Display inventory of the Torrent Duck

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Introduction

The Torrent Duck *Merganetta armata* is one of the least studied species in the family Anatidae. Unlike most waterfowl, Torrent Ducks are difficult to keep in captivity and consequently little is known about their display repertoire. A number of Torrent Duck displays have been described (Phillips 1953; Scott 1954; Johnson 1963; Wright 1965; Johnsgard 1966; Moffett 1970) but no attempt has been made to study the displays systematically. A basic display description can serve to illuminate the relations between individual races of Torrent Ducks and to indicate phylogenetic relationships within the family Anatidae (cf. Heinroth 1911; Lorenz 1941; Delacour & Mayr 1945; Johnsgard 1960, 1961a, 1965).

In this paper displays are taken to be ritualized behaviour patterns . . . ‘those peculiarly standardized and often exaggerated performances including all vocalizations and many movements and postures, which have become specialized and modified as social signals or releasers’ (Moynihan 1955). The terminology for comfort movements is that of McKinney (1965).

Methods

The following observations deal primarily with one pair (M1/F1) of the southern subspecies, *Merganetta armata armata*, that resided in the lake district on Rio Nalcus, Osorno, Chile, in the austral spring of 1975. Additional observations on an upriver pair (M2/F2) and a pair on Rio Chanleufue have been included. Both rivers had swift, highly oxygenated, clear, cold water that moved in an area of rapids over a substratum of rock, stones and gravel with only limited areas of sand and silt, characterized as rithtron in nature by Hynes (1970). During the study, individual males were identified by variations in the black and white feather pattern of the head and neck. Individual females could be identified by missing tail feathers which are molted throughout the year (Weller, 1968).

The drawings are based on super-8 mm films exposed at 24 frames per second. The sonograms of vocalizations were made from cassette recordings.

Display inventory

Male and female Torrent Ducks have a similar display repertoire and, although their vocalizations differ in that the calls of males are primarily clear-toned and those of females are harsh, both sexes stress a similar frequency range (3–5 kHz) which is above the background noise of the rapids (0–1–5 kHz).

*Pointing*, a series of evenly spaced horizontal thrusts of the head and neck is performed commonly by males and females. Both sexes often call just after the peak of the head thrust as the head is withdrawn. The male whistles a single clear ‘wheet’ (Johnsgard 1966) and the female emits a throaty ‘queech’ (Figure 1–2). These were the most common calls heard during daily activities and aggressive interactions. The male’s whistle carried well over the rapids but the female’s call was easily lost in the background roar.

All moves, including flight, swimming, or position changes, such as jumping off an emergent rock, were preceded by Pointing. The small (minimum neck extension) and irregularly spaced head thrusts appeared to aid in judging distance. Undisturbed, upriver flights were preceded by a long sequence of Pointing which began with a few, irregularly spaced head thrusts involving little neck extension. The body stance was relaxed and somewhat hunched (Figure 3a). Gradually, the bird became more erect and the head thrusts evenly spaced and more rapid with greater neck extension (Figure 3b–c). Often several minutes elapsed before flight and the birds moved from rock to rock Pointing as they swam. M1 and F1 often called while giving the emphatic head thrusts before flight and both vocalized during flight in a call-response pattern which probably served to maintain contact (‘queech-wheet’ . . . ‘wheet-queech’ . . . ‘queech-wheet’).

Pointing was also performed by seemingly wary birds. The head thrusts were directed at an angle of 30° to 45° above horizontal and each fully extended thrust was held in a ‘craning’ post with neck, head, and body feathers sleeked. Points could also be associated with rapid, cursory nibble-preens when a bird was frightened or wary; each Point alternated with a brief preen, usually of
the upper belly. The body was hunched, the feathers ruffled, and each Point and preen sequence occurred in less than a second. In the water, a wary bird often swam with its tail resting on the surface, Pointing with exaggerated head thrusts and sleeked head and neck plumage.

