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BEHAVIOUR OF THE RED-FOOTED CORMORANT (*Phalacrocorax gaimardi*)

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ABSTRACT

The pair bonding, recognition, defence, and courtship displays of the Red-footed Cormorant are described for the first time. Similarity in displays reinforces van Tets' contention that this species is a member of the *Stictocarbo* group. Its closest relatives seem to be the spotted shags of New Zealand waters and the European Shag. The Atlantic population of the Red-footed Cormorant is small and isolated, and it may differ from the much larger population along the Pacific coast by various behavioural and ecological features.

INTRODUCTION

One of the least known cormorants of the world is the Red-footed Cormorant (*Phalacrocorax gaimardi*), which breeds along the Pacific coastlines of Peru and Chile from near the equator to about 45°S (see Murphy 1936, Koepcke & Koepcke 1953, Johnson 1965, and Jehl & Rumboll 1976). A small, isolated population on the Atlantic coast is restricted to a small area of the Patagonian coastline (Doello-Jurado 1917, Zapata 1967) near Puerto Deseado, Santa Cruz Province, Argentina (40°S, 80°W). The largest colony in Argentina is located on the cliffs of Ilsa Elena (200 pairs) near the mouth of Ria Deseado, with an equal number distributed in four other locations 5-10 km farther upriver. About 70 km north of Puerto Deseado, a small colony of about 50 pairs breeds at Cabo Blanco; about 20 km south of Puerto Deseado, a small group of about 30 pairs breeds on Roca Olorosa in Bahia Oso Marino.

This population apparently does not migrate far in the post-breeding season, and extralimital transients are rare. Adults and juveniles seem to keep close to shore, and do not move more than about 300 km to the north and south (Jehl & Rumboll 1976). Although individuals have been seen

occasionally in the Straits of Magellan (Ogilvie-Grant 1898, Murphy 1936), no intervening colonies have been found in Tierra del Fuego, prompting many researchers to confer subspecific status on the Atlantic (*P. gaimardi ciniger*) and Pacific (*P. g. gaimardi*) populations. Humphrey & Bridge (1970) gave differences between the populations in culmen length, plumage, and bill colour, but because of small samples and other problems, it is difficult to tell if these population differences are real.

As part of a larger study of the biogeographic variation of this species throughout southern South America, I observed breeding behaviours in the Atlantic population in the late austral spring of 1985. These data help to show its behavioural affinities and phylogenetic relationships with the other members of the family.

METHODS

I observed courtship behaviour, pair bonding, and other related activities of Red-footed Cormorants in a colony of about 200 pairs on Isla Elena in Ria Deseado near Puerto Deseado, Argentina, during late January and February 1985. (See Zapata 1967 for a description of the colonies and de la Pena 1980 for descriptions of nests and nest sites.) Observation periods ranged from 1 h to 5 h; the total amount of time spent observing behaviour in the colony was equivalent to about 5000 bird-hours. When I began, breeding was still underway, but pairs were still forming and nests were still being initiated throughout the observation period. I observed courtship sequences of different lengths, about half ending in mounting. As I was unable to follow the progress of pairs or nests past the end of February, the courtship behaviour I observed may not represent the full range that may be associated with pairs that mate earlier in the season.

I observed courting pairs through 7x50 binoculars or a 45x telescope; I recorded behavioural acts in shorthand and on 35 mm slide film. I sexed birds by relative body size and behaviour, but I was confident in identification only by the position of individuals during mountings, and by observing certain behavioural displays traced to males or females. Behavioural terminology follows van Tets (1965), except where noted.

BEHAVIOUR

Locomotion

Adult Red-footed Cormorants moved rarely on land. Flat tops of rocks and islets were favoured resting spots (see also Coker 1919). On islets in the mouth of Ria Deseado, small flocks of juveniles and adults sometimes stood motionless on the sandy beaches. When approached on their resting areas by other cormorants (King and Imperial Blue-eyed Shags, *P. albiventer* and *P. atriceps*; Olivaceous and Magellanic Cormorants, *P. olivaceus* and *P. magellanicus*), adults would always take off and fly rather than shuffle two or three steps to the side; juveniles however seemed more likely to move away than fly.

