Robert W. Butler

The patient predator: foraging and population ecology of the Great Blue Heron Ardea herodias in British Columbia

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Robert W. Butler¹

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Abstract

This report presents the results of a six-year study (1986–91, including five breeding seasons and four winters) of the diet, food availability, foraging behaviour, use of habitats by age-classes and sex-classes, spacing of breeding colonies, and survival of the Great Blue Heron *Ardea herodias* on the Pacific coast of British Columbia. The general thesis of this study is that the availability of food energy largely dictates when herons use foraging habitats, the time of year that they breed, and which individuals survive.

Breeding herons were studied at a colony of 85–100 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. Field studies on Sidney Island included foraging behaviour, food availability, habitat use, and reproductive success. At other colonies, the reproductive success of herons and the chief foraging sites and locations of a nest predator, the Bald Eagle *Haliaeetus leucocephalus*, were recorded. In the nonbreeding season, the foraging behaviour, dispersion patterns, and habitat shifts of postbreeding adult and juvenile herons were studied in the Fraser River delta, a few kilometres south of the city of Vancouver.

Food was most available to herons in late May and early June, when daytime tides were the lowest of the year and fish prey was most abundant. Adult breeding herons ate mostly small fish caught along beaches. Fish were caught by solitary herons on beaches at an average rate of about one fish every two minutes. Herons reaped 3-4 times more food energy by eating the relatively larger shiner perch *Cymatogaster aggregata* than by eating other fish species. Adults caught fish about twice as fast as juveniles in autumn.

Most juvenile and adult herons foraged on beaches from March to October and in marshlands and grasslands from November to February. The switch from beaches to marshlands and grasslands occurred when the food availability to herons on beaches was below the level required to maintain their energy balance. Herons foraging in grasslands ate mostly Townsend's vole *Microtus townsendii* in autumn and winter, when vole densities were high. However, the number of herons on grasslands was not related to the time of day or to the diurnal period of vole activity.

Herons located colony sites near good foraging habitats, although all good habitats were not used by herons each year. The proximity of nesting eagles did not affect the spacing of colonies along the coastline, the size of heron broods, or the reproductive success of the herons. Herons that hatched eggs in the first two weeks of the breeding season had an 84% chance of successfully raising at least one chick to independence, compared with a 40% chance among nests with chicks hatching in the last 5-11 weeks of the season. It was estimated that 27% of the juveniles and 73% of the older herons present in August were alive the following February. Most chick deaths resulted from traumas and not starvation, as previously believed. However, the greatest mortality rate was in juveniles that became emaciated and were unable to avoid fatal accidents.

Résumé

Ce rapport présente les résultats d'une étude de six ans (1986–1991, dont cinq saisons de reproduction et quatre hivers) du régime alimentaire, de la nourriture disponible, du comportement alimentaire, de l'utilisation de l'habitat par classe d'âge et de sexe, de l'espacement des colonies de reproduction et de la survie du Grand Héron Ardea herodias sur la côte du Pacifique en Colombie-Britannique. La thèse générale soutenue ici est la suivante : l'énergie nutritive disponible est en grande partie déterminante du temps de l'année où les hérons utilisent des habitats d'alimentation donnés et se reproduisent, de même que des individus qui survivront.

Des hérons nicheurs ont été étudiés à une colonie comptant 85-100 couples sur l'île Sidney, près de la ville du même nom, et des visites périodiques ont été effectuées à quelque 40 autres colonies autour du détroit de Georgia (Colombie-Britannique). Sur l'île Sidney, les études de terrain ont porté sur le comportement alimentaire, la nourriture disponible, l'utilisation de l'habitat et le succès de la reproduction. À d'autres colonies, le succès de la reproduction du héron, de même que les principaux sites d'alimentation et la proximité d'une espèce prédatrice des nids, le Pygargue à tête blanche Haliaeetus leucocephalus, ont été notés. Pendant la période internuptiale, le comportement alimentaire, la répartition des individus et les changements d'habitat des hérons adultes ayant niché et des juvéniles ont été étudiés dans le delta du fleuve Fraser, à quelques kilomètres au sud de Vancouver.

C'est à la fin de mai et au début de juin que le héron trouvait à se nourrir le plus facilement, la marée diurne atteignant alors son niveau le plus bas et les poissons-proies étant le plus abondants. Les nicheurs adultes se nourrissaient surtout de petits poissons qu'ils capturaient le long des plages, le taux moyen de prises étant d'environ un poisson aux deux minutes dans le cas des hérons solitaires. Le perche-méné *Cymatogaster aggregata* procurait aux hérons 3–4 fois plus d'énergie nutritive que d'autres espèces de poissons relativement plus petites. À l'automne, les adultes capturaient des poissons presque deux fois plus vite que les juvéniles.

La plupart des hérons juvéniles et adultes s'alimentaient sur les plages de mars à octobre et dans les marais et les prairies de novembre à février. Les plages étaient abandonnées au profit des marais et des prairies lorsque la nourriture disponible ne suffisait plus au maintien de l'équilibre énergétique des hérons. Dans les prairies, le campagnol de Townsend *Microtus townsendii* constituait la principale proie des hérons pendant l'automne et l'hiver, la densité des populations de ce rongeur étant alors élevée. Toutefois, le nombre de hérons fréquentant les prairies n'était pas corrélé avec une partie quelconque du jour ou la période diurne d'activité des campagnols.

Les hérons établissaient leurs colonies près de bons habitats d'alimentation, mais ces derniers n'étaient pas tous utilisés chaque année. La proximité des pygargues nicheurs n'influait pas sur l'espacement des colonies le long du littoral, pas plus que sur la taille des couvées ou sur le succès de la reproduction. Les hérons dont les œfs éclosaient au cours des deux premières semaines de la saison de couvaison avaient 84 % de chances d'avoir au moins un petit qui survivrait jusqu'à ce qu'il soit autonome, cette proportion passant à 40 % lorsque l'éclosion avait lieu pendant les 5-11 dernières semaines de la saison. Selon les estimations, 27 % des juvéniles et 73 % des hérons plus âgés présents en août étaient toujours en vie au mois de février de l'année suivante. Chez les oisillons, la plupart des décès étaient attribuables à des lésions ou blessures et non au manque de nourriture, comme on le croyait auparavant. Toutefois, les juvéniles émaciés et incapable d'éviter des accidents fatals présentaient le taux de mortalité le plus élevé.

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Chapter 1. General introduction

"Waiting is not a mere empty hoping. It is an inner certainty"

A familiar scene on the south coast of British Columbia is the Great Blue Heron Ardea herodias standing on the shore waiting for the ebb tide to uncover the beach. As the tide ebbs, the heron moves onto the beach to catch fish. The heron catches fish by slowly wading in the shallows and standing motionless for many minutes until prey comes within reach of its formidable bill. With lightning speed, its neck uncoils, and a fish is caught between its mandibles. The wriggling fish is tossed into position and swallowed whole before the heron returns to stalking another fish. A breeding heron will repeat this behaviour about 100 times each day during the summer until the returning tide puts the beach out of its reach.

There are usually two low and two high tides along the British Columbia coast every day. The highest tide of the day is followed by the lowest tide, which is then followed by the intermediate high and low tides (Thomson 1981). There is also an annual cycle in which the lowest tide occurs near midday in June and near midnight in December. Thus, the rhythm of the tide schedules many events in the lives of animals, including herons, that forage in the intertidal zone during low tides.

Herons in British Columbia eat mostly small fish caught along beaches (see review by Verbeek and Butler 1989). In spring and summer, several species of fish swim into intertidal areas, where herons catch them, to spawn or give birth (Weibe 1968; Gordon and Levings 1984; Hughes 1985). The abundance, timing, and location of prey change with such factors as ocean temperature, salinity, and amount of dissolved oxygen in the water (Gordon and Levings 1984; Hughes 1985).

Along with tide patterns and prey abundance, how much food a heron consumes is dependent on its foraging skill. Learning to catch prey involves developing hunting skills (Quinney and Smith 1980), making the best use of foraging time (Draulans and van Vessem 1985), and selecting the most profitable prey in terms of food energy.

1.1 Aims of the study

The aims of this study were to explain the survival, habitat use, and reproductive behaviour of the Great Blue Heron in relation to the availability of its prey. The seasonal pattern of heron food availability, diet, and foraging behaviour is described in Chapter 2. The seasonal changes in habitat use by age- and sex-classes of herons are described in Chapter 3, and Chapter 4 compares two hypotheses of food availability and interspecific competition to explain the observed changes. The distribution of colony sites in relation to foraging habitats and heron predators is examined in Chapter 5. Chapter 6 explores the factors affecting the breeding success of herons. In Chapter 7, mortality rates among age-classes are described. The final chapter integrates findings of the previous chapters and discusses the implications of low tides, prey abundance, and foraging skill for the population ecology of the Great Blue Heron.

1.2 Study species

Great Blue Herons have inhabited the British Columbia coast for more than a thousand years. Their butchered remains are often found in archaeological sites on southern Vancouver Island and the Fraser River delta (Hobson and Driver 1989). Native people shaped long, hollow heron leg bones into drinking tubes, whistles, and ornamental objects (Stewart 1973).

Most herons vacate Canada and the northern United States for ice-free quarters in winter (Butler 1992). The subspecies A. h. fannini studied for this report lives year-round along the northwest coast of North America (Hancock and Kushlan 1984), where the climate is mild and intertidal food is available throughout the year.

Female Great Blue Herons lay clutches of about three eggs in southern latitudes and five eggs in the north. Herons on the British Columbia coast lay clutches of about four eggs. The mass of the clutch is smaller relative to the female's body mass (about 10%) than for most other North American herons (14–35%). The eggs of the Great Blue Heron have an incubation period of about 28 days

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(Vermeer 1969), and the chicks are dependent on their parents for food and care for up to 60 days. The entire breeding cycle therefore requires about 100 days, a longer period of parental attention than for any other North America heron. By the time the chicks leave the nest, nearly three months after the first egg is laid, each will have consumed over 14 kg of food and will weigh over 45 times its hatching mass (Bennett 1993). About one in 10 eggs will survive to become an adult; several studies have shown that survival of immature herons is low (Henny 1972; Bayer 1981a). However, once a Great Blue Heron reaches adulthood, it is likely to live for many years.

The Great Blue Heron has many adaptations for catching small fish (Willard 1977; Kushlan 1978). Its bifocal vision and wide field of view take in an area below and in front of its head. Its long bill has fine serrated edges for catching and holding prey. The specialized sixth vertebra that gives the characteristic kink in the heron's folded neck allows it to thrust its head forward with precision and lightning speed. Long legs enable the Great Blue Heron to wade after fish in deeper water than for any other North American heron. Powdery down feathers along the sides of its neck and belly disintegrate into a talc-like powder when preened, which aids in the removal of fish slime from its plumage (Voisin 1991).

There have been several descriptive foraging studies of Great Blue Herons (e.g., Krebs 1974; Kushlan 1976; Willard 1977; Hom 1983). However, quantitative descriptions of its diet are rare.

Most Great Blue Herons in British Columbia nest in colonies, but some pairs breed alone (Forbes et al. 1985a). Following Kushlan's (1986) terminology, a *colony* is a nesting group of herons, and a *colony site* is the geographical location where they build their nests. The advantages of colonial nesting are unclear. Lone pairs can expect to raise as many offspring in a lifetime as those nesting in colonies (unpubl. data).

1.3 Study areas

1.3.1 The coastal environment

The British Columbia coastline is a 27 000-km jumble of islands and fjords squeezed into a straight-line distance of 800 km. Although much of the coast is forested, with few beaches where herons can forage, herons reside along its entire length. A few wide, shallow beaches away from the pounding surf support most of the province's herons, which reach their greatest abundance around the Strait of Georgia. The oceanography, prey abundance, and distribution of birds in the Strait of Georgia were described in papers in Vermeer and Butler (1989).

