Displays and breeding behaviour of the Chiloe Wigeon *Anas sibilatrix*

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Many displays of the South American Chiloe Wigeon were similar to published displays of its close relatives, Eurasian and American Wigeon, Gadwall, and Falcated Duck, and differences appeared to be related to ecological and social factors. The loss of two courtship displays (Head-up-tail-up and Down-up) and the presence of an additional aggressive display (Wings-up) in all three wigeon species suggest that these features are related to their grazing lifestyle. Unlike the two northern wigeon, male Chiloe Wigeon have retained the Grunt-whistle display and did not perform Facing. Display bouts between male Chiloe Wigeon when their mates were incubating were interpreted as ritualized aggression, and some males directed courtship displays at other males in an aggressive context. Chiloe Wigeon actively maintained strong pairbonds through specialized Triumph Ceremonies, and males defended their mates vigorously, and usually successfully, during forced extra-pair copulation attempts. Both parents provided care for their ducklings and, from three days of age, ducklings directed displays to their parents and one another. These displays and family Triumph Ceremonies appeared to reinforce family bonds and encourage parental aggression towards other birds, showing convergence with geese and swans.

Keywords: Chiloe Wigeon, Anas sibilatrix, Displays, Grazing, Biparental Care

The Chiloe Wigeon *Anas sibilatrix*, a common bird of the open wetlands of southern South America (Weller 1968; Johnsgard 1978; Schlatter *et al.* 1983), is closely related to the American Wigeon *A. americana* and the Eurasian Wigeon *A. penelope*. Similarities in morphology, feeding habits, and display repertoires clearly distinguish these three species as a major subgroup of the dabbling ducks (tribe Anatini) (Delacour & Mayr 1945; Lorenz 1971; Johnsgard 1978) and systematists have sometimes given them separate status in the genus *Mareca* (Livezey 1991).

The displays of the wigeon are of special interest because these closely-related species have different social systems. The two northern species have seasonal pairbonds and female-only brood care (Cramp & Simmons 1977; Wishart 1983; Mayhew 1985), while the Chiloe Wigeon has biparental care, strong family cohesion, and probably long-term pairbonds (Johnsgard 1965; Kear 1970; Lorenz 1971). Displays and breeding behaviour of the American Wigeon and the Eurasian Wigeon are well known (Cramp & Simmons 1977; Wishart 1983; Mayhew 1985), but the behaviour of the Chiloe Wigeon has not been well described.

In this study, the displays of captive and wild Chiloe Wigeon were described and compared to the behaviour of the two northern wigeon and other close relatives (Gadwall *A. strepera* and Falcated Duck *A. falcata*) in order to examine the influences of different social systems and ecology on display repertoires (McKinney 1992).

Displays specialized for use in the Chiloe Wigeon social system were also compared to the signals of other waterfowl with similar social systems and feeding habits. Like the wigeon, swans and geese (tribe Anserini) feed almost exclusively on vegetable matter, often grazing on land, and have biparental care, long-term bonds, and cohesive family units (Johnsgard 1978). The Australian Wood Duck *Chenonetta jubata* is another grazing specialist with biparental care and long-term pairbonds (Kingsford 1986, 1990a,b). Possible convergence between Chiloe Wigeon and other grazing specialists raises interesting questions about the importance of phylogenetic, social, and ecological factors in shaping displays.

Methods

Wild birds

Wild Chiloe Wigeon were observed for over 500 h during three brood-rearing seasons (November-January 1985-88) at 11 sites in southwestern Argentina near San Carlos de Bariloche, Rio Negro province, and at one site near Claromeco, Buenos Aires province (McKinney & Brewer 1989; Brewer 1990). Birds were observed in shallow lakes, pools, flooded fields, and sheltered sections of large, deep lakes. Most wetlands were surrounded by grazed pastures and had filamentous algae and/or milfoil *Myriophyllum* sp. A few sites had some edge cover (*Juncus* sp.). Population sizes for the sites ranged from two to about 100 adults. Observations were made at all times of day, although mostly in the early morning, with 20-45 x spotting scopes or binoculars. Although wild birds were not marked, 35 broods were identified throughout the breeding season by brood age, size, location, and distinctive plumage of one or both parents (Brewer 1990).

Captive birds

Captive Chiloe Wigeon were observed in a large flight pen (55 x 27.5 x 3.6 m) at Cedar Creek Natural History Area, Bethel, Minnesota (see McKinney 1967) during spring and summer 1984-89. Each year, three to six pairs were released into the pen, with 19 adults and 45 ducklings observed during the course of the study. Five pairs (including five pinioned birds) were purchased from local aviculturists; the rest were raised by their parents at Cedar Creek Natural History Area and left full-winged. The oldest individuals studied were three years of age. Adults were individually marked with coloured plastic nasal saddles or discs, and two broods (nine ducklings) were individually marked for about two weeks by attaching small squares of coloured plastic tape to their foreheads with glue. Observations were also made on three hand-reared ducklings.

Captive Chiloe Wigeon were observed for over 520 h, including 68.5 h on marked ducklings. Most observations were made during three-hour watches starting just before sunrise, between 0515 h and 0530 h Central Daylight Time. Data were recorded directly onto data sheets or transcribed from cassette tapes. Vocalizations of captive birds were recorded with a Sony TCM 5000-EV cassette tape recorder and representative sonagrams were made with a Kay sound spectrograph 7800, and using SoundEdit 16 (Macromedia, Inc., San Francisco, California U.S.A.) and Canary 1.1 (Cornell Laboratory of Ornithology, Ithaca, New York U.S.A.) computer programs. An Elmo super 8 sound 10125-XL macro camera and a super VHS video camera were used to film behaviour. Movie film was later analysed with a Timelapse Data Analyzer 3420 projector.

Results

Stereotyped behaviour patterns (including vocalizations, movements, and postures) that are specialized as signals have been identified as displays (Moynihan 1955). Display terminology used in this paper is that of Johnsgard (1965) and McKinney (1965), unless otherwise noted. Displays are capitalized, and presented in boldface type when they are described for the first time in the text.

Courtship

Courtship was observed in captivity among paired and unpaired birds and in the wild when one or more males courted paired females, juveniles, and ducklings (Brewer 1991). I observed very little courtship between adults during the breeding season. Courtship between adult birds may occur more frequently during the southern fall and winter, as in other duck species (Rohwer & Anderson 1988), but data are not available for these periods. Courtship of ducklings and juveniles by unpaired, adult males was common during the breeding season in several study areas, and resulted in females forming bonds with adult males at an exceptionally early age (Brewer 1991). Most courtship took place on the water, although several group flights with one or two juvenile females and two to eight adult males were noted in late January.

The **Rakoo** display (**Figure 1**), performed broadside to the courted bird, included a loud, two-syllable call (**Rakoo Call, Figure 2A**; represented as "wiburr" by Lorenz 1971) given as the crest feathers were held erect, giving the head a very rounded appearance. The first syllable of the call was given with the neck slightly extended and the bill pointed slightly upward, the second syllable as the neck was brought forward and down to approximately 20-45° from the vertical, with the bill parallel to the surface. In other contexts (see *Pairbond Maintenance*), the two-syllable call was given in a more upright position.

Preen-behind-the-wing (**Figure 3**) was typically preceded by dipping the bill in the water and shaking the head, and the tail was often wagged after the display (performed broadside to the target). At close distances, a sharp whir could be heard as the wing was snapped open and the male placed his bill behind or just above the speculum. Males sometimes **Chittered** (**Figure 2B**) before they performed Preen-behind-the-wing. **Turn-the-back-of-the-head** (Johnsgard 1965) was seen rarely.

Males performed an exaggerated **Display Shake** (**Figure 1**) (called Introductory Shake by Johnsgard 1965) broadside to the target bird. These shakes were not consistently or often followed by other displays and, as suggested for American Wigeon by Wishart (1983), the term Display Shake is more appropriate than Introductory Shake.

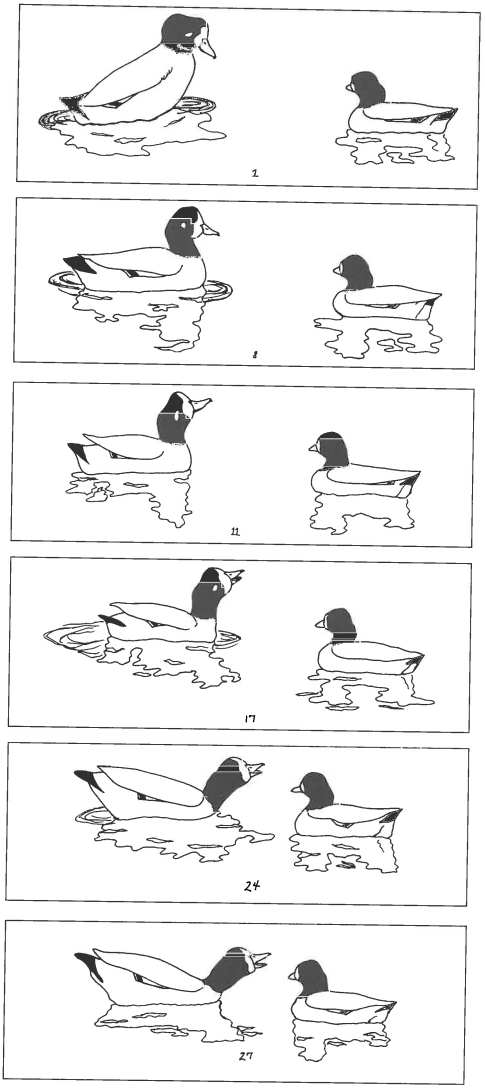


Figure 1. Male Chiloe Wigeon (left) performing a Display Shake (frames 1- 8) and Rakoo (frames 11-27) to a female. Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

A "true" **Grunt-whistle**, in which the male pulled his body up mostly out of the water, arched his neck so that the bill touched the water, and gave a low snort, was seen over 300 times, primarily when adult males courted ducklings in the wild. During this display, the bill was open slightly in or above the water when the call was given, but there was no sideways flick of the bill and no droplets of water

