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THE BREEDING BIOLOGY OF THE NORTHWESTERN CROW

ROBERT W. BUTLER, NICOLAAS A. M. VERBEEK, AND HOWARD RICHARDSON

In contrast to European *Corvus* species (Coombs 1978), the breeding ecology of the five North American species is poorly known. This is certainly true for the Northwestern Crow (*Corvus caurinus*), which is common on intertidal beaches and the adjacent coastline from Washington to Alaska (A.O.U. 1983). Drent et al. (1964) provided information on laying date, clutch-size, and nesting success of 12 pairs of Northwestern Crows on Mandarte Island, British Columbia. We began our studies of *C. caurinus* in 1973 (Butler 1974, Verbeek and Butler 1981, Verbeek 1982) and present here information about the breeding biology and productivity.

STUDY AREA AND METHODS

The study was conducted from April–August 1976–1983 on Mitlenatch Island (49°57′N, 125°00′W) (Butler 1974) and April–August 1976–1980 on Mandarte Island (48°38′N, 123°17′W) (Tompa 1964), British Columbia. Both islands are inhabited by large numbers of nesting sea-birds (Campbell 1976).

About 60 pairs of crows nested annually on Mitlenatch and from 13–25 pairs on Mandarte. Territories were delineated by marking and connecting the locations of displays and fights between nesting pairs on an aerial photograph (scale 1:5000) or a map (scale 1:1000). Territory size was determined with a planimeter.

Internest distances were measured on the ground with a measuring tape to the nearest 0.5 m or from an aerial photograph. We visited nests every 1–7 days. Nest dimensions were measured before first eggs were laid. The length and width of eggs were measured with Vernier calipers to the 0.05 mm to calculate egg volumes (Hoyt 1979). Eggs and nestlings were weighed with 50-g and 300-g Pesola balances to the nearest 0.5 g. Eggs were numbered with India ink and nestlings were marked with colored Scotch Brand® Plastic Tape on the legs until about 10 days old and then with unique combinations of colored, plastic leg bands. The length of the tarsus was measured by marking the end points on a piece of paper and measuring the distance with a ruler to the nearest 0.5 mm. The incubation attentiveness was obtained by watching individual nests for up to 3 h at various times during the day and recording when the females left the nest and returned to it to resume incubation. The data for brood attentiveness and feeding rates were obtained in the same way.

As only females incubate and brood nestlings, a common corvid habit (Goodwin 1976), we knew the sex of color-banded birds, even if only one member of the pair was banded. Males and females of unbanded pairs were distinguished by size (males are larger) or by various behavioral differences. For instance, males call more frequently, are more aggressive on the territory, and show the "pot-bellied" posture (see Coombs 1978) more intensely than females (pers. obs.). Yearlings were recognized by the brownish cast to the plumage on their

back, wings, and tail (Verbeek and Butler 1981). The data for both islands were pooled when they were not significantly different.

RESULTS AND DISCUSSION

Territory.—Shoreline territories generally included some shrubs or trees, which often held the nest, a section of meadow, and a stretch of beach. Inland territories, not present on Mandarte, differed only in that they lacked a stretch of beach. The mean territory size for both islands combined was 0.49 ± 0.20 ha (N = 61). Compared to other species, Northwestern Crow territories are very small: for instance, 26.7 ± 10.4 ha (N = 41) for the Eurasian Crow (*C. corone*) (Wittenberg 1968), 60 ha for the Black Crow (*C. capensis*) (Skead 1952), and 4 ha for the Little Raven (*C. mellori*) (Rowley 1967). The mean internest distance (17.8 ± 9.6 m, N = 97) between nests of *C. caurinus* in continuous habitat was correspondingly small. The shortest distance between two occupied nests was 4.4 m. Most of the food is obtained off the territory (unpubl.).

Pairs of Northwestern Crows defended nesting territories against all other adults, unrelated yearlings, and some related ones. Of 128 territorial encounters, consisting of displays, chases, and fights, among 14 neighboring pairs without yearling helpers, 104 (81.2%) were performed by males and 24 (28.8%) by females. The role of yearling helpers in territorial defence and reproduction has been discussed elsewhere (Verbeek and Butler 1981).

