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COLONIAL DEFENSE BEHAVIOR IN DOUBLE-CRESTED AND PELAGIC CORMORANTS

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ABSTRACT.—We examine the predictions, based upon the hypotheses of Coulson (1968), Hamilton (1971), and Vine (1971), that (1) species whose colonies are accessible to predators should form tighter groupings and have fewer isolated nests than those with reduced accessibility to predators, (2) nests at the center should be less subject to predation than those at the edge of a colony, (3) nests both in the center and with reduced accessibility should have the lowest predation pressure of all nests, and (4) individuals that nest in accessible locations should have more vigorous and more sustained antipredator behaviors than those individuals unlikely to come frequently in contact with predators. To test these predictions, we compare intrusions by two predators, the Northwestern Crow (*Corvus caurinus*) and the Glaucous-winged Gull (*Larus glaucescens*), at isolated and grouped nests of the cliff-face nesting Pelagic Cormorant (*Phalacrocorax pelagicus*) and cliff-top nesting Double-crested Cormorant (*P. auritus*) on Mandarte Island, British Columbia. Both crows and gulls preferred to visit the edge nests of both species, especially those on level ground. The steeper and more central the nest location, the less likely was visitation. Gulls were restricted by topography from entering the Pelagic colony, while crows were able to land in either colony. Predator success was high only in flat, accessible areas. Both cormorant species depend upon the habitat to deter predator access: the Double-crested Cormorant utilizes a defense regime of energetic and aggressive behaviors; the Pelagic Cormorant uses a much less effective defense and depends much more on the habitat as a necessary part of nest defense. *Received 11 July 1980, accepted 21 January 1981.*

WE here examine aspects of colonial nesting in relation to their effectiveness as protection against intruding predators. Nesting phenology (Nelson 1966, 1970), location within the colony (Coulson 1968), and the topography of the colony (Nelson 1967, Nettleship 1972) have been identified as actual or potential factors in determining the likelihood that a particular nest will be subject to predation. Hamilton (1971) hypothesized that the clumping of prey provides a significant defense against predation, and Coulson (1968) and Vine (1971) hypothesized that individuals at the center of a group will be at a lesser risk than those at the edge.

To test the hypotheses concerning the importance of nest location in predator avoidance, we examine the interactions between two species of prey, the Double-crested Cormorant (DCC: *Phalacrocorax auritus*) and the Pelagic Cormorant (PC: *P. pelagicus*), and two species of predators, the Northwestern Crow (*Corvus caurinus*) and the Glaucous-winged Gull (*Larus glaucescens*), at cormorant nesting colonies on Mandarte Island, British Columbia, Canada.

In this study, we had the opportunity to compare the activity and effect of a highly maneuverable predator (the Northwestern Crow) and a relatively clumsy predator (the Glaucous-winged Gull) as they attempted to steal eggs and small chicks from cormorant nests. Because the two species of cormorant prefer different nesting habitats and consequently have different structures for their colonies, we were able to compare the antipredator behaviors and their effectiveness for cormorants nesting on cliffs (Pelagic Cormorant) and for those nesting on level areas (Double-crested Cormorant) and for tightly clumped as well as loosely grouped nests.

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With the above variety of predators and nesting situations on Mandarte Island, we test here predictions from the hypotheses of Coulson (1968), Hamilton (1971), and Vine (1971), that (1) species whose colonies are accessible to predators should form tighter groupings and have fewer isolated nests than those with reduced accessibility to predators, (2) nests at the center should be less subject to predation than those at the edge of a colony, (3) nests both in the center and with reduced accessibility should have the lowest predation pressure of all nests, and (4) individuals that nest in accessible locations should have more vigorous and more sustained antipredator behaviors than those individuals unlikely to come frequently in contact with predators. To test these predictions, we compare intrusion pressure by predators and nest-defense behaviors for isolated and grouped nests of cliff-face nesting Pelagic Cormorants and cliff-top nesting Double-crested Cormorants.

METHODS

We conducted this study from 29 March to 2 August 1975 on Mandarte Island, British Columbia, Canada. Drent et al. (1964) describe the island and its breeding birds; van de Veen (1973) discusses the cormorant colonies in particular. We viewed the cormorants from blinds using 7 × 35 binoculars and a 45× telescope and recorded the behavioral data on tape cassettes for later transcription. Our observation periods were from 1 to 3 h long from dawn to dusk at various times of the day.