While on the nest, adults moved around the rim by shuffling, never lifting the base of the foot higher than the intertarsal joint. Red-footed Cormorants use a very modified form of Stepping to move around the nest

rim when changing incubation bouts. The bird initiating the change brings its head down on its breast with its neck held erect, and it steps around the nest rim by deliberately lifting its feet above the intertarsal joint. Stepping is used by other cormorants as an appeasement display when moving through the colony and near neighbours (pers. obs.).

Wing-spreading

I did not see this behaviour used by any adults or juveniles.

Nest-building

Red-footed Cormorants build their nests on sheer rock walls beneath overhanging rock ledges without any ground approach (see Fig. 43 in Koepcke 1953). For example, the small colony on Roca Olorosa in Bahía Oso Marino was 20 m above the level of the sea on the nearly vertical basaltic cliff faces. Unlike in the neighbouring Magellanic Cormorant colonies on Isla Chata, the birds could approach these nests only by air: once out of the nest, Red-footed Cormorant juveniles had no way to return except to fly.

Take-off

This display is considered to encompass three stages: Look, Crouch, Leap (van Tets 1965). When leaving the nest, a Red-footed Cormorant moves to the rim and Looks by holding its neck motionless over its shoulder with its body held upright, gular depressed by the hyoid, and its bill pointed away from the cliff (see Fig. 1a). This is very similar to the Twisting and Pointing display described by van Tets (1965) for the Pelagic (*P. pelagicus*) and Red-faced Cormorants (*P. urile*). The bird does a distinct Crouch, often repeatedly, by dropping its breast and raising its abdomen; the gular pouch is depressed by the hyoid and the bill is kept closed. The Leap is always horizontal and away from the nest, never up into the air. As soon as it leaves the nest, the bird utters a distinctive clear, warbling whistle which rises, then quickly falls in pitch. Coker (1919) likened this call to sparrow chirps, and Johnson (1965) described it as high-pitched and squealing. With only minor exceptions in calls and positions, these displays are quite similar to those reported for the European Shag, *P. aristotelis* (Snow 1963), and the Pelagic and Red-faced Cormorants (van Tets 1965, Dick pers. comm., Siegel-Causey, pers. obs.).

Landing

When landing at the nest, a Red-footed Cormorant flies up from below with its neck and head held 45°-60° from the horizontal and its bill wide open. As it approaches the cliff face, it brings its feet up in front of its body. Within about 30 m of the cliff, it gives a call similar to the Take-off call (Kink-throating, van Tets pers. comm.) but stops calling abruptly once on the ground. Immediately after landing, it extends its neck over the nest rim (or over the incubating bird), its neck feathers erected and the gular depressed by the hyoid (Post-landing posture of van Tets 1965). This pose is held motionless for a few seconds. I heard no post-landing vocalisations. The bird already on the nest would almost always lift its breast from the ground, drop its bill to the nest (Nest-indicating), and Nest-worry. Both adults would then Neck-twine and Allopreen (see Fig. 2). These post-landing behaviours resemble those used by the European Shag (Snow 1963) and other species of cormorants and shags (van Tets, pers. comm.).

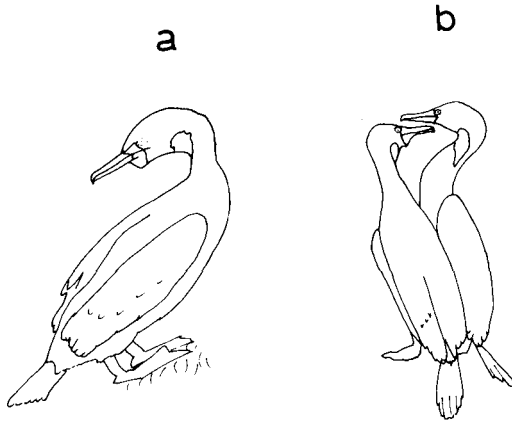


FIGURE 1 — Communication behaviour of the Red-footed Cormorant. (a) The Look phase of the Take-off display. (b) Throat-clicking during courtship. Note that the male on the left is Kink-throating. Figures are redrawn from photographs.