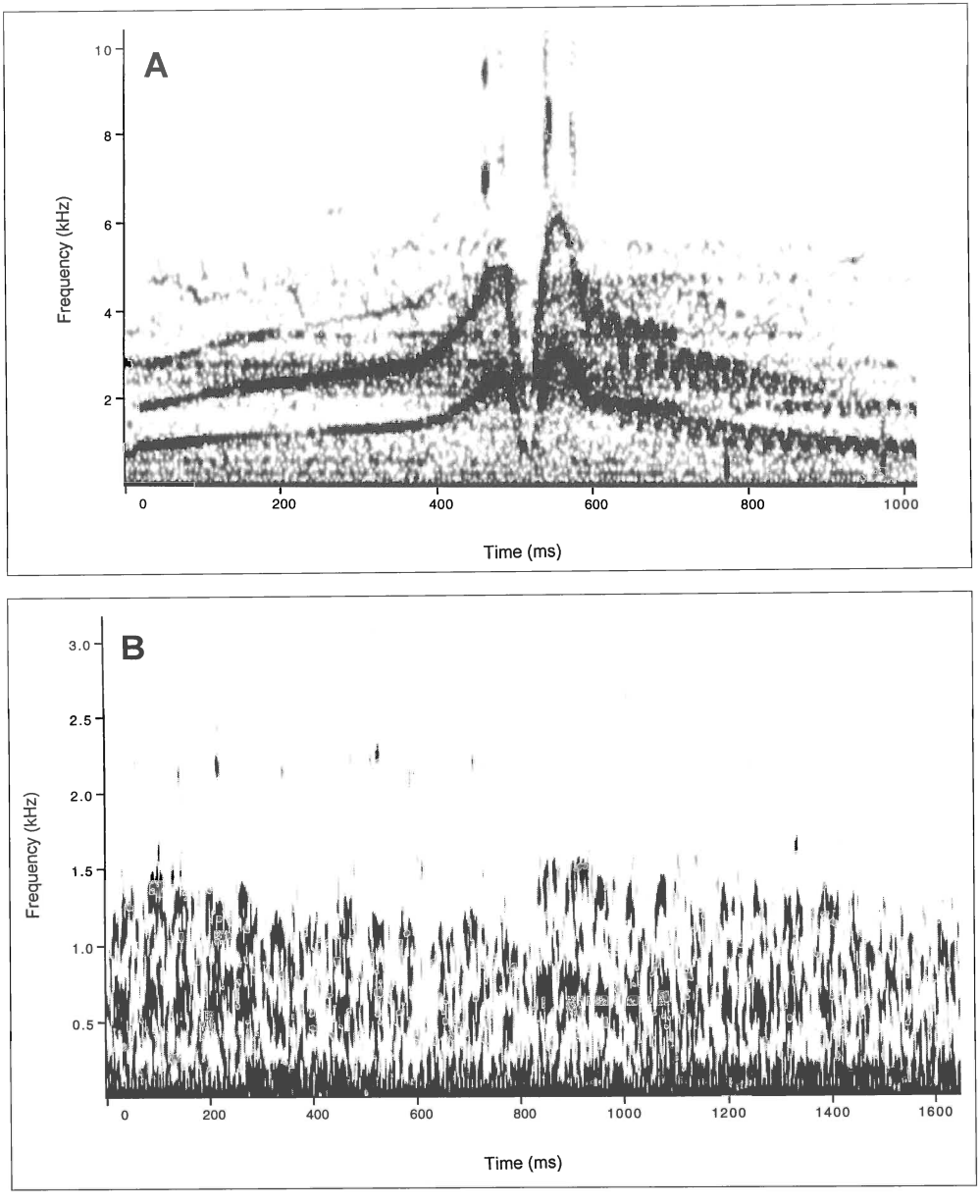


Figure 2. Loud Rakoo Calls (A) were performed by Chiloe Wigeon during courtship and pair maintenance displays. Males Chittered (B) as they accompanied their mates.

were flicked toward the target bird as they are in other *Anas* Grunt-whistles (e.g. Johnsgard 1965). Grunt-whistles were performed broadside to the target bird. This display has not been described previously for Chiloe Wigeon. Johnsgard (1965) noted that the Introductory Shake could be mistaken for a true Grunt-whistle in Chiloe Wigeon, but that no call was given and the bill did not strike the water. I recognize the displays that I describe here as Grunt-whistles, however, because both the call and bill striking the water were consistently present in the displays.

Females, juveniles, and ducklings responded to male courtship displays either positively by facing toward the male and **Chin-lifting** (**Figure 4**; Johnsgard 1965) or by threatening the male with an open bill (primarily adult females) or moving away from the courting male. During Chin-lifting, the bill was rapidly raised and lowered with the neck extended upward. In adult females, this display was sometimes accompanied by short **Honks**, like those described below for Triumph Ceremonies.

Pairbond Maintenance

Several displays seemed to function to keep members of a pair in close contact, and reinforce the strong pairbonds. Pairbonds continued to be reinforced during winter in captives, and persisted for at least four years for two pairs, three years for three pairs, and two years for six pairs. Only a few captive birds switched mates between breeding seasons. In the wild, nine pairs of parents remained together after they no longer tended ducklings. Pairbonds have been observed

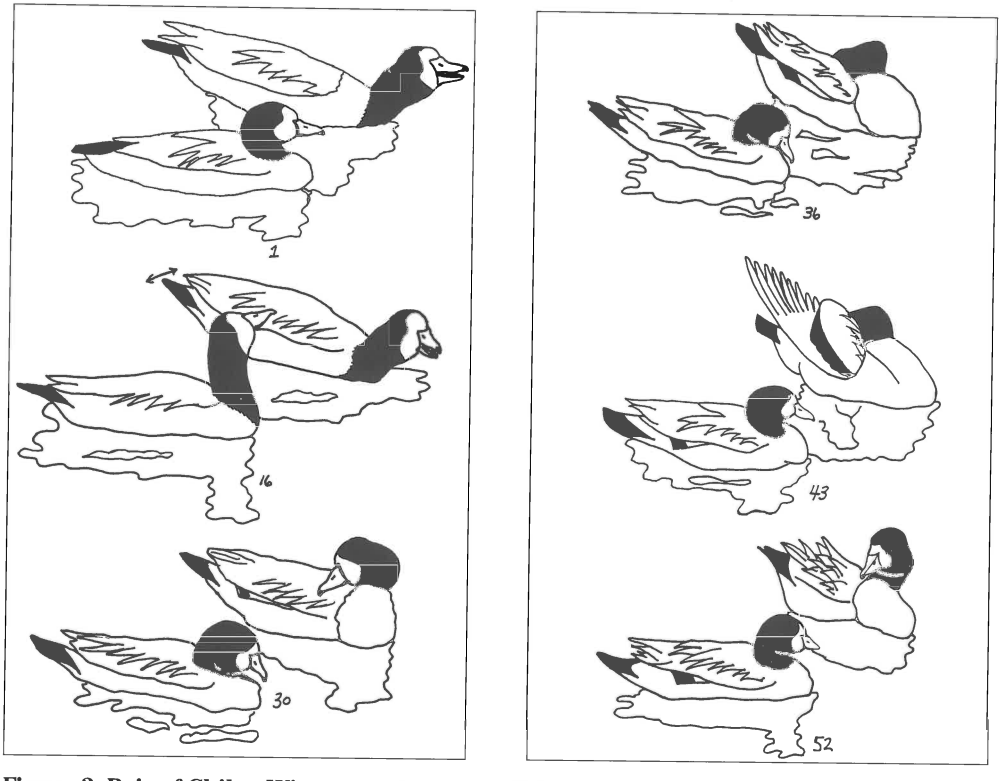


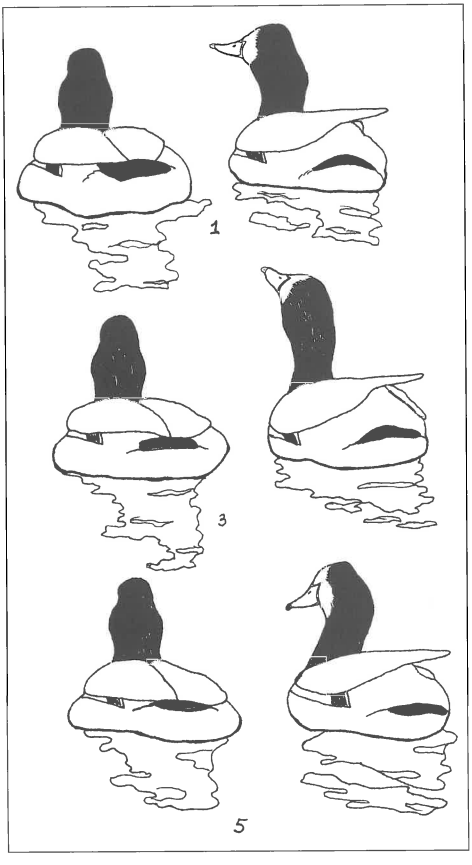
Figure 3. Pair of Chiloe Wigeon performing a Triumph Ceremony (frames 1-16) followed by male Preen-behind-the-wing (frames 30-52). Male is on the right. Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

among flightless birds in post-breeding moult (pers. observ.) and in fall and winter (Weller 1968), suggesting year-round maintenance.

In general, males and females of captive and wild pairs remained close to one another and tended to synchronize their activities. As the pair fed and moved together, males Chittered softly and females gave soft Honks. Flight was synchronized when males and females gave rapid **Head-shakes** and/or repeated **Head-thrusting** (McKinney 1965). Females sometimes gave rapid Honks during pre-flight displays and males infrequently Chittered.

Several courtship displays also maintained the pairbond. Preen-behind-the-wing was performed broadside to a mate when other wigeon were close or after Triumph Ceremonies (see below). In contrast to Johnsgard (1965, 1978), I did not see female Preen-behind-the-wing often (five times by four captive females in over 400 h of observation), and I did not observe members of a pair performing display preening to one another. Several paired males directed Display Shakes and Grunt-whistles at their mates.

When separated from their mates, females gave Honks and males gave Rakoo Calls, sometimes in response to one another's calls. Males sometimes searched for their mates by alighting in different areas of the pen or wetland, and then giving a series of Rakoo Calls. In captivity, males often gave Rakoo Calls, separated by 5-30 s, in an upright posture from the water (**Figure 5**) near where their mates were laying or during the first few days of incubation. Similar male behaviour was recorded in wild birds. Females did not give **Decrescendo Calls** when separated from their mates as do other *Anas* females (Johnsgard 1965).



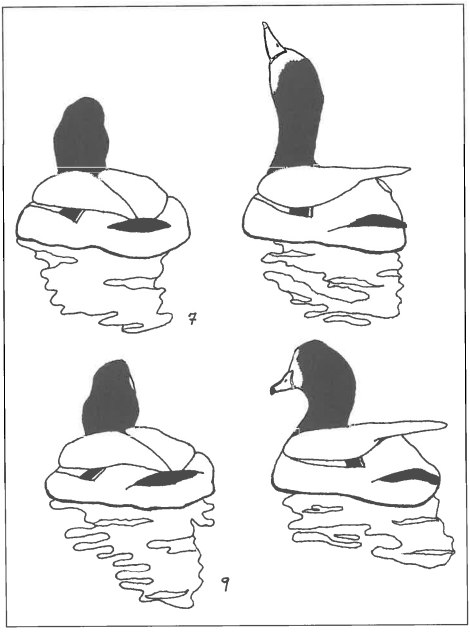


Figure 4. Female Chiloe Wigeon (right) performing Chin-lifting next to her mate. Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

After a separation and when other birds were near a pair, females sometimes Chin-lifted and males gave Rakoo Calls, initiating a **Triumph Ceremony** (**Figure 3**). During a Triumph Ceremony, the male gave one or several Rakoos as the female Chin-lifted and gave **Inciting Calls**, described as a whirring "errr" or "arrr" by Lorenz (1971) (**Figure 6A**), or Honks (**Figure 6B**). Males sometimes gave only the second syllables of the Rakoo Call during Triumph Ceremonies (**Figure 6B**), without returning to an upright posture before each call. Triumph Ceremonies might be preceded by male Snorts (**Figure 6C**). Males did not Chin-lift during Triumph Ceremonies, as Lorenz (1971) and Johnsgard (1965) reported.

During Triumph Ceremonies, the members of a pair remained close and often touched breasts as the calls were given. Males wagged their tails from side to side as they called, and at close range a loud, low buzz could be detected during the second syllable of the call. Females sometimes alternated threats or chases at other wigeon near the pair with Chin-lifts and Honks or Inciting Calls directed towards the mate, and Triumph Ceremonies frequently followed. The alternation of aggression with Chin-lifting in Chiloe Wigeon is similar to the **Inciting** displays of American and Eurasian Wigeon (Johnsgard 1965, Cramp & Simmons 1977; Wishart 1983), although female Chiloe Wigeon did not include threats as frequently during Inciting (e.g. 13 threats during 82 bouts of Inciting in 1986 for 6 females). Inciting was accompanied rarely by a movement of the female's tail from side to side (**Tail-wags**), and Inciting followed by male aggression was most common when a pair was attending a brood. Males sometimes followed the Triumph Ceremony with Preen-behind-the-wing (**Figure 3**), or chased or threatened other birds near their mates.

