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## DISPLAY AND SEXUAL BEHAVIOR OF THE BRANDT CORMORANT

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Descriptions of the display and sexual behavior of the Brandt Cormorant (*Phalacrocorax penicillatus*) have been extremely meager. Townsend (1925) noted certain posturings of this species but did not mention what I have called "advertising display," an essential feature of sexual behavior. Hoffmann (1927:20), in his manual, aptly describes in one sentence a certain part of the advertising display, and Michael (1935) describes some display actions seen in southern California.

The present study was carried on at certain breeding colonies along the coasts of Marin, Monterey, and San Diego counties, California. The work was done principally at Point Reyes, Marin County, and "Bird Rock" near Pacific Grove, Monterey County. About three hundred hours were spent afield over a period of eight years from 1933 through 1940.

All these colonies except the one at La Jolla, San Diego County, are on small, rocky islets close to the mainland. No landings were made. High seas rendered this impossible during most of the breeding season. For the same reason, and because most of the work was done on reserves, no birds were collected. Collection of displaying birds, if practical, would have facilitated identification of sex. However, it was found possible to make identification in other ways. Banding or marking adult birds by other means would also have been impractical.

Observations were made from the mainland with the aid of a telescope that magnified about 40 diameters. Although this had certain disadvantages, important advantages were gained. The birds were entirely undisturbed. Landing on small rocks where there are colonies flushes the incubating cormorants from the nests, exposing the eggs to the ever-watchful and bolder Western Gull (*Larus occidentalis*). Moreover, even if the exposed eggs were not robbed, the value of observations made at such times is questionable. My records show that under normal conditions the eggs are never left unattended. At the Point Reyes colony it was possible to approach within a few hundred feet without disturbing the birds at all, and from the elevation of the cliff there was an unobstructed view down into the nests (fig. 24).

Certain birds could be individually identified by means of a missing rectrix, asymmetry of head plumes, or unusually pale buff on the throat. This was not entirely satisfactory. The individual rectrices, which are easily observed when the tail is cocked in advertising display, can seldom be seen during the later stages of the cycle when the bird no longer indulges in frequent display. The plumes wear down in the course of the season and therefore are not a reliable mark for long.

Bent (1922:266) says, "Brandt cormorants seem to prefer to nest on the flat top of a rocky island, on a gradually sloping incline or more often still on a high rounding shoulder of rock." The exception to this rule is the colony at La Jolla where the birds nest on a cliff face (fig. 25). But even here the sites chosen are wide ledges or niches and are not nearly as precarious as the recesses generally chosen by the Pelagic Cormorant (*Phalacrocorax pelagicus*).

*The plumes and the gular pouch.*—Bent (1922:269) states that "the partial pre-



Fig. 24. Part of the colony of Brandt Cormorants and Murres at Point Reyes, Marin County, California; June 8, 1935.

nuptial molt of adults, at which the long nuptial plumes of the neck and back are acquired, occurs in February and March . . .” I found, however, that on the Monterey Peninsula these filaments become easily visible in early December. Weekly observations of adults in November and December over a period of eight years, made under standard conditions, bear this out. By July the plumes have become mere stumps, or have almost entirely disappeared, presumably through wear.

During the non-breeding season the gular pouch is a dull, blue-gray. At about the same time, or a little after the time that the filaments appear, it takes on a most brilliant cerulean blue. This color in turn is replaced for the most part by dull blue-gray in July.



Fig. 25. The Brandt Cormorant colony at La Jolla, San Diego County; March 23, 1938.

*The sexual cycle.*—The period of sexual activity roughly coincides with the aforementioned anatomical changes, although some abortive display which might be interpreted as sexual may be seen even in the non-breeding season. At Bird Rock intense sexual activity begins in January and continues into June. I have little data on the egg-laying period at this colony because the eggs are hidden from an observer by the walls of the nests. But this long protracted courtship season is reflected in the fact that small downy young may be seen there regularly for three months, from May through July.

The sexual cycle may be divided into three phases. These are not to be considered as necessarily following a time sequence, but are distinct divisions of behavior throughout the cycle.

Phase I, advertising display by males and "visiting" by females.

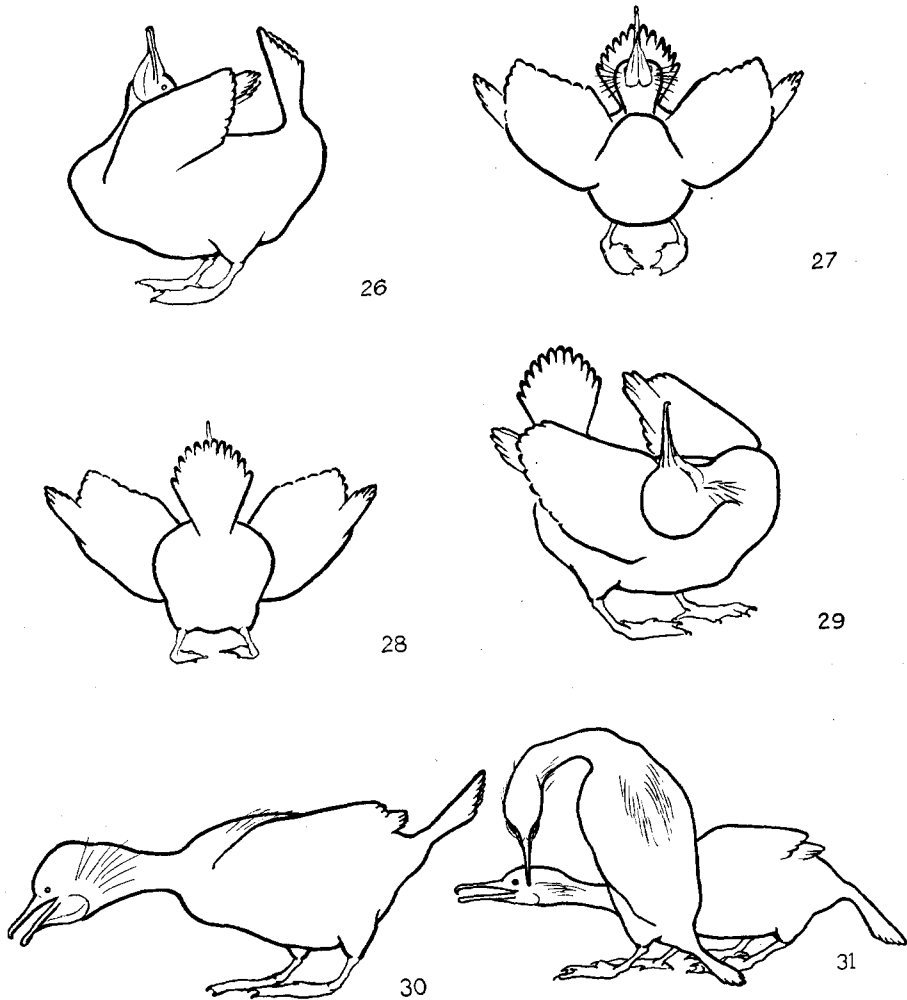
Phase II, pairing up, temporary or permanent, accompanied by mutual displays.

