A COMPARISON OF THE FEEDING AND NESTING REQUIREMENTS OF THE GREAT CORMORANT *(PHALACROCORAX CARBO* L.) AND DOUBLE-CRESTED CORMORANT *(P. AURITUS* LESSON) IN NOVA SCOTIA

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A comparison was made of nesting and foraging requirements of the Great Cormorant *(Phalacrocorax carbo)* and Double-crested Cormorant *(P. auritus)* in Nova Scotia.

P. carbo bred solely on barren islands and cliffs while *P. auritus* preferred to nest in trees on small islands. Occasionally, both species shared bare, rocky islands, in which case *P. carbo* nested around the boulder-strewn edges and *P. auritus* formed dense colonies on the tops. Nest-site segregation probably is related to species' sizes.

Diets determined from regurgitated pellets and from partly digested fish vomited by young birds showed: (1) *P. auritus* took more species of fishes than did *P. carbo;* (2) *P. auritus* utilized all species important to *P. carbo* plus large numbers of several others; (3) the relative frequencies of fish species common to both varied between birds; moreover, *P. auritus* took significantly smaller individuals of each of these species than did *P. carbo*; (4) *P auritus* took large numbers of eel-like fish not caught by *P. carbo*; (5) *P auritus* took large numbers of very small species, effectively reducing its mean prey size.

Diet dissimilarities mostly were the result of different foraging habitats. *P. auritus* fed both in shallow seawater (mean depth 5 m) and in freshwater; *P. carbo* was strictly marine, preferring deeper water (mean depth 11 m). However, the secretive eel-like fish, consumed solely by *P. auritus*, occupy a wide depth range, which suggests that foraging techniques also differ between cormorants. These different feeding depths and methods undoubtedly influence the mean diving times, mean resting times, and the ratios of these means, each of which differ significantly between species. As both species, outside of their area of range overlap, occupy very similar niches, it is proposed that their diet differences in Nova Scotia result from past competition.

Introduction

The cormorants comprise a highly successful, globally distributed family of fisheating birds represented by 28 species. Four occur in Canada of which two, the Doublecrested Cormorant *(Phalacrocorax auritus* Lesson) and the Great Cormorant *(Phalacrocorax carbo* L.), breed along the Atlantic coast. Both are prominently represented in coastal Nova Scotia where I have undertaken a comparative study of their nesting and feeding habits. Such investigations have been carried out previously for the individual species and reveal marked similarities in their niches. However, only *P. auritus* has been well studied in the area of sympatry (although notes for Nova Scotia are scanty). Relevant information on North American *P. carbo* is totally lacking.

It is my aim to assess niche overlap between these two cormorants both by analyzing their selections of nest sites and by determining the species and frequencies of their prey. I examine the differences found in terms of morphology and behavior of the birds, and consider some evolutionary implications. More practically also, it is my purpose to document the diets of these species in the light of the constant concern about their effects on fisheries.

Previous Knowledge of *P. carbo* and *P. auritus*

Investigations of cormorant biology have usually been prompted by economic concern over their effect on commercially important fishes. Such studies have been documented in Canada (McLeod and Bondar 1953), Scotland (Mills 1969), the Netherlands (van Dobben 1952), Russia (Dement'ev *et al* 1966), Australia (Serventy 1938), and New Zealand (Duncan 1968). The cormorants most frequently involved in the studies are *P. auritus* in North America and *P. carbo* in Europe.

The natural history of *P. auritus*, the eastern North American subspecies, has been the topic of two monographs, by Lewis (1929) and by Mendall (1936); these and other studies have been summarized concisely in Palmer (1962). According to these, *P. auritus* is primarily a ground-nesting bird, occasionally nesting in trees. It usually feeds in saltwater in the Atlantic region, occasionally venturing into freshwater. Taverner (1915) in Gaspé, Lewis (1929) in the Gulf of St. Lawrence, Mendall (1936) and Scattergood (1950) in Maine, Lewis (1957) in Nova Scotia, and Dunn (1975) in New Hampshire have recorded wide ranges of marine fishes in its diet, although the importance of individual species varied with location. Bottom-dwelling fishes were most favored, with myoxocephaline sculpins and pleuronectids occurring in all studies. South of Gaspé, the cunner *(Tautogolabrus adspersus)* represented over 40% of total numbers in some samples. Various gadids, the rock gunnel *(Pholis gunnellus)* and clupeids, particularly the alewife *(Alosa pseudoharengus)* were also of widespread importance. Freshwater fishes such as common sucker *(Catostomus commersoni)*, cyprinids including golden shiner *(Notemigonus crysoleucas)*, sticklebacks *(Gasterosteus* sp), and yellow perch *(Perca flavescens)* were also found by Lewis (1957). Small numbers of Crustacea such as shore crab *(Cancer irroratus)*, spider crab *(Hyas coarctatus)*, amphipods, and shrimp were noted along with remains of annelids and squid, probably representing digested-out remnants of fishes' diets. The diet of the western subspecies, *P. a. albociliatus*, has recently been investigated by Robertson (1974) who found that two species of gunnel, *Apodichthys flavidus* and *Pholis laeta*, and the Pacific sand launce, *Ammodytes hexapterus*, were heavily consumed along with shiner seaperch, *Lymatogaster aggregata*, and snake prickleback, *Lumpenus sagitta*.