The Pacific coast has the mildest climate in Canada: winters are characteristically mild and summers warm. Prevailing winds are from the west or northwest in summer and southeast or east in winter. During summer, high-pressure weather systems redirect storms to the north. In winter, Pacific cyclones track onto the coast from the west and southwest. These cyclones bring precipitation to the entire coast, usually in the form of rain. As a result, south coast summers are dry and winters are wet, whereas the north coast is wet throughout the year.

1.3.2 Sidney Island

Sidney Island (48°40'N, 123°20'W) is one of about a dozen large islands known as the Gulf Islands that lie in the southern Strait of Georgia between Vancouver Island and the mainland of British Columbia (Fig. 1). Sidney Island differs from most of the other Gulf Islands in having wide sand beaches and a large lagoon, instead of narrow, steep beaches. The island is 9 km in length and is made of sandstone, protected by an igneous intrusion along the east end. Wind and ocean waves have gnawed the northern and southern shores into near-vertical cliffs that rise about 30 m above the beach. Sand and gravel cascading to the beach below have been carried to the northwest by ocean currents to form a 91-ha lagoon near the northwest end of the island. About 60 ha of mudflat and 31 ha of eelgrass Zostera marina meadow are exposed during the lowest tides. Beyond the lagoon, the island tapers into Sidney Spit, which trails for about 1.5 km into Sidney Channel. It was in the lagoon that most herons foraged during this study. Much of Sidney Island was logged earlier this century, and now it is forested with grand fir Abies grandis, Douglas-fir Pseudotsuga menziesii, and western red cedar Thuja plicata. Few of the large Douglas-firs of the original forest remain. Interspersed in the second-growth coniferous forest are glades of red alder Alnus rubra and arbutus Arbutus menziesii trees, with dense growths of stinging nettles Urtica lyallii appearing in many areas since the reduction of fallow deer in 1989.

1.3.3 Fraser River delta

The Fraser River is the largest river on the British Columbia coast, and it enters the Strait of Georgia across a wide delta in the southwestern corner of British Columbia (Fig. 1). The geology, human history, and bird populations of the Fraser River delta (49°05'N, 123°00'W) have been described by Butler and Campbell (1987). The delta began to form about 9000 years ago following the retreat of glaciers from the coast. Today, it lies within the metropolitan area of Vancouver. Much of the delta has been diked to protect farmlands, houses, and industrial areas from high tides, but beyond the dikes lie a narrow marsh and about 8 km of beaches and mudflats. At low tide, the uncovered beaches of the delta are nearly 250 km² in area, and it is there that the greatest densities of herons in British Columbia reside year-round. Herons nest in remaining woodlots on the delta (Butler 1989) and forage on the beaches, mudflats, and farmlands and in the marshes. The largest colonies using the delta during this study were about 350 nesting pairs situated about 1 km south of the Canada-U.S. international border on Point Roberts, Washington, and about 150 nesting pairs located in Pacific Spirit Park, about 6 km north of the Fraser River delta (Fig. 1).

Figure 1 Location of major habitats and heron colonies in the Fraser River delta and on Sidney Island in the Strait of Georgia, British Columbia



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Chapter 2. Food availability, diet, and foraging rate

2.1 Introduction

The central theme of this report is that the seasonal availability of food energy is important in determining where herons locate their colony sites (Gibbs et al. 1987), when they breed (Powell 1983; Butler 1993), the number of young they raise (Sullivan 1988), how long they forage in a habitat, and which individuals survive. Thus, a description of seasonal prey availability is needed against which to compare many events in the herons' year. Most researchers have used estimates of food abundance as an index of food availability (reviewed by Daan et al. 1988), although measures of abundance do not necessarily mirror availability to predators (reviewed by Masman et al. 1989). Butler (1993) compared prey availability and consumption for breeding Great Blue Herons by estimating seasonal prey abundance on beaches (expressed in energy units) and energy consumption.

The purpose of this chapter is to describe the availability of heron food on beaches and in grasslands and to examine diet selection and foraging behaviour of herons on Sidney Island and the Fraser River delta throughout the year.

2.2 Methods

2.2.1 Availability of fish

The steps used to estimate relative abundance of food energy on beaches and relative availability of food energy to herons are outlined in Figure 2. Both variables are discussed in detail below.

2.2.1.1 Relative abundance of food energy

Relative abundance of food energy was determined by: (1) totalling the monthly biomass of those small fish most often eaten by herons and caught in beach seines by Gordon and Levings (1984) in habitats where herons foraged on the Fraser River delta; (2) converting the biomass estimates into energy units (Appendix 1); and (3) expressing the estimates for each month as a proportion of the annual total.

2.2.1.2 Relative availability of food energy

Relative availability of food energy is the estimated amount of food energy available to a heron foraging through the entire low-tide period each month. The metabolizable energy ingested each day by foraging herons was estimated by converting into units of energy the mass of fish caught per minute of foraging (Appendix 1) multiplied by the number of minutes of foraging time in the day. The average number of fish caught per minute of low-tide foraging by adults in eelgrass beds on Sidney Island (April-July) and the Fraser River estuary (August-November) was estimated using methods explained below (Section 2.2.3). Adult herons flew to beaches to forage during low tides during the breeding and nonbreeding seasons (Butler 1991, 1993). Therefore, the average number of minutes of foraging time when low tides (<1.7 m) exposed the eelgrass foraging areas was assumed to approximate the amount of time that herons foraged on beaches. This estimate was determined from tidal computer models at the Institute of Ocean Sciences in Sidney, British Columbia.

2.2.2 Availability of voles and abundance of herons

The Townsend's vole *Microtus townsendii* is the major grassland prey species of herons in the Fraser River delta (Taitt and Krebs 1983). I examined the hypotheses that: (1) the presence of herons on grasslands each hour during the day was related to the hourly activity of voles; and (2) the density of herons on grasslands each month was related to the density of voles. Vole and heron populations were censused in grasslands on Westham Island in the Fraser River delta between October 1986 and March 1987. The methods used to estimate vole densities and the Westham Island grassland have been described by Taitt et al. (1981). Most of Westham Island is cultivated with vegetable crops. The grassland where I studied voles and herons was a fallow field against a brackish marsh in the George C. Reifel Migratory Bird Sanctuary.

Voles were caught in Longworth live traps on three days every two weeks on a 0.25-ha portion of grassland. Traps were locked open between trapping sessions. Trap stations were placed in a square grid at 7.6-m intervals. Trap stations alternated with one and two live traps for a total of 39 stations and 60 traps. Each vole was identified by an individually numbered fish fingerling tag attached

Outline of the methods used to estimate relative food abundance and relative food availability to herons



to its ear. Daily activity of voles in the grasslands was measured by opening traps at dawn and checking them for voles once every hour until dusk in December (five days), January (four days), February (three days), and March (one day).

The number of herons on the grassland outside the trapping grid was counted each hour at the start of each trapping session. In addition, herons were counted on the grasslands two or more times each day in December (17 days), January (12 days), February (11 days), and March (eight days). The greatest number of herons counted in each month was compared with the monthly densities of voles.

2.2.3 Diet and foraging rate

The behaviour of herons feeding on fish was recorded from April to July in 1987 and 1988 on Sidney Island and from August to November in 1987, 1988, and 1990 on the Fraser River delta. The behaviour of herons feeding on voles was recorded from October 1986 to March 1987 in a grassland on Westham Island. On the beaches, I watched each heron for 10 minutes and recorded its age-class (juvenile or adult) using plumage characteristics (see Section 3.2), the time of each strike, whether strikes were successful, and the type of fish caught (e.g., gunnel, sculpin) and estimated the length of the fish as a proportion of the heron's culmen length. This method has some biases (Bayer 1985a), which I accounted for before analyzing the data (see details in Butler 1991). On the grasslands, I could seldom follow a heron long enough to record the interval between prey captures. Therefore, I watched up to three herons at a time for 10-45 minutes and recorded the number of voles caught by each heron per minute of foraging time.

I compared the species of fish eaten by herons with their relative abundance in the lagoon on Sidney Island as follows. Fish populations were sampled in an eelgrass bed in the lagoon on Sidney Island in the periods 23 April -24 June 1987 and 10 April - 28 July 1988. Most herons forage in the eelgrass beds when tides are low (Butler 1991) (see also Table 7). I devised a partial enclosure (Fig. 3) in which I could make repeated hauls and reduce the bias of underrepresenting hard-to-catch species (Appendix 2). The partial enclosure consisted of a three-sided or U-shaped chicken wire fence sandwiched between two layers of polyethylene sheeting measuring 1 m in height and 9 m along each side. It was held in place with stakes driven into the eelgrass bed on an ebbing tide once each month. The opening faced up the beach towards shore, so that fish missed by the seine would tend to swim into the partial enclosure. It was unlikely that many fish escaped, because the ends of the seine were pulled onto the shore before the middle of the net had left the enclosure. The beach seine was dragged into position along the inside perimeter of the fence and quickly hauled towards the opening. All fish caught in each seine haul were emptied into separate buckets of water to be counted, measured, and weighed later. This procedure was repeated until fewer than five fish were caught in a seine haul. Leslie-Ricker models (see Krebs 1989) were used to estimate the size of fish populations from these data.

Partial enclosure and the method used to estimate the relative abundance of fish in an eelgrass bed in Sidney lagoon. Shown are the dimensions and placement of the partial enclosure (A), the beach seine in place prior to sampling (B), and the beach seine being pulled ashore during sampling (C). This procedure was repeated until few additional fish were caught.



These models use the sizes of catches per seine haul to estimate the total population present in the partial enclosure. Nineteen beach seine hauls were made in eelgrass along the north and south shores of the lagoon each month to catch large samples of schooling fish that largely avoided the partial enclosure.

2.3 Results and discussion

2.3.1 Availability of fish

One factor affecting the quantity of food consumed is the length of the foraging period. The "window of opportunity" for herons foraging on fish was largely dictated by the duration of the low-tide periods, when herons could wade on beaches. The window was narrowest in December (about 5–10% of the daylight period) and widest in May or June in 1986, 1987, and

Relative abundance of heron food energy on beaches (A) and the relative availability of energy ingested per day by herons (B). Foraging data were collected from Sidney Island in April–July and on the Fraser River delta in March and August–November.



1988 (70–80% of the daylight period). As a result, herons could devote more time to foraging along beaches in spring and summer than in winter. The long legs of herons extended the foraging period by allowing them to wade in water before and after tides exposed and covered the eelgrass beds.

The relative abundance of food energy each month on beaches in the Fraser River delta was low in winter and early spring, increased rapidly to its highest point in May, and quickly fell in June, followed by a slow decline to the lowest level in December (Fig. 4A). The estimated amount of food energy that herons could potentially acquire by foraging during the entire low tide was therefore greatest in late May, when prey was most abundant and daytime tides were the lowest of the year.

The relative availability of energy ingested by herons between March and November closely mirrored the seasonal pattern of abundance (Fig. 4B). The threshold for maintenance energy (1560 kJ; Butler 1993) was crossed in April and September, and for egg production (1700 kJ; Butler 1993) in April.

2.3.2 Availability of voles and abundance of herons

The numbers of voles trapped on the 0.25-ha grid on Westham Island increased from about 22 in October 1986 to a peak of 95 in January 1987, then declined to about 60 in March 1987. The average number of herons per day on grasslands changed little from December to March (Kruskal-Wallis test, p > 0.05) and did not vary with vole densities: 7.0 individuals (SE = 1.9, N = 17 days) in December, 6.1 in January (SE = 1.9, N = 12 days), 7.4 in February (SE = 1.5, N = 11 days), and 8.4 in March (SE = 1.2, N = 8 days).

