The evolution of postcopulatory displays in dabbling ducks (Anatini): a phylogenetic perspective

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Although postcopulatory displays are widespread in animals, little is known about their function or the intended receiver. The postcopulatory displays of dabbling ducks are among the best described for any animal group. We documented the presence of initial and additional postcopulatory displays in nearly all dabbling duck species. We then reconstructed the evolution of postcopulatory displays in dabbling ducks using a phylogeny derived from mitochondrial DNA sequences. The display immediately following copulation (the initial display) is highly stereotyped in most species and shows extreme phylogenetic conservation. In contrast, the performance of additional displays is less stereotyped and less phylogenetically conservative. We review the possible functions of postcopulatory displays. Using evidence from display orientation, display form and phylogenetic reconstruction, we suggest that the most likely functions of postcopulatory displays in dabbling ducks are pair bond maintenance, individual identification, or signalling a successful copulation.

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The behaviour of animals before, during and after copulation has been studied more intensively in recent years because of interest in the mechanisms and consequences of sexual selection. For example, studies of copulatory behaviour may give clues to functional explanations for the diversity of mating systems (Thornhill & Alcock 1983; Choe & Crespi 1997), male intromittent organ morphology (Eberhard 1985), patterns of mate guarding (Alcock 1994), mechanisms of sperm competition (Birkhead et al. 1987; Birkhead 1988, 1996; Birkhead & Møller 1992, 1998) and cryptic female choice (Eberhard 1996). In addition to the major function of sperm transfer, intensive research on single species has shown that copulation may have social and/or physiological functions (e.g. de Waal 1987; Dewsbury 1988). Comparative studies of copulatory behaviour in groups of closely related species have led to new insights on the evolutionary history and adaptations of copulatory behaviour (e.g. Dewsbury 1975, 1985; Dewsbury & Pierce 1989; Langtimm & Dewsbury 1991). In this study we draw

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attention to a prominent but neglected aspect of copulatory behaviour: postcopulatory displays.

Male postcopulatory displays have been reported in many groups of animals (e.g. crickets, bats, primates, birds), but the adaptive significance, and even the intended receiver, of these performances is generally unknown (Smith 1977; Bradbury & Vehrencamp 1998). Possibilities for the function of postcopulatory displays include (1) facilitating species recognition, (2) reinforcing the pair bond, (3) facilitating repeated copulations, (4) calming the female and ensuring sperm retention, (5) signalling mate-guarding intentions to other males, (6) advertising male quality to other females, (7) reaffirming the male's identity to the female, or (8) signalling a successful copulation and lack of male intention to repeat copulation. These displays probably play important roles in reproduction and merit serious study. Surprisingly, even in birds, in which reproductive behaviour has been much studied, intensive research on postcopulatory displays does not appear to have been done on any species.

Although postcopulatory displays have been recorded in many groups of birds (e.g. grebes, pelicans, grouse, rails, pigeons), accurate descriptions of the behaviours are frequently lacking in the literature. Often copulations are rare, and the birds may be difficult to observe, or the activities following copulations may be fleeting or subtle.

Most waterfowl species (family: Anatidae), however, copulate while swimming on open water. Copulations in waterfowl are relatively frequent and easy to observe and record on film or videotape. In this group, postcopulatory displays are generally stereotypical, distinctive in form, and so convincingly homologous in closely related species that their value as taxonomic characters has long been recognized (Lorenz 1941; Johnsgard 1965). Indeed, homologous postcopulatory displays were key elements in the reclassification of several duck species (e.g. marbled teal, *Marmaronetta angustirostris*, and white-backed duck, *Thalassornis leuconotis*; Johnsgard 1961, 1967).

Many of Lorenz's (1941) conclusions on display homologies in dabbling ducks (tribe: Anatini) were affirmed and extended by other workers (e.g. Delacour & Mayr 1945; von de Wall 1963; Johnsgard 1965; McKinney 1965, 1978; Kaltenhauser 1971). However, a major limitation to these studies was the absence of a well-supported phylogeny for this tribe. While Lorenz identified several subgroups (wigeons, pintails, mallards, etc.), he was unable to infer the relative ages of these groups or the direction of evolutionary changes in behaviour. In this study, we used a phylogenetic hypothesis for the dabbling ducks based on mitochondrial DNA sequences (Johnson & Sorenson 1998, 1999), which makes explicit the relative ages and branching points in the dabbling duck phylogeny. We begin by reviewing available descriptive information on the postcopulatory displays of each species. We then infer when particular displays evolved and how postcopulatory displays have changed during the evolution of the dabbling ducks by mapping these displays on the dabbling duck phylogeny. We also consider evidence relating to possible functions of postcopulatory displays in ducks.

METHODS

Whenever possible the descriptions of postcopulatory behaviour are based on film or video records, but we used verbal descriptions by experienced observers for species with no films or tapes available. Many records taken from the literature (Table 1) included captive waterfowl in zoos or private collections, although some examined wild birds. Most of our own data (Table 1) were collected between 1965 and 1998 during studies of full-winged (i.e. nonpinioned) ducks breeding in flight pens (described in McKinney 1967) at the University of Minnesota's Cedar Creek Natural History Area, Bethel, Minnesota. The records of postcopulatory sequences were based on film (8 and 16 mm) and videotape recordings made on captive and wild birds, and subsequently analysed using frame-by-frame film projectors and slow-motion video playback of tapes. Very little individual variation in the form of postcopulatory displays was detected, so we focused largely on which displays were performed and in what sequence.

