DISPLAYS OF THE GARGANEY *ANAS QUERQUEDULA*: EVIDENCE OF MULTIPLE FUNCTIONS

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Male dabbling ducks use displays in two main contexts: courtship of females and hostile encounters with other males. Although the displays associated with each of these situations are fairly well documented, the use of particular displays in both situations has only been reported in a few species. The social behaviour of the Garganey (Anas querquedula) was investigated to provide a detailed account of the frequency with which displays are performed, study the orientation component of the displays, and examine the possibility that males of this species may use displays in multiple contexts. Displays that have previously been described as functioning only in courtship are also used by Garganey males in hostile situations. In particular, males direct the burp and laying-the-head-back toward rival males when competition for females is intense. Previous researchers have postulated that the presence of long-term pair bonds may contribute to the development of rivalries and, potentially, multiple use displays. Use of multiple function displays by Garganey males suggests that other factors may contribute to this behavioural phenomenon. Careful analyses of behavioural displays can also be useful in examining evolutionary hypotheses, although information on the displays of many other dabbling ducks is still needed to fully evaluate conflicting phylogenies.

Key Words: Garganey, social behaviour, courtship displays, multiple function displays.

Dabbling duck courtship involves two main components: intersexual choice, in which males display to females and females choose particular males for their mates, and intrasexual competition, in which males actively compete with each other for access to females. In many species of *Anas*, males use separate sets of displays for these purposes: 'courtship displays' to attract females, 'threat displays' and

'appeasement displays' to intimidate or appease rivals.

Certain displays, notably the down-up, combine courtship and threat functions, and recently it was discovered that displays formerly considered to have courtship function may also be used as threat displays in certain species (McKinney 1975; Davis 1997; McKinney *et al.* 1990). The proximate and ultimate factors favouring such multiple uses of courtship displays are not understood.

Research on display orientations of several species has suggested that the use of male-female courtship displays in male-male threat contexts may reflect intense male-male rivalries (McKinney *et al.* 1990). Such rivalries might be expected in sedentary species, perhaps especially in species with strong development of extra-pair courtship, bigamy, and long-term pairbonds (e.g. Sorenson 1992; Port 1998). On the other hand, for over 50 years ethologists have focussed attention primarily on courtship displays directed by males toward females (e.g. Lorenz 1941; 1971; Johnsgard 1965; 1978), and few studies have searched carefully for the presence of multiple function displays. This study performed such a search using captive Garganey *Anas querquedula*, a migratory species with seasonal pair-bonds, for which display orientations and contexts had not been examined previously.

Materials and Methods

Captive Garganey (11 males and 9 females) were observed at Cedar Creek Natural History Area, Bethel, Minnesota, for 198 observation hours from April to October, 1997-98, and May to July, 1999. From April through May, courtship was induced by removing all females from groups of Teal in triangular observation pens, then reintroducing one female to the males after a minimum of 24 hours. Most of this behaviour was recorded on videotape for later analysis. The breeding behaviour of four pairs was observed in a large (60 x 30 x 4m. high) flight pen that contained two large ponds surrounded by natural vegetation to provide cover, eight feeders, and a minimum of eight nest boxes (see McKinney 1967 for a detailed description). An elevated hide, situated midway along the south wall of the pen, provided an observation point for recording behaviour. Most birds studied were full-winged except for two males and one female that were pinioned, and all birds had full access to all areas of the pen.

Behaviour was recorded directly on data sheets, and complex, rapid actions and sequences were recorded on videotapes and later transcribed onto data sheets. Video recording equipment consisted of a Quasar SuperVHS digital video camcorder, as well as a Canon ES2500 Hi8 video camcorder with Azden ECZ-990 zoom microphone. SuperVHS tapes were analyzed using a JVC Vidstar VHS VCR and Mitsubishi colour TV. Calls were recorded using a Sony digital audio tape-recorder and parabolic microphone and analyzed using Soundedit 16 II (Schmidt 1994) and Canary 1.2 (Cornell Laboratory of Ornithology 1995) to obtain sonograms.

All displays discussed will be in bold type when first described. Unless otherwise noted, terms used to describe displays follow those of Lorenz (1971), Johnsgard (1965), McKinney (1970), and Cramp & Simmons (1977). Drawings of display postures were made free-hand from videotapes or slides. Sequence diagrams illustrate display sequences for behaviours that occurred within two seconds of each other.

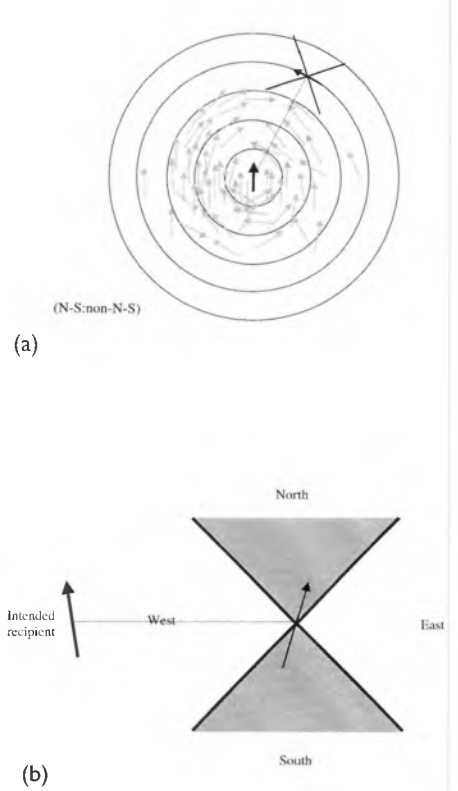

Figure 1. Illustration of display orientation measurements. (a) Target bird is represented by the large central arrow and all displays are mapped onto the concentric circles to illustrate distance from and orientation to the target bird. Circles indicate approximately one bird length distance and arrow heads represent the individual's head. (b) Northwest/southeast axes used to categorise body orientation of a displaying individual (NS=broadside; EW=facing toward/away from). These axes were overlaid on each displaying bird with the target bird always oriented due west (as noted on a).

