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THE COURTSHIP BEHAVIOR AND MIXED-SPECIES PAIRING OF KING AND IMPERIAL BLUE-EYED SHAGS (*PHALACROCORAX ALBIVENTER* AND *P. ATRICEPS*)

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ABSTRACT.—I compared the courtship behavior of King and Imperial Blue-eyed shags (*Phalacrocorax albiventer* and *P. atriceps*) for similarity and assessed their potential as a behavioral isolating mechanism between the two species. I could detect no differences in form or sequence of behavioral patterns, although there were some minor distinctions between forms. Observations were made near the end of the breeding season and may represent only the postbreeding behavior. I describe several new displays for King and Imperial shags, and contrast them with those known for the closely-related Antarctic Blue-eyed Shags (*P. atriceps bransfieldensis*). The courtship behavior of mixed-species pairs was nearly identical to conspecific pairs, and was difficult to distinguish. The observations do not support the existence of behavioral isolation between King and Imperial shags, but do support the contention that King Shags in Patagonia are color morphs of Imperial Blue-eyed Shags. *Received 15 Apr. 1986, accepted 10 July 1986.*

The specific status of the King Shag (*Phalacrocorax albiventer*) and its relationship with the Imperial Blue-eyed Shag (*P. atriceps*) is not well understood (Williams and Burger 1979, Brothers 1985). These two southern hemisphere cormorants are quite similar in appearance, differing only in external characters by plumage patterns of the cheeks and dorsum (Murphy 1936, Hellmayr and Conover 1948, Watson 1975). Both species breed along the Fuego-Patagonian coast, frequently within the same colony (Behn et al. 1955, Devillers and Terschuren 1978). Devillers and Terschuren concluded after extensive field observations that between 15% and 20% of the members of sympatric populations were intermediate in plumage characters, that mixed-species pairs exist, and that the King Shag should, at best, be considered as a subspecies of the Imperial Blue-eyed Shag. Much of their evidence, however, relied exclusively upon photographs and field observations of crowded colonies where juveniles and prebreeding adults could be confused with mated pairs. Rasmussen (1986) reported that Imperial Shags in juvenal plumage often superficially resemble King Shags, and such photographs may possibly represent experimental pairings between adults and juveniles, events that occur occa-

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sionally in cormorant colonies during the latter half of the nesting season (Lewis 1929).

One approach to elucidating this problem is to examine the courtship behavior of each species, and investigate in more detail the circumstances of mixed-species pairs. If these two forms are distinct species, there should be behavioral isolating mechanisms in zones of sympatry (see Bernstein and Gordon 1979). Here, I compare the courtship behavior of conspecific and heterospecific pairs of King and Imperial Blue-eyed shags and test for similarity.

METHODS

In late January 1985, I observed a colony of about 55 pairs of King Shags on Isla Escobar near Puerto Melo, Provincia de Chubut, Argentina (see Livezey et al. 1985 for a description of the area). During February 1985, I observed both King and Imperial shags at a staging area on Roca Foca and Isla de Cañadon del Puerto near Puerto Deseado, Provincia de Santa Cruz, Argentina (see Zapata 1967 for details). Both species breed on nearby Isla Chata, Bahia Oso Marino, in a colony estimated at 5000–10,000 nests, 80% of which were Imperial Blue-eyed Shags; the remainder were King Shags (Devillers and Terschuren 1978). I used 7 × 50 binoculars and a 45× telescope to observe courting pairs. I recorded behavioral acts in shorthand and on 35 mm slide film. I sexed birds by relative bill size and behavior (see Bernstein and Maxson 1982). Observation periods ranged from 1 to 5 h; the total amount of time spent observing behavior was equivalent to about 9000 bird-h. When I began, breeding was still underway, but all of these observations were made late in the breeding season. Thus, the courtship behavior I observed may not represent the full range associated with pairs mating earlier in the season.

As the ancestry of hybrids was unknown, I used only courtship sequences from conspecific and heterospecific pairs of King and Imperial Blue-eyed shags. Display terminology follows van Tets (1965) except where noted. Bernstein and Maxson (1982) described the behavior and habits of a closely related form, the Antarctic Blue-eyed Shag (*P. atriceps bransfieldensis*). I have relied upon their descriptions where possible and discuss only those displays not described there.

