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THE BREEDING ECOLOGY AND SOCIAL ORGANIZATION OF THE NORTHWESTERN CROW (CORVUS CAURINUS) ON MITLENATCH ISLAND, BRITISH COLUMBIA

by

Robert William Butler

B.Sc., Simon Fraser University, 1976

A THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in the Department

of

Biological Sciences

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The breeding ecology and social organization of the Northwestern Crow (Corvus caurinus) on Mitlenatch Island, B. C.

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Degree: Master of Science

Title of Thesis: The breeding ecology and social organization of the Northwestern Crow (*Corvus caurinus*) on Mitlenatch Island, B. C.

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Chairman: Dr. A. L. Turnbull

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Dr. R. M. Sadleir

Dr. Robert C. Brooke

Dr. R. W. Mathewes, Public Examiner

Date approved 23 April 1980

Abstract

The breeding ecology and social organization of the Northwestern Crow (Corvus caurinus) was studied from 19 May to 30 August 1976, 27 April to 26 August 1977, and 28 April to 19 July 1978 on Mitlenatch Island, British Columbia. Displays of the Northwestern Crow were similar to those of other species of crows. Nesting territories averaged 0.50ha. In 1978 nests that were built in continuous woodland were, on average, 21.8m apart. The location of many nests changed little from year to year which suggested strong site tenacity. Boundaries extended about 2-3m beyond the high tide line in territories that were adjacent to the beaches and crows from these territories dominated all other crows on the adjacent stretch of beach, although the intertidal was a communal feeding area. The male crow performed most of the territorial defense which, in beach edge territories, was positively correlated with decreasing tides during the nesting season.

Only forced copulations were seen. No courtship behaviour that terminated in copulation was observed.

Nest building began in April and most nests were built in shrubs although ground and tree nest sites were also used. Those nests built in beach-edge territories were significantly farther apart than nests built in inland territories. The composition and construction of 32 nests is described.

The eggs were laid beginning in late April after a mean of 8.6 days following the completion of the nest. Crows that established new territories waited significantly longer to lay

their eggs than crows that used the same territory from the previous year. Clutches were initiated over 37 and 32 days in 1977 and 1978, respectively. The mean clutch size was 3.7 and 3.8 eggs in 1977 and 1978, respectively. Clutches were significantly larger in beach-edge territories than inland territories. The eggs of C. caurinus were incubated only by the female and lost an average of 0.18 g per day (16.3% of original weight during incubation). The female crow was highly attentive to her eggs and only left them to be fed by the male and for short maintenance activities. Incubation lasted for 18 days. In 1977, 39% and in 1978, 52% of laid eggs hatched, which is much lower than for the Common Crow (C. brachyrhynchos) in California.

The female attentively brooded the nestlings until they were about 10 days old. The Northwestern Crow nestlings grew faster, on average, than Common Crow nestlings. The male performed about 66% of the feedings until the nestlings reached 7 days of age and afterward the female fed the nestlings about 66% of the feedings until fledging age. Most nestlings were lost in the first week of life, probably to other crows. About 52% of the hatched eggs fledged young in 1976-78, much higher than California Common Crows (13%). Fledging occurred in June and early July when the nestlings were 26 days old, on average, and weighed 318.1 g. Fledging success (no. of eggs laid that fledged young) was 27.1% in 1977 and 16.8% in 1978. Beach-edge territories lost significantly fewer nestlings and fledged significantly more young than inland territories.

Juvenile crows left the territory about 2 weeks after fledging and still begged food from their parents in late August when my observations ended.

The roosts comprised of the male roost, pair roost, yearling roost, and a family roost, on the territory and a communal roost off the territory.

The food of the Northwestern Crow came from the beach, the meadow, and the gull colony. The crows showed a significant preference for the beach as a food source over the meadow and gull colony.

Some yearling crows helped their parents raise the nestlings. However, most adult pairs did not have yearling helpers. Yearlings assisted in territorial defense and on one occasion fed the nestlings. In return they were fed by the adults. Those adults with helpers had larger clutches, more nestlings, and more fledglings than adults without helpers.

The presence of the Northwestern Crow nestlings coincided with the period of food abundance on the beach, in the meadow, and in the gull colony.

Although Northwestern Crow nests are clumped I suggest that the dispersion of nests on the island has arisen in response to the availability of nest sites and not a strategy to exploit the food supply.

I suggest that nesting asynchrony is a response to the ability of pairs to establish nesting territories in spring. Those crows that nested in new territories were less synchronous in laying their eggs than pairs reusing the previous years'

territory.

The Northwestern Crow appears to be a solitary nester that has incorporated some non-breeding yearling crows into the breeding effort. I suggest that its social organization is a response to the nature of the availability of the food resource.

Quotation

In a time when tides were absent from the earth, the Raven, Klook-shood, stole the daughter of Tu-chee, the East Wind, for his wife. As a marriage present, Tu-chee promised to bare the mud-flats for twenty days so that Raven, being a shiftless fellow, could find easy prey.

"Good", said the lazy Raven, "but you must bare the land to the cape"; to which the East Wind replied, "No, I will make it dry for only a few feet."

The haggling went on and on until Raven finally threatened to return the daughter. Tu-chee, alarmed, compromised and agreed to make the water leave the flats twice each day. So the tides were born, and so Ravens and crows now go to the flats to feed.

- based on a Makah legend
(Carefoot 1977)

Acknowledgements

I wish to express my gratitude to Dr. N.A.M. Verbeek for his enthusiasm, encouragement, and patience throughout this study. I would also like to thank Drs. R. Brooke, L. Dill, and R. Sadleir for their contributions as committee members. I am also very grateful to Mrs. T. Finlayson for her encouragement and assistance. I thank D. Flook for his comments on the thesis and Y. Yom-Tov and H. Richardson for their comments and discussion during the formative stages of this thesis.

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The Canadian Wildlife Service and NSERC supplied financial support through N. Verbeek.

In the field I was assisted by many people whose hospitality was greatly appreciated. Among these people were R. Colling, A. and B. LeChasseur, J. Linstead, G. McFetridge, H. and R. Moxley, and the people at Miracle Beach and Salmon Point Resorts. A special thanks is given to J. Kirbyson who shared common joys and sorrows for 2 summers.

N. Verbeek, R. Brooke, and J. Kirbyson allowed me to use their vegetation data for the plant community map. R. Brooke kindly let me use his drying oven. A. Philips identified fish in the throat samples.

Lastly, I wish to thank my wife, Sharon, who assisted me in the field, encouraged me at all times, and without whose help this project would not have been possible.

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1. Introduction

Each organism has a certain amount of time and energy that it can devote to maintenance, growth, and reproduction. Through natural selection those individuals that are best suited to efficiently exploit the available energy resources will have the best chance of survival. The way that an organism arranges its use of time, energy, and behaviour, form that species "exploitation system" (Verbeek 1973).

One effective method used by an organism to cope with a changing environment, and yet retain some degree of adaptation to it, is to vary the budgeting of its time and energy (Pianka 1974). Thus, a Northwestern Crow holds an exclusive territory only when food is abundant and from shortly before there are eggs until the young leave the nest. The energy resources also affect the social organization of birds (Crook 1965; Horn 1968; Lack 1968; and others). As Verbeek (1973) has pointed out, the degree of sociality among corvids is a function of the distribution of the food supply in time and space. As the resources become decidedly discontinuous, or "patchy", the various species of corvids become increasingly colonial and/or non-breeding individuals are incorporated into the breeding effort. The availability of food plays an important role in the evolution of mating systems (Orians 1969, Pitelka et al. 1974, Verner 1964, Verner and Wilson 1966), age at first breeding (Lack 1966, Verbeek 1977), size and type of territory (Brown 1964, Pianka 1974), clutch size (MacArthur 1958, Perrins 1965, Lack 1966) and population movements (Crook 1965, Holmes

1966).

On Mitlenatch Island seasonal variation of environmental factors such as precipitation, temperature, and tidal position create temporal differences in the availability of food. In the terrestrial habitats the meadow invertebrate populations respond to the primary productivity of the grasslands by increasing their numbers to a maximum population level shortly after the peak in grassland biomass. The meadows have differential exposure, drainage, amounts of sunlight, moisture, etc. This creates a "mosaic" of maturation stages of the grassland and thus the numbers of invertebrates that feed in the meadows.

The fish brought to the chicks and the seabird eggs have less temporal and spatial variability than the meadow invertebrates because they are synchronized in their breeding cycles and are therefore more predictable. However, these seabirds defend their nests which reduces the availability of the resources (eggs, chicks, etc.) to the crows.

The number of intertidal organisms are temporally and spatially variable in their distribution due to exposure to waves, sunlight, salinity, etc. (Carefoot 1977).

Field studies of the New World Jays (Corvidae, subfamily Garrulinae) have shown that their social organizations and breeding systems range from territoriality by breeding pairs in the Blue Jay (Cyanocitta cristata) (Hardy 1961) to cooperative breeding in the Mexican Jay (Aphelocoma ultramarina) (Brown 1963, 1970) and other species, and to colonialism in the Pinon

Jay (Gymnorhinus cyanocephalus) (Balda and Bateman 1971, 1972). Except for the Raven (C. corax), however, little is known about the social organization and breeding ecology of North American Crows (Corvidae, subfamily Corvinae) (Goodwin 1976).

The Northwestern Crow (Corvus caurinus) is distributed along the Pacific Coast of North America from Washington State to Alaska (Godfrey 1966). Observations have shown that the Northwestern Crow procures most of its food from the intertidal beaches on Mitlenatch Island during the breeding season (Butler 1974). Except for a few short papers and notes very little is known about the social organization and breeding ecology of Corvus caurinus.

This little-known crow thus offered a promising subject of investigation into the social organization and breeding ecology of a temperate species inhabiting an environment with an unstable food resource.

The purpose of this study was to investigate how the fluctuating food resource on the intertidal beaches, in the meadows, and in the gull colony has shaped the breeding ecology and social organization of the Northwestern Crow on Mitlenatch Island, British Columbia.

Study Area

Mitlenatch Island (49°57'N, 125°00'W) is located in northern Georgia Strait, British Columbia (Figure 1). The 35.5ha island is mostly composed of basaltic rock that forms two prominent hills: West Hill rises 54m above sea level and East Hill has an elevation of 32m above sea level. Joining these two knolls is an approximately 2.5ha meadow. On the northwest side of the meadow is Northwest Bay which has a steep intertidal slope of gravel and rock. Bordering the southeast edge of the meadow is Camp Bay, which has a low intertidal slope and is composed of gravel, sand, or mud, depending on the location. The tidal F' Island separates the mouth of Camp Bay in two. The remainder of the island has a varied topography with many exposed rises and knolls interspersed with vegetated basins and ravines. In 1958 a fire razed the island so that most of the island's vegetation is in early successional stages.

Mitlenatch Island lies within the Coastal Douglas-fir Zone of Krajina's (1965) biogeoclimatic scheme. Table 1 shows the weather trends for 1976-78. Figure 2 shows a climograph for Cortez Island which is about 6km northwest of Mitlenatch Island.

Figure 3 shows the major vegetation types on Mitlenatch Island and Table 2 shows the approximate area of the 6 major vegetation communities.

Recent estimates of the number of breeding seabirds (Campbell 1976) revealed that about 1632 pairs of Glaucous-winged Gulls (Larus glaucescens) nested on the exposed, rocky areas of the island, and about 286 pairs of Pelagic Cormorants

(*Phalacrocorax pelagicus*) and 200 pairs of Pigeon Guillemots (*Cepphus columba*) nested along the edge of the island in suitable habitat. Although all 3 species of seabirds supplied eggs, chicks, and food scraps for the Northwestern Crow, this study investigated only the interactions between the Northwestern Crow and the Glaucous-winged Gull.

Figure 1. Major landmarks on Mitlenatch Island.

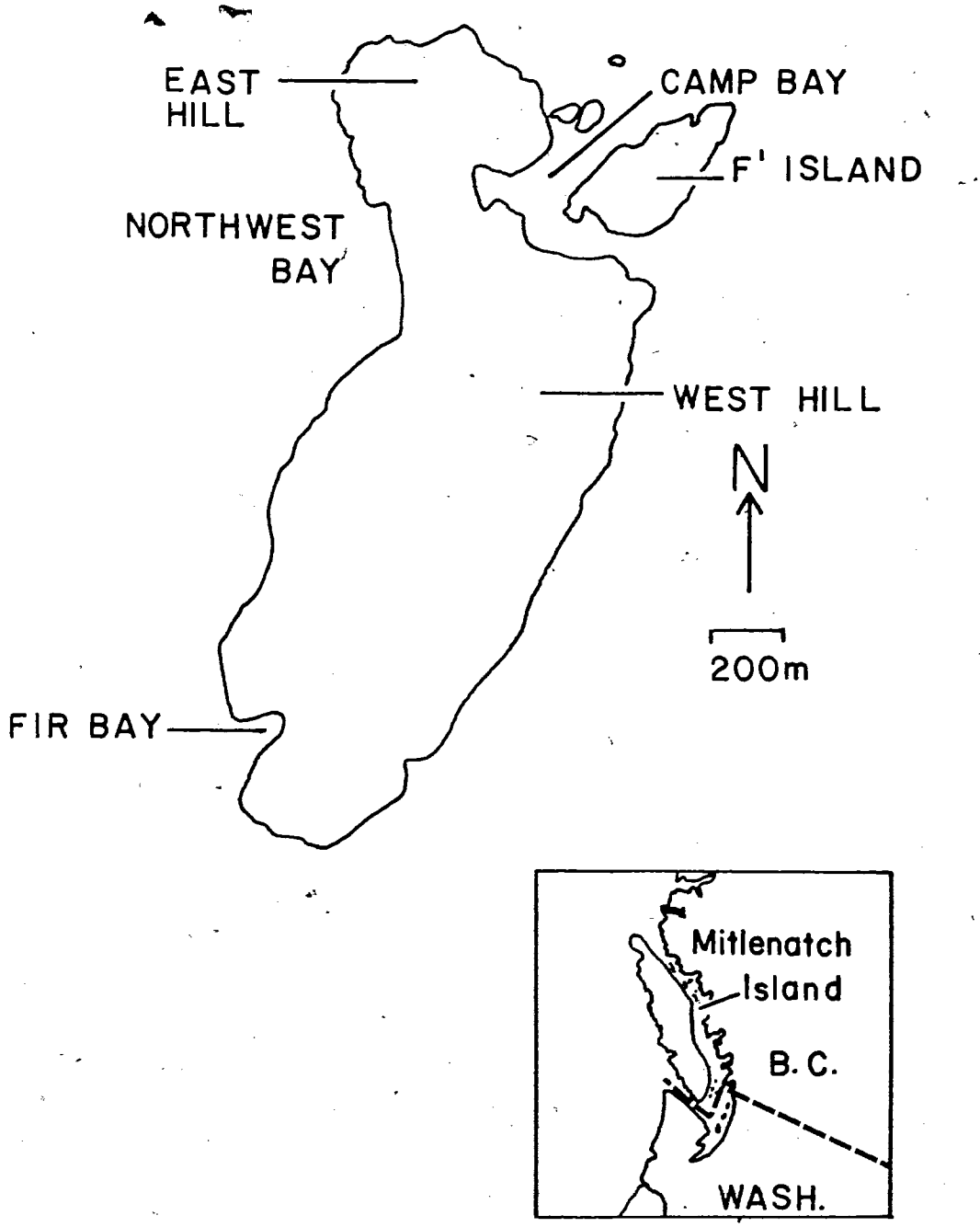

EAST HILL
CAMP BAY
F' ISLAND
NORTHWEST BAY
WEST HILL
N
200m
FIR BAY
Mitlenatch Island
B.C.
WASH.

Table 1. Mean temperature (^{o}C), mean daily precipitation (mm), and estimated mean maximum daily wind speed (km/h) at Cortez Island (April) and Mitlenatch Island (May-August)

	April[1]	May	June	July	August
Temperature					
1976	-	11.0	14.3	17.0	15.8
1977	9.7	11.9	16.4	17.1	21.9
1978	8.9	12.0	17.8	19.2	-
Precipitation					
1976	-	3.7	1.4	0.5	4.6
1977	1.1	1.6	0.6	1.0	1.1
1978	4.0	2.6	0.4	1.3	-
Wind Speed					
1976	-	36.0	19.5	23.0	23.0
1977	-	21.1	29.9	20.0	23.5
1978	-	21.3	16.5	15.0	-

[1] from Dept. of Environment, Monthly Record for Western Canada, Ottawa.

Figure 2. Climograph of mean values for Cortez Island (6km north of Mitlenatch Island). Intermittent summer weather records from Mitlenatch Island have shown that Mitlenatch receives less precipitation than Cortez Island. Data from Environment Canada, Monthly Record 1970-75. Numbers correspond to months.