Nest-prospecting

Early in the breeding season, pairs made flights around the pen or study area, apparently searching for nest sites. **Persistent Quacking**, evenly spaced, prolonged honks associated with nest-prospecting in other species (McKinney *et al.* 1990a), was given by one female in captivity in response to a similar call by a female Mallard *Anas platyrhynchos* in a nearby pen. Persistent Quacking was also heard once in Argentina as a female circled a wetland with her mate (F. McKinney , pers. comm.) . In comparison with many *Anas* species, this vocalization appears to be rare in Chiloe Wigeon.

Copulatory Behaviour

Most pair copulations (92 of 95) were observed in captivity and almost all

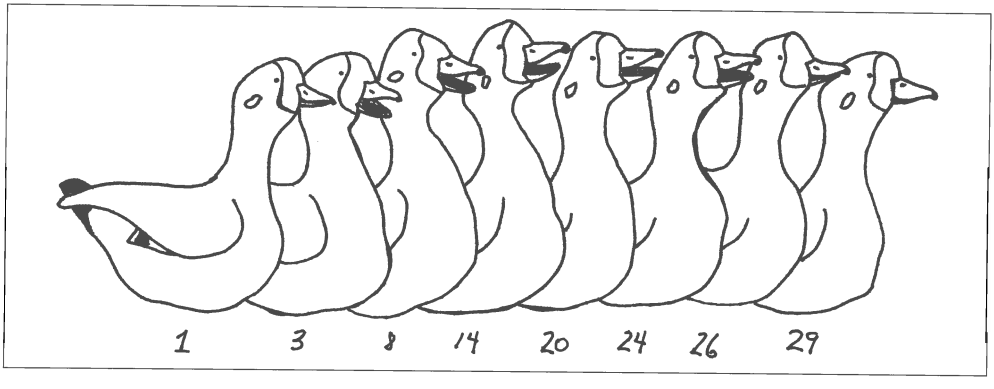


Figure 5. Male Chiloe Wigeon giving a Rakoo Call in an upright position, as he calls repeatedly while searching for his mate. Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

involved females in the laying or late pre-laying stages. **Pre-copulatory Head-pumping** was performed by males and females before 58 of 95 copulations. Following Pre-copulatory Head-pumping, females usually adopted a prone posture before copulation took place. Males initiated Pre-copulatory Head-pumping in all cases but one, and males sometimes Chittered as they head-pumped.

In 12 of 17 captive pairs, some pair copulations (n=37) occurred when the

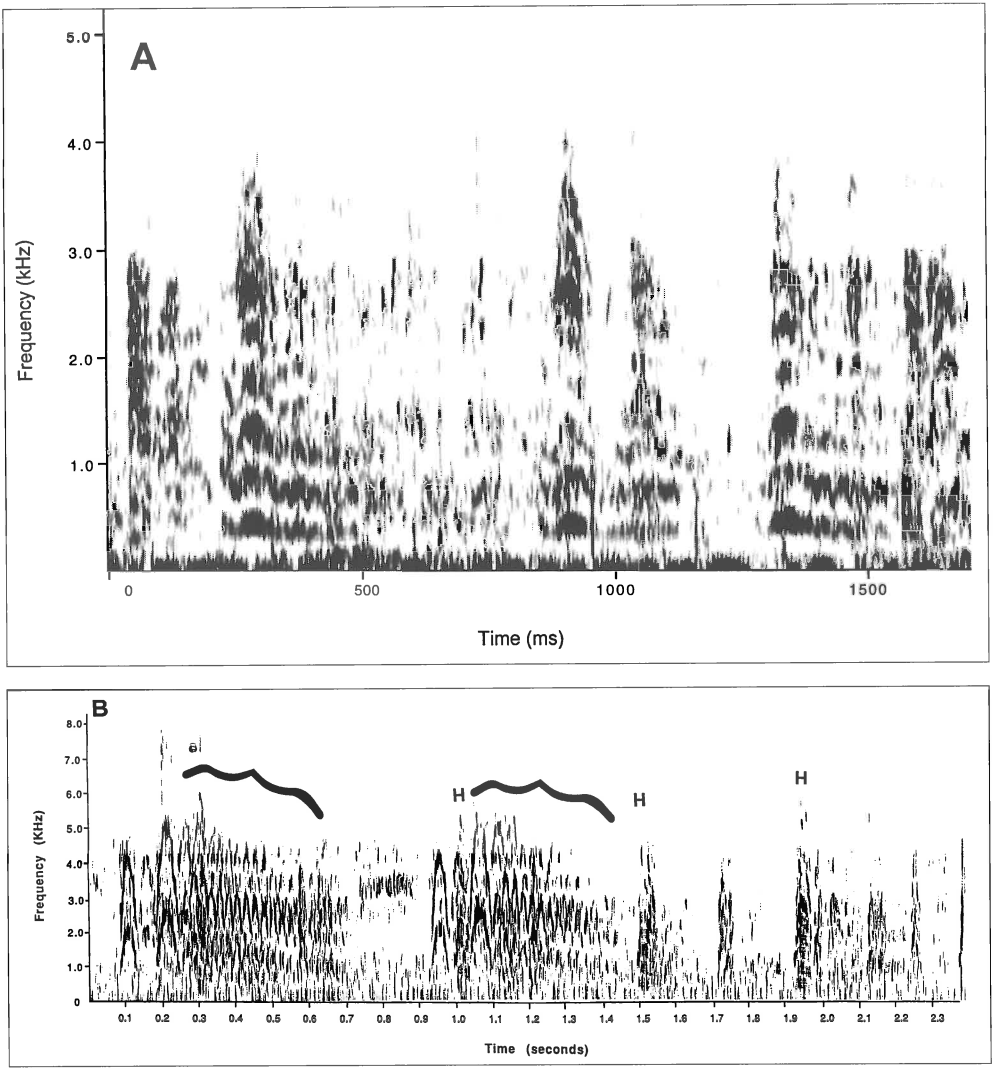
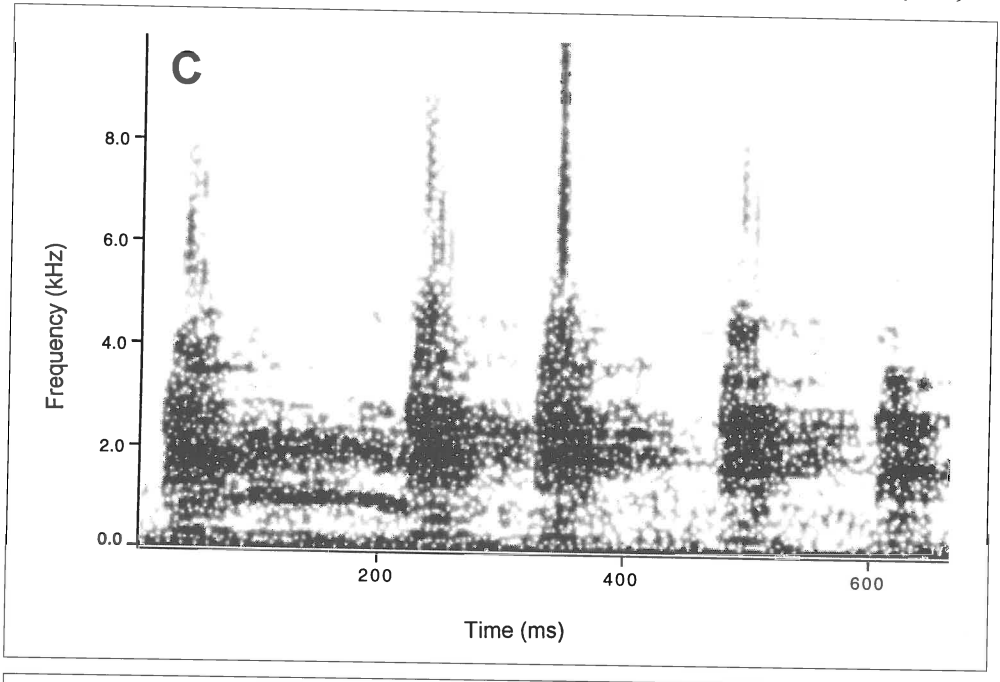
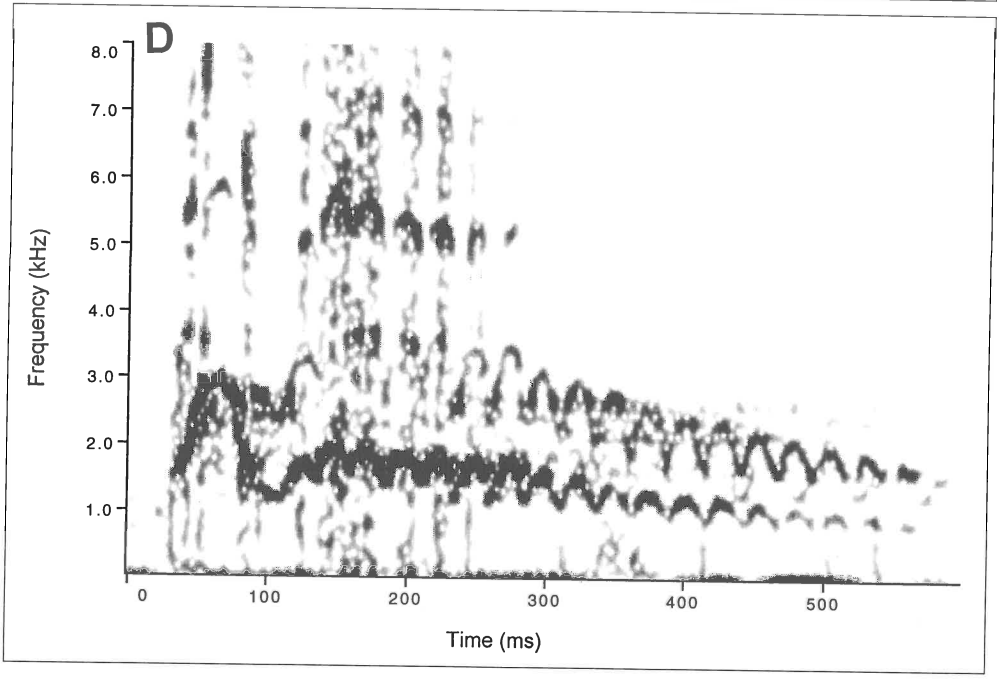


Figure 6. (A) Female Chiloe Wigeon gave Inciting Calls as they Incited near their mates. These calls are also given during Triumph Ceremonies. (B) Males gave the second syllable of Rakoo Calls (indicated by brackets) and females also gave Honks (indicated by H) during Triumph Ceremonies. (C) Triumph Ceremonies were preceded by male Snorts especially when other wigeon were nearby. (D) Males also gave the second syllable of the Rakoo Call as a post-copulatory display.

female did not perform Pre-copulatory Head-pumping or did not assume the prone posture, and the male rushed at his mate and attempted to mount her. When males tried to copulate under these conditions, females often attempted to move away and sometimes Honked. Despite female resistance, 62% (n=23) of





these forced pair copulation attempts appeared to be successful (sperm probably transferred as indicated by the male's tail-bend and thrust), including one that occurred immediately after a forced extra-pair copulation attempt. Other forced pair copulations occurred during the same period as forced extra-pair copulation attempts (described below).