Voles were caught in live traps significantly more often in late morning and late afternoon than at other times of day (Kruskal-Wallis test, KW = 25, p = 0.02, df = 12). However, the number of herons on the same grasslands each hour was not significantly related to time

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Table 1 New loss and assessed of each of the main mean appeales actor by Great Plus Herone during the 1097 and 1098 bread	na seasons on Sidney Island	

	Courtship		Egg		Small chick		Large chick		Total	
Species ^a	No. of fish	%								
Saddleback and crescent gunnels	20	41.7	188	40.9	56	34.6	175	65.3	439	46.8
Pacific staghorn sculpin	2	4.2	78	17.0	9	5.6	53	19.8	142	15.1
Shiner perch	0	0	20	4.3	68	42.0	11	4.1	99	10.6
Threespine stickleback	0	0	42	9.1	10	6.2	8	3.0	60	6.4
Bay pipefish	0	0	4	0.9	9	5.6	1	0.4	14	1.5
Tube-snout	11	22.9	1	0.2	0	0	1	0.4	13	1.4
Unknown	15	31.3	127	27.6	10	6.2	19	7.1	171	18.2
Total	48	100.1	460	100.0	162	100.2	268	100.1	938	100.0

^a See text for scientific names of species. Tube-snout is Aulorhynchus flavidus.

of day (KW = 8, p = 0.8, df = 12), to the time of day that voles were most often caught in live traps (KW = 7.0, p = 0.4, df = 7), or to the height of the tide (Butler 1991). The average heron required about 160 minutes to catch a vole (12 voles caught in 1938 minutes).

Herons hunted in grasslands between November and March (see Chapter 3), when voles were most abundant, the grasses were senescent, and flooding was frequent and widespread. Flooding and grassland cover are important components of foraging success by herons and birds of prey hunting small mammals in grasslands (Taitt and Krebs 1983; Masman et al. 1986). Water-filled burrows and short grass leave few places for voles to hide. However, herons did not hunt at the time of day when voles were most active on the surface of the grassland. Studying raptorial birds in the Netherlands, Daan (1982) found that their hunting success improved during periods of the day when voles were most active. The discrepancy between mine and Daan's (1982) study might have been that I counted all herons on grasslands rather than individuals that were hunting voles. Some herons preened feathers and rested on grasslands between bouts of hunting. Herons might hunt on grasslands when weather hampers their foraging success in the marshes. Adult herons gathered on grasslands significantly more often on days with high winds (N = 212 herons) than on calm days (N = 119 herons; $\chi^2 = 26$, p < 0.001). Bovino and Burtt (1979) found that in Tennessee, high winds reduced the foraging success of herons in open water habitats.

2.3.3 Diet and foraging rate

The quantity of food consumed by herons was determined largely by the prey species they selected, the amount of time spent foraging, and prey capture rate. Herons ate mainly eight species of fish in Sidney lagoon during the 1987 and 1988 breeding seasons (Table 1). Those most frequently taken were saddleback gunnel *Pholis ornata* and crescent gunnel *P. laeta*, Pacific staghorn sculpin *Leptocottus armatus*, and shiner perch *Cymatogaster aggregata*.¹ Gunnels were eaten at all stages of nesting, sculpins mostly when eggs and large chicks were in nests, and shiner perch mostly when small chicks were in nests (Table 1). The fish most frequently caught in beach seines during the herons' breeding season were the saddleback gunnel, crescent gunnel, threespine stickleback *Gasterosteus aculeatus*, Pacific staghorn

Table 2 Number and percentage of fish caught in beach seine hauls and eaten by adult Great Blue Herons in Sidney lagoon in 1987 and 1988

	Diet	Net hauls ^a		
Species	No. of fish	%	No. of fish	%
Saddleback and crescent gunnels	439	58.2	4627	70.3
Threespine stickleback	60	8.0	882	13.4
Pacific staghorn sculpin	142	18.8	452	6.9
Shiner perch	99	13.1	265	4.0
Bay pipefish	14	1.9	359	5.5
Total	754	100.0	6585	100.1

^a The number of each species caught in seine hauls was adjusted by its respective probability of being caught in one seine haul, as given in Appendix 2.

sculpin, shiner perch, and bay pipefish Syngnathus leptorhynchus (Table 2). The mean lengths and weights of most prey species in the lagoon increased each month, with the exception of the shiner perch: adult shiner perch left the lagoon in June, leaving recently born young (Table 3). Adult herons caught significantly (p < 0.0001) more sculpins ($\chi^2 = 16.7$) and shiner perch ($\chi^2 = 157.1$) than I caught in beach seine hauls (Table 2). Gunnels were the most frequently eaten species and occurred most often in seine hauls.

Shiner perch might have been preferred by herons because they were bigger than other species and therefore contained more food energy (Table 3) and also because they were easier to swallow. Adult shiner perch held about 100 kJ and were swallowed in <30 seconds, for a net gain of about 200 kJ of energy per minute of handling time. Herons traded off the large amount of energy gained by eating sculpins against the length of time it took to subdue them. Small sculpins (≤132 cm in total length) contained about 65 kJ of metabolizable energy and took an average of 80 seconds to subdue and swallow (SE = 12, N = 8), for a gain of about 48 kJ per minute of handling. Large sculpins (>132 cm) contained about 120 kJ and required an average of 157 seconds (SE = 52, N = 9) to subdue, for a gain of about 46 kJ per minute of handling. Gunnels held about 9 kJ and were swallowed in an average of 18 seconds (SE = 2, N = 49) after capture, for a gain of 30 kJ per minute of handling. The energetic payoff to herons of eating shiner perch over the other species was therefore substantial. To meet its daily energy needs of about 1560 kJ, a heron would have to catch only 15 or 16 shiner perch per day in May and June, compared with about 170 gunnels. As shiner perch were caught at an average of one every 4.5 minutes, a heron could meet its

¹ Source for names of fish species: American Fisheries Society (1991).

Table 3
Average length of fish caught in beach seines in April–July 1987 and
1088 and their estimated mass from length mass regression equations

	Total l	Mass (g)			
Species/month	Mean	SD	N	Mean	SE
Saddleback and crescent gunnels					
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
Threespine stickleback					
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
Pacific staghorn sculpin					
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
Shiner perch					
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
Bay pipefish					
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
Tube-snout					
April ^a	158.8	47.3	5	35.3	7.6

Table 4

Number and percentage of each prey species caught by adult and juvenile Great Blue Herons on the Fraser River delta in August, September, and October in 1987, 1988, and 1990

	Adul	Juvenile		
Species	No. of fish %		No. of fish	%
Shiner perch	82	63.1	27	35.1
Pacific staghorn sculpin	39	30.0	40	51.9
Saddleback and crescent gunnels	4	3.1	3	3.9
Unknown	5	3.8	7	9.1
Total	130	100.0	77	100.0

 $\chi^2 = 15.7$, df = 3, p = 0.002

Table 5

Average number of fish caught per minute by adult and juvenile Great Blue Herons on the Fraser River delta in August, September, and October in 1987, 1988, and 1990

	No. of fish caught per minute								
	A	dult		Juvenile					
Month	Mean	SE	N	Mean	SE	N			
August	0.87	0.10	42	0.59	0.09	31			
September	0.55	0.08	29	0.24	0.04	15			
October	0.52	0.14	28	0.43	0.18	8			

^a No tube-snouts were caught after April.

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Estimated daily consumption of fish by breeding herons in Sidney lagoon in 1987 and 1988

	Consumption					Proportion consumed		
- Nesting stage	No. of herons ^a (A)	No. of fish eaten/min/ heron ^b (B)	No. of minutes of foraging time/day ^c (C)	No. of fish eaten/day (A×B×C)	No. of fish in 81-m ² exclosure (D)	No. of fish/m ² (D/81 m ²)	No. of fish in 31-ha lagoon on day of sampling (D×310 000) (E)	% consumed by herons [(A×B×C/ E)×100]
Incubation Small chicks Large chicks	100 100 200	0.5 0.5 0.5	176 208 216	8 800 10 400 21 600	360 3 297 403	4.4 40.7 5.0	1 364 000 12 617 000 1 550 000	0.6 0.1 1.4

^a The Sidney Island colony contained 100 breeding pairs of herons. One adult foraged in the lagoon when tides were low, whereas the other tended the nest until chicks were large, when both parents foraged in the lagoon.

^b Herons caught fish at a rate of about one fish every two minutes of foraging (Fig. 5).

^c Low-tide foraging periods were estimated by Butler (1991).

daily energy requirement in slightly more than one hour. In contrast, although gunnels were caught about once every two minutes, a heron eating gunnels alone required the entire low-tide foraging period to meet its own energy needs. Clearly, catching shiner perch is important to provide the extra energy requirements of herons raising chicks. Herons prey on other fish when schools of shiner perch cannot be found.

During August, September, and October, herons caught largely shiner perch and Pacific staghorn sculpins on the Fraser River delta (Table 4). Adult and juvenile diets on the Fraser River delta were significantly different in August–October (Table 4), juveniles capturing fewer shiner perch. Capture rates by adults did not vary greatly throughout the breeding season (an average rate of about one fish every two minutes of foraging) (Fig. 5), but juveniles caught fish at about half the adult rate (Fig. 6 and Table 5). During the breeding season, adult herons consumed <2% of the fish in the lagoon each day (Table 6).

Little is known about the diet and foraging behaviour of herons in marshes during the winter. Herons catch small fish, including sticklebacks, sculpins, flounders, and smelt, in the marshes on Westham Island between November and March (A. Harfenist, unpubl. data). These species are abundant in the marshes during this period (Gordon and Levings 1984).

Foraging success rates of breeding Great Blue Herons in Sidney lagoon in 1987 and 1988



Figure 6 Foraging success rates of adult and juvenile Great Blue Herons on the Fraser River delta in August, September, and October in 1987, 1988, and 1990. Numbers indicate overlapping data points.



Chapter 3. Habitat use by age-classes and sex-classes

3.1 Introduction

Many studies have shown that colonially breeding herons forage within a few kilometres of their colony sites (e.g., Brandman 1976; Pratt 1980; Dowd and Flake 1985; Simpson et al. 1987). However, I know of no study that has described seasonal shifts in the distribution of ageand sex-classes. The purpose of this chapter is to describe how different age- and sex-classes of herons use foraging habitats on Sidney Island during the breeding season and on the Fraser River delta throughout the year.

3.2 Methods

3.2.1 Sidney Island

Herons can wade across about 91 ha of mudflats and eelgrass beds during the lowest tide in Sidney lagoon. 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 14 days at three periods in the 1987 breeding season. I observed birds on four days when most nests held eggs (12 April - 4 May), on four days when nests held small chicks (10-31 May), and on six days when nests held large chicks (16 June - 10 July). When nests held large chicks, 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.

3.2.2 Fraser River delta

On the Fraser River delta, herons can reach about 260 km^2 of intertidal marshes, mudflats, and sandflats, 66 km^2 of river, and 127 km^2 of farmlands, cultivated mostly for berry, vegetable crops, and pastures and drained by ditches. I censused herons in potential foraging habitats on the Fraser River delta from an airplane, car, and boat. These surveys covered habitats where herons were known to occur, although census efforts were uneven, and some herons in other habitats might have been overlooked.