BEHAVIOR

Take-off from land.—Departure from the nest or colony has the potential for disturbing neighbors and alarming the remaining mate and chicks. To reduce these problems, most cormorants use a ritualized display of three phases: Look, Crouch, and Leap (van Tets 1965). Bernstein and Maxson (1982) were unable to see the Crouch phase in Antarctic Blue-eyed Shags, but both King and Imperial shags I watched always employed a distinct Crouch before the Leap. In this phase the breast is dropped and the wings are partly opened; the Look and Leap phases do not differ substantially from that of other cormorants (see fig. 7 in van Tets 1965).

Hop.—This display is distinguished from normal locomotion by its ritualized slowness and in that the head and neck are pointed down toward the feet (see Fig. 10 in van Tets 1965). Although I observed this display

in both King and Imperial shags, Bernstein and Maxson (1982) did not observe it in the Antarctic Blue-eyed Shag.

Kink-throating.—This distinctive display is used by many cormorant species before landing. The hyoid is depressed forward, greatly enlarging the gular pouch, and is often accompanied by slight lateral headwaving (see Fig. 37 in van Tets 1965). Expansion of the gular pouch by the hyoid occurs in many contexts (during courtship, before take-off, in pair-recognition, etc.), and may not always be a distinct display. Instead, it may be employed as a behavioral adjunct by enabling the yellow gular pouch to be displayed as a visual signal. Both species always employed it when approaching their nests and about 60% of the time when landing near small groups of congeners. I saw it only about 10% of the time when the shags landed alone. Bernstein and Maxson (1982) did not see Kink-throating used during landing by the Antarctic Blue-eyed Shag, but this may have been a result of observational problems they encountered (Bernstein, pers. comm.). I was unable to detect any difference between King and Imperial shags in their use of Kink-throating before landing or during courtship.

Threatening.—King and Imperial shags used several displays in defense of their nest and its contents. When intruders were farthest from the nest, the most common display used was Snaking, a characteristic display of cormorants where the gaping bill is waved deliberately, often with the neck fully extended (Siegel-Causey 1978). When intruders came closer or were not deterred by Snaking, they used Thrusting (Siegel-Causey 1978), a rarer display. In this display, the head and neck are quickly extended at the intruder with the bill gaped and then retracted backwards. This threat was often repeated quickly 5–6 times by the defenders before subsiding into Snaking or motionless staring. Another display, Nest-indication, was given along with Snaking and Thrusting, possibly as redirected aggression. Bernstein and Maxson (1982) observed only Snaking in the Antarctic Blue-eyed Shag and did not see Nest-indication used during threats or fighting. Most other species of cormorants studied (van Tets 1965, Berry 1976, Siegel-Causey 1978) apparently use Nest-indication as a mild threat and to indicate site ownership. I detected no differences in threat behavior between King and Imperial shags off the breeding colony; I did not collect sufficient data for comparisons of defense behavior by either shag when in the breeding colony.

Male advertising.—Bernstein and Maxson (1982) described the male advertising display, Gargling, of Antarctic Blue-eyed Shags. The only difference I observed in King and Imperial Blue-eyed shags was that they rolled their head once from side-to-side at full Throwback position in 69% of the observations. Antarctic Blue-eyed Shags only occasionally did this (Bernstein, pers. comm.). This appears to be similar to what is de-

scribed as Gaping in the Great Cormorant (*P. carbo*) (see Fig. 26 in van Tets 1965), which is a bisexual recognition display. I never observed this movement in female King or Imperial shags, and males employed it only in conjunction with Gargling. Because of this high association with Gargling, I doubt that it constitutes a distinct display in either species. King Shags seemed to Gape more often (71% of observations) than Imperial Shags (56%) when at full Throwback, but I saw no differences in form between the species.

