S.E.=2.1, N=9). If fish caught during the day and night are the same size, then herons ingested about 3.6 times more energy per minute while foraging during the day as at night from August to November in the Fraser River delta. This assumption is discussed later. I assumed that herons caught the same species of fish during night and day on the Fraser River delta because sea perch and sculpins were caught in beach seines during day and night in eelgrass beds in the Yaquina estuary, Oregon (Bayer 1985b).

Foraging time (T) - The number of minutes that low (<1.7 m) tides uncovered the eelgrass beds each 24h from 1 September to 30 November 1987 was used as an estimate of the total amount of available foraging time on beaches.

Grasslands - I estimated the relative availability of foraging time of herons feeding on Townsend's voles (*Microtus townsendii*) in grasslands in November - January using the formula:

$$F_t = \frac{[(I_d \cdot T_d)]}{M} \times 100$$

where F_t is the percentage of the day required by a heron to meet its daily energy maintenance need, M is the estimated amount of energy needed for maintenance (=1560 kJ) using methods outlined in Chapter 5, I is the ingestion rate (kJ) of herons eating voles, and T is the number of daylight hours per day. How I determined ingestion rates is now explained in detail.

Ingestion rates (I) - Ingestion rates (I_d) during the day were estimated by multiplying the number of voles caught per minute of grassland foraging by the

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amount of energy (kJ) contained in an average vole. I watched 54 herons hunt voles in grasslands between 18 November 1985 and 17 January 1987. I estimated the average amount of metabolizable energy available to a heron eating voles by converting the mean weight (56g,SD = 12) of 61 voles caught into energy units (kJ). Voles were caught in live-traps on 2 December 1986 in grasslands used by herons on Westham Island in the Fraser River delta. I assumed that: (1) the average Townsend's vole contained the same amount of water (67%) and energy (23.5 kJ/g dry wt) as the Common vole (*M. arvalis*, Wijnandts' 1984), and (2) herons digested 78% of the energy in each vole (Castro *et al*. 1989). Therefore, the average metabolized energy available in a vole eaten by a heron was estimated to be (56g x 0.33 dry wt x 23.5 kJ/g dry wt. x 0.78 digestive efficiency=) 339kJ. These assumptions are discussed later.

Habitat Shifts, Dispersal and Mortality

I assumed that the decline in numbers of herons along an 89.4 km census route (Fig. 2-3) approximated their death and dispersal rate from the Fraser River delta. This assumption is discussed later. Four road censuses were conducted each month between August and February 1987-88, except in September (3 censuses), November (5 censuses) and August (6 censuses). Emaciated dead herons found by me or others in the Fraser River delta that had no abdominal fat stores and depleted pectoral muscle mass were assumed to have starved.

RESULTS

Spacing of Age- and Sex-classes

Breeding season - During low tides, most adult herons foraged in nearby Sidney lagoon (Table 4-1). Herons flying off the island fed in eelgrass and kelp beds on neighbouring islands within 10 km of the colony.

Table 4-1. Percentage of flights to and from the Sidney lagoon versus other sites off the island during low tides (<1.7 m) and high tides when the nests held eggs, small chicks and large chicks.

Stage	Low tides		High tides	
	Percent	N	Percent	N
Egg	94.1	271	27.2	213
Small chick	90.5	541	51.3	298
Large chick	62.6	460	10.3	78

During high tides, herons with eggs and large chicks in nests avoided the lagoon and flew mostly off the island (Table 4-1) to beaches and estuaries an average of 14 km (SD=8, range=6-27, n=13) from the colony-site. However, during the small chick stage, about half the flights at high tide were to and from the lagoon (Table 4-1).

Only females (18 cases) were recorded in the lagoon between 9 April and 31 May 1988. Males (2 cases) were first seen in the lagoon on 1 June in the company of females (11 cases). Seven male herons and no females were identified off the island in late afternoon and early evening before 1 June. I conclude that when nests held eggs and small chicks most females fed themselves and their chicks on fish caught in the lagoon during the day when tides were low and males fed themselves mostly off the island in the afternoon until the following morning when tides were mostly high. When nests held large chicks, both parents fed the chicks fish caught in the lagoon during low tide and off the island during high tides.

Yearling herons rarely visited Sidney Island during the breeding season. One was seen in the lagoon for about 3 weeks in late June-July in 1987, 1988 and 1989. A yearling occupied a nest in the colony in June-July 1989 but did not find a mate (I. Moul, pers. comm.). I found 1-8 yearlings among adults on fortnightly visits made in May-July 1988 to 4 estuaries and 6 beaches up to 27 km away from Sidney Island and on beaches and in marshlands in the Fraser River delta.

Non-breeding season - Adult female and juvenile herons in the Fraser River delta shifted from feeding mainly (92%) on the beaches in August to feeding mainly (56%) in marshlands in January. This trend was reversed in spring (Fig. 4-1). The number of herons counted on the beaches at low tide from August 1986 to April 1987 was significantly (t=7.6, p<0.001) and positively

100

MARSHLANDS

80

no
data

PERCENT

60

40

BEACHES

20

257 578 273 338 100 214 373 560

A   S   O   N   D   J   F   M   A
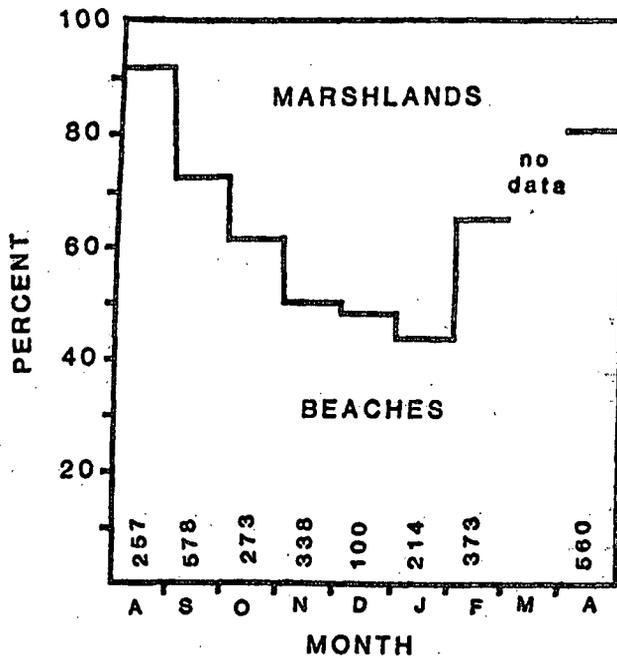
MONTH

Figure 4-1. Percentage of herons using marshlands and beaches in the Fraser River delta between August and April 1986-87. Numbers above months indicate the number of herons counted in that month.

correlated with the number of hours of available foraging time during low tide (Fig. 4-2). The marshlands were seldom covered by more than 30 cm of water for longer than 2h each day. Significantly more juveniles than adults used grasslands rather than marshlands (Table 4-2). Herons were mostly clumped on the beaches and in marshlands between September and February (Table 4-3).

In summary, herons used beach habitats mainly from March to October, and increasingly used marshlands and grasslands from November to January after which they began to return to beaches.

