Behavioural evidence of the systematic relationships of the Patagonian Crested Duck *Lophonetta specularioides specularioides*

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Despite recent advances in phylogenetic analysis, relationships among species of dabbling ducks remain uncertain. In particular, the placement of the Crested Duck *Lophonetta specularioides* remains in question. Although most researchers have placed the Crested Duck within the tribe Anatini, its placement within the tribe varies from study to study. A study was carried out to determine whether social displays used by the Patagonian Crested Duck *Lophonetta specularioides specularioides* could inform the phylogenetic debate. Detailed analyses of behavioural displays indicate that although many displays used by the Crested Duck are superficially similar to those of other dabbling ducks (genus *Anas*) they probably arose via convergent evolution. Such homoplasy provides evidence in support of mitochondrial DNA sequencing studies that place the Crested Duck in a position basal to the rest of the dabbling ducks and suggests that this species lacks close relatives.

Key Words: dabbling ducks, *Lophonetta*, phylogeny, Anatini, social display

The systematic relationships of the Crested Duck *Lophonetta specularioides* are still uncertain, although most evidence indicates that it is closely related to the dabbling ducks (tribe Anatini) and that it is the sister-species of the Bronze-winged Duck *Speculanas specularis*. Delacour & Mayr (1945) allied Crested Duck with shelducks (tribe Tadornini) because of shelduck-like aggressiveness, other reproductive behaviour and duckling coloration, separating it from Bronze-winged Duck, which they placed within Anatini. Johnsgard (1965, 1978) later placed both species within the genus *Anas*; however, most systematists continue to give them separate generic status. Based on a cladistic analysis of morphological characters, Livezey (1991) placed the Crested Duck and Bronze-winged Duck in one supergenus calling them the 'Proto-dabbling Ducks'. In Livezey's (1991) phylogenetic tree, *Lophonetta* and *Speculanas* represent a separate branch, basal to all the true dabbling ducks.

Molecular techniques have advanced knowledge of the ancestry of these two species by establishing their membership in a larger clade with the Brazilian Teal *Amazonetta brasiliensis* and four species of Steamer Ducks *Tachyeres*. In an extensive mitochondrial DNA sequencing study of dabbling ducks, Johnson and Sorenson (1999) placed *Amazonetta*, *Tachyeres*, *Speculanas* and *Lophonetta* together in a group of 'South American Ducks' in a basal position to one of the two major branches of dabbling ducks that includes the silver teal and blue-winged ducks. More recently, Donne-Goussé and colleagues (2002) found results similar to those of Johnson and Sorenson (1999) in a broader study of the Anseriformes.

If the phylogeny presented by Johnson and Sorenson (1999) is correct in aligning *Lophonetta* with the silver teal/blue-winged duck branch of the Anatini, it follows that some behavioural traits could be shared with this group. Either the display repertoire of *Lophonetta* could be unique (reflecting the absence of very close relatives) or it might share some homologous features with the silver teal/blue-winged duck clade. Furthermore, if *Lophonetta* exhibits displays that resemble those of the mallard/teal/pintail/wigeon clades, it may be possible to infer that these have evolved through convergent evolution. Indeed, such convergence was inferred by Kaltenhauser (1971) with respect to the Grunt-whistle (GW) display of typical dabbling ducks and the superficially similar display of *Lophonetta*.

Two races of *Lophonetta specularioides* are recognised (see below). In this paper the authors describe the displays of *L. s. specularioides,* the Patagonian Crested Duck, based on videotapes of captive birds, and compare them with the displays of other Anatini. Although captive birds may not perform displays at the frequency that might be observed in wild birds, the form of the displays is unlikely to differ between the two groups, and the authors feel that the displays described here reflect the overall behaviour of this subspecies. The objective of this study is to identify similarities of displays of *L. s. specularioides* and dabbling ducks and assess whether these represent

homologies or convergently evolved traits. Such detailed comparison of display features has been shown to be effective in illuminating behavioural homologies and homoplasies in other species (Wenzel 1992).

Methods

Ten hours of video tape were analysed for this study. Four hours were recorded at Cedar Creek Natural History Area, Anoka County, Minnesota (two pairs recorded in 2000); six additional hours were recorded at the Wildfowl & Wetlands Trust at Slimbridge, England (two pairs recorded in 1999 and a mixed-sex flock of five males and four females in 2001). Crested Ducks were filmed from a hide at both locations. Film of the birds in courting parties and in pairs was consistent with many of the displays described by other researchers.