Recognition and pairbonding.—King and Imperial Blue-eyed shags use various displays in recognition and pairbonding. Throat-clicking (Snow 1963, fig. 3b in Bernstein and Maxson 1982) was employed in many circumstances ranging from nest relief to maintenance of the pairbond. Although Bernstein and Maxson (1982) assigned different roles to each sex in Throat-clicking in the Antarctic Blue-eyed Shag, I saw no sexual differences in performance for either King or Imperial shags, nor could I see any differences in form between species.

A movement similar to Throat-clicking was employed only in courtship, usually preceding and following copulation. The female faced the male (unlike in Throat-clicking where the pair is side-by-side), repeatedly nibbled or bit the tip of the male's bill ("Bill-biting"), and waved her open beak. The male responded by remaining motionless or initiating another pairing display such as Allopreening or Head-wagging (see fig. 3a in Bernstein and Maxson 1982).

Pointing and Darting.—Although Bernstein and Maxson (1982) never observed these displays in the Antarctic Blue-eyed Shag, pointing and darting were among the most common recognition displays employed by King and Imperial Blue-eyed shags. In Pointing, the neck, head, and closed bill were stretched forward and upward, with neck and head feathers erected (see fig. 29 in van Tets 1965). In the context of a recognition display, it always was done very deliberately by either sex on the nest. It was held for 1–2 sec, and was followed by Nest-indication. In other cases, it was combined with Darting as a courting display, usually by the male standing or slightly crouching. I saw no intra- or interspecific differences in Pointing.

Both shags Darted by retracting their head and folding their neck medially over the back with their bill kept forwards. The bill was then moved from side-to-side. This display was repeated rapidly 2–5 times and then the cycle of Pointing-Darting started again. After 3–4 cycles, the male terminated the action with a modified Pointing display which differed by the mandible moved to curve upwards at the tip, held for about 2 sec. King and Imperial Blue-eyed shags performed the display similarly, differing only in the number of cycles (Kolmogorov-Smirnov Two-sample test, $D = 0.57$, $P < 0.01$) (Table 1).

TABLE 1

DURATION IN CYCLES OF THE POINTING/DARTING DISPLAY BY MALE IMPERIAL AND KING SHAGS[a]

Number of cycles	Imperial Shag	King Shag
1	0	3
2	1	5
3	5	14
4	12	2
5	6	2
6	1	1
7	5	1

[a] Only displays that were followed by the arrival of a female were counted.

The male, if alone, self-preened after Pointing-Darting in 86% of the observations, most often at the white alar bar or breast feathers. If done with a partner, mutual Allopreening, directed mostly towards the sides of the neck, occurred 95% of the time. I saw no difference between King and Imperial shags in self-preening behavior (Kolmogorov-Smirnov Two-sample test, $P > 0.10$) (Table 2) or Allopreening ($P > 0.10$) (Table 3). That males tended to preen their white alar bars after displaying strongly suggests a signal value for this display. It may have been derived from simple allopreening (both sexes preen their white alar bars), and later used for initiating and maintaining the pairbond.

MIXED-SPECIES PAIRS AND COURTSHIP SEQUENCES

Devillers and Terschuren (1978) reported a small number of mixed-species pairs allopreening and guarding nests and chicks at sites along the

TABLE 2

PRIMARY SITES OF SELF-PREENING AT THE CONCLUSION OF THE POINTING/DARTING DISPLAY BY MALE IMPERIAL AND KING SHAGS[a]

Preening site	Imperial Shag	King Shag
Neck	2	3
Breast	4	2
Abdomen	0	1
Upper wing	2	1
Alar bar	17	21
Back	1	0
Crissum	1	1

[a] A primary site was the first body area continuously preened after the display.

TABLE 3

PRIMARY SITES OF ALLOPREENING AT THE CONCLUSION OF THE POINTING-DARTING DISPLAY BY IMPERIAL AND KING SHAGS[a]

Preening site	Pairing[b]			
	Imperial × Imperial (N = 30)	King × King (N = 33)	Imperial × King (N = 7)	King × Imperial (N = 23)
Neck	11	13	4	10
Breast	7	5	1	5
Abdomen	0	1	0	0
Upper wing	2	1	0	1
Alar bar	8	11	2	9
Back	1	1	0	1
Crissum	1	1	0	3

[a] A primary site was the first body area continuously preened by the male after the display.
[b] The first species in the pairing caption represents the male.