Pointing occurred almost continuously during aggressive interactions but the head thrusts varied in neck extension and thrust rapidity (Figure 4a–d). F1, for example, averaged 1·4 head thrusts per second during 630 filmed seconds of aggressive interaction. Most head thrusts were either in the direction that the bird eventually went or toward a rival (Figure 4a). For example, a bird might Point toward an emergent rock, then it would jump into the stream, swim to the rock and then Point at the rival.

Often a Point by one bird immediately followed one by its mate. During aggressive interactions calls were so commonly given with Pointing that they formed a background noise (Point-wheet... Point-queech... etc.).

During tense confrontations, when rival males stood near each other on emergent rocks, the territorial male often performed slow, scooping head-thrusts lateral to the rival. Each thrust was angled 45° to 60° above horizontal and was held briefly at full neck extension (Figure 4b). Each head thrust appeared to be an individual performance rather than part of a series. Often the scoops alternated first to the left and then to the right, 10° to 20° off centre. Each scoop was usually associated with a 'wheeow' call rather than a 'wheet' (Figure 1a–b). The stressed frequencies (4–5 kHz) were preceded by an ascending slur and terminated by a descending slur. A call-response pattern occurred between mates, the male giving an extended head thrust and...
Torrent Duck display

Figure 2. Vocalizations of the territorial pair: two female 'queech' calls and one 'gaga-brr' followed by male's 'warble' (a), male 'warble' calls (b, c, d), male 'warble' call near nest (e), and male 'wheet' near nest (f). All calls are redrawn from sonograms with the river noise indicated in horizontal lines.

'wheow' call, the female giving a typical head thrust with 'queech' call (Figure 1c–d).

In an Upright posture, originally described by Scott (1954), the bird holds its body erect, feet widely spaced, and bill horizontal. Males erect their crest and cheek feathers emphasizing the black and white striations on the head and neck and drop their wings revealing the horn grey spur and exposing the specula. The posture was characteristic of aggressive interactions and was assumed by territorial owners and intruders of both sexes. When a bird moved from rock to rock during a confrontation it assumed an Upright on each rock and swam in an erect posture with head and neck held back and tail fanned above the water surface. Often it Pointed as it swam thrusting the head forward alternately to the right and left 10° to 20° off centre causing the bird to progress on a zig-zagging course.

The Upright was usually associated with Pointing although the birds called 'wheet' or 'queech' without Pointing while in this stance. In addition, the male whistled repeatedly in a series of slightly ascending then descending notes. Each note appeared similar to the 'wheet' vocalization in frequency but lacked the trailing finish (Figure 1h). Early in an aggressive interaction, just after the intruders were discovered, F1 emitted intense, repeated 'queech' vocalizations in an Upright and M1, also in an Upright, responded with repeated 'wheet'
calls that matched the rate of the female’s call (Figure 1f).

When two rival males faced each other during an interaction, the territorial male stood in an Upright and deliberately turned his head, with bill horizontal, so that one cheek was toward the intruder. After less than a minute he would methodically turn his head again to face the intruder directly.

**Barging** varies from a relatively fast and low approach with head held back, bill level, and breast only partially exposed to a slow, erect approach with neck extended vertically and breast completely exposed (Figure 4d). Males and females Barged during aggressive encounters and M1 was observed Barging before copulation.

During aggressive interactions **Pointing** was often associated with **Barging**. The head thrusts angled 30° to 45° above horizontal with almost no pause between thrusts (Figure 4d). F1 often made short distance Barges toward the intruder, rising extremely high in the water and Pointing rapidly. M1 often leaped after her and approached the intruders. Possibly F1’s Pointing in association with the high Barge was a threat toward the intruder and may have stimulated M1 to attack.

In the **Bent-neck** the bird’s neck is slightly curved and held rigidly extended with the head and bill bent sharply downward. The neck and head feathers are conspicuously depressed (Figure 5). On a rock, a performing bird appears tall and slim and often steps rapidly, high on its toes; in the water the bird paddles vigorously to hold a fairly
stationary, elevated posture as described and drawn by Scott (1954). During aggressive interactions the Bent-neck was performed by both sexes in the water, on rocks, and during flight.