The locations of herons on the beaches and marshlands were plotted on maps during aerial censuses between September 1986 and February 1987. Flights were made twice each month using a Cessna 172, flown at an altitude of about 90 m, when tides were about 3 m high. The census route covered the entire intertidal portion of the Fraser River delta from Semiahmoo Bay in the south to Iona Island in the north. Two observers sat on the same side of the airplane and independently marked the numbers and locations of all herons on a map. The greatest number seen by the observers was used to represent the number of herons present. Nearestneighbour 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 calculated for marsh and beach habitats (Krebs 1989:126-129).

The location of herons in ditches and grasslands within view of the roads was plotted on maps during a drive along a set route of 89 km once each week between 17 July 1987 and 31 March 1988, and once each month from 22 April 1988 to 7 March 1989. Age of herons was assigned by plumage colouration (see Butler 1992 for a detailed description). Plumage differences provide a reliable field method to age herons in the first three years of life. The differences were well illustrated by Milstein et al. (1970) for Grey Herons Ardea cinerea, a close European relative of the Great Blue Heron. Some markings to look for in the field are the white crown, long body plumes, grey-blue wing coverts, and black "shoulder patch" worn by adults (>24 months old). Juveniles (<12 months old) have grey crowns, no body plumes or shoulder patches, and chestnut-coloured edging to wing coverts. Yearling herons (12-24 months old) wear an intermediate plumage in which the crown stripe is small, body plumes are short, a few coverts are edged with chestnut-brown, and a small shoulder patch is present. Juveniles can be easily distinguished in the field from other age-classes, often without the assistance of binoculars or telescope. Yearlings are more difficult to separate from adults than from juveniles, but the brown feather edging and small white patch of feathers on the crown of the yearlings are quite noticeable through binoculars or telescope at close range.

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The plumages of the sexes appear identical. However, in British Columbia, the lengths of the culmen, tarsus, and folded wing of males are about 10% longer than those of females, and male body masses are about 15% greater (Simpson 1984). When a mated pair of herons is seen side by side, the size difference is almost always apparent. Gender was therefore assigned in this study from estimates of culmen lengths read off a graticule scale mounted in a telescope (Butler et al. 1990). The distance between the heron and the telescope was later measured using a tape measure, and the graticule scale measure was converted into actual beak lengths. The accuracy of this method depends upon several factors, including the angle of the culmen relative to the sight-line through the telescope and the distance between the heron and the observer. About 65% of females and 73% of males within 25 m could be sexed with 95% accuracy using this method (Butler et al. 1990). Records for the 25% of birds of unknown sex were discarded.

Habitats and the locations of herons along the banks of the Fraser River 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 (Bayer 1978).

3.3 Results and discussion

3.3.1 Sidney Island

Most adult herons foraged in nearby Sidney lagoon during low tide (Table 7). Herons flying off the island fed in eelgrass and kelp beds on neighbouring islands within 10 km of the colony. During high tides, herons with eggs and large chicks in nests avoided the lagoon (Table 7); most flew 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 7). The maximum number of herons counted in the lagoon during each week of the breeding season (12 April – 10 July) was negatively related to the height of the low tide (Fig. 7).

Only females (N = 18 observations) were recorded in the lagoon between 9 April and 31 May 1988. Males (N = 2 observations) were first seen in the lagoon on 1 June in the company of females (N = 11 observations). 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, whereas males fed themselves mostly away from the island. When nests held large chicks, both parents fed their chicks fish caught in the lagoon during low tide or away from the island during high tide. 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. Studies of coastal herons have shown that most pairs exchange duties during high tide (Paine 1972; Brandman 1976; Moul 1990).

Table 7

Number and percentage of flights to and from Sidney lagoon compared with other sites off the island during low tides (<1.7 m) and high tides $(\geq1.7 \text{ m})$ when nests held eggs, small chicks, and large chicks in 1987

	Low tides	High tides		
Stage	No. of flights	%	No. of flights	%
Egg	271	94.1	213	27.2
Small chick	541	90.5	298	51.3
Large chick	460	62.6	78	10.3

Yearling herons rarely visited Sidney Island during the breeding season. One was seen in the lagoon for about three 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. commun.). I found 1–8 yearlings among adults on fortnightly visits made in May–July 1988 to four estuaries and six beaches up to 27 km away from Sidney Island.

3.3.2 Fraser River delta

Great Blue Herons foraged along beaches close to their colony sites during the breeding season, from March to October, and in ditches, grasslands, and marshes during the nonbreeding season, from November to February, when food was least abundant on beaches and tides were low at night. A rapid shift of herons to grasslands and ditches occurred in November, and a rapid shift back to beaches occurred between March and April (Fig. 8). The farmland habitats, especially grassland fields with small mammal populations, used by large numbers of herons in winter might be essential to the maintenance of these populations.

The highest numbers and percentages of herons were found on beaches in June, July, and August (Fig. 8), the time of year when daytime tides were lowest (Thomson 1981). The demand for food by growing chicks reaches a peak in June, when they are about 4–6 weeks old (Bennett 1993). Sullivan (1988) showed that parents must increase their food provisioning rates to raise more than three chicks. Herons might nest near foraging sites to reduce their energetic costs of travelling between nests and foraging grounds or where they can balance their food needs with those of their chicks.

Significantly more juveniles than adults used grasslands and ditches compared with marshes (Tables 8 and 9). Moreover, 71.2% of the juveniles (N = 139) counted on roadside surveys between November 1986 and February 1987 were foraging, compared with 39.6% of the adults (N = 551).

Foraging herons were clumped in loose flocks on the beaches and in the marshes between September 1986 and February 1987 in the Fraser River delta (Table 10). The greatest densities occurred in Mud Bay, between the BC Ferry and Westport Terminal jetties on Roberts Bank, and between the jetties on Iona Island (Table 11). These three locations were near breeding colonies on the Nicomekl River (about 35 pairs), Point Roberts (about 380 pairs), and Pacific Spirit Park (about 145 pairs), respectively.

All 38 territorial herons along riverbanks of the Fraser River were adults. The highest densities of

Figure 7

Maximum number of herons counted in Sidney lagoon during the lowest tide each week of the breeding season. Numbers indicate overlapping data points in 1987 and 1988.



Figure 8

Percentage of herons on beaches, in grasslands, and in ditches on the Fraser River delta each month between July 1987 and March 1989



territorial herons occurred in river-edge marshes (Table 12), where the adults could wade for fish away from industry and agriculture. Nine territories that could be viewed both day and night were occupied by solitary herons every month of the year. Three of five territorial herons along riverbanks whose gender could be confidently assigned were adult males. Of 20 nonterritorial adults in marshlands during the nonbreeding season, 19 were females and one was male, significantly different from an expected 1:1 sex ratio (Fisher Exact Test $\chi^2 = 11.8$, p < 0.003). Not all territories were occupied each year. Three territories have not been used since the abandonment of a nearby colony site in 1992.

Table 8

Number and percentage of juvenile and adult Great Blue Herons found in ditches and grasslands each month in 1987, 1988, and 1989

Month	No. of juveniles	%	No. of adults ^a	%	Total no. of herons
February	10	19.6	41	80.4	51
March	7	17.9	32	82.1	. 39
April	2	66.7	1	33.3	3
May	4	100.0	0	0	4
June	3	75.0	1	25.0	4
July	5	71.4	2	28.6	7
August	2	66.7	1	33.3	3
September	11	78.6	3	21.4	14
October	16	72.7	6	27.3	22
November	8	15.4	44	84.6	52
December	14	29.8	33	70.2	47
January	2	7.7	24	92.3	26

^a Probably includes a small number of yearlings.

Table 9

Number of adult and juvenile Great Blue Herons counted in grasslands and ditches and in marshes of the Fraser River delta between July 1987 and March 1988 and between July and September 1988

Habitat	No. of adults	No. of juveniles
Grasslands and ditches	698	302
Marshes	158	16
2		

 $\chi^2 = 35.5, p < 0.001$

Table 10

Indices of aggregation of Great Blue Herons feeding in marshlands and on intertidal beaches of the Fraser River delta during the nonbreeding season in 1986 and 1987

	Index of aggregation $(\mathbf{R})^a$					
Date	Marshlands	N	Beach	N		
1986						
30 September	0.53**	69	0.59**	224		
29 October	0.96	73	0.87**	164		
12 November	0.98	105	0.83**	96		
27 November	1.25**	28	0.98	54		
10 December	0.80**	43	1.20*	22		
1987						
6 January	0.81**	45	0.73**	32		
21 January	0.95	46	0.57**	42		
6 February	0.97	27	0.74**	47		
20 February	0.63**	34	0.61**	84		

^a The spatial pattern ranges from clumped (R approaches zero) to regular (R approaches 2.15). When the pattern is random, R = 1 (Krebs 1989). *The spatial pattern is significantly (p < 0.05) different from random. **The spatial pattern is highly significantly (p < 0.01) different from

random.

Table 11

Dastribution of Great	Blue Her	ons cou	nted on tl	he intertid	al port	ion of
the Fraser River delta	between	August	1986 and	February	1987	and in
May 1987		-		•		

Location ^a	No. of herons	Area (km ²)	Density (no. of herons/km ²)
White Rock South	81	4.5	18.0
White Rock North	11	4.5	2.4
Crescent Beach	97	4.1	23.7
Mud Bay	306	6.8	45.0
Boundary Bay East	166	4.2	39.5
Boundary Bay West	185	7.8	23.7
Point Roberts	35	4.3	8.1
Tsawwassen	119	3.0	39.7
Roberts Bank Jetties	348	2.6	133.8
Roberts Bank South	56	3.3	17.0
Westham Island	152	7.8	19.5
Lulu Island	90	4.7	19.1
Sea Island	74	3.5	21.1
Iona Jetties	93	1.9	48.9

^a Locations correspond with surveyed sites beginning at Iona Island at the northernmost end of the delta and ending at the Canada–U.S. border. High-density foraging sites of herons from colonies appear in boldface type.

Table 12

Numbers and densities of territorial Great Blue Herons in three habitats along the riverbanks of the Fraser River delta on 10 January 1990

Habitat	Length of habitat (km)	No. of herons	Density (no. of 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

Chapter 4. Seasonal shifts in habitat use: a test of two hypotheses

4.1 Introduction

In the previous chapter, I showed that Great Blue Herons foraged in eelgrass beds from March to October and in marshes and grasslands from November to February. Two explanations for why herons shift between habitats are described in theories of habitat selection (Fretwell and Lucas 1970; Fretwell 1972; Sutherland and Parker 1985; Parker and Sutherland 1986). Herons might leave beaches when they have insufficient time to meet their daily energy needs by foraging on fish — the Foraging Time Hypothesis. Habitat shifts by herons might also occur when the best competitors establish exclusive feeding territories or dominate weaker individuals, who then move to marginal habitats — the Dominance Hypothesis. In this chapter, I test these hypotheses against empirical data.

4.2 Methods

I reasoned that herons would leave beaches to forage in other habitats when they could no longer catch sufficient prey to meet their daily needs. If dominance were important in determining when herons left beaches, dominance behaviour would have to reduce substantially the amount of food energy consumed by subordinates. The approach I took was to estimate the amount of the daily food intake lost to heron interactions.

I used interference, including territorial behaviour, as an indicator of intraspecific competition for food and foraging sites. Interference was defined as the immediate (although reversible) reduction in intake rate associated with increased interruption of foraging by other herons (Goss-Custard 1985). I noted the frequency and duration of chases, displays, and fights of foraging herons on beaches in the 1987 and 1988 breeding seasons at Sidney Island and from 1 August to 3 November in 1987, 1988, and 1989 on the Fraser River delta. The cost of this interference was determined by estimating the resulting reduction in food energy by subtracting the number of minutes of the low-tide foraging period lost to interference multiplied by the average amount of metabolizable energy ingested per minute while foraging on beaches in autumn (Appendix 1).