Because we were able to start this study before most cormorants had initiated courtship, we could map the nest sites completely in both colonies without disturbing the cormorants. We laid grid points at 5-m intervals along the entire cliff face extending from cliff shoulder to water line, encompassing an area of 16,300 m^2; within this grid, we measured nest positions to a precision of 0.1 m.

We completely restricted human entry into the colonies once the courtship commenced, so the location of new nests had to be estimated by eye. We checked the location of these nests on 21 February 1976, and found that no nest varied from the estimated position by more than 0.5 m. We adjusted nest-site estimates differing by more than 0.2 m to the February values.

For the purposes of analysis, we classed the position of nest sites within the colony according to how many nests were between a given nest and the periphery of the colony ("nest type"). For example, a section from edge to edge through a colony seven nests wide would produce the following sequence of nest types: 0, 1, 2, 3, 2, 1, 0.

We measured the slope of the ground surrounding a nest in degrees from horizontal by a Suunto clinometer. From an imaginary line running through the nest center, we made slope measurements on the quadrants of the nest edge. If the slope varied on different sides of a nest, we averaged all values on the quadrants for a representative slope.

We noted the behavior of both predator and cormorant, as well as the distance of the predator to cormorant at each defensive bout. This distance was measured in meters by eye using the nest diameter ($\bar{x}$ = 0.6 m) as a reference and the grid system where nests were not close together. We assume that the minimum distance (the "reaction distance") that an adult cormorant allowed a predator to approach its nest unchecked is representative of the adult's defense aggressiveness. Thus, the closer a cormorant allowed a predator to approach before it defended its nest contents, the less aggressive we assume this nest defense was. [Berry (1976) gives supporting observations for *P. capensis*.]

We recorded a crow or gull visit if the visitation elicited some behavioral response from a nestling or breeding adult or if the predator came within two nest diameters of a nest. A visit was termed successful if the predator carried away eggs, chicks, or food the adults vomited on the ground.

We normalized predator visits for interspecific comparison by dividing predator visits by the number of nests in the category (i.e. level areas, edge nests, etc.), and by the number of hours these nests were actually observed. We lumped nesting substrates into three classes: "level" substrates, <30°; "moderate" substrates, 30–60°; and "steep" substrates, >60°.

Every 2 days during the season we made a sight census of the number of nests, eggs, and chicks seen. We made these by viewing each nest through the telescope and waiting for the incubating bird to stand up. Once the parent was up, we could note the nest contents. At the end of the study, most chicks were 8–10 weeks old, and in the absence of any other information, we considered them to be "fledged" (*sensu* Lewis 1929).

We avoided the significant problem of investigator effects (see Kury and Gochfeld 1975) by observing

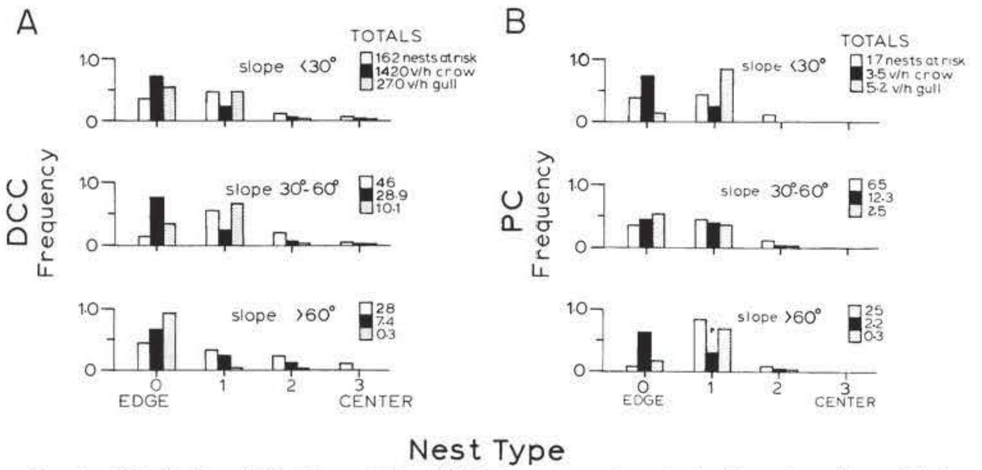

Fig. 1. Distribution of Double-crested and Pelagic cormorant nests at risk and predator visits by substrate slope and colony position. A. DCC = Double-crested Cormorant; B. PC = Pelagic Cormorant; clear bars = cormorant nests at risk of predation; solid bars = crow visits normalized to hours of observation; shaded bars = gull visits normalized to hours of observation; Nest Type = see Methods for explanation; Totals = cumulative number of nests and visits for each substrate category.

the nesting cormorants from blinds we constructed before the commencement of courtship and by totally restricting all human entry into the colonies during the course of this study.

