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Authors

SIEGELCAUSEY, D
HUNT, GL

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dean Venezuela, and specimens from the western tepuis of Territorio Amazonas are somewhat grayer than are specimens from the eastern tepuis of the Gran Sabana.

The definitive female plumage in the two subspecies is similar to that of the second basic male plumage of the same subspecies. Between the subspecies, the definitive male plumage of *duncani* is similar to, but still somewhat browner than, the definitive female or second basic male plumage of *homochroa*. Similarly, the second basic plumage of *duncani* is more similar to the first basic plumage of *homochroa*. Thus, reduced stripedness and gray coloration probably represent the derived condition, and heavily striped brown plumage is probably the primitive condition.

If this is true, then I would suggest that *duncani*, which inhabits the tops of the far older land mass of the tepuis, would have been the parental stock that "hopped" to and colonized the Andes after they were formed. A paler juvenile plumage and grayer definitive plumage was part of their adaptation to the drier paramo conditions.

Males of *C. h. oreophila*, the isolated Santa Marta population, in juvenile and first basic (in second pre-basic molt) and three females in second basic plumage are separable from the corresponding plumages of nominate *homochroa* in being somewhat paler brown. The type of *oreophila* was compared with the above three females by K. P. Parkes. It is distinctly grayer and probably represents the definitive basic plumage.

In contrast to our knowledge of plumage sequences for North American birds, one can generalize that such sequences are poorly known for neotropical species. The recognition of four sequential

plumages in male *Hemithraupis flavicollis* was so startling at the time that reviewers of Parkes and Humphrey's (1963) manuscript questioned the phenomenon (Parkes pers. comm.). The recognition of four sequential plumages in male *Icterus gularis* and now in both sexes of *Catamenia homochroa* perhaps indicate that a higher frequency of complex plumages is to be found among neotropical species.

I thank the curators of the following collections for the loan of material in their care: Carnegie Museum of Natural History, Field Museum of Natural History, Louisiana State University Museum of Zoology, Museum of Comparative Zoology, and the U.S. National Museum of Natural History. Mr. William H. Phelps, Jr., and Ramon Aveledo kindly hand carried the entire series of *duncani* from the Coleccion Phelps, Caracas to New York for this study. Kenneth C. Parkes reviewed the age plumage classes with me and made useful suggestions. The Photography Department at the American Museum of Natural History prepared the illustration.

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Breeding-site Selection and Colony Formation in Double-crested and Pelagic Cormorants

DOUGLAS SIEGEL-CAUSEY¹ AND GEORGE L. HUNT, JR.²

¹Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045 USA, and

²Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717 USA

The success of a breeding pair to raise eggs to fledged birds does not appear to be uniform over an entire colony; instead, there are certain regions (central area, steepest slopes, etc.) where the occupants have enhanced reproductive success (Coulson 1968, Nettleship 1972, Ryder 1980, Panov and Zykova 1982, Kharitonov 1983b). Fretwell and Lucas (1970) proposed a mechanism by which colonial birds could assess and choose optimal breeding sites from among a range of choices. A series of habitats are identified, each ranked by a unique suitability function that is a density-dependent measure of average reproduc-

tive success. That is, the average success of breeding birds decreases through the effect of density-dependent factors such as disease, neighbor conflict, predator awareness, etc. as the density of the habitat increases. At some density, the expected reproductive success in the optimal habitat will equal that experienced in some lesser, unoccupied habitat. Incoming adults intent on breeding should then colonize both habitats at an equivalent rate, rather than saturate the optimal habitat. Where breeding must be initiated within a narrow time frame, or nest sites are changed at a loss of the previously invested time and effort,