Phase III, incubation of eggs and rearing of young, with gradual diminishing of all the displays.

In phase I the male takes up a station on the rock. This station becomes the center of a future limited but definite territory, although there is evidence of some shifting about at first. To this place the nesting material is brought by the male even though he has not yet acquired a mate.

*The displays and associated behavior.*—The "advertising display" has two parts. The first of these may be called the "flutter." The bird squats, the breast almost, or actually, touching the rock. The neck is drawn back, the nape resting, or nearly resting, on the back, the bill pointed upward. The tail is cocked and spread. The feathers of the head and neck, together with the white filamentous plumes of that region, are decidedly ruffed out, giving a swollen effect (figs. 26 and 27). The longer back plumes are only very slightly elevated from the back. Neither the plumes of the head or back are nearly as showy as the head plumes of the Night Heron (*Nycticorax nycticorax*), or the long, voluminous and highly erectile plumes of the Snowy Egret (*Egretta thula*). Much display has been observed in individuals of *penicillatus* whose plumes have either been considerably worn or have not yet attained maximum length. In the flutter the gular

pouch bulges. As in other displays of the species this distention is achieved by expansion and depression of the hyoid apparatus. At close range it is possible to see the skin protruded at certain places by this action of the hyoid. The distended skin then exhibits



Figs. 26-31. Postures of Brandt Cormorants.

- 26. Advertising display; the flutter, side view.
- 27. Front view of the flutter.
- 28. Rear view of the flutter.
- 29. The flutter, with head twisted to one side.
- 30. Advertising display; the stroke.
- 31. Precoital postures; intense type.

the most brilliant cerulean hue. It may aptly be described as suddenly blossoming forth into this color and thus forming what is perhaps the most striking feature of the display, as seen through human eyes at least. The brilliant color, however, is missing along certain longitudinal lines on the pouch; the longest and most noticeable of these are indicated in the drawings.

As the bird assumes this squat and ruffed out position of the first part of the advertising display, the wings are lifted slightly off the back and rhythmically fluttered.

This is accomplished by raising the humerus up and out from the back. The radius and ulna remain in the folded position and there is no actual spreading of the primaries, the manus being held against the side. Even though the primaries are not spread, they are so oscillated behind the secondaries during the flutter that, from the rear, they suggest a feather duster in motion (fig. 28). There is movement of the slightly erected back plumes during the flutter but in the drawings they are masked by the flight feathers. A rather frequently observed variant to the usual flutter is with the head twisted to one side (fig. 29).

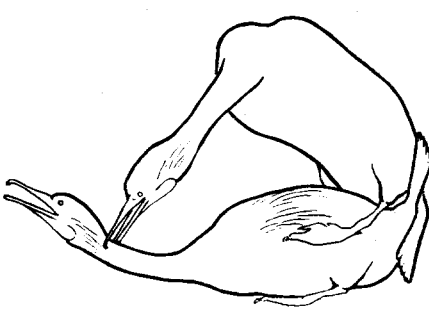
The flutter may be done for as long as twenty-five seconds before the second part of this display, the "stroke," is made. In the stroke the wings are partly replaced on the back; the head is thrust forward and downward in a hammer-like stroke; the bill, which at the end of the stroke almost, if not actually, touches the rock, is opened a bit; the gular pouch remains distended and the head and neck feathers, with the filaments, remain ruffed out (fig. 30). After a slight pause in this position, the head and neck are recoiled and the thrust is repeated. As many as fifteen strokes may be performed before the bird reverts to the flutter. More frequently just a few strokes are followed by a pause and then a flutter, and thus the display is repeated for an indefinite time.

While a male is advertising, various females come to him. I have called this "visiting." The females move about among the advertising males with thin, up-stretched necks, peering at one advertiser and then another and exhibiting a tentative air as they move hesitantly among the crowd of swollen-necked, fluttering, and stroking males. As the female approaches a group of males, there is a sudden increase in display activity, quiet males recommencing display and those already engaged in advertising intensifying their activity. As soon as a female reaches a male, either by a short flight or by walking, the two birds may be considered to have passed into phase II, whether the female remains for long or not.

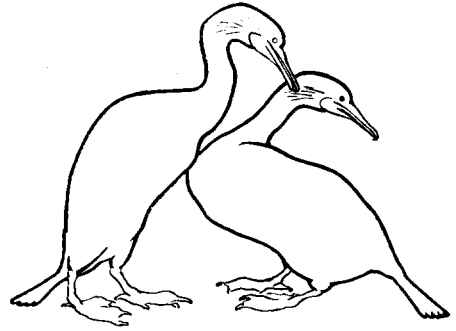
In phase II a number of bisexual displays are exhibited. Included are displays or posturings performed by both sexes, whether they are done synchronously or individually; the birds of the pair may even be temporarily alone. If pairing up is not accomplished and the female leaves, the male usually resumes advertising display and the female usually goes to other advertisers; the birds may be said to have reverted to phase I. The male does not advertise when the female is with him.

As the female approaches the male, the strokes of his advertising display merge into the prone (horizontal head and neck) position of the "lower precoital posture." The feathers of the head and neck are relaxed or even compressed to such an extent that the neck looks thinner than normal. The female at the same time assumes the "upper precoital posture," intermittently jabbing with her bill at the male's head or nape (fig. 31). The male, from time to time, slightly recoils the head and then stretches it forth again, an action somewhat reminiscent of the strokes of advertising display. The female may even *mount* at this point and behave very similarly to a male performing this act (fig. 32). But more often the female goes no further than is shown by the bird on the left in figure 33, while the male may rise to a partially erect posture. The female may then leave to go to another advertiser. Or the male may assume the upper precoital posture to which the female may or may not respond by taking the lower. If she does, the male may immediately mount. Thus there are instances of an almost immediate reverse mounting, although generally the male does not mount until sometime later. The upper and lower precoital postures may be assumed by *either* sex and *mountings* may even be done by either sex. However, my observations indicate that actual cloacal contact is made only when the birds are in the position usual to most species, that is, with the male uppermost.

