

FACTORS AFFECTING REPRODUCTION IN
GREAT BLUE HERONS (Ardea herodias)

By

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ABSTRACT

Reproductive success and size of 15 heronries were monitored from 1977 to 1980 in south coastal British Columbia. My main objectives were to inventory existing colonies, assess changes in colony status from historical information, and document factors important to reproduction. I collected data on banded herons at one colony to describe the movement of herons between and within heronries, and to identify the characteristics of individuals that related to reproductive success. Many heronries formerly identified were no longer present while others were at new locations or much larger in size. Heronry movements followed destruction of the nest trees or reproductive losses in several cases. Relocation normally occurred in the first or second year following heavy losses of young or adults. Disturbances by people sometimes forced herons to leave their nests and increased losses of eggs and young to predators. Severe predation continued after human disturbance had stopped. The number of young raised per successful nest was not a useful measure of reproductive success, since it varied little among colonies. The percentage of nests that succeeded, or numbers of young raised per breeding pair, provided better measures of reproductive success.

Marked herons at one colony were not attached to specific nests or mates, and many adults probably switched colonies each year. Unsuccessful pairs did not reneest in the same colony during the same breeding season. Although herons in central nests were more successful than those near the edge of the

colony, central nests were not occupied by birds which were dominant on feeding areas. Herons are probably attracted to colonies to find new mates each year, and to reduce the vulnerability of their young to predators. Although 78 percent of the herons in one colony fed in the nearest feeding areas, many chose to travel further to feed. These distant feeders suffered higher nest losses to predators, probably because they left their nests unattended more often than other locally feeding birds. Some evidence suggested that males travelled further than females, and were less attentive at the nest. Males may play a dominant role in initiating colony relocations. The lack of attachment of herons to nest sites or mates helps to explain the changes in size and frequent movements of heronries in coastal B.C.

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GENERAL INTRODUCTION

Great blue herons (Ardea herodias) are a large, conspicuous bird distributed across North America. Herons are predators and feed on a wide variety of fishes, amphibians, reptiles, mammals and birds. Their habit of feeding in marshes, open fields and tidal areas makes them easily observable, and they are a familiar sight in areas where they occur. Great blue herons normally nest in groups and, once located, heron colonies can be easily observed. Because of their wide distribution, easy observability, and their position near the top of the food chain, herons were considered a potentially good indicator species for monitoring environmental contamination (Canadian Wildlife Service 1971). This study was initiated by the Canadian Wildlife Service in 1977 primarily to identify and enumerate heron colonies in the lower mainland of British Columbia (Simpson and Kelsall 1978). My surveys were later incorporated into a nation-wide program to monitor great blue heron populations (Des Granges 1980) and to develop a distribution and abundance atlas for B.C. (Forbes et al. 1983).

There have been many studies of herons, most relating to their nesting or feeding habits, in this and other areas. In Chapter I, data collected at 15 heronries in south coastal B.C. is compared to historical data for the area and to results of studies in other areas. The effects of colony movements and changes in size, predation and human disturbance are assessed by comparing the reproductive performance of colonies subject

to varying influences from 1977 to 1980. In Chapter II, I document the behavior, movements and reproductive success of marked herons within one colony in 1978 and 1979. Some unexpected characteristics of individuals within this colony are related to results from Chapter I and aid in explaining some of the size fluctuations and movements of other heron colonies. Several factors considered important to reproductive success were assessed and other unforeseen factors were identified.

CHAPTER I

Location, Size, History and Reproductive Success
of Heronries in South Coastal B.C.

INTRODUCTION

Great blue herons (Ardea herodias) have been studied in many areas of North America. Many authors report the locations, numbers of nests and reproductive success in heronries within a geographical area (Des Granges 1981, Werschkul et al. 1977, Vermeer 1973, Benning 1969). Heron nests have been found in a variety of tree species, on man-made structures, in shrubs and even on the ground (Blus et al. 1980, Des Granges 1979, Vermeer 1970). Comparison of historical and annually collected data has shown that, although there are many long-standing heronries, colonies fluctuate dramatically in size, are abandoned or relocate frequently. The suspected reasons for this instability have included habitat destruction, disturbance from nearby human activity or avian predators nesting in or near the heronries.

Egg and nestling losses to predators and adult interactions with avian predators have been reported in many areas (Hjertaas 1982, Fry 1980, Koonz 1980, Bayer 1979, Werschkul 1979, Taylor and Michael 1971, Temple 1969, Dusi and Dusi 1968, Santy 1964). The effects of predation have varied from minor losses of adults or broods to complete destruction and abandonment of colonies. The response of herons to predators has generally been inconsistent and unpredictable. The role of predators in affecting heronry movements and reproduction has, therefore, been difficult to determine.

All researchers report the number of young raised per successful pair and some include an estimate of the percentage of successful pairs (see reviews by Parker 1980, Quinney and

Smith 1979, McAloney 1973). Most heronries produced at least 1.9 young per breeding pair per year, the number believed sufficient to maintain a stable heron population in the northern U.S.A. (Henny 1972). Although there is some geographic variation in the numbers of young fledged per successful nest, few differences have been found between colonies in the same area, between years or between disturbed and undisturbed colonies. In fact, the number of young raised per successful pair is a surprisingly stable statistic with "surplus" young reported for the majority of colonies. The lack of sensitivity of this statistic to varying conditions in heronries makes it a poor choice for assessing the reproductive health of a heron population.

Using data collected at 15 colonies from 1977 to 1980, I have investigated some of the factors that have been suggested to cause heronry relocations and fluctuations in size. I also examined the relationship between predators and heronries, and I propose a better method of assessing heron reproductive success.

METHODS

I studied 15 colonies, 11 of which were shown to me by naturalist clubs or individuals, and four which were found by ground or aerial searches. I visited the 15 study colonies 162 times from 1977 to 1979, 31 times (22%) prior to the adult herons' arrival, 66 times (41%) during egg laying and incubation, and 64 times (40%) during the pre-fledging period when

adults were seldom present. In 1980, three persons who had assisted me previously did the colony surveys. Visits were timed to minimize the disturbance to the colony while collecting data. I questioned residents and landowners in the area of each colony regarding its history, periods of abandonment, local movements, incidences of predation or human harassment, and changes in size.

I counted the total number of nest platforms (unoccupied nest sites) and the number of occupied nests in each colony in April prior to the development of dense deciduous foliage. I judged platforms to be occupied if there were incubating adults present or if there were obvious signs of activity on or under the nest (i.e. droppings, hair pellets, food items, broken branches, eggshells). I considered nests to be successful if there were one or more young present on the nest in late June or early July, just prior to fledging. At that time young birds were about two-thirds of adult size and were readily visible from the ground. The number of young birds was recorded for each nest where they could be accurately counted. I assumed that the numbers of young counted on these more visible nests were representative of all nests in each colony. I calculated the mean number of young fledged per successful nest (MYSN) based on this sample.

In two colonies, located in cottonwoods (Populus trichocarpa), many nests were no longer visible at fledging, so the number of occupied nests in April was used as an estimate of the number of successful nests each year (see "Results"). The Haney colony

was surrounded by dense coniferous forest so only a minimum nest count was possible and no fledgling counts were made.

I mapped eight colonies in 1978 and 1979 to obtain reproductive information on individual nests. I nailed numbered aluminum tags to the trunk of each tree containing one or more nest platforms, whether these were occupied or not. The location of each tree was plotted on graph paper by taking compass bearings and pacing the distance between trees. I recorded whether each platform was still present, and if it was vacant or occupied on each survey. Newly constructed nests were also labelled and mapped. In the large Point Roberts colony, the number of occupied nests was recorded in April 1978 and 1979 and a sample of 40 trees was labelled, mapped and checked at fledging. The change in numbers of occupied nests in those 40 trees was used to estimate the change in the entire colony between April and June. A similar estimate was made in the Coquitlam colony using 17 of the 35 nest trees in 1979.

The number and condition of dead young found on the ground in each colony was recorded and some specimens were collected. Evidence of predators or scavengers within the colonies such as scats, tracks, owl pellets, broken eggs and remains of herons was also recorded. Signs of human activity such as trails, tracks and fallen trees were also noted.

RESULTS

Heronry Locations, Sizes and General Descriptions

Figure 1-1 shows the locations of the 15 study colonies. I searched for nine additional colonies of uncertain status which were reported by Mark (1976). I found no evidence of an active colony at those sites in 1977, despite extensive ground and aerial searches and conversations with interested naturalists and persons who had reported the colonies. It is possible that some may have moved to distant, unreported locations. Three of the colonies (McGillivray, Gibsons and Chehalis) were abandoned the year I located them. The colonies I located on the Sunshine Coast represent the first written records of heronries in that area although many local residents were aware of them. I believe that the study colonies represented all of the larger heronries within the populated portion of the lower mainland. Smaller colonies, and those in remote areas, may well have been overlooked.

Colonies varied from 10 to 240 successful nests in the lower mainland (Table 1-1) compared to a range of three to 130 for colonies reported by Mark (1976) in the same areas. The average size of the four colonies reported previously by Mark (1976) was 62% larger during this study (Table 1-2).

Herons nested in stands of alder (Alnus rubra), broadleaf maple (Acer macrophyllum), cottonwood (Populus trichocarpa), Douglas fir (Pseudotsuga menziesii) and Sitka spruce (Picea sitchensis). Some nests were also found in western hemlock (Tsuga heterophylla), lodgepole pine (Pinus contorta) and

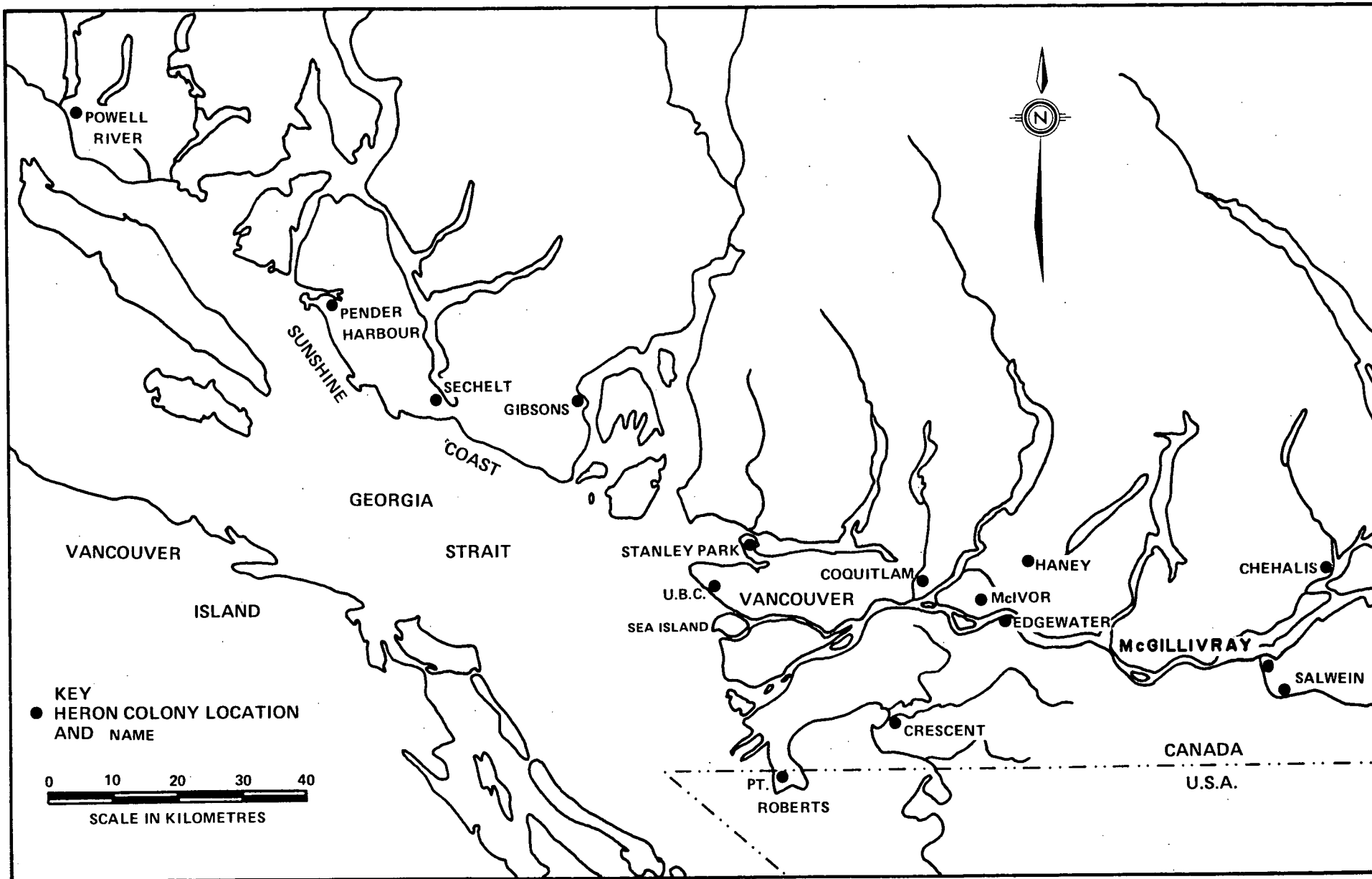


FIGURE 1-1. Heron colony locations in the lower mainland and Sunshine Coast areas of British Columbia.

Table 1-1. Number of successful nests in heron colonies surveyed in south coastal British Columbia.

