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Multiple Functions of Courtship Displays in Dabbling Ducks (Anatini)

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The displays of courting ducks have been described, analyzed, and compared by ornithologists and ethologists for a variety of reasons. Early comparative studies showed that stereotyped displays can be used as taxonomic characters and therefore behavioral evidence was used extensively to deduce relationships within the Anatidae (Lorenz 1941, Delacour and Mayr 1945, Johnsgard 1965). Ethological analyses of the form, contexts, sequences, and spatial orientation of duck displays have been used to infer motivation of the performer and signal functions of individual displays (e.g. Dane and van der Kloot 1964, Weidmann and Darley 1971, Simmons and Weidmann 1973, McKinney 1975, Standen 1980). Other authors have explored how ecological and social factors have influenced the evolution of display repertoires (McKinney 1965a, McKinney et al. 1978) or have used displays to test predictions from sexual conflict theory (Anderson 1984). In spite of the diverse objectives of these various lines of research, all depend on the gathering of accurate descriptive information on displays.

Most of the displays performed by male dabbling ducks (genus *Anas*) during social courtship have distinct orientation components that can be used to identify the target bird. Movie film analyses have shown that male displays may be categorized into three types: (Type a) displays that are directed at a specific female, (Type b) displays that are directed at rival males, and (Type c) displays that appear to be directed simultaneously at the female and at another male. Evidence of many kinds indicates that displays aimed at females function in pair formation (courtship displays) or pair-bond maintenance; those aimed at other males are agonistic and function in competition for mates or mate defense. Film analyses of courtship groups of Mallard (*Anas platyrhynchos*; Weidmann and Darley 1971), Green-winged Teal (*A. crecca*; McKinney 1965b), Chilean Teal (*A. flavirostris*; Standen 1976, 1980), Gadwall (*A. strepera*; Schommer 1977), and American Wigeon (*A. americana*; Wishart 1983) indicated that each major male display can be placed in only one of these three categories. Recent studies of White-cheeked Pintail (*A. bahamensis*) and Chilean Teal, however, have convinced us that some frequently used displays of these two species cannot be assigned uniquely to one category. We have found that major displays are used in *both* courtship (male-female) and agonistic (male-male) contexts, and apparently they serve multiple signal functions. We draw attention to this phenomenon because it has not been reported previously, and we stress the need to reexamine *Anas* signaling systems with special attention to the orientation components of displays.

In most male-female (type a) displays (e.g. grunt-whistle, bridling, head-up-tail-up; terminology for displays follows Johnsgard 1965), the long axis of the male's body is broadside to the female; in others (facing the female, turn-back-of-head), the male's bill is pointed directly at, or away from, the female. Lorenz (1941) noted that these displays often feature conspicuous plumage, and most are accompanied by loud whistles or grunting noises. During the grunt-whistle display, males direct a spray of water sideways, always aimed at the target female (von de Wall 1963). Simmons and Weidmann (1973) showed that similar directional bias is present also in three shaking movements that precede major displays. Such displays are thought to have evolved as signals that indicate the male's interest in a specific female and are designed to attract that female's attention to the performing male.

Male-male (type b) displays are presumed to serve threat or appeasement functions, and to allow assessment of potential competitors. In Mallards, bill-up postures with "rabrab" calls occur when males approach one another. Threatening with open bill or chasing often follows. The males face more or less

obliquely toward one another, and females may or may not be present (Weidmann and Darley 1971). Similar bill-up displays occur in other species in agonistic contexts. Subordinate male Green-winged Teal perform nod-swimming displays in response to approach by dominant males during social courtship, and apparently this functions as an appeasement signal (Laurie-Ahlberg and McKinney 1979).

A good example of a display (type c) that appears to give simultaneous signals to >1 bird is the down-up of the Green-winged Teal. The male orients broadside to the target female, but the display is given only when a rival male is present and very close (McKinney 1965b, 1975). Often there is a "3-bird lineup," with the long axes of both males and the female all parallel. The displaying male is positioned between the rival male and the female. Therefore, the down-up display of this species appears to signal both courtship interest to the female and threat to the rival male (McKinney and Stolen 1982). Standen (1980) concluded that the pointing or "greeting" display of the Chilean Teal has similar dual signal functions when performed in the presence of a female and a rival male.