Habitat Selection
Intraspecific foraging competition

Interference - Most breeding herons fed peacefully in Sidney lagoon during the day. I saw one interaction in over 2700 mins. of watching herons catch non-schooling fish. Interference increased when herons briefly flocked to pursue schools of Shiner Sea Perch (*Cymatogaster aggregata*). However, these interferences did not result in herons being chased from the lagoon. For example, on 28-29 June 1988 I recorded 41 interactions between about 50 herons that pursued perch for 23 mins. (0.04 interferences/heron/min.). Displaced birds flew a few meters away and began feeding on sea perch again about 30s later. The median capture rate in 27 of these groups was 0.2 sea perch per min. (range=0.04-1.7). Each sea perch contains an estimated 100.4 kJ of Metabolizeable Energy (ME) (Table 5-2, Chapter 5). Therefore, the estimated ME intake rate for herons feeding on sea perch was (0.2 fish/min. x 100.4 kJ/sea perch=) 20.1 kJ/min. The estimated energetic cost of an interference was (0.5 min. to start foraging per interference x 0.04 interferences/min x 20.1 kJ/min.=) 0.4 kJ/min/heron or 2% of the total ME
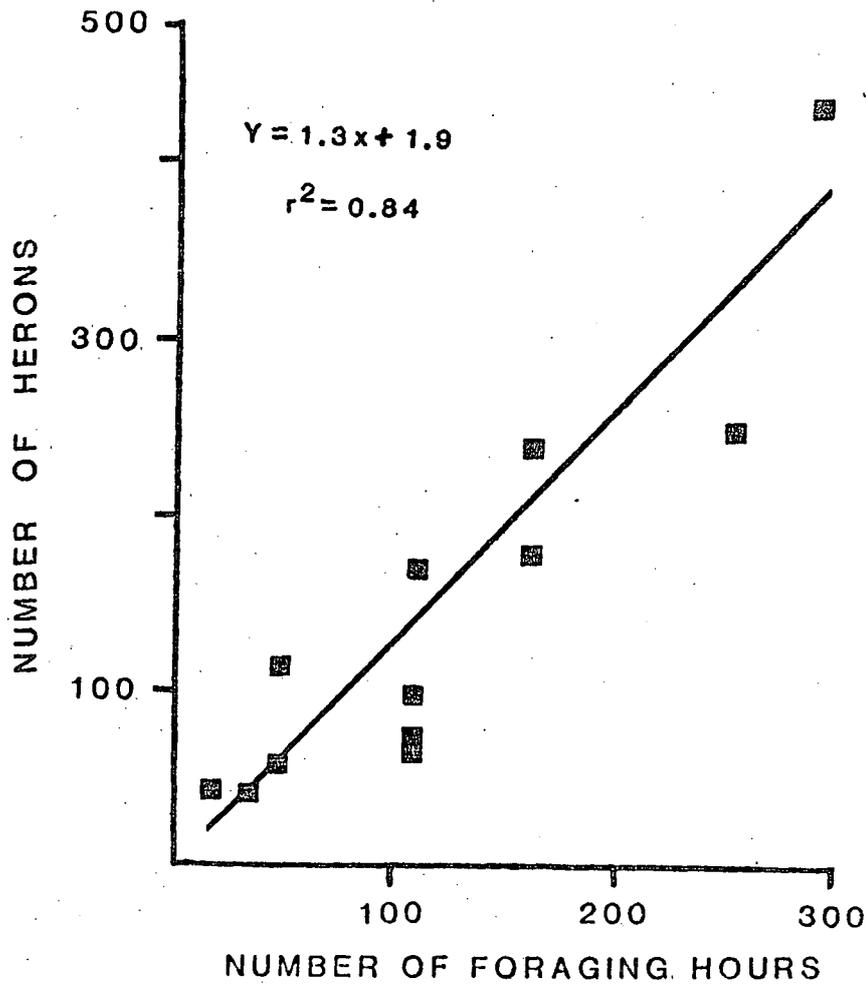
Figure 4-2. Numbers of Great Blue Herons counted on beaches in the Fraser
River delta in relation to the average number of foraging hours
at low tide (<2.3 m) from August 1986 to April 1987.

Table 4-2.   Number of adult and juvenile herons counted in grasslands and marshlands of the Fraser River delta between July 1987-March 1988 and July-September 1988.

	Adult	Juvenile
Grasslands	698	302
Marshlands	158	16

Table 4-3. Indices of aggregation of Great Blue Herons feeding in marshlands and on intertidal beaches of the Fraser River delta during the non-breeding season. The spatial pattern ranges from clumped (R approaches zero) to regular, (R approaches 2.15). When the pattern is random, R=1 (Krebs 1989).

		Index of Aggregation (R)			
Year	Date	Marshlands	n	Beach	n
1986	30 Sept	0.53**	69	0.59**	224
	29 Oct	0.96	73	0.87**	164
	12 Nov	0.98	105	0.83**	96
	27 Nov	1.25**	28	0.98	54
	10 Dec	0.80**	43	1.20*	22
1987	6 Jan	0.81**	45	0.73**	32
	21 Jan	0.95	46	0.57**	42
	6 Feb	0.97	27	0.74**	47
	20 Feb	0.63**	34	0.61**	84

* = the spatial pattern is significantly ($p < 0.05$) and ** = highly significantly ($p < 0.01$) different from random.

while feeding on sea perch. Therefore interference had little effect on the average ME intake rate of these herons although it could have affected some non-average birds who got continually displaced.

Adult and juvenile heron diets on the Fraser River delta were significantly different in August/ September (Table 4-4) because juveniles ate fewer sea perch. Interference from foraging conspecifics reduced the ME intake rates of adult and juvenile herons by about 1% of their average rate and therefore, interference was unimportant in autumn (Table 4-5). I conclude that interference by conspecifics maintains individual foraging distances but does not explain habitat shifts among herons foraging on beaches.

Territoriality - Adults held territories along riverbanks (n=38) on the Fraser River. The highest densities of territorial herons occurred in river-edge marshes (Table 4-6). Nine territories that could be viewed both day and night were occupied by solitary herons every month of the year. Three out of 5 herons could be confidently sexed along riverbanks and all were adult males. Nineteen out of 28 adults whose sex could be determined in marshlands during the non-breeding season were females, one was a male and the sex of 8 others could not be confidently identified. None were territorial. These values are significantly different from an expected even sex ratio in marshlands and along riverbanks (Fisher Exact Test X^2=11.8, p<0.003). These results support the prediction that it is usually adult male herons who defend feeding territories.

Table 4-4. Number of each prey species caught by adult and juvenile Great Blue Herons in August and September 1987, 1988 and 1990 (N=33 days).

Prey species	Adult		Juvenile	
	Number	%	Number	%
Perch	82	63.0	27	35.1
Sculpins	39	30.0	40	52.0
Gunnels	4	3.1	3	3.9
Others	5	3.9	7	9.0
Total	130		77	

X^2=15.7, df=3, p=0.002

Table 4-5. Daily Metabolizable Energy (ME) intake in kJ lost to interference by conspecifics in autumn.

	Adult		Juvenile	
	Mean	S.E.	Mean	S.E.
Estimated ME ingested				
Mean no. fish caught/min.	0.46	0.06	0.24	0.03
Mean ME/fish[a]	48.6	14.0	42.6	10.5
Mean ME/min.	22.4		10.2	
Cost of interference				
No. interferences/min.	0.01		0.01	
ME lost to interference/min.	0.22		0.10	

a – calculated by weighting the average metabolizeable energy per species (Chapter 5) by the proportion of the diet in Table 4-4.

Table 4-6. Numbers and densities of territorial Great Blue Herons in three
habitats along the riverbanks on the Fraser River delta.

	Length of habitat(km)	Number	Density (herons/km)
Forest edge	17.1	7	0.41
Marsh with or without forest	19.2	25	1.30
Industry/agriculture with or without marsh	62.1	6	0.10

Foraging success

Beaches - The mean daytime foraging rates of adults on the Fraser River delta declined significantly (t=4.9, r^2=0.24, p<0.001) between 1 August and 3 November. In August, adults needed an average of 1.9 mins (SE=0.5) to capture a fish versus 3.5 mins (SE=0.3) in September and 5.0 mins (SE=0.4) in October and early November. Juvenile foraging rates also declined, but not significantly (t=2.57, r^2=0.12, p=0.13). Juveniles needed an average of 3.3 mins. (SE=0.4) to capture a fish in August, 4.7 mins (SE=0.5) in September, and 6.0 mins (SE=0.9) in October and early November. Juveniles took 74%, 34% and 20% more time to catch a fish in August, September and October, respectively, than adults.

Foraging time

The average juvenile runs out of time (F_t>100%) to meet its daily energy needs on beaches on 5 days in September, 7 days in October and 12 days in November (Fig. 4-3). In contrast, the average adult meets its daily energy need during low tide on beaches on all but 2 days in September, 4 days in October and 7 days in November (Fig. 4-3).