All figures presented here were traced from film projected onto a screen using a Sharp Notevision PG A10X projector. Crested Duck displays were traced from an NTSC-format VHS copy (30 frames per second) of the original PAL video; all other displays were traced from Digital8 video (30 frames per second).

Results

General characteristics of social behaviour

The natural habitats used by this species are generally open lakes, creeks or sea shores. One race, Andean Crested Duck *L. s. alticola*, is resident in the high Andean lakes, nesting primarily above 4,000 m, from northern Peru and Bolivia to northern Chile and Argentina. The Patagonian Crested Duck inhabits lower altitudes in southern Chile, Argentinian Patagonia and the Falkland Islands and may migrate to the coast in winter, often forming large flocks outside the breeding season (Johnsgard 1978). They feed by dabbling or head-under in shallow water and are usually in habitats devoid of aquatic vegetation and much cover (these birds apparently do not rely on being able to escape detection by hiding). They are carnivorous, feeding on crustaceans, invertebrate larvae, clams (Weller 1972), and adult insects (F. McKinney, personal observation). Breeding birds are territorial and both sexes are very aggressive, chasing conspecifics and other, often larger, wildfowl species (Buitron & Nuechterlein 1989; Weller 1972). Pair bonds are strong, and mates cooperate in caring for ducklings (Buitron & Nuechterlein 1989). High levels of vigilance, co-operation by both adults and aggressiveness allow Crested Ducks to nest in close proximity with predatory birds such as gulls *Larus* spp. and skuas *Catharacta* spp. (Young 2005).

Many of the displays of this species are conspicuous and striking, and females have loud calls. Male courtship displays have pronounced orientation components with respect to the target female. The long tail is often conspicuously raised, exposing the black undertail coverts, and the male's crest is often erected during displays. Displays are described below; those performed with 'broadside orientation' occur with one side of the male's body directed towards the target female

(as opposed to facing towards or away from the target). Display durations are reported as mean (± s.d.). Displays described in this paper were consistent across all birds observed; however, due to the small sample size, additional variations in the displays may exist.

Male displays

Head-shake: (n = 286) This is a ritualised Head-shake; the basically lateral movements of the head are easily seen in slow-motion video but are tricky to differentiate from a rotary head-flick without video enhancement because the bill is pointed upwards during the head movement. (This upward bill-pointing component occurs in other displays of Crested Duck, e.g. Bill-Up Call, Decrescendo). McKinney (1965) noted that *L. s. alticola* performs similar head-shaking movements, which differ from those of *Anas* in the uptilting of the bill. The Head-shake is a very rapid movement, lasting an average of 0.504 (± 0.088) s, and it may be repeated up to seven times preceding a display (mean: 3.04 ± 1.46). It appears in introductory context at start of a display bout, but is probably better regarded as a preliminary to individual displays.

Kaltenhauser (1971) reported that males utter a single-note vocalisation during the Head-shake, and Jones (1948) noted similar behaviour in *L. s. alticola*. This study did not detect any vocalisations as part of the Head-shake, but our video was recorded from a minimum of 8 m (typically a much greater distance) from the birds. Quiet vocalisations may not have been recorded. Males did, however, point the bill upwards and give a single-note call *without* lateral head movements (see Bill-up Call below).

Head-flick: (n = 64) This display, involving a rotary movement of the head, differs in form from the Head-shake. The male lowers the bill close to the ground or water's surface when beginning this display, rolling the head from side to side as he brings the bill closer to the breast and neck. The Head-flick ends with the crest erect, forming a peak above the male's nape, which is similar to crest position at the end of a body-shake. This display differs from the Head-flick of *Anas* in that the bill is not lifted above horizontal, as it is at the culmination of displays by *Anas* (McKinney 1965). The duration of a Head-flick is almost double that of a Head-shake: 0.956 (± 0.144) s. Used much less frequently than Head-shake, Head-flick precedes a 'major' display (n = 10) just as often as it occurs following such a display (n = 11).

Body-shake: (n = 25) This is a typical ritualised swimming-shake, with a prolonged tail-wag at the start and head held low to the water's surface. Obvious rotary movements of the head initiate the full Body-shake; as with Head-flick, these rolling movements end with the crest erect and the bill brought close to the breast. (This shake is reminiscent of Wood Duck *Aix sponsa*; it is quite different from the shake of Hottentot Teal *Anas hottentota*, which ends with head forwards and down, A.N.P. Stevens, personal observation). On occasion, the Body-shake is preceded by a Head-flick (n = 7). It is one of the 'major' displays, is performed broadside to the female and lasts 2.065 (± 0.264) s.