RESULTS

Since the earliest studies on Mandarte Island, investigators have been impressed by the general difference between the nesting colonies of both species (Munro 1928, van Tets 1956). The Double-crested colony is active and noisy: crows and gulls forage for eggs and young amidst the nests; adult cormorants lunge and honk in defense. In contrast, the Pelagic colony is normally calm and tranquil, with an occasional crow to break the monotony; gulls rarely are seen.

Double-crested nests were found most commonly on level substrates (Fig. 1A—nest totals: Kolmogoroff-Smirnoff one-sample test, $P < 0.01$), Pelagic nests most commonly on steeper substrates and cliff faces (Fig. 1B—nest totals: same test, $P < 0.01$). This terrain affected the form of the colonies: the Pelagic colonies were much narrower and less dense (that is, fewer nests were between edge nests) than the Double-crested colonies (Fig. 1—nest types: $\chi^2 = 97.7$, df = 3, $P < 0.001$). We expected that the cliff face would dictate the dimensions of the Pelagic colony: our impression was that the rough and precipitous cliffs (substrates >60°) barred adults from constructing nests uniformly throughout the colony. Perhaps because of sample size, however, the location and density of nest sites in the Pelagic colony were not contingent upon substrate slope (Fig. 1B: $C = 0.19$, $\chi^2 = 5.05$, df = 4, $P > 0.08$). The distribution of nests within the Double-crested colony, which was located on the broad, level shoulders of the cliff, was unaffected by terrain (Fig. 1A: $C = 0.18$, $\chi^2 = 7.72$, df = 6, $P > 0.50$).

To test the first prediction, that species nesting in colonies accessible to predators should form tighter groupings than those nesting in colonies with reduced accessibility, we used a standard measurement of nest clumping, the nearest neighbor distance. Double-crested Cormorants nested closer to each other and had fewer

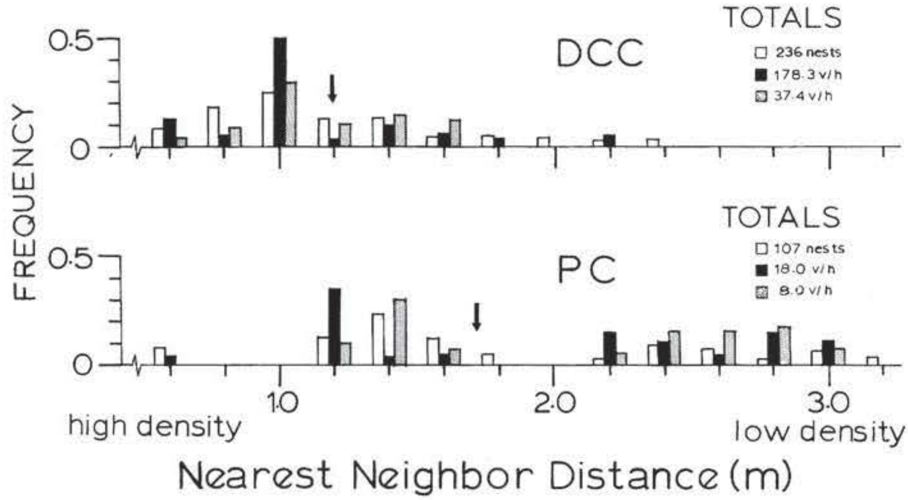

Fig. 2. Distribution of cormorant nests and predator visits by density of nesting. Abbreviations and symbols as in Fig. 1; arrows indicate mean nesting density for each species.

isolated nests than did the Pelagic Cormorants (Fig. 2: Cramér-von Mises two-sample test, $w^2 = 1.251$, $P < 0.001$). Some Pelagic Cormorants were greater than five nest diameters (3 m) from their neighbors and were truly isolated.