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 nonbreeding season. I assumed that adults and juveniles required the same amount of maintenance energy because they have similar body masses: juveniles are fully grown when they leave their nests (Bennett 1993).

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

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

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-hour 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 is explained in detail below.

The amount of energy needed for maintenance was estimated from Kendeigh's (1970) equation to be 1560 kJ (Butler 1993). Ingestion rates are the amount of energy (kJ) consumed per minute of foraging by adult and by juvenile herons, respectively. They were estimated by multiplying the foraging rates of adult and juvenile herons (see below) by the average amount of energy in their diets (see Section 2.2).

Low tides that uncover the eelgrass beds occur mostly during the daytime before November. Therefore, I used foraging rates of adult and juvenile herons on beaches on the Fraser River delta on 33 days between 1 August and 3 November in 1987, 1988, and 1989. I estimated the amount of food that could have been caught during high tides at night from nighttime observations of foraging herons at Sidney Island. The mean capture rate during high tides at Sidney Island in May-June was 3.6 times higher during the day ($\overline{x} = 2.6 \text{ min/fish}$, SE = 0.3, N = 81) than at night (\overline{x} = 9.4 min/fish, SE = 2.1, N = 9). If fish caught during the day and night are the same size, then herons on the Fraser River delta ingested about 3.6 times more energy per minute while foraging during the day than at night from August to November. Most foraging is done during the daytime at this time of year, so that the nighttime contribution to the overall energy

Table 13 Daily metabolizable energy (ME) intake lost to interference by conspecifics preying on nonschooling fish in autumn of 1988					
	Mean no. of fish caught/min (±SE)	Mean ME/fish ^a (kJ) (±SE)	Mean ME/min (kJ/min)	No. of interferences/min	ME lost to interference/ min ^b (kJ/min)
Adult Juvenile	0.46 ± 0.06 0.24 ± 0.03	48.6 ± 14.0 42.6 ± 10.5	22.4 10.2	0.01 0.01	0.22 0.10

^a Calculated by weighting the average metabolizable energy per species (see Appendix 1) by the proportion of the diet in Table 4.

^b This assumes that it takes one minute to resume foraging per interference.

budget is small. I assumed that herons caught the same species of fish during night and day on the Fraser River delta, because shiner perch and Pacific staghorn sculpins were caught in beach seines during day and night in eelgrass beds in the Yaquina estuary, Oregon (Bayer 1985b). These assumptions should not significantly affect the results. The number of minutes that low (<1.7 m) tides uncovered the eelgrass beds each 24 hours from 1 September to 30 November 1987 was used as an estimate of the total amount of available foraging time on beaches.

4.3 Results and discussion

Most breeding herons fed peacefully in Sidney lagoon during the day. I saw one interaction during more than 2700 minutes of watching herons catch nonschooling fish. However, interference increased when herons flocked briefly to pursue schools of shiner perch. Adults, vearlings, and juveniles joined flocks, but the size, frequency, and duration of flocks were highly variable. Flocks ranging from about five to 100 herons formed on most days in June and July. The duration of flocking ranged from about 10 to 60 minutes, but most flocks dispersed after about 20 minutes. Occasionally, Double-crested Cormorants Phalacrocorax auritus drove a school of shiner perch within reach of herons standing in shallow water. In these instances, flocks of herons followed the cormorants for long periods. Interactions between individuals usually occurred in these flocks. Individuals settling in tight flocks displayed with erected plumes and crown feathers, extended necks, and opened wings. Occasionally, jabs were made at each other with bills, accompanied by croaking calls. 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 shiner perch for 23 minutes (0.04 interactions/min per heron). Displaced birds flew a few metres away and resumed feeding about 30 seconds later.

The median capture rate in 27 of these groups was 0.2 shiner perch per minute (range = 0.04-1.7). Each shiner perch contains an estimated 100 kJ of metabolizable energy (ME) (see Section 2.3.3). Therefore, the estimated ME intake rate for herons feeding on shiner perch was (0.2 shiner perch/min × 100 kJ/shiner perch = 20 kJ/min. The estimated energetic cost of an interference was (0.5 min to resume foraging per interference × 0.04 interferences/min per heron × 20 kJ/min) = 0.4 kJ/min per heron or 2% of the total ME intake rate while feeding on shiner perch. The cost of interferences while foraging on nonschooling species was about 1% (Table 13). Therefore, interferences had little effect on the average ME intake rate of these herons, although they may have affected some that were repeatedly displaced.

Juveniles ate fewer shiner perch than adults on the Fraser River delta in August-October (Table 4), so that juveniles consumed slightly less food energy per capture than adults. Interference from foraging conspecifics reduced the ME intake rates of adult and juvenile herons by only about 1% of their average rate and was therefore unimportant in autumn (Table 13). I conclude that interference by conspecifics maintains individual foraging distances but does not explain habitat shifts among herons foraging on beaches.

The amount of foraging time available to herons during low tides declined over the autumn (Fig. 9). The average juvenile ran out of time ($F_t > 100\%$) to meet its daily energy needs on beaches on five days in September, seven days in October, and 12 days in November and required about 73–100% of the available time on most days over the same period. In contrast, the average adult could meet its daily energy needs during low tide on beaches on all but two days in September, four days in October, and seven days in November — in about 55–85% of the available time. Juvenile herons were therefore less efficient foragers than adults, requiring more foraging time to meet their energy needs.

These findings support the Foraging Time Hypothesis, rather than the Dominance Hypothesis. Interference by other herons was too infrequent to reduce the energy intake of herons substantially. These conclusions depend on several assumptions about herons foraging on beaches, all of which 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 the low-tide foraging period would have had to have been 6–165% (median 83%) longer on 10 days in November for juveniles to meet their daily energy needs. Tides were too high to allow herons to forage in eelgrass on a further two days.

My study joins other studies of birds in coastal environments in which tides play an important role in determining when and where birds fed throughout the year (Heppleston 1971; Burger et al. 1977; Connors et al. 1981). Herons are faced with a declining duration of low daytime tides (Fig. 9; Department of Fisheries and Oceans 1986–89) and diminishing prey populations (Gordon and Levings 1984) on beaches through autumn. Adult and juvenile herons store body reserves through autumn (Bennett 1993), and herons may increase their body reserves 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,

Estimated percentage of available low-tide (<1.7 m) foraging time required by adult and juvenile herons to meet their estimated energy needs of 1560 kJ over 24 hours each day in September-November 1987 and 1988 on the Fraser River delta



when they could hardly meet their daily energy needs on most days; most flew to grasslands after October (see Chapter 3), where they acquired about 73% of their daily energy needs each day in November and 65% of their daily energy needs each day in December and January. These findings suggest that herons leave foraging habitats when their food energy potential declines below a critical level (McNamara 1982).

Chapter 5. Heron colony spacing in relation to Bald Eagle predators and heron foraging habitats

5.1 Introduction

In previous chapters, I showed that Great Blue Herons gathered near shallow beaches with abundant prey during the breeding season. However, avoiding predators might also be important in locating colony sites. Lack (1954, 1966, 1968) postulated that food availability was more important than predators in determining the location of most breeding colonies of birds. However, heron predators are often difficult to observe or their populations are small, so that their impact on colony site spacing is poorly understood (Forbes 1989). Predators have caused colony site abandonments by herons (Dusi and Dusi 1968; Simpson 1984) and might affect the spacing of their colony sites.

The major predator of heron chicks, juveniles, and adults in British Columbia is the Bald Eagle *Haliaeetus leucocephalus* (Norman et al. 1989; Vermeer et al. 1989). Eagles nest in conspicuous places along the British Columbia coast and forage along intertidal beaches. Their nests are built over several months and used for many years (Stalmaster 1987), whereas herons build nests in a few weeks and frequently relocate colonies (Butler 1989). The purpose of this chapter is to examine the distribution of heron colony sites and reproductive success in relation to foraging habitats and Bald Eagle predators.

5.2 Methods

Great Blue Herons were studied at colony sites around the Strait of Georgia, British Columbia, in 1987, 1988, and 1989 (Fig. 10). I and three volunteers — André Breault, Ian Moul, and Philip Whitehead — visited the colony sites periodically, recording fledged brood sizes and estimating the number of nests used at the colony sites. I assumed that a nest was used if it held eggs or chicks, if there were hatched eggshells on the ground below the nest, or if the nest or the nest tree had feces splattered on the trunk or ground below the nest.

Shoreline around the Strait of Georgia was divided into "good" and "poor" foraging habitat as follows. Intertidal areas with eelgrass beds, kelp (mostly *Nereocystis luetkeana* and *Laminaria* spp.) beds, and marshes have high prey abundance (see Gordon and Levings 1984; Hughes 1985; Hay et al. 1989) and were considered to be good habitat. Shallow beaches without eelgrass, kelp, and marshes were considered to be poor habitat. All eelgrass beds, kelp beds, and marshes >10 ha in area in the Strait of Georgia were located during searches for heron colonies and from published maps (Hutchinson 1982; Hutchinson et al. 1989).

Herons departing from 29 colony sites were followed to their major feeding location when their nests held eggs and small chicks. The distance between the colony site and the centre of the feeding site was measured on 1:50 000-scale maps and compared with the distance to the nearest good foraging habitat (my criteria) of 31 randomly selected coastline locations away from built-up areas around the Strait of Georgia, using a one-way analysis of variance (ANOVA).

Eagle nests were found by ground searches (N = 6)nests) and air searches (N = 113 nests) (Vermeer et al. 1989) and through information provided by the general public (N = 74 nests). 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 sites were located ≤ 3 km from an eagle nest and assumed to be within an eagle's territory. I considered eagle nesting density to be high where three or more nesting territories were contiguous (i.e., nests were ≤ 6 km apart on average) and low where their nesting territories were not contiguous (i.e., nests were >6 km apart on average). Herons relocate nests more readily than do eagles. I tested the hypotheses that: (1) most herons established colonies far from eagle nests; (2) herons that established colonies near eagle nests had lower reproductive success than those far from eagle nests; and (3) herons located colonies near good foraging habitats.

5.3 Results and discussion

5.3.1 Colony sites and foraging habitat

Herons located colony sites near good foraging areas. The distance to 29 colony sites from their chief foraging areas was significantly shorter than the distance between 31 randomly chosen colony locations and the nearest good foraging habitat (ANOVA, F = 6.8, df = 56, p = 0.01). The feeding grounds of the 29 colonies were an average of 2.6 km from the colony sites (SD = 2.0).

Distribution of heron colonies, nesting Bald Eagles, and foraging habitats around the Strait of Georgia in 1987 and 1988



Twenty-nine of 35 colony sites used in 1987, 1988, and 1989 were near good foraging habitat (Fig. 10). The feeding sites of six small colonies were unknown, but all were within 2 km of the Strait of Georgia, where lone herons foraged. Not all good foraging habitat had associated heron colonies. Three apparently suitable feeding areas used in the past (Forbes et al. 1985b) had no colonies nearby during this study.

Gibbs et al. (1987) suggested that the spacing of heron colony sites in Maine resulted from dispersers

settling outside the foraging range of other colonies, 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 if the habitat were continuous.

This model assumes that herons deplete food supplies near their colony sites and that foraging habitats are fully occupied by herons (Gibbs et al. 1987). I agree

with Gibbs et al. (1987) that food supply determines the spacing of colony sites; heron colony sites were significantly closer to foraging areas than a random supply of locations along the coastline of the Strait of Georgia. Herons might be able to deplete local food supplies, thereby making unoccupied foraging habitats relatively more attractive. The fish populations in the lagoon in the 30 days between the small- and large-chick stages declined by about 370 000 fish per day (11 067 000 fish/30 days; Table 6). This decline includes emigration of fish to deeper water and mortality. An estimated 21 600 fish were eaten each day by herons during the large-chick stage (Table 6), or about 5.8% (21 600/370 000 × 100) of the fish in the lagoon between the small- and large-chick stages. However, many foraging habitats are not occupied each year in British Columbia. The dynamic nature of heron colony sites and colony membership (Simpson 1984; Butler 1989) likely results from disturbance by eagles and humans.