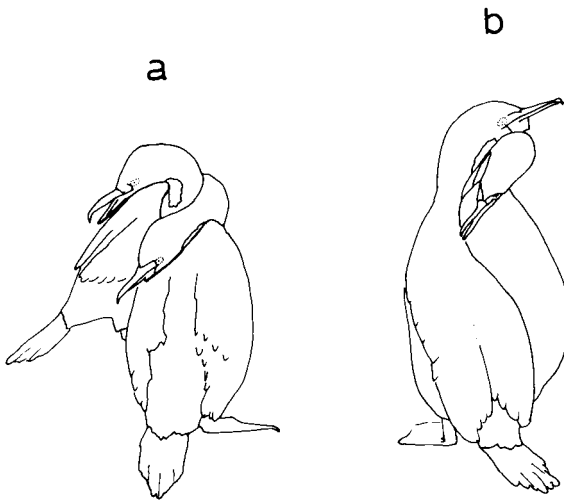


FIGURE 2 — Pairing displays of the Red-footed Cormorant. (a) Neck-twining and (b) Allopreening. Figures are redrawn from photographs that were part of a sequence observed between the same pair of birds.

Hop

The Hop, which is distinctive to gannets, boobies, darters, shags and cormorants, appears to be a symbolic, abbreviated flight (van Tets 1965) in that it comprises elements of the Take-off and Landing displays. For Red-footed Cormorants, the Hop display is an adjunct to the development of the pair bond. Males and females perform the display similarly. First, the head is pointed downwards with the neck stiffly arched towards the feet, the bill closed and the gular depressed by the hyoid, and the wings are slightly opened near the body. The bird makes a short jump upwards by making a sharp push with its feet. The feet leave the ground unevenly, often only one foot clearing the nest or ground. After the Hop, the bird does a Post-landing display, often very quickly.

At the beginning of the season, both sexes use the Hop frequently after landing and before take-off, before allopreening bouts, before and after mounting, to initiate nest relief, and in general, as a form of "punctuation" between other courtship displays. Later in the season, it seems to be used mainly before leaving the nest and at incubation changeovers.

Threat

Perhaps because the breeding season was well established, I saw little aggression among the Red-footed Cormorants. The calm of the colony was seldom broken by squabbling neighbours or by parents defending their nests, very similar to that observed in a Pelagic Cormorant colony (Siegel-Causey & Hunt 1981).

The usual threat display I observed consisted of very vague, lateral quivers of the head with the neck unextended; it was terminated by Nest-indicating. This display was used mostly as a primary threat, only rarely leading into other forms. The much rarer Thrust, presumably a higher-intensity threat, was used only in conjunction with the first display. If the defender was not already sitting down on the nest, it would drop its breast down to the nest rim and thrust its open bill weakly at the offender. As in the first display, Thrusting was followed by Nest-indicating. This cycle would often be repeated many times, but two or three repetitions were usually enough to drive away errant Red-footed Cormorants.

These threat displays resemble those described for the European Shag (Snow 1963) and other species of cormorants (van Tets, pers. comm.) but differ by their very low intensity. A derived form of the Thrust display, in which a weak Thrust and nest touch were combined into a single action, was seen directed by nesting adults at loafing juveniles and encroaching neighbours. It rarely was repeated and seemed to be used more in the context of site ownership and less as an agonistic display. I did not see Snaking used, although this display of waving the extended head laterally with opened bill at the invader is commonly used by other cormorants in defence (Siegel-Causey 1978). I also heard no vocalisations used with any agonistic display.

Male advertising

The displays used only by males during courtship were Darting and Throwback. In Darting, the male starts with his body semi-erect and wings closed. From this position he draws his head horizontally back and forth along the midline with small stiff movements, occasionally making a faint clicking noise in rhythm with the forward movement.

At the most forward position, he opens his bill slightly and displays the bright red gape. Darting was often repeated many times, but occasionally was interrupted by looking around to the side. This is similar to that observed in the Pelagic and Red-faced Cormorants (Dick, pers. comm.; Siegel-Causey, pers. obs.).

The male followed Darting with the Throwback, usually as the female approached. When both were at the nest, the male would Throwback after about four to five Dartings. In Throwback, the male stretches his neck along his back, points his slightly opened beak back towards the tail and rhythmically Kink-throats. The Throwback position is usually held for 3-5 seconds with the wings held tightly to the body. No calls are made. Occasionally, Throwbacks were combined with a single flip of the wings, similar to Wing-flapping of the European Shag (Snow 1963), Pelagic and Red-faced Cormorants (Snow 1963, Dick pers. comm., Siegel-Causey pers. obs.), in that the tips of the folded wings were moved sharply away from the body and brought immediately back. Although I often observed this display, I was unable to discern any pattern of its use by Red-footed Cormorants.