Predator behavior.—The crows and gulls approached the nests by air, landed nearby, and walked toward the nesting cormorants. Only rarely did more than one predator approach a nest at the same time, and we never saw any instances of coordinated attack among the predators (although this has been reported by Mendall 1936). As the predators approached the nest, the defending adult began its defense displays at some reaction distance. Both cormorants are larger than the nest predators and are able to defend themselves quite well (Lewis 1929). It was the nest contents that the predators strived for and what the parent defended. The parent rarely left the nest exposed during the nest defense but, in the course of a prolonged defense, would often stand up and vomit food upon the ground. At this juncture, the predator either snatched chicks or eggs from beneath the adult or ate the vomited food and then left the colony area. [Taylor (1894) describes this behavior.]

The second prediction is that central nesting cormorants should be less subject to predation than those at the edge of the colony. We found that both predators visited edge nests more frequently than center nests; the gulls, however, rarely ventured far beyond the edge nests and rarely were found in the inner reaches of the colonies (Fig. 1A: crow-DCC, Kolmogoroff-Smirnoff one-sample test, $P < 0.01$; gull-DCC, same test, $P < 0.01$; Fig. 1B: crow-PC, same test, $P < 0.05$; gull-PC, same test, $P < 0.05$). Crows preferred the Double-crested nests on the flat areas of the cliffs and Pelagic nests on the moderate slopes; gulls preferred the flatter and more moderate areas of either colony (Fig. 1A: crow-DCC, Kolmogoroff-Smirnoff one-sample test, $P < 0.05$; gull-DCC, same test, $P < 0.05$; Fig. 1B: crow-PC, same test, $P < 0.05$; gull-PC, same test, $P < 0.05$).

Crows infrequently landed in the densest colony areas but preferred the areas of intermediate density in both colonies (Fig. 2: DCC, Cramér-von Mises one-sample test, $w^2 = 1.250$, $P < 0.001$; PC, same test, $w^2 = 0.761$, $P < 0.01$). Gulls showed

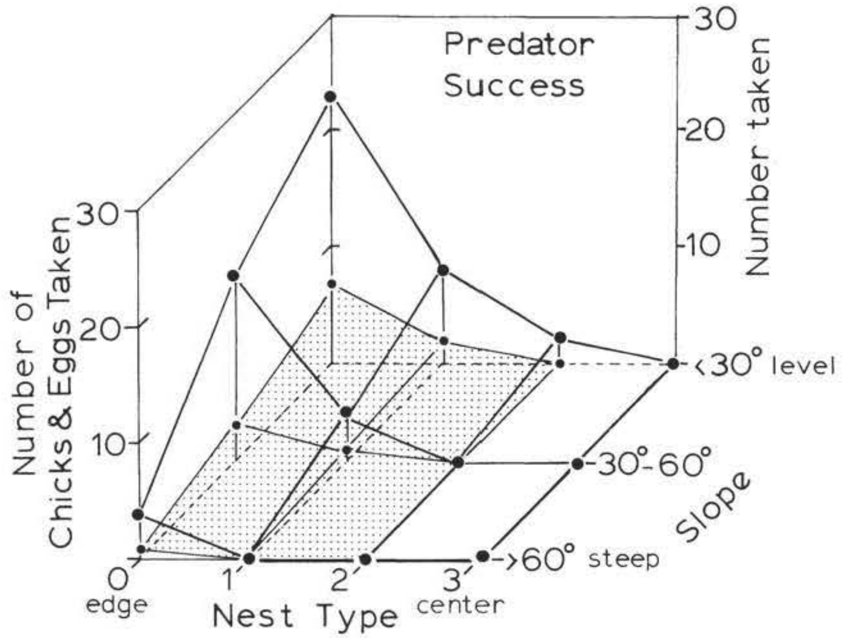

Fig. 3. Predator success in the Double-crested Cormorant colony. Clear surface = crow success; shaded surface = gull success; Nest Type = as in Fig. 1.

a similar pattern (Fig. 2: DCC, same test, $w^2 = 0.682$, $P < 0.05$; PC, same test, $w^2 = 0.462$, $P < 0.05$), but, as the totals indicate, they were less frequent visitors than were the crows and generally avoided the Pelagic colony.

The third prediction states that nests that are both central and inaccessible should have the least predation pressure. An edge nest on the flat shoulder of a cliff exists in a different habitat than does an edge nest on a steep cliff face, so it is informative to examine predator visits by nest position and substrate slope simultaneously. In the Double-crested colony, cormorants nesting at the flat edge of a colony received more crow and gull visits than at any other location, and the steeper core of the colony was mostly protected from predator intrusions (Fig. 1A: crows, Page's L test, $P < 0.02$; gulls, same test, $P < 0.05$). A similar pattern occurred in the Pelagic colony (Fig. 1B: crows, same test, $P < 0.05$; gulls, same test, $P < 0.07$) but, as before, at a much lower rate than in the Double-crested colony.