Knowledge of breeding biology, behavior, and population dynamics of *P. carbo* comes principally from studies of the central European race, *P. c. sinensis*, a smaller, more lacustrine, more tree-nesting bird (see Haverschmidt 1933; Portielje 1927; Kortlandt 1938; 1940; 1942) than *P. c. carbo*. Such information is scanty for the nominate race (see Witherby *et al.* 1943; Bannerman 1959; and Palmer 1962) although Erskine (1972) recently reported on phenology of the North American bird and found it to nest much earlier than *P. auritus*. *P. c. carbo* usually breeds on small, bald islands and cliffs. It occasionally nests in trees, for example on Lough Cutra, Co. Galway, Eire (Ruttledge in Bannerman 1959) and Durrell Point, P.E.I. (Godfrey 1954). It is largely a marine shoal feeder, although also venturing into freshwater in Britain. Descriptions of feeding habits in the New World consist of passing remarks by Lewis (1927) for Labrador and Salomonsen (1950) for Greenland that myoxocephaline sculpins were taken. In Europe, the following workers studied diets of marine feeding *P. carbo*. Steven (1933) in Corn-

wall, Pearson (1968) in the Farne Islands, Rae (1969) and Mills (1969) in Scotland, West *et al* (1975) in Ireland, and Madsen and Sparck (1950) in Denmark *(P. c. sinensis)*. Again species and proportions varied, but ground fish were in the vast majority. Pleuronectids were well represented in all studies with gadids of some importance in all but one. Various clupeids and the viviparous blenny *(Zoarces viviparus)* appeared regularly in three studies while salmonids, labrids, eels *(Anguilla anguilla)*, sand launce *(Ammodytes* spp), and gobies *(Gobius* spp) were important in individual areas though not widespread. Mills (1965) found brown trout *(Salmo trutta)*, Atlantic salmon *(Salmo salar)*, perch *(Perca Fluviatilis)*, and eel to be important prey species in freshwater in Scotland; these species were also noted by West *et al* (1975) although Irish cormorant feed much more heavily on marine fishes. Van Dobben (1952) in a detailed study of the feeding of Dutch *P. c. sinensis* found that the eel, roach *(Teuciscus rutilus)*, ruffe *(Acerina cernua)*, and bream *(Abramis brama)* were the principal prey. Moreover, he compared prey frequencies with actual fish frequencies in the Ysselmeer, showed a preference for larger fish, particularly eels, and illustrated influences of weather and season on diet composition. Crustaceans were reported by all of the previous workers. Steven (1933) found particularly large numbers of shrimp *(Crangon* sp) and prawn *(Pandalus* spp) implying that they were actively captured.
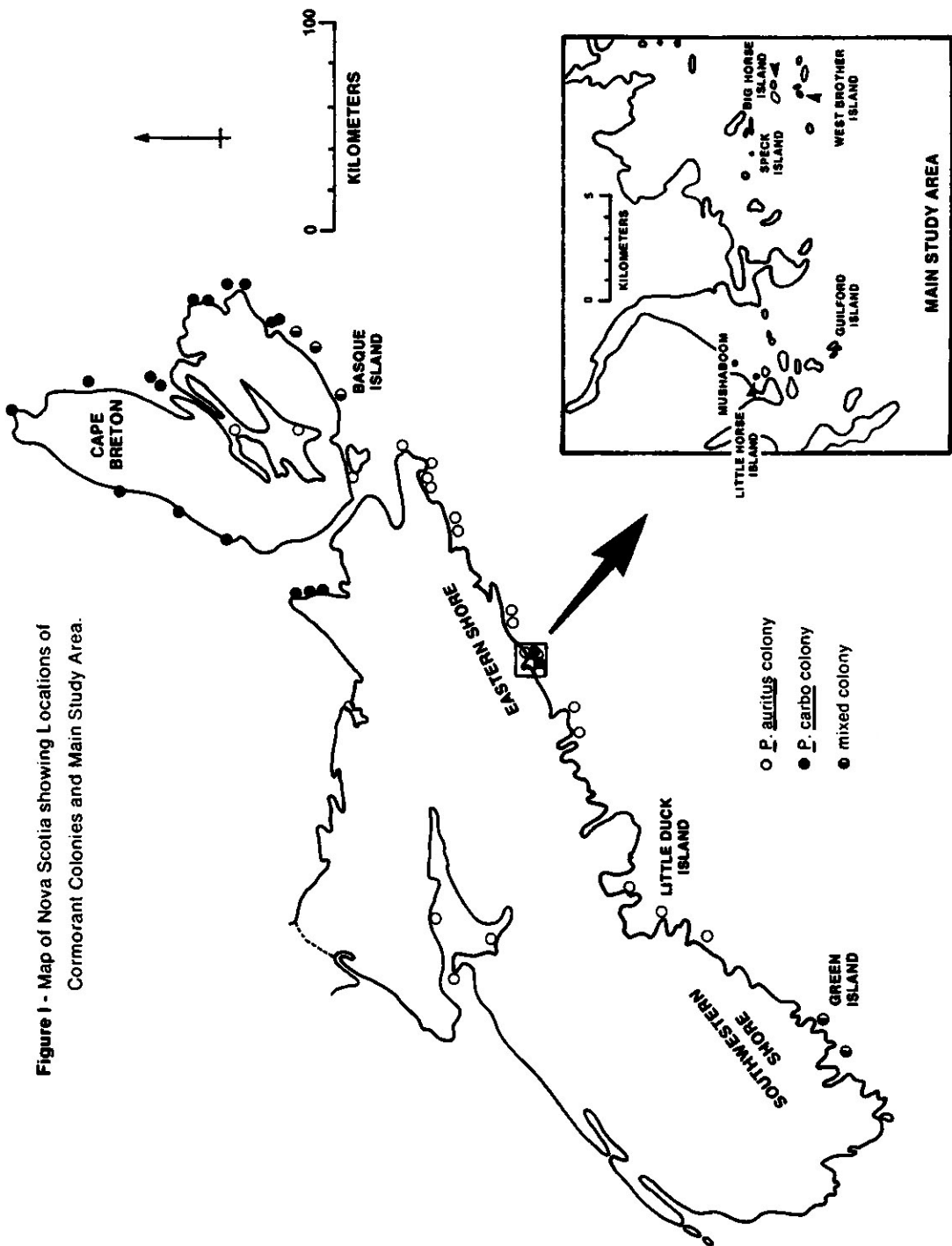
Competition between the two species is implied by the overlap of nesting habitat and food species. Lack (1945) studied this question in *P. carbo* and the Shag *(P. aristotelis)* in England and found them ecologically quite distinct. However, these species belong to separate behavioral groups (continental and marine, respectively) as outlined by van Tets (1965). More recently, Scott (1973) described differences in habitat requirements of sympatric Brandt's Cormorants *(P. penicillatus)* and Pelagic Cormorants *(P. pelagicus)*, both of the marine group. A unique feature of the present study is that both cormorants are continental forms.