Females bathed after copulation, and one female gave Preen-behind-the-wing broadside to her mate. Males gave post-copulatory displays after 27 of 58 pair copulations (47%) and after eight of 37 forced pair copulations (22%) (no female Pre-copulatory Head-pumping). The **Alert-broadside** posture in males, performed after 24% (n=23) of all copulations, was the most common (66% of post-copulatory displays). In this display, the head and crest were raised, with the neck slightly angled backwards, as the male remained motionless for a few seconds broadside to his mate. A call given from an upright posture broadside to the mate (single Rakoo Call or the second syllable of the Rakoo Call, **Figure 6D**), which occurred after 13% (n=12) of all copulations, was the next most common male post-copulatory display (34% of post-copulatory displays). One male gave Preen-behind-the-wing broadside to the mate after copulation. Post-copulatory displays were performed after 24 of 62 successful copulations (39%), but after only four of 33 unsuccessful copulations (12%).

Forced extra-pair copulations (FEPC), similar to those reported for other duck species (McKinney *et al.* 1983), were attempted by both wild and captive male Chiloe Wigeon. Males initiated FEPC attempts by approaching pairs, females that had just come off the nest, or even females on the nest. Sometimes males approached pairs several times before they initiated an FEPC attempt. As males approached a pair on water or on land, the female Incited and the pair frequently performed Triumph Ceremonies and gave Head-rubs (see below). Aerial approaches often led to aerial chases. When females were chased out of cover or off the nest, they gave loud Honks or **Squeals** and moved towards their mates, who usually gave Rakoo Calls and moved toward the female. During aerial chases, females gave Honks and Chin-lifted, and males gave Snorts, Rakoo Calls, and Rising Whistles. In wild birds, aerial chases lasted from 30 s to 5 min, except for two flights of about 20 min in which the pair and several pursuing males landed then flew several times.

Breeding was synchronous in captivity, and males frequently attempted FEPC when their mates were in cover or on the nest. In this situation, a male often gave a series of Rakoo Calls near where his female was in cover, attempted FEPC on a female in another part of the pen, then flew back to his former location and gave another series of Rakoo Calls. Data from 1986, when the most complete records were kept, show that most FEPC chases (74% of 308) and mounting attempts (80% of 25) were directed at late pre-laying or laying females. In the wild, 19 flights that involved one or more males and a pair were probably related to FEPC but the reproductive status of the females was not known. Only paired males were involved in the over 800 FEPC attempts observed in captivity; male status was unknown for wild birds except for one male that was tending a brood. Two captive males attending broods also attempted FEPC (n=16 attempts).

Mate defence was very strong and effective in Chiloe Wigeon, occurring during 383 of 420 (91%) FEPC attempts (data from 1986 and 1987). Males defending their mates on land or water gave Rakoo Calls, pecked other males, pushed them off the female, pulled their wings, and fought with them. During aerial chases, males defended their mates by flying at the chasing males and hitting them with their wings. Males also tried to remain between their mate and the chasing males. In the wild, females flew in an evasive pattern, sometimes circling high but remaining above the water. Males attempting FEPC sometimes fought with each other, and two wild males performed Bill-flipping bouts near an FEPC attempt. Only three of 40 FEPC mounting attempts in captivity were judged to be successful.

In the wild, two FEPC attempts were successful despite strong mate defence, when three to five males were involved and the female was mounted by two to three males simultaneously. Pairs performed frequent Triumph Ceremonies, sometimes including male Preen-behind-the-wing, when males were driven away or the pair was reunited.

Aggressive Interactions

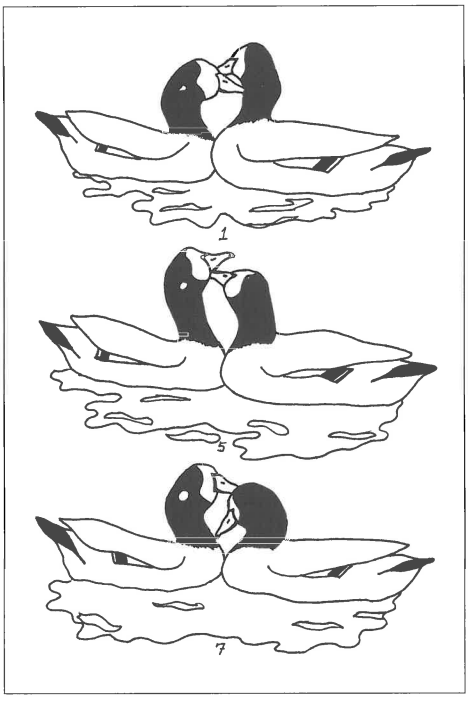
Although wild and captive Chiloe Wigeon were gregarious, breeding pairs did not tolerate the close proximity of conspecifics, or occasionally other species, and chased, swam-off (followed as if chasing), or threatened them. Males defended a moving territory around the female (and brood if present). Adults of both sexes and also ducklings threatened with the bill open and the head low (**Open-bill Threat**), as in other waterfowl (e.g. Cramp & Simmons 1977). In adults, Open-bill Threats were sometimes given in a **Wings-up** threat posture, when the tips of the folded wings were held up away from the body.

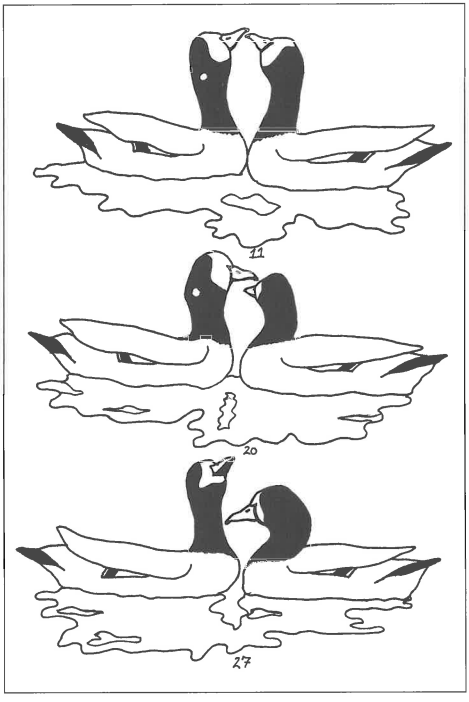
Males and females frequently rolled their heads side-to-side on their backs during hostile encounters. Usually several of these **Head-rubs** ("shoulder rubbing" of McKinney 1965) were performed in rapid succession, forming discrete bouts. Head-rubs sometimes preceded more overtly aggressive behaviour such as Open-bill Threats and chases, and they seemed to signal a lower intensity threat. Another less overt threat was **Tail-wag**, where the wing tips were lifted slightly and the tail was rapidly moved from side to side. Males sometimes gave Tail-wags when their mate was not present but they were close to other males. Tail-wags by females during Inciting, and by males during Triumph Ceremonies (**Figure 3**) and Bill-flipping (see below), seemed to signal aggression during joint threat displays directed at other wigeon. Snorts were given by males when a pair was approached by other wigeon, and often previous to a Triumph Ceremony, suggesting that they functioned as a threat.

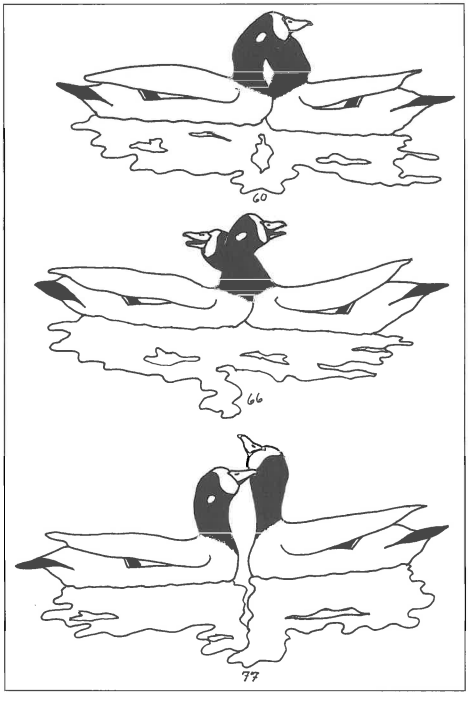
On rare occasions, five different males directed Display Shakes, Grunt-whistles, and Preen-behind-the-wing at other males, in addition to directing courtship displays at females. Males could have been using these male-male courtship displays as aggressive signals (McKinney *et al.* 1990b). Most of these displays were performed by one male and were directed at the same male; both of these males were paired to females and they were not homosexually imprinted.

In captivity, paired males briefly associated with each other (5-25 minutes in length) when their mates were on the nest during laying or incubation, and performed bouts of **Bill-flipping**, similar to Tandem-swimming in American Wigeon (Wishart 1983). Bill-flips were upward flips of the bill, with a brief pause when the bill was pointing upwards before it was brought down (**Figure 7**). Bill-flips were accompanied by **Pic Calls** (**Figure 8A**), short calls similar to whistles, given as the bill was brought upwards. Bill-flipping bouts frequently led to Rakoo Calls (often only the second syllable of the call) given with Tail-wags (**Figures. 7, 8B**). Males also Chittered as they were close to each other during these bouts. When a male was near his mate's nest, he also tended to give **Rising Whistles** (**Figure 9**; see below), a loud whistle increasing in pitch that appears to be modified from the first syllable of the Rakoo Call (**Figure 10A**). This behaviour possibly warned the mate of the presence of other males, as the Rising Whistle usually functions as an alarm call.

During male-male associations, males occasionally gave Open-bill Threats and pecked or chased each other, but more often, more subtle aggression was present (Head-rubs and swim-offs). These aggressive actions alternated with Bill-flipping bouts, indicating that Bill-flipping is a hostile signal. Comfort movements (preening the flank, back, or dorsal side of the wing) were also interspersed with periods of display activity. Bouts of Bill-flipping between two males are probably what Lorenz (1971) called "mutual chin-lifting" by a pair and Johnsgard (1965) described as the male's response to female







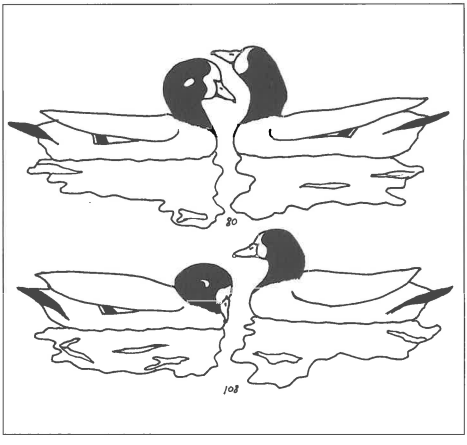


Figure 7. Male Chiloe Wigeon Bill-flipping bout, including Rakoo Calls (frames 60-66). Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

Inciting. This is further supported by Johnsgard's (1965) observation that the mutual calling bouts were accompanied by frequent aggressive signals (threats and the rubbing of the head on the back), as I observed in Bill-flipping bouts but not Triumph Ceremonies.

Fjeldsa & Krabbe (1990) also refer to infectious displays in wild Chiloe Wigeon in which males called and lifted their heads up and down. I observed Bill-flipping bouts on two occasions in the wild, once near a forced extra-pair copulation attempt and once when two males landed near a lone male, who was later joined by a female. One Bill-flipping bout was observed as an adult male followed a juvenile male late in the breeding season in captivity.