We reconstructed postcopulatory displays over a phylogeny for the dabbling ducks based on mitochondrial DNA sequences (Figure 1 in Johnson & Sorenson, 1999). In these reconstructions, we used unordered parsimony and MacClade (Maddison & Maddison 1992) to deter-

mine when gains and losses in displays occurred. In cases where more than one most parsimonious reconstruction was possible, we examined all possible reconstructions using MacClade (Maddison & Maddison 1992).

RESULTS

Comparative Review

We describe below the postcopulatory behaviour of 10 subgroups within Anatini (Johnson & Sorenson 1999), proceeding from the most basal to the most derived clades. Sources of information are detailed in Table 1.

We consider only male postcopulatory behaviour (Table 1). In contrast to many other waterfowl in which both partners perform postcopulatory displays (e.g. swans, geese, pochards), female dabbling ducks generally do not. Females usually begin to bathe, wing-flap and preen immediately after the male dismounts. We make a fundamental distinction between the 'initial display' performed by the male (usually accompanied by a single call) and 'additional displays', which may or may not follow. Only 'pair copulations' in which both partners were willing participants are included in this section. 'Forced copulations' (both intra- and extrapair) are discussed separately.

South American ducks

This group of seven species in four genera (*Amazonetta, Lophonetta, Speculanas, Tachyeres*) forms a well-supported clade, separate from other dabbling ducks. Copulatory behaviour is poorly documented in most of these species, and the possibility that each genus has distinctive displays cannot be excluded. The male Brazilian teal, *Amazonetta brasiliensis*, has an initial display that appears to be homologous to the Wings-up-bill-down (WUBD) of the blue-winged ducks and silver teals (Fig. 1d). In blue-winged ducks, WUBD was described as follows: 'The male points the bill downward at an angle of about 60 degrees to the horizontal, erects feathers of the head and neck, raises the wing-tips slightly as the tail is wagged, paddles the feet rapidly, and gives one or more calls: the Single Call or Male Decrescendo' (McKinney 1970).

Baikal teal, Anas formosa

This species has no close relatives (Johnson & Sorenson 1999), and its postcopulatory behaviour has not been described.

Silver teals and garganey, Anas querquedula

Analysis of videotapes of three species (*Anas versicolor, A. hottentota, A. querquedula*) shows that the male's initial display is a brief WUBD (Fig. 1c). This is often followed immediately by Erect-broadside (*A. hottentota*) or Erect-facing (*A. versicolor*) (Fig. 1g; also Figure 55 in Johnsgard 1965, page 195) accompanied by Repeated calls. In both of these Erect displays, the male's neck is stretched vertically while the head is held stiffly in one position as the calls are given. In *A. hottentota* the male's bill is turned slightly towards the female as the head is raised to the

Table 1. Post-copulatory displays of dabbling ducks

| Species | Initial display | | | | | Call(s) | | Additional displays | | | | | Swim displays | | | N | Source |
	Bridle	WUBD	Erect Broadside	Erect Facing	Erect THTF	Single	Repeated	Erect Broadside	Erect Facing	Lateral	THTF	Burps	Steam	Nod	TBH		
Amazonetta brasiliensis		1				1										3+	This study
Speculanas specularis																	
Lophonetta specularioides																	
Tachyeres pteneres																	
A. formosa																	
A. querquedula		1				1			2							3	A. Pearce, unpublished data
A. hottentota		1					2	2	2		3r				4r	16	A. Pearce, unpublished data
A. puna		1				1										3	Johnsgard 1965; Lorenz 1971
A. versicolor		1				1?	2		2							18+	This study; Johnsgard 1965
A. platalea		1?				1			2							?	Johnsgard 1965
A. rhynchotis																	
A. cyanoptera		1				1	2		2							2	McKinney 1970
A. discors		1				1	2	2r							2r	12	McKinney 1970
A. smithii		1				1	2		2r							7	McKinney 1970
A. clypeata		1				1	2		2r, 3r						2r, 3r	132	McKinney 1970
A. strepera						1	2		2							?	Johnsgard 1965; Schommer 1977
A. falcata					1												
A. penelope																	
A. americana			1	1r		1r										27	Wishart 1983
A. sibilatrix			1			1r			2?							58	Brewer 1997
A. waigiuensis																	
A. aucklandica																	
A. chlorotis	1					1			3					2	4	7	M. J. Williams, unpublished data; J. C. Elbert, unpublished data
A. capensis	1			1r		1		2				2r				100	This study
A. erythrorhyncha	1					1						2r				42	This study; Skead 1976
A. bahamensis	1					1						2				69	This study; L. G. Sorenson, unpublished data
A. georgica	1					1?										?	Lorenz 1971
A. acuta	1					1			2?			2?			2?	14	Smith 1963
A. bernieri	1					1								2	3	5	H. G. Young, unpublished data
A. castanea	1					1		2?	2?							?	Marchant & Higgins 1990
A. gibberifrons	1					1		2?								?	Marchant & Higgins 1990
A. crecca	1					1				2						?	von de Wall 1963
A. carolinensis	1					1				2						17	This study
A. flavirostris	1					1		2	2, 3	2?						65	This study
A. andium																	
A. sparsa	1					1				1r, 2						24	McKinney et al. 1978
A. undulata	1					1							2	3?	3	?	This study; Skead 1976
A. platyrhynchos	1					1							2	3?	3r, 4	37+	This study; Johnsgard 1965
A. diazi	1					1							2		3	?	Johnsgard 1965
A. rubripes	1					1							2		3	?	Johnsgard 1965
A. fulvigula	1					1							2		3	15	This study
A. superciliosa	1					1			3?				2		3, 4	?	Williams 1969
A. laysanensis	1					1							2	3	4	1+	This study; Johnsgard 1965
A. luzonica	1					1								2	3	?	Johnsgard 1965
A. zonorhyncha	1					1							2		3	?	Johnsgard 1965
A. poecilorhyncha	1					1								2	3	?	Johnsgard 1965
A. wyvilliana	1					1							2		3	?	Johnsgard 1965
A. melleri	1					1							2	3	4	20	H. G. Young, unpublished data