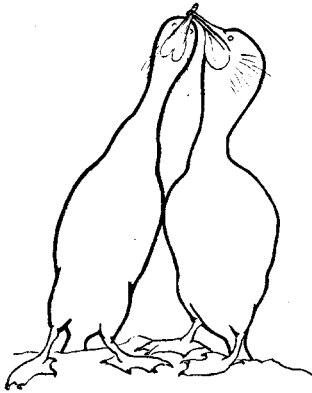
When the mounting bird gets off, both birds stretch up, one ruffing out, its gular



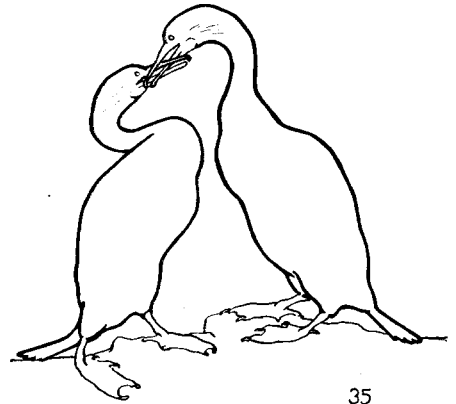
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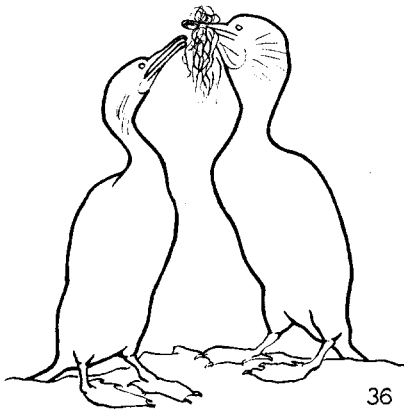
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Figs. 32-37. Actions involving both members of the pair.

- 32. Mounting.
- 33. Precoital postures; mild type.
- 34. The "stretch and ruff."
- 35. Billing.
- 36. Nest-material ceremony; arrival.
- 37. Placing the material.

pouch distended; the bills of the pair almost touch. I have called this the "stretch and ruff" (figs. 34 and 38).

A period of "billing" often follows. They nibble and grip each other's bill, and twist and sway together (fig. 35). This generally leads to rubbing the sides of the heads together, nudging the body, nudging the nape, and sometimes actually ruffing the feathers. An important feature at this stage is the nibbling by one bird at the other's gular pouch.

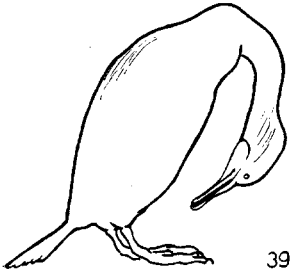
The male bird goes after nesting material if the female remains for any length of time. This almost invariably follows copulation with the male uppermost, and often



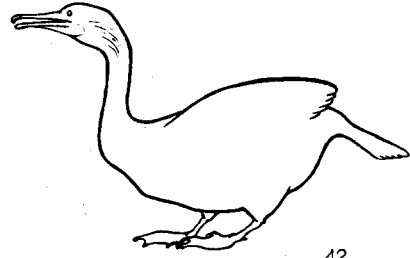
Fig. 38. The "stretch and ruff" (topmost pair); La Jolla, March 23, 1938.

it occurs when this has not yet been effected. As he returns to the station where he has left the female, the male alights with head high, gular pouch inflated, head and neck plumes and feathers erected, and back plumes slightly raised. The female rises from a squatting or lying position to take hold of the material in his bill. They sway from side to side, both holding the material, then arch down stiffly together and deliberately place it on the nest. Sometimes the female merely follows the male's head with hers as he places the material and there is no sway. This display I have called the "nest material ceremony" (figs. 36 and 37). A male in phase I may do what is essentially his part of this ceremony even though there is no female present to receive the material.

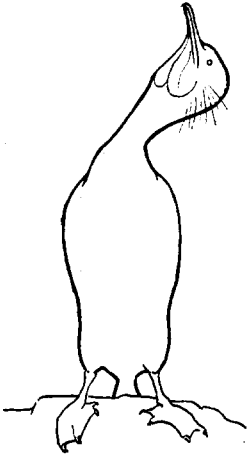
The "hop" is a display used in all three phases, although it is decidedly less frequent in the third. It has also been observed on perching rocks in the non-breeding season. The standing bird bows low, bending its neck stiffly down in front of it until the bill almost touches the rock between its webbed toes. In this bowed position it hops directly up, leaving the rock an inch or two. As the toes touch the rock again, the head and neck are swung upward until the bill is almost vertical. At the same time the



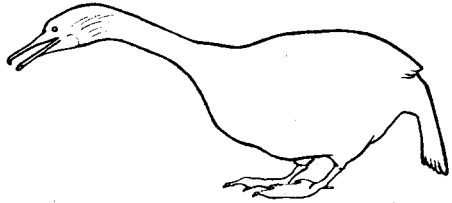
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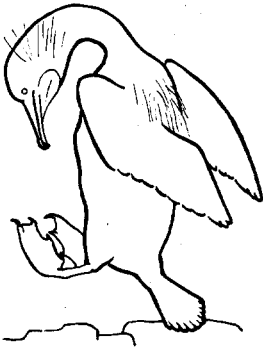
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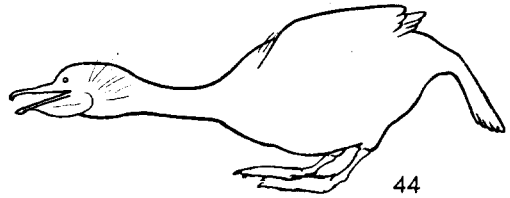
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Figs. 39-44. Hopping and threatening activities.

39. The hop; bowing.
40. The hop; inclining head after the bow.
41. Landing with a hop.
42. Threat gesture; beginning of fly-casting motion.
43. Later phase of fly-casting motion.
44. Climax of fly-casting motion; this position also used as a direct threat.

feathers and plumes of the head and neck are ruffed out and the gular pouch is distended. The neck is slowly and stiffly inclined a bit to one side (figs. 39 and 40), the bird holding this pose for about a second. Sometimes the bird performs the latter part of this display as it alights upon the rock from a flight (fig. 41). The hop is performed



by either bird in the course of display activities in phase II. Often a male going to another part of the rock to pick up unguarded nesting material lands with a hop; or he does this as he alights at his station either when it is empty or occupied by a usurper which he drives off. Sometimes when a female flies to an advertiser she lands with a hop. In the non-breeding season the hop, or landing with a hop, is associated with driving another bird from a perch.

Threat or intimidation displays used by both sexes occur during all phases of the sexual cycle as well as in the non-breeding period. They are of two types: the "threat gesture" and the "peck threat." In the threat gesture the neck is thrust forth, usually low along the rock and toward the object threatened. The head and neck feathers and plumes are ruffed out, the wings are slightly lifted off the back, the gular pouch is distended with the hyoid protrusion showing slightly more anteriorly than in other displays, and the bill is partly open. In this position the head is rapidly twisted on the axis of the neck, describing a short arc to right and left, while a loud, hoarse, trilling growl, or gargling sound, is uttered. Sometimes the head is thrust directly at the threatened object (fig. 44); sometimes it is thrown with a sort of fly-casting motion (figs. 42, 43 and 44). The peck threat is nothing more than an extremely rapid peck, or series of pecks, toward the threatened object. Occasionally a peck threat is used by a male against a female with whom he had been engaged in mutual displays in phase II, whereupon the female precipitately leaves.