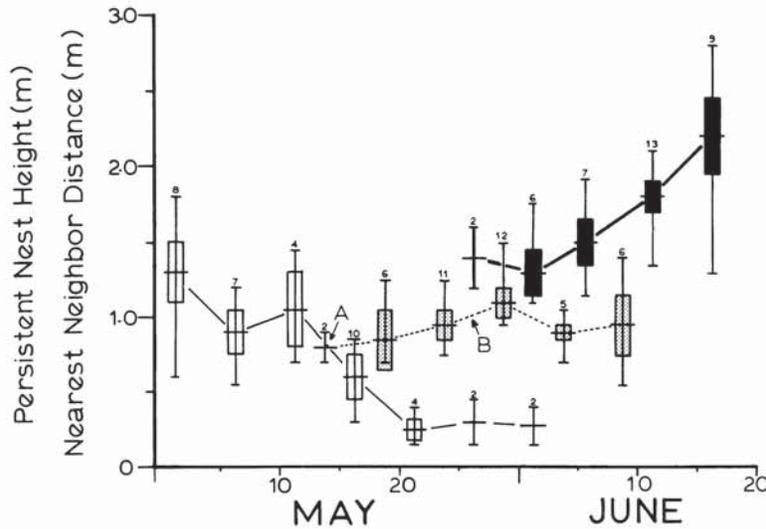


Fig. 1. Phenology of nest initiation in Double-crested Cormorant subcolony 1W. Open bars = persistent nests, shaded bars = interjacent nests, solid bars = peripheral nests. The vertical line is the range, the horizontal line is the mean, the length of the bar is the 95% confidence interval, and the superscript number is the sample size. The vertical scale for persistent nest measures height of nest in meters; the vertical scale for interjacent and peripheral nests measures nearest-neighbor distance in meters. Point A signifies habitat switching from persistent to interjacent nests; Point B, switching from interjacent to peripheral nests. Data were grouped in 5-day intervals.

midseason site shifts will be avoided. Mistakes in site choice will be maladaptive (see also Kharitonov 1971a).

We tested the predictions of this model using data collected in 1975 on the nest-site selection and colony formation of the ground-nesting Double-crested Cormorant (*Phalacrocorax auritus*) and the cliff-nesting Pelagic Cormorant (*P. pelagicus*) on Mandarte Island, British Columbia, Canada (see Siegel-Causey and Hunt 1981 for a description of the cormorant colonies and methodology). We tracked the daily growth of one Pelagic Cormorant subcolony (36 full-term nests) and three Double-crested Cormorant subcolonies (115, 52, and 37 full-term nests) from the first arrival of adults to chick fledging. To measure success, we used the proportion of chicks fledged to eggs laid because this better estimates reproductive effort than a simple success measure (e.g. number of young fledged per breeding pair). We used both field notes and photographs to follow the persistence and success of each nest under observation. We identified most adults in the colony using existing bands, rhamphotheca patterns, web perforations, and scarring. To minimize human interference, these colonies were last banded in about 1970. Therefore, we estimated age classes of both species using plumage characters described by van Tets (1959). We defined breeding habitats in terms of discrete classes of nests built by the breeding pairs.

On Mandarte Island, the Double-crested Cormo-

rant typically nested on the broad shoulders of the cliffs, wedged between the Glaucous-winged Gull (*Larus glaucescens*) colonies farther inland and the cliff face. The nest of the Double-crested Cormorant is composed of diverse objects (Lewis 1929, Mendall 1936), but large sticks greater than 15 mm diameter predominate. The materials are intertwined and covered with a thick, durable coat of guano that quickly hardens. At most other breeding localities, heavy winter storms remove the previous year's accumulation of nests, but Mandarte Island lies within the rain shadow of Vancouver Island and receives roughly $\frac{1}{2}$ the normal precipitation of the region (Drent et al. 1964). This and the elevation of the subcolonies (15-30 m above sea level) ensure that some nests are not washed away but are used for years, often reaching heights of 2 m or greater through yearly accumulations of materials. To test the Fretwell-Lucas model, we considered these high nests ("persistent nests") to be distinct habitats from those sites where breeding pairs began nests from bare ground.

The persistent nests were selected early in the season by the first arriving males and were strongly defended once occupied. In New England colonies, persistent nests were selected earliest (Mendall 1936) and seemed to provide the greatest chance for chick survival. Nesting on an elevated platform within the colony allowed the adult cormorants a better view of approaching predators and less contact with squabbling neighbors (Lewis 1929). Given this putative ad-

TABLE 1. Duration of nests initiated in areas commonly used for loafing and in the general Double-crested Cormorant colony area. Loafing areas were regions characterized by the continual presence of unattached adults.

Duration	Loafing areas	Colony
<1 day	115	30
1-7 days	29	11
>7 days	5	17

vantage, it would follow that new nests would be initiated only after all of the persistent nests were occupied. As predicted by the Fretwell-Lucas model, however, we observed that some adults began building new nests while there were still persistent nests available (Fig. 1: point A).