Grasslands - An average heron required about 160 mins. to catch a vole (12 voles caught in 1938 mins.) between 18 November 1986 and 17 January 1987. An average vole contained an estimated 339 kJ of metabolizable energy, so a heron ingested about 127 kJ per hour (339 kJ per vole/160 mins.) while feeding on voles caught in grasslands. There were about 9h of daylight each day in November and 8h of daylight in December and January at the latitude of this study (49°N). A heron preying only on voles ingested about 1144 kJ per day in November (127 kJ/h x 9h) and 1016 kJ per average day in December and January (127 kJ/h x 8h). Therefore, a heron obtained an average of 73%
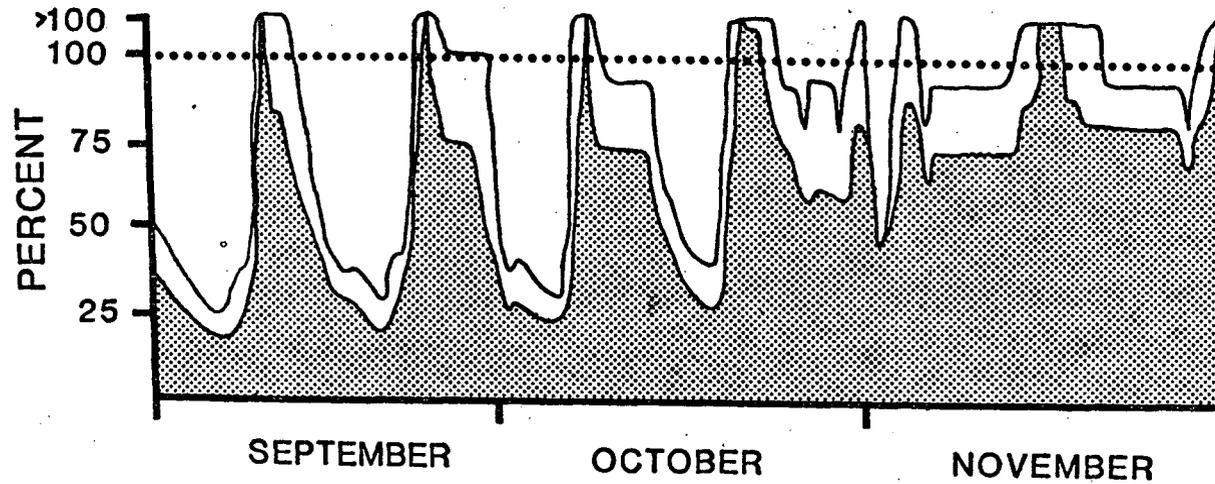
Figure 4-3. Estimated percent of available low-tide (<1.7 m) foraging time required by adult (stippled) and juvenile (open) herons to meet their estimated energy needs over 24 h (1560 kJ) each day in September to November 1987-1988.

of its daily need in November (1144 kJ/1560 kJ x 100%) and 65% in December
and January (1016 kJ/1560 kJ x 100%).

Habitat Shifts, Dispersal and Mortality

About one-third of all juveniles were seen in grasslands in September-
October and over three-quarters in November (Fig. 4-4). Most adults stayed
on beaches until November. Between November and February adult females used
marshlands rather than grasslands to a greater degree than juveniles
(X^2=32.1, p<0.001, Table 4-2). Proportionately more juveniles than adults
foraged during the day on 17 road-side censuses between November 1986 and
February 1987. Ninety-nine out of 139 (71.2%) juvenile herons were foraging
compared to 218 out or 551 (39.6%) adults (p<0.001).

Juveniles disappeared from the Fraser River delta at a faster rate
(Fig. 4-5) and more starved to death than adults. Twenty-eight out of 46
(60.9%) juvenile herons starved to death compared to 3 out of 16 (18.8%)
adults found between August and February (p<0.009).

These findings support the predictions that: (i) juvenile and adult
herons depart from beaches when there is too little foraging time during low
tide to meet their daily energy need and, (ii) juveniles vacate beaches
before adults in autumn.
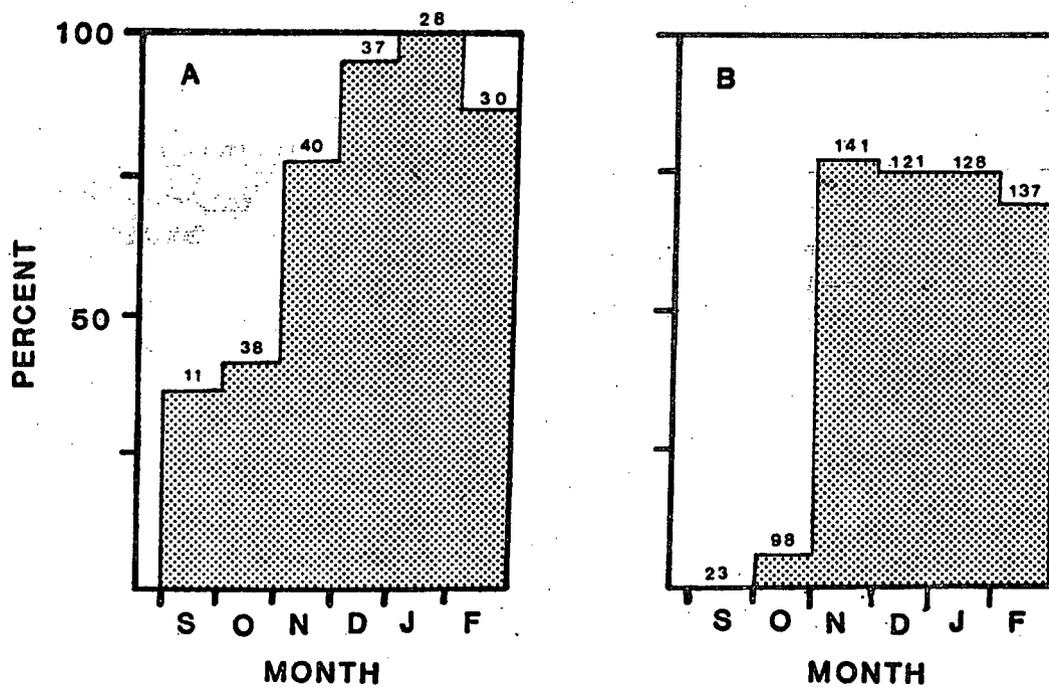
Figure 4-4.   Percentages of juvenile (A) and adult (B) herons counted on
grasslands (stippled bars) and beaches (open bars) during the
non-breeding season.   Numbers above bars are number of herons
counted.
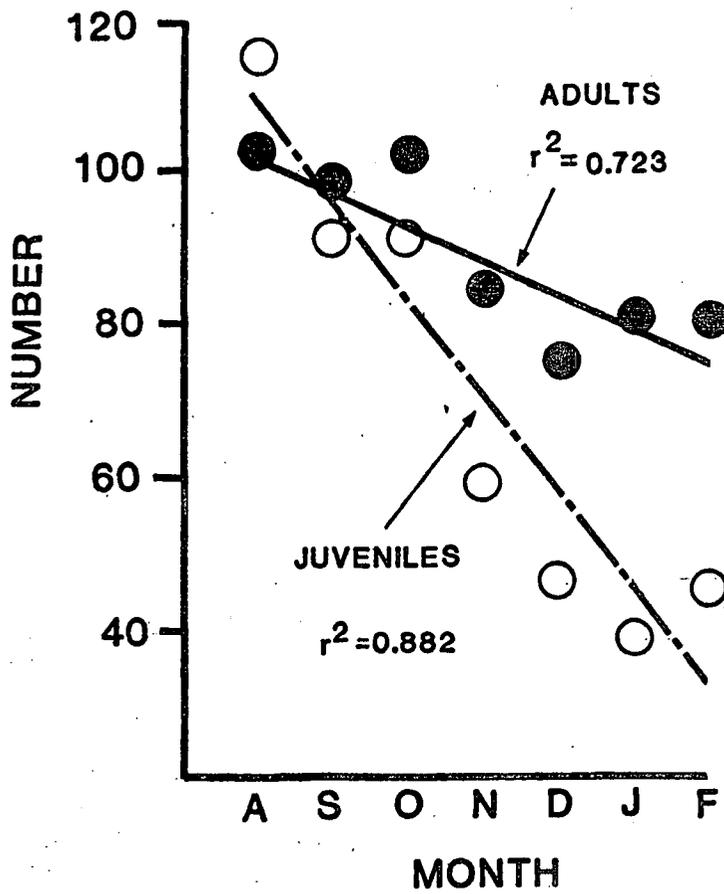
Figure 4-5.   Numbers of adult and juvenile Great Blue Herons counted each month on road surveys of the Fraser River delta.