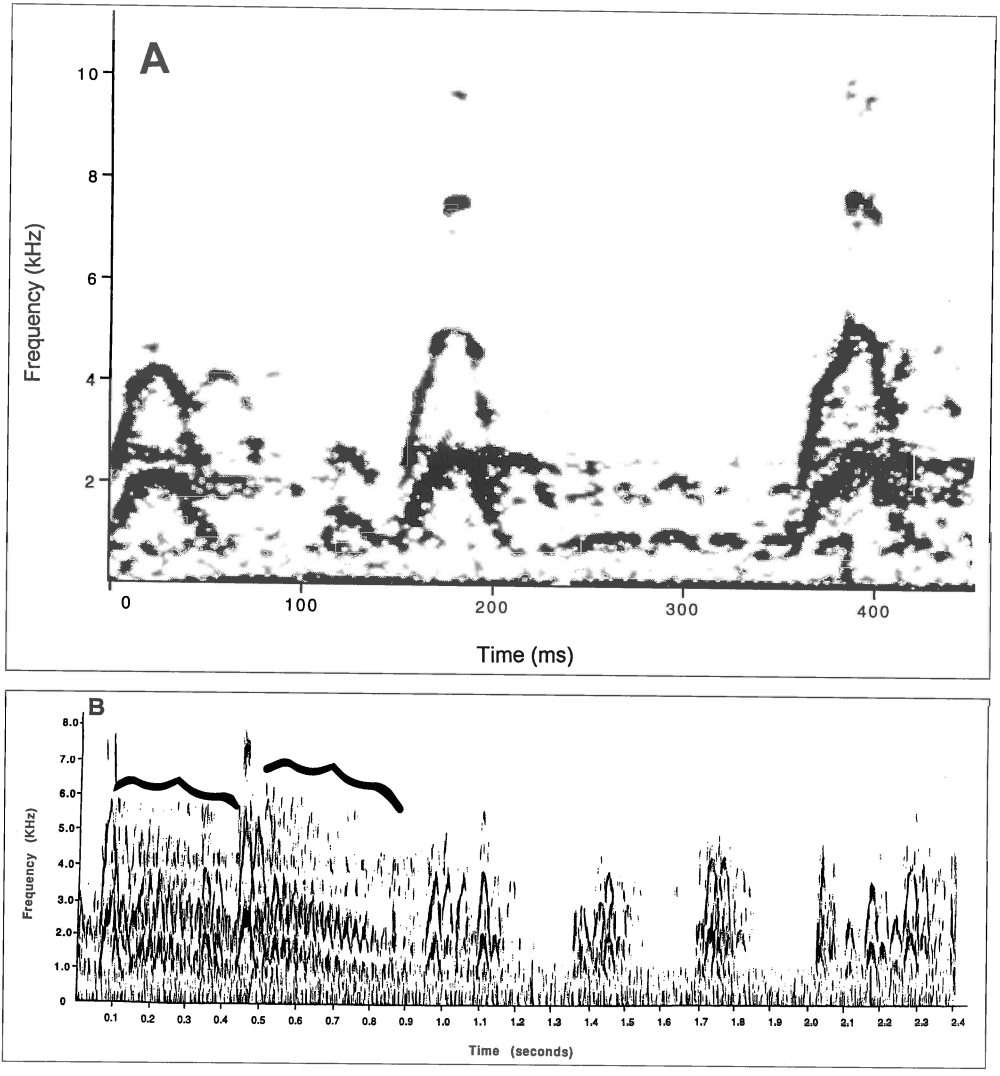


Figure 8. (A) Pic Calls of Chiloe Wigeon were given as the head was raised during Bill-flipping. (B) As two males performed Bill-flipping bouts, the second syllables of Rakoo Calls were also given (indicated by brackets).

Alarm Calls

Male Rising Whistles (**Figures. 9, 10A**) and a series of loud female Honks (**Figure 10B**) were given in response to approaching aerial predators, dogs, and humans as birds swam away from shore towards open water, or when males flew from danger. If the source of danger was very close, males gave shortened Rising Whistles in rapid succession. Five males gave a variation of the Rising Whistle, with three smoothly connected syllables that increased then decreased in frequency (**Figure 10C**), in alarm situations. At close range, males were also heard to give soft, repeated whistles as alarm calls (**Figure 10D**).

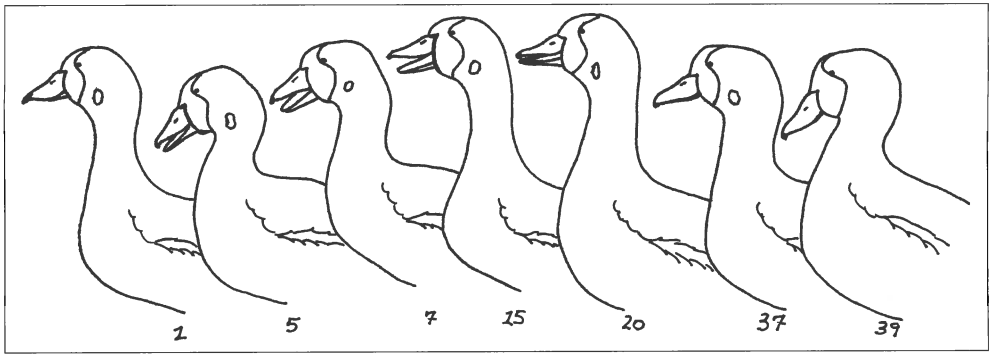


Figure 9. Male Chiloe Wigeon giving a Rising Whistle as an alarm call. Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

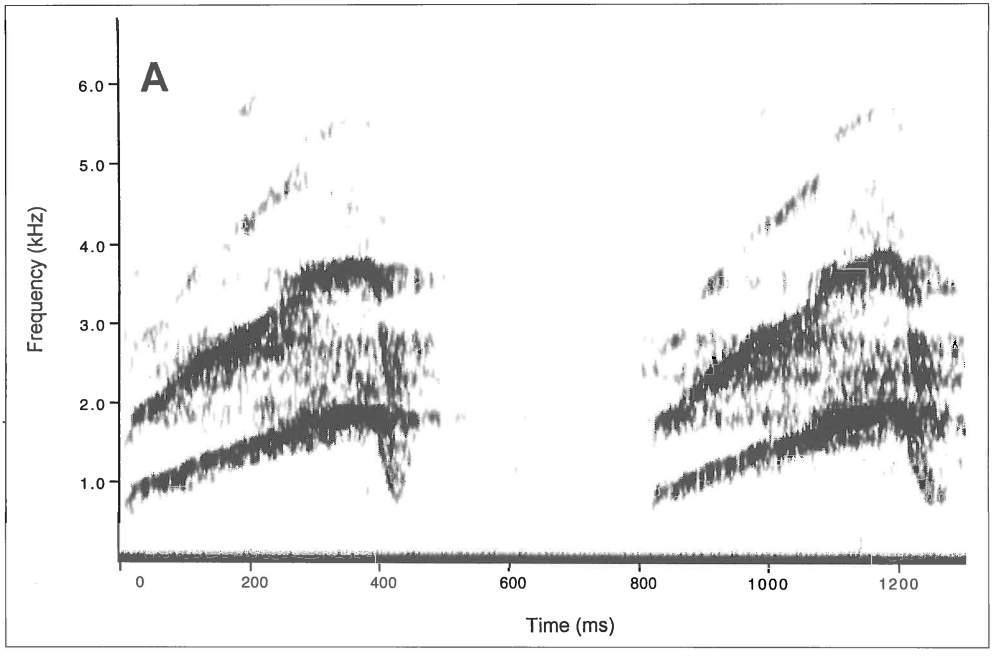
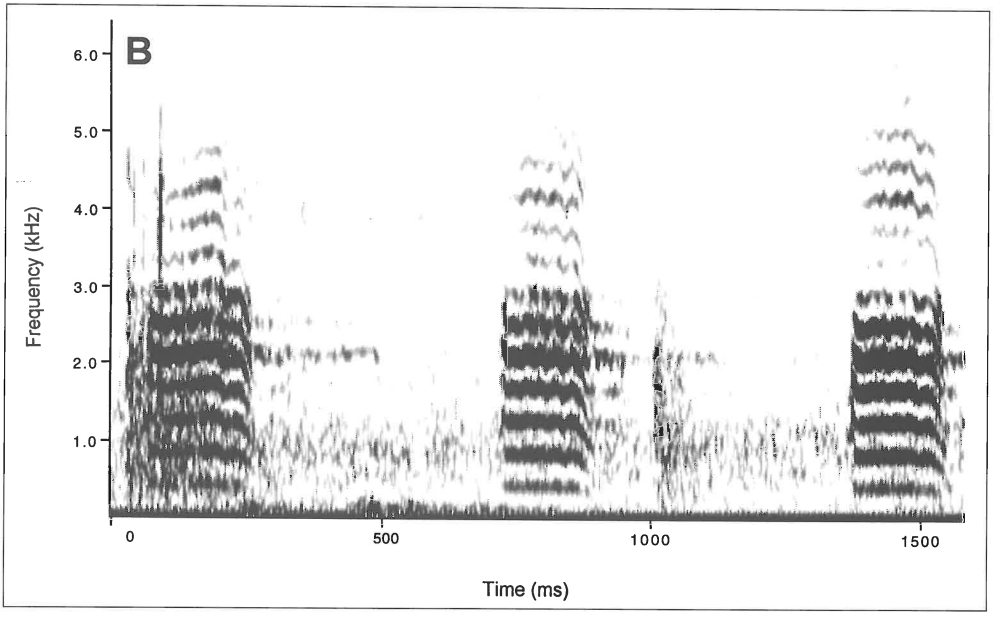
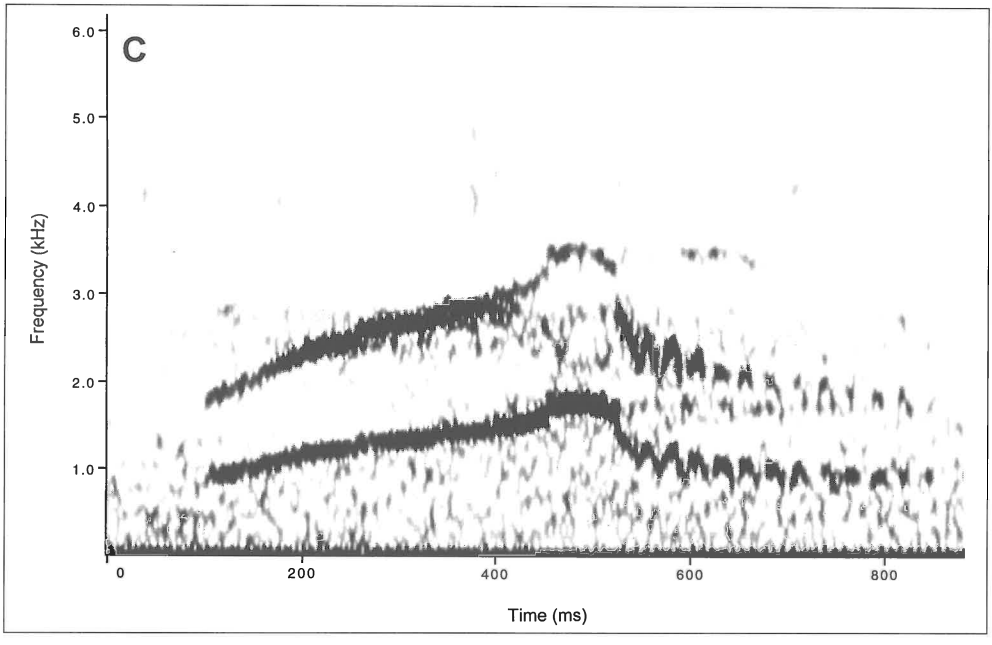


Figure 10. (A) Male Rising Whistles and (B) loud female Honks were given by Chiloe Wigeon as alarm calls. (C) Males also gave a variation of Rising Whistles and (D) soft, repeated whistles if danger was sighted.