Colony name	Number of successful nests			
	1977	1978	1979	1980
Coquitlam	169	162	31	26
Crescent	37	46	42	22
Edgewater	16	31	38	30
Haney	10*	10*	10*	10*
McIvor	8	8	5	6
Pender Harbour		25	33	0
Point Roberts	216	240	236	222
Powell River		6		19
Salwein	96	101	109	91
Sechelt		28	36	35
Stanley Park	19*	43	38	33
U.B.C.	82	103	118	130

* Minimum count due to visibility or other limitations--
see text.

Table 1-2. Comparison of past and present sizes of four colonies in the lower mainland.

Colony name	Before 1976		1977-1980		Mean % increase
	mean no. successful nests	N	mean no. successful nests	N	
Coquitlam	63	2	97	4	54
McGillivray	27	1	46*	1	70
Point Roberts	120	4	228	4	90
U.B.C.	80	3	108	4	35
			Mean		62

* Refers to occupied nests later abandoned, 1977.

cedar (Thuja plicata). In 11 colonies, herons nested in only one tree species (Table 1-3), although there were other trees of similar height in the same area. In all colonies, most successful nests were in the same tree species (Table 1-3) and in two cases, Coquitlam and Stanley Park, limited sites in the primary species may have forced herons to use other trees. I have used this characteristic of herons as indirect evidence that heronries at different locations, but in the same tree species, represent local movements of one population.

Historical and Present Colony Data

To assess long-term trends in the heron population, I compared past and present data. Mark (1974, 1976) summarized historical information on heron colony locations and sizes.

Table 1-3. Descriptions of the study colonies.

Colony name	Year	No. of successful nests*	Tree species	No. of nest trees
Chehalis	1979	47	Broadleaf maple	18
		31	Cottonwood	7
		5	Douglas fir	2
		1	Cedar	1
Coquitlam	1978	151	Sitka spruce	27
		7	Lodgepole pine	5
		4	Western hemlock	3
Crescent	1977	37	Douglas fir	5
Edgewater	1977	16	Cottonwood	3
Gibsons	1978	42	Broadleaf maple	14
		12	Red alder	11
Haney	1977	10	Douglas fir	2
McGillivray	1977	46	Cottonwood	10
McIvor	1977	8	Sitka spruce	1
Pender Harbour	1978	25	Red alder	23
Point Roberts	1977	216	Red alder	192
Powell River	1978	6	Douglas fir	2
Salwein	1977	96	Cottonwood	19
Sechelt	1978	28	Red alder	28
Stanley Park	1978	32	Douglas fir	3
		9	Cedar	5
		2	Western hemlock	2
U.B.C.	1977	82	Red alder	61

* Refers to occupied nests for colonies abandoned prior to fledging (Chehalis, Gibsons, McGillivray).

I used this and additional data from other publications and verbal reports to assess the history of the study colonies. I assume that varied locations of a colony within 10 kilometers in different years represent local movements of one population.

Chehalis Colony

This colony was active from 1957 to 1960 (Mark 1976). The colony had been abandoned shortly before my first visit on April 19, 1979. Eggshells found on the ground had been broken by predators or scavengers and no adult herons were observed. I found feathers of one dead adult bird. Residents confirmed that the colony was active in 1978 and that the herons had arrived, as usual, in March 1979. Bald eagles (Haliaeetus leucocephalus) which congregate in the area to feed on salmon (Oncorhynchus sp.) carcasses normally roost in the forested area where the herons nest and leave shortly before the herons arrive. Residents speculated that the herons abandoned their nests due to harassment by the eagles which left late in 1979. My observations of abandoned eggs and one dead adult support that conclusion.

Coquitlam Colony

Two colonies were recorded in Coquitlam. The Newberry Road colony had 78 nests in spruce trees in 1971 but was abandoned, probably in 1972, either because of an adjacent subdivision development (Mark 1976), or because of a juvenile banding program carried out by a heron research group working at the

University of B.C. In 1971, 94 of 190 nestlings were banded (Campbell et al. 1973).

The other colony, on the Essondale Indian Reserve (Fig. 1-1), was first recorded in 1973 when it contained at least 48 nests (Jerema 1973). Evidence indicated that there had been herons at that location for many years (Mark 1976). Judging by the size of the Coquitlam colony (over 160 nests in 1977 and 1978, Table 1-1), and apparent overcrowding, it is likely that the Newberry Road colony joined an existing colony at this location in 1972.

In 1979 and 1980 the earlier nesting site was abandoned. Bald eagles were nesting in the center of the vacated colony. Thirty-one occupied nests were located about one kilometer north of the old location. Reproduction in those nests appeared to be normal, but most young had fledged prior to the census in 1979. The status of the remaining 130 pairs that nested in 1978 is unknown.

Crescent Colony

The Crescent colony was referred to by Urhahn (1968), but no size or exact location was given. According to local residents, the Crescent colony was originally located in large firs in Crescent Park but was forced to move when the trees were felled. The birds occupied two more sites on private property, where they were unwelcome and the trees were felled, before they found sanctuary at their present location about 1970. The nest trees are all within 20 meters of a private residence. This location was abandoned for two years about

1972-73 when a pair of great horned owls (Bubo virginianus) occupied one of the nests (R. Nitsch, pers. comm.).

The Nitsch's observed eagles capturing young herons on three occasions. One eagle landed on a heron nest in 1978 and carried two young away. The eagle dropped one young heron in the Nitsch's back yard as it flew away. The Nitsch's deterred eagle attacks by firing a starter pistol when eagles approached.

Edgewater Colony

Mark (1976) recorded this colony as present in 1974. Mrs. M. Pastrick (pers. comm.) indicated that the colony was occupied from 1975 to 1976 and was visited regularly by the Langley Naturalists Club. Many crows (Corvus caurinus) were present in this colony at each visit. The shells of several eggs, apparently eaten by crows, were found in April of both 1977 and 1978.

Gibson's Colony

The colony was situated about 200 meters from a proposed sawmill site. The mill site was cleared to the outermost nest and extensive excavating began in 1978 and continued in 1979. The colony was occupied in April 1978 and again in May 1979 but was abandoned in both years. Many crows were seen in this colony. Eggs laid in 1978 were eaten on the nest platforms probably after the adults left, judging by the shells found on the nests. A possible previous nest site nearer the Gibson's town site was not reoccupied during this time. Two nests were

occupied and successful in 1980, indicating that more herons may return to this site in the future.

Haney Colony

Mark (1976) reported that this colony was first formed in 1974. It was also active from 1975 to 1976, according to U.B.C. Research Forest staff. Accurate nest and fledgling counts in this colony are impossible due to the dense coniferous foliage surrounding the nests.

A red-tailed hawk (Buteo jamaicensis) buzzed the colony in April 1977, and visitors reported that eagles harassed the colony. I found a decapitated young heron under the nests in June 1977, confirming predation by eagles or owls.

McGillivray Colony

The McGillivray colony was present since at least 1974 (Mark 1976). Local naturalists indicated that it was active until 1977, although no systematic records were kept. On March 10, 1977, 46 nests were occupied, although I described the birds' behavior as "very spooky and easily disturbed." Many nests were abandoned by May 6 and most (43) by May 18, 1977. An occupied eagles' nest was found 200 meters east of the colony in April 1978. The colony was not reoccupied in 1978 or 1979.

McIvor Colony

The McIvor colony could be one of several referred to by Mark (1976) in the Pitt Meadows area. Residents said it had been at this location since 1970 and averaged 10 nests a year.

Eagles frequently harassed the nests but no young were seen taken. At least five young fell from the nests in 1977. The nest tree was three meters from a private residence built in 1976.

Pender Harbour Colony

The Pender Harbour heronry was found on a property being subdivided for residential lots 200 meters south of Gunboat Bay. The colony had been at that location since at least 1963 when it was estimated to contain 75 nests (A. Joss, pers. comm.). It contained 43 occupied nests in 1978 and 45 occupied nests in 1979.

The colony was bounded on the east and north by subdivision lots and a new access road respectively, while the southernmost nests were exposed to view from Highway 101 by removal of the trees. The subdivision work began in the summer of 1977 and continued through the spring and summer of 1978. Extensive excavating and some blasting were required to install water mains in April and May and two water wells were drilled in June 1978. The work was completed in the spring of 1979 and there was no further road work or house construction after April of 1979. During the construction work in 1978, adult herons were frequently frightened from their nests.

I observed eagles taking young herons from their nests with adults present on two occasions in 1978 and three other eagle attacks were reported (M. Wise, pers. comm.). Ravens (Corvus corax) were commonly present in the colony and I

observed them taking six young from unprotected nests in 1978 and 1979. Ravens pulled young herons from their nests, in the absence of adults, and ate them on the ground. I found 14 eviscerated young on the ground in 1978. I also found evidence of three adult kills (feathers) including one banded adult (A83) in 1978. Eagles nesting in a large fir overlooking the colony appeared to use the herons as a convenient food supply. I found heron bones and feathers under the eagles' nest in 1978. Eagles did not nest there in 1979 but returned in 1980 when the heronry was abandoned.

In 1979 a total of 12 pairs, which attempted nesting, failed to fledge any young. Three nests were occupied by adults and abandoned prior to egg laying. Four other nests contained small young, judging by shells found on the ground, but the young were lost and the nests abandoned shortly after hatching. In such cases it is impossible to tell if loss of the young is the cause or the result of the abandonment. Two nests, each containing three large young, were robbed, probably by raccoons (Procyon lotor), between June 17 and 24. The nests were covered with feathers and chewed bones and raccoon tracks were found on the ground under the nests. I found four dead young under two other empty nests from which ravens had attempted to pull young on earlier dates. In one other nest three large young disappeared between June 20 and 24 prior to first fledging. I suspected eagles but no eagle attacks were observed in 1979.

Adult herons in the Pender Harbour area were banded in 1978 and 1979 at feeding areas. Many of the banded birds were observed in the colony (see Chapter II).

Point Roberts Colony

A colony of 165 nests (1948) and 185 nests (1949) was originally located near Raitt Road in Delta Municipality and was displaced a short distance by power line clearing (E. Taylor, pers. comm.). In 1959 a 100-nest colony in the same area was destroyed by clearing of the cottonwood and alder nest trees for a residential development (Mark 1974). Another colony of unknown size in south Point Roberts was recorded as destroyed by development about 1970 (Mark 1974). In 1973 a colony of 30 nests was located off Churchill Road just south of the Canada-U.S.A. boundary (Mark 1974). The Point Roberts colony containing over 200 nests (Table 1-1) was at this location from 1977 to 1980. If the nest counts from previous years are correct, it is likely that the colony split up from 1958 to 1973 and has recently re-congregated at the Churchill Road location. I believe that all the herons nesting in South Delta-Point Roberts are now at the one large colony.

Judging from tracks, domestic dogs and cats frequently visited the heronry. Some trees near the edge of the colony were felled by woodcutters and two nest trees had been chopped but not felled, probably by children playing with an axe.

Powell River Colony

The Powell River colony was located in a dense forest of immature Douglas fir and western hemlock behind Abbotsford Street Elementary School in 1978 and contained six nests (Table 1-1). Three former nesting sites were located, including one which contained 16 nests in 1974 (C. Burton, pers. comm.). Dense second growth forest in the Powell River area and limited access prevented location of other active heronries. The colony contained 19 active nests in 1980 (Table 1-1).

Salwein Colony

The Salwein colony was located in large cottonwoods about 100 meters from the Canadian Forces wet bridging practice area (Fig. 1-1). The area is a site of frequent mock combat maneuvers. The colony was first recorded in the B.C. Nest Record Scheme in 1976 and had an estimated 50 nests. The increased size in 1977 to 96 nests (Table 1-1) coincided with the abandonment of the McGillivray colony about eight kilometers away. I believe that many of the McGillivray herons shifted to the Salwein colony in the spring of 1977.

A pair of great horned owls nested in the colony in 1979. A red-tailed hawk harassed the herons in April and May 1977. Five dead and one live young were found on the ground on May 30, 1978.

Sechelt Colony

I located the Sechelt colony in March 1978 about 1.5 kilometers north-west of Porpoise Bay. The history of the

colony is unknown, but other reported locations include Four Mile Point on the north shore of Porpoise Bay, and Sechelt Marsh at the head of the bay. Dense undergrowth in the logging slash through which the colony is reached makes access difficult so it is unlikely that the colony suffers any direct disturbance from people.

I found six dead young on the ground and saw three others hanging from nests in 1978. All of the dead birds were intact. No crows were observed in the colony but I saw a red-tailed hawk harassing adults on two of the four visits in 1978. In 1979 I recorded two nest failures at Sechelt. No dead young were found under those nests although, under other trees, six dead young were found, of which one had been eaten.

Stanley Park Colony

There has been a heron colony in Stanley Park since at least 1921 when 39 nests were recorded at Brockton Point. Table 1-4 shows the locations and numbers of nests in the colony from 1921 to 1980. The exact date of the move from Brockton Point to the zoo area could not be determined. A newspaper article in 1928 stated that the dead spruce tree at Brockton Point, where the birds nested, was to be removed. A photograph of the tree showed 27 nests and 81 young during the "last" nesting season. It is probable that the colony has moved at least twice since 1921. The nest count in 1977 was probably an underestimate since I did not check other trees in the vicinity of the two large firs used that year.

Table 1-4. Size and locations of the Stanley Park colony from 1921 to 1980.

Date	Successful nests	Location	Source
1921	39	Brockton Point	Mark (1976)
1923	23	Brockton Point	Mark (1976)
1928	27	Brockton Point	Vancouver Sunday Province June 17, 1928
1959	25	Brockton Point	Mark (1976)
1961	25+	Exact location not specified	Mark (1976)
1966	28	Exact location not specified	Mark (1976)
1967	40	Exact location not specified	Mark (1976)
1968	25	Exact location not specified	Mark (1976)
1969	Active	Exact location not specified	Mark (1976)
1970	40	Exact location not specified	Mark (1976)
1971	30	Zoo area	Paine (1976)
1974	21	Zoo area	Mark (1976)
1977	19	Zoo area	Simpson and Kelsall (1977)
1978	43*	Zoo area	
1979	38	Zoo area	
1980	33	Zoo area	

* Twenty-nine nests in the two Douglas firs and 14 nests located in hemlock and cedar around the aquarium.

