Wilson Bull., 99(2), 1987, pp. 262–267

Nest-site quality and reproductive success of early- and late-nesting Double-crested Cormorants.—Reproductive success of some colonially breeding waterbirds can differ in nests positioned centrally or peripherally in a colony (see Knopf 1979 for review), the relative timing of breeding, and the age or experience of breeders (Dexheimer and Southern 1974, Ryder 1975, Blus and Keahey 1978, Blomme 1979, Hogan 1979, Knopf 1979, Potts et al. 1980, Parsons and Burger 1981, Ryder and Ryder 1981, DesGranges 1982, Debout 1985, Shaw 1986). In many species of cormorants and other colonial waterbirds, birds arriving at the colony early in the breeding season have bred before, and they select the best available nesting sites, often older nest foundations (McLeod and Bondar 1953, Blomme 1979). These early breeders generally nest in the colony center and raise the most young.

Little is known about the effects of nest-site quality in tree-nesting colonial waterbirds except that the clutch size in one colony of Double-crested Cormorants (*Phalacrocorax auritus*) increased with increased nest height (Blomme 1979). Factors important for ground-nesting cormorants such as the amount of exposure to rain (Potts et al. 1980) and ease of defense against intraspecific nest thieves and interspecific predators are probably important to tree-nesting species as well (Tenaza 1971, Potts et al. 1980). The nest-site quality for tree-nesters is presumably related to the strength of trees, which must be strong enough to withstand high winds and prevent the nest or chicks from being dislodged and lost. The aim of the study reported here was to determine whether the reproductive success of early and late nesting Double-crested Cormorants varied with the health and strength of the nest trees or their use as nest-sites during the preceding breeding season.

Study area and methods.—Observations were made at a colony of 1940 pairs of Double-crested Cormorants on Ile aux Loups Marins, an island of the Iles de la Madeleine Archipelago in the Gulf of St. Lawrence between 47°13′ and 47°39′N, and 61°23′ and 62°01′W. This 14-ha island is covered with 5–7 m tall conifers (*Abies balsamea* and *Picea glauca*) in which cormorants and Great Blue Herons (*Ardea herodias*) nest. Great Black-backed (*Larus marinus*) and Herring (*L. argentatus*) gulls also breed on the island (Léger 1984, Léger and McNeil 1986).

The trees used as nesting sites were checked for the presence of active nests every 5–6 days between 6 and 31 May 1980, and progressively less frequently until mid-July. Nest-building extended from the end of April to mid-July; 54% of the nests were built before mid-May, 19% in the second half of May, 15% in June, and 11% in July (Léger and McNeil 1986). Trees with nests were classified as (1) healthy (full of green needles), (2) morbid (needles beginning to fall), (3) dead (solid trees without needles), or (4) rotten or broken trees. The strength of the trees was judged "bad," "good," or "excellent," depending on their resistance to a lateral push. Observations by Burton (1978) and Pilon et al. (1983) permitted us to determine whether trees had been used for nesting during previous years. Nest contents were checked using a mirror fixed to the end of a 6-m metal pole.

The relationship between observed frequencies of early and late nests as a function of nest-site characteristics was examined using two-way contingency analyses (Nie et al. 1975, Legendre and Legendre 1983). Variables were divided into discrete classes using the PARTI program within the R package (Centre de calculs, Université de Montréal). The success of early and late nests was compared using tests of significance of percentages (Lamotte 1971) and *t*-tests for comparing mean values (Sokal and Rohlf 1981).