DISCUSSION

Validity of assumptions

This analysis is based on several key assumptions about herons foraging on beaches and in grasslands.

Beach-foraging herons - I assumed that: (i) herons can not change their food intake rate at a site (see Swennen *et al.* 1989), (ii) foraging time dictated by low tides and foraging skill were the only variables that significantly affected daily ingestion rates, and (iii) herons caught three times as many fish during the day as at night from August to November. The food intake rates of herons are also affected by high winds (Bovino and Burtt 1979), but my study took place when winds were generally light. I have less confidence in my estimate that three times as many fish are caught during the day as at night. My estimate is based on a small night-time sample (N=9) taken in summer. However, most foraging is done during daytime at this time of year and it is reasonable to expect that herons catch fewer fish at night than during the day. It is unlikely that herons caught larger fish at night than during the day because large fish move into deeper water during low tides when most herons feed.

All of these assumptions contribute additional error to my estimates of the amount of time herons need to balance their daily energy budgets. However, these errors do not greatly affect my conclusions because juveniles would require 6-165% (median 83%) more time on 10 days in November to meet their daily energy need. Tides were too high to allow herons to forage in eelgrass on a further two days.

Grassland-foraging herons - I assumed that: Townsend's voles eaten by herons in this study weighed an average of 56g, contained the same amount of water and energy per gram as the Common vole in Wijnandts' (1984) study, 78%

energy assimilation efficiency by herons, and herons caught voles at a rate of one every 160 mins.

Other studies have found similar body weights for Townsend's voles in the Fraser River delta between November and January (Beacham 1980). Moreover, the water and energy content is relatively constant between rodents (Cummins and Wuycheck 1971, Zwarts and Blomert 1990) and the digestive efficiency of herons is not significantly different from that of other birds (Castro et al. 1989). Each of these estimates has a small associated error. I have less confidence in my estimates of the rate that voles were captured by herons. Herons could be watched continually for about a half-hour on average (X=36 mins, SD=22, N=54), before they flew or walked out of sight. No heron could be watched long enough to determine the time interval between prey captures. Other factors, such as the activity of voles, the amount of vegetation cover, and especially the degree of winter flooding of grasslands, affect the vulnerability of voles to predators, including the Great Blue Heron. For example, Taitt and Krebs (1983) reported herons catching voles every 20 mins. in fields during heavy precipitation between November 1980 and February 1981 compared to 160 mins. in my study of the same field when flooding was not widespread. Thus, the availability to herons of voles in grasslands is probably more variable than the availability of fish on beaches.

Year-round Foraging Dispersion of Age- and Sex-classes

This is the first study to my knowledge that describes the year-round habitat use of Great Blue Heron age- and sex-classes. When nests held eggs and small chicks and food availability in the lagoon was high (Chapter 5), females fed close to the colony while males tended nests during the day.

Other studies have shown that most herons feed near their colony-sites (e.g. Brandman 1976, Pratt 1980, Dowd and Flake 1985, Simpson *et al.* 1987) but the sex of those herons was not known. When tides were high in late afternoon or evening, females in my study exchanged duties with males who then left the colony to feed alone on territories up to 27 km away until they returned the next morning. Other studies of coastal herons have shown that most pairs exchange duties during high tide (Paine 1972, Brandman 1976, Moul 1990). Both parents fed in the lagoon less often when the chicks were 3-4 weeks old than in earlier stages (Table 4-1). This shift in use of foraging sites coincided with a decline in food availability in the lagoon (Chapter 5).

Habitat Selection

Foraging efficiency, habitat shifts and dispersal – My study joins several others that indicate that foraging efficiency, daily use of time, and dispersal are closely interrelated in birds (e.g. Goss-Custard and dit Durell 1984, Weathers and Sullivan 1989, Sullivan 1989, Sullivan 1990). I showed that juvenile herons were less efficient foragers (Table 4-4), required more foraging time to meet their energy needs (Fig. 4-3), and departed from beach habitats sooner in autumn than adults (Fig. 4-4). I also indicated that proportionately more juveniles used grasslands than marshlands compared to adults (Table 4-2). Lastly, I showed that juveniles disappeared from the study area at a higher rate than adults (Fig. 4-5).

Foraging theory posits that animals switch feeding sites when their food intake declines to the average gain in the habitat (Charnov 1976). This theory predicts that herons should assess their foraging success on both beaches and in grasslands by sampling each habitat. Most adults

(94.5%, n=110) and juveniles (85%, n=35) roosted in marshes and fields during high tides in autumn rather than foraging in grasslands, contrary to the prediction of habitat sampling. Therefore, I used a hunger threshold to predict when herons departed beach habitats in autumn.

Herons are faced with a declining duration of low day time tides (Department of Fisheries and Oceans 1987, 1988) and diminishing prey populations (Gordon and Levings 1984) on beaches through autumn. Adults could meet their daily energy needs in about 55-85% of the available time during most low tides in September, October and November. Juveniles required about 73-100% of the available time on most days over the same period and had insufficient time on many days (Fig. 4-3). Adult and juvenile herons store body fat (unpubl. data) presumably on days when tides remain low for many hours to insure against predictable periods of shortage. This option ceased for juveniles on beaches after about mid-October when they could hardly meet their daily energy needs on most days (Fig. 4-3). Most juveniles flew to grasslands after October (Fig. 4-4) where they acquired about 73% of their daily energy need each day in November and 65% of their daily energy need each day in December and January. Presumably they met their energy needs by foraging in marshlands during low tides at night. These findings suggest that herons leave foraging habitats when their food energy potential declines below a critical level (McNamara 1982).

Individual differences among juveniles at the level of foraging efficiency I described can greatly affect their survival (Gill et al. 1975, Sullivan 1990). As winter approached, juvenile herons spent less time on the beaches and more time in grasslands (Fig. 4-4) where they hunted small mammals. I hypothesize that the low foraging success in grasslands left

especially juveniles emaciated and vulnerable to collisions with vehicles, telephone wires and fences.

It is unclear why more juveniles do not forage with adults in marshlands during the day. Juveniles might lack the knowledge of the best foraging times in the day (Draulans and Vessem 1985) or trade off low mean for high variance intake rates in grasslands (Caraco *et al.* 1980, Caraco 1981). Juveniles forage in marshlands at night (pers. obs. Richner 1986). Adults might leave marshlands on blustery days when their foraging success declines below some threshold (Bovino and Burtt 1979) or to exploit temporary bonanzas created when rains flood voles from their underground burrows in grasslands, or both.

Territoriality

Several studies have shown that adult herons defend feeding territories and that interactions are infrequent (Bayer 1978, Cook 1978, Richner 1986, Draulans and Hannon 1988). Mine is the first study to show that territorial herons were mainly and perhaps only males.

Density-dependent habitat selection models (Fretwell and Lucas 1970, Fretwell 1972) explain well the spacing of territorial herons. The greatest densities occurred in marshes along riverbanks where prey densities are probably greatest. Moreover, juveniles were excluded from territories in this and other studies (e.g. Bayer 1978, Richner 1986). These results are predicted from the ideal despotic distribution model (Fretwell and Lucas 1970, Fretwell 1972). Future studies are needed to examine if the average intake rates are greater in the high density habitats than in low density habitats, as predicted by the ideal despotic distribution.

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SUMMARY

1)   When nests held eggs and small chicks, breeding female herons at
     Sidney mostly fed within 2 km of the colony-site during the day when
     tides were low and, breeding males mostly fed along beaches from 6-
     27 km from the colony-site during late afternoon until the next
     morning when tides were high. Breeding males and females fed within
     2 km of the colony-site when chicks were large.

2)   The shift in habitat use by adult females and juveniles from beaches
     to marshlands and grasslands in autumn was best explained by a
     shortage of foraging time during low tides coupled with shrinking prey
     populations.