Backward-swim: (n = 42) This is a conspicuous component of male courtship, particularly in mixed-sex courting parties. The crest is held erect as the male manoeuvres such that his body remains parallel to (alongside) the moving female. This manoeuvre does not occur in *Anas* species, and it is a very basic difference because it must involve quite different foot movements. In this study, 29% of display occurrences were in response to a female Low-swim.

Double Grunt-whistle: (n = 18) The initial component of this 'major' display involves dipping the bill into water followed by a flick of the bill to one side, sending a spray of water in that direction (**Figure 1a**). A brief *whee* vocalisation is then given as the male lifts the body during the second stage of the display. The water spray is consistently directed towards the female, as occurs in *Anas*. Unlike most *Anas*, however, which combine bill-dip and rising of the body into one motion in the GW (**Figure 1d**), the Double Grunt-whistle (DGW) separates the bill-dip from the body raise, as noted by other researchers (Johnsgard 1965; Lorenz 1953; von de Wall 1963). The entire display lasts for an average of 1.59 (± 0.213) s, and it is typically preceded by a series of Head-shakes (3.7 ± 1.57). On four occasions, it was followed by a Head-flick.

Head-back/Tail-up + Turn-Head-Towards-Female: (n = 18) Another 'major' display, Head-back/Tail-up (**Figure 2a**) begins as the head is erected; the crest rises slowly as the head is moved back towards the scapulars. The tail is raised to about 45˚, making the dark undertail coverts conspicuous, as the head reaches the most extreme posterior position over the back. The tail remains lifted for the duration of the display. The male returns the head to an Erect position then gives a *wheoo* call, opening the bill conspicuously as he Turns the Head Towards the Female (THTF). Throughout the display, the male drifts backwards, apparently to maintain broadside orientation to the female. Following THTF, the male lowers both head and tail and returns to a natural swimming position. In one instance, a male performed Head-back without Tail-up or THTF (duration of Head-back = 0.8 s), in another, the male performed Head-back and Tail-up without THTF. The full display (including Tail-up and THTF) typically lasts 2.25 (± 0.547) s.

Preen-behind-wing: (n = 8) The form of Preen-behind-wing (PBW) is the same as in *Anas*, although the displaying bird is equally likely to raise the wing away from its mate as it is to raise the wing closest (**Figure 3**). As in *Anas*, PBW in the Crested Duck may be performed by both members of a pair (n = 4) and appears to function as a pair-bond maintenance display. On three occasions, this display followed a Prolonged Dabble.

Prolonged Dabble: (n = 26) This display is highly ritualised in form, but the duration is variable, ranging from 1.2 to 8 s (mean = 4.25 ± 2.66 s). The body is positioned broadside to the female and held in rigid position as the male dabbles. This display can occur while swimming or while standing at the water's edge (**Figure 4**). Males may give a Head-shake, Body-shake or Backward-swim immediately before beginning to Prolonged Dabble. On nine occasions, males performed

Figure 1. The Double Grunt-whistle (DGW) and Grunt-whistle (GW) displays; numbers indicate frame number of tracing; (a) traced from NTSC-format VHS copy (30 frames per second) of PAL video; (b-d) traced from Digital8 video (30 frames per second). (a) Crested Duck male performing DGW; (b) Falcated Duck male performing GW; (c) Gadwall male performing GW; (d) Spot-bill Duck *Anas poecilorhyncha* performing GW. Note the separation of Bill-dip + Head-shake from Swimming-shake in Crested Duck DGW; all *Anas* GW displays lack this component, blending Bill-dip + Head-shake with Swimming-shake.