A threatened male often replies in kind and the birds may grip bills. Unlike many land birds whose threat is so often mere bluff, Brandt Cormorants engage in genuine fights in which rival males push and pull each other, flap their wings about wildly and tumble over the rock. On such occasions the female of one of them, or the neighbors, or all, may add a few pecks, too. One fight that was timed lasted for three minutes.

Threat displays have been seen directed toward Western Gulls, sea lions (*Eumetopias jubata* and possibly *Zalophus californianus*), and Murres (*Uria aalge*). The threat gesture was used on many occasions by pairs on nests against gulls hovering over them. Large downy young with flight feathers protruding through the sheaths have been seen using the threat gesture toward a Western Gull which passed by their nest (Monterey County, July 3, 1940). The distance was too great to detect any sound that might have accompanied this action. Cormorants not on nests seem to give way before a sea lion advancing up the rock. But on several occasions birds on nests have been seen to use the threat gesture against an advancing sea lion which halted. At Point Reyes both the peck threat and the threat gesture have been observed to be directed against murres. A murre passing through a group of cormorants is pecked and threat-gestured from all sides. One male cormorant was more vicious toward a neighboring incubating murre when a female was with him than when he was alone. He once grabbed the murre and shook its whole body as a dog shakes a rat (Point Reyes, May 18 and 19, 1939). But the cormorant-murre relationship may not be entirely to the detriment of the murres. A downy young murre was so close to a cormorant on a nest with eggs that it could peck the tail of the cormorant (Point Reyes, June 23, 1939). During the years of observations at Point Reyes the murre numbers have kept up and the cormorant numbers, for some reason, have declined a little.

There are no displays peculiar to phase III (incubating and rearing of young) except the one of "nest relief." But as noted above, all of the displays carry over into this phase, though they diminish as the sexual cycle nears completion. Several minutes often elapse during nest relief. The relieving bird nudges the breast of the incubating bird or rubs its head on the sides of the latter's breast. This is interspersed with billing and self-preening. After some minutes the exchange is made, one bird often seeming to push the other off. The bird assuming incubation then pulls and tugs at the nesting

material and turns the eggs. This ceremony seems to be similar to those described for many other species. A male has been seen advertising from an incubating position while sitting on one egg. After nest relief this male mounted the female on the nest as she took her turn at incubation (Point Reyes, May 7, 1940).

*Call notes.*—Because of the constant sound of surf beating on the rocks, my data on call notes are meager. Except in the threat gesture, when the correlation of voice and action is easy to note, it has been almost impossible to associate a sound heard from the crowded rock with a particular display.

Calls are of two types: (1) a variable, low, hoarse, guttural, prolonged croak or growl or gargle, and (2) a high, clear, incisive *kauk* uttered in a series of three or more at regular measured intervals of about a second. The first varies from a pig-like grunt (also noted by Hoffmann, 1927:21) to sounds that have at times suggested to me certain notes of the Raven (*Corvus corax*). The second is louder and frequently carries across the open water and surf when no other call note does. The sound made during the threat gesture is of the first type and the gargling quality is perhaps due to the rapid twisting of the neck.

Both types of call have been heard at perching places at other than nesting time. Type one has been associated with disputes over perches. The *kauk* has been heard from a swimming bird. It also was definitely associated with a territorial dispute in one instance. On this occasion two advertisers at adjoining stations peck-threatened each other vigorously, once or twice gripping bills. When they finally broke away, one bird, in a squat position with pouch distended, thrust its head a little forward several times. At each thrust the gular pouch was further distended and the "hyoid angle" moved anteriorly, as in threat gesture, and at the same time the *kauk* was heard (Bird Rock, March 18, 1940). Nestlings utter rhythmic peepings. In a large colony they can be easily heard from some distance on calm days, no doubt due to the combined effect of many voices.

*Nesting material.*—Nesting material is gathered in four ways: (1) The birds go about on the rock picking up dry material that either comes from abandoned nests or has blown from the edges of other nests. (2) They thief material from a neighbor's nest, occasionally even in the presence of a bird on that nest, although generally in the absence of an unmated bird that has gone to get more material. Nesting material at a station is vigorously defended by threat displays. An unmated male never acquires much material because it is thieved in his absence. For example, Advertiser "P" was watched during two days as he alternated his display with bringing nesting material to his station. Bird "Pi", the male of a neighboring pair with two eggs, made a quick flight to P's station each time P left and thieved the material, so that P's nest made no progress during the two days (Point Reyes, May 16 and 17, 1939). There is continual pilfering of nesting material from neighbors in colonies of *Phalacrocorax auritus* (Lewis, 1929:31-33). When a female is present, however, she will defend the material from potential thieves by threat displays. (3) Cormorants sometimes gather land plants for the nest. The Farallon weed (*Baeria maritima*) has been found in nests on the Farallon Islands (Ray, 1934:79). Large beakfuls of land plants are carried from the edge of a cliff on the landward side of an islet at Point Lobos, Monterey County, to the nesting colony on a rock on the seaward side of the same islet. Chapman (1908:272) also noted this behavior at the same place when he visited California in 1903. (4) The principal method of gathering material is by diving for marine plants growing beneath the water. This is done particularly at certain places, or gathering grounds, near the colony. At Bird Rock, for instance, in the height of the season numbers of birds can be seen resting on the water in a restricted area near the mainland, either preparing to dive or pausing with material in their bills before flying back to the colony (fig. 45). Five



Fig. 45. Brandt Cormorant carrying nesting material from sub-marine gathering ground Bird Rock, near Pacific Grove, Monterey County, April 29, 1939.

counts of the time spent under water to gather the plants near Bird Rock averaged 23.4 seconds. Five counts made at Point Lobos averaged 25.2 seconds. Red and brown algae are gathered. The most important marine plant, however, is *Phyllospadix*, a plant resembling eel grass.