1: Initial display movement (with or without call); 2, 3, 4: second, third and fourth displays in sequence, respectively; r: rare; ?: incomplete record. N: Number of copulations observed. Displays recorded only once or twice in a species are not included.
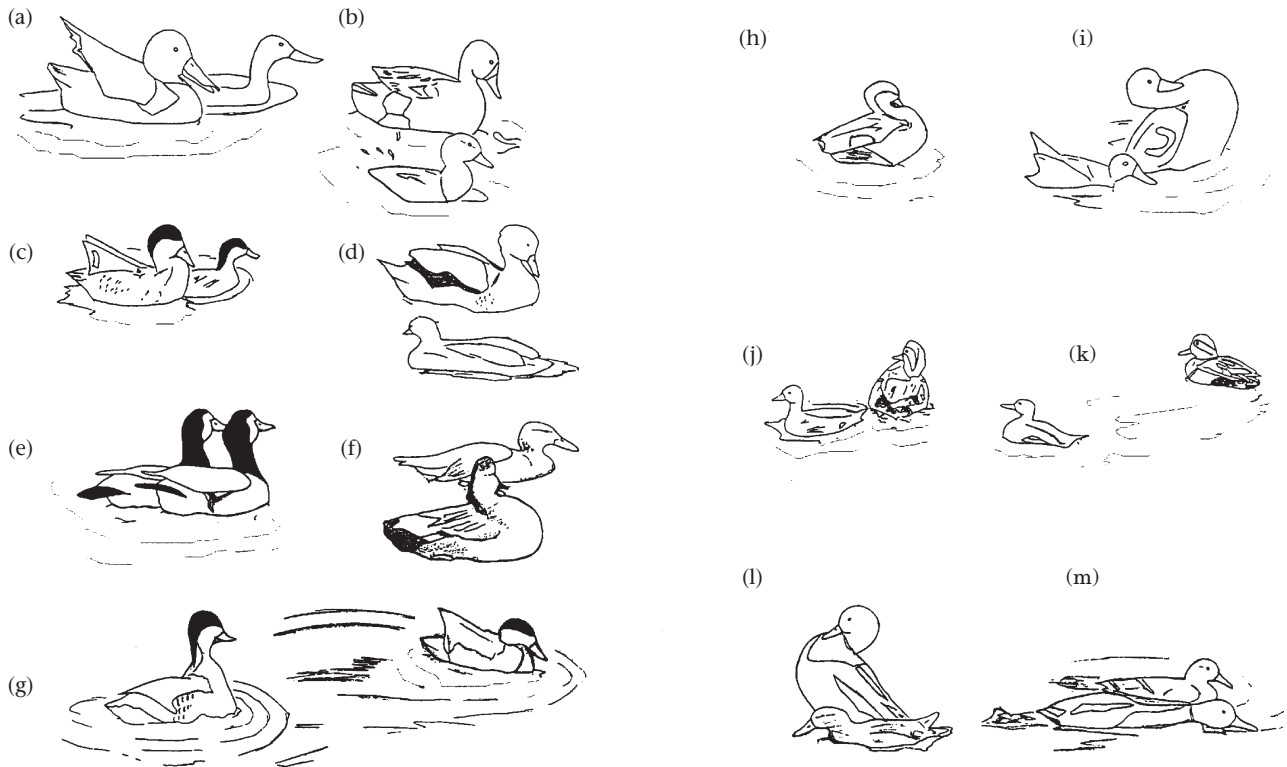
Figure 1. Postcopulatory displays of male dabbling ducks drawn from film and videotaped records. Wings-up-bill-down displays of (a) northern shoveller, *Anas clypeata*, (b) blue-winged teal, *A. discors*, (c) silver teal, *A. versicolor* and (d) Brazilian teal, *Amazonetta brasiliensis*; (e) Erect-broadside of Chiloe wigeon, *Anas sibilatrix*, male in foreground; (f) Turn-head-towards-female of gadwall, *A. strepera*; (g) Erect-facing of silver teal; (h) Bridle of red-billed pintail, *A. erythrorhyncha*, and (i) Cape teal, *A. capensis*; (j) Bridle and (k) Lateral Posture of American green-winged teal, *Anas carolinensis*; (l) Bridle and (m) Steam of mallard, *Anas platyrhynchos*.

Erect posture, but in *A. versicolor* the male's bill is in the central plane.

Blue-winged ducks

The six species in this clade include the shovelers and their close relatives. Males of at least four species perform WUBD as an initial display (Fig. 1a, b) (also see Figures 16, 17 in McKinney 1970). In *A. clypeata*, at least, this display is usually followed by Repeated calls. Erect-facing has also been recorded as an additional display in this clade.

Wigeons

In one intensive study of *A. sibilatrix*, postcopulatory displays were recorded after only 27 of 58 pair copulations (47%) (Brewer 1997). In this species, and in *A. americana*, the most frequent initial male display is Erect-broadside (Fig. 1e), apparently without any accompanying vocalization. Less frequently (or rarely) the male gives a single (Rakoo) call instead. Male gadwalls (*A. strepera*) give Turn-head-towards-female with a single call, then turn the body to Erect-facing (Fig. 1f). Although the behaviour of two species (*A. penelope* and *A. falcata*) is still uncertain, it appears that the wigeon group repertoire includes neither the WUBD of the blue-winged duck/ silver teal groups nor the Bridle of the teal/pintail/mallard groups (see below).