Parental Care and Family Interactions

Fourteen broods were observed in captivity and 37 broods were observed in the wild. Broods were escorted closely by both parents, and the behaviour of captives was similar to that of wild parents, except for the greater time wild parents spent in alert postures (Brewer 1990). In general, family members remained close to one another. Females gave soft **Brood Calls** (**Figures. 11A-C**)





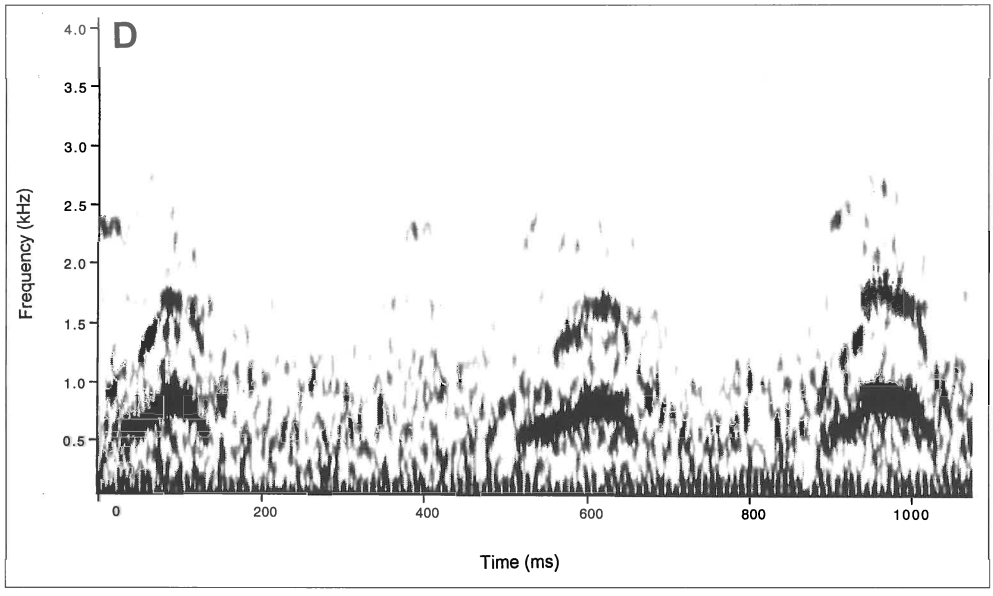
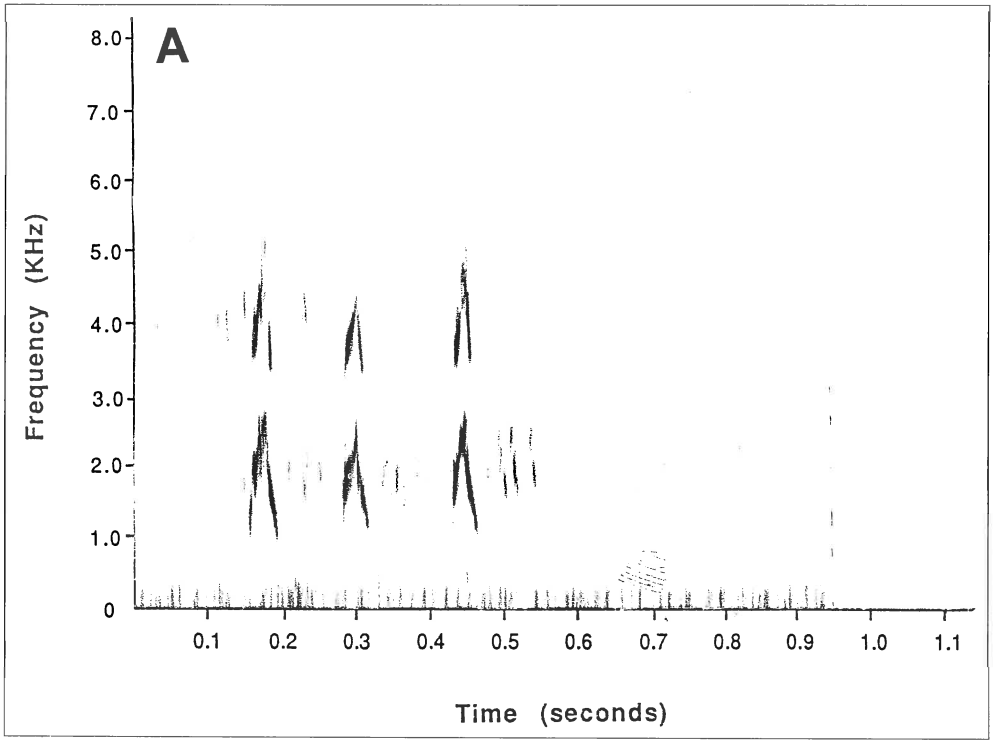
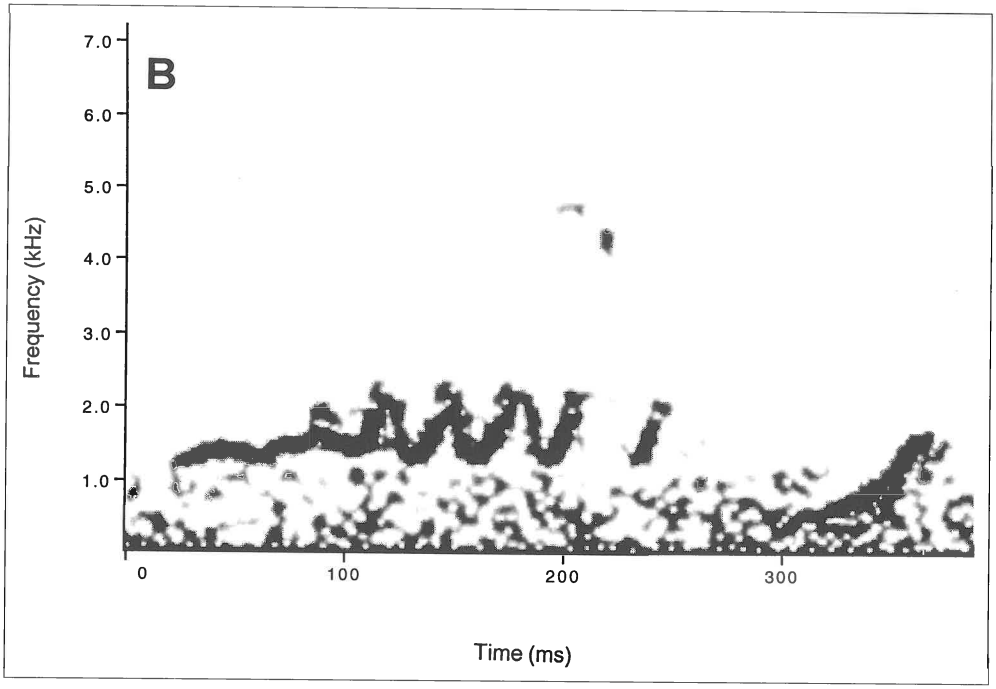
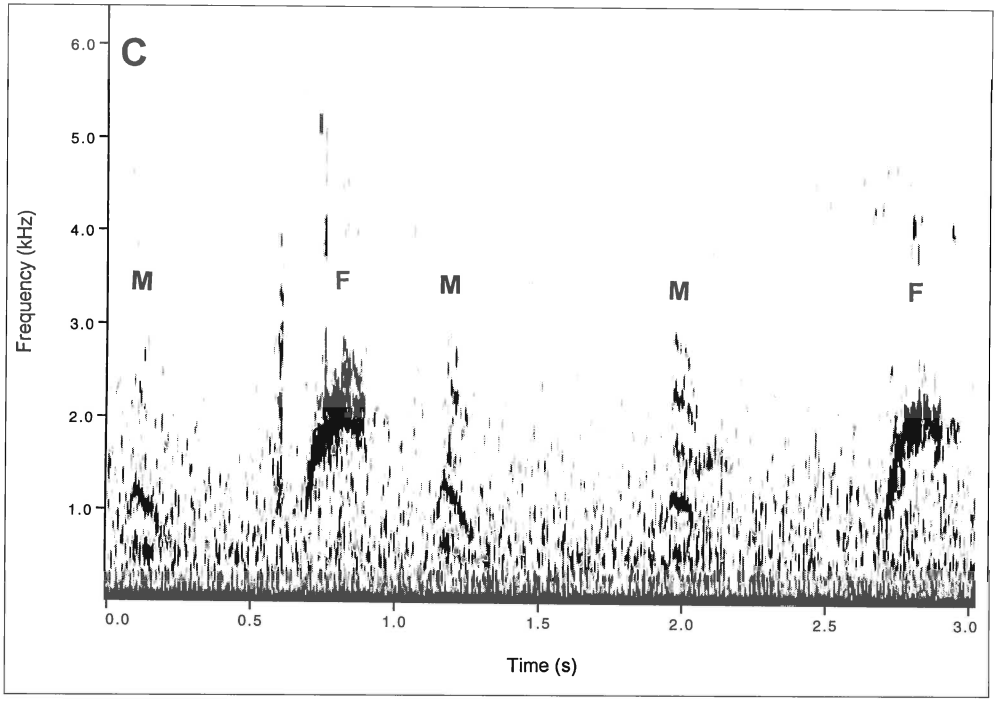


Figure 11. (A, B, C) Female Chiloe Wigeon gave Brood Calls (indicated by F in Figure 11C) and (C) males (indicated by M) called softly as they accompanied their ducklings.




B
Frequency (kHz)
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
100
200
300
Time (ms)


C
Frequency (kHz)
6.0
5.0
4.0
3.0
2.0
1.0
M
F
M
M
F
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Time (s)

almost constantly as they led and brooded ducklings, especially when ducklings were young. Males also gave soft calls similar to Chittering as they accompanied broods (**Figure 11C**).

Ducklings gave **Contentment Calls** (Kear 1968) almost continuously as they fed, swam, or rested near either parent and when ducklings became separated from their parents, they gave loud **Distress Calls** (Kear 1968). Both parents responded to Distress Calls by going to ducklings and calling to them (female Honks and male Rakoo Calls). When ducklings became very spread out, male parents sometimes gave Rakoo Calls and females gave loud Honks. The **Decrescendo Call** of females, a series of two honks of descending pitch, was heard in this study only when two captive females lost their single ducklings a few days after hatch. The females gave frequent Decrescendo Calls as they swam in the morning on the day that their only ducklings were found dead.

When a person, dog, or potential aerial predator was close, females with broods sometimes gave Squeals immediately followed by Honks (**Figure 12A**), in addition to Honks and Brood Calls (**Figure 12B**). Males with broods gave Rising Whistles, and families moved towards open water, or into the water if on land.