The male, almost exclusively, gathers the nesting material even when the birds are paired up. Females have been seen on a few occasions picking up dry material on the rock and bringing it to the nest. Both sexes arrange it at the nest. The nest is shaped in two ways: material is picked up from the outer side of the nest and laid on the rim; and birds lying in the nest tug violently at the packed material in the bottom of the nest, loosening it and laying it on the rim with gentle shakings. This tugging is a conspicuous action when one bird is alone on a large pile of nesting material. Nest building starts with the gathering of material by the male in phase I, reaches its highest development when the female remains with the male in phase II (the nest progresses rapidly at this stage because the female is there to guard it while the male goes for more material), and continues into phase III. Material was brought to a nest with young at a small colony (Monterey County) on July 2, 1940. A medium sized downy young bird has been seen reaching over the edge of the nest to drag up material and lay it on the rim (Bird Rock, July 27, 1939). Kortlandt (1940:434) observed a "quivering movement with twigs" in the young of *Phalacrocorax carbo* when two weeks old, and he says that at the age of about 4 to 5 weeks they pick up twigs and bind them into the nest.

*Territory.*—It is my opinion that the Brandt Cormorant, a colonial nesting bird, has a small but definite territory. Males proclaim this territory by advertising display, which has a positive effect on females. They also defend by threats and fights a few square feet around the station where they do this display. This area fulfills the concept of a territory because the male makes himself conspicuous there; the females come there; copulation and pairing-up occur there; the nest is built there; and the male is intolerant of other males at this place. Although this territory seems very small, the minimum between nest centers being about four feet, I believe that it has biological importance to the species and that it is a genuine territory, forming a unit of organization within the colony. Mayr (1935:31) defines territory as "an area occupied by one male of a species which it defends against intrusions of other males of the same species and in which it makes itself conspicuous." Tinbergen (1939:69) says, "whenever sexual fighting is confined to a restricted area, this area is a territory." (Also, compare Howard, 1920:198-200, and Tinbergen, 1936:6.)

## EXAMPLES OF BEHAVIOR SELECTED FROM FIELD NOTES

*Establishing territory.*—Bird Rock, April 14, 1939. A known advertiser was sitting at a station. Another bird landed with nesting material in its bill close beside this bird. The newcomer, as it landed, with the material still in its bill, peck-threatened the advertiser, forcing it to move off about four feet where it commenced the advertising display. The newcomer immediately put down the material and began to advertise also.

*Male advertising and females visiting.*—Bird Rock, 1939, bird "MR."

February 18. Bird MR with an identifiable gap in tail noted at a particular station.

February 20. MR is at the same station. He is one of a group of seven advertisers. 9:18 a.m.; MR goes to the gathering grounds and brings back fresh marine plants to his station. 9:32; goes a short distance and picks up dry material from the rock. He lays it down at his station with the nest material ceremony, although there is no female there. 9:35; advertises. 9:40; leaves the rock, apparently to go fishing. 10:15; returns. 10:28; steals the material of a neighbor that had just left its station. 11:32; a female comes to the group of advertisers. Four of these advertise violently. The female goes off toward another group.

February 23. 8:22 a.m.; a female comes to MR as he advertises. He assumes the lower pre-coital posture, the female the upper. 8:26; the female mounts. There is no coition. They stretch and ruff. MR hops. Soon the female leaves. 8:27; MR threat-gestures a cormorant passing rapidly by. 8:28; MR merges the stroke into the lower pre-coital posture as another bird approaches. They bill. MR again takes the lower posture. The female moves off to another advertiser. A third female comes and the same sort of actions follow.

In the course of the morning MR leaves his station to go for nesting material. While he is absent the material left at the station is stolen. During a second absence more material is stolen.

*Female visiting advertising males.*—Female B on Bird Rock was watched continuously from 9:12 a.m. until 12:23 p.m. on March 18, 1940. She made five rounds of visits to advertising males. Between the rounds she rested, preening and sleeping, at places away from the groups of advertising males. Twice she did this at the same spot—a small pinnacle of rock—twice at other places.

The first round took 18½ minutes, the second 8 minutes, the third 18, and on the fourth she was watched for 8 minutes before she was lost in the crowd of advertisers.

The advertisers of round II were different from those of round I. The groups on other rounds may or may not have been the same or may have overlapped.

Round I. She went to eight different birds, returning once to one of these. Three of them were advertising at the moment of her arrival.

Round II. She went to five males. Four of these were advertising at the time.

Round III. She went to four males. When she was with one bird, after she had taken the upper pre-coital posture and the male the lower, B hopped and nudged the male's nape. B was unusually vigorous with this male. Then the male hopped and they billed. The male's billing turned into a peck threat and B left precipitately.

Round IV. B went to two birds and then her identity was lost.

The reactions of all of these advertisers were the same; they gradually merged the stroke into the lower pre-coital posture as she approached and then assumed the full lower posture when she reached them.

Sometimes B merely stopped beside the male, but more often she took at least one jab at the nape of the male from the upper pre-coital posture before looking about and leaving for the next bird.

*Advertising males and a visiting female in which pairing-up seems to have been effected.*—Point Reyes, May 19 and 20, 1939. A group of advertisers, numbers 1-4, some with scraps of nesting material, some without, was watched continuously (fig. 46). There was a certain amount of fluidity in these stations, except No. 3. The No. 1 bird had a tendency to go a short distance away and advertise there for a few minutes and then return to his station, landing with a hop. No. 2, likewise, advertised from another place occasionally. As the observations started, 1, 2, and 3 were extremely vigorous in their advertising.

May 19. 11:32 a.m.; a female (individually identified by the length and number of plumes on the sides of her head; known as female No. 3) landed in the quadrangle and went to No. 3, taking the upper posture while the male took the lower. Presently she went to 2, and then back to 3. While she was with 3 the other birds advertised vigorously, making the strokes in her direction. Then she went to 2. Her upper posture was carried to the point of putting one foot on the male's back, but she did not actually mount. She then went back to 3 but soon to another bird outside the quadrangle. As she went to this other bird, 1, 2, and 3 advertised.

After she had returned to 3 for the fifth time the pre-coital posturing was most marked, but the male got up from the lower posture and they billed. The male then hopped and they arranged nesting material together; then female No. 3 took the lower pre-coital posture and the male imme-

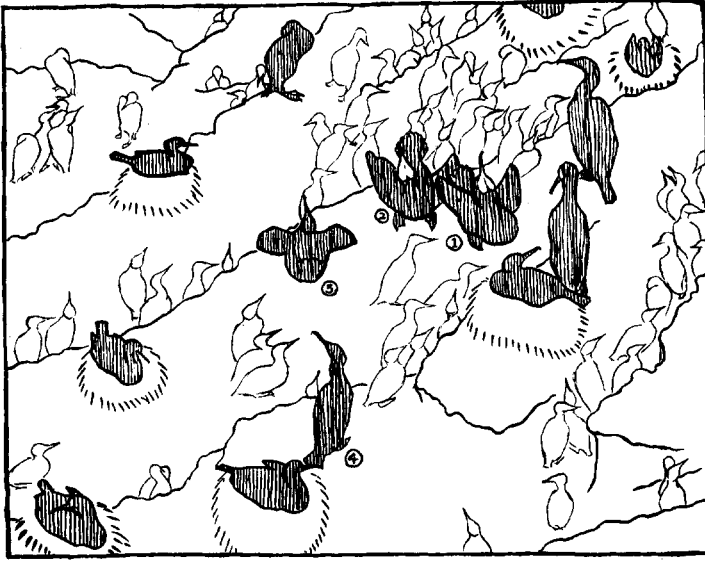


Fig. 46. Advertisers numbers 1-4 at their stations at Point Reyes colony, May 19, 1939 (drawn from a photograph). Numbers 1, 2, and 3 are fluttering. Murres shown in outline.

diately mounted. Insemination seemed probable. Almost immediately after this mounting the male went for nesting material. During the next two hours there were four more mountings with the male uppermost. These were distributed among thirteen trips by the male to get nesting material from under water. The observations for the day closed at 2:45 p.m. with both birds sitting quietly at the station.