Results.—From 6 May to mid-July 1980, 89 nests were checked. There were 50 nests of early breeders (established in early May), all in the center of the area occupied by the colony, and 39 nests of late breeders (June), all on the fringe of the colony, near breeding gulls. Late nesting cormorants built nests close to breeding gulls, and, when we visited the colony, the

TABLE 1

REPRODUCTIVE SUCCESS OF EARLY AND LATE NESTING DOUBLE-CRESTED CORMORANTS

	Early breeders (6–14 May)	Late breeders (June)
Mean number of eggs per nest	3.32 ± 0.09 (50)[a]	2.74 ± 0.88 (39)
Mean number of fledglings per successful brood	2.80 ± 1.10 (45)	1.87 ± 0.09 (30)
Mean number of fledglings per initiated clutch	2.59 ± 1.27 (49)[b]	1.41 ± 1.14 (39)
Percent of initiated clutches with fledged young	93.9	74.4
Percent of eggs that produced fledged young	68.6	51.4
Percent of eggs which produced fledged young from successful broods	72.0	67.0

[a] $\bar{x}$ ± SD (number of nests).

[b] The number of young in one of the 50 nests is unknown.

former flew away in greater numbers and for longer periods than did the early nesting birds in the center of the colony.

Reproductive success.—We define a clutch as "successful" if at least one young fledged, and a brood as "initiated" if at least one egg was laid. The mean clutch size, the mean number of fledglings per initiated brood and per successful brood (all t-tests, $P < 0.05$), the percentage of initiated clutches, and the percentage of eggs producing fledged young in initiated clutches (all tests of significance of percentages, $P < 0.05$) were significantly higher in early breeders (Table 1). Late nesting pairs abandoned proportionally more nests (9 out of 39) than did early breeders (3 out of 50). In successful broods, the percentage of eggs producing fledged young did not differ between early and late nesters ($P < 0.05$).

Nest-site quality.—When we considered all the nests built on Ile aux Loups Marins in 1980 (unfortunately we do not have data on their reproductive success), the values of the Wilks χ^2 calculated in the contingency analysis indicated that the health and strength of nest-bearing trees and their use as nest-sites in previous year(s) significantly discriminate between the early nests and late nests for which the reproductive success was observed (Table 2). More early nesters (May) used previously used nest sites than did late nesters (June and July), and proportionally more late nests than early nests were supported by healthy trees of excellent strength that were not used for nest-support during previous years. If we take the asymmetric uncertainty coefficient into account, however, previous use of trees accounts for the greater proportion of variation.

Discussion.—Our data on the reproductive success of early and late nesting Double-crested Cormorants agree with those obtained by Ellison and Cleary (1978), Blus and Keahey (1978), Knopf (1979), Hogan (1979), and Potts et al. (1980), who found that late breeding pelecaniform birds were usually younger, less experienced, and less persistent incubators and less successful in catching fish than were early breeders. Their nests were often left unattended and were thus more exposed to intraspecific actions of other breeders as well as to predation. At Ile aux Loups Marins, late nesting Double-crested Cormorants laid fewer eggs (1 to 4) than did early breeders (2 to 6), and they lost more eggs and nestlings. Similarly, late nesting Brown Pelicans laid fewer eggs and lost more young (Blus and Keahey 1978).

The proportionately greater nest abandonment in late nesting Double-crested Cormorants

TABLE 2

CONTINGENCY ANALYSIS OF VARIATION IN SITE QUALITY OF NESTS BUILT BY DOUBLE-CRESTED CORMORANTS IN DIFFERENT PERIODS IN 1980

Nest-site quality variable	χ^2 (Wilks)	Asymmetric uncertainty coefficient	Partitions	Periods			
				6–14 May	20–25 May	June	July
Formerly used trees	407.52[a]	0.120	Yes	583 (**0.72**)[b]	167 (**0.21**)	49 (0.06)	11 (0.01)
			No	193 (0.30)	120 (0.19)	171 (**0.27**)	151 (**0.24**)
Health of the trees	380.36[a]	0.110	Healthy	27 (0.12)	30 (0.13)	93 (**0.40**)	85 (**0.36**)
			Sick	54 (0.40)	29 (**0.22**)	27 (**0.20**)	25 (**0.19**)
			Rotten or broken	695 (**0.65**)	227 (**0.21**)	101 (0.09)	52 (0.05)
Strength of the trees	17.80[a]	0.005	Excellent	335 (0.52)	98 (0.16)	111 (**0.18**)	83 (**0.13**)
			Good or bad	439 (**0.54**)	187 (**0.23**)	110 (0.14)	79 (0.10)
Unconditional probability				0.53	0.20	0.15	0.11

[a] $P < 0.001$.