Both males and females vocalize during the Bent-neck. The male's 'warble' call is a highly variably series of clear notes (Figure 1g and 2a–e). Many of the warbled notes are given in ascending series at frequencies just above the roar of the rapids and consequently can be heard only at close range. This call may be used in close communication between mates whereas the stressed, high-frequency whistles function in communication over a greater distance. The female's 'gaga-brr' begins with three sharp calls that increase in intensity and are followed by a rapid unvarying staccato rattle (Figure 2a). Unlike the 'queech', this call carries well and is probably the call reported by H. Luthi (cited by Johnsgard 1966). During aggressive interactions Bent-necks were often performed simultaneously by mates so the 'gaga-brr' and 'warble' calls were often heard together (Figure 2a).

The Bent-neck varied in duration, and the longest performances usually occurred at the beginning of an interaction. When the upriver pair confronted M1 and F1 in the downriver territory, all four birds performed simultaneously. Separated by a metre or less, the two pairs often formed a tight group that wheeled in the current; each individual maintained a Bent-neck posture lateral to the rival of the same sex. Encounters such as these usually occurred in the water but sometimes all four participants crowded onto the same rock, each bird standing next to the rival but tilting its head and neck away as if to guard against a possible blow. Head-tilting was common at any time during interactions when one bird approached or 'crowded' a rival closely; but, the tilted head was particularly obvious during the Bent-neck because of the sleeked feathers.

On three occasions when no intruders were apparent on the territory, F1 assumed a Bent-neck with call apparently to 'summon' M1 when he was out of sight. The display in this context did not vary noticeably from that performed during aggressive interactions (Figure 5).

In the water a bird performing a Vertical-shake arches forward, dips its bill, and leaps vertically out of the water while shaking its head and holding its bill at or below horizontal. On a rock, the bird arches forward, swings its bill down, and straightens its body to a vertical posture while shaking its head (Figure 6). A single clear whistle is usually given by the male just before the display peak (Figure 6a, frame 7 and Figure 6b, frame 5) but I was unable to make a record of this vocalization.

During aggressive interactions, both sexes performed Vertical-shakes more often in the water than on rocks. The body was generally lateral to a rival so that the first swing of the head-shake following the bill-dip often sprayed water precisely at the rival, but remaining water droplets were also flung in the opposite direction on the return swing. Using the first head-shake to determine direction as in Simmons and Weidmann (1973), film analysis shows that 21 of 23 male Vertical-shakes were directed at rival males and 15 of 17 female Vertical-shakes were toward rival females.

Vertical-shakes were not performed in bouts (uninterrupted series of a single display type performed by one individual). Rivals occasionally displayed in rapid succession and pair members responded to each other's Vertical-shakes with the same display, particularly during the initial approach. For example, in one filmed sequence F1 displayed 0-7 second after M1 (Figure 6c–d).
Vertically-shakes were also performed by M.1 before copulation. In this context the display appeared similar to vertically-shakes performed in the water during aggressive interactions except that the male performed laterally to his female and directed the first shake toward her. The female also performed a vertically-shake on one occasion when M.1 did not respond after she assumed the Prone posture.

In separate instances M.1 and F.1 performed a single vertically-shake to the mate after vigorous bathing.

During incubation F.1 often performed a vertically-shake just after leaving the nest hole for a break. The vigour of the display varied from barely more than a swim-shake to a full display in which she jumped clear of the water.

Mule-kicks are performed in the water and on emergent rocks by both sexes during aggressive interactions. This display was first described by Scott (1954) and was later named by Moffett (1970). When performed in the water the bird arches up and kicks back with both feet sending a spray of water sometimes several metres in the air (Figure 7). The fanned tail flips up with the kick and occasionally the bird kicks again just before it hits the water. On a rock the body teeters forward as the feet kick back, but barely leave the substrate. The head is held low and forward before and after each kick and the tail rises slightly with the kick. Males but not females usually expose their specula before and after each kick.