Brown teals

The brown teal, *A. chlorotis*, male performs an initial Bridle with a single call, and this is followed by vigorous Nod-swim, Turn-body-towards-female (probably homologous to Erect-facing), and Turn-back-of-head. As in all species that perform postcopulatory Bridle, the male's head is slightly off-centre and the bill lies on the male's chest on the side towards the female at the peak of the display. The postcopulatory behaviour of *A. aucklandica* has not been described.

Pintails and Cape teal, Anas capensis

Males of all members of this group perform Bridle with a single call as the initial display (Fig. 1h, i). In Cape teal, the male's wings are fanned partly open during Bridle, exposing conspicuous white markings on the secondaries. In at least four pintail species, Bridle may be followed by a number of Burps (characteristic whistling calls each accompanied by raising of the head; Lorenz 1971), and in three species the male may swim around the female as he calls. Erect-broadside or Turn-back-of-head sometimes follow.

Grey teals

All three species (*A. castanea*, *A. gibberifrons*, *A. bernieri*) perform Bridle with a single call as the initial male

display. Additional displays recorded are Erect-broadside, Erect-facing, Nod-swim and Turn-back-of-head.

Green-winged teals

Three species (*A. crecca*, *A. carolinensis*, *A. flavirostris*) have Bridle with single call as the initial male display (Fig. 1j). In *A. carolinensis*, a frequent additional display is Lateral Posture, in which the male holds a position with his body broadside to the female, crest raised, and wings slightly fluffed up (possibly giving a call) but the head is not held erect (Fig. 1k). In this species, Nod-swim occurs rarely. In *A. flavirostris*, Erect-broadside, Lateral Posture and Face-female (probably homologous to Erect-facing) may occur as additional displays after Bridle. The behaviour of *A. andium* has not been described.

Mallards

All 13 species in the mallard group perform Bridle with a single whistle call. In many of these species, Bridle is immediately followed by Steam (Fig. 1l, m), in which the male swims around the female with his head forward just above the water's surface. Steam may be followed by Nod-swim and/or Turn-back-of-head. Unlike other mallard species, *A. sparsa* has not been recorded performing these additional displays, but instead the male often adopts a Lateral Posture similar to that of *A. carolinensis*. Also, unlike any other dabbling ducks studied to date, *A. sparsa* pairs often engage in a Mutual Greeting display after the male performs Bridle.

Postcopulation Display Patterns

In most species of dabbling ducks, males almost always perform a species-characteristic initial display (e.g. WUBD, Bridle) immediately after a successful pair copulation. Exceptions to this pattern are (1) members of the wigeon group, in which males often do not give any postcopulatory displays (e.g. 47% of copulations in *A. sibilatrix*), and (2) some pintails (notably *A. acuta*) and the gadwall in which postcopulatory behaviour appears to be quite variable (Smith 1963; Schommer 1977).

The most obvious display sequence, involving an initial display and an additional display, is the Bridle+Steam sequence typical of the mallard group (Fig. 1l, m). Other strong linkages are WUBD+Erect-facing in *A. versicolor*, Bridle+Lateral Posture in *A. carolinensis* (Fig. 1j, k), and Bridle+Erect-broadside in *A. f. flavirostris* and *A. capensis*. In most species, however, there is considerable variation in the presence and kind of additional displays.

A major difference between initial and additional displays is that initial displays tend to be brief, striking movements accompanied by a call (i.e. attention-getting displays) while additional displays tend to be quieter and more subtle. Initial displays have a strong orientation component, normally with the male's body (and especially his head) broadside to the female. Additional displays similarly have strong orientation components in relation to the female, but some entail the holding of a rigid posture either facing or broadside to the female (with a series of quiet calls in some species). Others

involve ritualized swimming manoeuvres. The male may swim around the female in a special posture (e.g. Steam, Fig. 1m), or he may swim away from her, with or without Turn-back-of-head or Nod-swimming.

Display Homologies

Wings-up-bill-down is a very distinctive display, readily identifiable in videotapes of silver teals and blue-winged ducks. The posture is adopted immediately after the male dismounts, while he is tail-wagging vigorously (presumably associated with reinversion of the phallus). In blue-winged ducks, a call accompanies the posture, but in silver teals (*A. hottentota* and *A. versicolor*) the call is delayed until the male adopts an Erect posture. The display of the Brazilian teal (Fig. 1d) appears to be identical in all respects to WUBD.

WUBD does not appear to be homologous to the Bill-down postcopulatory display of pochards (Aythyini; Johnsgard 1965). The latter posture involves deliberate stretching upward of the neck, with the bill pointing almost vertically downward, and it is held for some seconds as the male (and often the female also) swims stiffly along for several metres.

The vocalizations that accompany or follow WUBD have the same quality as the calls given by each species: 'peeew' or 'paaay' or 'raar' in blue-winged ducks, often followed by a series of Repeated calls (e.g. 'took-took, took-took' in *A. clypeata*; McKinney 1970). In *A. hottentota*, a series of quiet Repeated calls 'toc-toc-toc-toc-toc' has been recorded during Erect-broadside immediately after WUBD.