Study Area

Although the entire Nova Scotian coast was searched for cormorant colonies, this study was carried out principally on two islands off the town of Mushaboom, Halifax County, on the eastern shore during the summers of 1971 and 1972 (Fig. 1). Approximately 32 pairs of *P. auritus* nested in black spruce *(Picea mariana)* on Little Horse Island (50 x 150 m), along with Herring Gulls *(Larus argentatus)*, Great Black-backed Gulls *(Larus marinus)* and Common Eider *(Somateria mollissima)*. Seventeen pairs of *P. carbo* nested farther offshore on a small exposed rock (30 m diameter) off Guilford Island, with two pairs of Great Black-backed Gulls and a pair of Common Eider. Two other colonies were located 10 km to the east: *P. carbo (ca* 230 pairs) on West Brothers Island and *P. auritus (ca* 210 pairs) on an islet off another Horse Island, hereafter termed Big Horse Island. I visited these occasionally but their highly exposed location frequently made regular trips impossible. The substrate is rocky, and around all islands the depth of water is relatively shallow, to about 10 m, dropping rapidly farther offshore. Many shoals are also found throughout the region.

Methods

During the spring and summer of 1971, every cormorant colony in coastal Nova Scotia was located, censused, and described (Lock and Ross, 1973; Fig. 1), and a qualitative assessment was made of the suitability of each area for cormorant breeding. However, detailed studies of nest-site selection and feeding strategies took place in the main study area.

Figure 1 - Map of Nova Scotia showing Locations of Cormorant Colonies and Main Study Area.

Diets were determined principally from material found in pellets regurgitated round the nest. The oval pellets, ranging from 4 to 7 cm long, contained otoliths, larger undigested fish bones, rocks, and invertebrate remains (such as crab claws and polychaete mandibles), encased in a thick mucous membrane which is sloughed off from the stomach wall during regurgitation. Van Dobben (1952) found that pellets held the remains of a single fishing expedition, the usual daily number for a nesting cormorant. Neither Madsen and Sparck (1950) nor van Dobben found any indication that undigested remains were stored more than one day in the stomach or that any were ejected with the faeces. I found that pellets were rapidly devoured by scavenging gulls and crows so that those collected represented the cormorant's diet for that or the previous day. Examination of partly digested food, vomited by young cormorants when disturbed, provided further data on diet.

Regurgitations were collected and preserved initially in 5% buffered formalin; ethanol was later used. Each pellet was kept separate so that there should be no mixing of contents. The pellets' contents were sorted in trays under an illuminated magnifying glass, examined and, when necessary, measured by optical grid (one grid unit equals 0.071 mm) under a dissecting microscope.

Systematic collection of regurgitations and data on vomits were made on the two colonies off Mushaboom during the summer of 1971 in three sampling periods: May 30 - June 12; June 20 - July 4; and July 12 - July 22 respectively. Visits to each colony were made no oftener than every second day to minimize disturbance. Occasionally, owing to weather and sea conditions, colonies could not be visited for up to five days. Collections of pellets or at least observations of vomits were also made on other Nova Scotian colonies during the summers of 1971 and 1972.

Fish identification was possible using otoliths (fish ear-stones), which are species-specific, are digestion-resistant and, being white, are easily located. Moreover, their lengths are linearly related to fish length in a given species. A fish contains only a single pair of useful otoliths, one being the mirror image of the other. Totalling the number of otolith pairs and unpaired singles would thus give a minimum estimate of fish numbers in a sample. As occasionally only one member of a pair was found, the relationship between otolith disappearance and size was tested by comparing frequencies of pairs and singles in two arbitrary length ranges, 0-50 and 50-100 grid units. The differences between such frequencies for large and small otoliths were not significant at the 5% level for either species (χ^2 test for 2 x 2 table). Moreover, comparison of the two 2 x 2 tables by another χ^2 test (Pielou 1974, for examples) showed no significant difference in these frequencies between cormorants. Loss of otoliths, either through digestion, breakage or separation after regurgitation, could also mean fish going unrepresented. Assuming that each otolith in a given size range has an equal chance of being lost, the following expression can be derived for the number of fish unrepresented in a sample (see Ross 1973, for derivation).

$$\text{Fish lost} = \frac{b^2}{4a}$$

where b = the number of fish represented by pairs of otoliths, and
a = the number represented by singles.

Percentage fish loss was calculated for groups of all otoliths of the two size ranges found in each study period. Although percentages ranged from 3.8 to 18.3, nine of the twelve values were under 10%. As otoliths less than 1.8 mm long were not found, vomits were checked for the occurrence of small otoliths. One species with small otoliths, the cunner, was thus found to be very important in the diets of both cormorants. Therefore, the presence of this species was determined from its dorsal pharyngeal tooth plate whose width indicated fish size.

During the summer of 1971, diving and resting times were recorded for both species by watching the foraging bird continually with binoculars while dictating into a tape recorder the moments of surfacing and diving. Fishing depths were determined during the summer of 1972, using a depth sounder operated from a small boat.