The down-up (DU) is by far the most frequent courtship display of male White-cheeked Pintails. This display was identified by Lorenz (1941) as a head-up-tail-up, but reinterpreted as a down-up by von de Wall (1963) and Kaltenhauser (1971). In captives breeding in flight pens, we observed that down-ups are not only directed at females in courtship contexts but also at males in hostile contexts. In both contexts, the performing bird adopts a broadside orientation to the target bird, and the display is often followed by turning the head and then the whole body to face toward the target bird. When present, the "facing" component provides unambiguous confirmation of the identity of the target bird. Initially we suspected that these males were homosexually imprinted birds (Schutz 1965), but this was ruled out because the same individuals gave this display to females as well as males; and other behavior made it obvious that females were being courted, but males were being threatened.

Similar behavior has been documented (Sorenson unpubl. data) in a wild population of individually marked White-cheeked Pintails in 1985–1987 on Paradise Island, New Providence, Bahamas. In 3,894 down-up displays, 39% were directed at females ("courtship DUs") and 51% at males ("aggressive DUs"). The remaining 10% were not classified because the target bird could not be determined with certainty. Close temporal association of aggressive DUs with male-male hostility was confirmed: 77% of the male-male DUs were preceded or followed by other aggressive behavior (open-bill threats, chases, swim-offs, or fights). No aggression was associated with any of the courtship DUs. Furthermore, 18% of the aggressive DUs were performed by rival males when females were not in the vicinity or were absent from the pond altogether. Typically, when rival males met, they exchanged broadside DUs and, if one male did not retreat, they almost always escalated aggression. This suggests that the DU does indeed serve a threat signal function.

The displays of captive Chilean Teal were studied in detail by Standen (1976), who concluded that grunt-whistle and bridling displays are performed with the long axis of the male's body broadside to a female in courtship and pair-bond maintenance contexts. In flight pen studies of display orientations during interactions between pairs, Hart (unpubl.) found that these displays are also directed at males. In groups of 5–7 pairs of individually marked birds monitored during 1986–1988, 47% of 253 grunt-whistle displays and 44% of 209 bridle displays were directed (broadside) at males. The remaining displays were directed (broadside) at females. Many of the male-male displays were followed immediately by overt hostility, confirming that individual males perform these displays in both courtship and threat contexts.

Anas displays are typically highly stereotyped actions, and movie film analyses of captive birds have not detected differences in the form of these multipurpose displays when they are performed in courtship and agonistic contexts. Although wild White-cheeked Pintails may perform down-ups to both males and females (with or without the facing component), the turn is often omitted after hostile DUs given in male-male contexts. Down-ups directed at females or males in a courting party context are usually followed by facing. More detailed analyses may reveal other subtle differences in the form of the displays comparable to those found in the calls and postures of gulls and terns (Beer 1975, 1980; Veen 1985) and in the song-spread displays of grackles (Wiley 1975).

Displays with multiple functions are not likely a widespread, but previously unrecognized, phenomenon in dabbling ducks. Although there have been few detailed studies of display orientations, much attention has been given to the courtship behavior of *Anas* ducks over many years, and there are very few indications that male-male orientation of major courtship displays is a regular phenomenon. Several authors have reported that social courtship can occur in groups of males when no female is present (Lorenz 1941, Weidmann and Darley 1971, von de Wall 1965, McKinney 1975), but generally this is rare and, when it occurs, it could be triggered by the presence of one or more homosexual males. Recently, Kruijt et al. (1982) reported that male Mallards occasionally direct courtship displays at other males, and Bossema and Roemers (1985: 153) describe this for a trio involving 1 female and 2 males during a period of intense rivalry. More work on Mallards is needed to determine if such behavior occurs regularly. Almost all of the well studied Northern Hemisphere species of *Anas* are strikingly dichromatic, and it should be easy to detect if

males are directing the same displays to males as well as females. On the other hand, many Southern Hemisphere species (such as the White-cheeked Pintail and Chilean Teal) have greatly reduced dichromatism, and it is often difficult to be sure of the sex of target birds in groups of actively courting birds. Careful analyses of films of such species are needed.