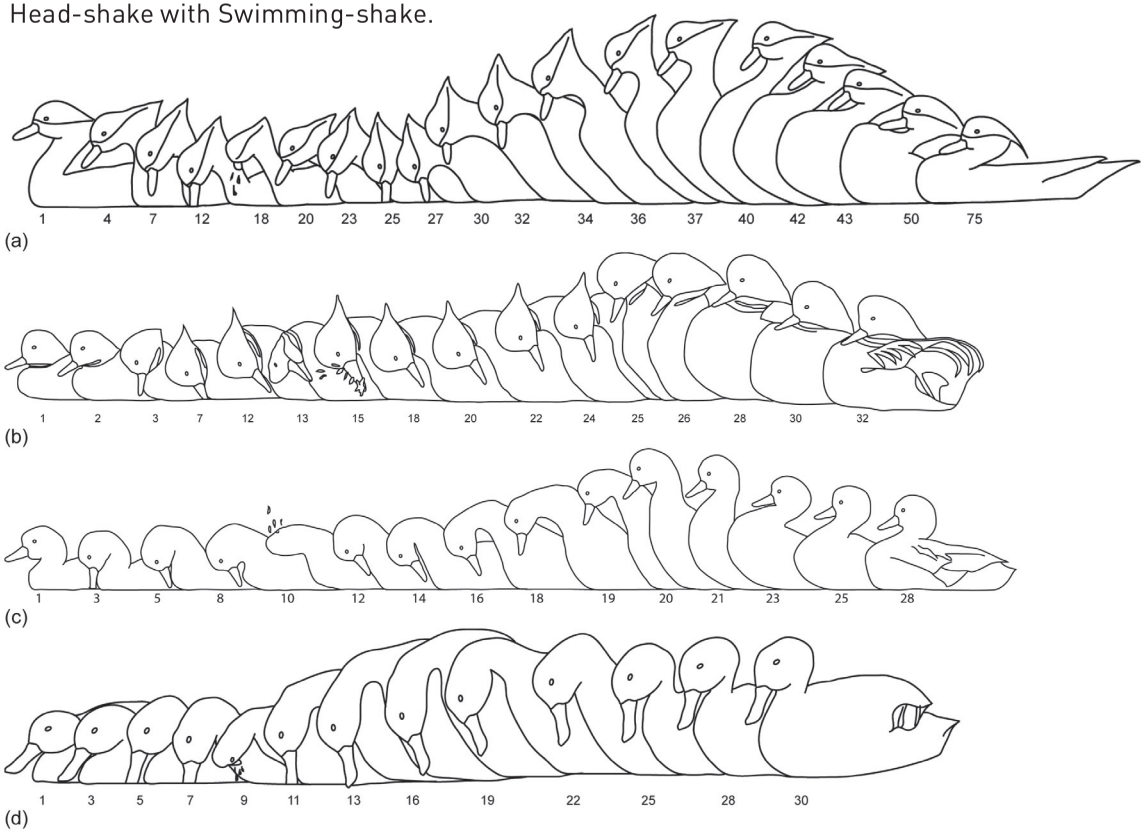
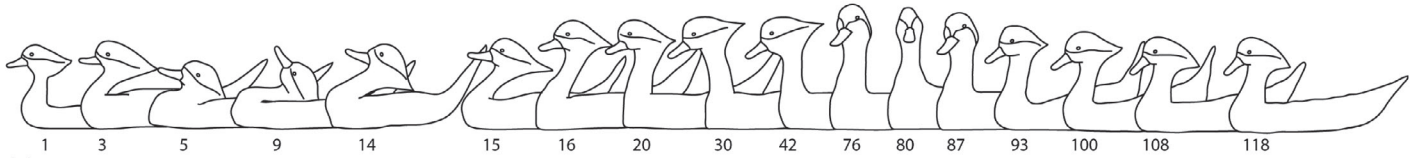
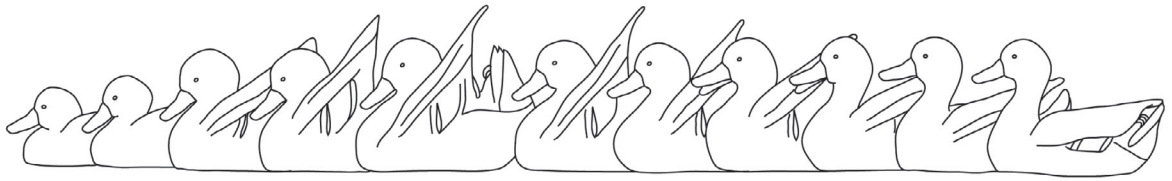


Figure 2. Head-back/Tail-up and Head-Up-Tail-Up (HUTU) displays; numbers indicate frame number of tracing; (a) traced from NTSC-format VHS copy (30 frames per second) of PAL video; (b) traced from Digital8 video (30 frames per second). (a) Crested Duck male performing Head-back/Tail-up plus Turn-Head-Toward-Female (THTF); (b) Mallard male performing HUTU without THTF. Note differences in movement of head and wings between the two species. Vocalisation occurs in frame 80 of (a), in frame 15 of (b).



(a)



(b)

Figure 3. Male Crested Duck performs Preen-behind-wing to his mate (in foreground).