Four *P. carbo* were collected off the Guilford Island colony on June 10, 1972, and four *P. auritus* specimens were obtained from the Federal Department of the Environment. These had been collected during June 1972 from the St. Mary's River and their stomachs removed to check on salmon depredation. All were weighed, then measurements recorded as follows: routine length of wing, tail, exposed culmen, and tarsus as in Godfrey (1965); *toe*: from end of the tarsus to the tip of the longest toe; *leg*: length of femur and tibia; *head*: distance from the preoccipital process to the most distal tip of the nail of the bill, the depth of the complete bill at the dorsal point of appearance of the exposed culmen, the depth of the hook of the beak from the tip dorsally to the most elevated level of the nail, the width across the maximum cranial bulge, and the distance between the squamosal processes; *vertical gape*: perpendicular distance from palate at cranio-facial hinge to point of maximum distension of the gular region; *horizontal gape*: maximum laterally distended width between the lower mandibles.

Areas were computed for the opened foot, the extended wing and the spread tail, using the weight of paper tracings. Maximum cross-sectional area of the body was estimated by measuring width and depth, then substituting these in the formula for the area of an ellipse. These various measurements were used to calculate parameters of diving and flying ability.

Results

Breeding Habitat   In Table I, the number of Nova Scotian colonies of each cormorant as well as the total number of breeding pairs are listed for the various habitat types. Two of the *P. auritus* colonies, recorded as arboreal, were composed predominantly of tree-nesters with some on the ground near fallen trees. Of the ground-nesters, one colony of *P. carbo* and two of *P. auritus* were found at the bases of dead and fallen trees. The remaining ground colonies were located on small, rocky, barren islands, of which five were occupied by both species.

Table I. Breeding habitats

Type of habitat	No. of colonies		No. of breeding pairs	
	P. carbo	*P. auritus*	*P. carbo*	*P. auritus*
Spruce trees on small islands	0	21	0	2839
Pilings	0	1	0	88
Level ground on small islands	11	8	1059	1190
Cliffs - mainland	7	0	307	0
Cliffs - island	5	0	627	0
	23	30	1993	4117

Certain nesting situations are clearly exclusive to each species in Nova Scotia. Only *P. auritus* uses trees or, in one case, old pilings, while *P. carbo* is the sole cliff dweller. The level ground of barren islands is the only nesting habitat common to both. However, since Godfrey (1954) found *P. carbo* breeding in trees and *P. auritus* on cliffs in Prince

Edward Island, it appears that these birds can utilize a wide range of breeding habitats elsewhere. A comparison of the locations of colonies with available nesting sites in Nova Scotia is necessary to determine if a preference exists.

Figure 1 reveals a patchy distribution of both species with substantial overlap only along the Atlantic coast from eastern Cape Breton Island to the southwestern shore. Unfortunately, the past history of cormorants in Nova Scotia is poorly known, owing either to lack of observation or to difficulties of previous observers in distinguishing the two species. My sole conclusion about the nesting preferences of allopatric cormorants is that the habitat utilized is the only one available in that location, example, cliff-nesting of *P. carbo* along the coast of western and northern Cape Breton, or the island-nesting of *P. auritus* in the Bras d'Or Lakes and Bay of Fundy. Similarly, in the area of sympatry, the five mixed colonies in Cape Breton and southwestern Nova Scotia are all on small barren islands, the only possible sites. However, along the eastern shore a large number of suitable small islands, both treed and barren, are unoccupied. Here *P. auritus* is an exclusive tree-nester. Moreover, it is well known in this area that, when these cormorants eventually destroy their trees with their droppings and by ripping off living branches, they move to nearby treed islands and do not breed as a colony on the ground, thus demonstrating a propensity for arboreal nesting. In contrast, the two colonies of *P. carbo* in this area are both on the ground, suggesting a preference for ground nesting.

A comparison of the censuses by Lewis (1957) and by Lock and Ross (1973) provides good examples of such preferences. Lewis recorded large colonies of tree-nesting *P. auritus* on both West Brother and Speck island, whereas Lock, 16 years later, found the trees mostly dead on both islands; no *P. auritus* occurred on West Brother and only a few remained on Speck. He found a large tree-nesting colony on nearby Big Horse Island, and *P. carbo* was nesting among upturned tree roots on West Brother.

The five mixed colonies were also examined for differences in nesting habitat. During aerial surveys I noted a clumped distribution of the species. To study segregation, I visited Basque Island and Green Island, both of which are flat-topped with rapidly shelving boulder-strewn sides. *P. auritus* bred in dense colonies on the exposed tops while *P. carbo* was situated around the edges, often sheltered behind rocks.

Food Studies Results of pellet analysis from the main study have been pooled for each study period (Tables II, III). Another diet composition based on vomits from nestlings is presented in Table IV. These show that 16 fish species were taken by *P. auritus* while *P. carbo* utilized only 11; nine were common to both. Comparison of the two methods of diet determination show that rock gunnel, a fish taken exclusively by *P. auritus*, was vastly under-represented in pellets. It was, in fact, a major prey of this cormorant, constituting between 25 and 50% of the fishes consumed. Other species important only to *P. auritus* were wrymouth *(Cryptacanthodes maculatus)* and a class of fish named "small gadoids" that could not be completely identified. As many as 50 individuals of this group could occur in a single pellet. An annotated list of fish species preyed on by cormorants in Nova Scotia is provided in Appendix I; this includes all available records.

All six of the dominant prey species of *P. carbo* also were consumed by *P. auritus*. To find whether relative frequencies of these fishes differed between cormorants, the frequencies of the six species (Tables II and III) were listed for both cormorants in a 2 x 6 contingency table for each study period. A χ^2 test for homogeneity (Bailey 1959) was then performed on each table to ascertain whether ratios of the two frequencies of the six fish species varied. Differences in these compositions were highly significant (P < 0.001) in the three periods, indicating different preferences of the cormorants among these species and/or different availability of the fishes.