Predator success.—The other component of predation pressure, predator success, was observed in the Pelagic colony only at two nests. These nests were situated upon a broad, level ledge at the top of the cliff face. Only vomit was retrieved by crows here; gulls enjoyed no success at all. Because of this small sample of predator success, only the results from the Double-crested colony are analyzed.

The Double-crested nests that suffered the fewest depredations were those at the steeper, central region of the colony (Fig. 3: Page's L test, $P < 0.05$). The nests in the most accessible areas were the least successfully defended; losses were disproportionately great when compared to the frequency of attack (see Fig. 1A). Edge-nesting Double-crested adults suffered a disproportionately high number of depredations from crows relative to the number of visits they received; center-nesting Double-crested adults received fewer crow depredations than expected (Fig. 3: Kolmogoroff-Smirnoff one-sample test, $P < 0.05$).

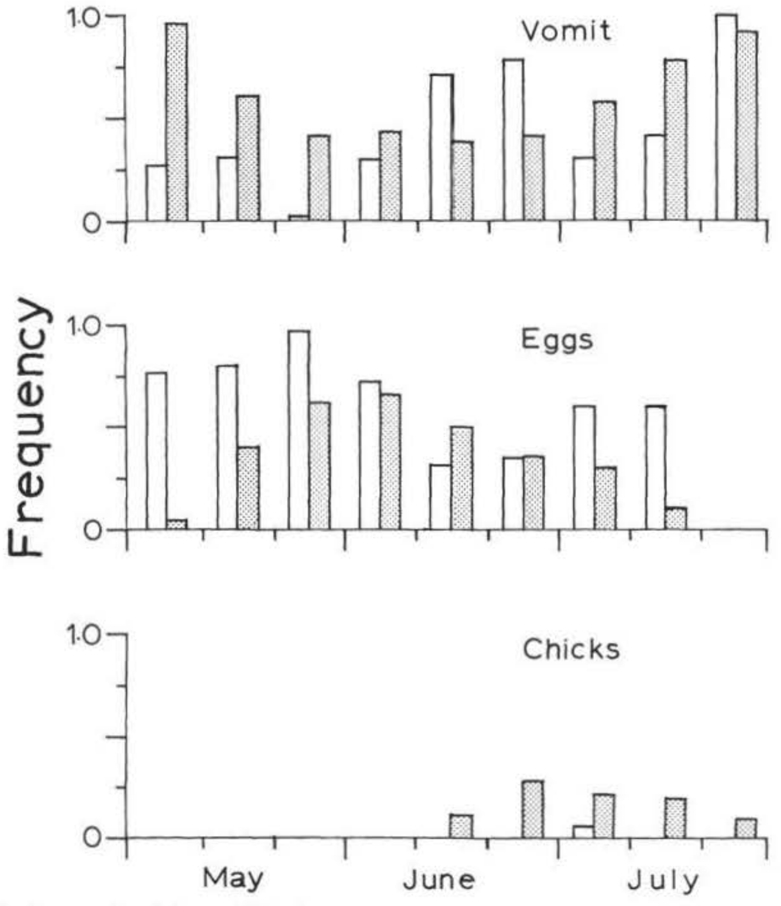

Fig. 4. Expected and observed Northwestern Crow success in the Double-crested Cormorant colony. Clear bars = observed frequency; shaded bars = expected frequency (see text for explanation).

The relative proportions of eggs, young, and vomited food taken by crows from the Double-crested colony are given in Fig. 4. We calculated the expected proportion of food items to be taken by counting the number of eggs, young, and nests (for the availability of vomit) present in each census period and lumping them into 10-day periods. The difference between the expected proportions and the actual proportion of items taken by predators is significantly different for eggs and for young but not significantly different for vomited food. Crows took eggs more than was expected at the start and at the end of the season; chicks were taken only in the first 10 days of July, and fewer than expected by their availability were taken (Fig. 4: eggs, Wilcoxon Matched-pairs signed-ranks test, $P < 0.025$; chicks, same test, $P < 0.05$; vomit, same test, $P > 0.06$). So few were the predators and so low their success in the Pelagic colony and so few were the gull visits in the Double-crested colony that similar analyses for these associations were not possible.