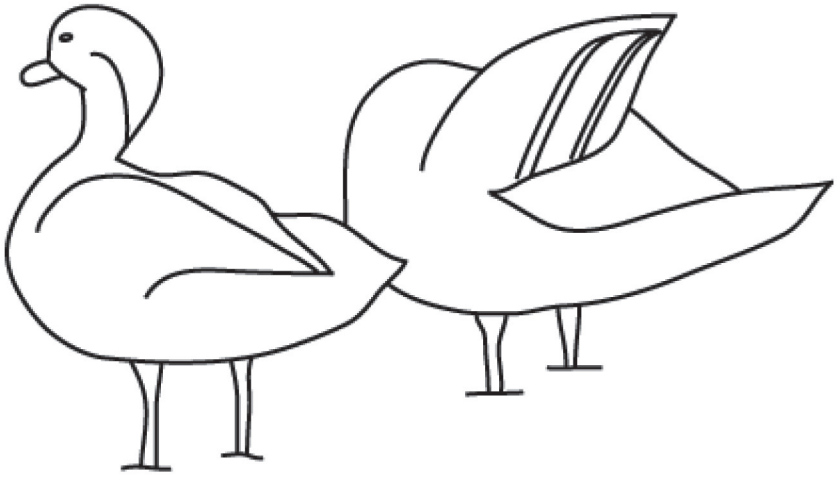
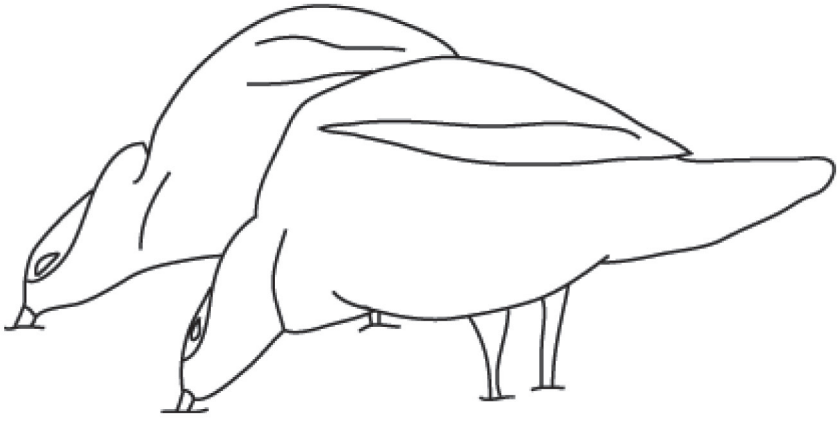


Figure 4. Crested Duck pair simultaneously perform Prolonged Dabble while standing in shallow water.



the Prolonged Dabble while doing a Backward-swim. When standing in shallow water, they may follow the Prolonged Dabble with a PBW display (n = 3).

Bill-up Call: (n = 33) When in large mixed-sex groups, males frequently (n = 30) respond to a female's bill-up Decrescendo with a single-note *pew* call, given with the neck erect and bill tilted almost to vertical (**Figure 5**). The vocalisation begins as the male lifts his head and culminates while the bill is 90˚ above horizontal; as the call ends, the bill is brought back to horizontal. Each display consists of one such bill-lift and vocalisation, with no repetition of either head movement or call.

Chin-lift: (n = 7) Once pair bonds have formed, an inciting female often elicits a Chin-lift response from her mate. The male typically lifts his bill to an angle 10˚ – 20˚ above horizontal. The bill may remain at this position or be repeatedly lifted further (the latter typically occurs in larger groups with several males). Rarely (n = 2), the male gives Chattering Calls during the Chin-lift. This response to inciting is also seen in Garganey *Anas querquedula* (Pearce 1999, 2000), wigeons *A. penelope* and *A. sibilatrix*, Falcated Duck *A. falcata*, Blue-winged Teal *A. discors* and Cinnamon Teal *A. cyanoptera* (Johnsgard 1965).

Chattering Call: (n = 59) This call seems to be quite diverse in function and consists of a rapid series of *che che che che* calls. Males may give this call while Chin-lifting when rivals approach, suggesting an agonistic function. They also call during pre-flight, usually with their mate. Pre-flight calling is often accompanied by slight head-pumping movements. Males may also call while their mates Incite, although this function is much less frequently used (n = 2). Male Falcated Duck, Cinnamon Teal and Cape Shoveler *Anas capensis* give similar calls during the Chin-lift (Johnsgard 1965). When performed during female inciting, these calls are similar to the Aggressive Calls of Garganey and appear to perform a similar function (Pearce 1999, 2000).