In a group consisting of one female and several males, the intended receiver of displays can be difficult to determine. This study used two indications: (a) link of the display to turn of the head or body to point at the target, and (b) association of the display with overt aggression. Whenever the target individual could be determined with confidence, display orientations were measured by mapping body position onto a target diagram with the receiving individual in the center and concentric circles separated by the length of one bird (**Figure 1a**). To analyse display orientation, a transparency with northeast/southwest axes was overlaid on each recorded body position with the target bird always due west of the performer (**Figure 1b**). Body orientation was then scored as 'northsouth' (in the shaded region of 1b) or 'eastwest' (lying directly on the axes or in the non-shaded region). All χ^2 analyses measure orientation against random orientation in which 50% of displays fall into the eastwest axis.

Results

Male Displays

Males direct displays toward both females and males, either individually or simultaneously, and many aggressive interactions among males occur during courting bouts or when an unpaired male approaches a male and his mate. During courtship, males continually change their positions in relation to other competing males and to the female that is the target of their displays. Males that are displaying frequently and energetically tend to remain very close to the female and appear to manœuvre so as to keep the

Table 1. Displays performed by males throughout the study. Numbers indicate the number of displays observed in each situation. Numbers in parentheses are listed in multiple columns; they represent the number of displays that were directed toward a pair and appeared to elicit inciting from the female and aggressive behaviour from the male. LTHB = laying-the-head-back, TBH = turn-back-of-head, TTT/THTT = turn-toward-target/turn-head-toward-target, PBW - preen-behind-wing.

Display Performed	Context in which display occurred				
	Courtship Interactions	Hostile Interactions	Pair Bond Maintenance	Breeding Behaviour	Unclear Target
Closed-bill threat	0	167	0	0	1
Open-bill threat	0	92	0	0	0
Chest-threat	0	9	0	0	0
Aggressive calling	0	1016	0	0	26
Bill fighting	0	83	0	0	0
Circular fighting	0	3	0	0	0
Burp	495 (212)	269 (212)	33 (212)	0	0
Burp-call	111 (106	63 (106)	0	0	45
LTHB	308 (105)	71 (105)	12 (105)	0	79
Independent Drink	0	18	36	0	16
Swimming-shake	98 (41)	51 (41)	0	0	52
Belly-preen	71	0	0	0	71
Wing-flap	46	15	38	0	13
TBH	19	0	4	3	0
TTT/THTT	108 (187)	134 (187)	0	0	0
PBW	0	0	39	0	0
Wings-up-bill-down	0	0	0	4	0

female away from other males. Particularly when the female has already expressed preference for a male by inciting, a second suitor will expend a tremendous amount of energy to prevent the female from inciting again beside that particular male. This includes threats toward the preferred male, chases and fights, and monopolisation of the female.

Burp. Three displays involve delivery of the characteristic rattling call of the male Garganey, referred to as burp, burp-call, and laying-the-head-back. The burp consists of head lifting and straightening of the neck with the call (**Figure 4a**) uttered at the height of the neck extension when the bill is held level to the water (**Figure 2**). This display is usually performed with lateral body orientation to the target individual (χ^2=76.05, $P < 0.001$, df=1) and head turned slightly toward the target bird, although some individual variation occurs (e.g. one male orients with his tail slightly toward the target individual and head turned laterally to it). Males performing the burp display often turn the bill (THTT) or body (TTT) to face the target individual before and/or after the burp.

The burp is often linked to a ritualised drink (44.2%), in which the bill is dipped into the water, then lifted and tilted above horizontal (see **Figure 2**). The exact sequence of displays associated with the burp varies, but the most common sequence consists of burp + tail-wag +

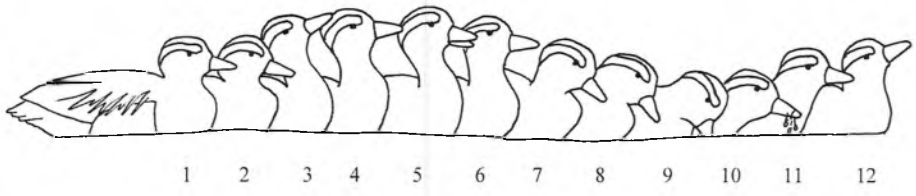

Figure 2. Male burp display: the burp-drink sequence. Positions 1-6 are involved in the burp, 7-12 with the drink. A call is given as the head is brought down from the erect posture (position 5).

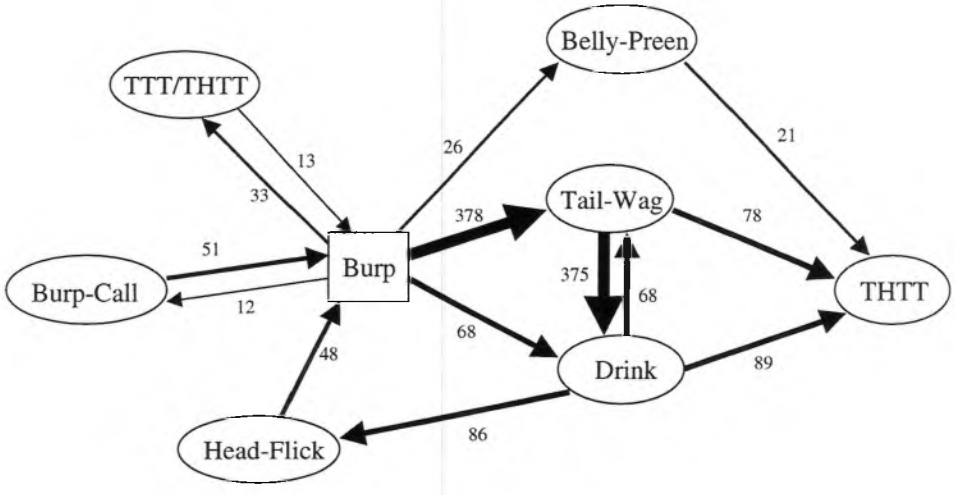

Figure 3. Sequences including the burp display. Thick arrows denote most frequent linkages; numbers indicate number of recorded instances for the particular sequence. TTT/THTT = turn-toward-target bird (i.e. whole body is turned) or turn-head-toward-target (i.e. head only).