Nests.—The nest of *C. caurinus* resembles that of the Common Crow, *C. brachyrhynchos* (Bent 1946, Emlen 1942). In 77 nests on Mandarte, cedar (*Thuja plicata*) bark formed part of the nest lining in 72 nests, moss in 45, sheeps wool in 33, grass in 7, and gull feathers in 2. Of 153 nests on Mitlenatch, 152 were also lined with cedar bark and 31 with moss, but 51 held gull (*Larus glaucescens*) feathers, 40 contained grass, 7 held crow feathers, 3 had paper, and 2 contained wool. The use of bark and wool in nests has been reported in other species of *Corvus* as well, for example in *C. corone* (Wittenberg 1968), the Raven (*C. corax*) (Coombs 1978) and the Pied Crow (*C. albus*) (Lamm 1958). Wool occurred in nests on Mandarte because domestic sheep grazed on nearby islands. The high proportion of gull feathers, especially on Mitlenatch, is unusual in the genus *Corvus*. Gull feathers were available on both islands, but perhaps they were used more on Mitlenatch than on Mandarte because of the lack of wool.

Four nests on Mitlenatch were dismantled and weighed. The twigs weighed 52 g in one ground nest and 202 g, 2805 g, and 1007 g in three tree nests. The cedar bark lining from those same nests weighed 236 g,

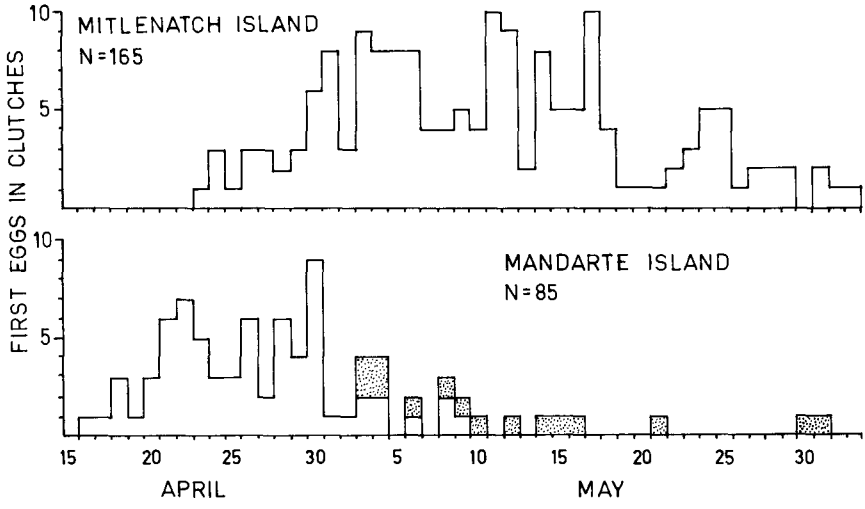

FIG. 1. Clutch initiation dates of Northwestern Crows on Mitlenatch Island and Mandarte Island. Stippled areas represent second nesting attempts. Second nesting attempts on Mitlenatch Island could not be determined with certainty.

15 g, 370 g, and 105 g, respectively, and the moss and grasses combined weighed 170 g, 19 g, 395 g, and 182 g, respectively. Ground nests in general contained fewer twigs and more cedar bark than tree nests. The mean measurements of 23 new tree nests were: 22.1 ± 5.0 cm high, 33.2 ± 4.8 cm in diameter, with a cup depth of 8.9 ± 1.2 cm and a cup diameter of 16.3 ± 1.6 cm.

Nests were built on the ground, in shrubs, and in trees. On Mandarte, 45% of 92 nests were built on the ground compared to 20% of 350 nests on Mitlenatch. The discrepancy between the two islands is in part due to differences in vegetation, Mandarte has few trees and tall shrubs, and in part because some ground nests on Mitlenatch may have been overlooked because of the rugged nature of the island. The percentages of nests built on the ground or in shrubs or trees vary from year to year—the reason for which is as yet unclear. When a sample of 114 nests for which the date on which the first egg was laid was known is divided into 58 early (first eggs laid prior to and including 26 April) and 56 late (after 26 April) nests, then there were significantly ($\chi^2 = 8.90$, df = 1, $P < 0.01$) more ground nests among early than among late nests.