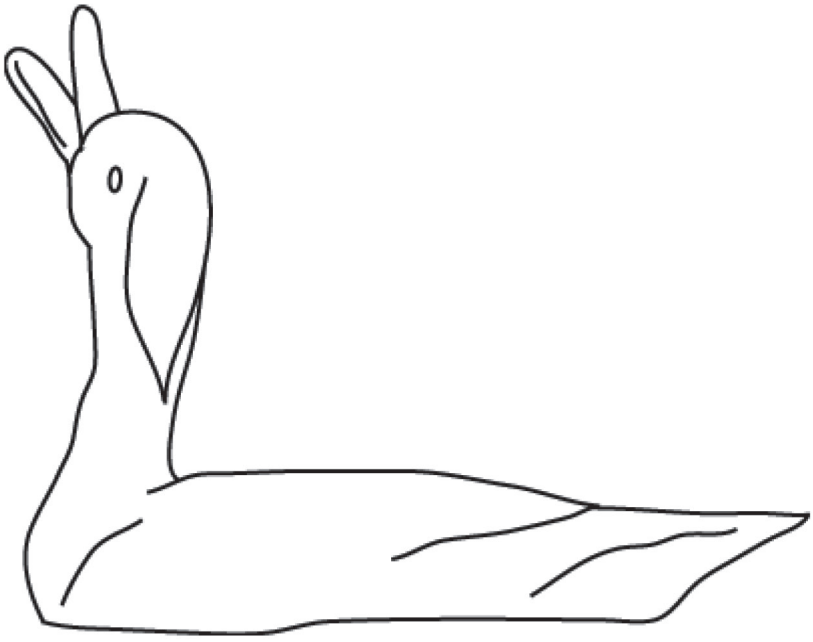
Open-bill-threat: (n = 9) This movement is much like that of *Anas*; the bill is held open as the head is thrust low in the direction of the bird being threatened. This display was exclusively used when chasing hetero- and conspecifics from the breeding territory.

Alarm Calls: (n = 3) Males give a long series of slow *pew pew pew pew* calls, opening the bill each time. While calling, males maintain an Erect posture with feathers, including the crest, held close to the body, giving the male a sleek appearance. This display is similar in form to the slow calling of most *Anas* when alarmed (e.g. slow-raeb in Mallards *A. platyrhynchos*, McKinney 1965; repeated 'toks' in Hottentot Teal, although they erect the crown feathers during the vocalisation, Pearce, 1999, 2000).

Female displays

Inciting (n = 55) This is a distinctive behaviour unlike that of other dabbling ducks but reminiscent of shelducks (Johnsgard 1965). The female swims in a circle around the male with her head forward and low over the water, angled slightly away from the preferred male. She then gives Open-bill Threat and loud *graaa* as head is brought back from

Figure 5. Crested Duck Bill-up display. Both males and female adopt this posture while vocalising; males give Bill-up Call and females give Decrescendo.



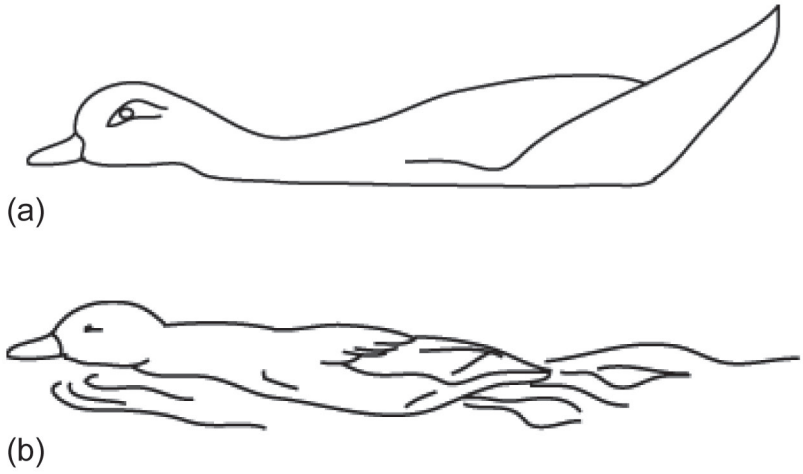
Open-bill Threat. This display is distinct from the Inciting of *Anas* in the lack of chin-lifting movements interspersed between threats (Johnsgard 1965). Duration of Inciting bouts ranges from 2 s to 42 s (mean: 10.09 ± 11.21 s).

Open-bill threat: (n = 10) Females perform the same movement as males, with a ritualised forward-and-down head movement.

Decrescendo: (n = 63) Johnsgard (1965) noted that the Decrescendo call is very mallard-like, usually with five or more syllables, descending gradually in pitch. It was found that Decrescendo calls typically consist of four notes (mean = 3.74), but can consist of 2–6 notes, with an emphasis on the second and third notes. During social courtship bouts involving several males and females, females gave pronounced Bill-up (**Figure 5**), with neck and bill extended vertically, when delivering these calls. This vertical movement of the bill is unlike that of any *Anas* species (Johnsgard 1965).