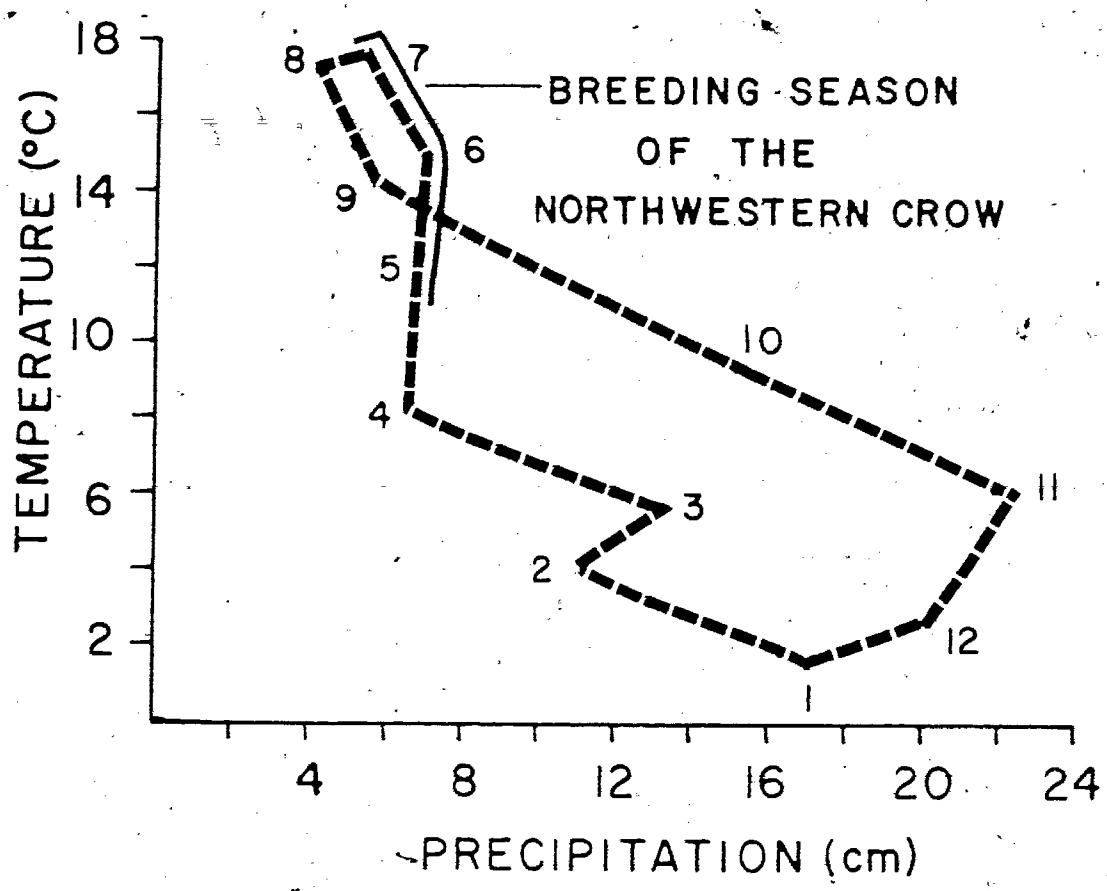

TEMPERATURE (°C)
18
14
10
6
2
4
8
12
16
20
24
PRECIPITATION (cm)
BREEDING SEASON
OF THE
NORTHWESTERN CROW
1
2
3
4
5
6
7
8
9
10
11
12

Figure 3. Major plant communities on Mitlenatch Island in 1978. Dashed lines (---) demarcate Glaucous-winged Gull nesting areas.

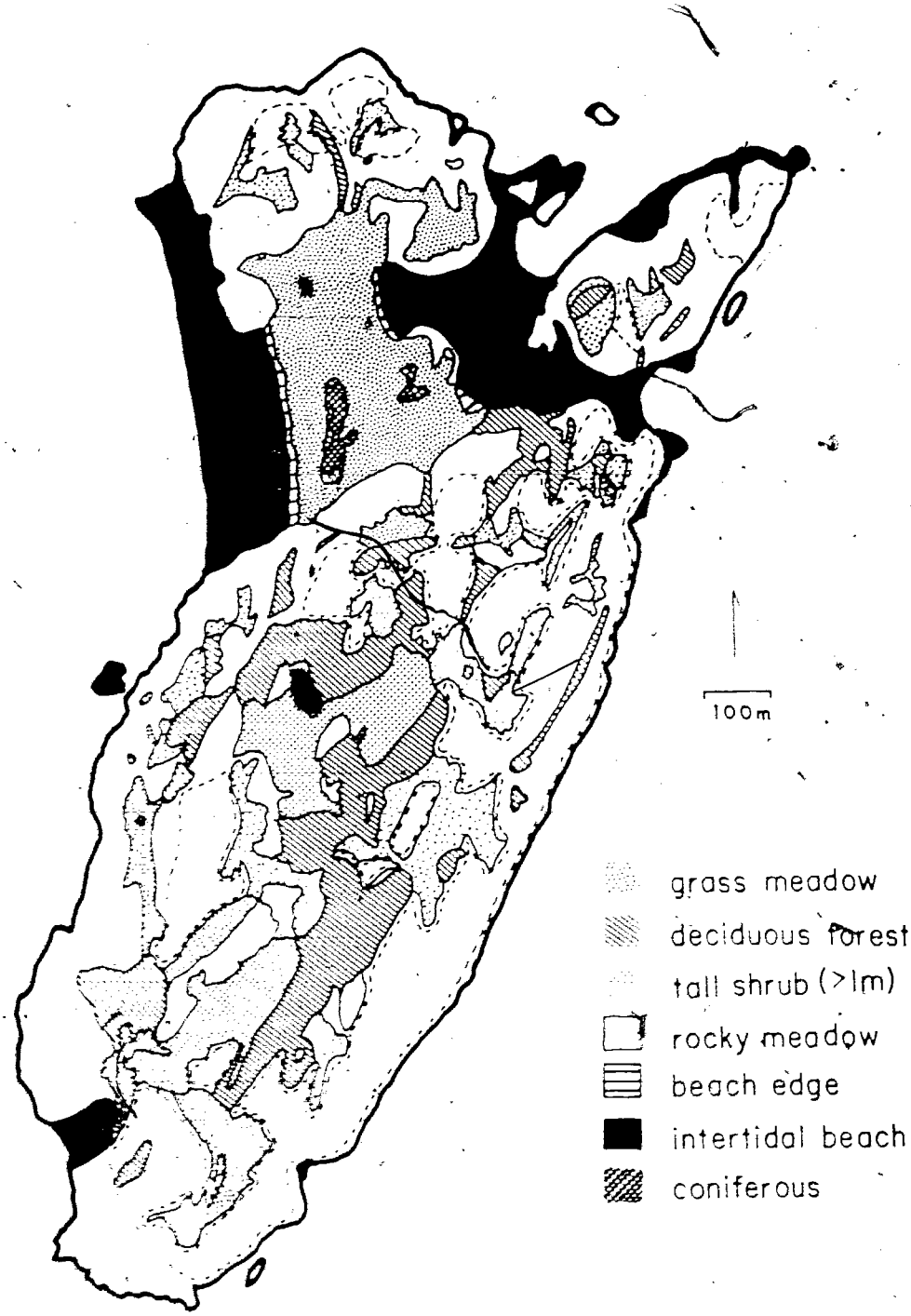

100m
grass meadow
deciduous forest
tall shrub (>1m)
rocky meadow
beach edge
intertidal beach
coniferous

Table 2. Approximate area of major vegetation communities on Mitlenatch Island

Community	Approximate Area (m^2)	% Area
rocky meadow	196,670	55.4
grassy meadow	74,195	20.9
shrub	48,280	13.6
deciduous forest	29,465	8.3
coniferous forest	2,840	0.8
beach edge	3,550	1.0

Methods

This study was conducted from 19 May to 30 August 1976, 27 April to 26 August 1977, and 28 April to 19 July 1978, and included 244 whole or partial days.

Nests were located in April and May in each season during nest building or egg laying and were visited once every 3 to 7 days while the nestlings fledged. Internest distances were measured on aerial photographs. The size of each crow territory was determined by plotting the territorial skirmishes on an aerial photograph and then calculating the area enclosed by a line joining those points. In 1977, 66 eggs in 23 nests were numbered with India ink so that weight changes during incubation could be determined for individual eggs. Nestlings were tagged with colored tape on one leg until they were about 14 days old at which time the tape was replaced with unique combinations of coloured, plastic bands and numbered, metal bands in 1977-78 (Appendix I). I did not capture and band adult crows.

Adult males were distinguished from adult females by their behaviour (males were more aggressive than females, only females incubated and brooded the nestlings, etc.). Adults are glossy and black, while yearlings (young from the previous year) have a brownish cast to their feathers, especially on the back and wings. Yearling Common Crows (C. brachyrhynchos) also have a brownish cast to their feathers (Emlen 1936).

Seasonal changes in the living and dead components of the plant biomass of the meadows was determined by clipping and immediately separating the green from the dead vegetation

in 10 plots (400 cm^2 each) at approximately 2 week intervals from 28 April to 13 July 1977. Each of those 10 plots was randomly selected from a checkerboard arrangement measuring 260cm x 280cm. Only every second plot was harvested to minimize the effect of collecting on adjacent plots. Each sample was air dried in the field and, later, oven dried for 24h at $80^{o}C$.

Nestling food samples were obtained in 1976 and 1977 using the pipecleaner method (Kluijver 1933). Nestlings that were extensively sampled for food were omitted from the growth rate and nesting success calculations.

I was able to determine the major food items of the crows on Mitlenatch Island by pellet analysis (Butler 1974), and direct observation. Based on this information I determined the relative importance of known and potential food items in the intertidal zone, the gull colony and the meadows. In the intertidal I counted the number of organisms that were known to be eaten or were highly suspected to be eaten by the crows in $1m^2$ plots. Five plots were placed randomly at the 1m and 3m tide levels each week between 28 April and 19 July 1978 on Camp and Northwest Bay beaches.

In the gull colony I determined the availability of food of the crows on a weekly basis by counting food items (fish, meat and viscera, invertebrates, etc.) along a 1 x 100m transect in a randomly chosen site from 28 April to 16 July 1978. All items were air dried and weighed. The contents of 56 Glaucous-winged Gull nests were also recorded once every 3 to

9 days from the initiation of egg laying (27 May) until most eggs had hatched and the crows' nesting season had ended (7 July).

Relative availability of the invertebrate fauna in the meadows was determined each week from April to July 1977-78 by sweep netting along an approximately 250m transect for one half hour on calm and sunny days. Ten pit fall traps were opened from dawn to dusk on the same day as the sweep netting took place. These sampling techniques were used because of the crows' diversified diet, which includes spiders, beetles, and caterpillars.

Results

1. Displays

The displays of the Northwestern Crow are generally similar to those of other corvids (Coombs 1960, Goodwin 1976).

defensive threat

The defensive threat (Goodwin 1976) of the Northwestern Crow involved the erection of the head and neck feathers, holding the head over the shoulders, and pointing the bill down at about a 10 degree angle from the horizontal (Figure 4a). This posture is the typical defensive threat posture of many corvids (Goodwin 1976). This display was mostly used by males when another crow entered or approached the territory, in defense of a food item, and before or after a fight or chase. Coombs (1960) called the similar display in the Rook (C. frugilegus) "feather fluffing". It appeared to be a display of uncertainty as to whether it should fight or flee.

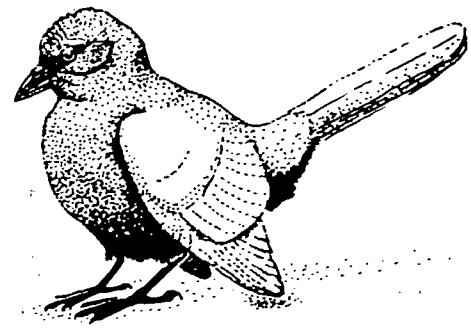
During escalation of a territorial dispute the tail was raised to a maximum of 45 degrees above the horizontal and the wings were drooped until they nearly touched the ground (Figure 4b). I could not hear any vocalizations. The relative intensity of the display could be determined by the angle of the tail; the greater the angle of the tail the greater the display intensity. Brown (1963) found that the Steller's Jay (Cyanocitta stelleri) erected its crest with increasing display intensity.

bowing

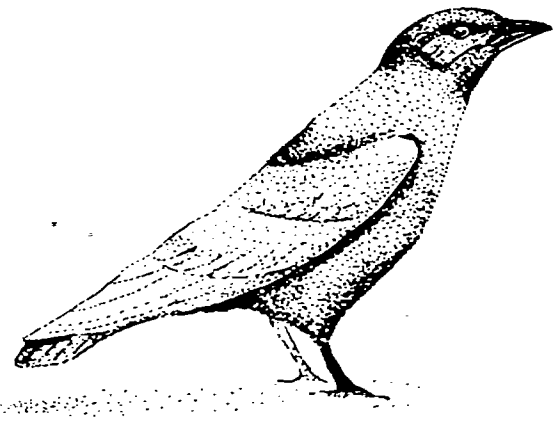
Bowing involved leaning the body forward while holding the

Figure 4. Social displays of the Northwestern Crow. a) mild defensive threat display (feather fluffing), b) intense defensive threat display, c) dominance display, d) subordination display. (see text for details. Displays a and c redrawn from photographs).

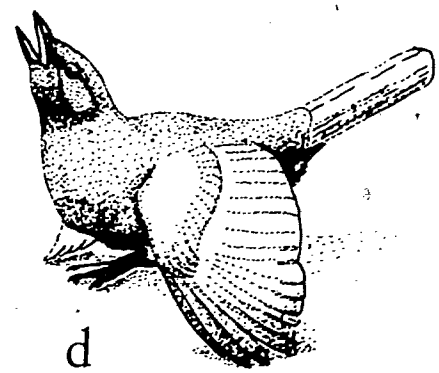
a



b



c



d

bill horizontal and partially fanning the tail. The breast feathers were drooped over the legs. While in this position the crow quickly snapped its head and forward part of the body up and down. With each raising of the body the crow uttered a drawn out "caw". Most often 3 bows of the body were given in about 3 secs. The Rook performs a similar display (Coombs 1960) but spreads its tail more widely than the Northwestern Crow. Goodwin (1976) refers to similar displays in other corvids as self-assertive displays although he does not mention any accompanied vocalization. Bowing was used to indicate territorial possession and social dominance. Both males and females performed the displays but it occurred mostly in males. Yearlings associated with territorial crows performed the display toward intruders on their parent's territory.

tail flipping

This display involved rapid spreading of the rectrices followed by their quick, but decidedly slower, closing. This behavior closely resembles the tail flipping display of the Carrion Crow (C. corone) (Coombs 1960). Tail flipping often followed a bout of bowing displays although it was also directed at rival or subordinate birds.

head-up

Dominant birds displayed to subordinates by holding their bodies in an erect posture so that the bill was directed slightly above horizontal and the head feathers were sleeked (Figure 4c). Males often performed this display in disputes over food items on the beach. Marler (1961) has shown that

variations in the head-up behaviour is used widely among passerines as a dominance display.

bill wiping

Bill wiping on a rock or perch often concluded a successful confrontation by a territorial male and may function as a displacement activity similar to grass-pulling behaviour between territorial male Herring Gulls (Larus argentatus), (Tinbergen 1960).

subordination

A submissive crow displayed to a dominant individual by crouching until the belly nearly touched the ground, raising the tail slightly above horizontal, and tilting the head so that the bill pointed nearly vertically (Figure 4d). The submitting bird uttered calls that resembled those of begging nestlings. This behaviour was seen only on rare occasions.

pre-copulation

Only forced copulation attempts were witnessed. One series of displays that ceased before coition so closely resembled that of the forced copulation attempt that I believe it was part of a copulatory behaviour. I have described this behaviour later (See courtship).

2. Territory

The Northwestern Crow defends a nesting territory against all adult crows and yearlings other than their own. The average area of 29 territories was 0.5 ha (range = 0.18-1.07) (Table 3). Nests were not always located in the center of a territory probably because of a shortage of suitable nesting sites. This created a clumping of nests in the shrubbery and treed areas with the territorial boundaries extending over the surrounding open areas. The mean distance to the nearest nest from 23 nests in continuous woodland in 1978, was 21.8m (range = 7.0-54.0). The distance between nearest nests, regardless of location in 1978, ranged from 7.0 to 168.0m (N=37) (Figure 5).

The location of the nests and the territorial boundaries were modified from year to year (Figure 6). Boundaries of nesting territories located adjacent to the beaches extended only about 2-3m into the intertidal. The remaining portion of the intertidal was a communal feeding area for all crows, although crows from territories adjacent to that stretch of beach showed a degree of dominance over other crows. This dominance was expressed by chasing or supplanting less dominant crows from their feeding location on the beach, although the same crows would at times alight within 2m of the dominant crow and continue feeding. One pair that nested adjacent to a stretch of beach terminated or initiated 25 of 29 intertidal feeding bouts in this area. Eight of these 29 feeding bouts resulted in the dominant bird chasing other crows on the beach upon return from its land based territory. Crows from territories located further inland

significantly avoided the beach adjacent to nesting crows and foraged on an unoccupied part of the beach ($X^2 = 24.6$, d.f. = 1, $p < 0.01$). Most territorial defense is performed by males (Table 4).

Table 3. Mean percentage of territorial area composed of beach, grassy meadow, rocky meadow, and shrub or tree. The beach category includes the area bounded by the upper limit of driftwood and an imaginary line 3m below the lower limit of driftwood. Grassy meadow is dominated by herbs and grasses, rocky meadow is dominated by exposed rock among grasses and herbs, and shrub-tree is enclosed by shrubs and trees that are taller than 1m.

	habitats					
1976	beach	grassy meadow	rocky meadow	shrub & tree	N	mean territory area (ha)
mean	10.9	63.5	16.7	8.9	9	0.41
range	(0.4-34.8)	(0-98.0)	(0-60.4)	(0.5-17.7)		(.18-.71)
1977						
mean	15.1	47.3	28.3	10.2	8	0.46
range	(0-34.8)	(0-77.0)	(0-69.8)	(2.4-18.0)		(.26-.71)
1978						
mean	6.9	41.0	37.0	15.1	12	0.62
range	(0-31.4)	(0-98.4)	(0-73.7)	(0.6-26.3)		(.31-1.07)
overall mean						.50

Figure 5. Internest distance (m) between 37 nearest nests located in all habitats in 1978.