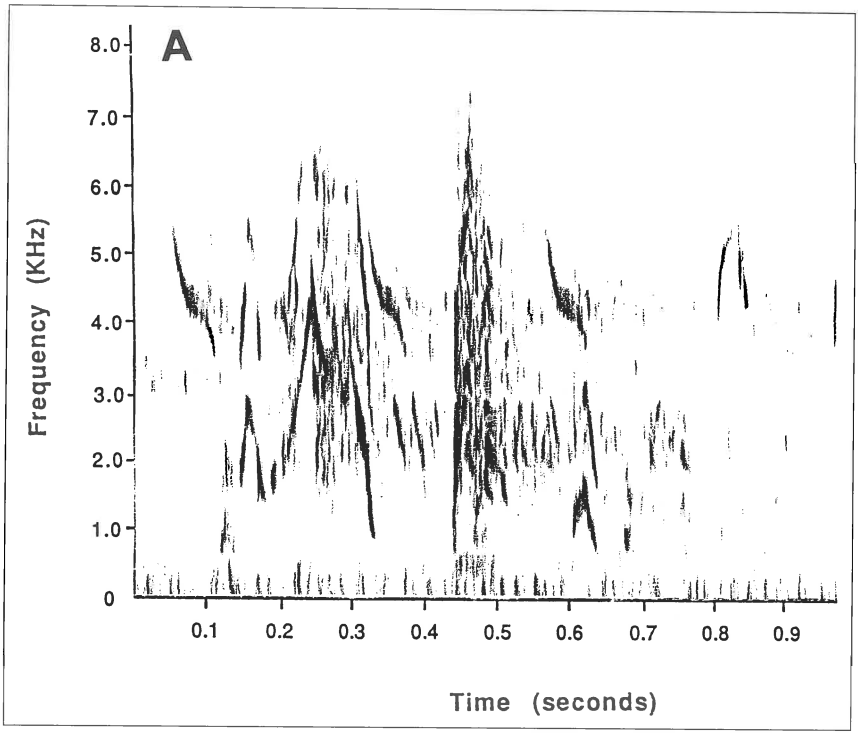
The female of one wild pair escorting ducklings performed a **Distraction Display**, similar to that of the American Wigeon (Beard 1964), in response to my approach. The female gave loud Honks as she flapped slowly across the water, beating her wings on the water's surface. The ducklings initially went to the male parent near some reeds, then went into the reedbed. The male then left the ducklings and made several short flights around the pond, giving Rakoo Calls and Rising Whistles. No Distraction Displays were observed in captivity, but parents mobbed and attacked a Belted Kingfisher *Ceryle alcyon* when it dived near a duckling.

Ducklings played an active role in maintaining bonds with their parents. On rejoining the family after a separation, ducklings sometimes directed **Chin-lifts** towards their parents and/or other brood members (**Figure 13**). These Chin-lifts were often accompanied by **Peeps** in young ducklings, and by high-pitched **Honks** (females) or **Trills** (males, probably a precursor to Rakoo Calls; **Figure 14**) in older ducklings. Although males first gave Trills when they were only three days old, these calls and the Honks of young females were more noticeable when ducklings were six to eight weeks old.

Family Triumph Ceremonies or male Rakoo Calls, sometimes accompanied by male Preen-behind-the-wing, followed some reunions as ducklings Chin-lifted. During family Triumph Ceremonies, all members of the family were very close, females Chin-lifted and Honked, males gave Rakoo Calls from a head-forward posture, and ducklings Chin-lifted and called.

Both parents were aggressive to conspecifics, other duck species, and other water birds near their broods, and ducklings sometimes gave bouts of Chin-lifting when other birds were near them. Ducklings as young as one week old Chin-lifted after their parents were aggressive to other birds and sometimes this led to family Triumph Ceremonies in which ducklings tended to be especially close to the male parent. Family Triumph Ceremonies were also initiated when parent females Chin-lifted or parent males gave Rakoo Calls after either or both parents threatened or chased another bird.

Limited evidence, from marked ducklings in two captive families (two male ducklings, and four male and three female ducklings), suggests that there were individual and sex differences in duckling behaviour. In each family, certain ducklings followed their parents less consistently and gave more Distress Calls. In the larger family, ducklings directed more Chin-lift bouts to their male parent (n=42 bouts) than to their female parent (n=16 bouts), although female ducklings directed more Chin-lifts to their female parent than male ducklings (mean = 6.25±2.50 SD bouts per male duckling and 5.67±2.08 SD bouts per female duckling directed at male parent; 1.75±1.71 SD bouts per male and 3.00±1.73 SD bouts per female directed at female parent).



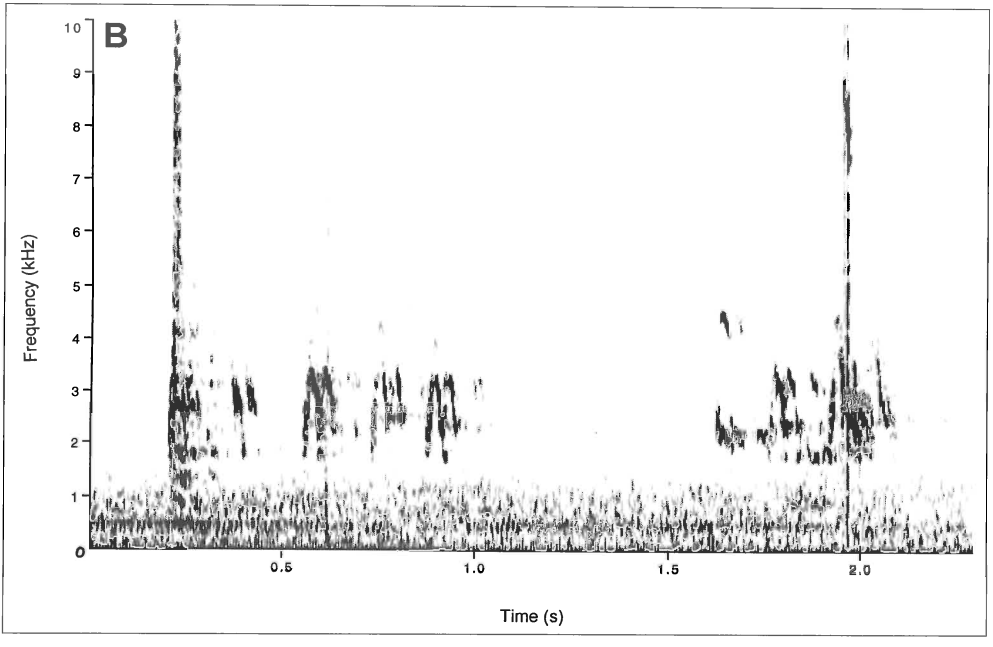


Figure 12. (A) A Squeal followed by a Honk and (B) Honks alternating with softer Brood Calls were given as an alarm by female Chiloe Wigeon with broods.

Adoption

Paired breeding adults of both sexes, but especially males, showed a keen interest in ducklings belonging to other broods of Chiloe Wigeon and other duck species both in captivity and in the wild. Males followed ducklings that were separated from their parents and gave Rakoo Calls and Rising Whistles near them, although they did not appear to be courting the ducklings. In captivity, two White-cheeked Pintail *A. bahamensis bahamensis* broods were sequentially adopted by two paired male Chiloe Wigeon. Each male escorted the brood

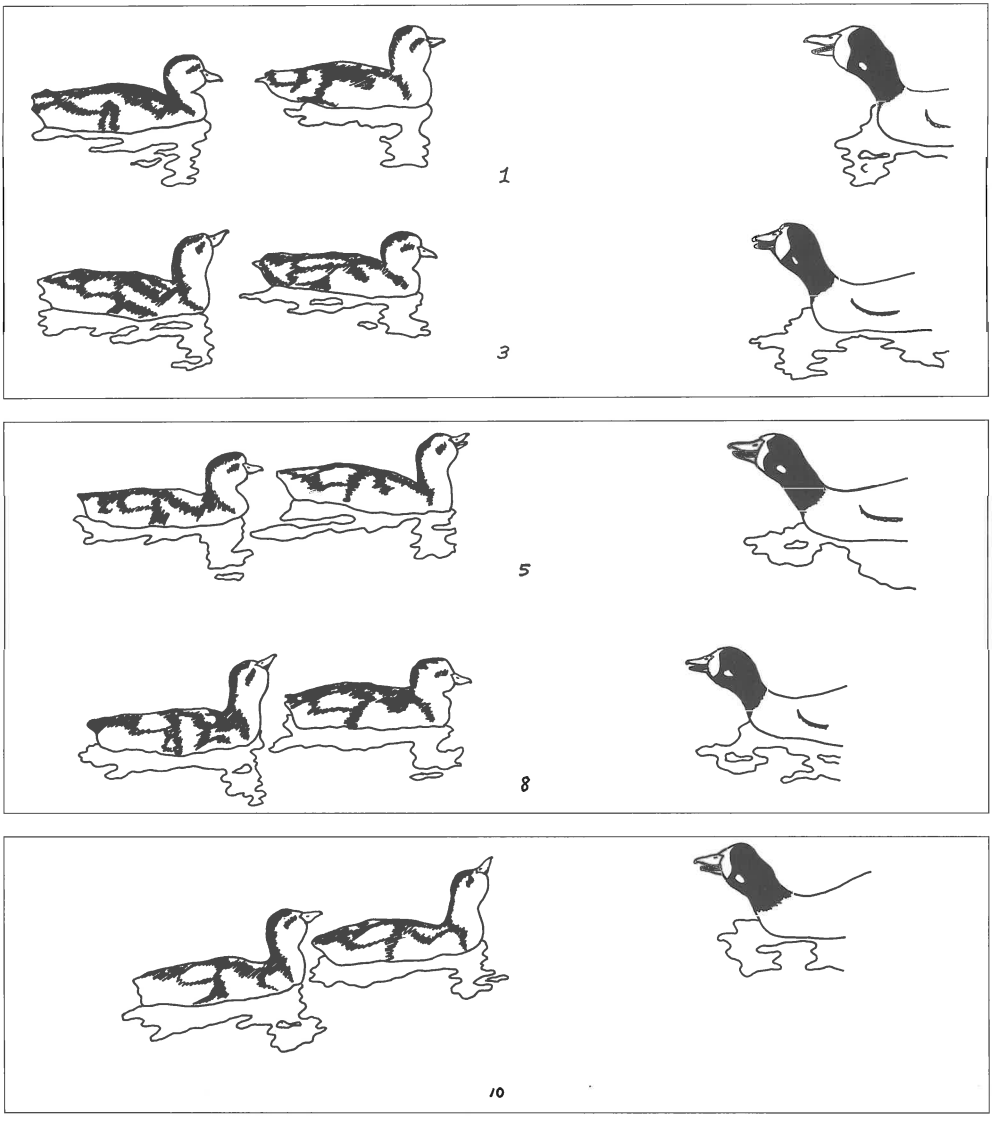


Figure 13. Chiloe Wigeon ducklings Chin-lift as their male parent rejoins them and gives a Rakoo Call. Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