If multiple use of major courtship displays does not occur typically in Northern Hemisphere *Anas*, its regular occurrence in the White-cheeked Pintail and Chilean Teal requires an explanation. We suspect that the phenomenon is related to the formation of bigamous pair bonds, long-term relationships between individual birds that are possible in sedentary populations, or both. The Chilean Teal and White-cheeked Pintail form bigamous bonds in captivity (McKinney and Bruggers 1983; McKinney 1985), and bigamy was documented in all three years of a field study (Sorenson unpubl. data) of wild White-cheeked Pintails. During the formation and maintenance of bigamous bonds, intense rivalries develop between individual males over particular females. Male-male displays, as well as other aggressive behavior, occur frequently as males try to dominate one another. In sedentary populations, the same individuals may interact with one another year-round and year after year, and complex dominance relationships may develop. Many populations of tropical and Southern Hemisphere *Anas* species (including White-cheeked Pintail and Chilean Teal) are nonmigratory.

At this stage we cannot explain the causal relationships between multipurpose displays and these factors. It is also possible that the multiple use of such widely distributed displays as the grunt-whistle, bridling, and down-up is the ancestral condition in *Anas*. New analyses of display repertoires that pay special attention to the orientation components of displays and the long-term relationships of the individuals involved are needed to address these questions.

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Taxonomic Status of the Coquette Hummingbird of Guerrero, Mexico

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An isolated population of small hummingbirds in the state of Guerrero, Mexico, was originally named as a subspecies (*brachylopha*) of the much more southerly *Lophornis delattrei*, the Rufous-crested Coquette (Moore 1949). The form was not reported again until rediscovered by Ornelas (1987) and remains known by only three male and two female specimens. Examination of two of the males indicates that the population deserves specific status as *Lophornis brachylopha* Moore, for which I propose the English name Short-crested Coquette.

Moore (1949) based his description of *brachylopha* on two male specimens from San Vicente de Benitez, altitude 1,500 ft (450 m) in the Sierra Madre del Sur approximately 70 km northwest of Acapulco, Guerrero. This was an extension of the range of the species *delattrei*, and of the genus *Lophornis* as then constituted, of ca. 1,900 km north from central Costa Rica. The subspecies was accepted by Friedmann, Griscom, and Moore (1950), and the species was included in subsequent guides to Mexican birds (Blake 1953, Davis 1972, Edwards 1972, Peterson and Chalif 1973). The descriptions in most of these guides, however, were apparently based on other populations of the species, as they largely ignored the distinctive characters ascribed to *brachylopha* by Moore (1949). This is especially true of the descriptions of the then unknown female! The Mexican range of the species was also noted by Eisenmann (1955), and the distinction of the form was affirmed by Hardy and Webber (1975). Despite this, the American Ornithologists' Union (1983) omitted any part of Mexico from the range of the species—presumably a lapse rather than a denial of Moore's description.

After Moore's (1949) description of *brachylopha*, nothing of significance was added to our knowledge of it until Ornelas (1987) collected three additional specimens, one male and two females, in 1986. These specimens were taken in mist nets in evergreen subtropical forest at Arroyo Grande, 13 km northeast of Paraiso, Guerrero, at an elevation of 1,350 meters. Paraiso is in south-central Guerrero, northwest of Acapulco and near Atoyac de Alvarez, and thus ca. 10 km northeast of the type locality (J. F. Ornelas in litt.).

Shortly after the reported rediscovery of *brachylopha*, I studied Moore's (1949) description of the taxon relative to specimens of *Lophornis delattrei delattrei* and *L. d. lessoni* in the National Museum of Natural History (USNM). It was readily apparent that the birds described were different—so different, in fact, that I wondered if they were actually the same species. It struck me that the stated differences were much like those one would record if specimens of *Lophornis ornata* of northeastern South America were compared with *delattrei*. Subsequently, I examined two of the three male specimens of *brachylopha* (MLZ 46069, UNAM P007047) and compared one or both of them with specimens of all species in the genus in the USNM, the American Museum of Natural History, and the Museum of Comparative Zoology. The diagnostic characters of males of *L. brachylopha*, emphasized by Hardy and Webber (1975), are the short crest, black bill, terminal tail pattern, and pale abdomen. Neither of the females was available for study, but Ornelas (1987) noted that they have the "throat completely white," which distinguishes them from *L. delattrei*.

The rufous crest feathers of *brachylopha* are wide and short (ca. 1 cm). The feathers on these two spec-