May 20. The male was first seen alone at station 3, then female No. 3 was alone there. 11:27 a.m.; both birds were at the station. 11:54; female No. 3 went to another advertiser and performed mutual displays with it. Then she returned to No. 3, landing with a hop, followed by the usual precoital postures. The bird with which she had just been, started to advertise, whereupon the female looked around at it and went back to this bird. During this action No. 1 advertised but No. 3 did not. (In fact after the first mounting on the previous day male No. 3 was never seen to advertise.) After a moment spent with this other bird the female flew back to 3 who was not advertising, although 1 was; she landed with a hop. They took the usual precoital postures and then both had a peck threatening bout with 4. Female No. 3 made another trip to the same bird she had visited twice before that day and to two other birds, all of them advertising as she went to them. With them she performed mutual displays with varying degrees of intensity but no mountings occurred.

12:24 p.m.; the female returned to 3. 12:32; No. 3 male mounted but copulation was not effected because the male, while still on the female's back, locked bills with No. 2 who pulled him off. 12:42; No. 3 female left the rock, apparently to feed. 12:54; No. 3 female returned. After 22 minutes of preening and mutual displays the male made two trips for nesting material and then mounted the female.

Observations ended with the female lying on a large pile of nesting material that had been accumulated. During the period of observation male No. 3 had threatened neighboring males, stolen their material, and threatened near-by murres.

To summarize: Female No. 3 went from one advertiser to another, taking the upper precoital posture each time and even putting her foot on the back of one male. But she kept returning to male No. 3, with whom, it appeared, she eventually paired. This male's advertising stopped when he apparently became paired up. The male went to get nesting material immediately after copulation had taken place. Other copulations followed, always with the male uppermost. The female seemed inclined to "go the rounds" even after pairing up, but she always returned to No. 3. Except for the one abortive mounting (putting her foot on the back of No. 2) at the beginning of the first day's observations, female No. 3 did not mount any bird. Station No. 3 was never left unattended in the course of the observations.

*The male defending his territory against intruding males.*—Point Reyes, May 17 and 18, 1939, pair "G." This was a pair that had a formed nest but which had no eggs. They frequently copulated,

with the male in the upper position. An unmated male had his station two neck-lengths away. In the absence of male G, "Neighbor," the unmated male, walked over to the female and copulated with her. (This was the only male I ever observed going to a female.) On the return of male G, a severe fight ensued resulting in Neighbor retreating to his station where he performed the advertising display. Neighbor later attempted to present female G with nesting material while male G was present. This also resulted in a severe fight, with Neighbor retreating to his station and advertising. When pair G were together at their nest, they threatened Neighbor, acting as a team. When female G went visiting other males (she performed mutual displays with them but no mounting was noted) neither male G nor Neighbor showed any interest and they remained at their stations.

#### COMPARISON WITH OTHER SPECIES OF PHALACROCORAX

*Nature of display.*—I am aware of no extensive published works on the display and sexual behavior of species in the genus *Phalacrocorax* other than those concerned with *carbo*, *auritus*, and *aristotelius*. *Carbo* has been the most studied.

*Carbo*, as observed in Holland by Haverschmidt (1933) and Kortlandt (1938, 1940), nests both in trees and on the ground, far more congenial places for study than the inaccessible rocks of the Pacific, the home of *penicillatus*. Haverschmidt and Kortlandt had the great advantage of working with color-banded birds. Lewis (1929) describes *auritus* nesting in trees, on bare rock and on the ledges of cliffs. When this species nests on the ground, the distance between nest centers varies, but often it is "about four feet" (*op. cit.*: 32). This is comparable to the distance between nests in *penicillatus*.

Kortlandt and Lewis mention sticks used in the construction of the nest. The latter mentions also various land plants as well as marine plants obtained by diving. No sticks are used by *penicillatus* in the colonies I have studied, nor was any tree nesting observed, there being no trees present.

Mendall (1936:39) describes "water courtship" in *auritus* and says that he has seen mounting take place while the birds were in the water. I have never seen aquatic mounting, but on one occasion (Bird Rock, July 27, 1939) I saw actions which might suggest elements of his description of water courtship.

*Carbo* and *auritus* perform a flutter of a similar nature and from much the same posture as the flutter of the advertising display described for *penicillatus*. Kortlandt calls this "wing-flapping" (*Flügelklappen*). Lewis (1929:23-24) says, "the wings [of *auritus*] are slightly raised from the sides so that they lie in approximately the same plane as the back . . . and the manus with its primary feathers is jerked quickly forward and outward, only to fall back into place almost immediately and jerk again . . ." *Aristotelius* starts the display from a similar posture but there is no wing movement (Selous, 1901:166 and 1927:59). All four species cock their tails.

Important accessories to the display of *carbo* are the spot of bare orange colored skin beneath and posterior to the eye and the white patches of the head and flanks. The flank patches are especially revealed as the wings are flapped. Selous (1927:58) mentions the gaping of *aristotelius* which reveals the "brilliant gamboge" interior of the mouth. Apparently the orange gular pouch of *auritus* functions in the display of that species, although Lewis makes no reference to it as having a particularly striking quality. Townsend (1925:93) makes special mention of the blue of the gular pouch of *penicillatus* saying that it "would flash out with great brilliancy," and that "there was every appearance of the inflation or pushing out of the gular pouch during the display." He says further that "in one case, seen in good light, the gular pouch during the display appeared to lie in longitudinal folds. In this case the mouth was slightly open and vibrating, and the vibrations were communicated to the gular pouch and to the white plumes standing out from the sides of the neck." No doubt these vibrations refer to the well known palpitations of Pelecaniformes which may serve the various species as a cooling device. Lewis (1929:34), on the other hand, does not believe that such is always

the purpose of these quiverings in *auritus*. In the Brandt Cormorant, at least, there is no indication that they have any relation to display. Kortlandt (1940:408) says of *carbo*: "In warm weather one often sees the 'throat-pouch-fanning' . . . whereby the throat-pouch shakes and, by this means, the pharynx forces out warm exhalations" (translation). Michael (1935:37) compares the distention of the *penicillatus* pouch to the "puffing out" of the throat of *Sceloporus* lizards. However, I am not sure that the tone of blue is the same, if Michael meant to imply this. But the general similarity is suggestive. The figures in the Kortlandt paper (1940) illustrating various phases of the sexual display do not show the throat bulging outward as does that of *penicillatus*. The pouch of *carbo* is described in some sexual situations as being "stretched out straight" (Kortlandt, 1940:425, figs. 21, 22). But it is protruded angularly in threat displays (*op. cit.*, figs. 12 ff.) and by begging young (*op. cit.*, fig. 26). There is an angular protrusion of the throat, caused by depression of the hyoid apparatus, in the begging of young *auritus* (Lewis, 1929:51-52).