Recognition and pairing displays

Male Red-footed Cormorants use a distinctive display to greet incoming females to the nest and to indicate nest relief. The neck is laid along the back, as in the Throwback display, and the bill is slightly opened, pointed back towards the tail, and then rolled quickly from side to side a few times. See Fig. 3. A single click is uttered on each roll. Except for the position of the neck, this behaviour appears similar to Gaping in the European Shag (Snow 1963). Both sexes of the European Shag use Gaping for recognition, but I observed only the male Red-footed Cormorant do it.

Throat-clicking is characteristic of Red-footed Cormorants returning to the nest, especially when bringing nest material, and often after copulation. The standing bird holds its body and neck semi-erect and its head horizontally over the back and neck of the sitting bird; its beak is closed, and its wings and plumage are close to the body (Fig. 1b). Kink-throating is done in conjunction with the emission of rhythmic clicks. After a few seconds of clicking, the bird slowly relaxes. Throat-clicking is often alternated with mutual Nest-worrying (van Tets 1965), which is a display where both partners make lateral quivering movements with their bills on or near the nest. Nest-worrying seemed to be used by Red-footed Cormorants in many contexts, for both sexes used this movement in greeting, as part of other recognition and courtship displays, and even between threat displays.

The most distinctive pair-bonding behaviour of the Red-footed Cormorant is Allopreening. It is initiated by either sex, generally by means of a behaviour similar to Bill-waving described for Blue-eyed shags (Siegel-Causey, in press). The initiator opens its beak about 45° and waves it near the face of the other bird horizontally so that it passes around the second bird's unmoving closed beak. Both then Neck-twine and gently nibble each other's long white neck patches. After 10-15 s, Allopreening stops, but usually it is repeated without Throat-clicking or Bill-waving. Repeated bouts last up to 4 minutes without either bird changing position or behaviour.

Although Bowing is a common behaviour in the European Shag and Pelagic Cormorant, I seldom saw it and could see little pattern in its use. All of these recognition displays appear similar in form to those of the European Shag (Snow 1963) and the Pelagic and Red-faced Cormorants (Dick pers. comm., Siegel-Causey pers. obs.).

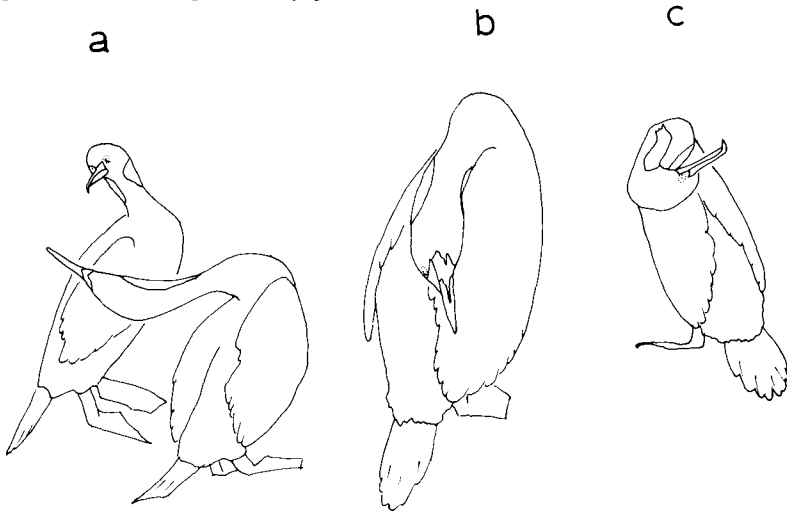


FIGURE 3 — The Gaping display of the Red-footed Cormorant. (a) Beginning, (b) rolling, and (c) ending phases of the display. Figures redrawn from photographs.