Table 2. Female displays performed during the study. See **Table 1** for legend.

Display performed	Context in which display occurred				
	Response to Courtship	Hostile Interactions	Pair Bond Maintenance	Breeding Behaviour	Unclear Target
Close-bill threat	0	201	0	0	3
Open-bill threat	0 (3)	104 (3)	0	0	0
Bill fighting	0	25	0	0	0
Circular fighting	0	2	0	0	0
LTHB	0	0	0	2	0
Independent drink	0	1	35	0	0
Swimming-shake	14	2	0	0	5
Wing-flap	0	0	36	0	7
PBW	0	0	13	0	0

drink + head-flick or turn-head-toward-target (**Figure 3**). The tail-wag often begins slightly before the drink, and ends after the drink is completed. The head-flick following the drink usually causes droplets of water to spray off the bill, but they do not appear to be directed toward the receiving individual, as in the grunt-whistle of other species of *Anas* (Johnsgard 1965; McKinney 1965).

Of 1009 burp displays, 26.7% were directed toward competing males, 56.2% toward a female, and another 21.0% toward a pair. When performed to a pair, it is difficult to determine which is the target bird and to classify burps as agonistic or courtship; possibly they serve a dual purpose, courting the female and sending a hostile message to her mate. Such displays often elicit hostile responses from the target pair, such as closed-bill and open-bill threats and aggressive calling from the male and inciting by the female.

Burp-Call. As with the more exaggerated displays (burp and laying-the-head-back), the burp-call is typically given with lateral body position in relation to the receiving individual (χ^2=32.06, $P<$ 0.001). The male swims near the target individual, vocalizing without lifting the head into an erect posture. The burp-call is often repeated (**Figure 4b**) and may be homologous to the repeated calls of blue-winged ducks (McKinney 1970), although the calls are not always evenly spaced. The vocalisation associated with the burp-call resembles the contact call males produce when their mates start laying and incubating (see below). However, it does not seem to be exclusively directed toward females, as are contact calls. Unlike the burp display, the burp-call is rarely followed by a ritualised drink (5.8%), but is more often linked to burp or laying-the-head-back displays (28.6%; **Figure 5**).

Laying-the-Head-Back (LTHB). In this display, the male quickly throws his head back, laying it on the scapulars, and gives a call when the bill is nearly horizontal in this position (Johnsgard 1965). He then raises the head into a burp position, uttering a second call as the head is brought down (**Figures 4c, 6**), typically into a ritualized drink. Lorenz (1971) and Johnsgard (1965)

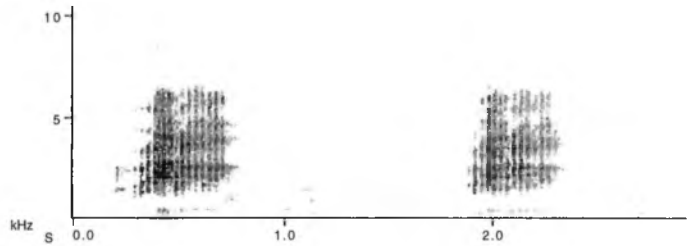

Figure 4a

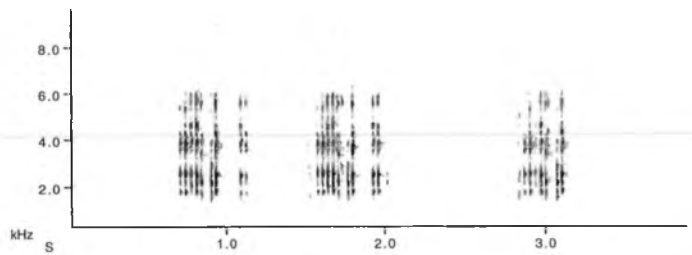

Figure 4b

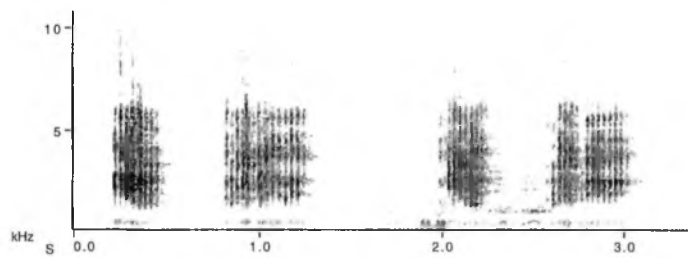

Figure 4c

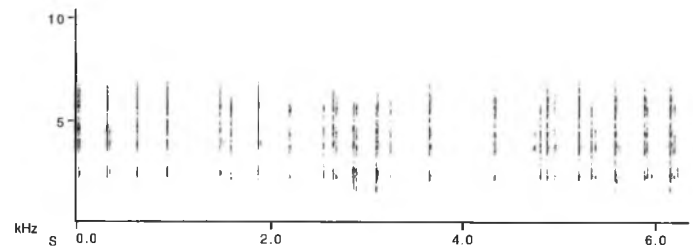

Figure 4d

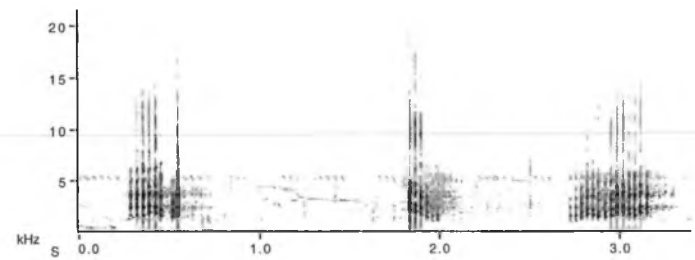

Figure 4e

Figure 4. Sonograms of male calls: (a) burp vocalisations given by two males during a courtship bout; (b) burp-call vocalisation with three repeated calls from the same male; (c) calls associated with laying-the-head-back, calls from two displaying males shown. Note the similarity in structure of the second LTHB call and the call given during the burp display. Both vocalisations are given at the height of vertical neck extension, just as the head is brought down; (d) aggressive calling by two rival males; calls from male A extend to a frequency of 7 kHz, those of male B only to 6 kHz. The calls consist of regularly spaced single notes; (e) contact call showing two components: burp-call (0.0 to 1.0 seconds) and LTHB (1.7 to 3.5 seconds) used to maintain auditory contact with a laying or incubating female.