This colony is unique in that it is in the center of a very high use recreation area and the nests are readily visible from the ground. The herons are apparently undisturbed by human activities on the ground. No avian predators or scavengers were observed at this colony although eagles, ravens and crows are present in the park.

U.B.C. Colony

A colony of 40 nests was reported on the north shore of Sea Island in 1941 and remained active until 1949. It was destroyed by airport expansion about 1950 (Mark 1976). The birds of that colony probably moved to the U.B.C. colony (Fig. 1-1). The U.B.C. colony was first enumerated in 1970 when it contained 125 nests.

In December 1970 a blind was built on the periphery of the colony for use in the summer of 1971 (Paine 1972). Occupancy of that blind resulted in the immediate abandonment of the three closest nests. The main group of birds returned to the colony one month late. Incubation, which began in early May, and the first nestling, observed on May 20, were equally late. During 1971 the colony contained about 55 nests, with another 20 located 200 meters north of the main colony. The "satellite" contained poor quality nests, and was an additional three weeks later than the main colony. The nest count was approximately 75, 50 less than in 1970 (Campbell et al. 1973). In 1972 the main colony was abandoned and the "satellite" contained 22 nests. No other nests were found and the decline was thought to be caused by "...losses to the

breeding population due to severe winters," (J. Krebs In: Campbell et al. 1974, p. 22).

In 1971, 106 of 176 young were banded (Campbell et al. 1973). In 1972, 57 of 62 young were banded. Those efforts would have involved climbing almost every tree in the colony and required several days of continuous disturbance each year. In 1973 and 1974 the research activity stopped, and the colony was recorded as being active with no nest counts (Mark 1974).

In 1977 there were 70 nests in the satellite colony while the main colony remained abandoned. A check on late nesting on July 19 revealed 12 additional nests approximately 100 meters northwest of the colony (Area A). The presence of loudly-calling unfledged young attracted attention to that location, and indicated that the group bred about three weeks later than the satellite colony, which had few unfledged young.

In April of 1978 the satellite colony had increased by 41 nests over the 1977 count. There were 19 inactive nest sites in Area A and another separate group (Area B) containing 24 nests, also inactive. If the majority of those 43 alternate nests had been active in 1977, then the observed increase in nests in 1978 can be explained simply by a shift of the peripheral birds back to one large colony.

It seems likely that the observed decreases in 1971 and 1972 were related to herons abandoning disturbed sites and relocating elsewhere in undiscovered sites. In 1979 all old locations of this colony were completely abandoned and a new and larger colony of 118 nests was formed about three

kilometers to the east. All the newly constructed nests were occupied in June 1979.

Four dead young were found on the ground and six dead young were seen on nests in 1978. I saw a raccoon eating a young heron on the ground in 1978 and raccoon tracks were common under the heronry. An eagle flew over the colony during one visit, but did not cause adults to leave their nests.

Reactions to Human Disturbance

In two colonies located within 20 meters of private residences (Crescent and McIvor), and one located in a highly developed park (Stanley Park), the herons were completely unconcerned during observational visits. In six other lower mainland colonies, which were surrounded by forest but close to populated areas, herons reacted to researchers by calling, raising feathers and standing but remained on or near their nests. At both Pender Harbour (April 1978) and McGillivray (March 1977) most birds fled as the colonies were approached.

When nest trees were climbed, birds flew from that tree and also from nearby trees. Most birds circled the colony giving continuous, loud calls when disturbed. However, on one occasion an adult bird actively defended its nest against the climber by physically blocking his path, striking at him and flaring its wings.

Reproductive Success

I measured reproductive success at most colonies from 1977 to 1980 by calculating the mean number of young fledged per

successful nest (MYSN) (Fig. 1-2). I compared MYSN between colonies and between years for the five lower mainland colonies, for which I had fledging estimates each year, by analysis of variance. There were no significant differences between years or between colonies. I compared MYSN between all colonies in 1978 and 1979 by analysis of variance. There were no differences between colonies in 1979 and few differences in 1978. The Pender Harbour and McIvor colonies had lower MYSN than the U.B.C. and Crescent colonies in 1978 ($p < .05$, Duncan's Multiple Range Test).

I followed the fate of individual nest platforms in eight colonies in 1978 and two in 1979. Although the status of some platforms was undetermined during each survey, minimum numbers of nests abandoned and newly occupied or constructed between surveys were obtained (Table 1-5). At most colonies, the number of additions exceeded the number abandoned over the nesting season. At Pender Harbour and U.B.C. the number of nests abandoned exceeded the number newly occupied, a significant difference from the combined proportion of other colonies (Table 1-5, $\chi^2 = 13.3$, 3 df, $p < .01$). Both of these colonies were completely abandoned the next year. Using abandonment data I was able to determine the number of breeding pairs, both successful and unsuccessful, and calculated the mean number of young fledged per breeding pair (MYBP) (Table 1-6). MYSN was significantly greater than MYBP ($t = 3.88$, 9 df, $p < .01$) by 15% on average and by up to 50% in cases where nest abandonment was high.

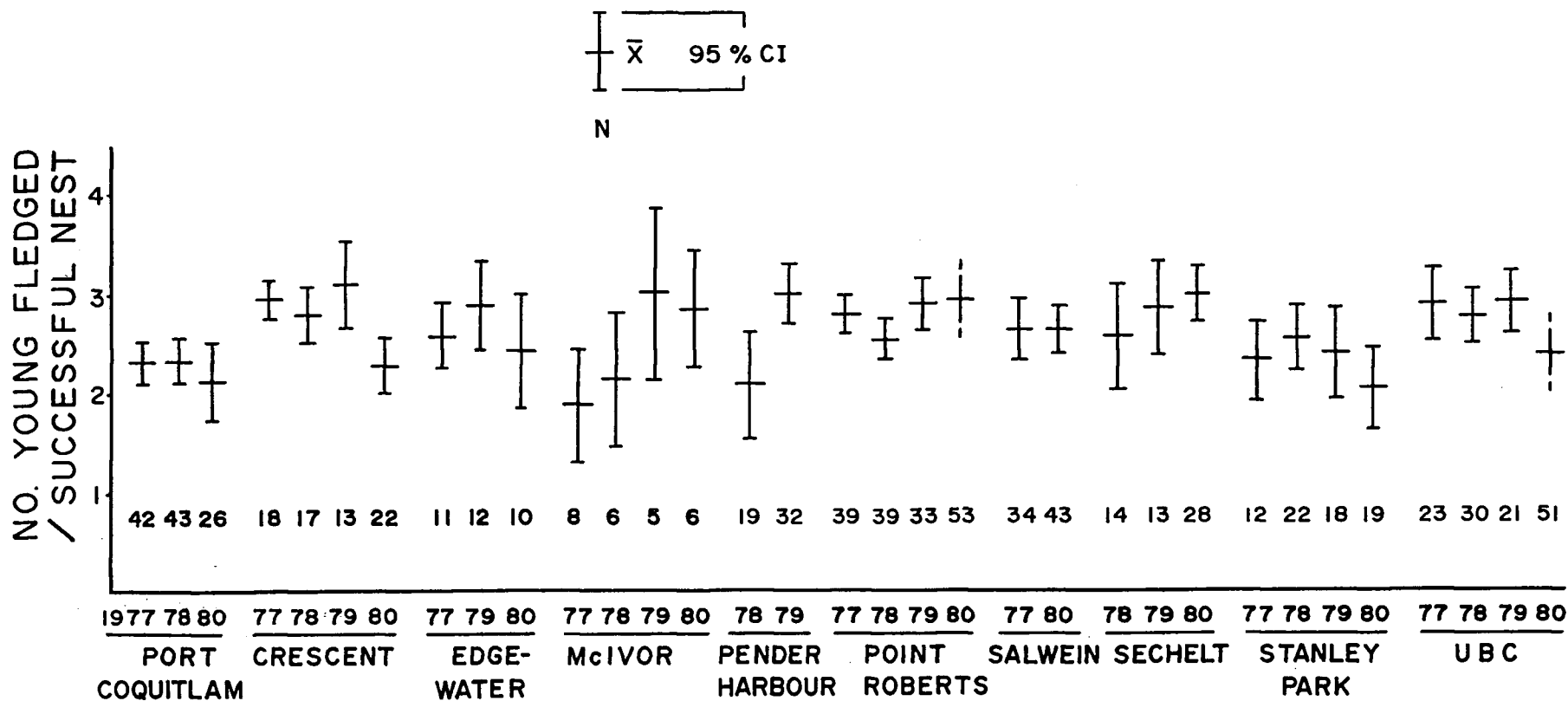


FIG. 1-2 Mean numbers of young fledged per successful nest at 10 heronries from 1977 to 1980.

Table 1-5. Number of nests abandoned and newly-occupied between survey dates at eight colonies in 1978 and two in 1979.

Colony	Time period	No. occupied in Mar/Apr	No. abandoned or fallen by Jun/Jly	No. newly occupied or constructed Mar-Jly	No. successful nests
Coquitlam ¹	Apr 7-Jun 27	141	9	30	162
Crescent	Apr 21-Jun 29	39	5	12	46
McIvor	Apr 12-Jun 27	9	1	0	8
Pender Harbour	Apr 30-Jly 17, 78	33	14	6	25
	Mar 31-Jly 13, 79	44	12	1	33
Point Roberts ²	Apr 21-Jun 29	221	21	40	240
Sechelt	Apr 19-Jly 17, 78	24	2	6	28
	Mar 27-Jly 14, 79	31	2	7	36
Stanley Park	Apr 5-Jun 28	43	1	1	43
U.B.C.	Apr 11-Jun 30	107	19	15	103

1. Estimated from 17-tree sample.

2. Estimated from 40-tree sample.

Table 1-6. Mean numbers of young fledged per successful nest and per breeding pair at eight colonies in 1978 and two in 1979.

Colony	Mean young fledged/ successful nest (MYSN)	Mean young fledged/ breeding pair (MYBP)	% difference
Coquitlam	2.3	2.2	4.5
Crescent	2.8	2.5	12.0
McIvor	2.1	1.9	10.5
Pender Harbour 1978	2.1	1.4	50.0
1979	3.0	2.2	36.4
Point Roberts	2.5	2.3	8.7
Sechelt 1978	2.6	2.4	8.3
1979	2.8	2.6	7.7
Stanley Park	2.6	2.6	0.0
U.B.C.	2.8	2.4	16.7
Mean (unweighted)	2.56	2.25	15.5

At most colonies the number of occupied nests and the percent of the total platforms occupied did not fluctuate much over the breeding season (Table 1-7). To determine the number of nests abandoned, each nest must be labelled and rechecked on subsequent visits. Counts of nests do not provide abandonment data because nest additions between surveys compensate for nest losses (Table 1-5). Labelling individual nests and repeated surveys are time consuming and may cause nesting disruptions and losses in colonies unaccustomed to human intrusions. I found that the number of nests abandoned and, thereby, the total number of breeding pairs at each colony, could be estimated using the percentage of platform^s occupied at fledging (Fig. 1-3). As the percentage of nests abandoned increased, the proportion of platforms occupied at fledging decreased, despite the confounding effect of nest additions.

DISCUSSION

Colony Sizes

The absence of nine previously reported colonies and the suspected amalgamation of the Newberry-Coquitlam and McGillivray-Salwein colonies suggest that the recent increase in sizes of existing heronries (Table 1-2) has resulted from the amalgamation of smaller colonies. Frequent reference to clearing for developments and power lines suggests that urban expansion and loss of forested nesting habitat is likely responsible for concentrating herons in fewer and larger breeding colonies.

Table 1-7. Number and % of nest platforms occupied during the breeding season at eight heronries.

Time period	<u>Coquit-</u> <u>lam¹</u>		<u>Crescent</u>		<u>McIvor</u>		<u>Pender</u> <u>Harbour</u>		<u>Point</u> <u>Roberts²</u>		<u>Sechelt</u>		<u>Stanley</u> <u>Park³</u>		<u>U.B.C.</u>	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Incubating April 1978	68	91			9	90	39	42	47	98	24	73	30	100	111	85
Young present May-June 1978			37 ⁴	95	8	80	43	46			28	88	31	100		
Fledging June-July 1978	78	94	46	87	8	80	25	27	51	91	28	88	30	97	103	77
July 1979							33	35			36	95				

1. 17-tree sample.

2. 40-tree sample.