Low-swim: (n = 22) Females in mixed-sex groups swim low in the water, with neck submerged and tail slightly lifted. Called Nod-swimming by Johnsgard (1965), Low-swim resembles the Steam of female mallards, in that the head is held out low over the water and there is no real nodding. In Steam, however, the female holds the length of the body low to the water's surface (**Figure 6b**), whereas in Low-swim the female conspicuously lifts the tail and

Figure 6. Female displays that elicit male courtship. (a) Crested Duck female performs Low-Swim; note lifted posterior end and tail. (b) Mallard female performs Steam; note position of entire body low in the water.



rump (**Figure 6a**). In both displays, the female tends to swim in circles around the courted male, and both Low-swim and Steam appear to elicit male courtship. On 12 occasions, Crested Duck males responded to a Low-swim with Backward-swim.

Preen-behind-wing: (n = 4) As with males, females may lift either the wing away from or closest to the male. This display often follows prolonged dabble (n = 3). Jones (1948) also recorded female PBW display in *L. s. alticola*.

Prolonged Dabble: (n = 5) This display is the same when performed by females or by males. In this study, females performed the prolonged dabble only when standing in shallow water with their mates.

Threat Calls: (n = 19) Threat calls consist of a prolonged series of *tuc tuc tuc tuc* notes, more quack-like than males' *che che* chattering calls. Females may give these calls with slight head-pumping, and they frequently give these calls during pre-flight movements.

Copulation behaviour

Pre-copulatory Pumping: The head movements made during Pre-copulatory Pumping are very *Anas*-like, as noted by Johnsgard (1965).

Copulation: (n = 4) On two occasions, the male dabbled at the female's back prior to mounting. The male wags his tail repeatedly after mounting the prone female, then moves the tail to the side (to right and left sides equally) for intromission and immediately dismounts. Duration of copulation, from mount to dismount, averages 8.25 s (± 2.63 s).

Post-copulatory Display: (n = 4) After copulation, the male dismounts and

gives a Head-back/Tail-up display. On three occasions, he followed the display with THTF, then maintained the erect-neck, tail-up position while swimming in front of the female. The male's head was turned to the side, as if to maintain position relative to the female (this is supported by the male turning his head to the other side when the female moved to that side). Unless disturbed by other birds, the male continues leading the female in this way for 14–17 s before returning to a normal swimming posture. The female alternates between bathing and Inciting as she follows the male during this display. The Head-back/Tail-up post-copulatory display was not described by either Johnsgard (1965) or Jones (1948), who both noted a mallard-like Nod-swimming display instead. Nod-swim was not observed in this study.

Discussion

Displays unique to *Lophonetta*

This study found two displays unique to *Lophonetta*: the Backward-swim and the Bill-up Call. Backward-swim is a conspicuous display in the Crested Duck repertoire. Males frequently perform this movement during courting bouts, particularly in large mixed-sex groups. It appears to function to maintain broadside orientation to the courted female, and other displays may be given while the male swims in this unusual manner. The Bill-up Call and other displays incorporating an exaggerated vertical movement of the bill (Decrescendo, Head-shake) are also unique to this species. No species of *Anas* have been observed performing such exaggerated head movements (bill lifted 90˚ above horizontal) during vocalisations, nor do *Anas* females tend to perform exaggerated movements during Decrescendo calls in the manner of Crested Ducks. The Bill-up Call also differs from Chin-lifting in *Anas* in the lack of repetition of either head movement or vocalisation. For example, various displays of the Mallard, Chiloe Wigeon *Anas sibilatrix* and Green-winged Teal *Anas crecca* involve uptilting of the bill, but none of these species raise the bill higher than 45˚ above horizontal, nor do their displays involve single bill lifts or calls (Johnsgard 1965).

Convergent display evolution

Double Grunt-whistle: The DGW involves two quite distinct movements – (1) dipping the bill and spraying water towards the female and (2) the vertical movement typically associated with a Swimming-shake. Lorenz (1953) and von de Wall (1963) discussed the two elements (Bill-dip + Head-shake and Swimming-shake) in the evolution of the GW. They noted that the bill-dip and rising of forepart of body *overlap* in most *Anas* (see **Figure 1d**), but occur one after another in Crested Duck (**Figure 1a**). Von de Wall also notes that the double nature of the GW can be seen in Falcated Duck and Gadwall *A. strepera* (**Figures 1b,c**). The two elements cannot be distinguished in members of the mallard/teal/pintail group because they have merged into one by overlapping (**Figure 1d**).