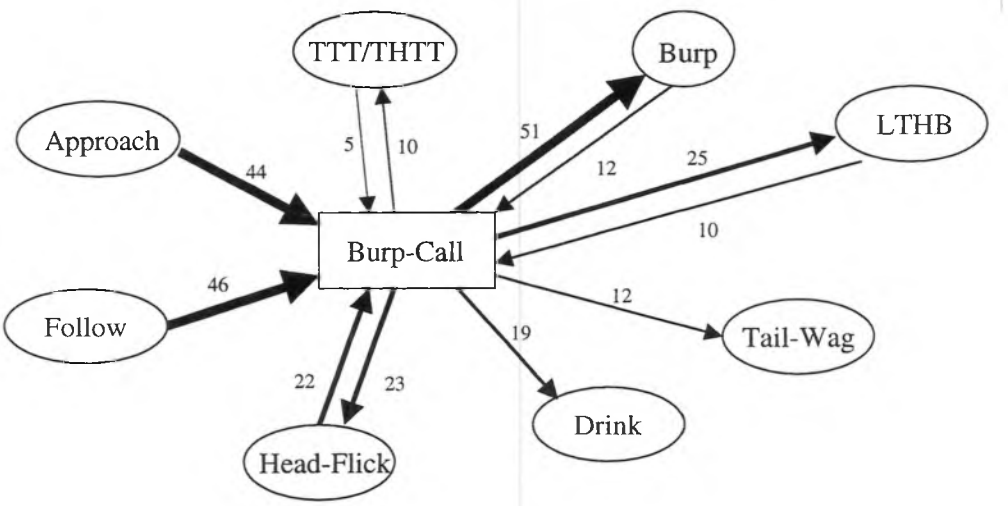

Figure 5. Sequences involving the burp-call. Abbreviations: turn-toward-target or turn-head-toward-target (TTT/THTT), laying-the-head-back (LTHB).

noted that this display appears to be a highly ritualised exaggeration of the burp display, and they suggested that it functions to change the shape and length of the trachea, altering the production of sound (Johnsgard 1971). The second call strongly resembles the call given during the burp display (see **Figure 4a**), and in both cases it occurs as the head is lowered from an erect position.

Intermediate forms between the burp and laying-the-head-back display movements were not observed; once the male begins the latter display, the head is consistently thrown into a horizontal position on the scapulars. Laying-the-head-back, like the burp, is often followed by a ritualised drink and tail-wag (44%), and the individual performing the display often turns his head or body to face the target bird before, or more often after, the display (**Figure 7**). Body orientation during LTHB is distinctly lateral to the intended recipient ($\chi^2 = 46$, $P < 0.001$).

As with the burp, males appear to use LTHB in both courtship and male-male interactions (**Table 1**), and the form of the display and orientation of the male are similar in both contexts. In hostile situations, the display usually occurs when the performer is threatened by the female as she incites beside her mate or when her mate gives aggressive calling. Paired males also perform laying-the-head-back displays broadside to males that persistently court their mates.

Swimming-Shake, Body-Shake. As noted by Johnsgard (1965), swimming-shake does not serve an introductory function to courtship bouts in the Garganey, as it does in the Mallard, Pintail, and Green-winged Teal groups (but not in

the blue-winged ducks, McKinney 1970, or Wigeons, Wishart 1983). Swimming-shake and body-shake (the same movement on land) are performed with lateral body orientation to the receiving individual (χ^2=46.296, P<0.001). They are performed laterally to females more often than to males (**Table 1**), occurring in sequences with burp and laying-the-head-back (**Figure 8**). These displays are occasionally performed with threats and aggressive calling, but courtship appears to be their major function.

Belly-Preen. When the individuals are on land, males may follow either a body-shake or one of the major displays (burp, laying-the-head-back) with a belly-preen, in which the bill is brought forward and briefly touches the belly in a preening posture (**Figure 9**). Typically, belly-preen is used in courtship situations, performed with broadside orientation to the female (χ^2=34, P<0.001). This display occurs in aggressive context only when linked with a burp or LTHB display; it is not used independently in hostile situations, as is often the case during courtship.

Wing-Flap. In this display, the bird lifts up out of the water and flaps the wings two-nine times (Mean=4.99±1.394, n=164), usually with the body oriented laterally to the target individual (χ^2=24, P< 0.001). This display is used by both sexes, primarily for pair bond maintenance (**Tables 1, 2**), and is only rarely used by males in aggressive interactions.

Closed-Bill and Open-Bill-Threats. The closed-bill threat consists of extending the neck horizontally and pointing the bill toward a target individual, often a male that has been performing hostile or courtship displays to a pair. The open-bill threat typically occurs during intense courtship bouts when many males are competing. Males rarely direct threat displays toward females (n=31), and such behaviour is typically in response to aggression from the female (closed-bill or open-bill threats or inciting next to her mate). Females use these displays to reject certain individuals, usually males that are persistently courting them. The posture adopted by females during this display is like that of the male, and is often interspersed with the bill-lifting component of inciting.

Chest-Threat. During agonistic encounters, one male may approach another male while giving aggressive calls, then attempt to gain a vertically superior position by lifting the breast onto the other bird's back. The movement resembles a mounting attempt during copulation, but it is strictly directed toward other males and only occurs during intense courtship bouts.