3)   Adult males spent the non-breeding season in territories along
     riverbanks and their spacing was predicted well by the ideal despotic
     distribution (Fretwell and Lucas 1970).

CHAPTER FIVE. TIME OF BREEDING IN GREAT BLUE HERONS

In the previous chapters, I examined how herons selected breeding and foraging habitats. Here, I focus on the relationship between food availability and time of breeding.

Lack (1954) postulated that natural selection favours adults whose nestlings are present when food is most available to the parents. This hypothesis predicts that early and late nesters should fare less well than those nesting on the average date. Several studies have supported Lack's (1954) hypothesis (see Perrins and Birkhead 1983), but early clutches are often the most productive (e.g. Cave 1968, Davies and Lundberg 1985, but see Noordwijk 1983).

Perrins (1965, 1970) proposed that food shortages during egg-laying prevent most females from breeding earlier so that young would be in the nest after the parents' food supplies had peaked. Several studies suggest that females breed when food becomes plentiful (Drent and Daan 1980, Daan et al. 1988) but it is not clear whether most young are in nests when food is increasing or decreasing in abundance (see Daan *et al.* 1988).

Tests of Lack's (1954) and Perrins' (1965, 1970) hypotheses have been hampered by methodological problems. Food abundance, rather than food availability, has been used as an index of food supply in most studies (Daan *et al.* 1988). Moreover, these hypotheses assume that food is in short supply to the egg-laying female (Perrins 1965, 1970) or adults with nestlings (Lack 1954), although many studies have found that breeding birds are not short of food (see reviews by Martin 1987, Linden and Moller 1989, Chapter 1).

A suitable species in which to compare timing of breeding is one in which food availability and prey consumption can be measured directly. The Great Blue Heron is a suitable species because: (i) it eats small fish whose populations can be sampled with beach-seine nets, and (ii) its rate of consumption of fish can be estimated (Simpson 1984, Bayer 1985).

The aim of this chapter is to relate the seasonal availability of food energy to the time of breeding of herons. First, I estimate the relative availability of prey energy to adult herons when they have eggs, small chicks and large chicks. I then examine if critical food shortages occur. Next, I compare the hypotheses that: (i) females begin to lay eggs after a threshold of available energy for egg production has been passed (Perrins 1965, 1970) and, (ii) chicks are in the nest when food for adults is most plentiful (Lack 1954).

STUDY AREA AND METHODS

Great Blue Herons were studied on Sidney Island (Figure 2-1). General methods used to: estimate foraging rates, sample prey populations, determine when eggs were laid, and estimate reproductive success, are outlined in Chapter 2.

Relative Availability of Energy to Adult Herons

Relative availability of food energy is the biomass of fish present in the lagoon expressed in units of energy (kJ), multiplied by the duration of low (<1.7 m) tides during each stage of the breeding season. It was estimated from the formula:

$$ME_s = ((F_s)(W_s)^.C)T_s$$

where ME_s is the amount of available energy in nesting stage S; F_s is the estimated number of the fish in the partial enclosure in nesting stage S, W_s is the average weight in grams of fish caught in the partial enclosure in nesting stage S; C is a constant multiplier for metabolizeable energy content of fish equal to 4.76 kJ/g dry weight, and T_s is the average number of minutes of low tide foraging in nesting stage S. Each of these terms in the equation is now explained in detail.

Number of fish in the lagoon (F) - A polyethylene fence lined with galvanized chicken-wire was erected around poles enclosing three sides of a 9x9 m portion of eelgrass (*Zostera marina*) bed on an ebbing tide in Sidney lagoon when nests held eggs, small chicks and large chicks (see **Nesting stages**, below) in 1988. A 1.5 x 18 m (6 mm stretched mesh) beach seine was then quickly and repeatedly hauled toward the opening. On each haul, the contents were quickly emptied into an empty bucket until most fish had been caught. These data (Appendix I) were used in Leslie and Ricker models (pp. 162-166 in Krebs 1989) to estimate the number of fish in the partial enclosure.

The Shiner Sea Perch (*Cymatogaster aggregata*) and Tube-snout (*Aulorhynchus flavidus*) avoided the partial enclosure so I estimated their numbers by assuming that the proportion of all species caught in 19 seine-hauls outside the partial enclosure each month was the same as in the partial enclosure prior to its installation. This assumption is discussed later.

Energy estimates in prey (W,C) - All fish caught in the partial enclosure were measured and samples were weighed to derive length-weight equations

for each species. The mean weight of all fish caught during each nesting stage (see below) was converted into units of energy as follows. I assumed that: (i) all fish contained 71% water (Holmes and Donaldson 1969), (ii) the assimilation efficiency of herons was 77% (Castro *et al.* 1989) and, (iii) each gram dry-weight of fish contained 21.3 kJ (Cummins and Wuycheck 1971). These assumptions are discussed later.

Nesting stages (S) - I estimated each nesting stage from the median date (14 May) that the first hatched eggshell was found below each nest. The chick stage was divided in half so that most nests held **small chicks** from 14 May to 8 June, and **large chicks** from 9 June to 1 July. Incubation requires about four weeks (Vermeer 1969, Brandman 1976). Therefore, the **incubation** stage was back-dated 28 days from the median hatching date to include the period 15 April to 13 May. **Egg-laying** was estimated to occur from 1-14 April.

Duration of low tides (T) - Foraging occurred while tides were low (<1.7 m) at Sidney lagoon. The number of minutes of low tide available to herons each day of the breeding season was generated by computer using tidal data housed at the Tidal Office of the Institute of Ocean Sciences.

Estimated Energy Consumption by Adults
Adult consumption - The length of each fish caught by herons was estimated as a proportion of the heron's culmen length (Chapter 2). The most significant bias in this method is the observer's ability to estimate the length of the prey (Bayer 1985). Observer precision was tested by showing a range of sizes of the four major prey species held between the mandibles

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of a dead heron to observers using telescopes 65-100 m away. Significant differences did not occur between observers (X^2=1.86, p=0.8, d.f.=4). Both correctly identified all fish and both underestimated the lengths of some fish sizes by one size-class. Therefore, I adjusted all fish length estimates by one size-class to reduce observer bias and then converted each fish into energy units following the methods outlined above.

Time of Breeding

Energy threshold for laying - Ciconiiformes require about 30% more energy above maintenance costs to fuel their activities (Kushlan 1977). The estimated maintenance cost from Kendeigh's (1970) equations for a caged 2100 g heron is 1200 kJ and her activity costs an additional estimated 360 kJ (30% of 1200 kJ) for a total daily energy need of 1560 kJ.

Twenty-seven heron eggs collected in B.C. near the beginning of the laying period contained a mean of 4.77 g of fat and 3.03 of carbohydrate and protein (P. Whitehead, unpubl. data). Each gram of fat contains about 39 kJ of energy while a gram of carbohydrate and protein holds about 18 kJ. Therefore, there are about 240 kJ [(4.77 g x 39 kJ/g)+(3.03 x 18 kJ)] in an average heron egg. The efficiency of converting metabolized energy into eggs is estimated to be about 70% (King 1973) so an average female musters about 312 kJ per egg (240kJ+(0.30x240 kJ)). Since herons lay eggs in two day intervals, a female requires about half the 312 kJ per day (Murton and Westwood 1977) or 155 kJ. She also requires energy for ovogenesis for a few days prior to egg formation (Murton and Westwood 1977). Therefore, a female heron must exceed a threshold of about 1715 kJ (1560 kJ/d for maintenance +155 kJ/d for each egg) for at least 10 days (Murton and Westwood 1977) to complete her 4 egg clutch where one egg is laid every two days.

Energy consumption by egg-laying females - Available energy to females before and while they laid eggs was estimated by multiplying the mean daily energy ingestion rate during the egg-laying stage (1-14 April) by the number of minutes that low (<1.7 m) tides uncovered the eelgrass bed each day from 1 February to 14 May.

Food demands of heron chicks - Six chicks were reared from the egg in captivity and fed fish *ad libitum* (D. Bennet, pers. comm.). They were moved into outdoor aviaries at about 3 weeks of age. I used three-day running averages of the weight of fish eaten to estimate the age when the maximum food demand occurred. Growth curves of captive and wild (Quinney 1982) chicks do not differ significantly (D. Bennet, pers. comm.).