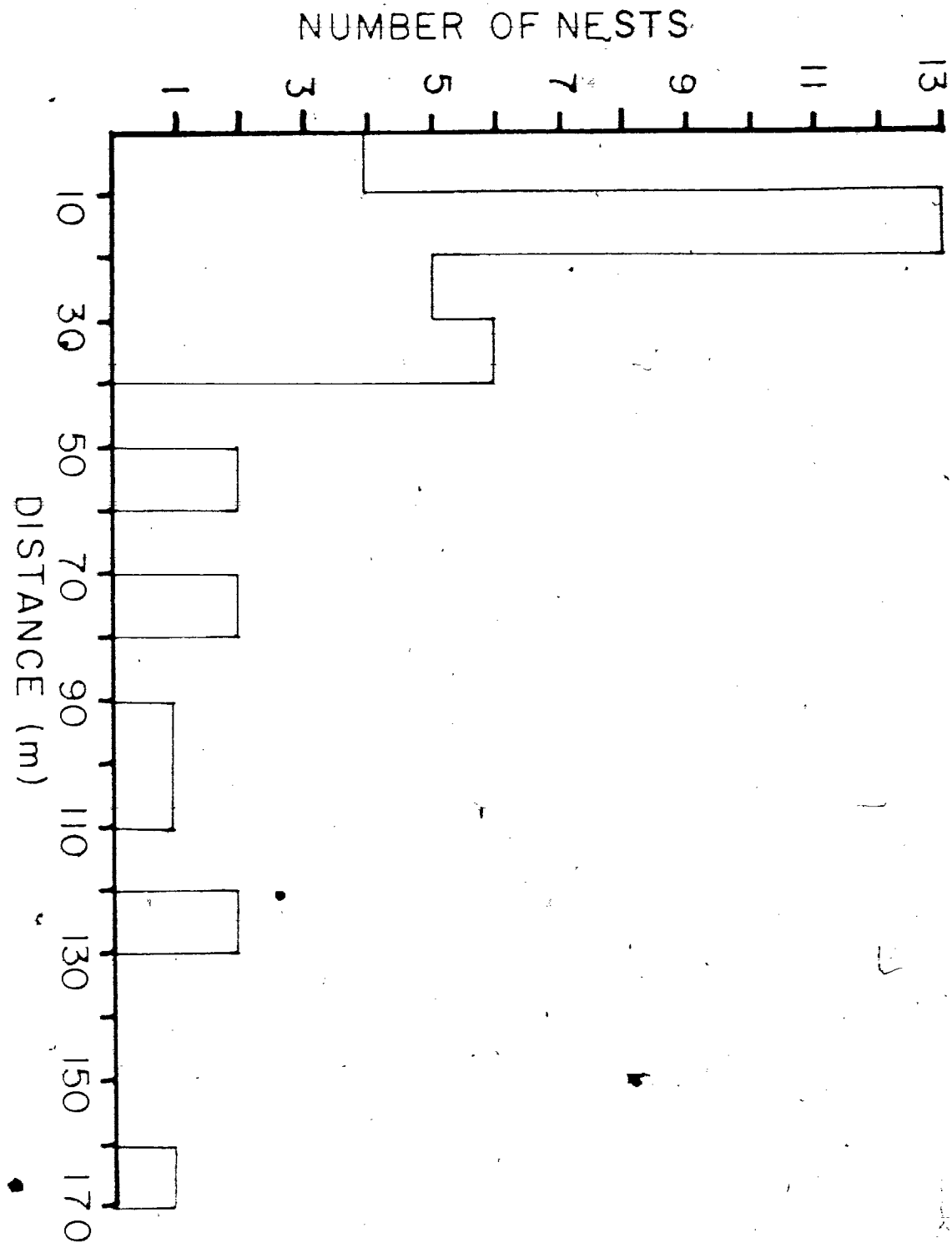

NUMBER OF NESTS
1
3
5
7
9
11
13
DISTANCE (m)
10
30
50
70
90
110
130
150
170

Figure 6. The locations of some nesting territories in 1976-78. Dashed lines (---) = territory boundary, closed dots (•) = nest site.

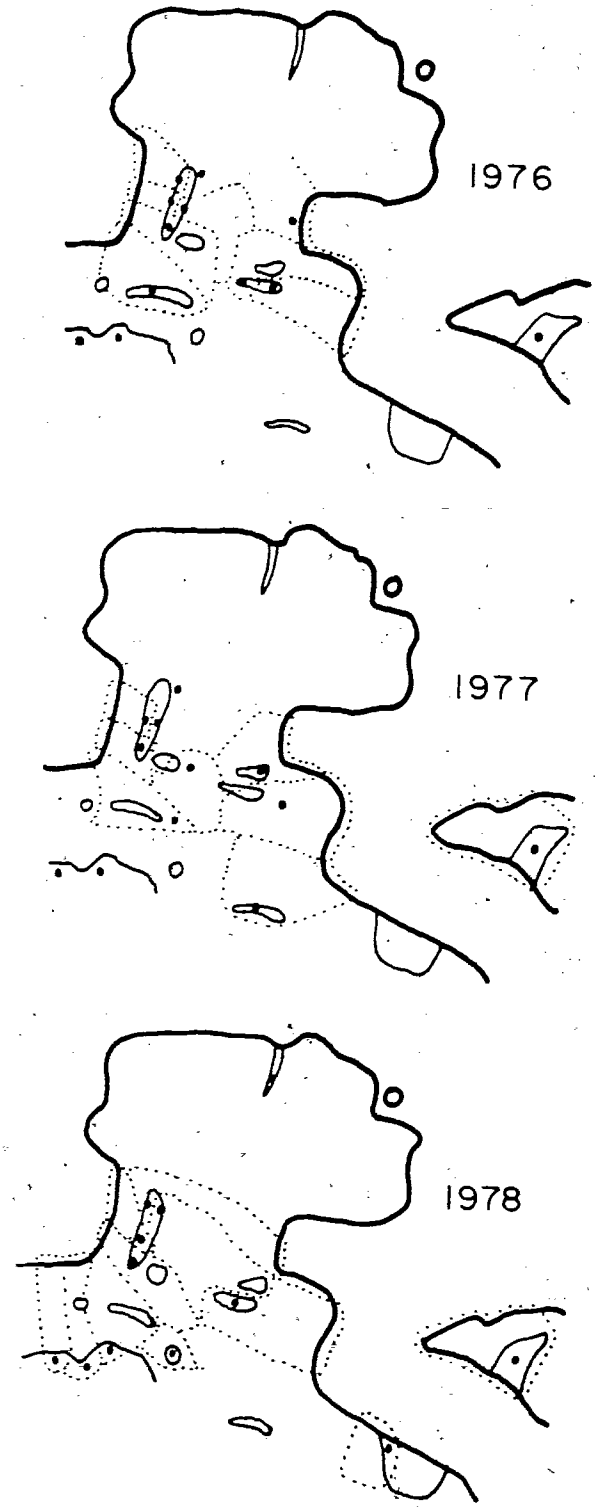

1976
1977
1978

Table 4. Observed participation in territorial defense encounters at 1 nest with a helper and 14 nests without helpers.

	Nests with helper	Nests without helper
male	21 (55.3%)	31 (79.5%)
female	12 (31.6%)	8 (20.5%)
helper	5 (13.1%)	- -
No. of defensive encounters	38	39

Territorial aggressiveness began to decline when the young were about to leave the nest. The first time that the male of a very frequently watched pair tolerated another crow on his territory was when his nestlings were 18 days old. After leaving the nest the young developed their flight abilities and began to follow their parents about the island. This resulted in minor skirmishes, mainly between adults. Trespassing young appear to be much more tolerated than adults. By mid-July most young began to feed regularly outside of the territory and by mid-August intruding adults and young were tolerated within 2m of the territorial pair. By this time the males returned to the territory for about ½h near sunrise and sunset where they called at passing crows but allowed penetration of the territory on the ground. As the tides dropped the crows moved from the territory on to the beach and crows holding beach territories encountered more trespassing crows during low tides than during high tides (Figure 7). Most low tides occurred in the late morning (Figure 8).

Figure 7. Number of encounters (fights, chases, displays) between 14 pairs of crows holding beach-edge territories and trespassing crows versus tidal position from 1 May to 30 June 1977-78. (Data based on 119h. of observation equally spaced through the day).

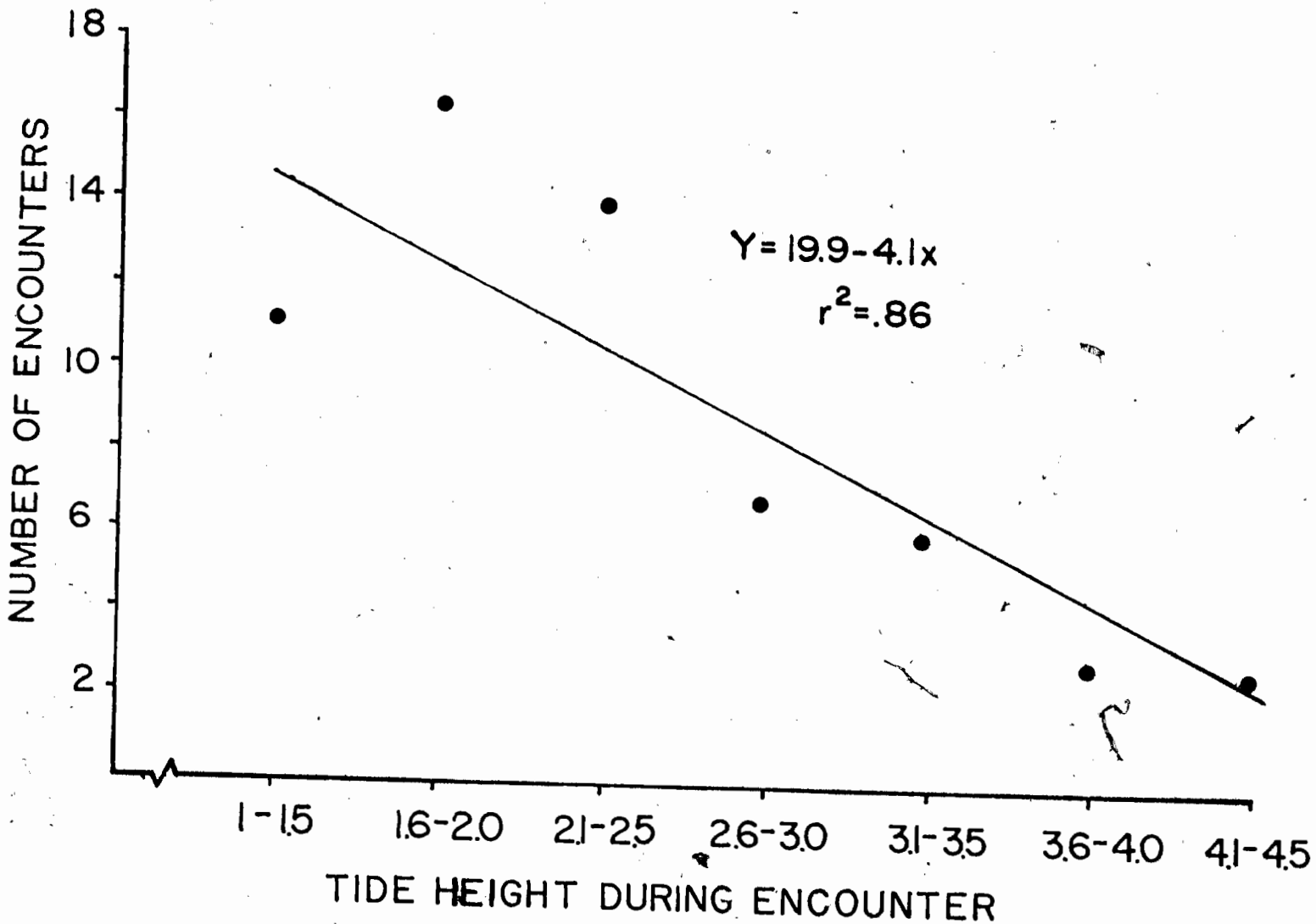
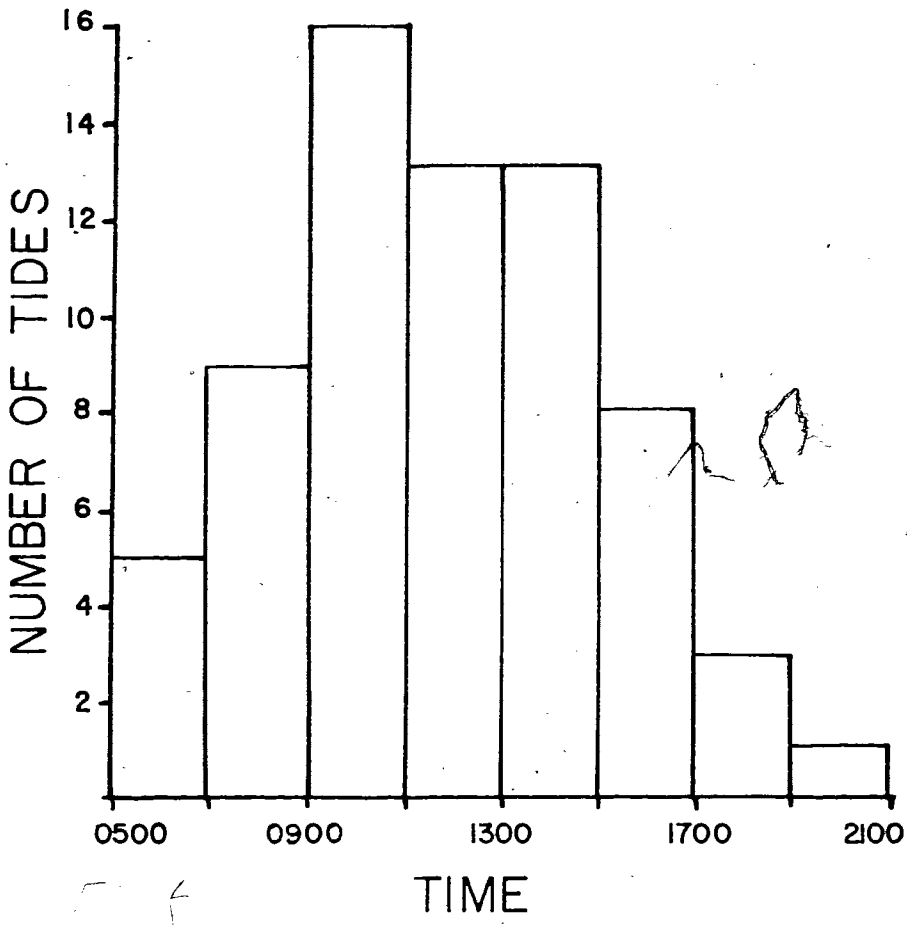

NUMBER OF ENCOUNTERS
18
14
10
6
2
Y= 19.9-4.1x
r²=.86
1-1.5
1.6-2.0
2.1-2.5
2.6-3.0
3.1-3.5
3.6-4.0
4.1-4.5
TIDE HEIGHT DURING ENCOUNTER

Figure 8. The number of tides below 2.5m between 1 May and 30 June 1977, versus time of day.


16
14
12
10
8
6
4
2
NUMBER OF TIDES
0500
0900
1300
1700
2100
TIME

3. Courtship

The female begged sporadically of the male during nest building and was not fed until after the nest was near completion or was finished. At one nest the pair finished building the nest on the morning of 1 May and the female began begging in the afternoon. The following morning she was fed for the first time on the territory. On 3 May the first egg was laid and the female vigorously begged and was fed several times. Goodwin (1976) states that in most, if not all corvids, begging is characteristic of laying or incubating females.

No copulations were witnessed although pre-copulatory behaviour was seen once. On 30 April 1978 a male crow flew to his territory with a Red Rock Crab (Cancer productus) pincer and passed it to the female. While she was engaged with caching the pincer the male found a snail (Haplotreme sp.) which he also passed to her. She repeated the storing behaviour with the snail but then walked away with it. The male followed her and together they pecked uneasily at the snail in a clump of grasses. Both birds then bowed forward with their tails spread, wings drooped, and their bills opened but directed downward. The female's tail quivered for approximately 2 secs. and then she resumed pecking actions at the snail. Tail quivering is a widespread pre-copulatory behaviour among corvids (Goodwin 1976). About 30 secs. later the female bowed once more and the male preened her back for 1-2 secs. Then he stepped onto and over her back to the opposite side. Both crows poked in the grasses for another 2-3 mins. and then departed. Interestingly this female's

eggs were never fertilized and were abandoned in the nest after 30 days of incubation. Rowley (1973) has suggested that courtship on the ground should occur in corvids with small nesting territories.

At one regularly watched nest the first egg hatched on 26 May and the lone surviving nestling fledged on 23 June. The female of that nest begged and was fed by the male until 5 June. The female begged for the following 7 days but was not observed being fed. Begging occurred on the nest until the first egg was laid and then begging and feeding occurred on the territory or on the beach. Verbeek (1973) has suggested that the female Yellow-billed Magpie (Pica nuttalli) vigorously begs to her mate during egg laying so that he will continue to feed her through the incubation period. I suggest that begging may also habituate predators to begging adults so that the begging young are ignored later in the season.

Mated pairs allopreen each other usually in the head and neck region. Solicitation behaviour involved one member of a pair approaching the other with its head and bill directed down and the nape feathers erected. A solicitor appeared to be entranced by the preening behaviour of its mate. Allopreening occurred throughout the nesting season.