Aggressive Calling. When males approach conspecific males, they often give evenly-spaced single-note calls (**Figure 4d**) without any obvious movement of the head or bill. Of the aggressive calling bouts recorded, 24.3% were preceded by approaching and 10.5% occurred after following another bird. These calls may precede aggressive displays and interactions (**Figure 10**), e.g. burp, bill-fighting, LTHB, or attacks.

Aggressive calling primarily occurs in the presence of other males (71.1%), occasionally when with a female (10.0%), or is directed toward a pair when the displaying male is attempting to court the female (16.4%). At times, aggressive calling is given with bill-lifting by the male, but this is not as prevalent in Garganey as are similar displays in other species of *Anas* (e.g. bill-up in Green-winged Teal, McKinney 1965; hostile pumping in blue-winged ducks, McKinney 1970).

Drink. The ritualised drink can be

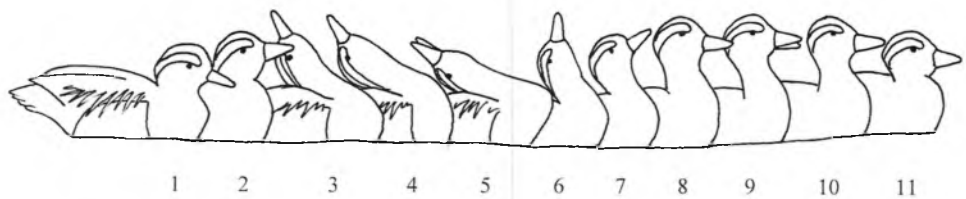

Figure 6. Sequence illustrating head and neck movements during the LTHB display; the shorter call (see Figure 4c) is given when the head is on the scapulars (position 5), and the longer call when the head is just being lowered (position 9).

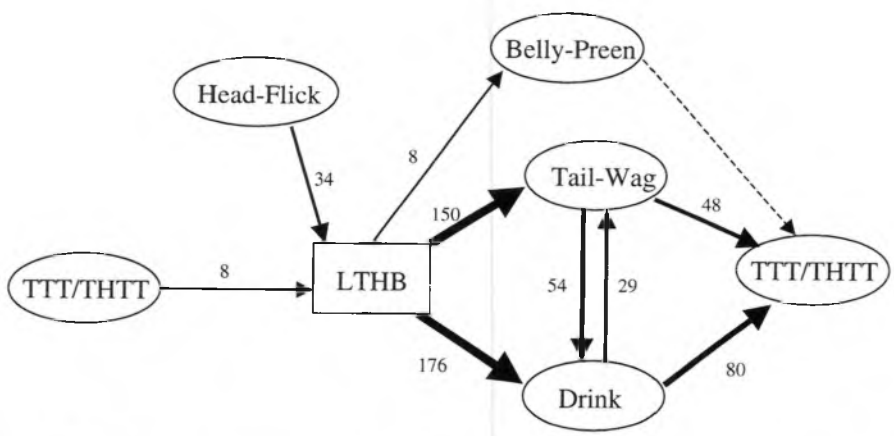

Figure 7. Flow diagram of sequences associated with LTHB. Dashed line represents a single recorded event.

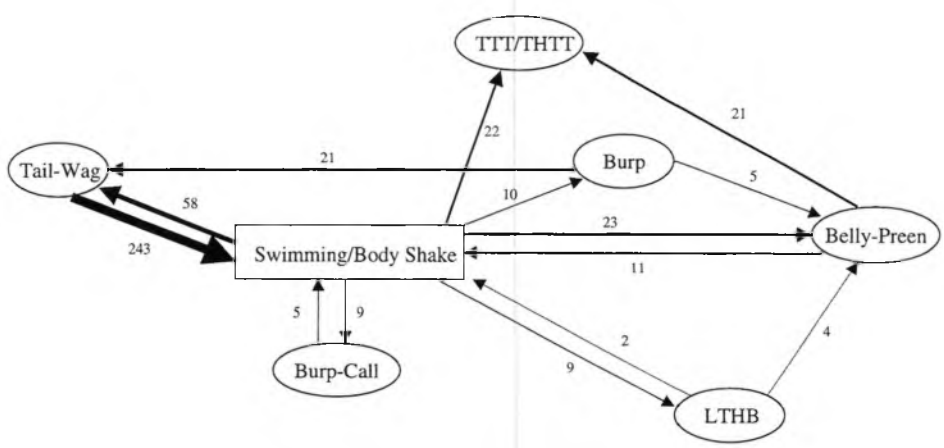

Figure 8. Display sequences that involve the swimming-shake or body-shake directed by a female toward a male. See **Figure 5** for explanation of abbreviations.

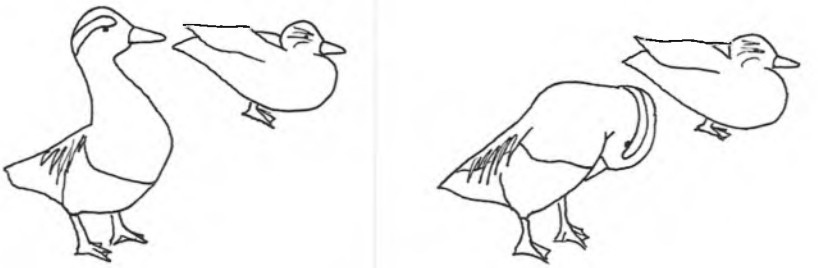

Figure 9: Male performing a burb + belly-preen sequence to a female (in background).