The average height of 51 tree nests on Mandarte was 1.9 ± 0.9 m and for 85 tree nests on Mitlenatch was 2.3 ± 0.9 m. The relatively few nesting

TABLE 1
MEAN VOLUME OF EGGS IN CLUTCHES IN WHICH THE LAYING SEQUENCE OF THE EGGS WAS KNOWN

Position of egg in clutch	Volume (cc) of egg		Significant difference between mean volumes of eggs
	N	$\bar{x} \pm$ SD	
1	27	16.6 ± 1.6	1 > 4 ($P = 0.007$), 1 > 5 ($P = 0.03$)
2	24	16.8 ± 1.5	2 > 4 ($P = 0.002$), 2 > 5 ($P = 0.002$)
3	33	16.1 ± 1.3	3 > 4 ($P = 0.03$), 3 > 5 ($P = 0.02$)
4	29	15.5 ± 1.3	
5	8	15.3 ± 0.9	

birds, linear arrangement of territories, and easy visibility on Mandarte provided an opportunity to determine the height of second nests when the first one was predated or disturbed. In all these cases (N = 26), except one, the first and second nest was built on the same territory. The mean height (1.6 ± 0.6 m) of first nests was significantly ($P < 0.05$, Mann-Whitney *U*-test) lower than the mean height (2.7 ± 1.2 m) of second nests.

Northwestern Crows built nests in new sites in most years. On Mandarte, 28.0%, 23.1%, and 26.7% of all nests used in 1978 (N = 25), 1979 (N = 26), and 1980 (N = 30), respectively, were built on top of nests of previous years.

Courtship begging.—The period between the start of courtship begging and egg-laying at five nests was 0, 1, 1, 5, and 7 days. Females begged on or off the territory but once the first egg was laid, courtship begging occurred on the nest or more commonly in its vicinity. Begging continued throughout incubation when the male arrived near the nest to feed his mate.

Eggs and incubation.—First eggs in clutches on Mandarte were laid 6–10 days earlier than on Mitlenatch (Fig. 1). In a sample of 158 eggs for which the laying interval was known, 133 were laid in daily intervals, 24 in 2-day intervals, and 1 in a 3-day interval. We never found 2 new eggs laid within a 24-h period. Laying eggs at daily intervals appears to be general for the genus *Corvus* (Holyoak 1967, Wittenberg 1968). When clutches were abandoned or predated, the first egg in replacement clutches (N = 10) appeared on average 13.6 ± 1.2 days later.

There was no significant difference in the mean egg volumes (Hoyt 1979) among first, second, and third eggs; however, the mean volumes

TABLE 2
MEAN NUMBER OF EGGS THAT HATCHED ON SUCCESSIVE DAYS IN CLUTCHES OF 3, 4, AND 5 EGGS[a]

Day of hatching	3-egg clutches		4-egg clutches		5-egg clutches	
	Eggs hatched		Eggs hatched		Eggs hatched	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
First	11	1.82 ± 0.57	23	2.43 ± 0.77	4	2.50 ± 0.50
Second	11	0.91 ± 0.51	23	1.22 ± 0.51	4	1.75 ± 0.43
Third	11	0.27 ± 0.45	23	0.26 ± 0.53	4	0.75 ± 0.43

[a] Nests were visited once per day; only clutches in which all eggs hatched were considered.

of first, second, and third eggs were significantly larger than those of fourth and fifth eggs (Table 1). No comparable data are available for other corvids.

The mean weight of 87 fresh eggs prior to full incubation was 17.8 ± 2.0 g. Emlen (1942) gave an average weight of 16.6 g for 157 fresh eggs of the Common Crow. Eggs lost 18.8% (0.19 g per day) of their initial fresh weight through incubation, and that agrees with 18% loss in weight for a typical bird's egg (Rahn and Ar 1974).

During 147 h of observation at 17 nests only females incubated and they spent an average of 86.0 ± 5.1% of each daylight hour on the nest. The mean inattentive period (N = 65) of females during incubation was 5.6 ± 3.3 min during which they defended the nest, drank, preened, defecated, or were fed. During 151 h of observation, 19 incubating females were fed by their mates an average of 1.4 ± 0.9 times per hour. The mean incubation period (N = 19) from the date of laying of the last egg until that egg and all other eggs in the clutch had hatched was 18.3 ± 0.85 days. One infertile egg was incubated for 33 days and weighed less than 9.0 g when it disappeared, and another infertile egg was incubated for at least 30 days before it was abandoned. Infertile eggs in nests with nestlings disappeared within 8 days.