[b] Values in parentheses represent the conditional probability. The conditional probabilities which exceed the corresponding unconditional probabilities are in bold-face type.

on Ile aux Loups Marins (see also Siegel-Causey and Hunt 1986) could have been due to egg or nestling predation as a result of human disturbance (Ellison and Cleary 1978, DesGranges and Reed 1981). Excluding abandoned nests, the percentage of eggs laid by late breeders that produced fledged young did not differ significantly from that of early breeders (Table 1). Similar data were reported by Knopf (1979) who found that lower reproductive success in late breeding White Pelicans was largely due to a higher frequency of nest abandonment.

The majority of the late nests in this study were in healthier trees than early nests. The strength of a higher proportion of these trees with late nests was also judged excellent (Table 2).

Little is known of nest-site quality of peripheral late breeders of any species. In ground-nesting Shags (*Phalacrocorax aristotelis*), Potts et al. (1980) found that the youngest birds bred on poor sites and had lower reproductive success, but the reproductive success of late breeders remained lower than that of early breeders on sites of equal or comparable quality. According to Blomme (1979), the reproductive success of Double-crested Cormorants increased with increasing nest height, but was not affected by nest size. DesGranges (1982), on the other hand, found that experienced adults built larger nests and reared the most young to fledging. The chances that eggs and young could be dislodged from the nest should decrease with nest size, but we do not have any data to test this. For tree-nesting cormorants in a windy region such as Iles de la Madeleine, however, nest stability should involve trees that are strong enough to withstand high winds. On a day of very high winds (up to 117 km/h) in 1979, 85 out of 1289 nests of Double-crested Cormorants were dislodged on Ile aux Loups Marins; most of them were in areas where trees were dead, rotten or broken, and pertained to early nesters (Léger 1984).

Siegel-Causey and Hunt (1986) found that first arrivals at a colony of ground-nesting Double-crested Cormorants selected existing nests over all other possibilities; site fidelity did not appear to be important. Among all the nests built on Ile aux Loups Marins in 1980, those built first were supported by trees in poorer condition than trees supporting later nests (Table 2 and Léger 1984). This suggests that early nesters selected trees that had been used in previous years, even if stronger (but unused) trees were available. Unfortunately, we do not have any data on the age of nesters. Taking into account the findings of McLeod and Bondar (1953) and Blomme (1979), however, we suggest that early arriving and early breeding cormorants were older, experienced, nesters that built their nests in preferred sites on previous years' foundations. Early nesters probably continue to use the same sites year after year until the tree is too weak to support their nest. The same tree may be occupied until a nest is lost due to wind action or because the tree has fallen. Early nesters may then renest on healthy or less damaged trees on the fringe of the area occupied by the colony, depending on the time in the breeding season. We also suggest that younger individuals breeding for the first time built nests on the fringes of the colony and laid later. Trees in this zone had been used for nest-support for the first time or had been used only fairly recently and were thus less damaged as a result of the direct and indirect effects of bird excrement on the vegetation.

Conclusion.—Many late nesting Double-crested Cormorants, despite being in relatively stronger trees, had a lower reproductive success than did early nesters. We eliminate tree condition as an operative factor in nesting success. What did cause nesting success of late and fringe-nesters to decline is unknown.