In the second part of its display analogous to the advertising of *penicillatus*, *carbo* throws the head backward but the bill instead of pointing upward is directed toward the tail. Then the head is brought slowly forward and back to the same position repeatedly; at this time the bird utters gurgling sounds ("das Gurgeln") (Kortlandt, 1940:423). In the third part ("dritte Phase") the head and neck are stretched forward and silently swung from side to side. *Carbo* makes no hammer-like strokes.

Reactions to this display by the opposite sex are of two kinds: (1) a stretching and ruffing out accompanied by a characteristic utterance; (2) a hopping all around and over the other member of the pair. This hopping is probably homologous to the "hop" of *penicillatus* but there is no bow and upward stretch and "the throat-sac is stretched out straight and the neck is presumably pumped up with air from the lungs" (Kortlandt, 1940:425). Kortlandt also says, "hopping is that expression-movement in particular through which the standing partner [male acting] makes known his desire for copulation." Possibly this function may be ascribed to the *penicillatus* hop, although it certainly occurs also in non-sexual situations. Selous (1901:166-167) describes a "great pompous hop" in *aristotelius*. Here also, apparently, the preliminary bow is missing. No hopping around or over the other member of the pair was noted in *penicillatus*.

*Carbo*, when mounting, "springs" upon the back of the prone bird, sometimes flapping the wings as it does so (Kortlandt, 1940:421). *Penicillatus* deliberately steps upon the back when performing such an act and has never been seen to beat its wings at this time.

Kortlandt describes threat displays of *carbo* analogous to those of *penicillatus*: "with feathers impressively ruffled, wings raised (almost like a swan), angularly forward projecting throat-sac" (1940:415). This is accompanied by a characteristic cry. There seems to be no head twisting. Kortlandt's phraseology, "Japanese wrestlers," in describing the way rivals grip bills and push and pull while fighting would apply well to *penicillatus*. Both species peck and bite fiercely and, in *carbo* at least, actually draw blood (Kortlandt, 1938:9). Selous (1927:70-71) describes a fight of this nature in *aristotelius*.

Pairs of all four species at the nest writhe and twist their necks together as part of the mutual display I have called "billing." Perhaps there is more nibbling at and clasping of each other's bills in *penicillatus* than in the other species. The focus of attention at the gular pouch in *penicillatus* is noteworthy; such focus does not seem to be mentioned for the other species.

*Identification of sex and the role of the sexes in display.*—Portielje (1927) and Haverschmidt (1933) state that the display of *carbo* ("Flugelklappen," "Gurgeln," and "dritte Phase") comparable to the advertising display of *penicillatus*, is done by

the females only. They called it a copulatory invitation and said that the males come and reply by stretching, ruffing out, and hopping.

Lewis shot an *auritus* while wing-flapping and found it to be a male. Haverschmidt thought Lewis was mistaken because *auritus* is closely related to *carbo*. Nevertheless Haverschmidt noted some reversals that he was unable to explain. Kortlandt, in his first paper (1938), said that either sex performs either display, called the birds the "sitting" and "standing partner," and said that coition could be effected with either bird mounting.

In the present study sex identification was made in the field by correlating the general body size and the length and depth of the bill with certain kinds of behavior. Measurements (in millimeters) of specimens of adult Brandt Cormorants (nearly all taken in central California) in the collections of the California Academy of Sciences and the Museum of Vertebrate Zoology revealed the following size differences:

	Maximum	Minimum	Average
Length of bill from gape			
20 females	98.9	88.5	92.75
26 males	108.2	89.6	101.33
Depth of bill			
18 females	10.8	9.1	10.10
26 males	13.8	10.6	11.74
Wing length			
22 females	276.	258.	270.00
27 males	305.	274.	291.22

Although these differences might seem too minute for field work, they proved helpful in the field when direct comparison could be made between the bills of members of a pair. The size differences were correlated with the following characteristics of behavior: (1) advertisers on stations were big billed; (2) the birds visiting them were small billed; (3) the big-billed birds usually mounted later in the cycle than the small-billed; (4) big-billed birds defended a territory, fought, brought most of the nesting material to the nest. Very occasionally it was impossible to distinguish a difference in bill sizes of members of a pair; in such event no data on them were used.

When the notes on 91 mountings were analyzed the following results were obtained:

	Small-billed bird mounts	Big-billed bird mounts
Coition probable	0	19
Coition doubtful	8	29
No coition	32	3
Total	40	51

Of course when the cloacae do not meet it is obvious that there is no coition; whereas it is almost impossible to make certain that it does occur. It was therefore concluded that the big-billed, advertising birds were males. All other displays, including both the upper and lower precoital postures and even mounting, are performed by both sexes.

In 1939 I reached the foregoing conclusions independently. In his paper of 1940 Kortlandt modified his earlier statement in regard to the roles of the sexes and says that in *carbo* the males alone perform the wing-flapping, except on rare occasions when a female might do it after pairing up, and that all other displays are entirely mutual, being done by both sexes. Advertising after pairing up is rare in *penicillatus* and on occasions when it has been observed and sex identification made the advertiser was a male.

Kortlandt finds that either sex may mount (as in *penicillatus*) with the important difference that in *carbo* the reversed position occurs "especially if the pair has been married for some time" (translation, 1940:421). He also says that "in the reversed



position the female less often seeks contact with the cloaca than does the male in normal copulation" (1940:429). In this latter respect his observations agree with mine. He continues by saying that this lack of cloaca seeking "is only a difference of intensity. Basically there is thus but a graduated distinction between the male and female sexuality in cormorants."

Kortlandt stresses the importance of voice difference in sex-recognition in *carbo* (the female has a particular utterance employed only in the breeding season). He also has found a difference in bill lengths, and in the width of the head, the males being larger as I had found in *penicillatus*. However, he remarked (in correspondence) that 5-10 per cent of his females have larger bills than their own mates.