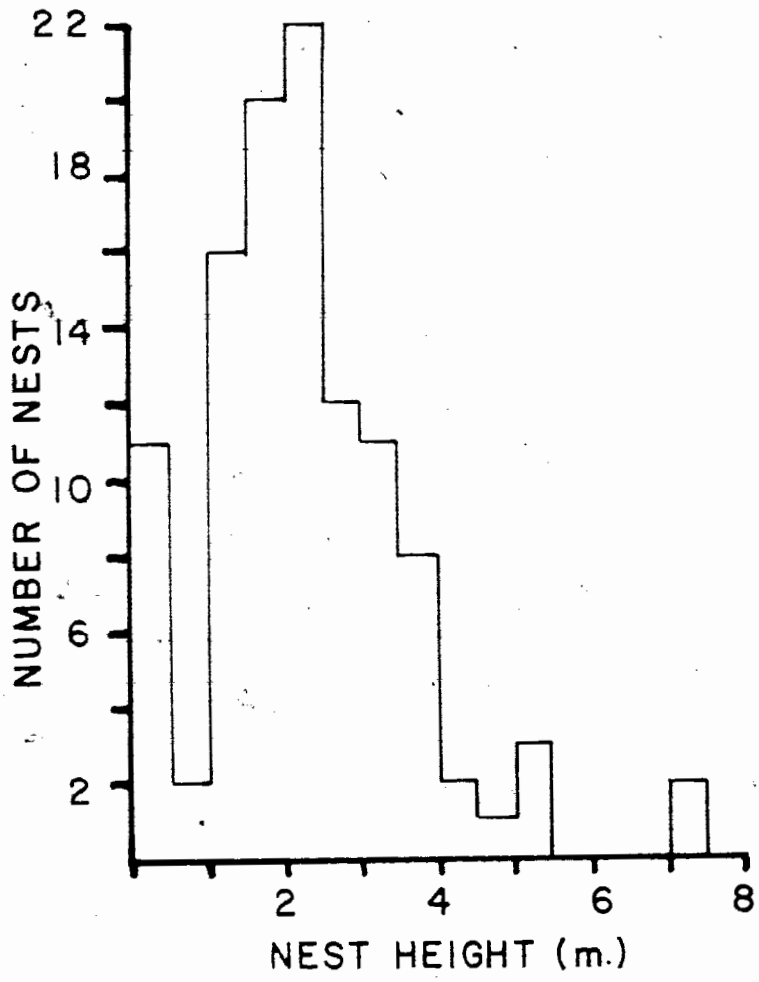
I saw one case of an attempted rape of a female by a strange male on 1 May 1977. The female was sitting on a post in the corner of her territory when a strange male arrived from the beach. The female moved to a new position on the post which allowed the male to alight. The male then spread his wings and

tail, pointed his bill down and opened it slightly but I did not hear him call. He then rocked his body up and down two times before stepping on to the female's back. The female pointed her bill up and crouched so that her back was horizontal. The male held her napewith his bill and attempted to copulate with her. The female began giving distress calls which brought her mate from the territory where he had been concealed by the tall grasses about 50m away. The rapist fluttered to the ground and was quickly chased from the territory by the male. Both members of the pair then flew to the center of their territory where the female begged and was fed by her mate. The raped female had not begun egg laying. Whether the rapist's nest contained eggs is unknown. Attempted rapes of incubating females occurs in the Rook (Coombs 1960), the Raven (C. corax) (Kramer 1932), the Carrion Crow (Wittenberg 1968), and the Yellowbilled Magpie (Verbeek 1973).

4. Nest

The nest of the Northwestern Crow is similar to that of the Common Crow (Bent 1946, Emlen 1942). A typical nest is made with sticks, blackberry vines, or grass stems on the bottom and sides. The first placed twigs are occasionally driftwood sticks. Inside this stick construction was a thin layer of grass and mud. In 1976 all 32 nests were built with about 0.5cm diameter twigs and lined with western red cedar (Thuja plicata) bark. Thirteen nests contained gull feathers, 12 held moss, 8 had grass stems and leaves, 7 contained crow feathers, 2 had wool fibres, 2 had trailing blackberry (Rubus ursinus) vines, and 1 had paper in its construction. The inner cup was composed of fine strips of cedar bark upon which a fine, loose mat of plant fibres was placed. One new, but unused, nest was dismantled and its parts were weighed. The outer structure of twigs and blackberry vines weighed 674g while the inner cup, made of earth, cedar bark, and grass weighed 338g. The overall nest weighed 1012g. There were 236 twigs, and 286 strips of cedar bark. The nest material came from both on and off the territory. Some twigs came from the beach while the remaining ones were broken from trees or shrubs near the nest. N. Verbeek (pers. comm.) has seen crows dismantling old nests and reusing the parts in new nests on Mandarte Island. Cedar bark was stripped from driftwood logs and moss was collected on the rocky meadows. The distance from the ground to the nest rim of 110 nests in 1976-78 is shown in Figure 9. Ground nesting has been reported in this species (Darcus 1930, Drent et al. 1964). The mean nearest internest

Figure 9. Distance from the ground to the nest rim of 110 Northwestern Crow nests in 1976-78. The first interval includes nests built on the ground.


22
18
14
10
6
2
NUMBER OF NESTS
2
4
6
8
NEST HEIGHT (m.)

distance to 10 nests located within 50m of the beach (i.e. mostly from territories that were adjacent to the beach) in 1978 was 69.8m (range = 3.0-168.0), while 27 nests located farther than 50m from the beach in 1978 had a mean internest distance of 29.3m (range = 7.0-96.0). Inland nests were significantly closer to each other than nests in beach territories (t-test, $p < 0.01$).

The mean measurements of 23 newly built nests in 1976 were 8.9cm (7-11) for an inner cup depth, a cup diameter of 16.4cm (14-20), an overall nest depth of 22.1cm (12-30) and an overall nest diameter of 33.2cm (24-45). In 1976, 15 nests were built in shrubs, 13 in trees, 4 on the ground, and 1 on a rock ledge. Two of the new nests were built on top of previous years' nests. In 1977 13 nests were built in shrubs, 11 in trees, and 7 on the ground. In 1978 the ground was very wet during nest building and only 2 nests were built there and both of these were built on top of the 1976 nest but no old nests were reused.

Nests in trees appeared to last 3 to 4 years while nests on the ground did not last the year. One nest had a second, presumably, new nest about 2m away and at the same height. Good (1952) found a nesting pair of Common Crows that partially built 4 nests before finally using one for egg laying.

Near Vancouver, B.C. I have seen Northwestern Crows building nests as early as 7 March. One pair built a nest in 19 days. On Mitlenatch Island in 1977 the first crows were lining their nests during the last 2 weeks of April. In 1978 the first nests were completed in the last week of April. Some evidence

suggested that more nest building occurred during sunny periods than on overcast ones. On 30 April the sky was cloudy during approximately 45 mins. of observation and no crows were nest building. By approximately 1015h the sky cleared and 4 pairs began gathering nest material and flew to their nest sites during 75 mins. of observation.

The female Northwestern Crow carried most of the nest material (17 out of 20 trips) and did most of the building although the male accompanied her while she tended the nest. It is uncertain why the male accompanies the female to the nest but it may be to guard against her being raped by other males or to act as a sentinel against predators. One pair of crows made 7 trips to the nest in 1 h during their most active nest building period. The mean time spent at a nest by 1 pair was 2.05 mins. (1-6) in 32 visits. Most building occurred in the morning or late afternoon to early evening and was interspersed with bouts of foraging.

5.. Eggs and Incubation

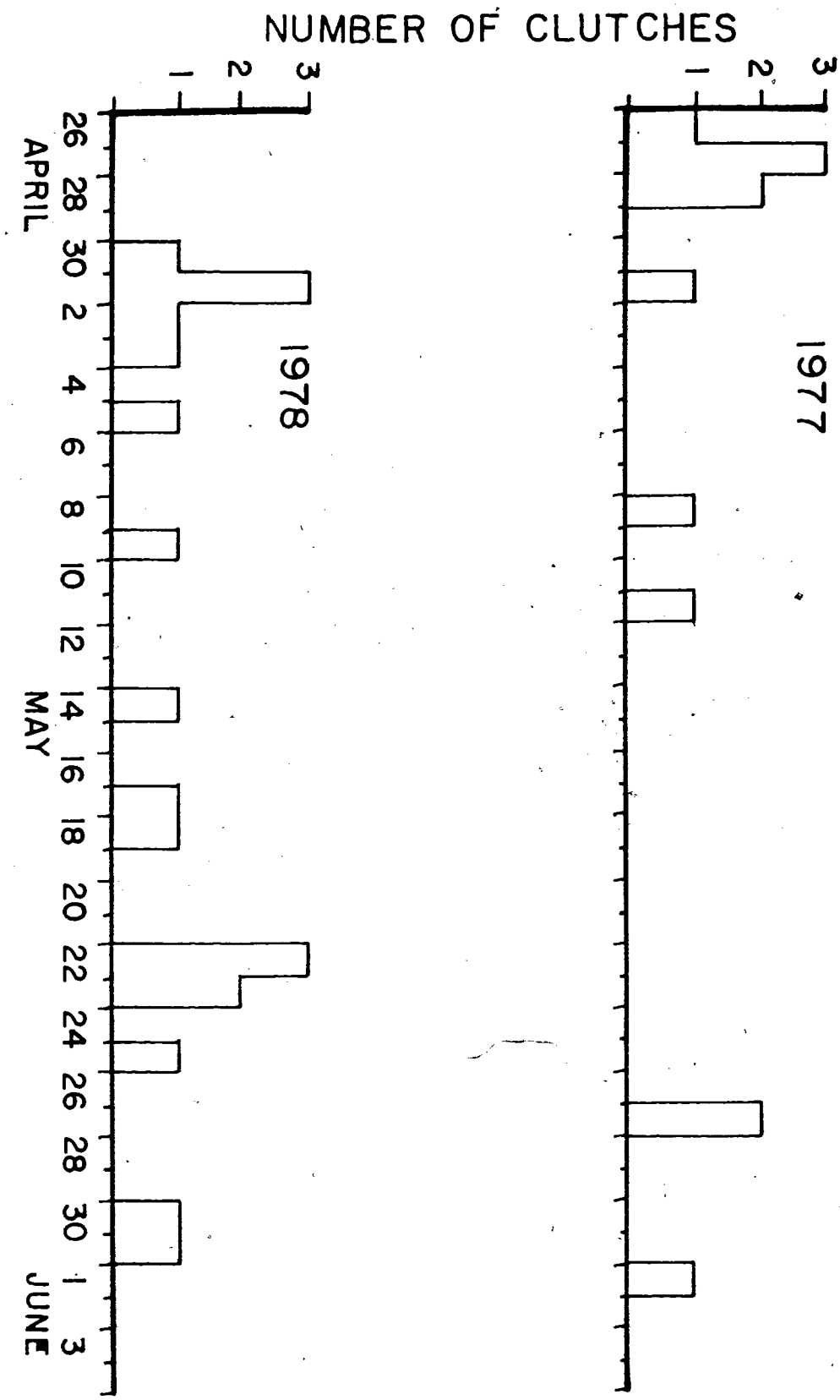
Female Northwestern Crows began to lay their eggs shortly after completion of nest building. The mean interval between nest completion and egg laying in 15 nests was 8.6 ± 1.5 days (1-20) assuming that the eggs were laid at a rate of 1 per day. Of these 15 nests, 6 were built in newly established territories (i.e. unoccupied areas in the previous year), 7 were built in the same territory as the previous year, and 2 were found in territories where the ownership was uncertain in the previous year. The mean interval between nest completion and egg laying was 12.3 ± 1.5 days (1-20, SD=6.6) in 10 newly established territories and 5.3 ± 1.5 days (2-10, SD=3.2) in 8 previously occupied territories. This difference is significant (t-test, $p < .001$) and may be due to higher metabolic costs required to establish a new territory. It is unknown whether one or both members of the pair were present in the same territory in successive years in the reused territories.

Breeding synchrony is best measured by the occurrence of first clutches in a population (Woolfenden 1973). Twelve first clutches in 1977 and 19 first clutches in 1978 were initiated over a 37 and 32 day span, respectively (Figure 10). Drent et al. (1964) reported a span of 6 weeks over which this species began egg laying on Mandarte Island. This is much shorter than Emlen's (1942) findings for the Common Crow. He found that egg laying in this species covered 58 to 60 days with all first clutches being initiated in the first approximately 23 days.

Drent et al. (1964) said that most clutches (16 of 18) of

the Northwestern Crow on Mandarte Island were initiated between the last week of April and the first week in May although the egg laying period lasted for 6 weeks. This is contrary to my findings for this species on Mitlenatch Island (Figure 10). The extended period of clutch initiation on Mitlenatch Island in 1977 and 1978 is apparently a result, in part, of territorial establishment. During territorial establishment and nest building in the spring of 1977 the weather was dry and warm (Table 1). Cortez Island, 6km north of Mitlenatch Island received 40% less rainfall in April 1977 than normal (Department of the Environment 1977). This allowed some crows to build nests on the ground (7 out of 31 nests). In 1976 and 1978 the weather was wetter (154% more rain than normal fell on Cortez Island in 1978) (Department of the Environment 1976-1978) and fewer nests were built on the ground (4 out of 33 in 1976, and 2 out of 65 in 1978). In years with dry spring seasons the competition for tree nest sites would be reduced because some crows could nest on the ground. The wet spring in 1976 and 1978 reduced the number of nest sites (on the ground) and competition appeared to be more severe for tree sites. Of the 7 pairs of crows in 1978 that began egg laying early (prior to 7 May), 6 built in the same territory as the previous year in 1977 (1 is uncertain). (I assume that at least one member of the pair returned to the territory because two crows banded as a nestling in 1965 and 1970 used the same territory in every year that observations were made). Of 12 pairs that began egg laying after 7 May 1978, 8 were in newly established territories

Figure 10. Clutch initiation dates for first clutches of the Northwestern Crow on Mitlenatch Island.


NUMBER OF CLUTCHES
1
2
3
1978
1977
APRIL
MAY
JUNE
26
28
30
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
1
3

(i.e. not used in 1977), 2 were in the same territory as the previous year, and 2 are uncertain.

The mean difference in dates of clutch initiation for nests built in the same territories in 1977 and 1978 was an average of 3.5 days (range = 1-9, N = 12). A comparative figure is not available for crows that changed territories because very few crows that were banded as nestlings in 1976 survived to adulthood in 1978.

The Northwestern Crow is single brooded but will lay replacement clutches when disturbed. Although the data are limited, egg laying appeared to occur at approximately 24h intervals, which is typical of most (if not all) corvids (Goodwin 1976) and passerines (Welty 1975). Eggs were laid in the early morning. The mean clutch size for 16 nests in 1977 and 25 nests in 1978 found during incubation or during laying prior to incubation was 3.7 and 3.8 eggs, respectively. Seven nests contained 5 eggs, 22 held 4 eggs, 8 had 3 eggs, 3 held 2 eggs and one contained 1 egg. The 1 egg clutch was laid in a poorly built nest that began to fall apart during incubation. The egg failed to hatch. This nesting attempt may indicate inexperience by 1 or both members of the pair. Drent et al. (1964) reported a clutch size of 4.3 eggs for 8 nests of this species.

Clutches were significantly larger (t-test $p<0.10$) in territories adjacent to the beach (mean = 4.0, N = 19, range = 2-5, SD = 0.97) than in the inland territories (mean = 3.5, N = 21, range = 1-5, SD = 0.81) when the data from 1977 and 1978 are pooled.

The mean weight of 11 eggs found before incubation had begun was 18.8g (17-20). Emlen (1942) gives an average weight of 16.6g for 157 fresh Common Crow eggs (12.5-21.3). The eggs of the Northwestern Crow lost an average of 16.3% of their weight during incubation, or 0.17g per day (Figure 11). This conforms closely to the figure of 18% weight loss during incubation given by Rahn and Ar (1974) for 475 species of birds. Parmalee (1952) found a weight loss of 2.8g (sic) per day (probably 0.28g) during incubation of Common Crow eggs.

Only females incubated and they appeared to be very attentive to their eggs (Table 5). The mean incubation period defined as the time between the laying of the last egg until that egg and all other eggs hatched in the clutch for four clutches was 18.0 days (17-20), which is slightly more than the 16.8 days (N=12, range = 16-18) for the Common Crow (Emlen 1942). One infertile egg was incubated for 33 days in 1977 and weighed less than 9.0g when it disappeared from the nest. In 1978 one female sat for at least 30 days on an infertile clutch of 3 eggs before abandoning them. Common Crows have been reported to sit on infertile eggs for up to 32 days (Emlen 1942).

The eggs in a clutch of the Northwestern Crow hatch asynchronously. On numerous occasions when I visited nests in the afternoon during the crows' egg laying stage I found 1 or 2 cool eggs but these same eggs were warm or the female flushed from the nest when 3 or more eggs were present. I also rarely saw one newly hatched nestling in a nest, that held 2 or more eggs, without a second nestling of the same weight or a

Figure 11. Weight loss of Northwestern Crow eggs during incubation.
(0 = 4 eggs, ■ = 3 eggs, ▲ = 2 eggs,
● = 1 egg).