Table II. Summary of numbers and percentages of fish found in *P. carbo* pellets during the main study, 1971

Fish species	30 May-12 June Actual numbers	Percent-age	20 June-4 July Actual numbers	Percent-age	12 July-22 July Actual numbers	Percent-age	Overall percentage
Pollock	28	20.7	76	26.6	51	22.1	23.8
Cunner	29	21.5	119	41.6	122	52.8	41.4
Winter Flounder	13	9.7	40	14.0	20	8.6	11.1
Long-horned Sculpin	22	16.3	13	4.2	5	2.1	6.0
Short-horned Sculpin	35	25.9	14	4.8	17	7.4	10.1
Cod	6	4.5	16	5.5	14	6.2	5.5
Plaice	1	0.7	4	1.4	1	0.4	0.9
Smelt	-	-	1	0.4	-	-	0.2
Small Gadoids	1	0.7	3	1.1	1	0.4	0.8
Ocean Pout	-	-	1	0.4	-	-	0.2

Table III. Summary of the numbers and percentages of fish found in *P. auritus* pellets during the main study, 1971. The "small gadoid" class has been omitted from the percentage calculation in order to make this column more comparable to that of **Table II** for the larger fishes

Fish species	30 May-12 June Actual numbers	Percent-age	20 June-4 July Actual numbers	Percent-age	12 July-22 July Actual numbers	Percent-age	Overall percentage
Pollock	129	37.6	47	29.0	52	21.4	30.5
Wrymouth	79	23.1	46	28.4	48	19.8	23.3
Short-horned Sculpin	50	14.5	17	10.6	64	26.3	17.5
Winter Flounder	30	8.8	7	4.3	10	4.1	6.3
Cod	18	5.3	5	3.1	7	2.9	4.0
Long-horned Sculpin	3	0.9	3	1.8	3	1.2	1.2
Cunner	27	7.9	27	16.7	55	22.7	14.7
Smelt	1	.3	—	—	—	—	0.1
Rock Gunnel	1	.3	8	4.9	4	1.6	1.7
Ocean Pout	—	—	1	0.6	—	—	0.1
Herring	—	—	1	0.6	—	—	0.1
Common Sucker	3	.9	—	—	—	—	0.4
Silver Hake	1	.3	—	—	—	—	0.1
Small Gadoids	17	NA	353	NA	414	NA	NA

Table IV. Summary of contents of cormorant vomits from nestlings observed in the main study area during the summer, 1971 (12-22 July)

| | Cormorant Species | | | |
| | P. carbo | | P. auritus | |
Fish species	Numbers	%	Numbers	%
Cunner	38	71.7	5	16.2
Sculpins (ssp)	7	13.2	8	25.8
Pollock	1	1.9	0	0
Winter Flounder	4	7.5	0	0
Rock Gunnel	0	0	15	48.4
Wrymouth	0	0	1	3.2
Sand Launce	0	0	1	3.2
Eel	0	0	1	3.2
Herring	3	5.7	0	0

Otolith length (or tooth-plate width of cunner) were recorded for all examples of the six dominant species plus wrymouth found in pellets. The frequency distributions of these dimensions were examined for each cormorant in the three study periods (see Ross 1973) and observations are summarized in Appendix I. The means of the various distributions for the six dominant species are presented in Table V. In all but one of the 18 pairs of means, those for *P. carbo* are larger than those for *P. auritus*, indicating that *P. carbo* took significantly larger fish (P < 0.0001, sign test).

Table V. Mean length of otoliths (pharyngeal tooth plate width for cunner) of the six important fishes taken by both cormorant species. All measurements are in grid units

Cormorant species and study period	Pollock	Cod	Winter Flounder	Long-horned Sculpin	Short-horned Sculpin	Cunner
30V-12VI						
P. carbo	94.5	120.7	47.1	82.2	74.6	184.8
P. auritus	80.7	72.5	43.3	82.0	52.6	149.1
20VI-4VII						
P. carbo	91.8	115.6	41.9	80.9	76.1	168.1
P. auritus	77.9	79.8	27.9	59.0	62.9	145.6
12VII-20VII						
P. carbo	76.5	120.8	40.4	75.9	63.8	146.1
P. auritus	80.2	100.3	36.2	73.7	52.4	143.1

Lists of fish remains also were made at other cormorant colonies, including West Brother and Green island for *P. carbo,* and Big Horse, Little Duck, Basque and Green islands for *P. auritus.* Diet compositions were broadly similar to those found in the main

study although several new species were encountered. However, at the *P. auritus* colony at Little Duck Island, the proportion of cunner was much higher than in the Mushaboom area (79% as compared to 15%). Observations also have been made of the diet of *P. auritus* on the St. Mary's River. Lewis (1957) identified the contents of 20 stomachs while I checked five stomaches of birds shot by technicians of the Department of the Environment in 1972. Small fish such as sticklebacks and cyprinids were very important.

The cormorants also regurgitated various items other than fish. Rocks occurred in 66 and 48 % of the *P. carbo* and *P. auritus* pellets respectively. Gastropods, seaweeds, and sand dollars also were eaten, for unknown reasons. Other molluscan, crustacean and annelid remains most likely represent the diets of captured fish. Rock crabs, *Cancer irroratus*, with some spider crabs, *Hyas coarctatus*, were represented in considerably different proportions in pellets of the two cormorants (11% for *P. carbo* compared to 1% for *P. auritus)*. This suggests either that the fish eaten had different diets or that *P. carbo* was actively hunting crabs. The former appears to be more probable as crab remains were almost always associated with those of large sculpins, but in three instances crabs in *P. carbo* pellets bore punctures in their carapaces possibly caused by the nail of the bird's beak. Bivalve remains, mainly blue mussels, *(Mytilus edulis)*, were also much better represented in *P. carbo* pellets, reflecting the larger percentage of cunner taken.

Diving Behavior Differences in mean depth (Table VI) were highly significant (P < 0.001, Mann-Whitney U-test). This result is supported by the fact that *P. carbo* was rarely observed fishing near shore and invariably flew toward open water to forage. *P. auritus* was often encountered diving just beyond the surf. A good example was provided by the *P. carbo* and *P. auritus* of West Brother and nearby Big Horse Island respectively. *P. carbo* moved almost exclusively westward from their colony to feed around outer shoals; *P. auritus* flew north toward the main shoreline when foraging.