Thus with the exception of the sexually different voices in *carbo*, and the fact that the swollen-necked stroke as well as the flutter is an exclusively male action in *penicillatus*, and that mountings with the female uppermost occur more frequently early in the cycle in *penicillatus*, rather than late (as implied by Kortlandt), the bisexual character of the behavior is apparently quite similar in the two species.

*Discussion.*—It is of course entirely possible that I have missed sounds made by *penicillatus* during sexual actions. If I have not, the most striking difference between this species and *carbo* is the distinct sounds made by the two sexes of the European Cormorant and the lack of any sounds made during these actions by *penicillatus*. Moreover, pairing-up is impeded in *carbo* when a bird has a "divergent" voice, although copulation is not (Kortlandt, 1940:430). Lewis (1929), also, records a very definite "song" uttered by *auritus* while wing-flapping.

At the La Jolla colony observations were made on advertising male Brandt Cormorants at close range, about 100 feet, and although the two types of call notes already described could be heard, one of them associated with threat display, no sound could be detected from advertisers. However, a variety of sounds uttered by several individuals of *Phalacrocorax auritus* perching at an even greater distance from me could be easily heard. One of these notes was undoubtedly that which Lewis (1929:61) calls "the 'cane-tube' croaking or rattling," because "it sounds like a rather rapid series of clicks, made in a hollow cylinder of cane or bamboo. It forms part of the male's courtship address, but is also used in other ways during the nesting season." From a distance of more than a hundred feet and under the same general surf conditions as at La Jolla, sounds uttered by a pair of Pelagic Cormorants (*Phalacrocorax pelagicus*) during displays have been heard by me.

Might it not be possible that in *penicillatus* voice has not been particularly evolved, display effects being achieved by striking posture and the brilliance of the pouch alone, whereas *carbo* has developed a striking pattern of plumage and posture, but particularly voice, and *auritus* perhaps has some degree of all three qualities, pattern, posture, and voice?

The male *auritus* selects both territory and nest site (Lewis, 1929:87). The female *carbo* goes from one wing-flapping male to another and, when a female remains, the male gets nesting material (the male, as in *penicillatus*, is the principal gatherer of material). But the male *carbo* also takes a "circular flight," always returning, however, to his own nest and never flying to other females (Kortlandt, 1940:431).

Noble, Wurm and Schmidt's (1938) description and illustration of the Night Heron's gaining "dominance" and "billing for dominance" suggests certain mutual display postures of the Brandt Cormorant. I am not sure, however, whether or not it would be correct to ascribe "dominance" reactions to the latter species.

Several writers have mentioned the importance of nesting material in the sexual cycle of various species. The material often serves some other purpose in addition to forming a structure to hold the eggs. When a Brandt Cormorant is stretched out in the

prone position of the lower precoital posture, very frequently it picks up and nibbles pieces of material. It seems probable that this should be considered a "substitute activity" as characterized by Lack (1941:429). Unpaired male Brandt Cormorants bring nesting material to their stations, place it there with the nesting-material ceremony and advertise over it. This activity of bringing material in phase I is functionless as far as constructing a nest is concerned, since the material never accrues because of pilfering. Thus the activity might be interpreted as of symbolic display, that is, in which an act normally playing some other part in behavior is introduced into display (Lack, 1940:173). But when a female remains to guard, a nest rapidly takes shape and what was an activity without function in phase I becomes functional if the pair becomes permanently mated and passes into phase III.

Since the display of the male in bringing material to the nest is essentially the same in phase I, before he is paired up, as it is in phase II when a female enters into the ceremony, the use of the term "symbolic display" applied to it in phase I may seem questionable. In phase II the manner of gathering and "presenting" the material remains the same and it is the external situation which has changed. On the other hand, when we consider the many times that "precoital postures" do not lead directly to coition, it may be that the prone position assumed by either sex is a symbolic display in the sense meant by Portielje (1927). This writer refers to various actions of *carbo* as symbolic. Among these he interprets wing-flapping as symbolic of copulation. Kortlandt (1940:423) comments that "it is remarkable that an almost exclusively male behavior [wing-flapping] should arise from the copulation position of the lower bird, that is to say from a predominantly female position!" As a female approaches an advertising male *penicillatus* the latter gradually merges the swollen-necked strokes into the thin-necked thrustings of the lower precoital posture (see above). Appreciating these actions together with the general bisexual behavior of both *penicillatus* and *carbo*, perhaps the phrase "reversed symbolic display" has meaning.

Reverse mounting has been described for the Great Crested Grebe (Huxley, 1914:505), the Moorhen (Selous, 1902:197), and the domestic pigeon (Whitman, 1919:97). I have witnessed it also in Band-tailed Pigeons (*Columba fasciata*) in the wild state (unpublished observation). In discussing the reverse mounting of the grebe, Huxley suggests the possibility of genital products passing either way. In the case of the Brandt Cormorant it does not seem necessary to postulate this, as it seems fairly well indicated that no cloacal contact is made when the female mounts.

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#### SUMMARY

This study of the Brandt Cormorant (*Phalacrocorax penicillatus*) was made on the coasts of Marin, Monterey, and San Diego counties, California, in the breeding seasons from 1933 through 1940.

Display of three types was observed: (1) advertising performed by males and responded to by females, (2) mutual and bisexual displays performed by both sexes, and

(3) threat displays by both sexes. In many of these the distended gular pouch is conspicuous.

The sexual cycle may be divided into three phases: (I) advertising display by males during which the females visit them, (II) pairing-up, temporary or permanent, attended by mutual displays, (III) egg laying and rearing of young.

Females move about on the crowded rock occupied by the colony, passing from one advertising male to another, sometimes remaining with each for a few minutes only. Males do not advertise when females are with them. When the pairs, now in phase II, are together they perform a series of mutual displays. Immediately upon the female's arrival the *male* assumes the lower pre-coital, female-like posture, the female the upper pre-coital, male-like posture. The female may even mount and behave very much like a male. Reversal, with the male mounting, may occur immediately following this or not until later. It seems well indicated that insemination occurs only with the male uppermost.

Males gather most of the nesting material; both sexes arrange it. The material is gathered by the male even before a female is present. Threat displays are used to guard territory and nesting material. Prolonged fights have been observed.

This colonial bird has an individual territory, although the area defended is only a few square feet around the nest. The males advertise at this place and keep other males away; the females come there for copulation and the nest is built there.

Reverse mounting has been noted by other observers for other species. Recent work by Kortlandt on *Phalacrocorax carbo* in Holland records "wing-flapping" by males only, while all other displays and mounting are performed by both sexes, as in *P. penicillatus*. In *P. carbo* there is an important sex difference in voice not noted for *penicillatus*.

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*Carmel, California, December 1, 1941.*