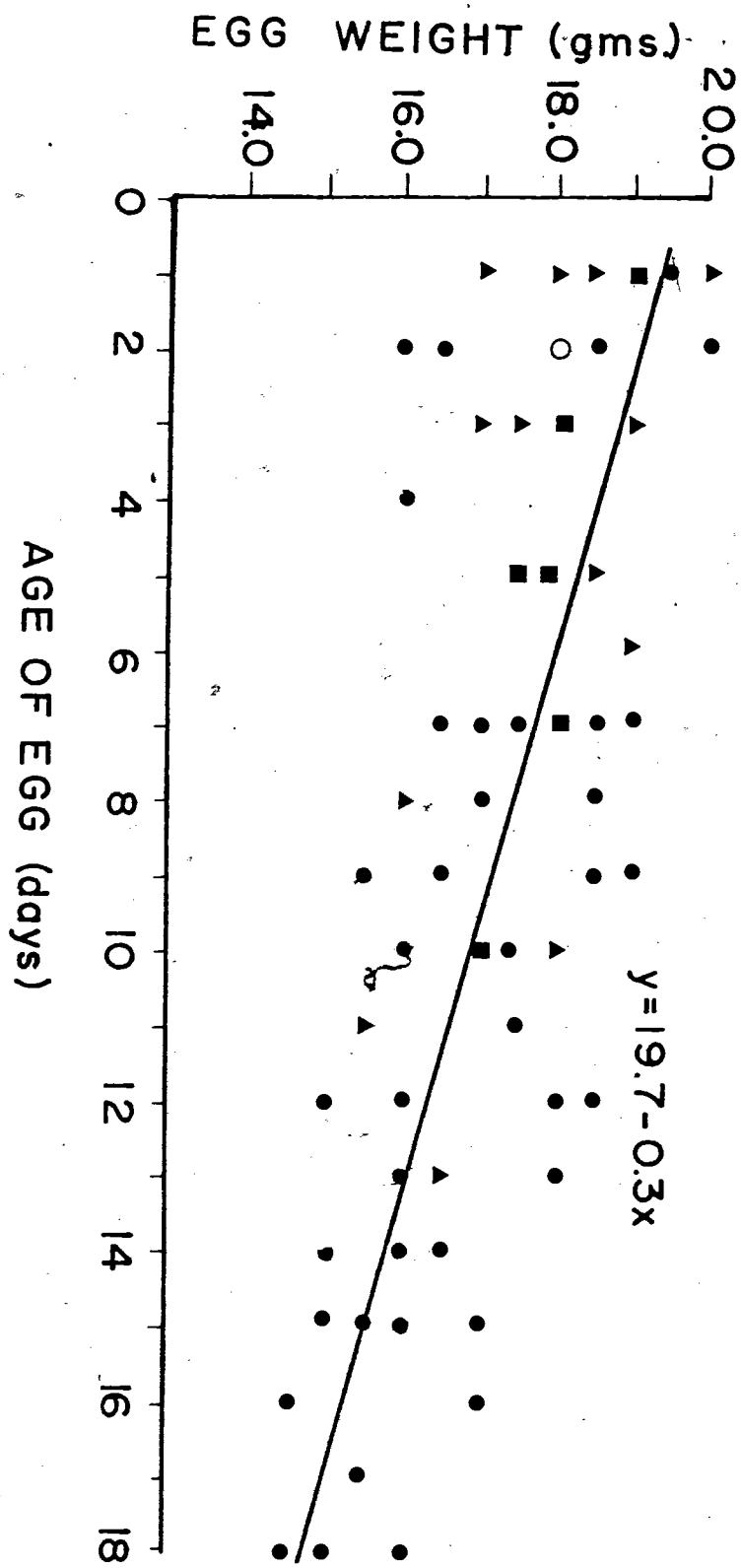

EGG WEIGHT (gms.)
14.0
16.0
18.0
20.0
0
2
4
6
8
10
12
14
16
18
AGE OF EGG (days)
y=19.7-0.3x

Table 5. Nest attentiveness of 3 female Northwestern Crows to their eggs during incubation in 1976 and 1978.

Age of egg[1]	No. of obs. mins.	No. of mins. on nest	% attentive
1	120	112	93.3
5	161	154	95.7
6	120	112	93.3
7	338	284	84.0[2]
14	240	233	97.1
15	120	100	83.3

[1] number of days following the commencement of full incubation.

[2] part of the time was spent off the nest pursuing a crow that had penetrated into the territory.

dipping egg. This evidence suggests that females begin full incubation after laying the third egg in most clutches.

Table 6 shows the fate of 146 eggs from 39 nests in 1977 and 1978 from laying until hatching. Emlen (1942) found that 68 out of 77 (88%) eggs that were laid in 22 Common Crow nests hatched compared to 45.8% (average of 1977 and 1978) in this study. Nice (1957) obtained a hatching success of 60% for a large number of open nesting, altricial birds. I also found a higher degree of hatching failure (average of 1977 and 1978 = 17.9%) in the Northwestern Crow than Emlen (1942) found for the Common Crow (12.0%).

Table 6. Summary of the egg stage of the Northwestern Crow in completed clutches (percent of eggs laid)

	1977	1978
Number of nests	16	23
Number of eggs laid	59	87
Number of eggs lost	17 (28.8)	38 (43.7)
Number of eggs remaining at time of hatching [1]	42 (71.2)	49 (56.3)
Number of eggs failing to hatch	11 (18.6)	15 (17.2)
Number of hatched eggs	31 (52.5)	34 (39.1)

[1] assuming an incubation time of 18 days for infertile eggs

6. Nestlings

a) brooding

Only the female Northwestern Crow brooded the nestlings. She remained very attentive to the nestlings until they were about 10 days of age (Table 7), after which the female increased her share of feeding the nestlings. The female Common Crow broods the nestlings for 9 to 14 days (Emlen 1942). When the ambient temperatures exceeded 20°C the young spread themselves over the nest rim in an attempt to cool themselves in a similar fashion to Scrub Jay nestlings (Woolfenden 1978).

b) growth of the nestlings

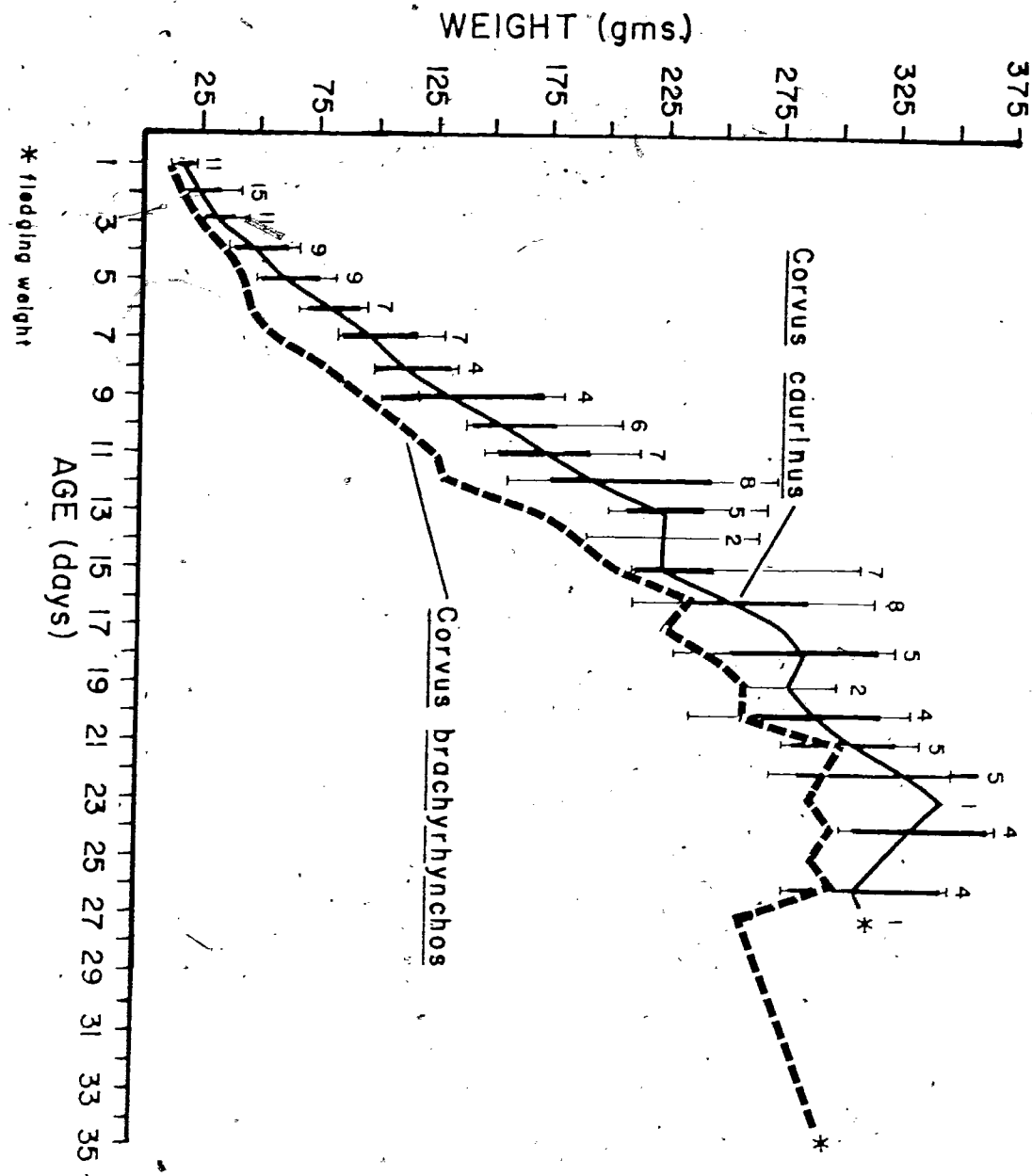
There is a trend, based on small samples, for Northwestern Crow nestlings to gain weight more quickly than Common Crow nestlings (Figure 12). The weight of Common Crow (Emlen 1942) and the Northwestern Crow nestlings declined in the last week to 10 days of nestling life. Using Ricklefs (1967) method of estimating the asymptote of growth cruves the Northwestern Crow fledges at 318.1g and the Common Crow at 300.0g. Interestingly, though, the Northwestern Crow nestlings fledge about one week earlier than Common Crow.

For the first three days after hatching the nestlings were pink skinned and their eyes were closed. Tufts of down feathers grew from the head, dorsal region and the wings, and the chicks held their heads up for less than about 10 s during gaping. They uttered weak squeaking calls. By the fifth day the young were grey colored, their eyes were tiny slits, and the first pin feathers began to erupt through the skin. Their eyes opened

Table 7. Nest attentiveness of 3 female Northwestern Crows during brooding in 1976-78.

nestling age (days)	No. of obs. mins.	Female on nest	Percent attentive
1	381	359	94.2
2	140	129	92.1
3	315	298	94.6
5	210	188	89.5
8	40	32	80.0
9	98	90	91.8
11	123	64	52.0
12	122	62	50.8
13	105	43	40.9
14	236	12	5.1
17	70	21	30.0
18	200	27	13.5

Figure 12. Weight gain by nestling Northwestern Crows in 1977 versus the Common Crow derived from Emlen's (1942) study.


WEIGHT (gms.)
25
75
125
175
225
275
325
375
AGE (days)
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35
Corvus caurinus
Corvus brachyrhynchos
* fledgling weight

and the iris was blue coloured by day 7. Parmalee (1952) said that the eyes of 8 Common Crow nestlings began to open between the 10th and 12th day although one bird's eyes began to open by the 6th day. Emlen (1942) found that the eyes of Common Crow nestlings in California were slits by 8 days of age and began opening when they were 11 days old. The iris of the Northwestern Crow began to turn brown by 80 days of age.

The feathers of Northwestern Crow nestlings first erupted from the sheaths by day 9 which is 6 days earlier than the Common Crow (Emlen 1942). On day 12 the nestlings crouched at my presence at the nest and gaped reluctantly. This same behaviour begins at 18 days in the Common Crow (Emlen 1942). Secondary flight feathers were approximately one quarter unsheathed by 15 days, half unsheathed by 18 days and the wing tips were longer than the tip of the tail near fledging at 20 days.

The tarsus grew quickly and attained adult length at fledging (Table 8). Most of the growth (92.6%) in length occurred before day 18 and at about this age the nestlings began to defecate over the nest rim. Nestling crows leave the nest before they can fly and must have strong, well developed perching abilities at this age.

c) egg and nestling loss

Fewer eggs and nestlings were lost in 1977 than in 1978 (Tables 6 and 9). Egg losses in 1976 are unknown but nestling losses were higher than in 1977. Losses appeared to occur mostly in the early stages of nestling life probably because of the

Table 8. Changes in tarsus length with age in nestling Northwestern Crows in 1977.

Age (day)	N	mean	range	mean daily increment gain
1	4	12.4	11-15	-
2	4	12.5	11.5-13.5	0.1
3	5	13.4	12-15	0.9
4	6	16.3	14-20.5	2.9
5	5	20.8	17.5-24	4.5
6	6	24.3	21-29	3.5
7	3	26.2	25-27	1.9
8	3	30.0	27-35	3.8
9	3	31.3	25-38	1.3
10	1	37.0	-	5.7
11	2	40.0	39-41	3.0
12	5	40.0	33-44	0
13	1	43.0	-	3.0
14	4	44.3	40-48	1.3
15	4	44.6	42-47	.3
16	4	46.5	45-48	1.9
17	2	50.0	48-52	3.5
18	4	51.0	49-53	1.0
19	2	50.5	49-52	-.5
20	3	50.0	49.5-50.5	-.5
21	2	50.0	49-51	0
22	1	50.0	-	0
23	1	49.0	-	-1.0
24	1	50.0	-	1.0
25	0	-	-	-
26	1	53.0	-	1.5
27	1	52.0	-	-1.0

Table 9. Outcome of 107 eggs followed from hatching to fledging in 1976-78.

	1976	1977	1978	Total
No. of nests	17	13	12	42
No. of eggs hatched	42	31	34	107
No. of nestlings lost	20 (47.6)	10 (32.3)	22 (64.7)	52 (48.6)
No. of nestlings fledged	22 (52.4)	21 (67.7)	12 (35.3)	55 (51.4)
Mean fledging age (days)	27.2	24.8	25.9	26.0
N	11	6	8	25
Range	22-33	23-27	22-31	22-33

combined effect of weather, inattentiveness by the female, the ease of predation on small, helpless young, and other factors. The Carrion Crow in Scotland is highly suspected of intraspecific egg and nestling predation (Yom-Tov 1974). Of 47 nestlings that went missing at a known age 27 (57.5%) occurred within the first week of hatching, 13 (27.7%) between 8 and 14 days of age, 7 (14.9%) from 15 to 21 days, and none older than 21 days from hatching. Nestlings older than 15 days either died in the nest as runts (N = 4) or fell from the nest (N = 3). I fixed pipecleaners snugly around the neck of one 15 day old nestling that had fallen from a nest. Its 3 remaining nest mates also had pipecleaners fitted and I left the birds for 2h to see if the fallen bird would be fed. Although it begged vigorously for the 2h it was never fed although its 3 nest mates were fed. All the nestlings weighed approximately 210 g.

7. Fledglings

Fledging is a gradual process in the Northwestern Crow. At a weight of about 300g the nestlings moved on to the nest rim and into the branches of neighbouring trees and shrubs. I considered that a nestling had fledged when it left the nest during my inspection or perched on the nest rim or was outside the nest. For about 2 to 3 days the young moved back and forth from the nest to the branches until an average age of 26 days when they permanently left the nest. From the shrubs and trees near the nest the young crows begged and called to their parents for food. The first time that a fledgling took to the air from the trees or shrubs was 33 days in 1976 and 37 days in 1977. The fledglings' iris was grey-blue and the lining of the mouth was watermelon-red. The first flight of the young crow was awkward and the adults followed the young calling loudly. Glaucous-winged Gulls that came within about 5m of the young crows were swooped at by the adult crows. When the adults were out of sight of the young the fledglings slept, preened their feathers, or picked and tugged at twigs and leaves. Upon the approach of the adults the young let out a clamour of begging "gaaa-gaaa-gaaa" calls at a rate of about two calls per second while fluttering their wings and stretching their necks in the direction of the adult. The young begged to any passing adult until they were about one week old after which they begged only to their parents. Verbeek (1973) found that young Yellow-billed Magpies begged to strange adult magpies and also to Acorn Woodpeckers (Melanerpes formicivorus) until they were 6 days old,

after which they begged only to their parents.

After about 15 to 20 days of being fed on the territory the fledglings attempted to follow their parents to other locations on the island.

Emlen (1942) found that the Common Crow nestlings fledged on about the 35th day when they weighed about 300 g. The Northwestern Crow nestlings on Mitlenatch Island fledged, an average, at about 318g on the 26th day. The Northwestern Crow on Mandarte Island fledged in about 35 days (N. Verbeek, pers. comm.). In 1977 the first departure from the territory of 10 fledglings from 5 nests occurred at an age of 18 days after fledging (4-25). The low value of 4 days was a fledgling from a nest built on the ground that walked into the gull colony. More young fledged in 1977 than 1978 due primarily, to higher egg and nestling losses in 1978 (Tables 6 and 9).

a) fledging success

Fledging success is defined as the proportion of eggs laid that produce fledglings (Woolfenden 1973). The fledging success of all eggs that were laid by Northwestern Crows on Mitlenatch Island was 27.1% in 1977 and 16.8% in 1978. Emlen (1942) did not give a fledging success figure, as defined by Woolfenden (1973), but reported that 13% of 88 eggs that hatched fledged young. Comparable values for the Northwestern Crow on Mitlenatch Island were much higher, 52.4% in 1976 (N = 17), 67.7% in 1977 (N = 13), and 35.3% in 1978 (N = 12). The reasons for this large difference are not known. Verbeek and Butler (1980) have shown that adult Northwestern Crows that have yearling helpers fledged significantly more young than crows without

helpers but the helper system is not widespread among Northwestern Crows on Mitlenatch Island and would not greatly change the population's overall fledging success.

Upon departure from the territory family groups began to mingle. The mean number of days between fledging and family mixing for 10 fledglings from 5 nests in 1977 was 37.6 days (8-48). Table 10 shows the weekly survival of fledglings in the 9 weeks following fledging in 1976 and 1977. By the end of August most young were feeding themselves although they begged sporadically to their parents. In Vancouver Northwestern Crow young were still begging, although rarely, on 23 September 1978.

Although both mortality and dispersal are probable causes for the decrease in sightings as the weeks progressed, clearly the juvenile Northwestern Crows remained on Mitlenatch Island for a long time.