Acknowledgments.—We express our thanks to J. Brabant, P. Drapeau and J.-F. Léger for their help in the field, to F. Rankin for permission to work on Ile aux Loups Marins, and to N. Bernstein, K. L. Bildstein, N. David, J. Downing, M. P. Harris, and D. Siegel-Causey for improving the final version of the manuscript. We are also indebted to A. Leduc for invaluable advice and guidance in statistical processing and data analysis. This study has been supported by scholarships from "Fonds F.C.A.C." (Gouvernement du Québec) and the Natural Sciences and Engineering Research Council of Canada, and a grant from the Fisheries and Marine Service of the Department of Environment (Canada).

LITERATURE CITED

BLOMME, C. 1979. Status and breeding success of Double-crested Cormorant in two North Channel (Lake Huron) colonies in 1979. Ont. Field Biol. 35:70–78.

BLUS, L. J. AND J. A. KEAHEY. 1978. Variation in reproductivity with age in the Brown Pelican. Auk 95:128–134.

BURTON, J. 1978. L'alimentation estivale du Fou de Bassan, du Grand Cormoran et du Cormoran à aigrettes aux Iles de La Madeleine, en relation avec les pêches commerciales. Unpubl. report presented to the Fisheries and Marine Service of the Department of Environment (Canada) by the Centre de Recherches écologiques de Montréal.

DEBOUT, G. 1985. Quelques données sur la nidification du Cormoran huppé, *Phalacrocorax aristotelis,* à Chausey Manche. Alauda 53:161–166.

DESGRANGES, J.-L. 1982. Weight growth of young Double-crested Cormorants in the St. Lawrence estuary, Quebec. Colonial Waterbirds 5:79–86.

——— AND A. REED. 1981. Disturbance and control of selected colonies of Double-crested Cormorants in Québec. Colonial Waterbirds 4:12–19.

DEXHEIMER, M. AND W. E. SOUTHERN. 1974. Breeding success relative to nest location and density in Ring-billed Gull colonies. Wilson Bull. 86:288–290.

ELLISON, L. N. AND L. CLEARY. 1978. Effects of human disturbance on breeding Double-crested Cormorants. Auk 95:510–517.

HOGAN, G. G. 1979. Breeding parameters of Great Cormorants (*Phalacrocorax carbo carbo*) at mixed species colonies on Prince Edward Island, Canada. M.Sc. thesis, Brock Univ., St. Catherines, Ontario.

KNOPF, F. L. 1979. Spatial and temporal aspects of colonial nesting of White Pelicans. Condor 81:353–363.

LAMOTTE, M. 1971. Initiation aux méthodes statistiques en biologie. Masson et Cie, Paris, France.

LEGENDRE, L. AND P. LEGENDRE. 1983. Numerical ecology. Elsevier, New York, New York.

LÉGER, C. 1984. Les cormorans à aigrettes (*Phalacrocorax auritus*) des îles de la Madeleine, Québec: croissance, alimentation des jeunes et caractéristiques de nidification. Mémoire de Maîtrise, Univ. Montréal, Montréal, Québec.

——— AND R. MCNEIL. 1986. Choix de l'emplacement des nids de Cormorans à aigrettes (*Phalacrocorax auritus*) aux îles de la Madeleine, Québec. Can. J. Zool. In press.

MCLEOD, J. A. AND G. F. BONDAR. 1953. A brief study of the Double-crested Cormorant on Lake Winnipegosis. Can. Field-Nat. 67:1–11.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. SPSS statistical package for the social sciences. McGraw-Hill, New York, New York.

PARSONS, K. C. AND J. BURGER. 1981. Nestling growth in early- and late-nesting Black-crowned Night Herons. Colonial Waterbirds 4:120–125.

PILON, C., J. BURTON, AND R. MCNEIL. 1983. Reproduction du Grand Cormoran (*Phalacrocorax carbo*) et du Cormoran à aigrettes (*P. auritus*) aux îles de la Madeleine, Québec. Can. J. Zool. 61:524–530.

POTTS, G. R., J. C. COULSON, AND I. R. DEANS. 1980. Population dynamics and breeding success of the Shag, *Phalacrocorax aristotelis,* on the Farne Islands, Northumberland. J. Anim. Ecol. 49:465–484.