Northwestern Crows begin to incubate before the clutch is complete, so that the eggs hatch asynchronously (Table 2). In clutches of three eggs, 1.82 ± 0.57 eggs hatched on the same day, the remaining eggs hatched the following day or rarely after 2 days (Table 2). In contrast, in four- and five-egg clutches, incubation did not start until about 2.5 eggs had been laid (Table 2). Lockie (1955) found that Jackdaws (*C. monedula*) began to incubate clutches of four eggs when on the average 2.6 eggs had been laid and Wittenberg (1968) stated that *C. corone* started to incubate when about two eggs had been laid (clutch-size not specified).

TABLE 3
SUMMARY OF NORTHWESTERN CROW BREEDING DATA ON MANDARTE AND MITLENATCH ISLANDS

	Mandarte			Mitlenatch		
	N	N/nest	%	N	N/nest	%
Nests[a]	67			120		
Eggs						
No. eggs	267			479		
No. eggs/nest		4.0			4.0	
No. eggs hatched	208		78	345		72
No. eggs hatched/nest		3.1			2.9	
No. eggs lost	13		5	45		9
No. eggs lost/nest		0.2			0.4	
No. eggs not hatched	46		17	89		19
No. eggs not hatched/nest		0.7			0.7	
Young						
No. young lost	101		49	207		60
No. young lost/nest		1.5			1.7	
No. young fledged	107		51	138		40
No. young fledged/nest		1.6			1.2	
Successful nests[b]	54		81	93		76

[a] Only nests with completed clutches (three or more eggs) in which at least one egg hatched.
[b] Nests from which at least one young fledged.

There was no significant difference in the mean clutch-size and hatching success in the two island populations (Table 3). In a total of 187 nests, there were 44 clutches of three eggs, 101 of four eggs, and 42 of five eggs. The mean clutch-size (N = 187) was 4.0 ± 0.7 eggs. Of a total of 746 eggs, 7.8% were lost to predators, 18.1% failed to hatch, and 74.2% hatched. There are surprisingly few comparative data available for other species of *Corvus*. Wittenberg (1968) found that about 10% of the eggs of *C. corone* failed to hatch.

Nestlings.—Hatching was designated as day 1. At hatching, the nestlings were naked except for tufts of down feathers on the head, dorsal region, wing stubs, and tail and they weighed an average of 14.9 ± 2.1 g (N = 62, Fig. 2). The logistic growth curve

$$\left(W = \frac{A}{1 + e^{-K(t_w - t_0)}}\right)$$

most closely fits the data (Fig. 2). In this equation, W is the weight of the nestling in grams on day t_w, A is the asymptotic weight achieved by the