Cormorant behavior.—The fourth prediction is that nesting cormorants exposed to predator approach and isolated from potential neighbor assistance in defense should be more aggressive in defense than those that are protected by the presence of other nests (central nesters), protected by habitat (cliff nesters), or both. Using

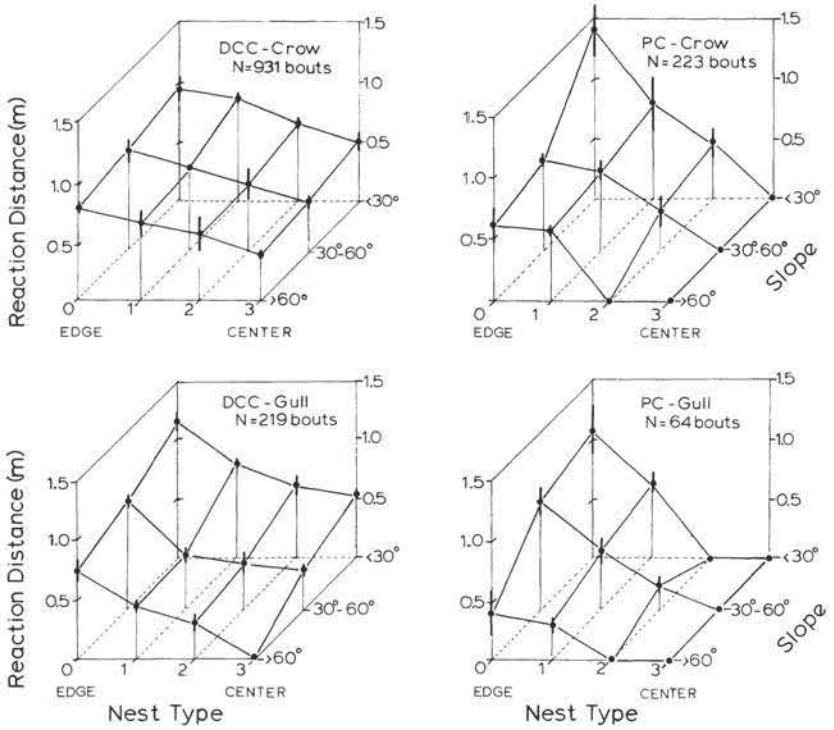

Fig. 5. Cormorant defense against predator intrusions. Reaction distance = see Methods for explanation; solid ball = mean value; solid bar = 95% confidence interval; other abbreviations as in Fig. 1.

reaction distance as an index of defense aggression (see Methods), we found such a pattern in the Double-crested colony (Fig. 5: crow, Page's L test, $P < 0.05$; gull, same test, $P < 0.05$) and in the Pelagic colony, even though the predator visits there were much reduced (Fig. 5: crow, same test, $P < 0.05$; gull, same test, $P < 0.05$). Double-crested defense aggression increases through the breeding season but drops abruptly (see Fig. 6). The reaction distance means in the last 10 days of May and the first 10 days of July are different ($t = 2.24$, df = 39, $P < 0.05$); the means of the first 10 days and the second 10 days of July are also different ($t = 2.70$, df = 74, $P < 0.01$).

DISCUSSION

The defense behavior of cormorants has several components. Clumping in space is achieved by nesting in dense aggregations or on crowded ledges. It has been demonstrated here that being a member of a crowd rather than an exposed individual results in fewer predator visits (Fig. 2). Veen (1977) attributes a similar occurrence in *Sterna sandvicensis* to neighbor assistance. Similarly, nesting on slopes steep enough that the only level areas are occupied by a nest or by an adult cormorant or by its neighbors means that predators are barred from landing or forced into close conflict with the nesting cormorant. But such habitat-selection options may not be available to all colony members: nest sites are limited on very steep slopes, and the geometry of a colony demands that there always be birds on the periphery. There-