The new nests ("interjacent nests") were constructed among the core of persistent nests and placed often less than one nest diameter (0.7 m) away from an existing nest. At this distance, neighbors could touch bills while sitting on the nest. [We measured the length of full stretch ($\bar{x} = 0.38$ m, $s = 0.04$, $n = 31$) by observing fights between nesting adults within a measured grid.] In time, this resulted in areas of high density (<1 nest/m²), which, in certain cases, has been implicated in increased chick survival (Siegel-Causey and Hunt 1981, Kharitonov 1983a, Zykova and Panov 1983). We observed another shift in nest habitat similar to the conditions described above (Fig. 1: point B). Although interjacent sites were still available, some breeding pairs chose to build nests at the periphery.

Nests in the third group ("peripheral nests") were at the edge of the colony always greater than two nest diameters from the nearest nest. Peripheral nests often were isolated from the main aggregation by the irregular topography of boulders and erosion gullies. This nest habitat was clearly marginal to the persistent and interjacent nest sites because the environment limited dense nesting, hid incoming predators, and, by being on the edge of the colony, increased the individual predation pressure (see Coulson 1968, Kharitonov 1971a). Furthermore, birds breeding here had to contend with the continual theft of nest materials by transient nest builders.

Roughly equal proportions of 2-yr-old birds (distinctive by their brown heads and breasts) and birds with adult plumage built "ephemeral nests" of small size and variable composition throughout the breeding season. Some birds attracted potential mates, performed preliminary pairing behaviors, and attempted copulation. Although these events are normal preliminaries in the nesting sequence (van Tets 1965), none of the ephemeral nests lasted longer than about two days. Ephemeral nests were more likely to be built near loafing areas than near active nests. These loafing areas were usually at the periphery of the colony area, but habitat inclusions such as low rock

TABLE 2. Regions of highest turnover in nest ownership in the Double-crested Cormorant colony. Nests at the periphery were defined as those with one or no nests between them and the colony limits; central nests were all other nests.

Turnovers	Periphery	Center
1	7	18
2	10	8
3	5	0

walls and broad boulders placed some of these areas within the colony limits. Nests of any type built near loafing areas did not last as long as those sited in the general colony area (Table 1; $\chi^2 = 30.04$, $df = 2$, $P \ll 0.001$). Nest sites characterized by high turnover (two or more sequential occupants) were typically located near these inclusions and loafing areas (Table 2; $\chi^2 = 9.80$, $df = 2$, $P < 0.01$).

Pelagic Cormorants typically nested seaward of the Double-crested Cormorants along the cliffs of the western edge. The nest is composed of dried grasses and seaweed and is cemented into a durable mass through yearly accumulations of guano (Bent 1922). Although most nests were protected from winter storms by overhanging ledges, none of them grew appreciably as did nests in the Double-crested Cormorant colony. Nest building was not as protracted nor were the materials as bulky as those used by Double-crested Cormorants.

Unlike the Double-crested Cormorant colony, the availability of potential nest sites was restricted by the cliff habitat: there were only a few ledges and outcrops on the sheer face broad enough for a nest. As in the Double-crested Cormorant colony, persistent nests were the first occupied. We observed a habitat shift as one interjacent nest was initiated (PC31) when there were still two empty persistent nests (PC11 and PC27). We believe that all of the nest sites were occupied after one week from the first arrivals, because later breeding pairs initiated nests only at abandoned nest sites. Ephemeral nests appeared only on ledges normally used for loafing, and none lasted longer than one day. Unlike the Double-crested Cormorant colony, turnover in nest-site ownership was rare: only 3 of 36 nests were reused by another adult pair during the breeding season. The remaining 33 nests were occupied continuously during the breeding season by the initiating pair.

The relation between individual reproductive success and nest density at the time of initiation (Fig. 2) further affirms the predictions of the Fretwell-Lucas model. As persistent nests were occupied through time, the density of nesting increased (Fig. 2). Later-arriving males had more neighbors to contend with, each aggressively defending its nest area against intruders. Even females intent on copulation used elaborate pairing and recognition behaviors to avoid being

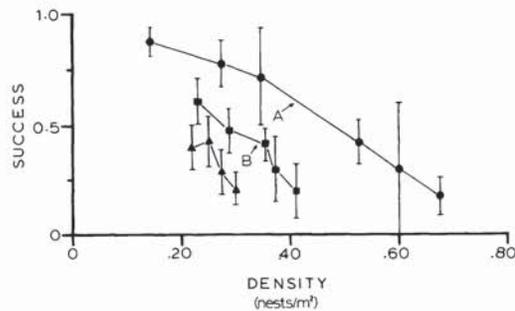


Fig. 2. Model plot of nest success to breeding density. Circles = persistent nests, squares = interjacent nests, triangles = peripheral nests. The position of the symbol denotes the mean; the length of the vertical line is the 95% confidence interval. Points A and B are as in Fig. 1.

attacked as they approached (see also van Tets 1965). Fights for possession and nest defense increased in number and the general level of aggression within the colony rose rapidly during this period (see Siegel-Causey and Hunt 1981: fig. 6).