3. Nests in two large Douglas firs only.

4. Sample of nests examined by a tree climber in 1977.

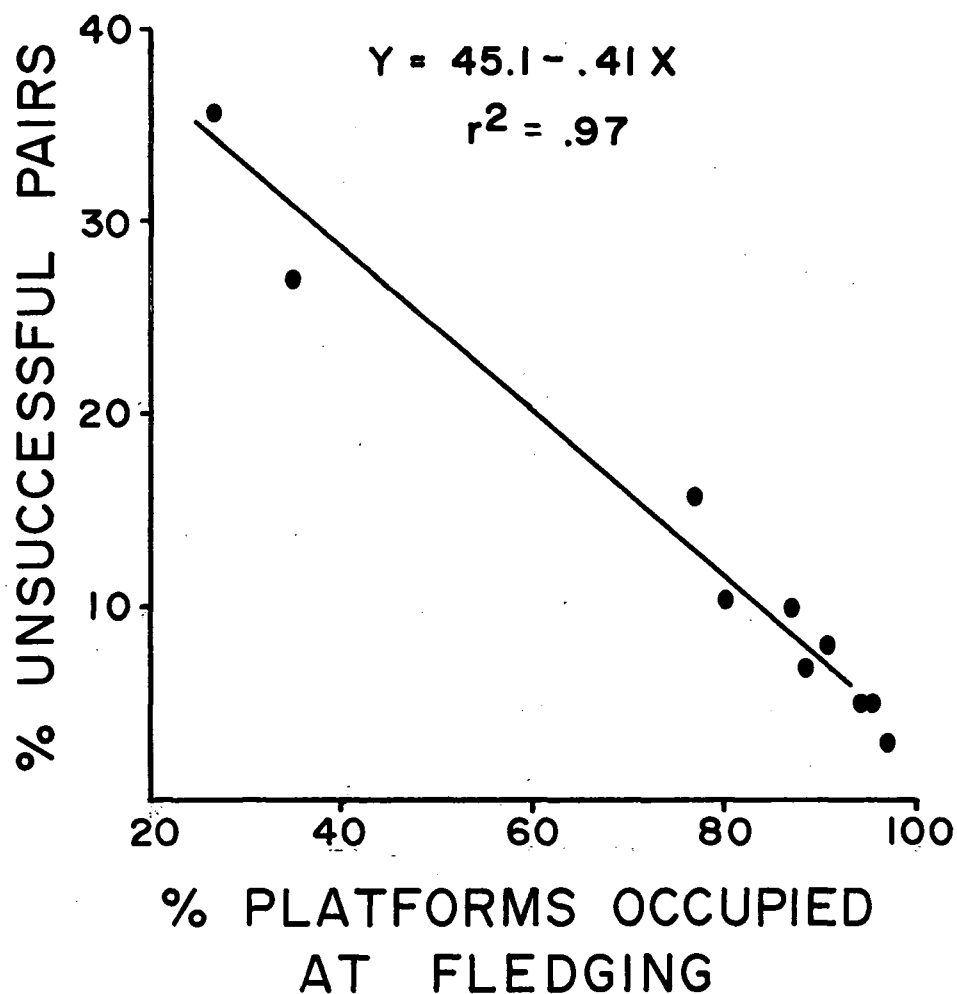


FIG. 1-3 The relationship between the percentage of nest platforms occupied at fledging and the percentage of unsuccessful pairs at eight colonies in 1978 and two in 1979.

Data for nine colonies in the lower mainland from 1977 to 1979 showed that the smallest decreased in size from eight nests to five, one decreased due to abandonment of its original site, one remained static and the other six increased in size from nine to 138%. In 1980, most colonies showed slight declines, ranging from six to 17% (Table 1-1). These fluctuations can best be understood by considering the circumstances and history of each colony.

The increase in the U.B.C. colony in 1978 was probably the result of the return of adults from alternate nesting sites to one central nesting area. In 1979 the entire colony relocated and contained 118 active nests. In 1980 it increased to 130 nests, five more than the previous high count of 125 nests in 1970. The same phenomenon may be responsible for changes at the Crescent colony. Complete abandonment in 1972 and 1973 suggests that the colony has some undiscovered alternate nesting site. Interchange between sites could account for year-to-year variations in numbers of occupied nests, independent of actual changes of population. The large increase in size of the Stanley Park colony from 19 to 43 nests indicates again the apparent mobility of great blue herons in choosing nest sites. Based on previous years' data (Table 1-4), 38 nests is not unusually large for the Stanley Park colony. The low nest counts of 1971, 1974 and 1977 could well be the result of failure to locate other nests in the general area.

Colonies in the Sunshine Coast area have shown similar fluctuations. Successful nests at Pender Harbour and Sechelt

increased by almost one-third from 1978 to 1979 (Table 1-1), although historical data indicated that the Pender Harbour colony may have been larger previous to the subdivision development there. In 1980 the Pender Harbour colony was completely abandoned while the Sechelt colony remained stable and the small Powell River colony tripled in size (Table 1-1). The Coquitlam colony dropped from 162 nests in 1978 to 31 nests in 1979. Such massive changes in colony size from year to year cannot be explained in terms of adult mortality or recruitment. The death of 260 adult herons in Coquitlam could scarcely have gone unnoticed.

The abandonment of the McGillivray colony and the concurrent increase at the Salwein colony lends further support to the idea of the adult movement between colonies. It may be inferred that, although herons prefer to nest in groups, the presence of one group does not preclude the existence of others in the same locality. In fact, the presence of one concentration is often associated with one or more alternate sites among which breeding adults may relocate from year to year.

Reactions to Human Disturbance

Marked differences were noted in the response of herons in some colonies to the presence of people. These ranged from no reaction, to standing and calling, to taking flight. Those varied reactions to the same stimulus imply that herons have different tolerance levels to humans in different locales.

In general, colonies located close to areas of human activity showed less response than those in more remote areas.

Some individuals within colonies were also more tolerant or less afraid than others. I believe that many of the herons at Pender Harbour which successfully raised young in 1978 did so because they remained on their nests despite the disturbance from construction nearby.

Nesting herons could benefit from a close association with people if predators are less tolerant of humans. The deterrence of eagle attacks by landowners probably reduced predation at the Crescent colony. The presence of people and residences near other colonies may have inhibited the activity of some predators. The scarcity of predators at Stanley Park may result from intense human activity.

Predation

I observed avian or terrestrial predators in every heron colony except Stanley Park. I recorded eagle or owl nests at five colonies, eagle or hawk harassment at seven, crows or ravens at seven and mammalian carnivores at three. Predators are probably attracted to heronries because of the young and eggs in the nests and by the food items and young falling from the nests.

I believe that predation was a significant cause of nest failure at some heron colonies, especially at Pender Harbour. Fourteen eviscerated young found at Pender Harbour in 1978 were probably killed by ravens. Seven intact young found at

Sechelt probably fell accidentally from their nests since they were not eaten. My other observations implicated predators in five of 12 nest failures at Pender Harbour in 1979. Heavy losses to predation at Pender Harbour were probably predisposed by the frequent absence of adult herons from the nests which, in turn, was caused by the construction work nearby. Predators apparently became accustomed to the readily available food supply afforded by unprotected nests. The eagle attacks witnessed occurred with adults in attendance at the nests, however, indicating that any inhibition that may be provided normally by adults, was not operating. The loss of three adults further reinforces that conclusion. Other studies have indicated that complete nest losses are probably caused by predators (Dusi and Dusi 1968, Pratt 1972). I concluded that predators were unusually successful in the Pender Harbour colony and were persistent at vulnerable nests until all young were removed.

Many observations have been made on the interactions of avian and other predators with herons and heron colonies. Occupancy of heron nests by predatory birds has been cited as the cause of colony abandonments both in this study (Chehalis, Crescent, Coquitlam and McGillivray colonies) and others (Mark 1976, Vermeer 1973). In contrast, great horned owls and bald eagles have been recorded as nesting in or near 10 different heronries without causing abandonment (Vermeer 1972 and 1973, Bayer 1979, Koonz 1980). The Salwein colony had a pair of great horned owls nesting in one of the "heron" nests but

that colony had a successful nesting season in 1979. Eagles nesting near the Pender Harbour colony in 1978 did not cause herons to abandon nesting.

The variation in the effects of predators on nesting success may be due to differences in the relationships of the species in different areas. Both owls and eagles have been reported to prey upon or harass adult and nestling herons (Bayer 1979, Werschkul 1979, Krebs 1974). Crows, ravens and turkey vultures (Cathartes aura) also prey on young herons (Taylor and Michael 1971, Temple 1969, Dusi and Dusi 1968), but have never been suspected of causing colony abandonment. It may be that the intensity of predator interactions determines the response of a nesting colony. Presumably if predation causes significant losses in reproduction or adult mortality it would be to the advantage of the herons to relocate, provided that predation is reduced at the new location. The abandonment of heronries at U.B.C. in 1979, and Pender Harbour in 1980, suggests that herons move to a new site if nests lost at the old site exceed 15% (Table 1-5) or if the number leaving a colony exceeds the number entering during the breeding season. The reduction of nest losses in the U.B.C. colony, following relocation, may have related to lower predation at the new site.

Observations of eagle-heron interactions in 1980 suggested that herons may show radically different responses to eagles at different locations, possibly related to the level of predation suffered by the herons. Feeding herons at Pender Harbour

rarely allowed an eagle to approach within 100 meters without fleeing, whereas those at Sechelt reacted only by assuming an alert posture even upon the close approach of an eagle (Forbes 1980). Heron responses to eagle harassment similar to those at Pender Harbour are described by Bayer (1979). Eagle predation on both adult and juvenile herons was observed at Pender Harbour but not at Sechelt. Those observations again suggest that herons may alter their response to certain predators as a result of previous experience.

Reproductive Success

Reproductive success was assessed at all colonies using the mean number fledged per successful nest (MYSN). Although the number of young fledged per breeding pair (MYBP) is a better estimate of heron productivity, MYSN has been the standard used in many previous reports (see reviews by Parker 1980, Quinney and Smith 1979). Our fledging rates were similar to the results of others and few differences were found among study colonies using MYSN.

Nest losses were the most important parameter determining the reproductive status of a colony. The effect of the disturbance at Pender Harbour was not reflected by MYSN. Successful pairs raised as many young as adults in undisturbed colonies (Fig. 1-2). Reproductive losses were reflected by increasing the percentage of unsuccessful pairs (Table 1-5). Pender Harbour had proportionately more unsuccessful nests than six other colonies in 1978 (Table 1-5, $\chi^2 = 38.4$, 1 df, $p < .001$). Pender Harbour also had proportionately more nest

failures than the Sechelt colony in 1979 (Table 1-5, $\chi^2 = 6.73$, 1 df, $p < .01$) or the U.B.C. colony in 1978 ($\chi^2 = 7.49$, 1 df, $p < .01$). Those results show that some adults lose all their young under adverse conditions, while others are unaffected. At Pender Harbour in 1978, tolerance of disturbance and tenacity at the nest were probably important factors determining the success or failure of different nesting pairs.

Determining nest abandonment requires repeat inspections of individually labelled platforms at each colony. This is a tedious and time-consuming job and may represent a considerable disturbance to nesting herons in non-urban colonies. The proportion of platforms occupied in each colony can be used to estimate the number of nests abandoned, particularly just prior to fledging when platform occupancy is generally high (Table 1-7). The low platform occupancy at Pender Harbour in 1978 (27%) and 1979 (36%) was probably related to disturbance from work in the adjacent housing development. Nest abandonment decreased platform occupancy while construction of new nests, further from the disturbance than existing platforms, increased the number of apparently suitable nest sites.

Platform occupancy can be used to estimate the number of unsuccessful pairs at each colony and provide a more meaningful index of the population and productivity of herons than MYSN. For example, if surveys had been undertaken for the first time in 1980, low platform occupancy at Gibsons and Coquitlam would have indicated substantial nest abandonment. The relationship between platform occupancy and nests abandoned

(Fig. 1-3) can be used to estimate the number of nest failures at colonies where there is a large proportion of vacant nests. For colony sites which are completely abandoned (e.g. Pender Harbour and U.B.C.) I would expect to find alternate nesting sites.

I tested this relationship using data collected elsewhere by Des Granges and Laporte (1981, 1983) and Parker (1980). I noted that 33 small (<20 nests) colonies frequently had no unsuccessful nests (15) or were completely abandoned (2). I excluded data from these colonies. I approximated nest occupancy at fledging by subtracting unsuccessful nests from the number reported to be occupied in May for each colony. Figure 1-4 shows the relationship obtained using that data and the combined regression line. Analysis of covariance showed that the means of residuals from the combined regression line were the same for all studies. This relationship may be useful in estimating nest failures in heronries in other areas which have low platform occupancy at fledging.