Mule-kicks occurred commonly throughout an interaction but were most frequent during active confrontation and were most commonly performed in the water. In contrast to a vertically-shake, one individual often performed two or three Mule-kicks in a rapid series. Rivals of the same sex often Mule-kicked at each other.

A bird performing the Mule-kick usually faced away from but kicked toward a rival. Film analysis shows that 60 of 69 Mule-kicks by males and 26 of 30 by females were directed at a rival of the same sex.

Members of a pair often Mule-kicked in sequence; the female led more commonly than the male.

Wing-flaps are preceded by a gradual erection of body feathers while the bird stands in an Upright. The breast projects forward and the wings are drawn rapidly up, back, and flicked forcefully forward. After one to three flaps the wings are held loosely at the side with primaries extended and specula exposed. The wings are then folded, one at a time into position. In contrast to the Wing-flap the comfort movement of wing-flapping involves more than three flaps and lacks the pronounced emphasis on the forward flap (Figure 8).

Wing-flaps were performed on rocks by
both sexes during aggressive interactions. The 29 filmed Wing-flaps included 17 single, 11 double, and 1 triple flap display. Eighteen of these displays were performed by females and of these 12 faced a rival female suggesting that a directional bias might exist. On several occasions the female actually struck a rival with one wing. The possibility of being struck could explain the tilted head in the Bent-neck posture since Wing-flaps were often performed as a bird crowded a rival.

The Shudder-shake varies in form from a brief 'shudder' after body feather erection to a tight body rotation with head-flick (Figure 9). It differs from the loose maintenance body-shake which begins with a conspicuous and prolonged tail-wag and develops into a shuffling shake, head-flick, and tail-wag. The Shudder-shake was performed on rocks by both sexes while they were in the Upright. Occasionally it was also observed in the water during a Barge. No directional bias was obvious either during field observations or in filmed displays.

Open-bill threats are used by many anatids but were seen rarely in Torrent Ducks (less than 10 records). In all observations a stationary male or female faced a rapidly approaching rival with arched back, depressed tail, and lowered neck.

In the Body-bend, originally described by Phillips (1953), the breast is lowered in a continuous motion while the bill tilts upward until the head rests against the back and the fanned tail is lifted to a vertical position. The

legs are flexed as the bow deepens and the primaries lift exposing the specula (Figure 10). At the display peak, the head and neck are framed by the specula (more apparent in the male) and the female's 'gaga-brr' and the male's 'warble' are similar to the calls accompanying the Bent-neck.

Body-bends were performed in the water or on rocks by males and females during aggressive interactions and by the male after copulation, around the nest area, and following a reunion with his mate. The display was slow and the peak was held for 1 to 3 seconds (based on 88 filmed displays). It was performed throughout aggressive interactions usually on a rock simultaneously by both pair members. Film analysis shows that of 50 female and 38 male Body-bends, 21 were performed simultaneously with a mate. Often one member of a pair initiated
Figure 10. Body-bends performed during an aggressive interaction in characteristic synchrony by mates with ‘gaga-ber’ and ‘warble’ calls. The numbered line indicates which frames were used.

and held the bow until its mate also performed the display (Figure 10). The Body-bend did not seem consistent in orientation; sometimes a bird faced the rival and sometimes it faced its mate.

Duck M1 performed partial Body-bends after reunions with F1 and after 4 of the 12 observed copulations (Figure 11). Though the associated call seemed similar, the display in these contexts was not as extreme as it was when performed during aggressive encounters; it was performed in the water, the head and tail reached a 45° angle above the water, and the specula were not displayed.

When M1 and F1 were searching for a nest and later when F1 was incubating, M1 often performed Body-bends in or out of the water. The Body-bend in this context was more developed than the post-copulation Body-bend, but less developed than those performed during aggressive interactions; the tail was lifted to a vertical fanned position, the head to a 45° angle, and the specula were not displayed (see photograph in Moffett 1970.)