RESULTS

Relative Availability of Food Energy in the Lagoon

Herons caught tube-snouts (*Aulorhynchus flavidus*), sticklebacks (*Gasterosteus aculeatus*), sea perch (*Cymatogaster aggregata*), pipefish (*Signathus griseolineatus*), sculpins (*Leptocottus armatus*) and gunnels (*Pholis ornata* and *P. laeta*). The average length, weight and estimated energy contained by these fish through the breeding season is shown in Tables 5-1 and 5-2.

Table 5-1. Average lengths of fish caught in beach seines April-July 1987-88 and their estimated weights from length-weight regression equations.

	Total length (mm)			Weight (g)	
	Mean	SD	N	Mean wt(g)	SE
Pholis ornata					
April	87.0	28.1	18	1.8	0.2
May	80.8	19.7	141	1.3	0.1
June	99.0	17.2	92	2.6	0.1
July	94.3	16.5	73	2.3	0.1
Gasterosteus aculeatus					
April	60.8	6.1	27	1.8	0.8
May	67.2	5.5	98	2.6	0.4
June	70.4	4.4	42	3.0	0.7
July	73.8	4.8	12	3.5	1.2
Leptocottus armatus					
April	64.1	15.2	21	2.9	3.2
May	66.4	24.5	47	3.1	1.7
June	90.9	38.5	66	6.4	1.5
July	95.8	22.9	58	7.6	1.5
Cymatogaster aggregata					
May	110.0	34.2	15	24.9	6.7
June	104.1	12.1	119	21.1	2.4
July	52.1	5.3	50	12.0	3.7
Sygnathus griseolineatus					
April	138.0	58.0	7	3.9	0.7
May	156.7	48.2	118	4.4	0.2
June	173.1	39.2	31	4.8	0.4
July	173.1	39.2	31	4.8	0.4
Aulorhynchus flavidus					
April	158.8	47.3	5	35.3	7.56

Table 5-2. Estimates of Metabolizable Energy (calculated from weights from Table 5-1) available to herons from the major prey species each summer month in the lagoon at Sidney.

	Metabolizeable energy (kJ)	
	Mean	SE
Pholis ornata		
April	8.6	0.2
May	6.2	0.1
June	12.4	0.1
July	11.0	0.1
Gasterosteus aculeatus		
April	8.6	1.0
May	12.4	0.5
June	14.3	0.9
July	16.7	1.5
Leptocottus armatus		
April	13.8	4.1
May	14.8	2.2
June	30.5	1.9
July	36.2	1.9
Cymatogaster aggregata		
May	118.5	8.6
June	100.4	3.1
July	57.1	4.7
Synathus griseolineatus		
April	18.6	0.9
May	20.9	0.2
June	22.9	0.5
July[a]	22.9	0.5
Aulorhynchus flavidus		
April	168.0	9.7

a – no pipefish were caught in seines in July so I assumed those caught by herons were the same size as in June.

Numbers of prey individuals were greatest by far when herons had small chicks in nests (Table 5-3). Low tides exposed the eelgrass habitat for the longest period when large chicks (9 June-1 July) were in nests (Table 5-4). However, the relative availability of food energy was greatest when small chicks were present (Figure 5-1).

Seasonal Energy Consumption by Adults, Chicks and Egg-laying Females

Adults - Adult herons ingested nearly four times more food energy per day when small chicks were in their nests (Table 5-5) than when they were laying ($p < 0.001$), or incubating eggs ($p < 0.001$), and nearly three times as much as when raising large chicks ($p < 0.05$, Kruskall-Wallis ANOVA and multiple comparison test; p. 200, Zar 1984). The surge in energy consumption resulted from the large number of sea perch in the diet (Table 5-6).

Chicks - The greatest food demands by 6 captive-reared chicks occurred at about 37 days of age. The median hatching date at Sidney was 14 May. Therefore, the estimated peak food demands fell 37 days later on about 20 June when large chicks were in nests, and when ingestion rates were relatively low.

Egg-laying females - Egg laying began when the females' estimated daily energy ingestion exceeded their energy threshold for egg-laying for 7 days in 1987 and 9 days in 1988 (Figure 5-2). Moreover, available energy fell below the egg-laying threshold for 10 continuous days in late February-early March compared to only 1-2 days in early May (Figure 5-2).

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Table 5-3. Extrapolated minimum populations of fish in the partial
enclosure in Sidney lagoon.

Period	Extrapolated population[a]	S.E.
Incubation	360	48
Small chicks	3297	6
Large chicks	403	5

a - See Appendix I.

Table 5-4. Number of low (<1.7 m) tide minutes per average day in which
            herons could forage in the lagoon eelgrass beds during the
            breeding season.

Breeding stage	Number of minutes per average day
Egg laying	151
Incubation	176
Small chick	208
Large chick	216

Table 5-5. Estimated Metabolized Energy (ME) intake (kJ) per average day by an adult heron averaged over four periods of the breeding season on Sidney Island in 1987-88. N is the number of herons watched.

	Breeding period											
	Egg-laying			Incubation			Small chick			Large chick		
	x	SE	N	x	SE	N	x	SE	N	x	SE	N
ME intake rate (kJ/min)	7.7	3.7	27	6.8	1.1	155	20.5	3.7	48	7.4	0.7	109
Mins. available to forage per day	151			176			208			216		
Estimated intake/day	1163	555		1197	194		4264	764		1598	151	
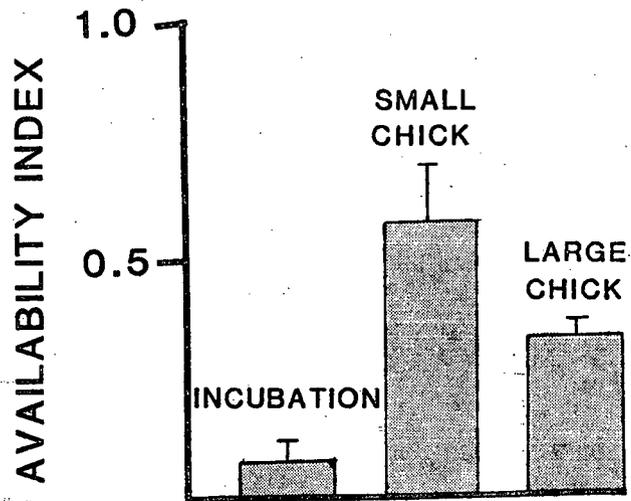
Figure 5-1. Index of food availability during the breeding season of the
Great Blue Heron. Percent availability is estimated from the
product of numbers of minutes when low tides (<1.7 m) exposed
the foraging habitat and the size of the fish population
converted into units of energy. Vertical lines are standard
errors.
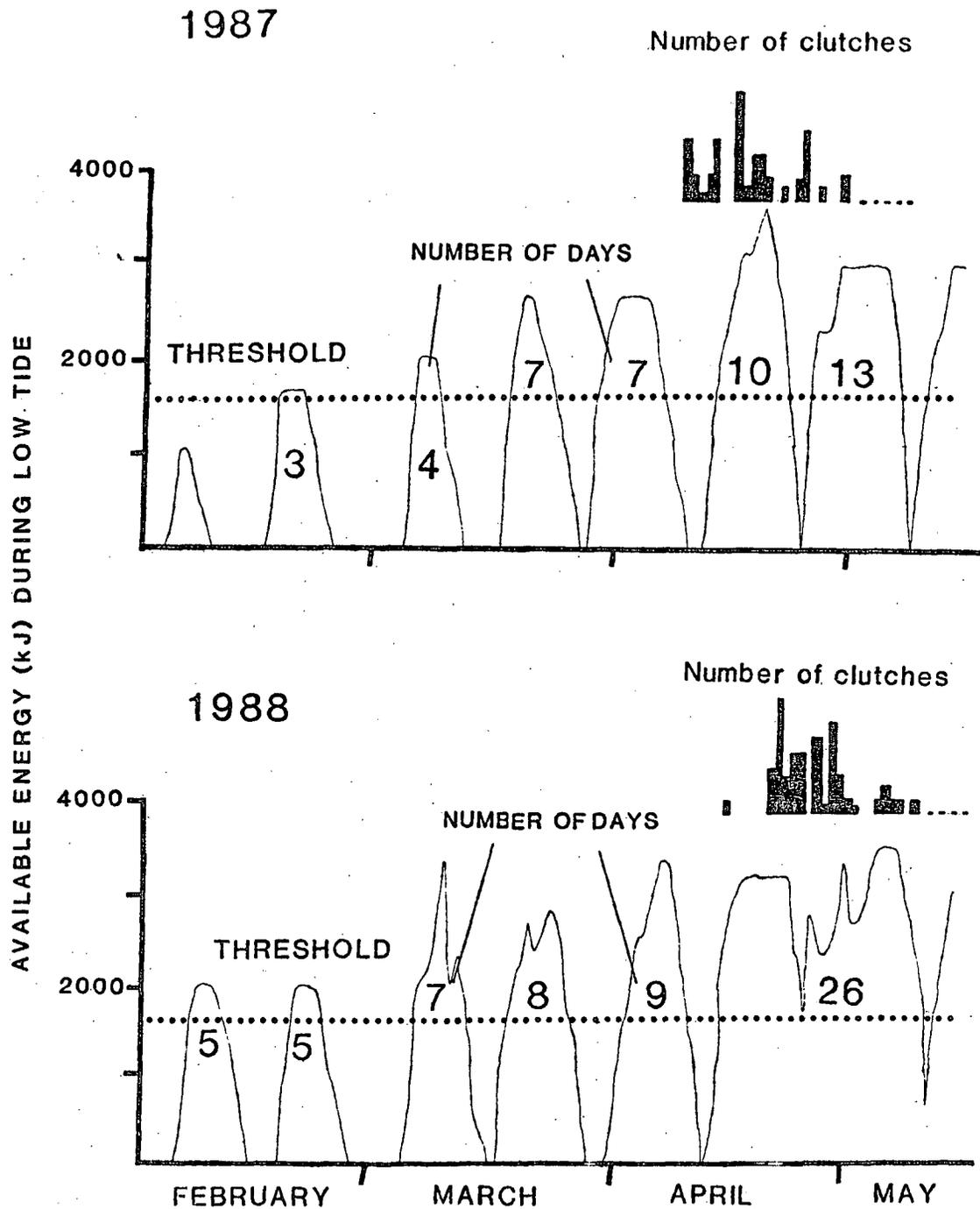
Figure 5-2. Numbers of days that available energy exceeded an estimated energy threshold for egg laying and the estimated dates when clutches were laid in 1987 and 1988.