Herons might raise more young by nesting closer to foraging sites. Large broods require adults to make more trips to feed nestlings than smaller broods (Sullivan 1988). It makes intuitive sense for herons to nest as close as possible to food supplies so that they spend less time flying and more time foraging. 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 the 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 for differences in reproductive success to be detectable. Herons carry large amounts of food each trip and make few trips to feed young. Marion (1989) reported individual Grey Herons feeding up to 38 km from colony sites in France, but he did not relate flight distances to reproductive success.

5.3.2 Colony sites and eagles

Herons did not establish colony sites away from areas with high densities of nesting eagles (Fig. 10). In fact, very similar numbers of herons occupied colonies where eagles nested at high density (497 herons in 19 colonies) and at low density (515 herons in 13 colonies). More importantly, the proportion of colony site abandonments proved to be slightly lower in high-density eagle areas than in low-density areas (Table 14).

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 sea coasts, of which herons are of minor consequence (Vermeer et al. 1989). Heron colony sites are located near foraging habitats with an abundance of small fish (Hughes 1985; Hay et al. 1989). These biologically productive habitats also attract the prey species taken by eagles.

The mean brood size was identical in colonies near and far from eagle nests (Table 15). More importantly, the mean percentage of successful nesting pairs was nearly identical in colonies near and far from nesting eagles (Table 15).

Table 14

Number of successful and failed heron colony sites where eagles nested in high and low density in 1987, 1988, and 1989

Eagle nest density ^a	No. of successful sites ^b	No. of failed sites ^b
High	23	5
Low	17	6
<u></u>	· · · · · · · · · · · · · · · · · · ·	

^a High density — nests ≤6 km apart; low density — nests >6 km apart.
 ^b Successful sites — ≥1 nest that fledged chicks; failed site — <1 nest that fledged chicks.

Table 15
Percentage of successful (≥1 fledgling) nesting pairs and mean brood
sizes of colony sites that produced fledglings near (≤ 3 km) and far
from (>3 km) an occupied Bald Eagle nest in 1989

Proximity to	% successful r	oairs	Brood size			
eagle nest	Mean	SD	N	Mean	SD	N
Near	81.1	11.9	12	2.6	0.4	12
Far	85.1	13.7	7	2.6	0.4	7

At one heron colony 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. Eagles attacked the Sidney Island colony in all years from 1986 to 1990. They killed at least three adult herons in the colony in 1989 and five in 1990. The colony abandoned the site twice during the egg stage in 1989. In 1990, the Sidney herons abandoned their eggs after one attempt and renested about 6 km away on Vancouver Island. Eagles also attacked herons in seven of 21 other colony sites in 1988 and in nine of 23 colony sites in 1989.

The analysis of heron nesting success might have been more sensitive if I had used more than two categories of eagle nest abundance and accounted for the effects of other predators. Raccoons Procyon lotor, Red-tailed Hawks Buteo jamaicensis, and Turkey Vultures Cathartes aura occasionally prey upon heron eggs and chicks in British Columbia (Simpson et al. 1987; A. Breault, pers. commun.). Most importantly, the proximity of nesting eagles might be a poor indicator of predator pressure for herons, or breeding herons might not be able to avoid eagles. 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 or, conversely, the territorial behaviour of nesting eagles might reduce the number of attacks on herons by other eagles. On 9-10 April 1987, when female herons were laying or incubating eggs in most colony sites, over one-third (293 of 797) of the eagles counted from aircraft in the Gulf Islands were immature-plumaged birds. There was slightly more than one eagle per kilometre of coastline on average (797 eagles along 750 km of shoreline) in the southern Gulf Islands in 1987 (data in Vermeer et al. 1989).

My study did not determine adult mortality in colonies near and far from eagle nests. The demographic consequences of differential adult mortality in colonies might be far more important than differences in offspring production. Anecdotal evidence suggests that herons abandon colonies more readily when adult herons are killed than when chicks are taken. Eagles repeatedly took heron chicks at the Sidney colony from 1987 until abandonment in 1990. Adults in other nests raised offspring through this period and abandoned the colony in 1990 when at least five adults were killed.

5.3.3 Colonial nesting, mate finding, and food availability

This study has shown that herons locate colonies near foraging habitats and that the presence of Bald Eagle predators is unimportant. However, it does not explain why herons clump nests together into breeding colonies. It seems paradoxical that Great Blue Herons should lead such a solitary existence and yet breed in colonies. Colonies were thought to serve as sources of information on the whereabouts of dispersed food (Krebs 1974), centres to find mates at the start of the breeding season (Simpson et al. 1987), and a means of reducing nest predation (Lack 1968; van Vessem and Draulans 1986). Evidence is weak or equivocal for food finding and predator avoidance (Mock et al. 1988; Forbes 1989), and the mate-finding hypothesis has not been examined. I provide a hypothesis here to explain how colonial nesting, mate finding, and food availability might be related.

Simpson et al. (1987) posited that colonial nesting among herons reduced the time spent in finding mates and that herons exhibited low site and mate fidelity because of the frequent movements of colonies and mates, and therefore that colonies served as a central mate-finding site. They suggested that herons remained in colonies after finding mates because colonies reduced predation pressure on some herons. However, they did not explain how colonial nesting might have arisen, so I provide a hypothesis here.

Many herons select new mates each year (Simpson et al. 1987) and nest near food supplies. As the breeding season approaches, herons gather where food is plentiful (see Chapter 3). Female herons select their mates by approaching unpaired males displaying at nest sites (Mock 1976). A female heron that minimizes the time and energy spent in finding a mate will have more energy to devote to the breeding effort. She can reduce her time and energy in the search for a mate if males are in one location. Males displaying together would benefit from the mutual attraction of potential mates and be rewarded by raising more young by nesting earlier than dispersed males (see Table 18).

Chapter 6. Effects of nest site selection and time of breeding on breeding success

6.1 Introduction

Herons using nests on the periphery of colony sites raise fewer offspring than herons in centrally located nests (Simpson et al. 1987). The time of year that eggs are laid is also important in determining the number of young raised (Pratt and Winkler 1985). The arrival of herons at colony sites in British Columbia at the beginning of the breeding season has not been documented. The purpose of this chapter is to describe the arrival of herons in the colony before eggs are laid and to evaluate the effects of time of egg laying and nest size on nesting success of Great Blue Herons on Sidney Island.

6.2 Methods

6.2.1 Arrival of adults at colony sites

The arrival of Great Blue Herons prior to egg laying was documented at the Sidney Island colony in 1987 and 1988. Visits were made to the colony site in February and March to search for birds feeding in the lagoon and to determine their presence on nests in the evening. In 1988, a polyethylene blind was built on the ground on the perimeter of the colony site, and a 100-m-long covered walkway was extended through the forest to allow access unnoticed by herons. This blind was used to observe herons at nests and had no noticeable effect on the settlement or nesting success of herons. Observation periods from the blind began prior to the arrival of the first heron each evening. Each observation period lasted for about 1.5 hours.

6.2.2 Nest diameter

All nests were numbered with an aluminum plate nailed to the base of each tree in February before the herons arrived at the Sidney Island colony. The diameter of each nest (in centimetres) was estimated using a graticule scale in the eyepiece of a telescope directly below the nest (Butler et al. 1990). All nests were built in the canopy of red alders about the same distance from the ground. The vertical distance between the telescope and nests was measured with a rope hung from one nest.

6.2.3 Date of hatching and number of chicks raised to independence

On most visits to the colony, we approached no closer than 50 m from its edge until the eggs had hatched, because herons are very sensitive to visits early in the season. Herons throw eggshells from nests upon hatching, giving a clear indication of the date on which eggs in each nest began to hatch. Most nests were far enough apart that we could assign eggshells to the respective nests. The eggs in the few nests that were close together hatched at different times, so that we could assign eggshells to nests by listening for the noises of the newly hatched young. The hatching dates for about 10 closely located nests with eggs that hatched within a few days of each other might have been incorrectly assigned, but the error would be of only a few days. Once the first chick was heard, near-daily visits to gather eggshells were made. Two observers were used, to reduce the total search time to about 10 minutes.

Young herons could be seen in the nest near the end of May, when chicks were about three weeks of age. At that time, I made visits about every five days to count the number of chicks in each nest. I recorded the date that the chicks were first seen in branches around the nest as the fledging date and used the number of chicks seen at this time as the number that departed successfully.

6.3 Results and discussion

6.3.1 Arrival of adults at colony sites

Herons began to gather near colony sites around the Strait of Georgia in late winter. In 1988, 40 herons gathered on log booms about 500 m from a colony site near Crofton on 25 February, 50 herons were seen in a field about 1 km from a colony site on Point Roberts on 29 February, and 24 were seen in a field about 2 km from a colony site on the Nicomekl River on 2 March. All gatherings occurred when tides were high.

Herons on Sidney Island visited nest sites in the late afternoon in spring. For example, 43 herons foraged through the low tide in Sidney lagoon about 1 km west of the colony site for most of the afternoon of 21 March 1987. Beginning at 15:55, individuals left the beach and flew to a small island about 800 m from the colony site to perch in trees. Between 17:06 and 18:32, four herons

Table 16

Time of first arrival, number of hours spent at colony site, number of territorial interactions, and number of occupied nests at the Sidney Island colony site in 1988

Date	First arrival time (PST)	Time spent by herons in colony (h)	No. of terri- torial inter- actions/h	No. of nests with adults
17 March	19:00	0.7	0	29
21 March	18:56	0.3	0	14
22 March	_a	0	0	0
23 March	19:08	0.8	0	10
24 March	19:09	1.2	0 -	10
25 March	18:59	1.5	0.7	8
26 March	19:12	1.1	1.8	14
30 March	<19:00	1.1	0	15
8 April	19:29	2.1	14.2 ^b	15
9 April	-	24.0	10.5 ^b	49
15 April	-	24.0	2.0 ^b	60
16 April	-	24.0	n.d.	61

n.d. = not determined

^a No birds arrived.

^b Observations were made for 2 hours 8 minutes on 8 April, 2 hours on 9 April, and 1 hour on 15 April starting at 19:15.

arrived from off the island and joined the flock perched in the trees. At 18:38 and nearing dusk, 43 herons flew en masse into the colony site, followed by three others three minutes later. I could hear "bill snapping" and "roaring" vocalizations (*sensu* Mock 1979) until darkness fell at about 19:20 and the colony went silent. From a distance I could see individuals on 10 nests in the fading twilight, and I suspect that these herons were males prospecting for nest sites. The colony site was vacant the following morning.

In 1988, herons flew directly into the colony site from off Sidney Island. They arrived alone near dusk and spent increasing amounts of time in the colony site from about mid-March until 9 April, after which they remained all day (Table 16). Territorial displays were infrequent until late March, when the first pairs were seen at nests (Table 16). No herons foraged in the lagoon at night in March in 1987 or 1988.

The arrival of herons at colony sites begins before they can meet their energy needs by foraging along nearby beaches during the day. The maintenance requirement of an average heron is about 1560 kJ/day (Butler 1993). In 1987, herons at Sidney Island could meet their maintenance energy needs by foraging in the lagoon on about 12 days in March and about 23 days in April. In 1988, herons could meet their energy needs in the lagoon on about eight days in February, 15 days in March, and 28 days in April (Butler 1993). Pair formation began in late March, and the first eggs were laid in the first week of April (Butler 1993).