Tail-wagging involves continuous and rapid wagging movements. It is often punctuated by Body-shakes and appears to be a pronounced continuation of the normal Tail-wagging associated with Body-shakes. Whenever the pair, M1 and F1, stood near a potential nest site they looked at each other and Tail-wagged vigorously for 5 to 10 minutes. After incubation began the female continued to Tail-wag whenever she returned to the nest after a break. The male, who usually accompanied the female back to the nest area, also wagged his tail but not as vigorously.

In the Prone the female’s body rides low in the water and her tail rests on the surface. Her head and neck are drawn in and her bill slants down until it touches or almost touches the water. The posture is characterized by its stillness. F1 assumed the Prone in the water before every copulation although once she assumed it on a rock and then dropped into the water.

Taxonomic relationships and display context

Delacour and Mayr (1945), in a major reorganization of anatid phylogeny, placed Torrent Ducks in a separate monotypic
Torrent Duck display

Johnsgard (1966) suggested Cairinini Torrent Duck on the basis of osteological features and placed it in the tribe Anatini. Woolfenden (1961), also using osteological evidence, returned the species to separate tribal status but agreed that it has Anatini affinities. The trachea, an apparently conservative taxonomic character, indicates relationship to the Anatini, Cairinini, or Tadornini but not to the Oxyurini as suggested by Delacour and Mayr (Johnsgard 1961a). After observing Torrent Ducks in the field, Johnsgard (1966) suggested Cairinini affinities. Brush (1976) analysed S-carboxy keratins from feathers and suggested affinities with Cairinini or Tadornini.

Although anatids have been classified primarily on the basis of morphological, osteological, and biochemical evidence, displays have been used to indicate phylogeny (Heinroth 1911; Lorenz 1941; Delacour & Mayr 1945; Johnsgard 1960, 1961b, 1965). Although I saw no displays that are considered conservative, taxonomic indicators (e.g., Grunt-whistle, Head-up-tail-up, Bridling, Decrescendo of Anatini), the following discussion compares context and form of Torrent Duck displays with those of Anatini, Cairinini, and Tadornini.

The Vertical-shake appeared to function in two contexts: pair bond maintenance and territorial encounters. The directional change of the head-flick, towards the mate before copulation and towards an intruder during an encounter, suggests this duality. The display may also indicate the territorial status of the performer since it was performed more often by the territorial male than by the intruder.

In form, the display resembles the Grunt-whistle of Anas, the Display-shake and Double-display-shake of Aix, and the Whistle-shake of Tadorna tadorina. Although it incorporates a directed spray of water and a whistle at the display peak, the Vertical-shake differs from the Grunt-whistle in that the head shakes several times and remains erect rather than returning to a normal position. The Display-shake and Double-display-shake involve a slight head shake or rotary movement of the head and neck as the bird rises from the water but no subsequent spray of water and the head and neck return to normal position as in the Grunt-whistle. The Whistle-shake of Tadorna is very similar to the Vertical-shake; the head and neck are lowered and rapidly jerked back with head shaking to an erect posture, with an associated whistle by the male display as the name implies.

In context, the Vertical-shake resembles the Whistle-shake of Tadorna but not the Grunt-whistle, Display-shake, or Double-display-shake in that both sexes perform in situations other than pair formation, such as pair bond maintenance and agonistic encounters.

The Body-bend was performed in a pair-maintaining context during daily activities and agonistic encounters. The male appeared more diligent in pair bond maintenance and performed solo Body-bends after copulation and separation and around the nest area. During encounters both pair members performed simultaneously. This display may also indicate territorial status since it was performed more often by the territorial pair than by the intruding pair.

The Body-bend does not resemble displays of either Cairinini or Tadornini, but it is superficially similar to the Head-up-tail-up and Down-up displays of Anas species except that in the Head-up-tail-up the bill is lowered and in the Down-up the tail is lowered rather than raised. In contrast to these displays, the Body-bend was performed by both sexes in contexts other than pair formation. Blue Ducks Hymenolaimus malacorhynchos, are tentatively associated with Anatini and perform a display similar to the Body-bend in form and context (Johnsgard 1965; Williams 1967). The Blue Duck display does not involve the extreme raising of the head and tail and usually incorporates a vertical head pump.