At Pender Harbour and U.B.C., where the numbers of nests abandoned exceeded those of platforms occupied during the breeding season in 1978 or 1979, the colonies were abandoned the following year. I did not collect data on nest abandonments at U.B.C. in 1979 but the 100 percent platform occupancy at fledging suggests that there were few abandonments and MYBP increased at the new location. MYSN did not change following colony shifts at U.B.C., Coquitlam and McGillivray-Salwein (Fig. 1-2). Since the number of young raised per successful

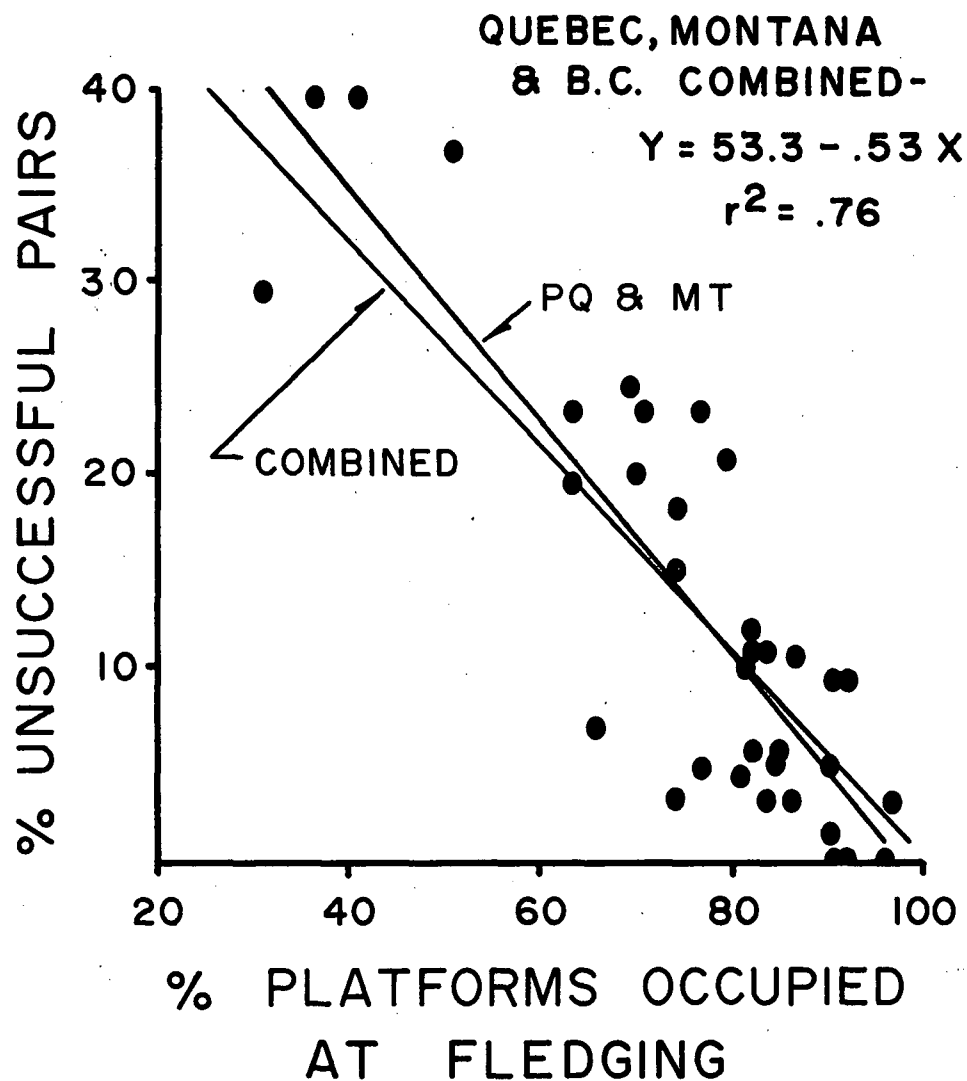


FIG. 1-4 The relationship between the percentage of nest platforms occupied at fledging and the percentage of unsuccessful pairs at colonies in Quebec and Montana.

Note: Data from DesGranges 1981 and 1983 and Parker 1980.

nest does not change when heronries are severely disturbed or relocate, it is probably a poor indicator of reproductive success. Numbers of successful and abandoned nests, which can be estimated using percent platform occupancy at fledging, more accurately represent the reproductive success of heronries.

CONCLUSIONS

Frequent heronry abandonments, changes in size, and relocations have resulted in concentrating herons into larger colonies at fewer locations than were historically present in the lower mainland. Many of these changes may have been caused by urban development. Sudden large changes in colony sizes between years probably result from movement of adults between colonies. The frequent, and in some cases apparently unprovoked, movements of heron colonies suggest that such occurrences may represent a normal part of a heron's life cycle.

Human disturbance at colonies unaccustomed to people increases predation, since adults are easily frightened from their nests. Heronries which have adapted to human activity suffer less predation since birds do not readily flush from their nests, and predators may be inhibited by human activities. Some nest predation occurs in most heronries, but disturbances which frighten adults from their nests increase losses of eggs and young and reduce the number of successful nests. Heavy predation continued at one colony after a construction disturbance stopped. Responses of herons to predators varied

in relation to the severity of predation. When large numbers of young or adults are lost, heronries relocate.

The number of young fledged per successful pair is an insensitive measure of reproductive success. It did not vary between colonies even when a colony was severely disturbed. Disturbance affected reproduction by increasing the number of unsuccessful pairs. The number of unsuccessful pairs cannot be estimated by nest counts at two periods because nest additions usually exceed nest losses within a colony. To avoid the need to label individual nests and do repeat counts, the percent of nests abandoned can be estimated from the percent of platforms occupied at fledging. This method is applicable in other areas, at least for larger heronries (>20 nests). Nest losses, which can be estimated using platform occupancy at fledging, are more important than the numbers of young fledged per successful pair in assessing heron reproductive success and population status.

CHAPTER II

Movements, Behavior and Breeding Success
of Banded Herons at Pender Harbour

INTRODUCTION

Results in Chapter I showed that characteristics of breeding birds, such as nest tenacity, were important to reproductive success. Studies of another colonial bird have shown that selecting the same colony, mate and nest site each year is associated with increased breeding success (Coulson and Thomas 1983). Other characteristics of parents, such as feeding areas used, feeding success and social dominance, might also influence reproduction, but no information exists for herons because individuals have not previously been reliably identified in colonies or on feeding areas (Quinney and Smith 1979, Mock 1976, McAloney 1973, Pratt 1972 and 1970, Henny and Bethers 1971). Marked birds would also confirm the movements of herons between colonies, for which there is considerable circumstantial evidence (Chapter I).

One of the principal theories attempting to explain colonial nesting suggests that colonies act as information centers for food finding (Custer and Osborn 1978, Ward and Zahavi 1973). This theory proposes that adjacent individuals within colonies follow each other to good feeding sites. Krebs (1974) and Des Granges (1978) showed that arrival and departure frequencies and flight directions of herons at colonies were significantly clumped, suggesting that birds were travelling together to and from feeding areas. More recent studies, based on the movements of adults to and from heronries, have shown that many herons have predetermined feeding areas or join aggregations of feeding birds adjacent to the

colony (Pratt 1980) and that departure and arrival clumping is related to the time of low tide (Bayer 1981). The lack of identifiable individuals within heronries has prevented the direct testing of the information exchange hypothesis.

More general studies have related feeding sites to heron colony locations. Most larger heronries are located within 10 kilometers of productive marshland or tidal feeding areas, and most breeding herons have relatively predictable feeding areas (Thompson 1979a, Werschkul et al. 1977, Vermeer 1973). Some breeding herons, however, do not use the closest feeding areas and travel much further to feed (Parris and Grau 1979, Thompson 1979b). Some researchers have observed that many great blue herons have feeding sites which they frequent and sometimes defend (Pratt 1980, Piefer 1979, Hedeem 1967). Feeding territory defence is most pronounced in winter when herons have dispersed from the breeding colonies and exclusive territories are large and obvious. In contrast, the large feeding flocks, observed in summer, suggest that herons are not territorial. Some reports suggest that communal feeding occurs at seasonal prey concentrations and tidal habitats which, because of their limited availability, are not worth defending (Bayer 1978, Stingle 1978). Bayer (1978) also suggested that the greater mortality for young herons over winter (Henny 1972) may result from their exclusion from winter feeding areas by more dominant territorial adults. Although feeding area information exchange could potentially be useful to colonial birds, the

need for such a mechanism among herons, many of which have specific feeding sites or territories, is questionable.

In order to obtain information on mate selection, feeding areas and movements, I banded 60 percent of the adult herons at the Pender Harbour colony (Simpson and Kelsall 1979).

I compared the reproductive success of banded individuals to their feeding success; feeding, mate and nest site selection; movements; and social dominance. Using data from banded birds I was able to assess the results and conclusions of others who have used less direct methods to study great blue herons.

METHODS

Adult herons were captured in net-covered box traps located on top of the bait tanks at three sites in Pender Harbour (Simpson and Kelsall 1979) (Fig. 2-1). Each bird was marked with a number-coded red plastic leg band (Sladen 1978) and a conventional aluminum band on the left ankle. The numbered leg band allowed positive identification of individuals at distances up to 200 meters. The sex of each banded heron was determined from morphological characteristics (Appendix I). Banded birds were identified in the nesting colony, on two tidal feeding areas and at three trap sites within Pender Harbour (Fig. 2-1) during the summers of 1978, 1979 and 1980 (Kelsall and Simpson 1980). Sightings and recoveries of dead birds within Pender Harbour and from surrounding areas were also recorded. Most

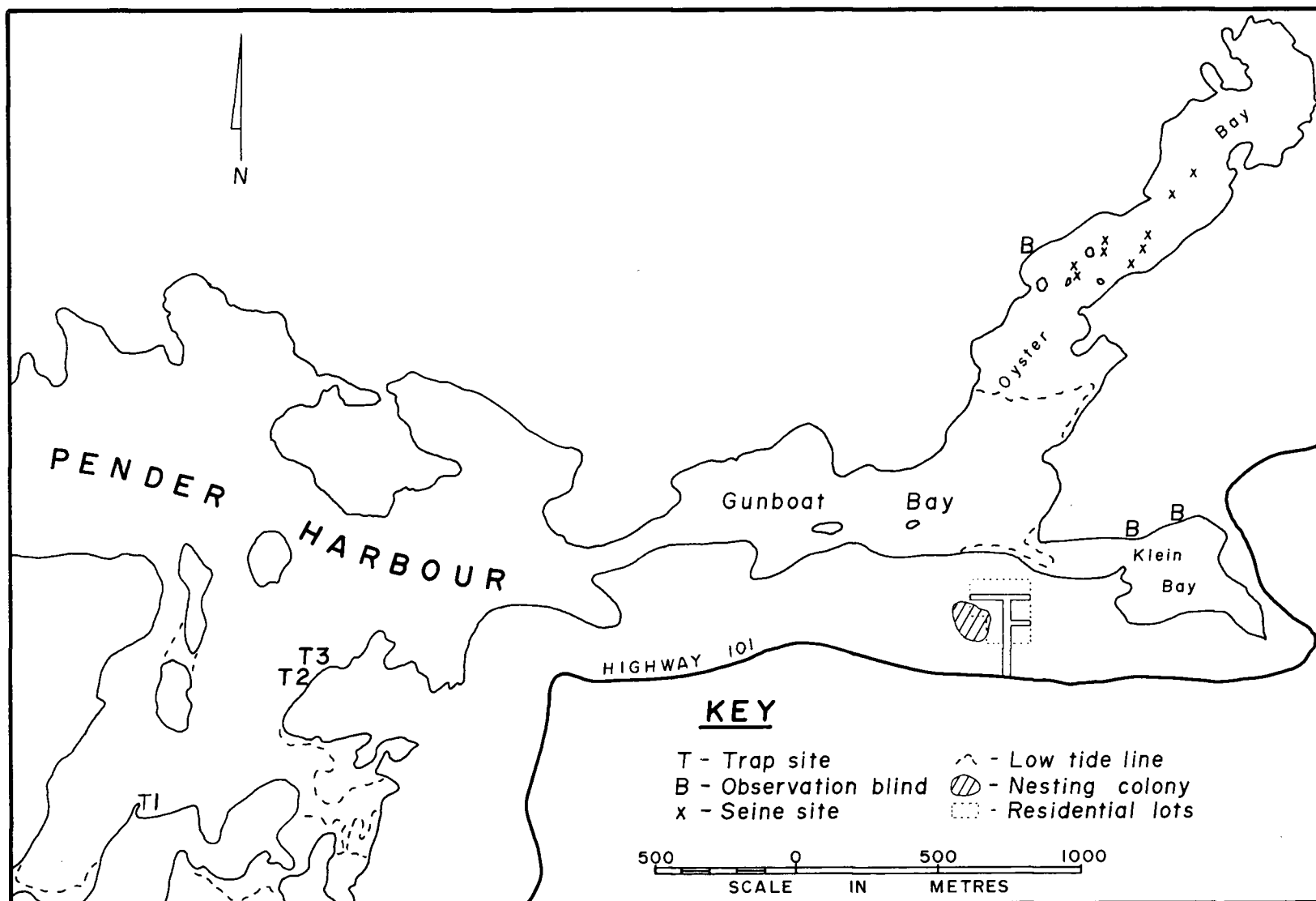


FIG. 2-1 Locations of traps, observation blinds and seining sites at Pender Harbour.

sightings were at the bait tanks and tidal feeding areas during May, June and July 1979.

I defined a nest platform as an occupied nest or a structure which had obviously been a nest in the past. The locations of platforms in the colony were plotted by measuring the distances and taking compass bearings between litter and dropping marks under each. All trees containing platforms were numbered and the band numbers of herons occupying each nest recorded in 1978 and 1979. The geometric center of the colony was determined by taking the mean X-coordinate and mean Y-coordinate of occupied platforms in each year. The distance of each platform from the colony center was then calculated for 1978 and 1979 by simple algebra.

In 1979 I visually subdivided the colony into three sectors--north, east and west. The north sector contained 18 occupied nests and 16 banded birds; the east, 15 nests and 15 banded birds; and the west, 12 nests and 13 banded birds. Each banded bird seen in the colony was then related to a nest site, a nest distance from center measure and a sector within which its nearest neighbors were located.

Feeding rates of herons on two tidal feeding areas were determined using telescopes from blinds located on the shore from April to August 1979 (Fig. 2-1). Observers recorded the size and species of each prey item during manipulation by herons prior to swallowing. The length of each item was estimated by comparison with the bill length of the heron (Krebs 1974). I established the weight-length relationship for each

prey species by measuring fish captured using a beach seine in Oyster Bay. The biomass caught by herons during each 10-minute observation period was estimated by converting each fish-length to a weight and summing all weights. Eleven replicate trials showed that biomass estimates did not differ significantly for three different observers concurrently recording information on the same heron ($F_{2, 30} = .076$, $p > .92$). The average weight of prey caught over several trials was used for comparison of individuals and groups of individuals using analysis of variance. Other factors thought to affect feeding rate were also recorded for each 10-minute trial, including tide direction and level, substrate, water depth and date.

I also observed herons feeding at night on bait tanks from April to July 1979. Most bait tanks had overhead lighting, and this was supplemented by spotlights mounted at leg level to make band numbers readable. Size estimates of herring caught were unreliable because all herring were longer than a heron's bill. I estimated the total weight of fish caught in 10 minutes by multiplying the number caught by the mean weight of samples of fish taken from the bait tanks in April and July.