Some authors believe that the first Great Blue Herons and European Grey Herons to arrive at colony sites are males, whereas others have disputed this claim (Meyerriecks 1960 and references therein; Voisin 1991). It seems sensible that male Great Blue Herons should arrive ahead of females at colony sites in British Columbia to scout for nest sites or the arrival of mates. The arrival of females might occur after they can obtain sufficient food energy to produce eggs (Butler 1993).

Table 17

Number of nests with brood sizes of 0-1, 2, and 3-4 chicks in the Sidney Island colony in 1987 and 1988

	No. c	of nests	
	1987 b	rood size	
1988 brood size	0-1	2	34
0–1	5	6	3
2	9	9	3
3-4	4	7	. 9

Table 18

Number of fledged chicks	in nests a	t each	hatching	week	on	Sidney
Island in 1987 and 1988						

			No. of	f fledge	ed chicks		
Hatching week	0	1	2	3	Mean	SD	Total
1	4	1	9	6	1.9	1.1	20
2	10	6	28	23	2.0	1.0	67
3	9	1	9	8	1.6	1.3	27
4	1	1	0	1	1.3	1.5	3
5	4	0	2	0	0.7	1.0	6
6	2	0	4	1	1.5	1.1	7
7–11	6	0	1	0	0.3	0.8	7
Total	36	9	53	39			
Nests ≥1 chick		-			2.3	0.6	101
All nests					1.7	1.2	137

6.3.2 Nest size and location

The diameter of nests did not significantly influence the date nests were settled (ANOVA, F = 2.2, p = 0.1) or the number of chicks they held in late July (F = 0.9, p = 0.5). The number of chicks raised in a nest in 1987 did not significantly influence the number raised there in 1988 (Table 17). Therefore, I conclude that the number of offspring raised in a nest is independent of nest size or previous use. Van Vessem and Draulans (1986) also showed that the size of nests in the heron colonies did not significantly affect the number of fledging-aged chicks it held.

6.3.3 Date of hatching and fledging success

Most herons in the Sidney Island colony hatched their eggs in May over a 19-day period in 1987 and a 12-day period in 1988. Herons that hatched eggs early in the season raised more offspring than late-nesting pairs. Van Vessem and Draulans (1986) found similar results for Grey Herons breeding in Belgium. The average fledged brood size declined as the season progressed (Table 18). The decline in the number of fledglings each week was largely a result of an increase in failed attempts. The probability of failing to raise a brood was 0.16 (N = 87) in the first two weeks, 0.33 (N = 30) in the third and fourth weeks, and 0.60 (N = 20) in the fifth to eleventh weeks (Table 18). Chicks that hatched early in the season stayed in nests significantly longer than chicks hatched later (Fig. 11). The date that chicks began to leave nests ranged from 4 June to 15 August; the average date of nest departure for chicks in all colonies was 30 June (SE = 3days).

Figure 11 Number of days that chicks remained in nests versus the date of hatching in May 1987. Numbers indicate overlapping data points.



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Chapter 7. Local survival of age-classes

7.1 Introduction

Lack (1954) posited that heron populations were regulated by density-dependent mechanisms that limit the number of adult herons that breed each year. He showed that the number of nesting pairs in the River Thames drainage crashed following harsh winter weather and rebounded to former levels following mild winters. From this evidence, Lack proposed that populations increased when food became more available to the survivors, who raised more offspring. Eventually, the population would reach a point where food limited the number of adults that could breed in a colony.

A second view is that heron populations are regulated by territorial behaviour in which strong competitors exclude weaker individuals, who then settle in poorer habitats (Marion 1989; but see von Schantz 1991). However, it is unclear if territorial behaviour reduces the breeding success of nonterritorial individuals. Moreover, most herons are not territorial (Butler 1994).

A third view is that juvenile populations of herons are decimated in winter by their inability to catch enough food (Butler 1994). In this view, breeding populations are too low for density-dependent effects on breeding success to appear.

In order to develop a general theory of population regulation for herons, it is necessary to determine where in the life cycle population levels are established. Henny (1972) and Bayer (1981a) presented data from the recovery of herons banded as chicks to show that about twice as many bands were found from herons in their first year of life than from herons in their second year, and three times as many as from herons three years of age and older. However, their method uses many assumptions that require justification (Lakhani and Newton 1983).

In this chapter, I compare the relative mortality rates at different stages of life and describe the causes of mortality for Great Blue Herons.

7.2 Methods

7.2.1 Mortality during the breeding season

I estimated the relative mortality at various stages of the life cycle of herons by determining the proportion of individuals that succumbed during the various breeding stages and estimating the disappearance rate of juveniles and adults from the Fraser River delta. The stages I used were eggs and chicks, juveniles (<12 months old), and older herons (≥12 months old). Clutch sizes were estimated by climbing to nests to record their contents in three colonies and by viewing nest contents in permanently installed mirrors above about 40 nests at the UBC colony site about 25 km north of the Point Roberts colony (see Fig. 1). I estimated the average natality by multiplying the mean number of eggs laid by females in three colonies around the Strait of Georgia by the minimum number of breeding females.

7.2.1.1 Minimum number of breeding females

I visited the largest colony site on the Fraser River delta, located on Point Roberts, in 1987 through 1991 and counted the number of nests. Point Roberts is located on a peninsula along the southern edge of the Fraser River delta and extending into the United States. The colony is located about 1 km south of the Canadian border in a red alder woodlot.

The rationale for this method is as follows: Great Blue Herons form monogamous pair bonds for one breeding season (Mock 1979). However, colonies could be an amalgam of pairs that successfully nested early, pairs that failed and did not renest, pairs that failed early and renested, and pairs that nested late. Some late-nesting pairs might be failed breeders from another colony. I assumed that all successful pairs bred only once, as insufficient time is available for a second brood at this latitude. I also assumed that all pairs that failed to nest did not renest, although other studies have shown that failed and abandoned attempts are followed by second and third attempts (Brandman 1976; Mock and Parker 1986). I also assumed that all females attempted to breed, because very few adults were seen far from colony sites. Therefore, mine are minimum estimates.

7.2.1.2 Number of lost eggs and chicks

The number of lost eggs and chicks is defined as the difference between the number of eggs laid and the number of chicks that fledged from all nests in which eggs were laid.

Table 19 Estimate	9 ed egg, chick, and juve	nile losses from	n the Point Roberts co	olony between	1987 and 1991			
Year	Minimum no. of breeding females	No. of eggs laid ^a	No. of eggs and chicks lost ^b	% lost/ egg laid	No. of fledged chicks	% fledged/ egg laid	No. of juveniles gone missing ^c	No. of yearlings ^d
1987	183	732	311	42.5	421	57.5	306	115
1988	335	1340	670	50.0	670	50.0	487	183
1989	256	1024	538	52.5	486	47.5	353	133
1990	350	1400	665	47.5	735	52.5	534	201
1991	387	1548	697	45.0	851	55.0	619	232
Total	1511	6044	2881	47.5	3163	52.5	2299	864

^a I assumed each female laid an average clutch of four eggs (see Table 20).

^b The number of eggs and chicks lost is the difference between the number of eggs laid and the number of fledged chicks.

^c I assumed that a constant percentage of 72.7% of all fledglings died before reaching breeding age (i.e., no. of fledged chicks × 0.727). ^d Calculated as No. of fledged chicks – no. of juveniles gone missing.

7.2.1.3 Fledging success

A sample of about 50 nests was used to represent the average fledged brood size of the entire colony. The number of offspring raised in nests was not related to the size of the nest or its location in the colony (see Section 6.3.2). Therefore, the first 50 nests encountered in the colony that were visible from the ground were used as the sample. The total number of chicks raised in the colony was estimated by multiplying the average fledged brood size in the sample by the number of occupied nests.

7.2.2 Mortality during the nonbreeding season

The numbers of juvenile and older herons were recorded during weekly road surveys of grasslands and beaches in the Fraser River delta, as described in Section 3.2.2. I assumed that no juveniles that emigrated from the Fraser River delta returned there, and that there was no immigration. This assumption is based on band recovery data that showed that: (1) all 16 bands recovered from adults in the delta were banded as chicks in the delta; and (2) none of the 56 recoveries of herons banded as chicks in colonies within 500 km of the Fraser River delta has been recovered in the delta.

I estimated mortality as 1 – local survival of juveniles from the slope of the regression line of the number counted each month on road surveys. Adult and yearling herons were lumped together because they could not be distinguished at a distance in the field.

7.2.3 Causes of mortality and physical condition

The causes of mortality were quantified from 43 nestlings and 118 injured and emaciated juvenile herons brought to me and to wildlife rescue facilities near the Fraser River delta and on Vancouver Island. Gross postmortems were performed by a veterinarian on 43 nestlings found below nests in seven colonies and on 29 juveniles (K. Langelier, pers. commun.). Of the 43 nestlings, 13 were less than half the size of a fledglingaged chick, 10 were one-half to three-quarters size, and 20 were three-quarters to full size.

Forty-seven herons found on the Fraser River delta were used to develop a condition index, as follows. The lengths of the wing chord, exposed culmen, and tarsus were measured with a ruler. The carcass was weighed with a Pesola spring balance, and the wet mass of the visceral fat surrounding the gut was determined using an

electronic pan balance. The relationship between visceral fat mass (VF) and body mass (BM) was VF = 0.031BM -42.813 (r² = 0.56, p = 0.003). The body mass at which the average heron had depleted all of its visceral fat was estimated from this equation to be 1381 g (y-intercept). Herons with no visceral fat (i.e., body mass ≤ 1381 g) were considered to have depleted their nutrient stores, whereas herons with body masses above the regression line were considered to have nutrient stores.

7.3 **Results and discussion**

7.3.1 Mortality rates

The minimum number of breeding females in the Point Roberts colony increased from 183 birds in 1987 to 387 in 1991. The percentage of chicks raised to fledging age per egg laid averaged 52.5% (Table 19).

Juveniles disappeared from the study area over the autumn and winter more rapidly than did older herons (Fig. 12). The slope of the regression line (b = 13.2, SE = 2.2) indicates that 72.7% of the juveniles counted in August had vanished by February. The slope of the regression line for older herons declined more slowly (b = -7.5, SE = 2.0), indicating that 27.3% disappeared over the same period. Therefore, less than half (47.5%; Table 19) of all eggs and chicks were lost in the nest stage, compared with about three-quarters (72.7%) of all surviving juveniles and about one-quarter (27.3%) of older herons (Fig. 12).

I am confident that my estimates of mortality in the nesting stage are reasonable, because nest contents can be determined accurately from the ground (unpubl. data). However, I am less confident in my estimate of mortality of juveniles and older herons. My estimate of local survival (Fig. 12) includes an unknown number of yearlings and therefore is probably low, and it did not account for juvenile herons that survived after departing the Fraser River delta. Nonetheless, the number of yearlings in the population is likely small compared with the number of adults, so that eliminating them would increase the estimated adult mortality rate only slightly. Similarly, the number of dispersing juveniles that survive is probably lower than the number of nondispersing juveniles. My estimates of mortality were similar to those from analysis of band recovery data from other parts of North America (Henny 1972; Bayer 1981a).

Figure 12

Number of juvenile and older herons counted on the Fraser River delta between August 1988 and February 1989



7.3.2 Causes of mortality

Of 96 eggs laid in 23 nests, 14.4% failed to hatch. Of 43 nestlings found below nests, 23 died from a trauma, most likely during falls from the nests. A remarkable finding was that of the broken wings or legs found in 31 chicks, nine breaks were partly healed, indicating that they had occurred before the falls from the nests. Another striking finding was that nearly half of the 43 chicks' stomachs (N = 21, 48.8%) were not empty; nine stomachs were one-quarter full, four were half full, one was three-quarters full, and seven were very full. Eleven of the chicks had ingested twigs, and six had eaten alder cones. Seven chicks had gastric nematodes. Only 15 chicks were judged to be thin, of which six had food in the gizzard and four likely died from starvation.