In a 4 year study of the Florida Scrub Jay (Aphelocoma coerulescens) Woolfenden (1973) found 74% of the young of the year survived the first month, 69% the second month, and 62% lived through the third month. The comparable figures for 54 Northwestern Crow fledglings are similar (first month = 86.6%, second month = 73.6%) to Woolfenden's (1973) findings. Of the 22 colour banded young Northwestern Crows from 1976, 3 were seen in the study area in 1977 and 2 (of the same 3) returned as adults in 1978. In 1977 31 nestlings were colour banded of which 7 returned as yearlings in 1978.

Because the beach appeared to be the favoured feeding location for nesting crows we might expect that nests located

Table 10. Weekly survival of colour-banded fledgling Northwestern Crows.

Week	No. of individuals (%) seen		
	1976 N = 22	1977 N = 31	1976+1977 N = 54
1	20 (90.9)	31 (96.9)	51 (94.4)
2	20 (90.9)	26 (81.3)	46 (85.2)
3	20 (90.9)	26 (81.3)	46 (85.2)
4	20 (90.9)	24 (75.0)	44 (81.5)
5	20 (90.9)	23 (71.9)	43 (79.6)
6	19 (86.4)	20 (62.5)	39 (72.2)
7	19 (86.4)	20 (62.5)	39 (72.2)
8	18 (81.8)	20 (62.5)	38 (70.4)
9	18 (81.8)	20 (62.5)	38 (70.4)

near the beach would be more successful (produce more young) than nests located further from shore. To compare nesting success in territories adjacent to the beach and those further away I divided the nest distances into those located 0-50m and those 51-250m from the beach. All nests within 50m of the beach are not necessarily in territories that abutt against the beach but it does include all nests within territories that are adjacent to the beach. Nests located within 50m of the beach lost significantly fewer eggs to predation (1.05 (N = 21) versus 1.77 (N = 17) (1-tailed Mann-Whitney U test, $p < 0.01$), and fledged significantly more young (1.25 (N = 32) versus 0.47 (N = 23), Mann-Whitney U test, $p < 0.01$) than nests in nonadjacent territories. There is also a trend for nestlings in beach territories to grow faster than nestlings in inland territories. The reasons for these differences are several. The increased flight distance to unoccupied portions of the beach might result in a decreased feeding rate of the incubating and brooding female by the male. She therefore might spend more time off the nest foraging for herself. This would leave the eggs and young more vulnerable to predation and cold.

Not only did the interior nesting crows fly further to the intertidal but they also avoided those portions of beach that were adjacent to crow territories along the shore.

3. Roosting

The seasonal differences in sociality among the adults, yearlings, and young of the year plus the changes in roosting sites of the 3 age classes created a complicated roosting picture. The size of the roost varied from one bird in June to 200 birds by August. Two main types of roosts occurred: territorial roosts and communal roosts. The territorial roost consisted of a male roost, a pair roost, a yearling roost, and a family roost. The communal roost involved all crows at the end of the breeding cycle although it was mostly occupied by adults that I believed were non-breeding birds or those that failed early in the season.

a) Territorial roost

i) Male roost

The male Northwestern Crow roosted in the shrubs or trees on the territory at night while the female sat on the eggs or nestlings. The roost site was within 1m of the tops of the bush or tree and it was used regularly judging by the droppings on the branches below. One male flew each night to the area used later in the season as a communal roost probably because his territory lacked a suitable roost site. When the nestlings fledged and were capable of good flight the males abandoned their territorial roosts for the communal roost.

ii) Pair roost

The female brooded the nestlings until they were about 10 days old and then she joined the male on his territorial roost. When the male abandoned the territorial roost she accompanied

him to the communal roost.

iii) Yearling roost

Yearling helpers roosted with the male until the young fledged from the pair's nest. It is not certain where the yearlings roosted each night following the fledging date of the nestlings although they were seen occasionally at the communal roost.

iv) Family roost

After fledging the young remained on the territory for about 10 to 25 days where they roosted in the shrubs and trees. As their flying skills improved they tried to follow the adults to the communal roost. A few days later the young were seen at the communal roost for the first time.

b) Communal roost

From late June to early July the fledglings began to leave the territories during the day and followed their parents around the island. At this time the adults and the occasional yearling gathered in dead snags in a preroosting site located on an elevated part of the island where they jostled for positions, made a great deal of noise, and displayed vigorously. Several times in an evening several hundred crows would take to the wing and circle above the roost while they called loudly. The tempo of displaying crows increased with each new arrival. Although the yearlings sat among the adults they did not display and easily gave up their position to any adult. On windy nights the adults curtailed their displays and usually sat still.

The communal roost was also used by up to 13 crows from

Hernando Island which joined the roost during good weather.

In 1977 the young birds arrived at the roost for the first time on 14 July without their parents. They perched at different locations than the adults and yearlings. On 28 August the young gathered as a group without the adults on Northwest Bay beach and tugged at driftwood twigs before they chased each other in the wind to the preroost site. Some juveniles flew to the roost alone as early as 2h before sunset while the earliest adult arrived 30 mins. prior to sunset on clear evenings.

The vigorous displaying and jostling among the adults and lack of displaying by yearlings and juveniles is possible evidence that the communal roost serves a social function in establishing a hierarchy amongst flock members. With the coming winter it may be "evolutionarily wise" for the members of the flock to establish the hierarchy early in the season while the food resources are still relatively abundant and not to waste energy later during more stressful times. Further study is needed to ascertain the advantages accrued by creating a hierarchy in the Northwestern Crow. Swingland (1977) has shown that when the weather became severe dominant Rooks (Corvus frugilegus) forced lower ranking individuals from the sheltered parts of the roost. These Rooks lost more energy at night than the dominant birds through exposure and this was exacerbated on the feeding grounds during the day. He also showed that the mortality of young Rooks was higher than for adults in winter.

9. Food of the Northwestern Crow

a) feeding areas

The food sources of the Northwestern Crow are the intertidal beaches, the grassy meadows, and the seabird colony. Table 11 shows the amount of time that 5 pairs of adults spent at the 3 food sources during the egg, nestling, and fledgling stages. I stress that this is the amount of time spent at each region and not the amount of time spent foraging there. However, because the crows spent most of their day foraging I feel these figures are fairly representative of the actual amount of time spent foraging. On a seasonal basis, crows spent more time on the beach than in the meadow and gull colony. The meadow shows a decline in use during the nestling stage. This may be a result of the large allocation of time spent on the territory (i.e. in the meadow) during the egg stage for nest defense and not a decrease in the intensity of foraging activity there. The gull colony shows a gradual increase in usage through the nesting season of the crow.

i) intertidal

Most crows concentrated their intertidal food searching in either Northwest or Camp Bay. To determine the importance of the 2 bays as sources of food I divided the beaches into 2 regions. I chose the 1.2m tideline as the division between the portion of beach exposed by high, low tides (HLT) (i.e. tides $\geq$ 1.2m) and low, low tides (LLT). The 1.2m tide line was chosen because above this level, in Northwest Bay, the beach was mostly gravel and below this level the beach was mostly covered

Table 11. Amount of time spent by 5 pairs[1] of crows on the beach, in the meadows, and the gull colony in 1977-78 (N = 3477 mins.). Females were excluded during incubation and brooding seasons.

	Beach		Meadow		Gull Colony	
	No. mins.	%	No. mins.	%	No. mins.	%
Egg stage	276	44.0	292	46.6	59	9.4
Nestling stage	1367	60.1	657	28.9	251	11.0
Fledgling stage[2]	262	45.6	213	37.0	100	17.4
Mean	635	49.9	387	37.5	137	12.6

[1] All pairs nested in territories that were adjacent to the beach.

[2] Up to 17 days following fledging.

in Ulva sp. and other marine algae. Casual observation had shown that the algae zone was much used by crows and the gravel beach was mostly ignored. During 26 ebbing and flooding tides I counted the number of crows feeding in Northwest and Camp Bays during HLT and LLT (Table 12). The crows concentrated their feeding activities at Camp Bay during HLT and at Northwest Bay during LLT. Crows that nested adjacent to the beach tended to stay on that portion of beach during all tides.

It is uncertain why the crows moved between the two beaches as the tides changed. The search and handling times were always greater in Northwest Bay except during HLT when the handling times were shorter (Table 13). (I define search time as the amount of time taken between finishing feeding on one item and of the capture of a new item. Handling time is the amount of time taken from the capture of the item until it had been completely swallowed.) I found different marine organisms were present on Northwest Bay than Camp Bay and this may explain why the crows switched beaches. It is more probable, though, that the majority of crows preferred Northwest Bay because it was closer to their nests.

ii) meadows

The crows fed in the grassy meadows mostly within the territory although they also perched in shrubs to reach invertebrates on the leaves. Only on rare occasions during high tides did the crows leave the territory to feed in other parts of the meadows. Invertebrates were picked from the rocks, and plant stems and dug out of the ground. Portions of the meadows

Table 12. The number and (percent) of crows using Northwest Bay and Camp Bay when the tide was $\geq$ 1.2m (HLT) and when the tide was < 1.2m (LLT). (N = 26 ebbing and flooding tides).

	Northwest Bay	Camp Bay
LLT	119 (57.2)	89 (42.8)
HLT	54 (21.9)	193 (78.1)

Table 13. Search and handling times (secs.) for randomly chosen adult Northwestern Crows during HLT and LLT in Camp Bay and Northwest Bay. (See text for details).

	Camp Bay		Northwest Bay	
Tide Position	Search	Handling	Search	Handling
LLT	50.9 (N=32)	4.6 (N=16)	99.8 (N=26)	9.3 (N=23)
HLT	28.8 (N=79)	23.0 (N=7)	83.0 (N=26)	4.9 (N=12)

were vegetated with dense, tall grasses. These areas were avoided by the crows. As the meadows dried out and the insect populations declined the crows spend more time in the gull colony. It was not easy to separate the foraging time in the gull colony from that performed in the meadows because the gulls do nest in some grassy meadows. I arbitrarily included all meadows within the gull colony as part of the seabird colony.

iii) gull colony

The gull colony provided food intermittently for the crows. During courtship the male Glaucous-winged Gull feeds the female on their territory (Vermeer 1963) on an average of once every 10h (Henderson 1972). This food was sometimes stolen by groups of crows that swooped at the gulls that had dropped their courtship food. Usually one or 2 crows swooped at the gulls in an attempt to drive them away from the food or allow another crow to fly in and steal the morsel. Large amounts of food seemed to attract more crows than smaller amounts.

The Glaucous-winged Gulls laid their eggs in late May and early June. Some of these eggs were taken by the crows from abandoned nests and from occupied nests during disturbances in the colony. Seabird eggs are eaten by many corvids. Vermeer (1963) mentioned predation of Glaucous-winged Gull eggs by Northwestern Crows on Mandarte Island. Fish Crows (C. ossifragus) and Common Crows prey extensively on the eggs of Laughing Gulls (Larus atricilla) (Monteyechhi 1977) during human disturbances. Ravens regularly patrol Black-legged Kittiwake (Rissa tridactyla) nesting colonies in search of eggs

while Carrion Crows prey on the eggs of the Black-headed Gull (Larus ridibundus) (Montevechhi 1979). It is difficult to accurately quantify the degree of egg predation by the crow because my disturbance to the nesting gulls while examining the number of eggs in their nests probably increased the chance of egg predation by the crows. I also marked gull nests with stakes. Artificial nests that were marked with stakes have been shown to assist Corvus corone in locating them (Picozzi 1975).

The adult gulls feed their chicks with increasing biomass as the chicks grow (Henderson 1972). Because some of this food is stolen from the gulls by the crows it may be one reason why the crows increase their foraging activity in the colony during the chick stage.

One of the greatest causes of L. glaucescens mortality in the chick stage is due to attacks by the adults (Vermeer 1963). Young gulls are attacked by neighbouring gulls if the young venture away from their parents' territory. These carcasses are scavenged by the crows (Butler 1974).

Northwestern Crows were seen carrying 1 to 4 day old gull chicks on several occasions but I never witnessed a crow killing them. When the young gulls weighed approximately 400g (about 15 days old; Vermeer 1963) both the adults and chicks showed little concern about the presence of the crows in the colony.

b) food sources and feeding rates at the nest

The food brought to the brooding female and the nestlings by the male was located on and off the territory (Table 14). Later, when the female assisted in the feeding of the young the

food still was located on and off the territory. To find the role of the territory as a food source I observed one pair of nesting crows from when the first egg hatched (26 May) until the one surviving nestling fledged (22 June) and recorded where the food was found by the pair. Sources of food were only scored for the original site, so, for example, if the male fed the female who in turn took the food to the nestlings I recorded the source where the male found the food only. A single feeding could have come from on the territory, off the territory, or from both on and off the territory. I considered the crow's territory to end at the high tide mark on the beach and included a portion of meadow and shrubbery. Because the attractiveness of the beach as a food source roughly increases with an ebbing tide I decided to also see if more food came from the beach at a low tide than from the meadows on the territory. I arbitrarily chose a 2.5m tide line to separate the beach into an area exposed by high, low tides (HLT), and low, low tides (LLT). Of course the HLT portion of the beach is exposed during all LLTs but the pair of crows tended to feed along the water's edge at all times. When given a choice the pair of crows fed on the beach (Chi-Squared Test, $p < 0.005$) (Table 14). Approximately 70% of the nestlings' food is located on the territory during HLT and 20% during LLT.

The males from 4 nests made the most number of trips (66%) to feed the brooding female and the nestlings in the first week of the nestlings' life (Table 15). After about 10 days of brooding the female assisted the male in feeding the nestlings.

Table 14. Location of food brought to the brooding female by the male, and by the male and female to feed the nestlings at one nest in relation to tidal position. (See text for details).

	tidal position			
	LLT		HLT	
Food source	No. of trips	%	No. of trips	%
On territory	4	20	28	70
Off territory	13	65	2	5
Both on and off the territory	3	15	10	25
Total	20		40	

Table 15. Nestling feeding rates by the male and the female at 4 nests in 1977-78. (percent).

Nestling age (days)	Mean feedings per hr.					No. obs. mins.
	N	male	N	female	Total	
0-7	44	1.8(66.7)	22	0.9(33.3)	2.7	1431
8-14	13	1.1(33.3)	26	2.3(66.7)	3.4	677
15-21	8	0.7(32.0)	17	1.6(68.0)	2.3	672
22-28	6	0.8(40.0)	9	1.2(60.0)	2.0	456
						3236

A feeding was only scored for the last adult that touched the food although at one nest that could be observed from a close distance the male only fed the nestlings under the age of 2 days and so some feeding scores may be biased against the male.

In a 14h day an adult crow visits the nest approximately once every 23 minutes, on average, to feed its nestlings. This is nearly double the approximate rate of once every 35 minutes for the Common Crow (Good 1952).

c) nestling food

Fifty-three samples of food fed to 7-day-old and older nestlings were obtained using the pipecleaner method (Kluijver 1933) (Table 16). Of these 53 samples 63.9% had items found on the beach, 30.6% from the meadows, and 5.5% from the gull colonies. These figures agree closely with the amount of time that the crows spent on the beach during the nestling stage (Table 11). Only the gull colony figure is low in relation to the time spent there (5.5% versus 11.0%). As mentioned earlier, this is probably because some meadow foods (invertebrates) were caught in the gull colonies but recorded as meadow food. In addition, gull eggs that are fed to the nestlings would not appear in the food sample using the pipecleaner method, because only the egg content is eaten. The method also has limitations.

d) adult and yearling food

Little-neck clams (Protothaca staminea and Venerupus semidecussata) were eaten after they were dropped on large rocks (Butler 1974). To determine the size of clams selected by the crows in this study I randomly collected 117 Little-neck Clam shells that had been dropped by crows on the upper beach and

Table 16. Food items in 53 throat samples collected from nestling Northwestern Crows in 1976-78.

Food item	No. of samples containing item	%
mollusc and/or gastropod viscera (probably Protothaca staminea and P. semidecussata)	22	27.9
Hemigrapsus nudus and H. oregonensis	17	21.5
Anoplarchus purpurescens	12	15.2
Rubus ursinus	7	8.9
spiders (Order phalangida)	7	8.9
Cancer productus	6	7.6
Geometridae larvae	6	7.6
spiders (Salticidae)	5	6.3
Noctuidae pupae and adults	4	5.1
moss, grass stems, leaves	4	5.1
leaf hoppers (Cercopidae)	4	5.1
Diptera larvae	3	3.8
shrimps (Spirontocaris spp.)	3	3.8
bread from humans	3	3.8
spiders (Mimetidae)	3	3.8
beetles (Scarabidae)	3	3.8
gull meat and feathers	3	3.8
ants (Formicidae)	2	2.5
Pugettia gracilis	2	2.5
unknown crab sp.	2	2.5
wasp adult and larvae (Hymenoptera)	2	2.5
Nereis sp.	2	2.5
beetles (Elateridae)	2	2.5
sculpin (Cottidae sp.)	2	2.5
Shield bug (Pentatomidae)	2	2.5
fish (Tonicella lineata)	1	1.3
Mosquitoes (Culicidae)	1	1.3
Diptera (Empididae)	1	1.3
shrimp (Callianassa sp.)	1	1.3

Table 16 (cont'd)

Clingfish (*Liparid florae?*)	1	1.3
unknown fish	1	1.3
unknown spider	1	1.3
spiders (*Oxyopidae*)	1	1.3
wasp (*Sphecidae*)	1	1.3
beetle (*Coleoptera*)	1	1.3
spiders (*Mecicobothridiidae*)	1	1.3
Edible Mussel (*Mytilus edulis*)	1	1.3
fish (*Clinocottus acuticeps* or *C.embrynum*)	1	1.3
grasshopper (*Acrididae*)	1	1.3

measured their greatest length on a ruler (mean = 31.6mm S.D. = 2.3 range = 27.0-39.0). When a clam was dropped rarely did both valves break so I feel that my sampling method accurately represents the range in sizes of clams dropped by the crows. I also dug eight plots (50x50x6cm) in all habitats of the little-neck clams and sorted all clams larger than 5mm in length from the sample. I chose a plot depth of 6cm because this is about as far as the crows dug into the beach. Of 217 clams dug from the beach 87 (40.1%) fell within the range of shells at the drop stations on the beach (27.0-39.0mm).