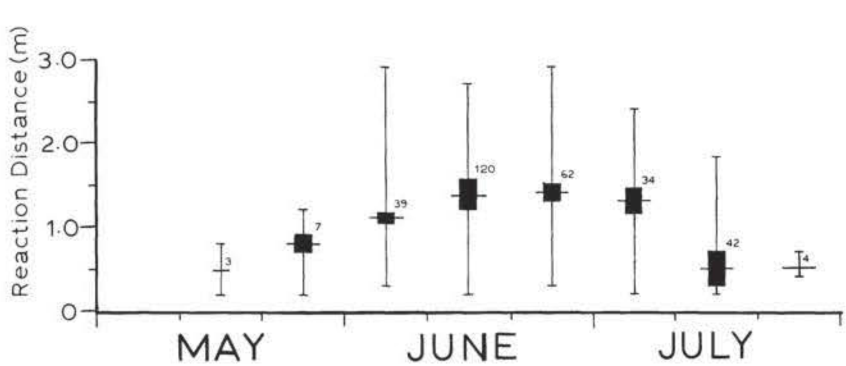

Fig. 6. Phenology of Double-crested Cormorant defense behaviors. The vertical line in each diagram indicates the range of values; the horizontal line, the mean; the solid box, the 95% confidence interval; the superscript number, the sample size; reaction distance = see Methods for explanation.

fore, there should be intense competition for protected nests in the steeper core of the colony. The colony should then grow from these nests by accretion of breeding pairs building nests around them; isolated nests will appear late in the season on more level areas as the other possibilities are used up (Lewis 1929, Mendall 1936, Siegel-Causey and Hunt MS).

Agonistic behaviors provide an additional element of defense. Some of these defenses may arise over the course of evolutionary time and may constitute such species-specific characters as preference (or ability) for nesting on steep cliffs, the incorporation of highly visible defense behaviors, etc. Other defenses, such as aggressive behaviors, may become intensified over the breeding season as conditions require. These behaviors will need to be plastic so that the adult may minimize the energy expenditure required to repulse predators. The adult cormorant should increase the amount of energy used in nurture and defense as the embryo develops, for there are physiological constraints on the birds' ability to start new broods late in the season. In addition, the investment of time and energy in offspring accumulates as the season progresses (Trivers 1972). When we examined the phenology of Double-crested defense behaviors, we found (Fig. 6) that the aggression level (measured by reaction distance) increases with time and then drops suddenly. This drop-off coincides with the period when the chicks have matured and have grown to a size such that predators are unable to carry them away (Lewis 1929, Drent et al. 1964).

Behavioral analysis shows that Pelagic Cormorants employ defense behaviors that are less aggressive than those of the Double-crested Cormorant (Fig. 5) and may be appropriate only for cliff habitats. In support of this, a small colony of Pelagics nesting atop drift logs on Race Rocks, British Columbia in 1975 did not lay an egg that was not eaten by gulls (W. Campbell pers. comm.). This low-level defense behavior may be possible only when topography provides the major deterrent to predators. Thus, there seems to be a trade-off between using minimal defense against predators and being limited by lack of nest sites at places that exclude predators.

Double-crested Cormorants employ an aggressive defense against predation and commonly nest on wharf pilings, treetops, and broad ledges. They are physically unable to nest at commonly used Pelagic nest sites (Mendall 1936) and venture only slightly over the cliff edge. Double-crested Cormorants, in comparison with Pelagics, employ a defense strategem of direct aggression. This is best shown for gull-Double-crested Cormorant interactions.

Crows are more common and more successful predators than are gulls in both cormorant colonies. They are not restricted from cliff landing by their size and weight as are gulls and may land at most nest sites in either colony. Crows still prefer to visit Double-crested nests over Pelagic nests, however, regardless of the minimal Pelagic defense. This may be because of the greater availability of food from the more densely nesting Double-crested Cormorants.

The pattern of predator visits and nesting density (Fig. 2) indicates that the crows avoid areas of highest density, where the proximity of nests places the intruder in conflict with not only the victims, but their neighbors. The lowest density areas, isolated nests, also are not preferred. Should the initial attack fail, the number of nearby alternative victims will be small in lowest density areas, and the predator must expend more time or effort moving to new prey than when it switches to neighbors. The predator also increases its chances of detection by other nesting cormorants as it traverses greater areas of the colony looking for food. The trade-off between increasing its rate of success (high density) and decreasing its chances of being attacked (low density) apparently results in the crows selecting some intermediate cormorant breeding density.

The food choice of crows (Fig. 4) probably is determined by the quality of the adult's defense. We expect that, as the parental investment in time and energy into offspring increases, their defense of offspring also will increase. This increased defense may be enough to force a predator to avoid offspring and choose an alternate item, such as vomited food. Late in the season, the chicks can defend themselves and are too large to be carried away. Thus, chick predation by crows always should be rarer than that upon eggs or vomit, even at the end of the season when parent defense is low.

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