Many authors have reported starvation as a major cause of chick mortality among nesting herons (Quinney and Smith 1979; Pratt and Winkler 1985). However, no postmortems were conducted in these studies. The results of the present study suggest that differences in food provisioning by parents were not an important cause of chick mortality. The majority of chicks died from falls from the nests, and many had previously broken wings or legs. Similar fractures occur after leaving the nest. These findings are not consistent with Lack's (1954) hypothesis that brood reduction mediated by asynchronous hatching of eggs adjusts Grey Heron brood sizes to the parents' ability to find food.

The percentage of eggs lost to predators ranged from 0 to 11% in the Sidney colony in 1987 and 1988 (Butler 1989). The rate of loss at other undisturbed colonies is not known but is probably low, as most nests contain chicks. Crows mostly scavenge unguarded eggs in nests that have been temporarily or permanently abandoned by adult herons. The upper estimated limit (11%) of eggs lost to predators in the Butler (1989) study is about 2-3 times greater than the 2-4% loss reported by
 Table 20

 Mean clutch size in Great Blue Heron colonies on the British Columbia coast

		Clutch size		•	
Colony	Year	Mean	SD	N	
Nicomekl	1986	4.4	0.6	14	
Nicomekl	1988	4.2	0.8	23	
Crofton	1986	3.9	0.7	51	
UBC	1987	4.2	0.6	23	
UBC	1989	3.7	0.6	13	

Quinney and Smith (1979) and 5% estimated by McAloney (1973).

Most (41%) of the 118 herons turned in to wildlife rescue facilities had fractured bones, and many (22%) were emaciated. About 9% had lacerations to heads, wings, or legs, about 8% were caught in fishing gear, and 5% each had been shot or suffered from traumas. Eighteen percent had bumblefoot, were poisoned, had been caught by dogs, had burns to the head, had bone dislocations, or had a fish stuck in the gullet. However, few herons died directly from starvation. Postmortems of 29 juveniles showed that only four (13.8%) likely starved to death (K. Langelier, pers. commun.). The remaining 25 (86.2%) either starved following an accident or died of accidental causes. It is possible that emaciated juveniles were more likely than well-fed juveniles to suffer accidents and subsequently starve.

The findings that about 5% of juvenile herons turned in to wildlife rescue facilities had been shot indicate that Great Blue Herons in Canada and the United States continue to be persecuted even though they have been protected by legislation since 1916. The effect of a 5% mortality from illegal shooting of juveniles on population levels of herons is unknown. Shooting of adult herons resulted in declines in the number of breeding pairs in Europe (Voisin 1991: 196–198). When legislation forbade shooting herons, their populations increased in the former breeding range.

Thirty herons in the present study had depleted their nutrient stores, and 17 herons carried nutrient stores (Appendix 3). Twenty-eight of 30 herons with depleted nutrient stores had sternums projecting sharply from their breasts. On average, the body mass of these herons was 19.2% lower than expected, and the most depleted individual was 33.1% below its expected body mass. On the other hand, the body mass of 17 herons with nutrient stores was on average 15% greater than expected, and the heaviest individual was 41.7% above the expected body mass. There was no significant difference in the lengths of wings of herons with and without nutrient stores. However, herons without nutrient stores had significantly shorter culmens (one-tailed t = 3.1, df = 45, p < 0.005) and tarsi (one-tailed t = 2.3, p < 0.001) than did herons with nutrient stores.

Chapter 8. Conclusions

The aims of this report were to explain the survival, habitat use, and reproductive behaviour of the Great Blue Heron in relation to the availability of its food. Food availability affects the time of year when herons breed (Butler 1993), the number of eggs a female lays, and the size of broods (Powell 1983; Powell and Powell 1986; Sullivan 1988). The present study indicates that food availability strongly affects the spacing of heron colonies (Chapter 5), the use of habitats by herons (Chapter 4), and heron survival (Chapter 7). In this final chapter, I attempt to pull together the results of the previous chapters by discussing the responses of Great Blue Herons to food availability throughout the year.

The evidence presented in this report supports my general thesis that the seasonal pulse in food availability establishes when herons forage (Chapter 4), the amount of food they consume (Chapter 2), and their breeding success (Chapter 6). Heron food arrives in seasonal pulses created by the inshore migrations of small fish preparing to reproduce coupled with long periods of low-tide foraging bouts during the day (Chapter 2). The sudden arrival of millions of fish beginning in April provides female herons with the food energy needed to make eggs (Butler 1993). Most females in a colony lay their eggs over about a three-week period. However, laying dates between colonies can be at least six weeks apart, perhaps reflecting different arrival times of small fish. Local differences in sea temperature on beaches near colony sites might result in staggered immigrations of fish populations on nearby beaches. The availability of shiner perch was critical for the successful breeding of herons at Sidney Island. This species provided most of the food energy for adults and chicks. Shiner perch swim into shallow waters in late spring to give birth to live young that reside there until autumn. Large schools use eelgrass beds and estuarine marshes on the British Columbia coast. and it is near these habitats that herons located colony sites.

Breeding herons flew to Sidney lagoon to forage mostly when tides were low. Other studies of coastal nesting herons have also shown that foraging activity was largely centred around low-tide periods (Brandman 1976; Bayer 1981b). The regularity of low tides provides a general calendar by which herons can schedule seasonal activities such as breeding and dispersal. Individual herons can fine-tune their own activities to their consumption rates, which result largely from the level of prey abundance and their foraging skill. The daily activity of herons was scheduled around the low-tide foraging period so that other activities, such as courtship, preening, and resting, occurred at other times of the day. In addition, the seasonal use of beaches (Chapter 3) and the timing of egg laying (Butler 1993) occurred during the months when daytime tides were the lowest of the year.

In autumn and winter, most adult herons continue a similar regime, by flying to marshes to forage during low tides and scheduling their rest periods during high tides. This option was not available to juveniles, because few of them used marshes (Chapter 3), most foraging on small mammals in grasslands instead. Juvenile herons catch about half as many prey per minute as do adults (Quinney and Smith 1980; Chapter 2) and might forage in grasslands because they are unable to catch sufficient food in marshes in winter.

My hypothesis that food availability outside the breeding season determines the number of juveniles that survive and subsequently establishes the size of breeding populations requires further testing. The mechanism of population limitation provided by Butler (1994) is that few juveniles have the foraging skills required to survive food shortages in winter, which results in wide-scale mortality of this age-class. The best-skilled juveniles should survive longer and will determine the rate of growth of breeding populations two years hence.

My study results concur with those of Sullivan (1989) and Catterall et al. (1989) in suggesting 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; Ens 1992). In my study, dominance was less important. I conclude that food availability mediated through foraging skill explained well much of the behaviour of the Great Blue Heron.

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 (Chapter 3), where they hunted small mammals. I hypothesize that their low foraging success in grasslands left juveniles emaciated and vulnerable to collisions with vehicles, telephone wires, and fences (Chapter 7).

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 van 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 or to exploit temporary bonanzas created when rains flood voles from their underground burrows in grasslands, or both.

Future studies might examine the relationship between age-related foraging success and survival. Recently fledged herons have poor foraging skills. Young that leave the nest when food is plentiful on the beaches and tides are low for long periods of the day will have the longest time to learn to catch prey and the greatest chance of survival. Adults forage at about twice the rate of juveniles (Quinney and Smith 1980; Chapter 2) and have nearly three times the survival probability (Chapter 7). Thus, learning to recognize and catch prey is paramount in the survival of juveniles and ultimately in determining the number of recruits into subsequent breeding populations.

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Appendices

Appendix 1

Method to estimate the amount of metabolizable energy ingested from prey of Great Blue Herons

Metabolizable energy is the amount of energy absorbed during digestion by herons. The steps used to estimate the amount of metabolizable energy in fish eaten by herons are outlined in Figure 2. The length of each fish caught by herons was estimated as a proportion of the culmen length (see Section 2.2.3) and converted into mass using length-mass regressions from samples of the major prey species caught in beach seine nets. The mass of all fish was converted into units of energy by multiplying by a constant of 4.76 kJ/g dry weight derived from the follow assumptions: all fish contained 71% water (Holmes and Donaldson 1969) and each gram dry weight of fish contained 21.3 kJ of energy (Cummins and Wuycheck 1971), of which 77% was assimilated by herons (Castro et al. 1989). These assumptions have been discussed elsewhere (Butler 1993).

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Appendix 2

Probability of capturing all individuals of the most numerous fish species in a partial enclosure in Sidney lagoon on each seine net haul in eelgrass habitat on 19 May 1988

	Saddlebac crescent gi	k and innels	Threes sticklel	pine back	Pacific st sculp	aghorn in	Shiner p	berch	Bay pip	efish
Haul	No. caught	Prob.	No. caught	Prob.	No. caught	Prob.	No. caught	Prob.	No. caught	Prob
1	390	0.41	74	0.74	4	0.67	2	1.00	10	0.53
2	121	0.54	18	0.92	0	0.67	0	1.00	1	0.57
3	117	0.66	7	0.99	0	0.67	0	1.00	4	0.79
4	74	0.74	0	0.99	0	0.67	0	1.00	0	0.79
5	103	0.85	0	0.99	1	0.83	0	1.00	3	0.95
6	85	0.94	0	0.99	1	1.00	0	1.00	0	0.95
7	57	1.00	1	1.00	0	1.00	0	1.00	1	1.00
Total	947		100		6		2		19	

Prob. = probability (cumulative)

Appendix 3 Length of wing chord, culmen, and tarsus and body mass and expected body mass of 47 herons found dead or that died following rehabilitation attempts in the Fraser River valley

Wing chord	Culmen	Tarsus		Expected
length	length	length	Body mass	body mass
<u>(mm)</u>	(mm)	(mm)	(g)	(g) ^a
490	123	160	1190	1778
511	128	162	1300	1895
480	134	160	1425	2034
480	135	155	1450	2056
451	117	160	1155	1638
440	116	148	1150	1615
470	120	149	1225	1708
472	123	142	1300	1778
475	122	160	1300	1755
497	191	169	1630	2197
455	117	142	1235	1638
460	125	145	1390	1824
460	117	150	1250	1638
470	119	151	1300	1684
485	123	150	1375	1778
482	116	152	1250	1615
485	131	175	1550	1964
489	114	147	1270	1568
510	134	167	1650	2034
469	126	157	1550	1848
403	116	149	1410	1615
494	140	172	1950	2174
475	132	159	1800	1988
460	120	160	1550	1708
520	130	168	1775	1941
450	121	145	1600	1731
490	133	167	1800	2011
487	124	163	1700	1801
447	112	141	1510	1522
483	112	157	1520	1522
429	117	129	1710	1638
492	132	163	2080	1988
478	108	137	1500	1429
480	134	165	2140	2034
460	124	154	1900	1801
486	134	153	2150	2034
490	113	160	1650	1545
438	112	150	1650	1522
488	124	173	2000	1801
442	95	115	1340	1126
473	135	154	2460	2058
533	148	172	2900	2361
476	139	173	2650	2151
517	134	149	2510	2034
490	136	152	2570	2081
440	114	139	2000	1568
454	130	175	2750	1941

^a Expected body mass was estimated by inserting the culmen lengths (CL) into the equation BM = 23.2CL - 1087.9 ($r^2 = 0.31$, p = 0.0001), where BM is the body mass in grams and CL is the culmen length of 33 herons with >1 g of visceral fat.

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