The mean shell size of these 87 clams was 29.6mm (S.D. = 2.4). I then measured 250 clam shells from cracking stations on 5 crow territories (50 shells per territory) and found a mean shell size of 39.8mm (S.D. = 6.3, range = 29.0-60.0). Shells found on cracking stations on territories were significantly larger than those found on the beach cracking stations (z-test $p < 0.05$). The reasons for these differences are uncertain. The Northwestern Crow stored food when it was superabundant. Perhaps a large clam is more energetically profitable to store than smaller ones and so these are taken to the territory for caching. Stored clams that I located and those that I saw the crows carrying to their territories appeared to be larger than those eaten on the beach. Large clams were generally deeper in the beach substrate and more difficult for the crows to remove.

Blennies (Anoplarchus purpurescens) were captured in tidal pools and under marine algae. The crows carried these fish to the upper beach where they directed several blows at the

writhing fish. The blennies were then swallowed whole.

Red rock crabs (Cancer productus) were captured under algae on the beach or by wading into the water. The crows tossed these crabs ashore and with a few quick shakes removed the legs and pincers. Sometimes the crabs were lifted into the air and dropped onto the rocks to crack them open.

Nereid sp. worms were pulled from the beach substrate and then broken into several pieces before they were consumed.

The glaucous-winged Gull fed along the beach and on occasion tried to steal Red Rock Crabs from the crows. Usually the gulls lost crabs, that they had caught, to the crows. The gulls also caught Cockles (Clinocardium nuttalli) at very low tides and dropped these onto the rocks to open them. The crows often stole parts of these clams from the gulls.

Besides gull eggs adult and yearling Northwestern Crows fed on fish scraps in the gull colony. These were picked from around the nest of gulls and cormorants. When a large amount of scraps were found by the crows they would make as many trips as necessary to fly the remains to the territory where it was stored. Some of this food was stolen from the young gulls shortly following a feeding but more often following a disturbance which caused the gull chicks to regurgitate their food. Seldom did this regurgitated food appear in the food samples taken from nestling crows.

Blackberries (Rubus ursinus and R. laciniatus) were eaten by crows in late June. I found remains of these berries in 80% of 86 regurgitated crow pellets in July 1973 (Butler 1974) but

only 7 of 53 (8.9%) of the nestling samples contained them. Seven Coast Garter Snakes (Thamnophis elegans) were killed and partially eaten near the beach by the crows. Only adult crows were observed killing the snakes although a yearling did carry a carcass killed by an adult. Coast Garter Snakes also eat nestling crows (Campbell 1969).

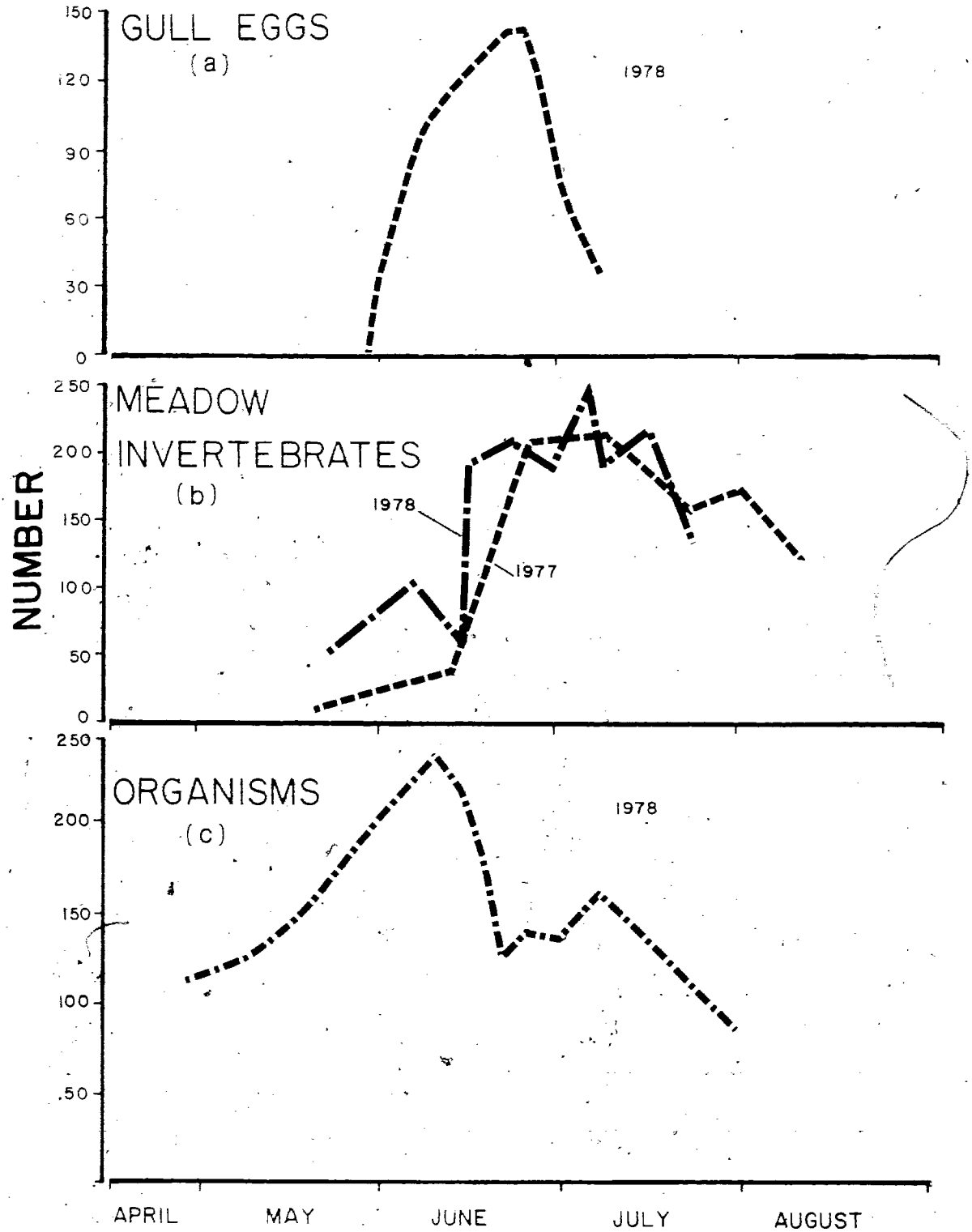
e) food caching

Food caching is widespread in the Corvidae (Turcek and Kelso 1968; Goodwin 1976). In 5 out of 6 observations of food storing the food came from the beach and on one occasion the food came from the gull colony in 1977. Food storing was not only performed by the adults. Three yearlings stored food on their parents' territory and in one case a juvenile stored food also. In this instance the young bird had been fed 5 times in rapid succession after which it picked up a piece of clam from under its parent and carried it to a foreign territory where it pushed the meat into a crack in a rock. After walking to and from the storage site four times it was finally chased away by an adult. In all cases where I returned to the cache, the food was gone within 24h. Cached foods included Red Rock Crabs, sculpins (Cottidae), and Little-neck Clams.

f) timing of the nestling period

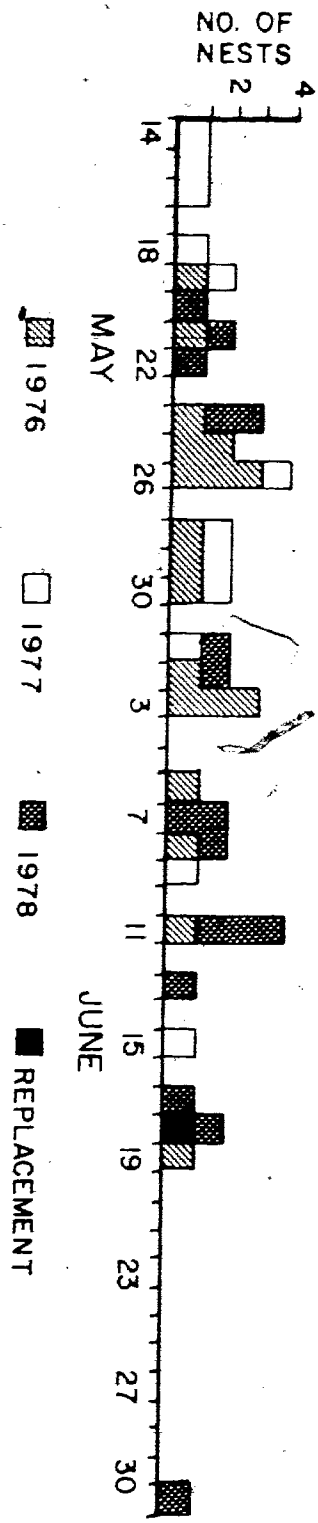
During the breeding season the food of the Northwestern Crow on Mitlenatch Island came from the beaches, the meadows, and the gull colony. The timing of the nestlings' presence coincided with the maximum number of available foods at these three sites (Figure 13). The major food items showed only small changes in size over the period that the crows preyed

Figure 13. Seasonal abundance of gull eggs in 56 Glaucous-winged Gull nests (a), invertebrates in the meadows (b), and the number of organisms on the beach (c). Camp and Northwest Bay beach organisms were sampled in 1978 (see methods). The meadow invertebrates were collected along a 250m transect using a sweepnet (1977) and a sweepnet and pit traps (1978). Gull eggs were counted in 1978.


GULL EGGS
(a)
1978
150
120
90
60
30
0
MEADOW
INVERTEBRATES
(b)
1978
1977
NUMBER
250
200
150
100
50
0
ORGANISMS
(c)
1978
250
200
150
100
50
APRIL
MAY
JUNE
JULY
AUGUST

upon them and so the number of items probably closely approximates the available biomass, too. In 1977, 66 days elapsed between the dates of the first nestling and the last fledgling while in 1978 49 days elapsed. The occurrence of nestlings is extended over several weeks as a result of the extended egg laying period (Figure 14).

Figure 14. Dates of first nestlings in 49 Northwestern Crow nests in 1976-78.


NO. OF NESTS
2
4
14
18
22
26
30
3
7
11
15
19
23
27
30
MAY
JUNE
1976
1977
1978
REPLACEMENT

Discussion and Conclusions

10. Timing of the breeding cycle

The 4 major ultimate factors that appear to influence the timing of breeding in the Northwestern Crow are the length of day, and the seasonal cycles of temperature, precipitation, and oceanic tides. With increasing daylength the crows can spend more time performing activities. The longest active crow day is about 15 hours. The hottest month is July and the driest month is August (Figure 1). Low tides occur mainly during the night in winter and during the day in summer (Figure 15). The seasonal cycles of precipitation, temperature, and daylength affect the productivity of the grasslands and the numbers of invertebrates that live there. The standing crop of the grasslands reached a peak in the third week in May in 1977 (Figure 16) and the greatest abundance of invertebrate fauna followed shortly after (Figure 13). The maximum number of Glaucous-winged Gull eggs are laid in the first week of June in colonies in Georgia Strait (Drent and Guiguet 1961, Vermeer 1963, personal observation).

These 4 ultimate factors (daylength, temperature, precipitation and tides) not only create a seasonal abundance of food but, in addition, there is also a larger number of daylight hours available to exploit it. The Northwestern Crow probably begins nest building in late March on Mitlenatch Island. The eggs are laid from the last week in April to the first week in June and most eggs hatch from mid-May to late

Figure 15. The number of low tides (< 2.5m) that occurred during the day and the night versus the months of the year.

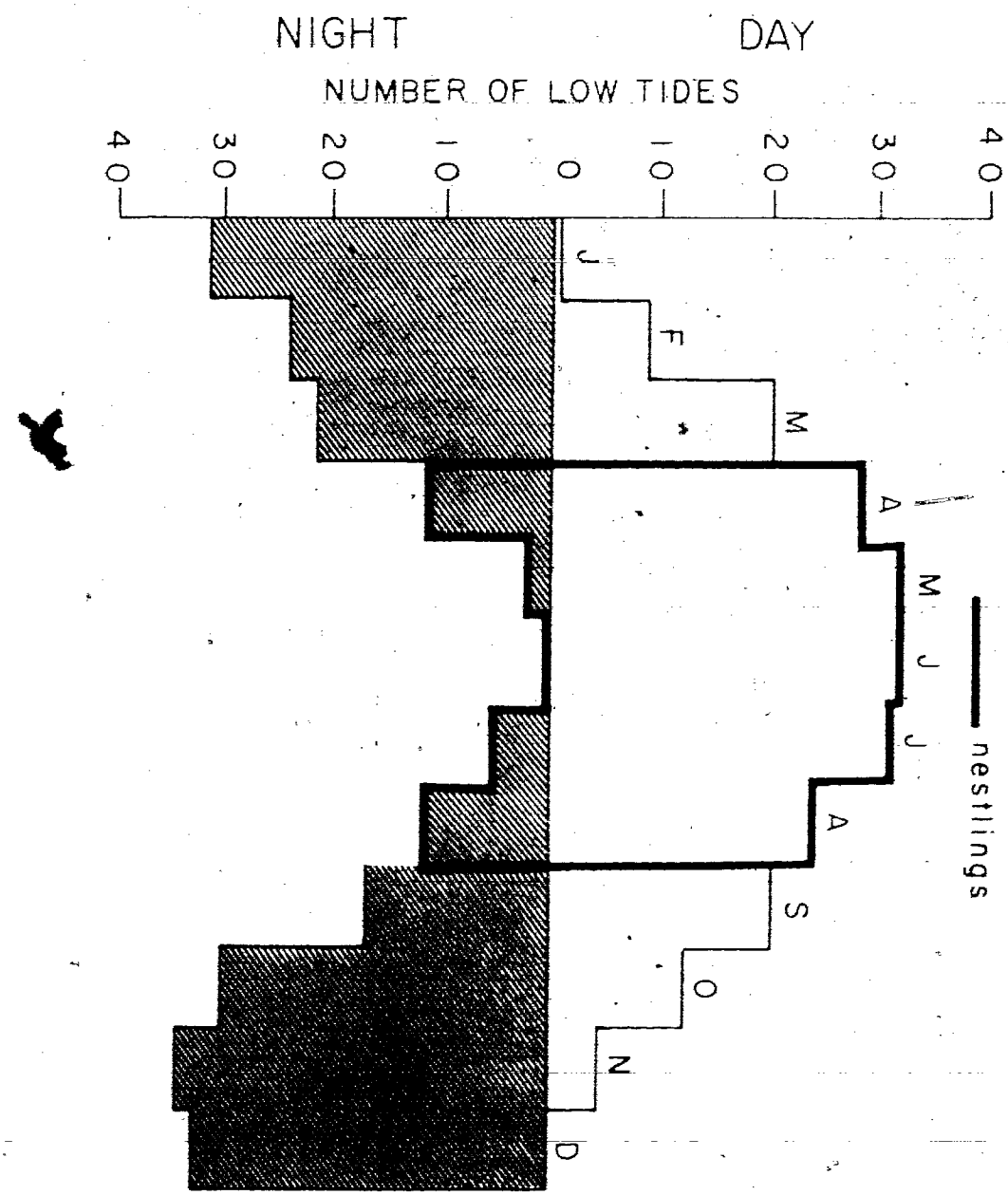
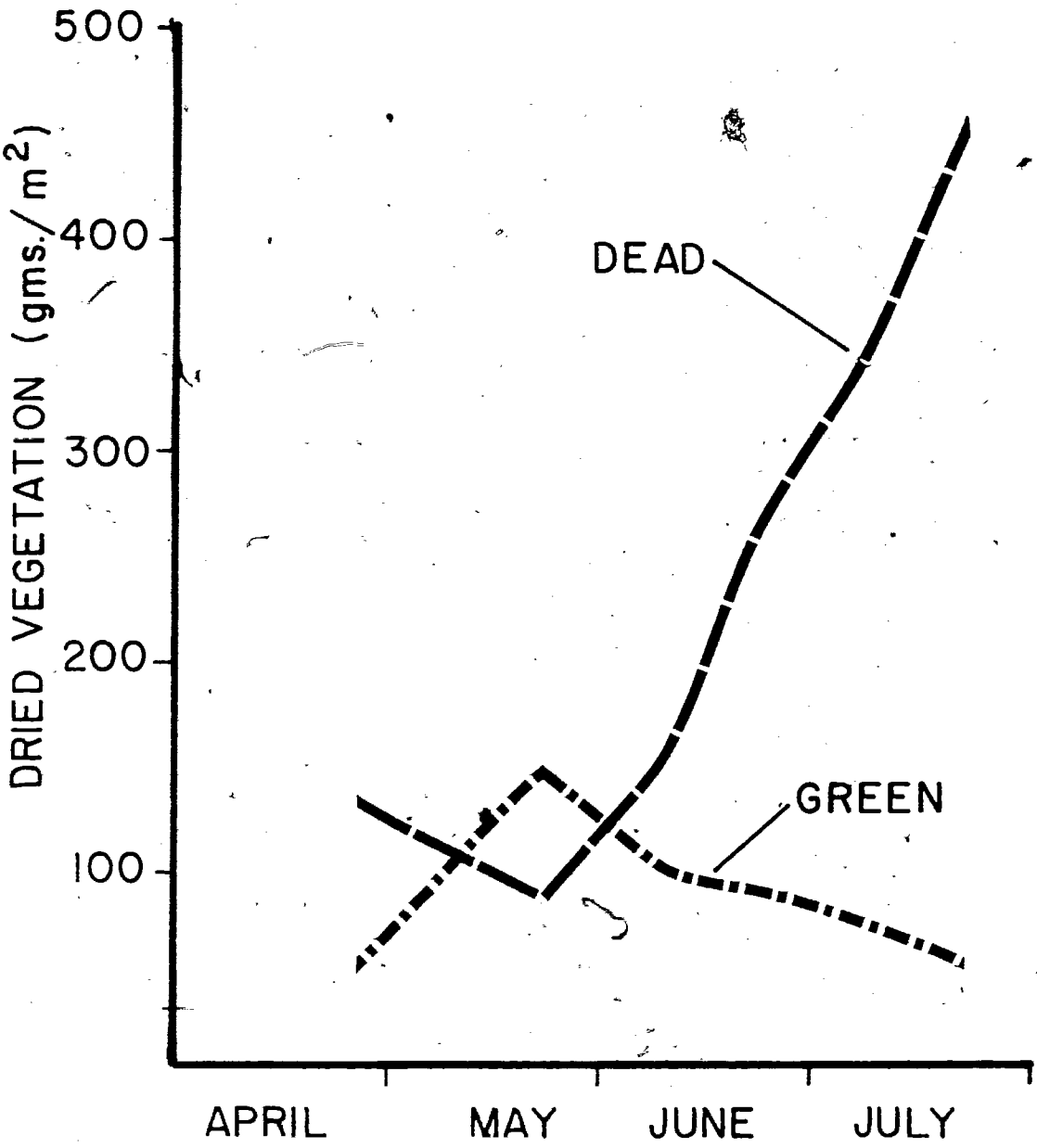

NIGHT
DAY
NUMBER OF LOW TIDES
40
30
20
10
0
10
20
30
40
J
F
M
A
M
J
J
A
S
O
N
D
nestlings

Figure 16. Standing crop of the grasslands in 1977. Each point represents the mean weight of dried vegetation collected from 10 randomly chosen 400cm^2 plots arranged in checkerboard fashion. (See methods for details).