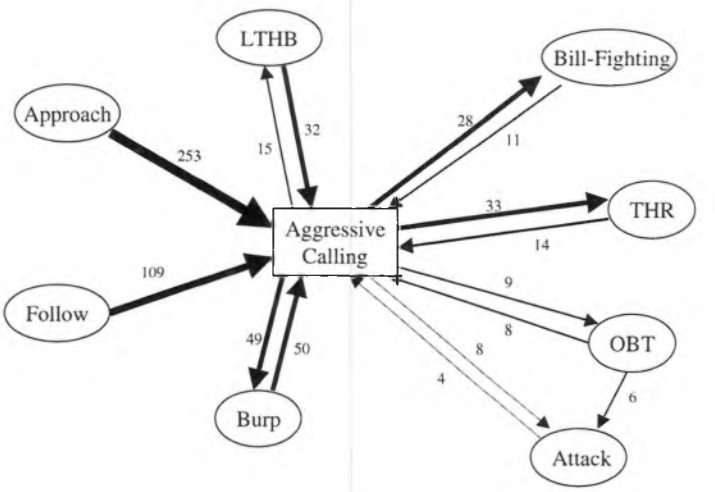

Figure 10. Flow diagram illustrating sequences typically associated with aggressive calling. All behaviours are performed by the aggressor and directed towards the target.

distinguished from the normal drinking movement by the deliberately vertical dip of the bill into the water and the rapidity of the subsequent up-tilting of the bill to a 45 degree angle above horizontal (see **Figure 2**). It is often linked to burp or LTHB when these displays occur on water (see **Figures 3, 7**), but at times (n=18) it is used alone, preceding or following aggressive calling or open-bill threats, apparently serving an agonistic function (threat or appeasement). When performed independently of other displays n=71), it occurs between members of a pair, particularly when they meet after a separation. Birds maintain lateral body orientation during this display (χ^2=10, *P*=0.002).

Bill-Fighting. Instead of breast-to-breast fighting as in Mallards *A. platyrhynchos* (Lorenz 1971), or grasping at the back of the neck and flailing wings as in African Black Ducks *A. sparsa* (McKinney *et al.* 1978), bill-to-bill fighting appears to be characteristic of the Garganey. Bill-fighting often follows aggressive calling by males and can occur between males, between males and females, and rarely between two

females. Both birds attempt to move into a position above that of their competitor, extending their necks and bodies vertically to do so (**Figure 11**). Generally, the individual that fails to maintain a high position flees from its opponent, and often is chased as it leaves.

Circular-Fighting. On rare occasions, males interact by circling each other on the water. These dashing movements, termed circular-fighting by McKinney (1970), are common in blue-winged ducks. In Garganey, circular-fighting is associated with competition for mates rather than territorial defense, as it usually is in blue-winged ducks. There is no evidence that Garganey males defend breeding territories.

Attack. Occasionally, closed- and open-bill threats and aggressive calling escalate into an attack. Attacks usually involve biting of the feathers along the nape of the neck, or biting and pulling of wing and tail feathers as the attacker chases the other bird. Males attack both males and females, although attacks on males are more common.

Turn-Back-of-Head (TBH). This display is used relatively infrequently by the Garganey. In many species of *Anas* the male typically swims in front of an inciting female while keeping the nape of the neck directed toward her (Johnsgard 1965). Garganey males, however, more often maintain a broadside position to the female while swimming than leading her, and thus they keep the side of the head directed to her. Males were not seen to deliberately turn the side of the head toward the female while leading her, as described by Lorenz (1971) and Bauer & Glutz von Blotzheim (1968). Males appear to use TBH as a post-copulatory display (see below).

Figure 11: Two males bill-fighting; note the relative vertical positions of the two individuals. The bird that maintains a higher position with respect to its competitor most often wins the fight.

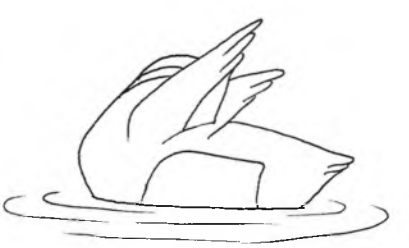

Figure 12: Male performing preen-behind-wing display to female (in foreground, not pictured).

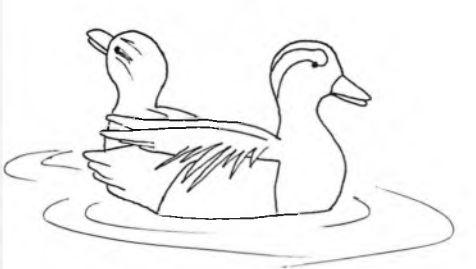

Figure 13: Post-copulatory display: wings-up-bill-down. The male holds this position for less than a second while giving a burp vocalisation.

Turn-Toward-Target (TTT). Males use the turn-toward-female display (Johnsgard 1965), in which the head and body are turned to point at the female, as part of courtship sequences and they often direct a similar movement toward rival males in hostile encounters. Turn-toward-target appears to reinforce the directionality of the display when used in sequence with major displays (e.g. burp, burp-call, laying-the-head-back, swimming/body-shake). This display also occurs as part of the post-copulatory sequence (see below).

Turn-Head-Toward-Target (THTT). Often, males turn only the head to direct the bill toward the target bird. This movement also precedes or immediately follows the major courtship displays (e.g. burp, laying-the-head-back; **Figures 3, 7**) and is similarly used in hostile interactions with rival males.

Male response to inciting. A male responds to a female inciting beside him in several ways. He may lead her with TBH or, more often, by slightly turning the side of the head to the female while remaining more or less broadside to her. More rarely, when many competing males are present, the male gives aggressive calls as he swims close to the female, performing bill-lifting movements like those given by the female during inciting (see **Figure. 14**). These movements may be homologous to the hostile pumping of blue-winged ducks (McKinney 1970). Alternatively, in response to persistently aggressive behaviour by another male, the male retreats, often swimming to a corner of the pond where he is more secluded. The female may remain next to him, actively inciting by bill-lifting in his direction and occasionally threatening the other male(s). The male does not appear to be directing the back of his head toward the female in these situations.

Preen-Behind-Wing. This display most often occurs when the members of a pair are beside each other (n=30). One individual lifts a wing (often, but not necessarily, the wing nearest its partner), briefly placing the bill behind it in ritualised preening posture (**Figure 12**).The partner often responds with a similar display. Typically the display occurs following interactions in which other males attempted to court the female. Placement of the bill on the outside of the wing, as reported by Lorenz (1971), was not observed. A male that has persistently courted a female for several hours may begin to perform this display as though a pair bond has formed, even though the female has not responded to them in kind. Similarly, a female that is interested in an already-mated male occasionally performs this display to that male but, in such instances, the displays are rarely reciprocated and the male may show aggressive behaviour toward the female.