Bridle is a very striking display readily homologized across species. Postcopulatory Bridle corresponds to the Independent Bridle display performed by males of six *Anas* species during courtship (*A. crecca*, *A. carolinensis*, *A. flavirostris*, *A. castanea*, *A. gibberifrons*, *A. chlorotis*) (von de Wall 1963; Johnsgard 1965; Kaltenhauser 1971; Marchant & Higgins 1990). No differences have been detected in the form of this courtship display and that of postcopulatory Bridle in these *Anas* species. In all these species, a loud whistling call is given at the peak of Independent Bridle.

Erect-broadside and Erect-facing occur as initial displays primarily in the wigeon group. Similar displays involving erect body postures can also occur as additional displays in many species, and in the swim phase they can be accompanied by specialized swimming displays such as Nod or Turn-back-of-head.

Vocalizations characteristically accompany initial postcopulatory displays. A single loud whistle coincides with the peak of the movement in species that perform Bridle. In the blue-winged ducks, silver teal and wigeons, the vocal quality of the initial call varies between species and is similar to the quality of courtship or contact calls in each species.

A series of Repeated calls is also given in silver teal and a number of blue-winged ducks as additional calls after the initial vocalization. In the pintail group, males may give several Burps as additional displays.
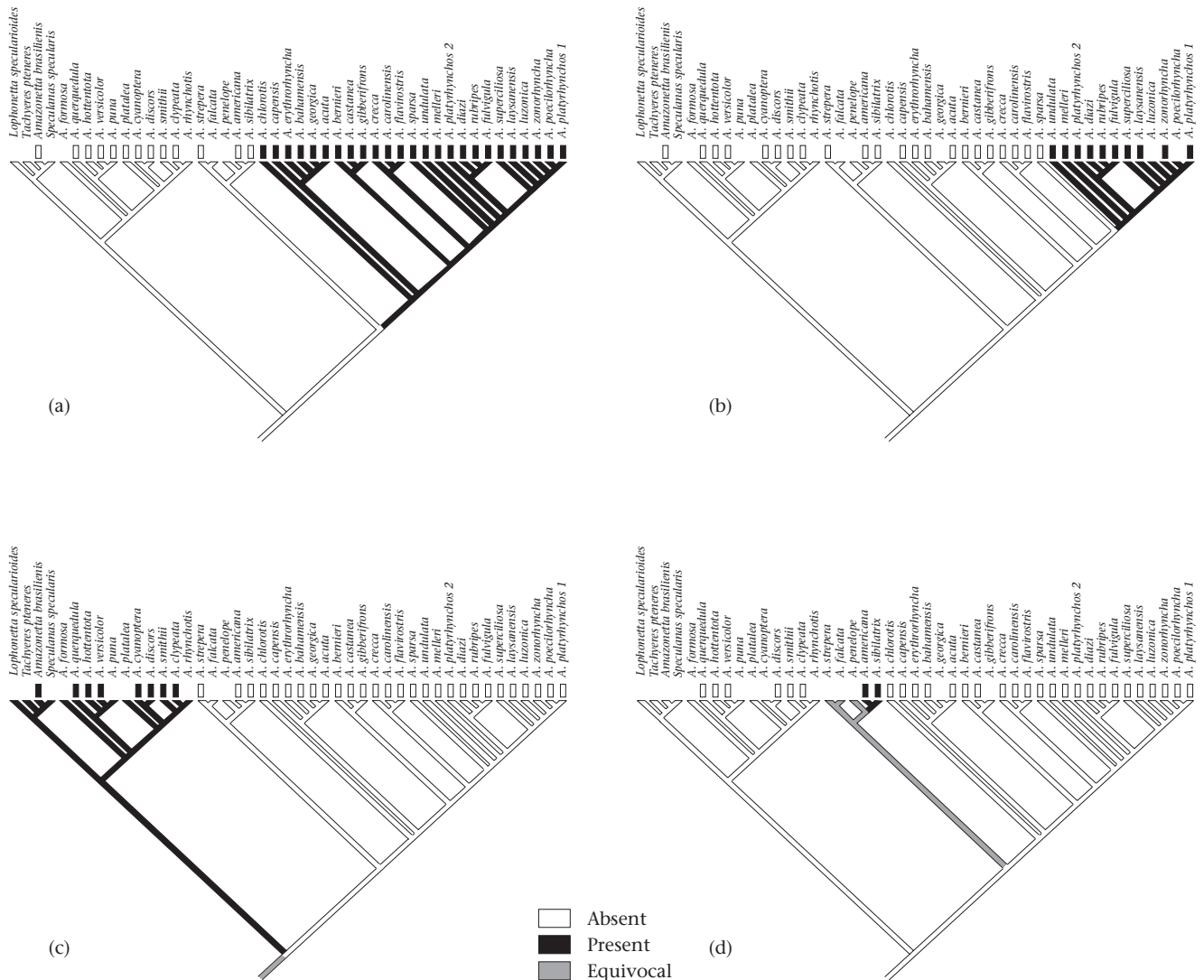
Figure 2. Phylogenetic reconstruction using unordered parsimony of initial postcopulatory displays. The phylogeny is based on mitochondrial DNA sequences (Johnson & Sorenson 1999). (a) Bridle, (b) Bridle+Steam sequence, (c) Wings-up-bill-down, (d) Erect-broadside. *A.: Anas*.