The authors concur with Lorenz (1953) and von de Wall (1963) in their suggestion that both displays probably

arose as these components became linked in the birds' display repertoires. However, the authors disagree with von de Wall's (1963) and Johnsgard's (1965) assessments of the DGW and GW as homologous displays. The distinct differences in the form of DGW and GW suggest that these two displays evolved independently, and are thus convergent, not homologous, displays.

Head-back/Tail-up: The erect neck and lifted tail of this display are reminiscent of the Head-Up-Tail-Up (HUTU) display of *Anas* (Johnsgard 1965 described it as a specialised HUTU), however, like the DGW, the specific body movements involved in these displays indicate that Head-back/Tail-up and HUTU are unlikely to be homologous. The Head-back/Tail-up display of *Lophonetta* begins with a lifted head, which is then laid back, almost touching the scapulars. Only when the head is raised again does the tail begin to lift. In the *Anas* HUTU, the head and tail are raised simultaneously, and the head is never moved to a position just over the back (**Figure 2b**). Duration of the tail-up component also differs between these displays: *Anas* males lower the tail prior to any THTF movement, whereas Crested Duck males hold the tail at an upward angle until THTF is complete. In addition, the wings are typically lifted as much as 45° during the HUTU (Stevens 2002), a movement that does not occur in the Head-back/Tail-up display of the Crested Duck. Although both displays involve vocalisation, Crested Duck males call when they face the female during the THTF component of Head-back/Tail-up, whereas *Anas* males call as the head, wings and tail are lowered from HUTU (**Figure 2**), prior to THTF. Such striking differences between the *Anas* HUTU and the *Lophonetta* Head-back/Tail-up provide strong evidence of convergent evolution.

Prolonged Dabble: The Prolonged Dabble is another display that appears to have evolved independently in *Lophonetta*. A ritualised dabbling display performed broadside to the female is present in several species of *Anas* (e.g. Blue-winged Teal, McKinney 1970; Speckled Teal *A. flavirostris*, McKinney *et al*. 1990; Hottentot Teal, Pearce 1999), as well as in *Lophonetta*, but the details of the displays differ. In *Anas*, the display always involves erection of feathers along the back, whereas nape and back feathers are held close to the body by the Crested Duck. Additionally, only males appear to perform the Lateral Dabble in *Anas*, and it seems to function as a courtship display in these species. In contrast, both males and females perform the Prolonged Dabble in the Crested Duck, often simultaneously, and it appears to function as a pair-bond maintenance display. Thus, the resemblance between Prolonged Dabble and Lateral Dabble appears to be superficial, as the details of these displays are quite dissimilar.

Low-swim: Female dabbling ducks may use a low-profile display to attract the attention of males and elicit courtship displays. Such behaviour occurs in the mallard group as well as in the Crested Duck, but the form of the display used differs. Although females of both species swim with the bill just over the surface of the water, the position of the rest of the body differs markedly. This distinction, coupled with the absence of a low swimming

display in other *Anas*, suggests that the Low-swim of the Crested Duck and the Steam of the mallard group evolved independently.

Evidence of convergent evolution of displays in *Lophonetta* and *Anas* has previously been described by Kaltenhauser (1971), who strongly disagreed with Johnsgard's (1965) placement of *Lophonetta* between pintails and mallards. She argued that these various courtship displays evolved convergently, based on anatomical features and ethology, and the authors concur with her assessment. Very few behaviours exhibited by *Lophonetta* appear to be homologous to those of *Anas*: Open-bill Threat, Chin-lift, Chattering Calls, Alarm Calls, Head-shakes (McKinney 1965), and PBW (McKinney, 1992). Most of these behaviours are associated with agonistic interactions and pre-flight movements, thus they occur in some form in all wildfowl and are likely to be ancestral to the dabbling duck group.

Crested Duck displays may have evolved to be particularly exaggerated, showy and vocal in response to their environment. Open spaces on mountain plateaus are likely to be windy (H.G. Young, personal observation), thus loud vocalisations would be needed to communicate over substantial distances. Visually, exaggerated movements, particularly those that emphasise the colour contrast between the black undertail coverts and buff flank feathers, probably enhance signal transmission over large distances. In addition, the Backward-swim may have evolved in response to running water in the Crested Duck habitat – it effectively allows males to maintain their position relative to a female under conditions that would otherwise separate the two individuals.

The unique display repertoire exhibited by *Lophonetta* supports its placement in a position basal to the *Anas* and suggests that this species lacks close relatives. Detailed behavioural data are unavailable for Bronze-winged Duck but would provide a key piece of evidence to address questions about species' relationships and behavioural evolution within this group.

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