Post-Copulatory Displays. The following account is based on observations of four copulations in one individual pair. As in all species of *Anas*, mutual pre-copulatory head-pumping typically preceded treading in pair copulations. After the male dismounted, he turned his side to the bathing female and gave a burp vocalization while briefly holding a wings-up-bill-down posture (n=4; **Figure 13**) similar to that of other blue-winged ducks (McKinney 1970). He then wagged his tail and turned-toward-the-female while continuing to hold his head erect. The male either bathed (n=1) after completing the post-copulatory sequence or swam directly away from the female while giving TBH (n=3).

Contact Calls. Males maintain contact with a laying or incubating mate when she is on the nest by swimming nearby (within

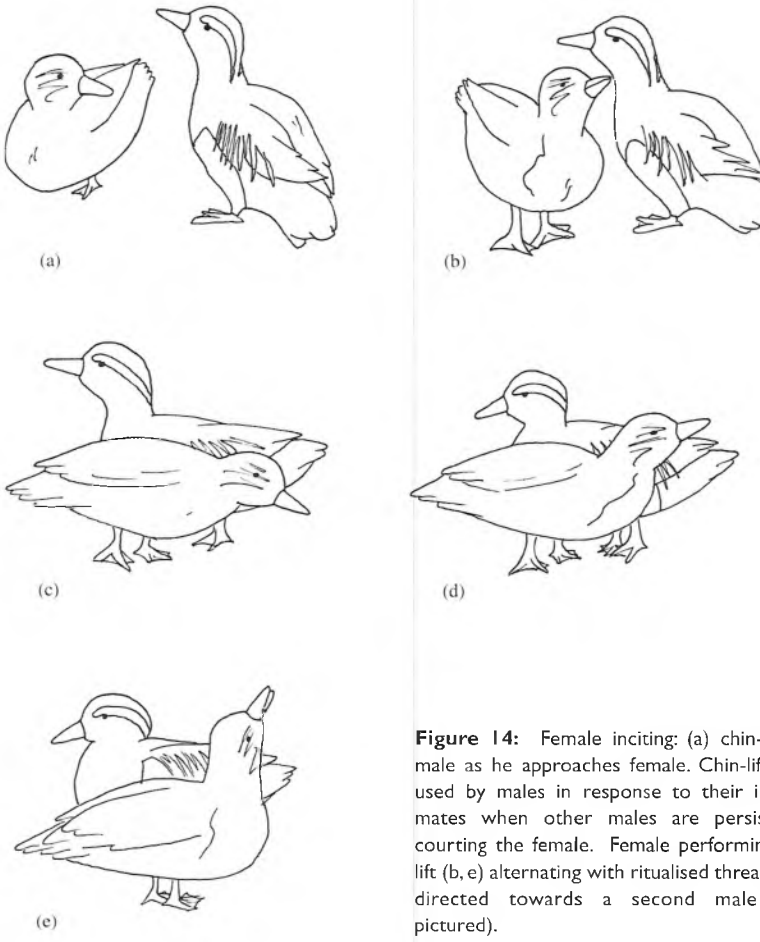

Figure 14: Female inciting: (a) chin-lift by male as he approaches female. Chin-lifting is used by males in response to their inciting mates when other males are persistently courting the female. Female performing bill-lift (b, e) alternating with ritualised threat (c, d) directed towards a second male (not pictured).

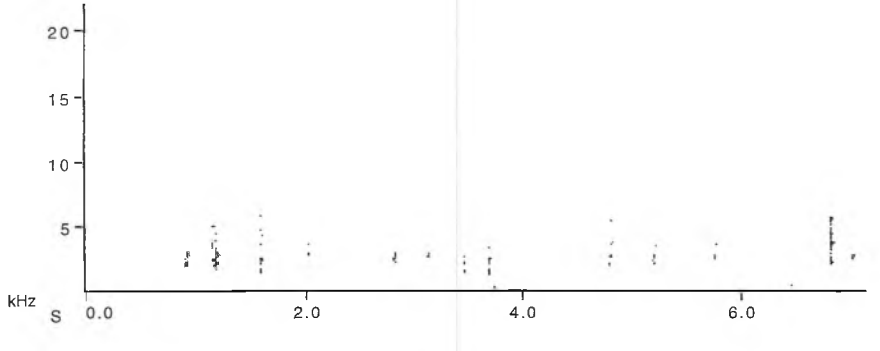

Figure 15: Sonogram of female calling during the bill-lift component of inciting.

seven metres) and periodically uttering bursts of contact calls. Mainly burp-calls are given, but burp or LTHB displays can be interspersed between burp-calls (**Figure 4e**). This behaviour persists until late in incubation, generally becoming less frequent two weeks after onset of incubation and ceasing completely by hatch.

Forced Copulations. Male Garganey pursue forced extra-pair copulations (FEPCs) similar to those reported in many waterfowl (McKinney *et al.* 1983; McKinney & Evarts 1997). FEPCs (n=8) occured on land and on water with equal frequency, and the female's mate often remained near the struggling female, very alert and attentive, but only occasionally attempting to prevent the attacking male from copulating by forcing him off the female. Females tried to escape from the pursuing male by taking flight, diving, or sneaking into cover. Following FEPC attempts, the female's mate usually joined her, and they sneaked onto land, occasionally into cover, where they preened and performed pair bond maintenance displays, particularly preen-behind-wing. Forced pair copulations (FPCs) were not observed.

Female Displays

Several agonistic and pair bond maintenance displays are used equally by both sexes (**Tables 1, 2**). These displays are described above and are not mentioned in this section.