Displays after Forced Copulations

Forced extrapair copulations (FEPCs) occur in many species of dabbling ducks and are a secondary male reproductive strategy in some, and perhaps many, species (McKinney et al. 1983; McKinney & Evarts 1997). The presence of male postcopulatory displays was used as a criterion to judge whether FEPC attempts were successful in several early studies, but this poses problems (McKinney et al. 1983). For example, the female's mate may actively defend her from males attempting FEPCs, and males may be inhibited or prevented from performing displays while under attack. In one observational study of captive mallards, 58 of 71 (81.7%) apparently successful FEPCs were not followed by postcopulatory Bridle+Steam displays, including 10 cases in which the female's mate did not defend her (Cheng et al. 1982; McKinney et al. 1983). This suggests that performance of displays is not usual after FEPCs, at least in this species.

Forced pair copulations (FPCs) have been recorded in many species of ducks (McKinney & Evarts 1997), but they are relatively infrequent, and reliable data on the presence or absence of postcopulatory displays are scarce. Barrett (1973) observed 33 FPCs in eight pairs of captive mallards and judged that 11 (33%) were successful based on the presence of displays.

Phylogenetic Conservation of Displays

A clear pattern emerges when initial postcopulatory displays are reconstructed on the molecular tree (Fig. 2) indicating strong phylogenetic conservation. Wings-up-bill-down occurs only in one major clade of dabbling ducks (blue-winged ducks, silver teal and the Brazilian teal; Fig. 2b). If present in *Speculanas*, *Lophonetta* and *Tachyeres*, WUBD would be reconstructed as having only one origin and not being lost. However, if the display is absent in *Speculanas*, *Lophonetta* and *Tachyeres*, an independent origin in *Amazonetta* would be inferred. This
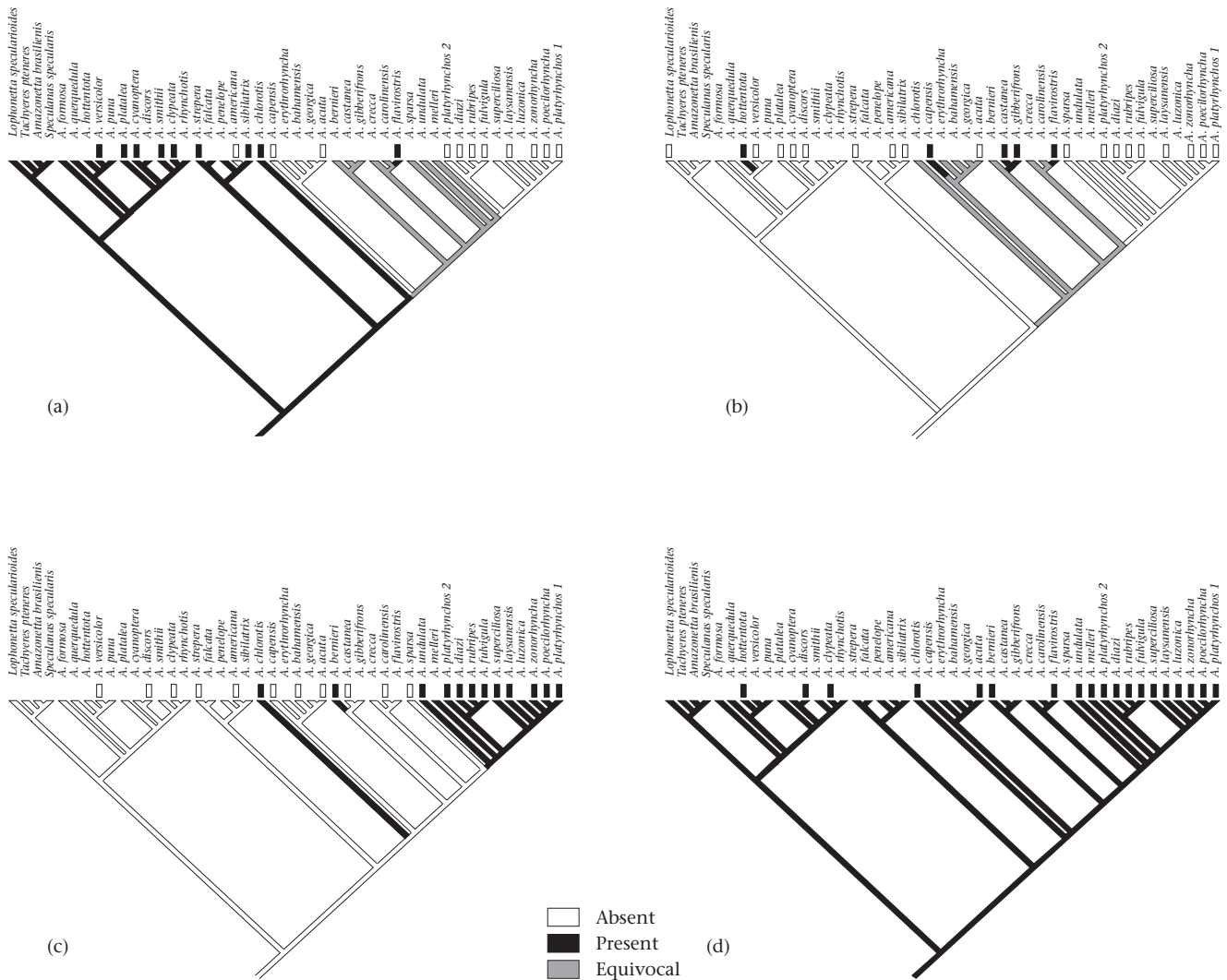
Figure 3. Phylogenetic reconstruction using unordered parsimony of additional postcopulatory displays. The phylogeny is based on mitochondrial DNA sequences (Johnson & Sorenson 1999). (a) Additional Erect-facing, (b) additional Erect-broadside, (c) Nod, (d) Turn-back-of-head. *A.: Anas*.

would be the only case of independent origin of an initial postcopulatory display in the dabbling ducks. In either case, this display is extremely conservative, being found throughout the blue-winged ducks and silver teals. Erect-broadside as an initial display occurs only in the gadwall and wigeon clade, evolving once. Bridle evolves only once in the clade containing the brown teals, pintails, grey teals, green-winged teals and mallards. The tight linkage of Bridle+Steam occurs only in the mallard group.