I established nine seine sites in Oyster Bay in March 1979 (Fig. 2-1). Six of those sites were used consistently from March through September. Wooden stakes were used as markers and as anchors for the net during seining. Each site was seined on the ebb and flood tide for at least three consecutive

days each month. The number and species of fish captured at each site were recorded. Specimens were taken to confirm identification of each species and a sample of each species was weighed and measured to determine their mean weight and length each month. The change in prey biomass per month was estimated by adding the total weight caught for each species (number caught x mean weight) for all seine sites. Prey abundance was then expressed as a mean weight caught per set each month.

The dominance and aggressiveness of some banded herons were determined by recording interactions between herons on feeding areas. The retreating bird was deemed the loser. In cases where there was no clear winner the interaction was called a tie. Herons with the greatest proportion of wins were given the highest rank for dominance; those with the greatest number of interactions were given the highest rank for interactions.

For most banded herons the number of young fledged was determined by counts made in the colony. I had reproductive information for both 1978 and 1979 for 14 banded herons. Reproductive data from 1979 was used for comparison with colony, sighting, feeding rate and social interaction data, most of which was also collected in 1979.

RESULTS

Capture and Banding

We captured a total of 79 different herons--68 in 1978 (Simpson and Kelsall 1979) and 11 in 1979. During June 1979 an average of 14 birds were counted in Oyster Bay and 26 in Klein Bay each day (Fig. 2-1). The proportion of banded herons feeding in those bays was $54 \pm 3\%$ (95% C.I.) in 1978 and $53 \pm 6\%$ in 1979. I estimated that about 125 birds used the Pender Harbour area each year, based on the ratio of banded to unbanded birds. In 1979, counts of the proportion of birds banded were also made in the nesting colony (60%) and on the bait tanks ($62 \pm 11\%$).

Resightings and Movements of Banded Herons

All but three banded birds were resighted at least once. Resightings averaged 21 times per bird with a maximum of 61 sightings. Five banded herons moved the 24 km between Sechelt and Pender Harbour from 1978 to 1980. One individual (band number A84) moved from Pender to Sechelt and back within 13 days while another (A82) moved from Sechelt to Pender to Secret Cove, 11 km south, within 33 days. Two individuals, each sighted 11 times at Pender in June and July 1979, were seen at Sechelt in July 1979 or May 1980. One individual (A43) was never again seen at Pender Harbour (banded in June 1978) but was sighted twice at Sechelt in both 1979 and 1980. Another heron (A48) was seen at Pender Harbour in both 1978 and 1980, but not in 1979. Forty-eight banded herons seen at the Pender Harbour colony in 1978 or 1979 and alive in 1979 averaged 25 sightings each. Eighteen others, not seen at the colony, averaged 12 sightings each. Two of those herons (A94 and A57)

were seen 50 and 42 times respectively and, although they were never identified in the colony, I suspect that they were two of four unidentified banded herons nesting at Pender Harbour in 1979.

Feeding Areas and Nesting Status of Banded Herons

I classified all banded birds as local feeding or distant feeding, based on the number of sightings at Pender Harbour from 1978 to 1980. Herons with 15 or fewer sightings at Pender Harbour were classed as distant feeding (DF) birds and those over 15 as local feeding (LF) (Fig. 2-2). I also classed 48 banded herons seen at the colony in 1978 or 1979 as colony birds, and 18 not seen, as non-colony birds. Overall there were 36 colony LF birds, five non-colony LF birds, 12 colony DF birds and 13 non-colony DF birds (Table 2-1). In 1978, 75% (N = 21) of the colony birds were LF, and 81% were LF (N = 44) in 1979. For both years combined, LF birds had more successful nests than DF birds (Table 2-2), although the difference was not significant for either year alone. DF herons in successful nests raised as many young as LF herons in both years. I examined the sighting records of all unsuccessful DF herons to determine if they were classed as DF birds because they left Pender Harbour or fed less often after losing their young. Only one individual (A55, Table 2-3) had significantly fewer sightings after losing its nestlings compared to sightings for successful DF birds. Most DF herons lost their young late in the nesting season so it is unlikely that they were misclassified.

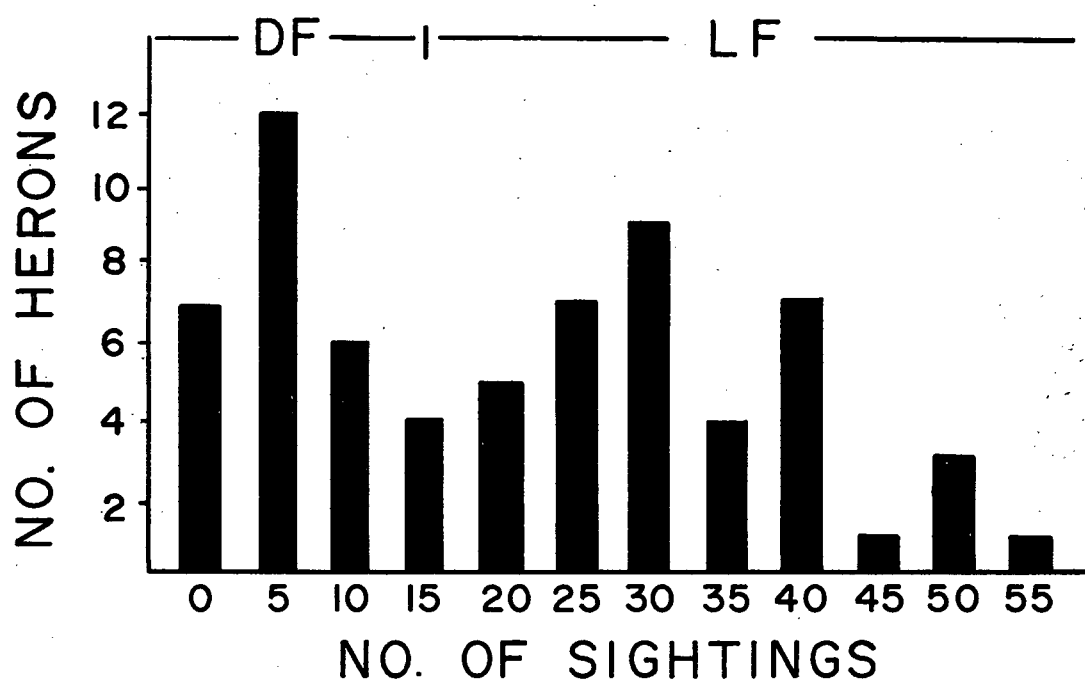


FIG. 2-2 Frequency distribution of the number of sightings of 41 local feeding (LF) and 25 distant feeding (DF) banded herons at Pender Harbour.

Table 2-1. Number of sightings of banded herons at Pender Harbour from 1978 to 1980 categorized by frequency of observation, sighting location and presence in the colony.

	Local feeding (>15 sightings)		Distant feeding (≤15 sightings)	
	Colony (seen at colony)	Non-colony (not at colony)	Colony	Non-colony
No. of banded birds	36	5 ¹	12	13 ²
No. of sightings on tide flats	797	137	37	29
No. of sightings on bait tanks	316	21	38	35

1. Includes A94 and A57 suspected colony birds--see text.

2. Includes five seen at Sechelt and one recovered May 1979 on Texada Island.

Note: With one noted exception includes only birds known to be alive in June 1979 or later and for which feeding status was known.

55

Table 2-2. Comparison of the reproductive success of local feeding (LF) and distant feeding (DF) herons at Pender Harbour in 1978 and 1979.

		No. success- ful	MYSN	SD	No. unsuc- cessful	χ^2	p
1978	LF	13	1.8	.73	2		
	DF	3	2.7	.58	2	1.67	> .10
1979	LF	27	3.0	.76	7		
	DF	3	2.7	.58	5	3.65	> .05
1978 and 1979	LF	40			9		
	DF	6			7	6.75	< .01

Note: Three herons for which LF or DF status was undetermined (A68, A76) or questionable (A55, Table 16), not included.

Table 2-3. Comparison of the number of sightings of distant feeding (DF) herons to determine if unsuccessful birds were seen less often than successful birds after their young were lost.

Bird	Sightings before date young lost	Date young lost	Sightings after date young lost	χ^2	p
A21	0	June 19	3		
SDF	17		14	1.95	< .1
A27	4	June 24	3		
SDF	22		20	0.03	< .8
A38	0	May 20	0		
SDF	5		37	1.89	< .1
A46	5	June 24	0		
SDF	22		20	2.35	< .1
A54	2	June 16	0		
SDF	17		25	2.76	< .05
A55	5	May 20	4		
SDF	5		37	6.17	< .02

Nest Sites, Mates and Feeding Areas of Banded Herons

Twenty-one banded birds were identified on nests in the colony in 1978 and 44 in 1979 including, for both years, 18 banded pairs. In 1978, I identified five pairs where both mates were banded. None of these pairs definitely remained together in 1979. Seven of the birds were identified with different mates in 1979, two were not seen in the colony and one was paired with an unidentified banded bird. Of the 21 herons identified on nests in 1978, 13 were on different nests in 1979, one on the same nest and seven were not seen in the colony. I did not observe any adults moving between nests within one nesting season. Eight pairs lost all their eggs or young in 1979. None of the 13 banded birds involved in these pairs attempted to reneest in the Pender Harbour colony in 1979, although I did observe two unsuccessful attempts at late nesting by unbanded individuals.

Successful nests were much closer to the center of the colony than unsuccessful nests in 1978. In 1979, however, there was little difference between these groups (Table 2-4). The mean distance of all occupied nests from the colony center was about 30 meters in both years.

I examined nest position and feeding locations of banded herons to determine if banded herons nesting close together also fed in the same areas in Pender Harbour. Herons that nested in the same sector of the colony did not feed in the same areas. In fact, herons from each sector of the colony were uniformly distributed among the four principal feeding areas in Pender Harbour (Table 2-5).

Table 2-4. Mean distances (m) of successful and unsuccessful nests from the center of the colony in 1978 and 1979 at Pender Harbour.

	Successful			Unsuccessful			Median test
	\bar{x}	SE	N	\bar{x}	SE	N	
1978	24.1	1.96	25	42.5	4.41	14	p < .001
1979	29.4	1.71	33	31.6	3.36	12	p < .56

Table 2-5. Total number of banded herons from each sector of the Pender Harbour colony seen feeding together on four different days in 1979.

Feeding location	Number of herons from each sector			χ^2
	North	East	West	
Klein Bay	10	21	15	
Oyster Bay	18	11	13	
Trap 1	18	15	15	
Trap 2	9	8	9	6.05 (p > .3)

I also examined the feeding locations of banded pairs in 1979 to test if the male and female tended to use the same foraging zone. In eight of the 11 pairs, the male and female differed significantly in their frequency of sightings at five different feeding locations (Table 2-6). One member of each of the three pairs which did not differ significantly had few sightings, making a valid comparison difficult. The members of banded pairs, which fed mostly within Pender Harbour, therefore used different feeding areas in 1979.

Table 2-6. The number of sightings for each member of 11 banded pairs at five feeding locations in Pender Harbour in 1979.

Banded pair	Feeding status	Feeding locations					χ^2	df	p
		Klein	Oyster	T1	T2	T3			
A26	LF	18	0	11	0	0	6.1	2	< .05
A37	LF	15	5	3	0	0			
A65	LF	16	0	0	0	0	26.4	1	< .05
A35	LF	3	21	1	0	0			
A33	LF	6	11	2	0	0	1.4	1	> .05
A21	?	2	1	0	0	0			
A54	DF	1	1	0	0	0	2.1	1	> .05
A93	LF	28	1	1	1	1			
A59	LF	24	13	13	6	0	19.5	3	< .05
A71	LF	39	8	0	0	2			
A63	LF	21	2	0	4	0	0.2	1	> .05
A90	DF	6	1	0	1	0			
A70	LF	18	5	7	0	1	14.6	2	< .05
A64	LF	0	8	6	0	0			
A78	LF	20	3	4	0	2	24.8	3	< .05
A77	LF	1	16	10	0	1			
A86	LF	11	11	2	0	1	12.0	2	< .05
A79	LF	2	18	11	0	0			
A95	LF	4	22	15	1	0	33.7	2	< .05
A66	LF	26	2	10	1	0			
A99	LF	12	1	0	7	0	14.6	3	< .05
A56	LF	6	17	12	0	1			

Note: Includes only pairs with ≥ 20 sightings in 1979 and categories combined if expected < 1 .

Feeding on Tidal Areas

We completed 907 10-minute feeding trials from April to August 1979. Several environmental factors influenced feeding rates of the herons (Table 2-7). Most of those factors reflect individual choice and could be considered inherent in the feeding rates of different individuals. Herons captured more prey on ebbs tides, and in deeper water (Table 2-7). The biggest source of variability in feeding rates, however, was the change in prey abundance with time. The mean weight of prey caught per feeding trial and prey abundance, estimated from seine sampling, increased from April to June then decreased in July and August (Fig. 2-3). Catch rates did not differ between May, July and August. I compared the catch rates of banded herons which successfully raised young with those that failed in 1979. Catch rates did not differ during June or during the combined May, July, August period (Table 2-8). I also compared the prey capture rates between successful herons, which raised from one to five young, to determine if birds which fledged more young had higher prey capture rates. There was no relationship between the feeding rates of the parents and the number of young raised ($F_3, 407 = 1.5, p > .22$). Other data also suggested that food availability and catch rates of herons did not limit the reproductive success of herons at Pender Harbour. A single female successfully raised two young after her mate died on June 9, 1979. Despite the fact that the maximum food demand of young birds occurs in late June, just prior to fledging, this single female was able to supply the needs of her young.

Table 2-7. Factors affecting the weight (gm) of prey caught by herons on tidal feeding areas.