Table 5-6. Numbers of each of the main prey species eaten by Great Blue
Herons during the 1987-88 breeding season on Sidney Island.

Species	Courtship		Egg		Small chick		Large chick		Total	
	N	%	N	%	N	%	N	%	N	%
Gunnel	20	41.7	188	40.9	56	34.6	175	65.3	439	46.8
Stickleback	0	0	42	9.1	10	6.2	8	3.0	60	6.4
Sculpin	2	4.2	78	17.0	9	5.5	53	19.8	142	15.1
Sea Perch	0	0	20	4.3	68	42.0	11	4.1	99	10.6
Pipefish	0	0	4	0.9	9	5.5	1	0.4	14	1.5
Tubesnout	11	22.9	1	0.2	0	0	1	0.4	13	1.4
Unknown	15	31.2	127	27.6	10	6.2	19	7.0	171	18.2
	48		460		162		268		938	

In summary: (i) energy demands of the chicks occurred several weeks after the peak in availability to their parents, and (ii) female herons laid their eggs soon after the estimated egg-laying threshold had been exceeded. I conclude that my findings best support the energy threshold hypothesis (Perrins 1965, 1970).

DISCUSSION

Validity of Assumptions

In this analysis I assumed that: (i) the relative abundance of fish in the partial enclosure represented the fish population elsewhere in the lagoon, (ii) the proportion of tube-snouts and sea perch caught in seine hauls in the lagoon closely reflected their abundance relative to other species in the lagoon, (iii) each fish contained 71% water and 21.3 kJ per gram dry weight of which 77% was assimilated by herons, (iv) I found eggshells below nests on the day they hatched, and (v) female herons required 1560 kJ per day to maintain themselves and an extra 155 kJ each day to produce an egg.

Departures from all of these assumptions contribute additional error to the estimates of energy availability and consumption. However, these errors do not alter my conclusions because the relative abundance of prey populations was more than eight-fold greater when small chicks were in nests than when large chicks were present (Table 5-3). Other studies of intertidal fish populations in British Columbia have found similar seasonal patterns in abundance (Weibe 1968, Kelsall and Simpson 1980, Hughes 1985). The additional errors from estimating water and energy content of fish, assimilation rates and maintenance energy requirements of herons are probably also low (see Kahl 1964, Dunn 1975, Kushlan 1977, 1978, Castro et al. 1989). For example, a sample of 12 prey fishes in my study contained 71-73% water and 3 seaperch

contained about 3 kJ less energy than my estimate (118 kJ) using values from the literature.

I have less confidence with my estimates of energy consumption early and late in the nesting season. My energy threshold estimate for egg-laying using published values (1715 kJ) was greater than my field estimate (=1163 kJ) of energy ingestion by laying females but the error around my estimate was great (Table 5-5). Moreover, existence energy of herons held in outdoor cages at the University of British Columbia is about 270 kJ lower than the 1200 kJ maintenance energy estimate derived from Kendeigh's (1970) equations (D. Bennet, unpubl. data). Thus, my estimates of energy required for maintenance and the threshold for egg laying are probably slightly higher than what female herons require. Also, a large change in the position of the threshold is required to make small change to the number of days when food availability exceeds the threshold in Figure 5-2.

Time of Breeding

My results are best explained by Perrins' (1965, 1970) hypothesis that: (i) energy availability determines when females will lay eggs and, (ii) chicks are in the nest after food availability to their parents has peaked. However, most females laid eggs several days after the estimated threshold had been crossed (Figure 5-2). Some of this variability probably arose from females being in different body condition (see Drent and Daan 1980, Perrins and Birkhead 1983). Thus, the Great Blue Heron faces an impossible optimization problem: once females cross the threshold for egg laying, insufficient time remains for the chicks to match their food demands with the peak in the food supply. Chicks are fed only by the female when food is most available and by both parents after food availability peaks.

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It is unlikely that photoperiod or air temperature are significant influences (see refs. in Orell and Ojanen 1983) on when herons breed because laying dates are not synchronized between nearby colony-sites. For example, in three years of this study, 3 colonies in the Fraser River delta (30-40 km to the north) and a colony in Victoria (25 km to the southeast) hatched eggs 2-3 weeks earlier than Sidney. Moreover, a colony near Crofton (35 km to the west) hatched eggs in the same week as Sidney. I hypothesize that the asynchrony in laying dates between colonies results from differences in inshore movements of local fish populations.

The daily duration of low tides determines how much food herons acquire on beaches throughout the year (Chapter 4, Figure 5-2). In Chapter 4, I proposed that female herons might store energy on winter days when tides were very low to safeguard against predictable periods of food scarcity. Here, I propose that as periods of food scarcity become less frequent in spring, female herons devote less foraging time to maintaining their energy balance, and more time to the breeding effort.

Future Directions

Future work might examine the strength of the relationship between egg-laying date and food availability to the female. Food manipulations of wild and captive herons offer the best prospects.

The bonanza in food energy available when sea perch are plentiful in May might allow females to recover body condition from egg-laying and chick-rearing and begin their feather moult. Sea perch are abundant between May and September in eelgrass beds.

SUMMARY

1) The greatest amount of energy available and consumed by adults occurred in May when young chicks were in the nest.

2) The greatest energy demands of chicks occurred in late June about one month after energy was most available to their parents.

3) The timing of breeding in Great Blue Herons in British Columbia is best explained by the availability of energy to the egg-laying female (Perrins 1965, 1970) rather than to the demands of the chicks (Lack 1954).