Fuego-Patagonian coastline. At various sites on or near Puerto Deseado used by courting King and Imperial Blue-eyed shags from the nearby breeding colony on Isla Chata (see Devillers and Terschuren 1978 for details of the colony), mixed-species pairs constituted about 8% of the 451 pairs observed. Male King and female Imperial courting pairs comprised two-thirds (N = 23) of these pairs. I saw no differences in the forms of courtship and recognition displays among any of the conspecific and heterospecific pairings. If a behavioral isolating mechanism does exist, it must instead be a difference in courtship sequence, rather than one involving different displays.

To examine the courtship sequences of each class of pairings, I accumulated male-to-female and female-to-male behavioral dyads for each courtship sequence that ended in mounting. I constructed contingency tables using the dyadic frequencies, and from them constructed conditional probabilities of the various male–female and female–male transitions. Transitions occurring most frequently in each pairing are in Fig. 1. Because of small sample sizes and the unknown applicability to courtship patterns used early in the breeding season, I was unable to test for higher-order patterns or gender differences.

There are no differences among courtship sequences used by hetero- and conspecific pairs of King and Imperial Blue-eyed shags (Hilton's G test: 1a–1b, $P > 0.20$; 1a–1c, $P > 0.10$; 1a–1d, $P > 0.10$; 1b–1c, $P > 0.10$; 1b–1d, $P > 0.25$; 1c–1d, $P > 0.10$) (Fig. 1). There were some qualitative distinctions between conspecific pairs of King and Imperial Blue-eyed shags: King Shag males often initiated Head-wagging after a female began Throat-clicking (Fig. 1a), and Imperial Blue-eyed Shag females

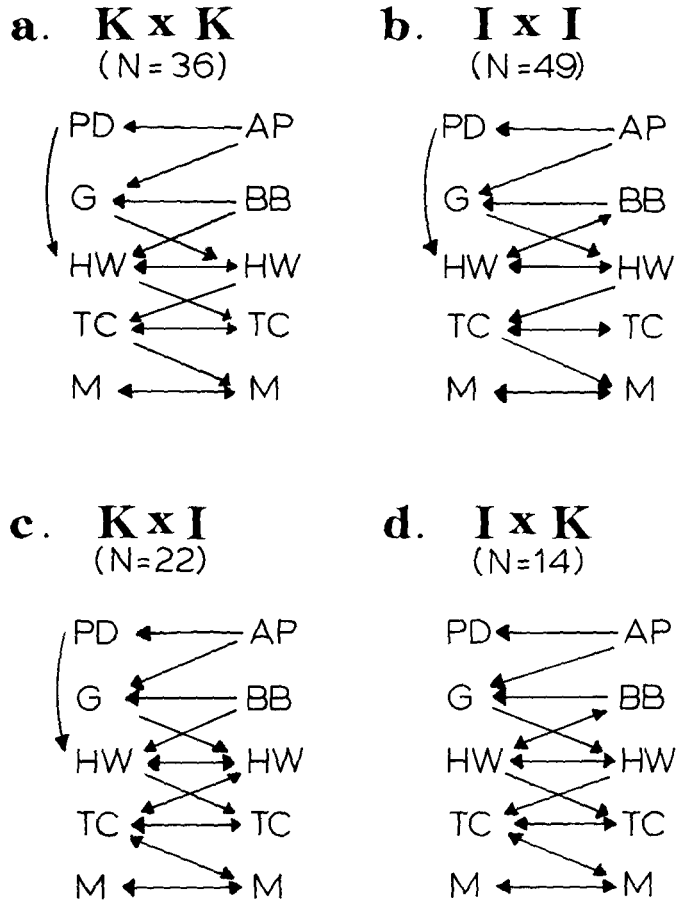

FIG. 1. Sequence diagrams for the courtship behavior of King and Imperial Blue-eyed shags. Sequence captions are male species × female species: (a) King × King, (b) Imperial × Imperial, (c) King × Imperial, (d) Imperial × King. Sample sizes are given in parentheses. Behavior sequences for each sex run from top to bottom in each column; interaction directions are indicated by arrows. AP: Approach and head alignment; BB: Bill-biting; G: Gargling; HW: Head-wagging; M: Mounting; PD: Pointing-Darting; TC: Throat-clicking.