Table VI. Observations on depth and rhythm of diving activity

Foraging depth (m)

Species	Mean depth	Range	N
P. carbo	10.7	4.6-19.8	22
P. auritus	4.7	1.5- 7.9	25

Diving and resting times

Species	Mean diving time in sec.	Mean resting time in sec.	N	Ratio of mean diving and resting time
P. carbo	51.0	13.9	34	3.67: 1
P. auritus	25.1	10.3	86	2.43: 1

Differences in mean diving times, mean resting times and dive/rest ratios (Table VI) were also highly significant ($P < 0.001$, Mann-Whitney U-test). Diving times undoubtedly correlate with feeding depths, while the resting time would reflect the recovery period after these exertions. Interestingly, the dive/rest ratios are highly dissimilar, suggesting differences in either physiological efficiencies or underwater behavior.

Comparative Morphology Means of each of 14 linear measurements were determined for both *P. carbo* and *P. auritus* and the ratios taken for each pair. The average of these ratios of means *(P. carbo: P. auritus)* is 1.17:1, with a range of 1.07:1 - 1.36:1. The extreme values are associated with tail length and cranial bulge which both showed much smaller differences than expected (1.07:1) and with vertical gape which was proportionally much greater for *P. carbo* (1.25:1). The ratios of the three beak measurements, exposed culmen (1.36:1), depth at exposed culmen (1.26:1), and hook depth (1.26:1) were consistently greater than average.

Mean weight of the four specimens of *P. carbo* was 3480 g with a range of 3090 - 3714 g. As the four *P. auritus* specimens had their stomachs removed, their whole weight was first estimated by adding 15% to their eviscerated weight. Their mean estimated weight was 1860 g with a range of 1786 - 1928 g which is similar to findings of Lewis (1929) and Mendall (1936).

Calculations concerning diving and flying abilities are listed in Table VII. Storer (1971) indicated that underwater speed and manoeuvrability are functions of the ratio of maximum cross-sectional area to foot area. The difference between species is striking, implying that *P. auritus* travels faster and/or more efficiently under water. Aerial efficiency and manoeuvrability are guaged from wing loading (body weight divided by total area of wings and tail). *P. auritus* carrys less weight per unit area of flight surface than *P. carbo*. This is expected for birds of similar proportion differing only in size, since weight varies as the cube and area as the square of linear dimension.

Table VII. Calculated parameters of diving and flying ability

	P. carbo		*P. auritus*	
	Range	Mean	Range	Mean
Wing loading (g/cm^2)	1.37-1.51	1.44	0.88-1.10	0.98
Ratio of cross-section to foot area	1.38-1.79	1.57	1.18-1.23	1.21

Discussion

Pronounced differences in the breeding and feeding requirements of *P. auritus* and *P. carbo* result from morphology and feeding behavior of these species.

Nest sites are distinctive in Nova Scotia since *P. auritus* largely utilizes trees while *P carbo* is an exclusive ground-nester. Along the Atlantic coast, *P. auritus* nests mainly in trees and only occasionally on the ground. However, in other sections of its range ground-nesting predominates, although trees are used wherever possible (Palmer 1962). *P. carbo* has tree-nesting races, *e.g.*, *P. c. sinensis* (Kortlandt 1942; van Dobben 1952) but this behavior is exceptional in *P. c. carbo*. As both species belong to the group of cormorants characterized by this arboreal capability (see van Tets 1959), it appears that

the tree-nesting propensity was ancestral but has since been suppressed in *P. c. carbo*. Clearly, the primary advantage of arboreal nesting to *P. auritus* is protected from terrestrial predators. Ground nesting itself provides little benefit to *P. carbo* other than a reduced chance of young falling out of the nest. Instead, I proposed that *P. carbo* breeds on the ground because it finds tree nesting difficult, possibly because its greater weight strains branches or increased wing loadings leads to landing problems. However, its large size is of advantage as it allows greater metabolic efficency which, considering the cormorant's wettable plumage (Rijke 1968), is important if cold waters are to be fished. Moreover, this could explain why *P. carbo* remains year round in or near the breeding range, and does not undergo a lengthy migration like *P. auritus*.

Present-day competition cannot be invoked as a mechanism to segregate nest sites as preferences of the two Nova Scotian cormorants do not change outside of the area of range overlap. It initially appeared that some degree of competitive displacement might occur on mixed colonies where the limited, suitable breeding habitat has forced both to share a barren island. However, even here different nesting sites appear to be preferred. I observed that *P. auritus* on the Blue Gull Rock colony did not occupy vacant nesting sites of the type used by *P. carbo*, suggesting a preference by *P. auritus* and not a simple physical exclusion by the larger, earlier nesting *P. carbo*. However, Erskine (1972), in tracing the history of the *P. carbo* colony at Crystal Cliffs, noted that *P. auritus* initially bred there and was replaced by *P. carbo*. In contrast, the Cape Tryon, P.E.I. colony has contained both species since 1941; although proportions fluctuate, neither species is approaching extirpation. As detailed observations of the nesting sites of these colonies have not been made, further speculation is not warranted.

Food spectra of the two cormorants show a degree of overlap as expected; however, differences exist which are remarkable for such similar species.

1) *P. auritus* preys on a larger number of fish species than *P. carbo*. In the main study area, *P. auritus* took 16 species and *P. carbo* only 11, while, based on all records in Nova Scotia, the numbers were 23 and 13 respectively.

2) *P. auritus* utilizes all the important species taken by *P. carbo* plus large numbers of several other species. The proportions of the various common species differ greatly between the two birds.

3) *P. auritus* takes a large number of eel-like fish not caught by *P. carbo*. These include wrymouth, rock gunnel, sand launce and American eels.