In contrast to initial displays, the phylogenetic reconstruction of additional displays indicates a less taxonomically restricted distribution of these displays (Erect-broadside, Erect-facing, Turn-back-of-head, Nod-swim) (Fig. 3). This may reflect the widespread use of such displays in courtship repertoires of dabbling ducks and some other waterfowl (e.g. Turn-back-of-head in *Aix sponsa*).

The level of homoplasy (i.e. convergence and reversals) of postcopulatory displays is much less than most other

behaviour in dabbling ducks. The average consistency index (CI) for the initial postcopulatory displays is 1.0 (i.e. all four initial postcopulatory displays show one gain and no losses on the tree). In contrast, the average CI for additional postcopulatory displays is 0.44 (range 0.20–1.0). In addition, the CIs for initial postcopulatory displays are much higher than the CIs for either male courtship displays (mean CI 0.72, range 0.17–1.0, for 17 displays from Johnson 1997) or other nondisplay behaviour (mean CI 0.15 for five nondisplay behaviours; from Foster et al. 1996). Thus, initial postcopulatory displays in dabbling ducks contain more phylogenetic information than courtship displays or nondisplay behaviour. Interestingly, the precopulatory display in dabbling ducks (Head-pumping) is universally conserved in the group, making the displays associated with copulation among the most phylogenetically conserved behaviours known in this group.

DISCUSSION

Phylogenetic Patterns

Recent research on waterfowl phylogeny based on morphological (Livezey 1986, 1991, 1997) and molecular characters (Madsen et al. 1988; Sraml et al. 1996; Johnson & Sorenson 1998, 1999) allows for the evaluation of phylogenetic signal in behavioural characters. Postcopulatory displays have proved to be very informative in waterfowl systematics and this is confirmed by the present analysis of Anatini. The initial displays performed immediately after copulation show extreme phylogenetic conservation. However, displays given after the initial display are more variable both within and between species. Reasons for these differences are not completely clear; perhaps species stereotypy and phylogenetic conservation are related in some way. These patterns bear further investigation in other behaviour and in other taxa.

While two major groups of dabbling ducks can each be defined by the presence of a particular initial display (i.e. WUBD and Bridle), the nature of the initial display in the wigeons+gadwall group is more puzzling. In *A. sibilatrix* and *A. americana* the initial display (Erect-broadside) is performed after only roughly half the copulations. It is likely that this Erect-broadside initial display is homologous to the Erect-broadside additional displays found in several species of blue-winged ducks as well as several teal and pintail lineages. Perhaps the wigeons actually lack an initial display such that the Erect-broadside that is performed is essentially an additional display. This view is consistent with the pattern of intraspecific variability in this and other wigeon postcopulatory displays.

In the gadwall, the initial display is Turn-head-towards-female often followed by Erect-facing. Turn-head-towards-female is derived in the gadwall and perhaps is a combination of Erect-broadside and Erect-facing. It may be that the lack of an initial display in the gadwall/wigeon group led to the evolution of a novel initial display in the gadwall.

Given the apparent conservation of initial postcopulatory displays, there are clear expectations for the behaviour of species that have not yet been examined. WUBD is likely to be found in *A. puna* and *A. rhynchotis*. If WUBD in the Brazilian teal is truly homologous to the same display in the blue-winged ducks, we would predict that WUBD (or a more ritualized form of this display) should be present in *Tachyeres*, *Lophonetta, Speculanas* and *A. formosa*. Similarly, postcopulatory Bridle is likely to be present in *A. aucklandica* and *A. andium*. Detailed information on the postcopulatory displays of *A. penelope* and *A. falcata* would indicate whether they have displays similar to *A. americana/sibilatrix* and *A. strepera*, respectively, or have unique postcopulatory behaviour (perhaps including some combination of additional displays observed in other species). This would be relevant to our interpretation of display evolution in this group (see above).

While WUBD does not appear in the courtship repertoire of the blue-winged ducks, it is interesting that some postcopulatory displays unique to mallards/teals/pintails also appear in courtship in some species (notably Bridle and Nod-swim). In addition, some other more widespread postcopulatory displays are also performed during courtship by many species (e.g. Turn-back-of-head). We are unable to determine whether these displays first evolved in the context of courtship or postcopulation. The origin of Bridle in the context of copulation is clearly in the ancestor of the mallard/teal/pintail clade. However, Independent Bridle may have evolved at the same time and have been lost twice (in the pintails and mallards) or it may have been derived three times (once in each of the three teal lineages; Johnson 1997). The latter scenario seems possible given the presence of Bridle in the postcopulatory displays of all these species. Similarly, while courtship Nod-swim evolved in the same mallard/teal/pintail ancestor as Bridle (Johnson 1997), postcopulatory Nod-swim appears to have been gained three times independently within this group. In either case, a major shift in courtship repertoires appears to have occurred in the ancestor to the mallards/teals/pintails.