500
400
300
200
100
DRIED VEGETATION (gms./m²)
DEAD
GREEN
APRIL
MAY
JUNE
JULY

June when the food is most abundant. Fledging occurs from mid-June into July.

It is generally believed that the breeding season of birds is timed so that the presence of the nestlings coincide with maximum food availability (Lack 1954, Perrins 1970). The amount of time that the crows can spend foraging in the meadows and seabird colony is governed, mostly, by the number of daylight hours. However, on the beach the varying heights and occurrences of the tides within the daylight hours creates a second constraint on the availability of food on the beach. The time and tide components create daily, weekly, monthly, and annual cycles of food availability on the beach. In June (when the nestlings are present) more intertidal organisms are available to the crows on the beach than at any other time of the year (Figure 13) and furthermore, the low tides also occur during the daylight hours (Figure 15). The weekly and daily tidal cycles appear to have little or no effect on the timing of nesting. The crows showed no correlation between egg laying and the position of the tides on a weekly basis. These trends then, create a seasonal cycle of food abundance which, in turn, is exploited by the nesting crows.

11. Role of non-breeding helpers

From observations of colour-banded Northwestern Crows, nesting appears to first occur at 2 years of age or older. This is characteristic of most crows (Goodwin 1976). Northwestern Crows were aged by the brownish cast to the feathers of yearlings, and by individual colour band combinations. Because many yearlings were also helpers the words helper and yearling are used synonymously here.

On Mitlenatch Island the ratio of adult pairs known to have helpers versus pairs without helpers was 3 to 6 in 1976, 4 to 13 in 1977, and 3 to 22 in 1978. The role of the helpers consisted of various degrees of participation between years and between nests. In 1978 the yearling at two closely watched nests escorted their parents to the territory when a disturbance occurred there but seldom defended the territory alone. Unlike in 1978, the yearling at one nest in 1977 was involved in 38 encounters (chases, fights, and/or displays) toward intruding crows of which 5 (13.1%) were by the yearling alone.

In addition to physical encounters, the yearlings uttered alarm calls that brought the adults to the territory. Although the yearlings expended only a small amount of energy in physical defense of the territory their presence probably also served as a deterrent to other crows. One yearling spent 30 of 956 mins. alone on its parents' territory while they foraged elsewhere during the nestling and fledgling periods. Off the territory the yearlings were subordinate to all adult

crows but were dominant over intruders on the territory. Helpers uttered alarm calls, mobbed, or assisted their parents in chasing Ravens, Bald Eagles (Haliaeetus leucocephalus), Glaucous-winged Gulls, and River Otters (Lutra canadensis). The presence of a yearling helper did not significantly change the territory size of its parents.

One yearling fed its parents' nestlings once in 1976. No other feeding was observed. On Mandarte Island one helper fed the nestlings 23 of 171 (13.5%) times while other helpers never assisted in feeding the nestlings.

The behaviour of the parents towards the yearlings appeared to be fickle. On one day the yearling is tolerated near the nest while on the next it is not. Only on one occasion was a helper seen at the nest without its parents.

Adult Northwestern Crows readily store large food items. (Butler 1974). A yearling stored food on 2 occasions during 2512 mins. of observation in 1977 and 2 yearlings stored food on their parents' territory once in 1978.

Helpers received food from their parents by begging and being fed, or begging from a feeding adult who then abandoned the food item to the yearling. All begging was directed toward the territorial male throughout the nesting season. In 1977 a yearling was fed 7 times in 2425 mins. of observation but 2 yearlings at 2 nests in 1978 were never fed in 1065 mins. of observation.

Helpers associated with territories fed on these territories and therefore competed for its food with the adults. Yearlings that were unattached to territories

remained on the beaches or in the unoccupied regions of the island. As the nesting season progressed helpers move farther afield from their parents' territories. Roosting occurred on the territory with the male.

When the yearling became an adult in the following year it attempted to establish a territory. The data are too small to determine where all returning helpers establish themselves in relation to their parents' territory. However, one former helper nested within 300m of its parents' territory of the previous year. Only territories located adjacent to the beach had helpers (7 of 34). A similar trend existed on Mandarte Island (Verbeek, pers. comm.)

Not all nests had helpers from year to year, probably because all the previous young did not survive the winter. From banding information and nest site tenacity I assume that yearlings only help their parent(s) in the next year. Adults with helpers tended to have large clutches, more nestlings, and produce more fledglings per pair than adults without helpers (Table 17). A similar trend exists on Mandarte Island but these trends are significant only if the Mitlenatch and Mandarte Island data are pooled (Verbeek and Butler, ms.).

Table 17. Reproductive success of pairs with and without helpers in 1977 and 1978.

	with helpers	without helpers	t[1]
Number of nests[2,3]	6	22	
Eggs laid	25	79	
Mean clutch size	4.2	3.6	1.36
Mean no. nestlings/pair	3.5	1.8	3.26
Mean no. fledglings/pair	2.0	0.6	1.31

[1] Significant difference exists ($p < 0.05$) between means tested with Student's t-test

[2] Only 28 nests had continuous nestling data although helpers assisted at 7 of 34 nests.

[3] Only first clutches were considered and only those nests whose eggs were not abandoned.

12. Nesting synchrony

The prolonged initiation dates of egg laying (Figure 10) resulted in pronounced asynchrony in the nesting stages between pairs of crows. No more than 3 females ever began laying on the same day in 1977-78. Yom-Tov (1975) has suggested that synchronization in nesting Carrion Crows reduced the degree of cannibalization of eggs and chicks. He showed that nests that were clumped tended to be more synchronized than dispersed nests. It would be expected that because of asynchronous egg laying and the fact that nests were built close together that the fledgling success of the Northwestern Crow would be lower than for the Carrion Crow. However, fledging success of the 2 spp. does not differ greatly. Both species of crows lay 4 to 5 eggs (Goodwin 1976). The fledging success (number of young that fledged from hatched eggs) in the control of Yom-Tov's (1974) study was 58% versus a mean of 48.6% (35.3%-58.1%) in my study. The two closest nests in my study were within 4m of each other and yet the first eggs in these two nests were laid 20 days apart. Asynchrony in the Northwestern Crow is probably a result of the ability to establish a territory. Those crows that nested in the same territory between 1977 and 1978 were more synchronized in egg laying than the crows that established new territories. (I assume that if the territorial boundaries changed little between years then the same pair occupied that territory because 2 adults banded as nestlings prior to this study have always occupied the same territory). The mean of the range

of egg initiation dates in nests built in the same territory between 1977 and 1978 was 1.6 days (N = 5) and 6.4 days (N = 5) in newly established territories. This may be a result of higher metabolic costs required to establish a new territory.

The higher degree of egg and chick loss in nests located greater than 50m from the beach is probably a result of reduced feeding rates due to the increased flying distance between the nests and the food supply, although inexperience may also be involved. Females from 2 nests within 50m of the beach and one nest greater than 50m from the beach were incubating 5 to 7 day old eggs on 11 and 12 May 1978. Over this period the weather was wet and windy. The females at the two beach nests were, on average, 88.9% attentive to their eggs and spent an average of 6.9 mins. off the nest in 10 shifts (N = 626 mins.). The female from the inland nest was 59.4% attentive and spent an average of 27.2 mins. off the nest in 12 shifts (N = 802 mins.). Unfortunately the number of times that the female was fed by the male from the distantly located nest could not be made but I presume that she was feeding herself more than the females near the beach. Casual observation of other similarly located nests showed a similar trend.

13. Nesting dispersion

Generally it has been concluded that nesting dispersion and feeding dispersion are influenced by abundance of food and predator avoidance (Crook 1965, Lack 1968). Verbeek (1973) theorized that communal and colonial breeding in corvids was a method of exploiting a less abundant or a more abundant but patchy food supply, respectively. The food of the Northwestern Crow comes mostly from the beach (Table 9). The intertidal food is most abundant in June (Figure 13) and appears to be somewhat homogenous in its spatial distribution. For example, while I examined the abundance of organisms in the beach quadrants each week I noticed a consistency in their numbers between quadrants within the same habitat. There was no apparent clumping of organisms within a given habitat. Also, I have shown that some crows feed on the same stretch of beach most times. Both of these points, although somewhat indirect, suggest that the food supply has little spatial variability in numbers of individuals.

The tide controls the crows' accessibility to the food on the beach. Thus, kelp crabs (Pugettia sp.) which live in the lower intertidal will be available less often than shore crabs (Hemigrapsus sp.) on the upper beach because the upper beach is exposed by tides more often. So, in effect, any given species whose numbers fluctuate little from season to season are available in a proportion equal to the amount of time it is exposed by the tide. An organism that has seasonal fluctuations in abundance will also be available in a

proportion equal to the amount of tidal exposure but it has seasonal constraints too. The picture gets complicated, indeed, when one compares the many possible combinations of seasonal and tidal rythyms of intertidal food availability to the crows.

Fisher (1954) suggested that coloniality enhanced efficiency in exploiting an unevenly distributed food supply. Several studies (Horn 1968, Hunt and Hunt 1976, and others) have shown that colonial nesting birds gain information from each other on the whereabouts of locally abundant food. Because the beach food of the Northwestern Crow probably shows only minor spatial fluctuations the only advantage of colonial nesting is on a temporal level. That is, the behaviour of nesting neighbours indicates when the tide is low. But surely a crow that nests within 250m of the beach knows when the tide is low and does not need clues from its neighbour. I suggest that the apparent coloniality in the Northwestern Crow on Mitlenatch Island may be an artifact created by the nature of the availability of the food supply. The birds are simply trying to nest as close to the food source as possible. Brown (1964) stated that territoriality in birds will occur when the resource is defendable. This means that the food supply must be somewhat predictable in its location and abundant for the length of the nesting season. When this does not occur birds generally exploit the resource communally or colonially (Brown 1974, Verbeek 1973). If hypothetically the tide was always low I would predict that the nesting dispersion of the crows would not change greatly. Instead, the beach would become

exclusive territory of the pairs that nested adjacent to it.

Brown (1974) and Verbeek (1973) suggested that as food resources became less predictable an exclusive territory would unlikely supply the needs of the pair. This would favour the evolution of coloniality or communiality. From the classic all-purpose territory Brown (1974) envisages a colonial route depicted by small nesting territories and a large home range where flocks of up to 100 birds "roll" over the landscape searching for food. The resident pairs only defend the vicinity of the nest such as in Pinon Jays (Gymnorhinus cyanocephalus). An alternate communal route involves the incorporation of nonbreeding "helpers" into the breeding effort and maintenance of exclusive territories. This culminates with the Mexican Jay (Aphelocoma ultramarina) in which up to 11 helpers are involved in the breeding effort of one pair. Verbeek (1973) described the evolution of coloniality as a function of abundant, but patchy food resources, and communiality a result of less abundant food. The major food resource of the Northwestern Crow is on the beach (Table 11). The food availability there fluctuates between rich and lean periods with the ebbing and flooding of the tides. According to Verbeek (1973) the nature of this resource would favour communiality. During high tides the beach food is unavailable and the crows rely on the meadow invertebrates. The meadow food appears to be fairly predictable in distribution and abundance or the crows would not hold an exclusive territory. Therefore the important factor in the availability of the food supply appears to be

the fluctuation between rich and lean periods of the beach food.

The Northwestern Crow appears to follow both routes of coloniality and sociality (Brown 1974) if coloniality is defined only by internest distances. However, I see the definition of coloniality to incorporate both internest distance and the benefits it accrues. I have argued earlier that the Northwestern Crow probably benefits little from its coloniality and I feel it has followed the route to communiality.

APPENDIX I - Colour band combinations of crows on Mitlenatch Island from 1976-78. Band prefixes are 704- in 1977 and 1978.

Nest Number	Colour combination	Date banded
1	left white, right green	18 June 1976
	left green/green	18 June 1976
4	left green	17 June 1976
5	right green	17 June 1976
	left green, right green	17 June 1976
6	left green, right white	17 June 1976
8	left blue, right green	17 June 1976
	left green, right yellow	17 June 1976
	left yellow, right green	17 June 1976
11	left green, right red	17 June 1976
	left red, right green	17 June 1976
12	right green/green	18 June 1976
	left green/red	18 June 1976
17	left green, right blue	17 June 1976
26	right green/red	18 June 1976
	right red/green	18 June 1976
30	right green/blue	18 June 1976
	left green/yellow	18 June 1976
	right green/yellow	18 June 1976
32	right yellow/green	18 June 1976
34	left green/blue	18 June 1976
	right red/green	18 June 1976

Nest Number	Colour combination	Date banded
4	left blue/white,right -03515	3 June 1977
	left white/white,right -03518	3 June 1977
6	left yellow/blue, right -03506	3 June 1977
	left yellow/yellow, right -03507	3 June 1977
8	left red/blue, right -03509	3 June 1977
	left red/yellow, right -03508	3 June 1977
10	left blue, right -03503	3 June 1977
11	left blue/red, right -03514	3 June 1977
	left blue/blue, right -03515	3 June 1977
12	left white/blue, right -03516	7 June 1977
	left white/red, right -03517	7 June 1977
14	left -03501, right yellow	1 June 1977
	left -03502, right red	1 June 1977
20	left -03521, right blue	8 June 1977
	left -03522, right white	8 June 1977
28	left red/red, right -03509	3 June 1977
31	left -03525, right yellow/yellow	14 June 1977
	left -03524, right yellow/blue	14 June 1977
	left -03526, right red/yellow	14 June 1977

Nest Number	Colour combination	Date banded
34	left white, right -03504	3 June 1977
	left yellow/red, right -03505	3 June 1977
35	left yellow, right -03519	7 June 1977
	left red, right -03520	7 June 1977
38	left red/white, right -03511	3 June 1977
	left blue/yellow, right -03512	3 June 1977
39	right red/blue	15 June 1977
	right red/red	15 June 1977
37	left -03529, right blue/blue	2 July 1977
	left -03528, right blue/yellow	2 July 1977
40	left -03530, right blue -red	11 July 1977
	left -03531, right blue/white	11 July 1977

Nest Number	Colour combination	Date banded
12	left yellow/-03532	4 June 1978
14	right red/-03533	8 June 1978
	right blue/-03534	8 June 1978
	right -03536/red	8 June 1978
16	left yellow/-03538, right red	25 June 1978
	left blue/03535	25 June 1978
9	left red/03539, right red	3 July 1978
	left blue/03540, right red	3 July 1978
20	left -03546/yellow, right red	3 July 1978
42	left -03547/red, right red	3 July 1978
44	left -03548/blue, right red	3 July 1978
	right yellow/03549	3 July 1978
55	left red, right red/-03550	3 July 1978
	left red, right blue/-03551	3 July 1978

Appendix II - Parasites found in Northwestern Crow nests.

From the last week of April to 14 May 1977 14 fleas were collected from several crow nests that had been in use in 1976. G.P. Holland (pers. comm.) identified the fleas as "... close (to), if not identical to Ceratophyllus niger Fox ..." but he said that all of the 7 females had incised sternums VII where this structure is ordinarily entire. This is generally considered a "simple variation" within the species. Nonetheless C. niger is endemic in western North America occuring on many species of birds, especially Passeriformes, but this is the first record from crows. A true crow flea (C. rossittensis swansoni Liu) has been found on Asio otus and Corvus brachyrhynchos (Holland 1954). This flea is the New World equivalent of C.r. rossittensis Dampf which occurs on Corvus cornix, C. corone, and Asio otus in Europe. C. rossittensis formerly swansoni) has not been recorded in B.C. although it has been found in Montana (Jellison and Good 1942).

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