Factor	Level	\bar{x} wt. caught/ 10-min. trial	SD	N	F	Signif.
Tide direction	Ebb	13.86	10.5	556	9.4	.002
	Flood	11.48	12.3	336		
Location	Klein	13.09	11.7	539	3.1	.079
	Oyster	11.71	9.4	309		
Water depth	Dry	5.19	3.4	9	7.7	.000
	Ankle	11.95	11.1	161		
	< knee	12.60	9.9	378		
	> knee	12.31	9.6	211		
	Feather	17.55	16.2	148		
Bottom substrate	Algae	12.58	5.8	20	7.6	.000
	Eelgrass	14.26	11.6	717		
	Marsh	14.17	16.1	4		
	Mud	8.30	9.5	147		
	Oysters	10.33	11.9	16		
	Rock	2.19	2.1	3		
Grand mean		13.15	total	907		

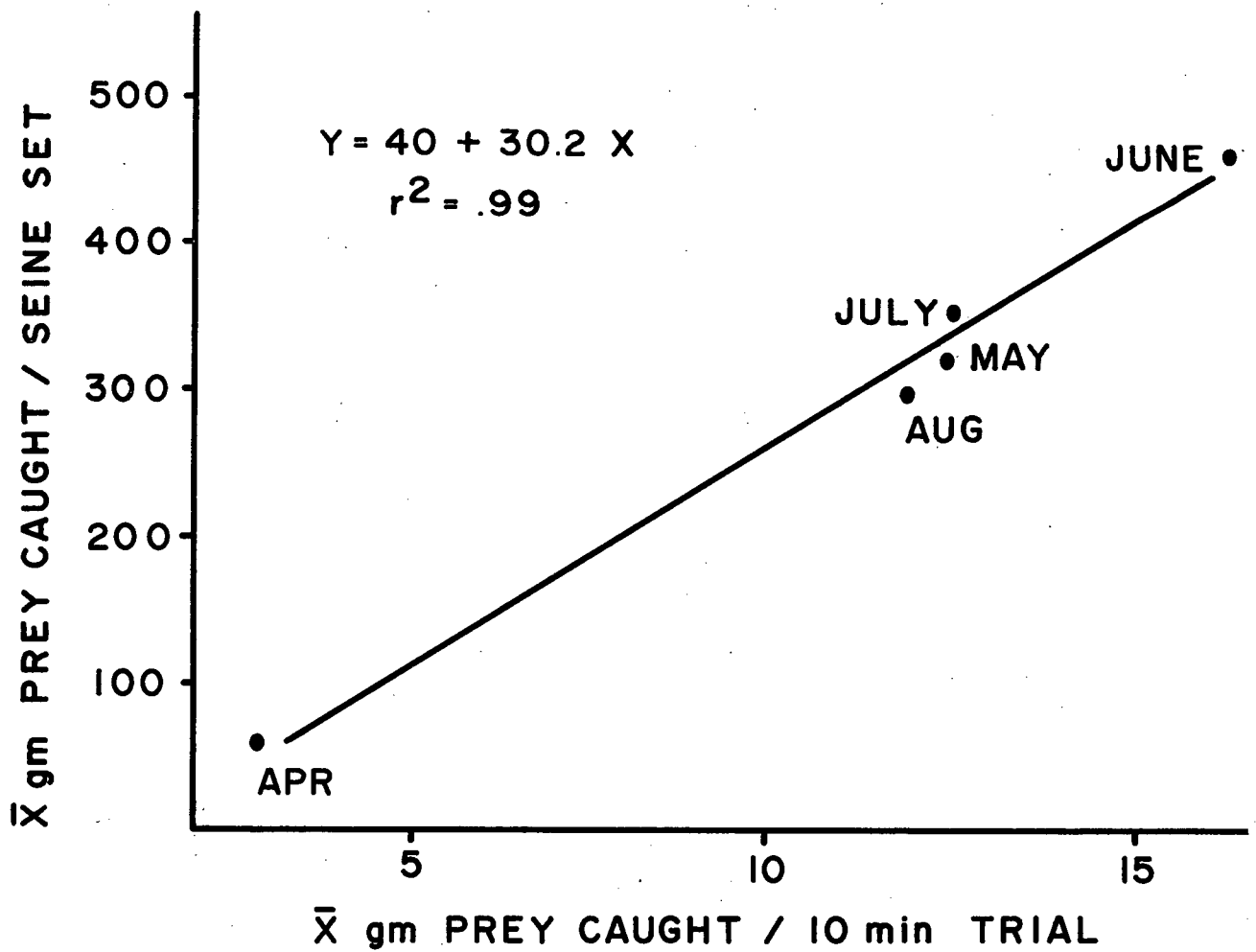


FIG. 2-3 Correlation between prey caught by herons (N=907) and prey caught by seining (N=244) for five months in 1979.

Table 2-8. Comparison of the weight of prey caught by herons which successfully raised young and those that failed to raise young in 1979.

Time period	Reproductive status	\bar{x} wt. caught/10-min. trial	SD	N	F	Signif.
June	Successful	16.47	9.9	70	2.6	.110
	Failed	13.01	5.9	24		
May, July, August	Successful	13.49	8.1	182	1.0	.319
	Failed	14.98	10.0	38		

Feeding at the Bait Tanks

Observations of herons feeding on the bait tanks in April (N = 15) and June (N = 6) showed that catch rates were much higher (392 ± 64 and 186 ± 22 g, respectively) than on natural tidal areas ($2.97 \pm .33$, N = 54 and $16.18 \pm .79$, N = 314, respectively) for 10-minute feeding trials. Herons at the bait tanks frequently captured two or three herring in a single strike. I saw two herons capturing herring then releasing them apparently after their hunger was satiated. Feeding success of herons on the bait tanks varied greatly depending on the number and behavior of fish in the tank. The bait tanks did provide an extraordinary and attractive food source for herons at Pender Harbour.

Aggressive Interactions

Most aggressive interactions (82 percent) occurred on the bait tanks because of the crowding of birds competing for favorable feeding sites. Forty-nine evening counts made from

mid-June to mid-July 1979 on two bait ponds showed a mean of 10.5 herons with a maximum of 24 and a minimum of six birds using each pond. Other interactions (18 percent) were recorded on tidal feeding areas during feeding trial observations. I recorded 572 aggressive interactions involving 51 banded herons in 1979. Although the average was 11.2 interactions per bird, the distribution was skewed right, so that only 16 herons were involved in more than 10 interactions. I was also able to classify 38 of those 51 birds as successful or unsuccessful breeding and local (LF) or distant feeding (DF) in 1979.

Successful LF herons consistently won more aggressive interactions than failing DF herons, but there were few failing birds of known status and the difference was not significant (Table 2-9). Successful and LF birds were involved in more encounters than failing or DF herons (Table 2-10). Differences in numbers of interactions for DF and LF birds probably relate to their differing frequency of observation at sites where interactions were recorded. For LF birds, the lower number of interactions for failing herons may relate to their avoidance of confrontations with other birds. I found no relationship between the distance of a nest from the colony center or the number of young raised and the dominance or interaction rank of the parents.

Table 2-9. Comparison of the dominance of banded herons with different reproductive success and feeding areas at Pender Harbour in 1979.

Reprod. status	Local/ distant feeding	N	\bar{x} % wins	Kruskal- Wallis H.	Signif.
--	LF	38	45.6		
--	DF	13	30.2	2.13	0.14
Succ.	LF	27	47.2		
Fail.	LF	6	23.8	2.59	0.11
Succ.	DF	3	18.6		
Fail.	DF	2	50.0	0.08	0.77
Colony	LF	33	42.9		
Colony	DF	5	31.1	0.67	0.41
Succ.	--	30	44.3		
Fail.	--	8	30.4	0.74	0.39

Table 2-10. Comparison of the total number of aggressive interactions for banded herons in relation to reproductive success and feeding areas at Pender Harbour in 1979.

Reprod. status	Local/ distant feeding	N	\bar{x} no. inter- actions	Kruskal- Wallis H.	Signif.
--	LF	38	13.2		
--	DF	13	5.5	5.76	0.02
Succ.	LF	27	15.8		
Fail.	LF	6	4.2	6.47	0.01
Succ.	DF	3	7.3		
Fail.	DF	2	1.0	1.33	0.25
Colony	LF	33	13.7		
Colony	DF	5	4.8	3.21	0.07
Succ.	--	30	15.0		
Fail.	--	8	3.4	9.15	0.01

Table 2-11. Changes in reproductive success for eight males and six females from 1978 to 1979.

		Reproductive status	1978	1979
Males	Fail.		1	1
	Succ.		7	7
Females	Fail.		0	3
	Succ.		6	3

Sex and Reproductive Success

All 79 captured herons were sexed using the discriminant function shown in Appendix I. The banded group included 42 males and 37 females. For herons not nesting at Pender Harbour there were significantly more male DF birds (10) captured than female DF birds (three) (binomial, $p < .05$).

I obtained reproductive information for both 1978 and 1979 for eight males and six females (Table 2-11). Their reproductive performance was similar, but that of females was less predictable. Two females at Pender Harbour in 1979 exhibited greater nest tenacity and defence than males. One female raised two young after losing her male partner. Another female defended her nest against scavenging ravens for two days after her young were lost to raccoons.

DISCUSSION

Colony Formation

Most herons known to nest at Pender Harbour foraged close to the colony site. The food demand of young herons ensures that foraging parents return regularly to their nests and, if the maximum time away from the nest is to be used for gathering food, feeding sites must be close to the colony. Werschkul et al. (1977) found that heron colonies in coastal Oregon are placed adjacent to good feeding grounds and colony size was related to the size of the adjacent estuaries. Colonies are probably formed by groups of herons which congregate at the large estuaries to feed. Locally-feeding herons formed the majority of the Pender Harbour colony in both 1978 and 1979 and probably determined its location.

Most herons nesting at Pender Harbour in 1978 selected a new mate and nest site in 1979. This is in sharp contrast to other colonial species, especially gulls, which show considerable colony, nest and mate fidelity between years (Southern and Southern 1982). It has been shown that kittiwakes (Rissa tridactyla) have improved reproductive success if they mate with the same individual each year (Coulson and Thomas 1983). Factors which can cause mate switching, such as death of the former mate or unsuccessful reproduction, did not cause herons to switch at Pender Harbour. Eight of 10 individuals paired in 1978 were still present in the colony in 1979 and all five banded pairs were

successful in 1978 yet none remained together in 1979. This lack of nest site and mate fidelity coincides with results in Chapter I which suggested that breeding herons frequently move between colonies and establish new nests. Changes in locations and numbers of nests during the nesting season resulted from unsuccessful birds leaving and new birds entering the Pender Harbour colony rather than from movements within the colony. Those facts again suggest that herons show little attachment to specific nesting sites. Because of this lack of predictability of nests or mates, heronries are important assembly areas for herons to find new mates and nest sites each year.

Although herons nesting in peripheral nests had poorer reproductive success (Table 2-4), central nests were not occupied by herons more dominant on the feeding areas. The nest position of pairs in a colony is largely dependent on the males, which select and defend nest sites early in the breeding season prior to the formation of pair bonds (Rodgers 1978, Meyerriecks 1960). Others have observed that older, established nests and those furthest from the ground are the first occupied by displaying males, probably to aid in attracting females (Parker 1980, Rodgers 1978, Henny and Bethers 1971). Nest height may also be important in colonies where average heights are low ($<4\text{ m}$) or in tree species such as cottonwood and Douglas fir where there is a large difference between the lowest and highest nests and there are many nests per tree. Higher nests should be less vulnerable to tree-climbing predators since

lower nests would be encountered first. Alternately, higher nests may be more vulnerable to avian predators which come from above. At Pender Harbour there was generally one nest per tree (Table 1-3), nest heights varied little ($\bar{x} = 26$ m, $SD = 1.51$, $n = 65$) and there was no relationship between nest occupancy or reproductive success and nest height. Parker (1980) noted that returning herons occupied nests in all parts of the colonies and did not group together. Later arriving birds were then able to occupy sites between established pairs, who had reduced the territory defended to the area immediately surrounding their nests (Rodgers 1978). The final position of a nest in a heronry is dependent on where subsequent birds choose to nest. At Pender Harbour there was a large number of vacant nests. Early arriving birds which chose nests near the center of the available sites may still have ended up near the edge of the colony if later arriving birds nested mostly to one side. This suggests that all sites are equally available to any individual. The possible advantages of joining a colony, which are derived mainly from the proximity of neighbors (Wittenberger 1981), would therefore be equally available to each of its members. Herons are attracted to colony sites to find mates, to locate their nests near good feeding sites and to reduce the vulnerability of their young to predators by nesting in groups.

Predation, Reproductive Success and Adult Survival

Predation was probably the primary cause of nest failure at Pender Harbour. Predation typically results in the loss of entire nests (Jenni 1969, Dusi and Dusi 1968), in comparison to starvation or sibling rivalry, which reduce the number fledged per successful nest (McAloney 1973, Pratt 1972, Owen 1960). Higher losses among peripheral nests (Table 2-4) also implicate predators as the cause. Nests near the edge of a colony are the first encountered by predators and, because they have fewer close neighbors than central nests, the advantages of swamping are reduced (Wittenberger 1981). Predators have been considered important causes of nest failure for great blue herons in other areas, and for colonial species in general (Hjertaas 1982, Ward and Zahavi 1973, Milstein et al. 1970).