Courtship

Males invite prospective females to approach by Darting and Throwbacks, rarely by Wing-flipping. The female responds by sidling closer to the male and Hopping. The male then Throwbacks only, the female responding by Hopping and Throat-clicking. Intensive bouts of Allopreening follow, the male occasionally doing Throwbacks, rarely Wing-flipping. Mounting is usually preceded and followed by the male Throat-clicking and the female Nest-worrying. Although reverse mountings have been reported in cormorants (see Bernstein & Maxson 1982), I have not seen it in the Red-footed Cormorant. The cycle of Allopreening, Throat-clicking, and Mounting persists over a few days, gradually being replaced by nest building and pair-bond displays. In its barest outlines, this sequence of courtship behaviours matches that described for the European Shag (Snow 1963).

DISCUSSION

Murphy (1936) summarised the evidence to that date on the affinities of the Red-footed Cormorant, and identified the spotted shags (*P. punctatus* and *P. featherstoni*) as its closest relatives, apparently on the grounds of general similarity and proximity. At the same time, von Boetticher (1935), struck by the fact that only the Red-footed Cormorant and the Great Cormorant

(*P. carbo*) have 14 tail feathers, introduced a new subgenus *Poikilocarbo* for the Red-footed Cormorant and retained the latter species in the subgenus *Phalacrocorax*. As little other than the number of tail feathers was presented for justification, and such monotypic groupings do not help in assessing relationship, this work was ignored by systematists.

In van Tets' (1974) reorganisation of the Phalacrocoracidae, the Red-footed Cormorant is referred on behavioural evidence to the subgenus *Stictocarbo* along with the spotted shags and the Magellanic, Pelagic, and Red-faced Cormorants. Only partial ethograms of the spotted shags are available for comparison (van Tets, pers. comm.), but other evidence from skeletal morphology (Siegel-Causey, pers. obs.) indicates that they and the European Shag are the closest relatives of the Red-footed Cormorant. I expect that when the behaviours of the spotted shags are better known, the similarities between the spotted shags and Red-footed Cormorant will be closer than those observed between it and the European Shag.

Whether Atlantic and Pacific populations of Red-footed Cormorants differ in behaviour is also not known. Although not very well described, the nest-site selection and nest-building behaviours, certain vocalisations, and the courtship display of Bill-waving appear similar (Doello-Jurado 1917, Coker 1919, Murphy 1936, Koepcke & Koepcke 1953, Johnson 1965, Zapata 1967). The foods eaten, the size of the feeding and resting flocks, the distances of winter dispersion, and the strength of the ties to a particular colony or nest site appear to be quite divergent between Atlantic and Pacific populations (Coker 1919, Bullock 1935, Murphy 1936, Olrog 1948, Johnson 1965, Markham 1971, Jehl & Rumboll 1976). The Red-footed Cormorants of the Atlantic coast are apparently more sedentary and more social than those of the Pacific coast. How far these differences are due to genetic divergence or to environmental differences between coastlines is not known.

The species of the *Stictocarbo* group so far studied are, by their behaviour, clearly more closely related to one another than to other cormorants. Among these cormorants, there appears to be two distinct behavioural groups: the Magellanic, Pelagic, and Red-faced Cormorants; and the European Shag, Red-footed Cormorant and, provisionally, the spotted shags.

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SHORT NOTE

Notes on the feeding habits of the New Zealand Dotterel

Buller wrote in 1873 (*A History of the Birds of New Zealand*) that the New Zealand Dotterel (*Charadrius obscurus*) feeds mainly on small crustacea, mollusca and sandhoppers. In 1888 (second edition) he added insects to this list. Some interesting feeding habits and many specific items of prey have been recorded since then, though most works just quote Buller.

Hutton & Drummond (1923, *Animals of New Zealand*, 4th ed.) specified craneflies and grasshoppers as being important food items. In 1963 McKenzie & Sibson (*Notornis* 10: 350) recorded the taking of a cricket and a moth. New Zealand Dotterels have been seen feeding in rock pools and in grassland, tossing aside pieces of dry cowdung, by Edgar (*Notornis*, 16: 86) and worms are mentioned as part of their diet by Power (1971, *Waders in New Zealand*). Raking soft sand to flush sandhoppers was described by Jones (*Notornis* 22: 324), who also witnessed foot-trembling by New Zealand Dotterels (*Notornis* 31: 208). Heather watched New Zealand Dotterels on Great Barrier Island feeding on the little black mussel (*Xenostrobus pulex*)