Pointing appeared to coordinate the pair’s movements before flight and during aggressive encounters. It probably evolved from simple head movements used to judge distance before a move. Possibly the fast-water environment intensified selection favouring vigorous head thrusts as intention signals. Other river specialists such as the African Black Duck Anas sparsa (McKinney et al. 1978), Salvadori’s Duck Anas waigiuensis and the New Zealand Blue Duck (Kear 1972) have head thrusting intention displays but all incorporate a vertical component that Pointing lacks. Mutual head thrusting between pair members during aggressive encounters is common in Tadornini but not in Anatini or Cairinini and probably threatens a rival as well as coordinates the pair.

Vocal duetting occurs between pair members of Tadornini but not Anatini or...
Cairinini. The combined head thrusting and duetting by pair members of Tadornini is similar to mutual Pointing and calling of Torrent Ducks. The 'wiwiwiwi' - 'r-brrr' duet in Tadornini (Heinroth 1911) seems strikingly similar to the 'warble' - 'gaga-brrr' Torrent Duck duet. Male and female vocal dimorphism in Torrent Ducks appears to be similar to that of Tadornini. Tadornini and Cereopsis are the only tribes where the females vocalize in a rattle-like 'brrr' as in the 'gaga-brrr' of the female Torrent Duck (Heinroth 1911; Veselovski 1970). The variable whistle of the male 'warble' is similar to that of the male Andean Goose Chlorophaga melanoptera and Abyssinian Blue-winged Goose Cyanochen cyanopterus.

The 'queech' female call is only vaguely similar to the quacks of Anas species. The repeated 'queech' call in Figure 1 superficially resembles a Decrescendo but the decreasing emphasis on each succeeding burst of the call is lacking and the call occurred during an aggressive interaction when F1 was with her mate who matched the rate of her call in 'wheets'. When the male was absent she called repeatedly an even-spaced 'queech' or a single 'gaga-brrr'. Johnsgard (1966) suggested that female Torrent Ducks, like Cairinini females, have a reduced vocal repertoire but my observations suggest that rather than being reduced, they are difficult to hear over the river noise.

The Bent-neck was performed during aggressive approaches early in the encounters and during the most intense display bursts. It appeared to 'rally' the pair members since a Bent-neck by one prompted the other to perform as well. This was also true when F1 assumed the Bent-neck to summon M1 even though no intruders were apparent. He responded immediately by joining her as if an intruder was there.

The Mule-kick appeared to function as a highly directed, defensive 'parry' during active display bursts of aggressive interactions. It was performed while facing away from a rival and the kick, usually directed towards the rival, moved the performer away while splashing the rival. Significantly, this display was performed more often by intruders than by territorial holders.

Mule-kicks by the female were less directed and were often followed by mule-kicks on approach toward a rival by the pair male, suggesting that the display may serve an 'inciting' function as well.

The Bent-neck, Mule-kick, and Wing-flap displays do not have obvious parallels in Anatini, Cairinini, or Tadornini with possible exception of the erect, threatening posture of the Ruddy-headed Goose Chlorophaga rubidiceps (similar to Bent-neck) and the Wing-flap display of the Andean Goose.

In summary, my observations support separate tribal status for the Torrent Duck and do not support a close relationship with Anatini. This conclusion agrees with Johnsgard (1966) and with Brush (1976). An association with either Cairinini or Tadornini seems possible but the Vertical-shake/Whistle-shake similarity, mutual head thrusting, vocal duetting, and vocal dimorphism suggest a closer relationship to Tadornini.

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Summary

Observations on the display repertoire of a territorial pair of Torrent Ducks Merganetta armata armata on Rio Nalcus, Oscorno, Chile, from 18 September to 26 November 1975 support the view that Torrent Ducks belong in a monotypic tribe Merganettini. Described and illustrated displays include: Pointing, Barging, Upright, Bent-neck, Vertical-shake, Mule-kick, Body-bend, Wing-flap, Shudder-shake, Tail, wagging, Prone, and associated vocalizations.
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