Intended Receiver

In Anatini, as is generally the case in all waterfowl, copulations occur when the pair is alone or at least some distance from other birds. Consequently it is very unlikely that male postcopulatory displays are designed for communication with either male or female conspecifics other than the male's partner. Initial postcopulatory displays (WUBD, Bridle, Erect-broadside) are brief, attention-getting displays with strong orientation components in relation to the female. Initial displays are accompanied by brief vocalizations similar to those used by males of each species during courtship and/or as contact calls. Therefore initial postcopulatory displays are apparently designed as attention-getting signals directed to the male's own partner.

Although additional male postcopulatory displays are generally more variable in their presence/absence and in the kind of display performed, they are similar to initial displays in having strong orientation components directed towards the male's partner. For example, Nod-swim and Steam displays are generally performed as the male swims around the female, Turn-back-of-head as he swims away from her, and Erect-broadside and Erect-facing displays have characteristic orientations to the female. Additional displays tend to be quiet, subtle performances suited for close-range signalling and, as with initial postcopulatory displays, the intended receiver appears to be the male's partner.

Review of Functional Hypotheses

Examination of evolutionary patterns and general forms of postcopulatory displays can provide insights into hypotheses concerning their function. Functions of postcopulatory displays are largely unknown in animals, so we review the eight major hypotheses outlined in the Introduction in relation to the potential functions of

these displays in dabbling ducks. Because postcopulatory displays are generally subtle and appear to be oriented towards the male's mate, we consider it unlikely that these displays function as a mate-guarding display towards other males (hypothesis 5) or to signal male quality to other females (hypothesis 6).

A function of species recognition (hypothesis 1; Johnsgard 1962) is not supported by the phylogenetic distribution or nature of postcopulatory displays. If these displays aided females in distinguishing males of their own species from males of other species, we would predict that these displays would vary between closely related species. However, these displays are conserved among close relatives and show little evolutionary change in body movements. In addition, if species recognition is important to female dabbling ducks, it seems more likely that selection would favour a precopulatory signal of species' identity.

The hypothesis (2) that postcopulatory displays may reinforce the pair bond is consistent with the evolutionary conservation of initial postcopulatory displays. In addition, postcopulatory displays are found throughout waterfowl except for the muscovy, *Cairina moschata*, several oxyurids, and the musk duck, *Biziura lobata* (Johnsgard 1965; Johnsgard & Carbonell 1996). All of these exceptions have weak or nonexistent pair bonds, supporting the idea that postcopulatory displays might have a role in maintaining pair bonds. Furthermore, comparative evidence in other waterfowl suggests relationships between postcopulatory performances and pair bond maintenance (McKinney 1975). Swans, geese and whistling ducks, which have especially strong, long-term pair bonds, have elaborate mutual postcopulatory displays, and females of two shelducks species (*Tadorna cana*, *T. ferruginea*, in which adult sex ratios are female biased and females compete strongly for mates) are notably vocal after copulation (Johnsgard 1965).

It could be that repeated pair copulations are important for males in species with a high frequency of forced extrapair copulations. If postcopulatory displays were important in obtaining repeated copulations (hypothesis 3), then we might expect them to be more prominent in species with high extrapair copulation frequency, but this correlation remains to be evaluated in waterfowl.

Another possibility is that postcopulatory displays calm the female and ensure sperm retention (hypothesis 4). Recently much attention has been given to the possibility that female birds have some control over which sperm fertilize their eggs (Birkhead & Møller 1993, 1998; Birkhead 1996; Gowaty & Buschhaus 1998). Perhaps the quality of a male's postcopulatory displays influences the probability that the female retains his sperm. If females are choosing between the sperm of different males based on the performance of postcopulatory displays, we might expect females to solicit extrapair copulations and males to perform postcopulatory displays after all copulations. There is no evidence, however, that dabbling duck females solicit copulations from extrapair males. In addition, postcopulatory displays are performed more often after nonforced pair copulations (although they do

occur after some forced extrapair copulations; McKinney & Evarts 1997).

Males may be signalling their identity to the female partner through postcopulatory displays (hypothesis 7). Tonal qualities in the calls accompanying postcopulatory displays may show individual variations that allow the female to identify the male and assist in maintaining the pair bond. The fact that these displays are performed only by males in Anatini, and occur immediately after dismounting, is also consistent with an identification function. To test this hypothesis more fully, documentation of individual variation in vocalizations or display performance is needed.

A final possibility is that male postcopulatory displays simply signal to the female that, from the male's perspective, copulation has been successfully completed (hypothesis 8). Other displays in waterfowl that show extreme conservation (e.g. precopulatory head pumping) often tend to have a simple contextual meaning. In contrast, courtship displays may be under the operation of sexual selection, and thus might be expected to evolve more rapidly than other signals (Lande 1981). It may be that displays used for relatively simple messages and by all species in a clade are more conserved than displays that are involved in courtship. In addition, the fact that postcopulatory displays are not given after 'aborted' copulation attempts is further support for this idea.

By reconstructing evolutionary changes in postcopulatory display repertoires in dabbling ducks, we demonstrate that postcopulatory displays show extreme phytogenetic conservation. While the functions of postcopulatory displays are still largely unknown, we find pair bond maintenance, individual identification and signalling successful copulation as the most likely explanations for the functions of postcopulatory displays in dabbling ducks. Further observational and experimental studies should examine individual variation in both visual and vocal components and situational influences on display sequences. Analysis of the context of these displays (in relation to the success of copulation and the presence of other individuals), the sequence of behaviour before and after these displays, and the status of the focal pair and other pairs in the population will also be useful for understanding these displays. These studies can be combined with our present analysis and other more extensive phylogenetic analyses to determine what role these displays might play in reproduction.

Acknowledgments

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