4) *P. auritus* takes significantly smaller individuals than does *P. carbo* of the fish species common to both cormorants; however, the differences in mean sizes of the various species are small. *P. auritus* also takes substantial numbers of much smaller species such as rock gunnel, stickleback, sand launce, mummichog, and an undertermined group described as "small gadoids". These further reduce the mean prey size of this species.

The observed differences in diet result primarily from dissimilarities in foraging habitats. The greater diversity of prey of *P. auritus* is largely the result of its feeding in fresh as well as saltwater; *P. carbo* is strictly marine. In the sea, *P. carbo* fishes at an average depth of 11 m as opposed to 5 m for *P. auritus*. Correspondingly, the latter forages closer to shore where it would more often encounter the smaller fish species, *e.g.*, mummichog and stickleback. It also might find the "small gadoids" here, possibly fry of squirrel hake *(Urophycis chuss)* or tomcod *(Microgadus tomcod)* which inhabit estuaries or very shallow water (Bigelow and Schroeder 1953). It is unlikely that *P. carbo* deliberately rejects these small species. The depth difference also could account for the greater proportion of the deeper-water, long-horned sculpin taken by *P. carbo* and the presence of American plaice in its diet.

Habitat differences do not explain why *P. auritus* specializes in taking eel-like fishes, as these occupy a wide depth range. However, considering the complete absence of this group from the diet of *P. carbo*, it appears that *P. auritus* must have a different foraging technique which allows the capture of these secretive, burrowing fish.

The larger *P. carbo* with its disproportionately larger beak and more voluminous gullet is clearly better adapted for the taking of larger fish including such difficult species as long-horned sculpins which have powerfully erectile head spines. The smaller *P. auritus*, with its much smaller beak, is well designed for catching and manipulating small fish and can probe more easily down holes and around rocks in search of eel-like fish. Moreover, the greater speed and manoeuvrability of this species, implied by its ratio of cross-section to foot area, also would be advantageous in the pursuit of small, darting fish.

The form and life habits of fish taken by both cormorants in other areas are largely similar to those found in the present study although naturally fish species vary with location. However, in Great Britain, *P. carbo* takes eels and rock gunnel while not utilizing them here. It is not known whether this results from different foraging behavior of the cormorants or different availability of these fish. The British *P. carbo* also eats considerably more crustaceans (Steven 1933) which are minimally important here.

The two species differ strikingly in diving behavior, largely because of differing hunting depths. *P. carbo* dives for approximately twice as long, rests on the surface slightly longer, and has a much larger dive/rest ratio (3.67:1) as compared to *P. auritus* (2.43:1). The findings for *P. auritus* agree with casual notes made by Lewis (1929) and Mendall (1936); however, the observations on *P. carbo* differ considerably from those published for the British bird, which usually dives for 20-30 sec, as opposed to an average of 51 sec, here, and probably never ventures below 9.5 m (Dewar in Witherby *et al* 1943). Stonehouse (1967) in a study of various New Zealand cormorants found that *P. c. novaehollandiae*, in 2-3 m of water, had a mean diving time of 21 sec, mean resting time of 7 sec, and a dive/rest ratio of these means of 3.0:1. Depth undoubtedly accounts for these dissimilar diving times. The differing dive/rest ratios of *P. carbo* and *P. auritus* are difficult to interpret without knowing underwater behavior and lengths of diving sessions. Stonehouse (1967) considered that this ratio indicated physiological efficiency in New Zealand cormorants. However, I concur with Scott's (1973) contention that such a conclusion based on field studies may not be warranted as the birds usually work well within their physiological limits. These limits could probably only be determined in the laboratory. Therefore, in the present study, no conclusions or speculation on this aspect will be advanced.

Although *P. carbo* and *P. auritus* are largely different ecologically in Nova Scotia, it is problematic whether these dissimilarities are fortuitous or result from competition. Lack (1945; 1971) supports the former theory and Andrewartha and Birch (1954) the latter in considering the niches of the highly similar *P. carbo* and *P. aristotelis* in Great Britain. Pearson (1968), in examining this situation for the Farne Islands, stated that competition may occur under adverse conditions but does not appear to exist at present. Lack's conclusion was also supported in a brief review of Holarctic cormorants by Cody (1973).

From the present study, I propose that competition occurred when *P. carbo* invaded *P. auritus* range in Atlantic Canada. It is likely that *P. auritus* was the original colonizer of this area, judging from its greater abundance in Eastern Canada, very wide North American distribution, and pleistocene fossil record (Wetmore 1956; Brodkorb 1958). *P. carbo* probably arrived later, since it has smaller numbers, an extremely restricted North American range, and no fossil record. Moreover, North American and British *P.*

carbo are morphologically identical which would be expected only if these populations had been recently separated. However, from Lack's (1945) description of its habitat, *P. carbo* in Britain forages in the same shallow-water marine and freshwater environments as does *P. auritus* in Nova Scotia. All other races of *P. carbo* also prefer this environment (Serventy 1938; van Dobben 1952; Rand 1960; Williams 1964; Dement'ev *et al* 1966; Stonehouse 1967; Etchecopar and Hue 1967). Since the *P. carbo* in the present study is solely marine and fishes greater depths than in Britain, it appears likely that competition from the better-established *P. auritus* led to the evolution of a preference for deeper water by *P. carbo*. The possibility exists that *P. carbo* was preadapted to this foraging area during colonization of Greenland and Iceland prior to invasion of North America. This cannot be conclusively checked in the literature although Salomonsen (1950) described it as a shallow-water bird in Greenland.

Central to the hypothesis that competition induced separation of the two species is the concept that food was limiting. Considering the present number of cormorants, their opportunistic nature, and the general abundance of the fishes on which they feed, it seems most unlikely that this would be the case. However, it is well known that cormorant numbers were vastly reduced by human disturbance (Gross 1945; Erskine 1972). In the past, with less human interference, numbers may have been much higher, strengthening the interaction of the two cormorants and leading to resource partitioning.