often continued Bill-biting after males initiated Head-wagging (Fig. 1b). Mixed-species pairs showed the influence of both partners, and the only distinction observed was that male Imperial Shags always preceded Gargling with the Pointing-Darting display (Fig. 1d). In contrast, male King Shags frequently skipped Gargling and went straight to Head-wagging (Fig. 1c). None of these differences, however, was significant.

DISCUSSION

In addition to my inability to find differences in form or sequence of courtship displays, the courtship sequences employed by heterospecific pairs were generally indistinguishable from those seen in conspecific pairings. Allopreening between different species has not been reported in the Phalacrocoracidae prior to Devillers and Terschuren's (1978) investigation, and hybrids in the family are rare. It appears that for King and Imperial Blue-eyed shags, the behavioral barriers to introgression are weak or nonexistent. If assortative mating occurs, it must be accomplished by other means, perhaps through morphological differentiation or allopatry.

In the Emperor Shag (*P. albiventer purpurascens*), pairbonds frequently were broken between and among seasons, and mate retention did not seem to be influenced by reproductive success (Brothers 1985). Antarctic Blue-eyed Shags show a similar rate of mate change (Bernstein and Maxson 1982), unrelated by age of partner, prior or subsequent breeding success (Shaw, in press). This low mate fidelity could allow greater latitude in mate choice, and serve to maintain the presence of mixed-species pairs. Devillers and Terschuren (1978) found heterospecific pairs at each sympatric colony they visited.

Some of the King and Imperial Blue-eyed shags I observed may represent immature birds practicing courtship or attempting maladaptive pairings. Although Rasmussen (1986) reported similarities in cheek patch patterns between juvenile Imperial Shags and adult King Shags, confusion between the two seems unlikely except at a distance. The overall appearance of first-year birds is very different from that of their elders (Shaw, pers. comm.) in coloration of the gular pouch, development and coloration of caruncles, and absence of nuptial plumage and filoplumes (see Derenne et al. 1976). Furthermore, early breeding in King and Imperial shags is uncommon.

Emperor Shags on Macquarie Island generally breed by their fourth year, although a few attempt breeding as soon as they attain adult plumage at 2 years of age (Brothers 1985). Antarctic Blue-eyed Shags on the South Orkney Islands were able to raise successful broods at 3 years of age, but the mean age of pairs was higher, about 6.5 years (Shaw 1985b). The youngest birds were mostly paired with older mates, only equaling or exceeding their age by age five (females) or age seven (males) (see fig. 2 in Shaw 1985b). Birds less than 7 years of age arrived at the colony significantly later than older birds, and younger pairs nested generally on the periphery with a lower reproductive success (Shaw 1985a). Juvenile or inexperienced birds may comprise one or both courting partners of a mixed pair; assortative pairing may become more common with the mean age of the pair as morphological discrimination develops. If this is the

case, then mixed pairings should occur only in pairs involving younger birds. Similar demographics may contribute to the scarcity of mixed-species pairs along the Fuego-Patagonian coast and the absence of strong behavioral isolating mechanisms between King and Imperial Blue-eyed shags.

The differences in courtship and pairbonding behavior of King and Imperial Blue-eyed shags compared with Antarctic Blue-eyed Shags are difficult to explain. Although my investigation was based only on observations of adults in breeding plumage, about half represent pairs off the breeding colony near the end of the breeding season (February). Nonetheless, these sequences did not deviate significantly from those seen on the breeding colony on Isla Escobar earlier in the season. These differences, if not artifacts of observational error, indicate that the relationship between King and Imperial Blue-eyed shags may be closer than currently postulated between Imperial and Antarctic Blue-eyed shags. In that case, King and Imperial Blue-eyed shags should probably be considered, as suggested by Devillers and Terschuren, as subspecies or color morphs of a single species, *Phalacrocorax atriceps.*

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