Inciting. As in other species of *Anas*, females frequently use this display to indicate preference for, or attachment to, a particular male. In the Garganey, there are two major components: the **bill-lift** and the **ritualized threat** (**Figure 14**). The bill-lift component involves rapid tilting of the bill to an almost vertical position in the direction of the female's mate. The female often incites next to or somewhat behind her mate, and she is generally oriented to face him. Bill-lifting alternates with a closed-bill threat component as the female turns toward nearby individuals (typically male Garganey but occasionally females or heterospecifics), extends her neck, and points her bill in their direction. Calls consist of repeated monosyllabic notes (**Figure 15**) during the bill-lifting movement (not the single notes described by Lorenz 1971).

Female Laying-the-Head-Back. Lorenz (1971) and Bauer & Glutz von Blotzheim (1968) reported that females as well as males perform LTHB. In this study, the female performed this display immediately before adopting the prone position prior to all four copulations observed. After brief bursts of pre-copulatory head-pumping, the female gave a laying-the-head-back display, accompanied by a single loud quack (Lorenz 1971 noted a double call). The form of the female's display appeared to be similar to that of the male, although the female's head did not reach a fully horizontal position (**Figure 16**). The male responded to this behaviour by immediately approaching and mounting the prone female. Further observations of copulations are needed to determine whether this female display is always present.

Decrescendo Calls. Females of all species of *Anas* use the decrescendo call (Johnsgard 1965). Although it is present in the Garganey, it was rarely heard during this study, and Lorenz (1971) rarely recorded it. Females use the call to maintain contact with their mates when they are out of sight.

Repulsion. Females that are incubating and no longer receptive respond to

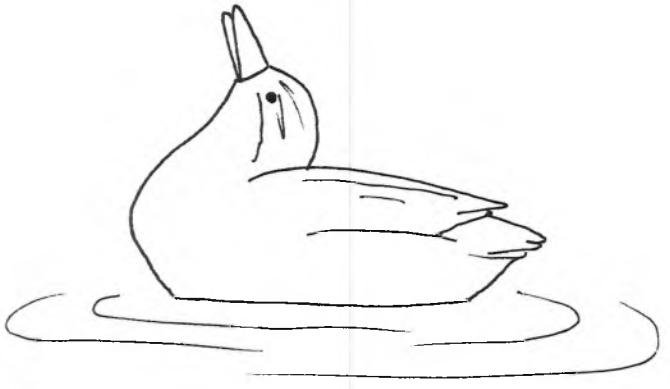

Figure 16. Female performing the laying-the-head-back display.

courtship or harassment by males with repulsion displays. The female erects the feathers along her crown and body and utters loud calls while attempting to avoid the males.

Distraction Display. Females flushed from the nest late in incubation rarely move far from the nest site. They give unusually loud calls and flop around moving both wings in a paddling motion, either on water or on land.

Discussion

Previous reports of Garganey behaviour (Lorenz 1941, 1971; Johnsgard 1965; Bauer & Glutz von Blotzheim 1968; Cramp & Simmons 1977) have described the burp and laying-the-head-back in the context of courtship but did not report these displays being directed toward males. This study shows that males do indeed direct these displays toward both males and females. Like the Hottentot Teal, *A. hottentota* (Pearce 1999), White-Cheeked Pintail, *A. bahamensis*, and Chilean Teal, *A. flavirostris* (McKinney *et al.* 1990), Garganey males direct burp and laying-the-head-back displays toward females during courtship and toward rival males in agonistic situations. In all of these species, temporal association of the display with overt aggression or linkage with a head-turn or full-body-turn to face another bird unambiguously identifies it as the target.

McKinney *et al.* (1990) speculated that species using courtship displays in multiple contexts may have long-term pair bonds or remain relatively sedentary, allowing rival males to interact and compete for females over several years. In contrast, the Garganey is a strongly migratory species, and such long-term rivalries are unlikely to be present in wild populations of this species. However, strong competition for mates occurred in the captives and it is possible that development of intense male rivalries contributed to the use of displays in multiple contexts. Several of the males regularly competed for females and were repeatedly involved in courting bouts that escalated to more aggressive interactions, although use of courtship displays in male-male competitive interactions was not limited to strong rivals.

At this juncture, careful analyses of films and videos for many species of *Anas* are needed. The benefits of such detailed studies are two-fold. First, to determine whether the use of courtship displays in hostile contexts is a wide-spread phenomenon. Once species with multiple-use displays have been identified, possible correlates of the behaviour can be examined and it is possible to begin to understand the proximate and ultimate factors that underlie such broadly functioning displays.

Second, detailed studies of species-typical behaviours may provide critical evidence for phylogenetic investigations. Along with morphological and molecular sequencing data, it is now well established that behaviour can provide important information on phylogenetic relationships among taxa (Prum 1990; McKitrick 1992; de Quiroz & Wimberger 1993; Paterson *et al.* 1995; Zyskowski & Prum 1999). When using behavioural characters for phylogenetic inquiry, it is essential to use as complete a record as possible of the behavioural repertoire for each species. Displays that are observed only rarely may provide the key to phylogenetic relationships. For example, the occurrence of wings-up-bill-down as a post-copulatory display confirms the relationship of the Garganey to the blue-winged ducks (Johnson *et al.* 2000). Such information is invaluable when evaluating conflicting hypotheses, such as the phylogenies proposed by Livezey (1991, 1997) and Johnson & Sorenson (1999). Livezey (1991, 1997), using morphological data, placed the Garganey in a cohort consisting of the Green-winged Teals, Silver Teals, Pintails, Grey Teals and Brown Teals, whereas Johnson & Sorenson (1999), using mitochondrial DNA sequence data, placed the Garganey with the Silver Teals and Blue-winged Ducks, in agreement with the earlier judgements of Lorenz (1971) and Johnsgard (1965, 1978). Until this study, however, the behavioural repertoire of the Garganey was not sufficiently well documented to allow researchers to use behaviour to fully evaluate the conclusions from the morphological and molecular phylogenies. Many other species of dabbling ducks remain relatively poorly studied, which continues to hinder a full phylogenetic analysis using behavioural characters.

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