CHAPTER SIX.   GENERAL DISCUSSION

The aims of this thesis were to consider the factors that determine where herons locate their breeding colony-sites, how age- and sex-classes use foraging habitats through the year, and to examine the relationship between food availability, habitat selection and time of breeding.   I discuss and integrate my main conclusions now.

Choice of Colony-site

Three main conclusions emerged from this study.   First, colony spacing is best explained by the distribution of feeding sites and not by the presence of a key predator the Bald Eagle (Chapter 3).   Twenty-nine of 33 colonies were near rich intertidal feeding areas.   The average distance to the feeding grounds of a sample of 22 colonies was 2.4 km (Chapter 3).   In contrast, the number of breeding pairs of herons, the number of successful nests and the size of broods did not vary significantly with eagles nest densities.   Herons might be unable to avoid eagles, my analysis might be too coarse or the power of the test might have been to weak, to detect a significant difference.

Several studies have shown that the number of breeding wading birds is positively related to the area of their feeding habitat (e.g. Werschkul *et al.* 1977, Kushlan 1978, Chapter 3).   Others have shown that colony spacing in continuous habitat is positively related to the number of breeding pairs (Fasola and Barbieri 1977).   However, I disagree with Gibbs *et al.* (1987) assumption that heron breeding habitats in general are near their carrying capacity.   In my study, three foraging areas used by breeding herons in the past were not used during this study (Chapter 3).   Forbes *et al.* (1985a) found that reproductive success did not vary significantly with the number of breeding pairs in a colony, and I found no evidence that food was limiting at

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the colony level among breeding herons (Chapter 5). At the individual level, brood reduction adjusts the size of broods to the food provisioning ability of the parents.

I hypothesize that the number of suitable feeding territories spaces breeding male herons through the habitat (see Marion 1989) and that their choice of colony sites is constrained by how far they will fly to nest. I assume that male territory holders exclude all other males from settling in the habitat when territories shrink to a minimum size (Fretwell and Lucas 1970). This explains the distribution of colonies and the relationship between colony size and the area of foraging habitat without having to assume that regional populations are at their carrying capacity of their habitat.

Colony Formation

Predators have been suggested to play an important role in the formation or maintenance of nesting colonies of birds (Lack 1968, Forbes 1989) although not all others agree (see review by Forbes 1989). Egg and nestling survival is often used as a measure of the effectiveness of colonial nesting against predators (see reviews by Wittenberger 1981, Perrins and Birkhead 1983, Wittenberger and Hunt 1985). For example, Vessem and Draulans (1986) ruled out colonial nesting as an anti-predator adaptation in Gray Herons because egg and chick survival did not differ significantly in colonies of different sizes and adults did not mob predators. However, colonial nesting might have arisen primarily to favour the survival of adults (Forbes 1989). Herons that nest close to one another would increase their vigilance and reduce the chances of being caught by eagles (see Pulliam and Caraco 1984). This hypothesis predicts that heron nests should be more clumped in eagle areas than elsewhere

in their range. Thus, Lack's (1968) hypothesis needs to be examined for herons from the perspective of adult survival.

Habitat Selection

My second main conclusion is that herons in my study have a set of preferred foraging habitats that shift seasonally, as dictated by tides and food. Because of a strong seasonal movement of small fishes to inshore waters, shallow tidal lagoons, kelp beds and eelgrass beds are the preferred feeding habitat for breeding female herons. I showed that the number of herons feeding on beaches was significantly correlated with the number of hours of low tides each month of the year (Chapter 4). Moreover, juveniles and later, post-breeding adults vacated beaches for marshlands and grasslands when their estimated energetic needs could no longer be met on beaches (Chapter 4). Great Blue Herons might have a flexible social system, like some other birds (see Stacey and Koenig 1990), and behave differently elsewhere in their range.

Time of Breeding

My third main conclusion is that the time of breeding is established by the seasonal availability of food to egg-laying females and not by the energetic demands of their chicks. Egg-laying began about 9 days after an estimated energy threshold for egg production had been crossed by egg-laying females, whereas the greatest energy demands of the growing chicks occurred about one month after the food energy available to the adults had peaked (Chapter 5). The surge in food energy to females feeding in the lagoon occurred in May (Table 5-5) when sea perch arrived in shallow waters. This surplus might be used to recover body condition and prepare to moult the flight feathers. Herons elsewhere in British Columbia (Simpson 1984) and in

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California (Brandman 1976) have chicks in the nest when fish are abundant. However, mine is one of the first studies in which food energy availability, rather than food abundance, has been shown to be related to energy demands of egg-laying adults and growing chicks (see Daan *et al.* 1988). My index of food availability is more accurate than indices of food abundance used in other timing of breeding studies because it combines estimates of prey abundance with those of foraging time by herons. This is important because the longest low tide foraging periods in early June did not coincide with the peaks in abundance of all the major prey species. I assumed that all herons fed on the beach continuously through each low tide. Further studies might address how variation in the amount of time individuals spend foraging during low tide affects their timing of breeding.

Inter-related Patterns of Ecology & Behaviour

Empirical evidence from many scattered sources indicate that an individual's fitness is related to the combined effects of its choice of habitat, spacing patterns, dispersal and foraging efficiency (Catterall et al. 1989). The distribution and availability of food resources is the most important factor underlying the ecological and behavioural relationships between age-classes of Yellow-eyed Juncos (*Juncos phaeonotus*) shortly after the breeding season (Sullivan 1990) and Silvereyes (*Zosterops lateralis*) in winter (Catterall et al. 1989). I now extend the examination of ecological and behavioural relationships throughout the year using age- and sex-classes of the Great Blue Heron as an example.

Adult versus juvenile tactics

Juvenile herons are poorly suited to foraging on beaches in autumn and winter because of their low foraging efficiency and spend more time than adults hunting voles in grasslands (Chapter 4). The resultant pattern is one of low food consumption, narrow limits on their use of habitats and high rates of mortality, compared to adults.

Juvenile herons might specialize at catching small mammals in grasslands in winter and return to beaches the following spring as yearlings to feed on fish returning to inshore habitats. Age-related shifts in use of habitats and foraging specialization are well documented in other animals (Partridge and Green 1985). Through the summer and autumn yearlings might improve their feeding skills so that they can catch the food necessary for good winter survival and reproduction as 2-year-olds.

Adult females have high foraging efficiency (Chapter 4) which makes them well suited to foraging on beaches during the breeding season and into autumn, and in grasslands and marshlands in winter (Chapter 4). As a result, adult females have high food consumption, use of a wide range of habitats, and low rates of mortality compared to juveniles.

Some adult male herons foraged on territories through the year (Chapter 4). During the breeding season, some males travelled up to 27 km each night between territories and their nests (Chapter 4). When nests held large chicks, males foraged with females near the colony. Post-breeding males returned to their territories to spend the autumn and winter (Chapter 4). Thus, males were mostly solitary feeders on territories. The foraging efficiency of territorial males is unknown.

My study concurs with those of Sullivan (1989) and Catterall et al. (1989) that food availability is the most important factor shaping the behaviour of

age- and sex-classes. In many species, dominance is an important feature of individual fitness and survival for all age- and sex classes (e.g. Monaghan 1980, Bildstein 1983, Arcese and Smith 1985, Catterall *et al.* 1989). In my study, dominance is important to adult males on feeding territories but unimportant to adult females and juveniles feeding in marshlands and grasslands.

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Appendix I.   Regression equations of catch per unit effort (Y) versus cumulativecat ch (X) and extrapolated minimum population[a] in the partial enclosure for four frequently eaten prey species[b] eaten by Great Blue Herons in Sidney lagoon in 1988.

Stage	Regression	Correlation coefficient	Extrapolated population	S.E.
Eggs	Y = 45.28 - 0.12X	- 0.72	349	48
Small chicks	Y = log 2.6 - 0.001X	- 0.96	3258	6
Large chicks	Y = 183.67 - 0.64X	- 0.99	287	5
Fledglings	Y = 14.73 - 0.30X	- 0.76	49	6

a -   *Pholis ornata, Gasterosteus aculeatus, Leptocottus armatus, Signathus griseolineatus.*

b -   does not include mobile fishes, principally *Cymatogaster aggregata*, also eaten by many herons.