The size relationship of the birds, particularly their beaks, is in the range noted by Hutchinson (1959) and elaborated by MacArthur (1972) for closely related sympatric species; this is usually associated with different prey sizes (Hespenheide 1971). The size difference of these cormorants could have been one of the factors which moderated their interaction sufficiently to favor ecological segregation rather than extinction of one of them. The ratio of beak sizes (approx. 1.2:1) occurs in other pairs of cormorant species such as *P. aristotelis* and *P. carbo* in Great Britain and *P. penicillatus*, *P. auritus* and *P. pelagicus* on the Pacific coast of Canada.

The different dates of clutch initiation (Erskine 1972) may be further manifestation of past competition for food. Although it was not investigated, separation of laying and hatching dates could serve to separate peak food demand periods for the cormorants.

The suggested mechanisms by which ecological segregation of *P. carbo* and *P. auritus* were accomplished involve considerable circumstantial evidence and speculation. Further evidence would be provided by a wider study of the habitat requirements of each species throughout its whole range. Studies of foraging behavior, diving physiology, and metabolic rate would aid in defining each species' advantageous attributes.

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Appendix I

Annotated list of fish species taken by cormorants in Nova Scotia.

Atlantic Cod *(Gadus morhua)*

Taken in small but roughly equal numbers by both cormorants. May be uncommon in the shallow waters fished by them. The frequency distributions of otolith length indicate a wide range of sizes taken with little evidence of modal points.

Pollock *(Pollachius virens)*

Large, highly visible schools throughout the Mushaboom area. Well represented in both cormorants' diets in approximately equal amounts *(eg.* 23.8% of fish taken by *P. carbo).* Length distributions show major peaks in both June study periods, probably representing second summer fish. The few larger otoliths could be those of third summer fish. During July study period another modal point, suggesting fry, appears in both distributions.

"Small Gadoids"

Taken in large numbers by *P. auritus* (51.2% of all fish recorded in main study). Assumed to be gadid fry as aging of otoliths indicate fish of the year.

Cunner *(Tautogolabrus adspersus)*

Very abundant and widely distributed in shallow water among rocks and around holdfasts of marine algae. The most important species in the diet of *P. carbo,* making up 41.4% of total numbers and occurring in 80% of the pellets examined. Relatively fewer taken by *P. auritus.* Proportions of Cunner eaten increased during the study periods by an equal amount in both species. The frequency histograms of pharyngeal tooth plate widths reveal a broad, fairly uniform distribution, resulting from the slow growth of this fish which allows many year classes to be eaten.

Rock Gunnel *(Pholis gunnellus)*
A small eel-like species of great importance to *P. auritus* (25-50% of total numbers).

Wrymouth *(Cryptacanthodes maculatus)*
A little-known, secretive blenny consumed exclusively by *P. auritus* and representing as much as 20% of its diet in the main study. Frequency distributions show a wide range of sizes, suggesting the slow growth of the species. Readings of some otoliths revealed fish aged up to 7 years were consumed.

Long-horned Sculpin *(Myoxocephalus octodecemspinosus)*
Caught in larger numbers by *P. carbo* (10.1% of fish taken) than *P. auritus*. A wide range of sizes are taken.

Short-horned Sculpin *(Myoxocephalus scorpius)*
Much more important to *P. auritus* than to *P. carbo*. Proportions vary considerably with study period, (from 10.6 - 26.3% of larger fish taken by *P. auritus*). A wide variety of sizes taken.

Winter Flounder *(Pseudopleuronectes americanus)*
Of moderate importance to both cormorants although a slightly larger percentage taken by *P. carbo* (11.1%). A restricted range of otolith sizes found, possibly owing to the cormorants' ability to handle only smaller fish.

Herring *(Clupea harengus)*
Large schools common in the summer in the Mushaboom area. As only small numbers were taken by both cormorants, capture probably occurred when birds fortuitiously pass through schools while diving for the bottom.

American Smelt *(Osmerus mordax)*
A schooling species usually restricted to coastal regions. Very small numbers taken by both cormorants.

American Eel *(Anguilla rostrata)*
Very small numbers taken by *P. auritus*.

Silver Hake *(Merluccius bilinearis)*
One taken by *P. auritus* in main study.

American Sand Launce *(Ammodytes americanus)*
One recorded for *P. auritus* in main study, although more important at Green Island.

Ocean Pout *(Macrozoarces americanus)*
Taken rarely by both cormorants. A specimen weighing 630 g was regurgitated by a *P. carbo* nestling on West Brother Island.

American Plaice *(Hippoglossoides platessoides)*
Taken rarely by *P. carbo* in the main study.

Gaspereau *(Alosa pseudoharengus)*
Taken in small numbers by *P. auritus* from Basque Island and the St. Mary's River although probably very important during spawning run.

Mummichog *(Fundulus heteroclitus)*
    Of minor importance to *P. auritus* on Basque Island.

Mackerel *(Scomber scombrus)*
    Two individuals regurgitated by *P. carbo* nestlings on West Brother Island. Probably caught by chance, like Herring.

Grubby *(Myoxocephalus aeneus)*
    Two individuals regurgitated by *P. auritus* nestlings on Basque Island.

Sticklebacks *(Gasterosteus sp)*
    Of major importance to *P. auritus* on St. Mary's River. Occurred in 18 of 25 stomachs examined.

Common Sucker *(Catostomus commersoni)*
    A freshwater species occasionally straying into estuaries. Taken in small numbers by *P. auritus* in main study.

Golden Shiner *(Notemigonus crysoleucas)*
    This and other unidentified cyprinids taken occasionally by *P. auritus* on St. Mary's River. Occurred in 7 of 25 stomachs.

Yellow Perch *(Perca flavescens)*
    Of minor importance to *P. auritus* on St. Mary's River. Occurred in 3 of 25 stomachs.

White Perch *(Roccus americanus)*
    Lewis found one taken by *P. auritus* on St. Mary's River.