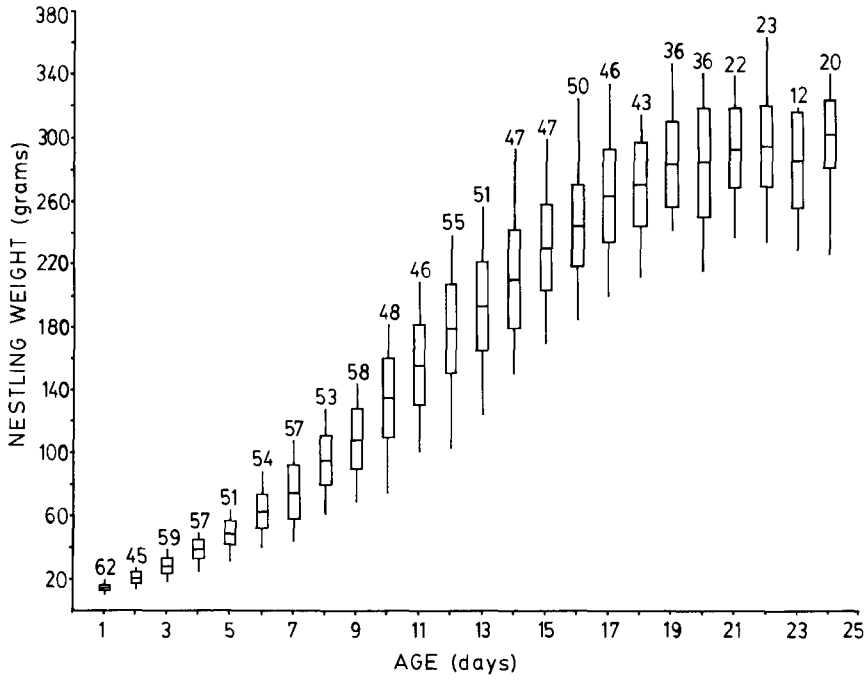

FIG. 2. Change in weight of nestling Northwestern Crows on Mitlenatch Island in 1979 and 1980. Only nestlings that survived to fledging are included. Open bar represents standard deviation around mean, solid line depicts the range and numbers above each point represents the sample size.

average nestling, e is the base of natural logarithms, K is a constant proportional to the specific rate of growth and t_o is the age in days at the point of inflection on the growth curve (Ricklefs 1967). For the Northwestern Crow, A = 305 g, K = 0.298, ½A is 10.8 days, and the time required to grow from 10–90% of A is 14.8 days. The eyes began to open as early as day 5, and they were wide open and a blue iris was apparent at a mean age of 9.0 ± 1.8 days (N = 18), at which time the young weighed an average of 114.7 ± 42.7 g (N = 18). The eyes of nestling Common Crows are slits by day 8 and fully open by day 11 (Emlen 1942). Only females brooded nestlings and they remained very attentive to the nest until the young were about 10 days old (Table 4).

A marked change in behavior occurred when the young were about 12 days old. Prior to that age nestlings begged for food when we jiggled the nest but after that age the same nestlings crouched in the nest and begged reluctantly or not at all. This change in behavior coincided with the timing

TABLE 4
BROOD ATTENTIVENESS OF THREE FEMALE NORTHWESTERN CROWS

Nestling age (days)	Min obs. N	% attentive
1–5	1046	93.1
6–10	138	88.4
11–15	586	30.9
16–18	270	17.8

of the female's increased share in feeding of the young (Table 5) and her reduced nest attentiveness (Table 4). The tips of the folded wing extended beyond the tip of the tail on about day 20 when some nestlings in tree nests began to climb into branches adjacent to the nest. The tarsus attained an adult length of about 50 mm at 16–18 days (Fig. 3) at which time the nestlings began to defecate over the nest rim.

Forty-nine nestlings in 20 nests on Mandarte left the nest permanently at an average age of 32 ± 2.5 days, while 55 nestlings on Mitlenatch did so at an average age of 26 ± 3.4 days. The nestling period on Mandarte agrees well with that of several, slightly larger, other species: 35 days for *C. brachyrhynchos* (Goodwin 1976), 32–33 days for the Rook (*C. frugilegus*) (Goodwin 1976), and 30–36 days (Wittenberg 1968) and 30–34 days (Coombs 1978) for *C. corone*. Premature nest departure on Mitlenatch was presumably due to our presence near nests, whereas on Mandarte the nestlings were observed from a distance.

Fledglings.—Northwestern Crows that fledged from tree nests stayed in trees and shrubs near the nest, whereas fledglings from ground nests moved to nearby trees. Three flightless nestlings from a ground nest moved approximately 30 m through tall grass to reach a nearby tree. Young crows

TABLE 5
FEEDING RATES OF NESTLINGS IN FOUR NESTS BY THEIR PARENTS

Age of nestling	Male		Female	
	No. feedings	Feedings/hour $\bar{x}$ ± SD (%)	No. feedings	Feedings/hour $\bar{x}$ ± SD (%)
1–7 days	44	1.8 ± 0.3 (66.7)	22	0.9 ± 0.4 (33.3)
8–14 days	13	1.1 ± 0.2 (33.3)	26	2.3 ± 0.1 (66.7)
15–21 days	8	0.7 ± 0.2 (32.0)	17	1.6 ± 0.2 (68.0)
22–28 days	6	0.8 ± 0.3 (40.0)	9	1.2 ± 0.2 (60.0)