DF herons had more nest failures than residents but, in successful nests, raised as many young as residents (Table 2-2). DF birds must have chosen areas outside Pender Harbour for feeding. Two of those individuals were seen only at the bait tanks while the others were seen so irregularly at tidal areas that I doubt if they could have supported nestlings without alternate feeding areas. Thompson (1979b), in Montana, and Parris and Grau (1979), on the Great Lakes, showed that some great blue herons travelled up to 20 or 30 km, respectively, to feeding areas from their nesting sites. If those distances apply to herons at Pender Harbour, some breeding birds may have been feeding as far away as Sechelt. Since short term movement

between Pender Harbour and Sechelt was seen, such long distance foraging by breeding adults seems possible.

Yom-Tov (1974) experimentally manipulated the food supply of breeding crows and found that nest losses increased when food was placed further from the nest. He suggested that when food is dispersed the nestlings are more vulnerable to predation because the parents spend more time far away from the nest. DF herons may have more nest failures because they spend more time away from their nests while foraging for food.

The reasons why DF herons fed in areas far away from their nests, apparently at the risk of losing their young, are not clear. Although LF herons were not clearly dominant over nesting DF birds, it is possible that DF herons were forced away from Pender Harbour by competition from LF birds. Several LF herons excluded all other herons from selected parts of the bait tanks. Differences in number of interactions between LF and DF herons probably relate to their different occurrence on feeding areas (Table 2-1). Fewer interactions for DF herons was probably a result rather than a cause of their observed lower use of feeding sites within Pender Harbour.

Bayer (1978) found that some herons which maintain feeding territories over winter had better survival than non-territorial herons. DF herons nesting at Pender Harbour may have travelled to distant feeding areas to maintain preferred territories. Improved winter survival may have been more important to the individuals than decreased reproductive success. My data was insufficient to test if DF birds had

above average over-winter survival and I did not distinguish between territorial and non-territorial herons within Pender Harbour during the winter.

Colonial Nesting and Information Exchange

Krebs (1974) postulated that transfer of feeding information may be one of the principal advantages to colonial nesting in herons. There was no evidence to suggest that herons at Pender Harbour used any type of feeding area information exchange. Neither paired herons nor neighbors tended to feed in the same areas as would be expected if herons followed each other to good feeding sites (Krebs 1974). In fact, pairs tended to feed in different areas (Table 2-6).

Prey abundance and distribution was predictable and feeding rates of herons did not vary greatly on local tidal areas (Table 2-7). Large tides, in June, expose the maximum estuarine habitat coincident with the peak prey abundance, peak adult feeding rates (Fig. 2-3) and maximum food demand of the young herons. Reproductive synchrony and timing at the Pender Harbour colony probably ensures that the food demand coincides with the seasonal changes in supply. A single adult successfully raising two young suggests that food is not limiting. I found no evidence of the reduced brood sizes normally associated with food limitation and starvation (Des Granges 1979, Pratt 1972, Owen 1960), nor was there any relation between feeding rates of parents and number of young fledged. Under those favorable circumstances there is no need for herons to "share" feeding area information.

Although much of my information indicates that many herons at Pender Harbour had specific feeding areas (Table 2-6), other data also shows their ability to exploit extraordinary or unusually abundant food supplies. Sightings of four of the 13 DF non-colony birds (Table 2-1) suggest that they came from frequently used areas outside Pender Harbour. Bird A43 was resighted only at Sechelt, suggesting that it may have been a DF heron from the Sechelt colony when it was captured in 1978. The movements of A82 and A84, and the sighting data for A48, show that they frequented other areas and only occasionally visited Pender Harbour. Those birds were probably attracted to Pender Harbour by the abundant food supply at the bait tanks. Some of the breeding DF herons at Pender Harbour may have had similar movement habits. If those birds occasionally located extraordinary feeding sites, that information could be transferred to other neighboring adults in the colony when they returned to feed their young.

Local food shortages have occurred at heronries in other areas (review by Des Granges 1979) possibly due to unpredictable declines in prey abundance or poor weather conditions. If the local food supply at the Pender Harbour colony were to fail, DF herons in the colony could lead other colony members to alternate feeding areas. A local food shortage would be required to adequately test the information exchange hypothesis using great blue herons at Pender Harbour.

Sex and Reproductive Success

Great blue heron pairs share the responsibility of incubating and feeding the young. Adult herons tend the nest continuously during incubation and for the first three to four weeks after hatching (Pratt 1970). From June 1 until fledging both parents return regularly to feed the young, but do not maintain constant vigilance at their nests.

I have some information which suggests that differing habits of males and females may affect reproduction. Significantly more males than females were captured in the DF non-colony group at Pender Harbour. Although there is no information on the sex ratio in the great blue heron population, there are generally more females than males in populations of large colonial species (Coulson and Thomas 1983). Band recoveries at Pender Harbour suggest that adult mortalities were divided equally between females (seven) and males (six). If we conservatively assume an equal male/female ratio in surrounding areas, more DF males must have travelled to the bait tanks in Pender Harbour to increase their capture frequency. It is possible that male DF herons feed at greater distances from their nests than females and are, therefore, less attentive at the nest site.

If individual herons maintain similar reproductive effort from year to year, changes in reproductive success probably relate to other factors such as the effort of the mate. Three of six females successful in 1978, failed in 1979 when paired with different males. Only one of seven males involved in

successful 1978 matings failed in 1979 (Table 2-11). Although those observations are not significantly different, they suggest that female reproductive success can be affected by the behavior of their male partners. Other observations of female tenacity at the nest and ability to raise young alone suggest that females maintain a higher and more consistent level of reproductive effort than males. The suggested differences in the movements and nest tenacity of males and females may indicate that males have greater responsibility for finding food, while females have greater responsibility for tending the young.

CONCLUSIONS

The Pender Harbour heron colony was composed of a core group of LF herons which fed principally in the two adjacent tidal estuaries during the day and at live bait fish ponds at night. Herons with feeding areas outside Pender Harbour (DF) constituted about 22 percent of the Pender Harbour colony. Most herons selected a new mate and nest site from 1978 to 1979. The colony shifts and size fluctuations noted in Chapter I undoubtedly relate to the lack of attachment of breeding herons to nesting sites or mates. Central nest sites were most successful but differences in individual dominance, determined at feeding sites, were not related to nest site occupancy. Herons are probably attracted to colonies primarily to find suitable mates, to locate their nests near good feeding

sites and to reduce the vulnerability of their young to predators by swamping.

DF herons suffered more nest failures than LF birds, but fledged as many young as LF herons in successful nests. The frequent loss of entire clutches, higher losses in peripheral nests and direct observations of predators in the colony confirmed predation as the primary cause of nest losses. DF herons probably spent more time away from their nests while foraging for food, and thereby exposed their young to heavier predation.

DF herons nesting at Pender Harbour may have been less dominant at feeding sites than LF birds, so it is possible that they were forced to use more distant feeding sites by intraspecific competition. Other research indicates that herons which maintain feeding territories have better overwinter survival. DF herons nesting at Pender Harbour may have continued to use distant feeding areas to maintain territories which were valuable for winter survival even though their reproductive success was lowered.

Exchange of information about feeding areas did not appear to be occurring in the Pender Harbour colony. Prey abundance and distribution was predictable in time and space, based on results of seine sampling and observations of feeding herons. Peak prey abundance and feeding habitat availability occurred coincident with peak food demands of young herons in the colony. Under those circumstances there was obviously no need for any information exchange to locate good feeding areas.

Local food shortages and starvation have been observed in other heronries. Under those conditions, LF herons could follow DF birds to alternate feeding areas. Food shortages and unpredictable supply should be demonstrated before the information exchange hypothesis for colonial nesting can be tested using great blue herons.

Indirect evidence suggests that males may be wider ranging than females. Because males may spend less time at the nest and leave the nest unattended, reproduction for some females may be limited by this behavior of the male. Since males initiate nesting and colony formation, their movements may also be responsible for some of the observed colony instability.

GENERAL DISCUSSION AND RECOMMENDATIONS

Heronries frequently change locations or fluctuate in size dramatically. Such movements and changes in size have previously been associated with disturbing influences or predation and were considered unnatural or detrimental occurrences. Great blue herons differ from other colonial species because colonies are not composed of discrete groups of birds which return annually to the same site. Each year varying numbers of herons gather and form colonies near good feeding sites but not necessarily at previously used locations. The lack of mate and nest site fidelity, observed at one disturbed colony, may be indicative of herons generally and probably contributes to the observed instability of many heronries. Colonies which relocated bred successfully at new locations and may, at least temporarily, have avoided some of the predators which frequented established heronries. The greatest distance moved by a heronry was 10 kilometers, but most moves were under five kilometers in this study. Activities which may cause relocations should be avoided unless there is suitable similar habitat available within 10 kilometers. The proximity of preferred feeding areas to potential nesting areas may be important in determining the maximum distance a heronry might move.

Human disturbances had the effect of increasing the success of natural predators in heronries and frequently resulted in colony relocations. Although some heronries adapted to human activities, others, away from regular human activity where

adults fled from people, should be undisturbed during the nesting season (April-July).

The percentage of nests successful was the best statistic to assess reproduction in heronries. The method of determining the numbers of successful and unsuccessful pairs, without causing a major disturbance in the colonies, should be further explored. Colony censuses should include an accurate count of occupied and vacant nest platforms during fledgling counts. In colonies adapted to human activities the relationship between nest occupancy and numbers of breeding pairs could be further examined.

Banding of individuals, at one colony, has shown that breeding herons have differing habits which relate to reproduction, over-winter survival and food-finding. Males may have greater responsibility for foraging and food-finding while females may provide more nest defence. Although distant feeding herons had lower reproductive success than local feeders, they may have gained long-term advantages by maintaining territories important for over-winter survival. Birds which travel further to feed may also have more options in choosing colonies in which to nest. Further studies using banded herons could better define the roles of males and females and the importance of distant feeders to formation of colonies and location of feeding areas.

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APPENDIXDiscriminant function used to determine
the sex of banded herons at Pender Harbour

Morphological measurements (bill, head plume, tarsus, tail and wing length and weight) were obtained from 19 dead and 79 living great blue herons. Measurements were taken to the nearest mm using a steel tape, and weight to the nearest 25 g.

1. Bill: measured from the tip of the bill to the point at which the skin of the forehead joins the bill.

2. Head plume: measured from the attachment on the skull to the end of the longest plume.

3. Tarsus: with the left leg extended to approximately 130° at the knee joint, measured from the joint indentation on the ankle to the joint indentation on the knee.

4. Tail: measured from the base of the pineal gland to the end of the longest tail feather.

5. Wing: with the bird restrained and laid on its right side, measured from the leading edge (elbow) of the left wing to the end of the longest flight feather.

6. Weight: restrained birds were laid in the cradle of the dial scale.

Dead specimens were collected mainly during the winter in south coastal B.C. Sex was determined during autopsy by Dr. A.C. MacNeill, Agriculture Canada, Health of Animals Branch. Laparotomies were done to determine sex of three adult living birds captured at Pender Harbour in 1978.

Incisions were made in the left abdominal wall using xylocaine local anesthetic and gonads observed using a high intensity microscope light.

Using measurements from dead or laparotomized males (eight) and females (13) a linear discriminant function was developed after the method of Rao (1973). The function was used to determine the sex of 32 banded herons, which were members of the 18 banded pairs in the Pender Harbour colony in 1978 or 1979. Assigned sexes for each paired bird were examined to ensure that each pair consisted of a male and a female. Additional information such as observations of copulation was used in correcting the sexual classification of three individuals. Following this verification, measurements of the entire group of now classified birds were used to develop a second discriminant function which was applied to the remaining banded birds.

The measurements I used in determining the sex of banded birds are shown in Table 1. Two measurements were discontinued during the course of the trapping due to difficulties in obtaining consistent measurements (tail length) or obvious large variations unrelated to age or sex (head plume). Two of three laparotomies attempted on adult birds were successful. Difficulties in restraining large herons, poor field laboratory conditions and extended handling time precluded further attempts. Two of the three birds involved have been observed since and one successfully raised four young in 1979. Laparotomy is a viable, although probably unnecessary,

technique in determining the sex of living herons, given proper equipment and working conditions. Table 2 shows the coefficients of the linear discriminant function developed using measurements of dead (known sex) and paired living herons. Both functions are evaluated for each individual and the one with the lower value determines the sex (Rao 1973). Of 53 individuals of known sex (dead or paired birds) 52 (98%) were correctly classified. Table 3 shows the morphological measurements of classified herons. Using posterior probabilities over 70% of the birds could be classified with 95% confidence. I used this technique to assign sexes to all the banded herons at Pender Harbour.

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Table 1. Morphological measurements of 79 great blue herons captured at Pender Harbour in 1978 and 1979.

	N	Min.	Max.	Mean	SD
Bill length (mm)	79	116	146	132	8.34
Tarsus length (mm)	79	133	180	160	11.02
Wing length (mm)	79	462	544	500	18.01
Tail length (mm)	68	170	230	195	12.56
Weight (kg)	79	1.87	2.97	2.34	.25

Table 2. Coefficients of the linear discriminant function based on measurements of known sex and paired great blue herons in British Columbia, 1979.

Variable	Male	Female
Constant	-855.71	-745.97
Bill length	3.07	2.64
Tarsus length	- 0.43	- 0.49
Wing length	2.65	2.56
N	24	29

Table 3. Morphological measurements of known male and female great blue herons in south coastal British Columbia.

	Sex	Min.	Max.	Mean	SD	N
Bill length (mm)	M	129	146	137.0	4.43	24
	F	112	131	123.9	4.72	29
Tarsus length (mm)	M	155	177	165.9	6.72	24
	F	135	165	152.0	7.04	29
Wing length (mm)	M	470	544	505.7	13.75	24
	F	465	500	483.0	8.69	29
Weight (kg)	M	1.53	3.07	2.48	0.29	24
	F	1.90	3.27	2.11	0.34	29

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