RYDER, J. P. 1975. Egg-laying, egg-size, and success in relation to immature-mature plumage of Ring-billed Gulls. Wilson Bull. 87:534–542.

RYDER, P. L. AND J. P. RYDER. 1981. Reproductive performance of Ring-billed Gulls in relation to nest location. Condor 83:57–60.

SHAW, P. 1986. Factors affecting breeding performance of Antarctic Blue-eyed Shags *Phalacrocorax atriceps*. Ornis Scand. 17:141–150.

SIEGEL-CAUSEY, D. AND G. L. HUNT, JR. 1986. Breeding-site selection and colony formation in Double-crested and Pelagic cormorants. Auk 103:230–234.

SOKAL, R. R. AND R. J. ROHLF. 1981. Biometry. Freeman, San Francisco, California.

TENAZA, R. 1971. Behavior and nesting success relative to nest location in Adélie Penguins (*Pygoscelis adeliae*). Condor 73:81–92.

RAYMOND MCNEIL AND CLAIRE LÉGER, *Centre de recherches écologiques de Montréal* and *Dépt. Sciences biologiques, Univ. Montréal, C.P. 6128, Succ. "A," Montréal, Québec H3C 3J7, Canada.* *Received 10 June 1986, accepted 6 Nov. 1986.*

Wilson Bull., 99(2), 1987, pp. 267–268

High basal metabolic rate in Sanderlings (*Calidris alba*).—Physiological data from a number of species permit the estimation of basal metabolic rate (BMR) from allometric equations (Lasiewski and Dawson 1967, Aschoff and Pohl 1970, Kendeigh et al. 1977). Here I report BMR for Sanderlings (*Calidris alba*) taken on their wintering grounds on the Peruvian Coast and compare these results with estimates of BMR from three allometric equations.

Methods.—Nine Sanderlings (all adults, sex unknown) were caught with mist nets on Villa beach, near Lima, Peru, on 21 August 1984 at 22:00. They were kept in the laboratory over night at 19°C. BMR for each bird was measured the next day beginning at 8:00. BMR was estimated from oxygen consumption of the birds during 30-min periods. All individuals were in a postabsorptive (without food in their stomachs) condition, and they had been resting in a dark 1-l metabolic chamber for at least 1 h prior to the experiments. The temperature in all the determinations was 25 ± 1°C [SD] (see Castro et al. 1985).

I tested the accuracy of the apparatus by measuring oxygen consumption in a strain of laboratory mice of known basal metabolism. The results fitted the expected values.

Results.—Mean body weight was 50.44 ± 4.59 g [SD]. Mean oxygen consumption was 1.98 ml/g/h ± 0.53, equivalent to 48.15 kJ/day assuming a conversion factor of 20.1 kJ per liter of oxygen consumed (fat and carbohydrate metabolism, Dawson 1974).

These results are 12–28% higher than those predicted by the equations of Aschoff and Pohl (1970), Lasiewski and Dawson (1967), and Kendeigh et al. (1977) (Table 1).

Discussion.—Few measurements of shorebird BMR have been published. Thus it is difficult to know whether the high values reported here might be representative of shorebirds in general. Johnston and McFarlane (1967) showed values for 2 individuals of the Lesser Golden-Plover (*Pluvialis dominica*). One of them had a value 14% lower than that predicted using Aschoff and Pohl's (1970) equation, but the other had a value 28% higher than predicted. Johnston and McFarlane rejected the second measurement, arguing that the bird in question "evidently never reached a basal level" based on allometric predictions. Kendeigh et al. (1977) reported a value for *Charadrius dubius* that was 34% higher than that predicted by Aschoff and Pohl (1970). Kersten and Piersma (in press) report values for three other species of shorebirds that run an average of 34% over those predicted by Aschoff and Pohl's (1970) equations. Thus it appears likely that shorebirds have higher metabolic rates than