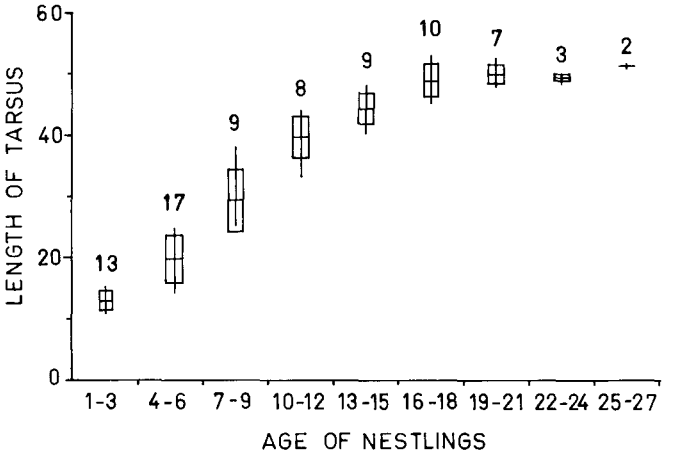

FIG. 3. Change in tarsus length with age of nestling Northwestern Crows on Mitlenatch Island. (Explanation as in Fig. 2.)

clamored toward adults carrying food and eventually began to follow closer to the food source 2–3 weeks following nest departure. Once the young could fly the offspring of two or more families mixed together.

Fledging success, defined as the number of eggs hatched that fledged young, was low on both islands (Table 3). Significantly ($P < 0.05$) more young fledged on Mandarte than on Mitlenatch but the percentage of nests that fledged at least one young was about the same (Table 3). Among 47 nestlings that disappeared at a known age, 27 (57%) were lost within the first 7 days following hatching, 13 (28%) between 8 and 14 days, and 7 (15%) between 15 and 20 days. None disappeared after 21 days. Similar results have been reported for *C. corone* (Tenovuo 1963) and *C. monedula* (Zimmermann 1951).

Mortality among fledgling Northwestern Crows based upon sightings of colorbanded young on Mitlenatch was low in the 9 weeks following fledging. Thirty-eight (75%) of 51 fledglings seen in the first week following fledgings were still alive 9 weeks later. All 38 juveniles were seen at least once during each of the 9 weeks. Among 12 fledglings from early nests (fledged on or before 15 June), 11 were seen between 22 July and 26 August (median date 22 August), while among 14 late nests (fledged after 15 June), only seven birds were seen between 1 July and 26 August (median date 13 July). Mitlenatch is separated from the nearest land by an often windy 5 km of water and it is very unlikely that fledglings attempted to leave the island during those first 9 weeks. Attacks by Glau-

cous-winged Gulls (*Larus glaucescens*) were a major source of mortality on both islands when the fledgling crows landed on gull territories.

Ten fledglings on Mitlenatch were observed almost daily following departure from the territory. They were first seen to feed themselves at an average of 27.6 ± 7.4 days after fledging. On Mandarte one fledgling was fed sporadically 77 days after fledging.

SUMMARY

Northwestern Crows (*Corvus caurinus*) were studied during April–August 1976–1983 on Mitlenatch and Mandarte islands in Georgia Strait, British Columbia. Nesting territories ($\bar{x}$ = 0.49 ha) and internest distances ($\bar{x}$ = 17.8 m) were small compared to other species of *Corvus*. Nests were built on the ground or in shrubs and trees. Nests built early in the season tended to be ground nests as compared to those built later. The average height of tree nests was 2 m. About 25% of the nests each year were built on top of nests of previous years. Most eggs were laid at daily intervals. The mean weight of fresh eggs was 17.8 g and eggs lost 18.8% of their initial weight during the incubation period ($\bar{x}$ = 18.3 days). Fourth and fifth eggs were significantly smaller than first, second, and third eggs. Incubation began when an average of 2.3 eggs had been laid in a clutch. The mean clutch-size was four eggs. Hatching success was 74%. Nestlings weighed 14.9 g at hatching and 300 g about 4 weeks later. About 79% of the nests fledged one or more young.

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DEPT. BIOLOGICAL SCIENCES, SIMON FRASER UNIV., BURNABY, BRITISH COLUMBIA V5A 1S6, CANADA. (PRESENT ADDRESS RWB: CANADIAN WILDLIFE SERVICE, BOX 340, DELTA, BRITISH COLUMBIA V4K 3Y3, CANADA.) ACCEPTED 5 MAR. 1984.