When the nesting density of the persistent nests reached about 0.4 occupied nest/m², some newly arriving birds shifted to building interjacent nests at about 0.2 nests/m² (Fig. 2). Interjacent nests had to be built from bare ground, but presumably at a lesser cost than fighting for a persistent nest. Kharitonov (1983a) observed similar behaviors in *Larus ridibundus*: pairs attempting to establish territories in the dense core of the colony shifted to the "pericentral" areas, where the competition for space was lower. Later attempts at center nesting were always rebuffed by the central nesters.

The nearest-neighbor distance was highly correlated with the date of nest initiation and nesting density, and the reproductive success with time (Table 3). When the linear effects of the nest initiation time and the placement of nests were removed, the partial cor-

TABLE 3. Multiple correlations of reproductive success, date of nest initiation, breeding density, and nearest-neighbor distance in the Double-crested Cormorant colony.* Coefficients were calculated from 240 nests. RS = reproductive success, NI = date of nest initiation, NND = nearest-neighbor distance, D = nesting density.

	RS	NI	NND	D
RS	1.000			
NI	-0.538**	1.000		
NND	-0.210*	+0.574**	1.000	
D	-0.262*	+0.064	-0.552**	1.000

** = $P < 0.05$, * = $P < 0.01$.

TABLE 4. Partial multiple correlations of reproductive success to breeding density.* Abbreviations are as in Table 3.

Linear effect removed	RS-D
NI	-0.464**
NND	-0.271*
NI + NND	-0.245*

* = $P < 0.05$, ** = $P < 0.01$.

relation of individual reproductive success with nesting density was still significant (Table 4: $r = -0.245$, $P < 0.05$).

Pelagic Cormorants, nesting in an extreme habitat where possible nest sites are limited, do not show the pattern seen for Double-crested Cormorants. Although some differential success was observed in the Pelagic Cormorant colony, it seemed more related to breeding experience than to nest-site selection. We showed earlier that, for the Pelagic Cormorant and other cliff-nesting birds, the habitat provides a defense against predators (Siegel-Causey and Hunt 1981). In the context of the Fretwell-Lucas model, the cliff face rather than nest type may constitute a single discrete habitat. Because nest sites are limited here, the habitat may saturate before the theoretical optimum density is reached; thus, no corresponding habitat shift is observed. Rodgers (1980) noted a temporary saturation of nesting territories for the Little Blue Heron (*Egretta caerulea*) and a corresponding hiatus in nest initiation.

The selection of nest sites within the Double-crested Cormorant colony appears to progress as predicted by Fretwell and Lucas (1970) through shifts in nest-site habitats, but it is not immediately clear by what mechanism new arrivals are able to assess the suitability (i.e. future success) of a particular habitat type. Previous studies have shown that for some species, center-nesting birds are generally the older, more experienced breeders; young and inexperienced birds are more likely to be found at the edge of the colony (Kharitonov 1971a, b; Veen 1977). Past experience of breeding in a particular habitat and the level of aggression needed to secure a nest site may be the means by which breeding adults assess the immediate suitability of a habitat. Adult Double-crested Cormorants on Mandarte Island are highly philopatric, and previous experience seems to affect nest-site selection in future years (van de Veen 1973). A similar mechanism also may operate in the Pelagic Cormorant colony, but it appears that the habitat quickly saturates, preventing further colonization.

It is difficult to reconcile the success/density relationship we found here with previous results in a neighboring colony where the highest chick survival was in the areas of greatest density (Siegel-Causey and Hunt 1981). In contrast to this neighboring colony, the Double-crested Cormorant subcolonies we

discuss here were new additions to the main breeding population on Mandarte Island, formed by recent expansions (van de Veen 1973). A colony location in a marginal part of the island or a greater proportion of younger parents may have prevented the formation of a large core of experienced breeders able to participate in group defense or other activities known to enhance chick survival. Further studies with marked and known-age birds will be necessary to clarify these problems.

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