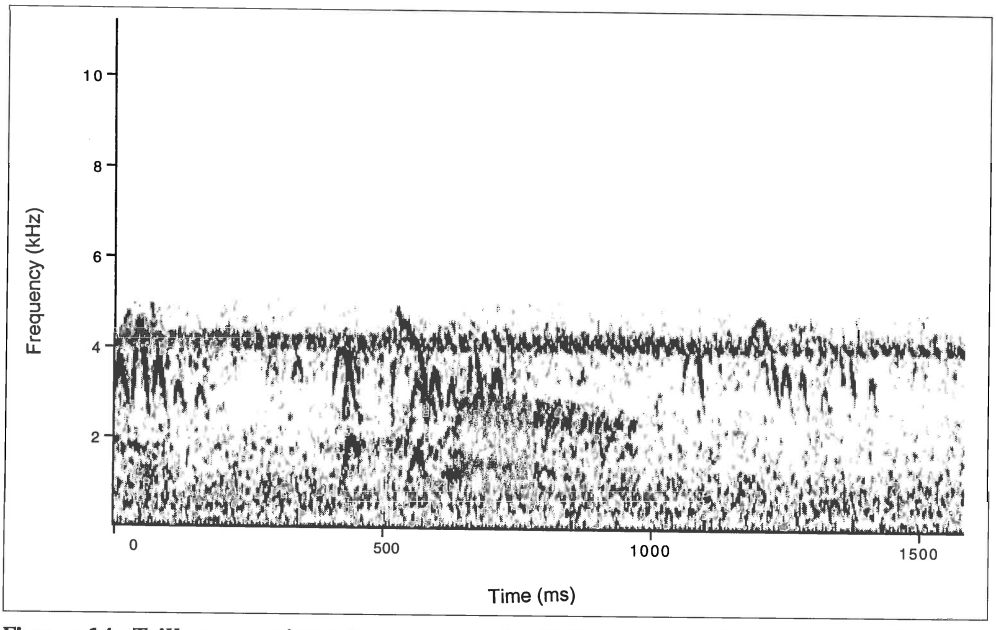


Figure 14. Trills were given by young male Chiloe Wigeon during family Triumph Ceremonies. The thin band alternating around 4 kHz represents background noise.

and drove other birds away, although both continued to maintain their bonds with their incubating mates. The first male escorted the brood for six days, until his own brood had hatched. The second male continued to escort the pintail brood for almost a month after his own brood had hatched, dividing his time between the two families.

In five other cases, pairs attempted to adopt Chiloe Wigeon ducklings (**Table 1**). For pairs with broods (n=4 pairs), adopted ducklings remained permanently with their new families. One pair without ducklings attempted unsuccessfully to get an unaccompanied brood to follow them. Males and females played an active role in some adoptions by approaching ducklings and by chasing away parents when they attempted to retrieve their offspring. In other cases, ducklings joined a different brood and were accepted by the parents of the brood they joined. Most adoptions involved young ducklings (**Table 1**).

Table 1. Conspecific adoptions of Chiloe Wigeon ducklings.

Location	Duckling age	Circumstances
Captivity	1 day	Two ducklings joined older brood of four; true parents chased away by adopting parents.
Captivity	2 days	Paired male with brood of five actively adopted broods of two and three; true parents chased away.
Captivity	9 days	Two ducklings joined a brood of five when female parent removed temporarily; true parents chased away by adopting parents.
Wild	1 day	Eight ducklings joined brood of nine during alarm; ducklings did not respond to true parents.
Wild	2 days	Pair without ducklings tried to lead eight ducklings away from where their parents had temporarily left them; ducklings rejoined their parents when they returned.

Table 2. Proposed display homologies of the wigeon, Gadwall, and Falcated Duck.[1] C = display common, R = relatively rare, X = frequency unknown or variable, - = absent, ? = unknown. Displays of Chiloe Wigeon that differ from their homologues are indicated with an asterisk and discussed in the text.

	Gadwall and Falcated Duck	American and Eurasian Wigeon	Chiloe Wigeon
Male Displays:			
Head-up-tail-up	C	–	–
Down-up	X	–	–
Grunt-whistle	C	–	C
Facing	C	C	–
Turn-the-back-of-the-head	C	X	R
Display Shake	C	C	C
Slow Whistle	C	C	C*
Fast Whistle	C	C	C*
Alarm Call	C	C	C
Soft calls	?	?	C
Post-copulatory call or posture	C	C	C
Chin-lifting or Bill-flipping	C	C	C*
Tandem-swim	?	X	C
Courtship as aggression to males	?	?	R
Female Displays:			
Chin-lifting	C	C	C
Inciting	C	C	C*
Alarm Call	C	C	C
Brood Call	C	C	C
Distraction Display	X	X	R
Persistent Quacking	C	R	R
Decrescendo Call	C	R	R
Displays of both sexes:			
Pre-copulatory Head-pumping	C	C	C
Pre-flight Head-shake or thrust	C	C	C
Preen-behind-the-wing: male	C	C	C
female	X	X	R
Triumph Ceremony	C	C	C*
Tail-wags	C	C	C
Open-bill Threat	C	C	C
Wings-up	–	C	R
Head-rubs	–	–	C
Duckling Displays:			
Distress Calls	C	C	C
Contentment Calls	C	C	C
Chin-lifting and Peeps	X	?	C
Honks	?	?	C
Trills	?	?	C
Family Displays (both parents):			
Triumph Ceremony	–	–	C

[1]Information for Gadwall is from Lorenz 1971 and Cramp & Simmons 1977; for Falcated Duck, Lorenz & von de Wall 1960 and von de Wall 1963; for American Wigeon, Johnsgard 1965, Kear 1968, and Wishart 1983; for Eurasian Wigeon, Kear 1968, Lorenz 1971, and Cramp & Simmons 1977; for Chiloe Wigeon, Johnsgard 1965, Kear 1968, Lorenz 1971, and present study.

Discussion

The display repertoire of a species can be shaped by ecological factors (e.g. Crook 1964) and by changing signalling needs related to the social system, resulting in specialized repertoires for males and females (McKinney 1975). The comparative method is useful in investigating the influence of these factors, but interpretations must be made in the context of phylogenetic relationships (Harvey & Pagel 1991). The Gadwall, Falcated Duck, and three wigeon species are members of a phylogenetic group that is basal to the major *Anas* types according to recent evidence from comparative morphology (Livezey 1991) and DNA sequencing of mitochondrial genes (K. Johnson, pers. comm.), confirming previous analyses using behavioural data (Johnsgard 1962; Lorenz 1971). These five species share a number of similar displays that are probably present in all species due to common ancestry, including pre-flight and pre-copulatory displays, aggressive displays, adult calls, duckling calls, and several courtship and pair maintenance displays (**Table 2**). The three wigeon species have apparently lost Head-up-tail-up and Down-up, male courtship displays present in Gadwall and Falcated Duck (Lorenz & von de Wall 1960; von de Wall 1963; Cramp & Simmons 1977). As suggested by Kaltenhauser (1971) for other *Anas* species, the loss of these major aquatic courtship displays may be related to displaying on land as well as water, which occurs in the three wigeon species (Cramp & Simmons 1977; Wishart 1983; Mayhew 1985; this study) but not in Gadwall and Falcated Duck.

Although males perform ritualized Display Shakes in all three wigeon, a "true" Grunt-whistle display was used frequently only by Chiloe Wigeon, especially when wild males courted ducklings (Brewer 1991). Chiloe Wigeon Grunt-whistles, however, did not include the sideways flick of the head and spray of water droplets seen in Gadwall and Falcated Duck. Similar displays have been noted rarely in American and Eurasian Wigeon, and in hybrids between wigeon and other *Anas* species (Johnsgard 1965; Kaltenhauser 1971; Lorenz 1971; Wishart 1983). Facing or Turn-toward-the-female is present in Gadwall (Cramp & Simmons 1977), Falcated Duck (Lorenz & von de Wall 1960), and the two northern wigeon (Cramp & Simmons 1977; Wishart 1983), but is absent in Chiloe Wigeon. Male Chiloe Wigeon raised the irridescent green feathers on the side of the head in broadside displays to females rather than displaying the prominent, light-colored patch on the forehead that is shown off during Facing in the two northern wigeon, or the specialized head feathers prominent in Turn-toward-the-female, especially for Falcated Duck. Turn-the-back-of-the-head, common in the American and Eurasian Wigeon, Gadwall, and Falcated Duck, was infrequent in breeding Chiloe Wigeon, and not among the displays directed at ducklings during courtship (Brewer 1991).

Additional features of the displays and display repertoire of the three wigeon species are probably related to their specialized feeding behaviour. The wigeon are well known for their consumption of plant material on land and water, and their bill morphology is convergent with that of geese (Phillips 1923; Munro 1949; Johnsgard 1965; Weller 1968; Owen & Thomas 1979; Wishart 1983; Mayhew 1985; Jacobsen 1993). Grazing on land requires more time feeding, as plant material is a poorer source of protein than invertebrates (Wishart 1983; Mayhew 1985). Grazing in open areas is dangerous in terms of predators, and is costly in terms of vigilance (e.g Mayhew 1987; Jacobsen & Ugelvik 1992; 1994). Food is usually patchily distributed, and competition for choice patches may occur. These aspects of a grazing lifestyle favour high male vigilance, especially while the female feeds during laying, joint threat behaviour by pairs, and noisy calling to keep mates in close contact and repel competitors.

Behavioural specializations in grazing waterfowl can be seen especially in displays associated with aggressive interactions and maintenance of pairbonds. Aggressive behaviour in Chiloe

Wigeon was frequent and well-developed, as it is in the northern wigeon. Open-bill-threats, Tail-wags, and aggression during female Inciting are shared by the wigeon and their close relatives, but Wings-up has been noted only in the wigeon (**Table 2**). Geese and swans also raise or flick the wings as an aggressive display (Johnsgard 1965), and Wings-up may represent a convergent strategy for aggression associated with grazing. This display is seen often in American and Eurasian Wigeon (Cramp & Simmons 1977; Wishart 1983), but in Chiloe Wigeon, Head-rubs may replace Wings-up, especially when expressing a lower-intensity threat.

In breeding wigeon, aggressive behaviour occurs during the defence of waiting areas near the nest site (Eurasian Wigeon), breeding territories (American Wigeon), or moving territories around the female (Chiloe Wigeon) (summarized by Anderson & Titman 1992; this study). Ritualized aggression between males (Tandem swimming and Bill-flipping bouts) has been noted for American and Chiloe Wigeon (Wishart 1983, **Figure 7**), but not Falcated Duck. Small flocks of Eurasian Wigeon males observed in the breeding area (Hilden 1964) and observations mentioned by Wishart (1983) for Gadwall may represent a similar phenomenon to Tandem-swim and Bill-flipping bouts. Chiloe Wigeon males also vigorously defended their mates during forced extra-pair copulation (FEPC) attempts. In contrast to geese (e.g. Mineau & Cooke 1979) and the northern wigeon (Dementiev & Gladkov 1967; Cramp & Simmons 1977; Wishart 1983), FEPC attempts were frequent in Chiloe Wigeon. For American Wigeon, Wishart (1983) reported defence during only three of six FEPC attempts, and pairs attempted to avoid interactions with other males by crouching or hiding. Wild Chiloe Wigeon pairs usually did not have this option due to the lack of suitable cover. Prevention of cuckoldry through vigorous defence of the mate, and possibly through forced pair copulations, may be especially important in Chiloe Wigeon because males provide care for ducklings. In addition, because pairbonds are long-term, strong mate defence may be important to promote the condition of present and probably future female breeding partners.

Pairbonds in all three wigeon are especially strong (Heinroth 1911; Delacour & Mayr 1945; Lorenz 1971; Cramp & Simmons 1977), although male American and Eurasian Wigeon desert their mates during incubation (Cramp & Simmons 1977; Wishart 1983) and only Chiloe Wigeon appear to have long-term pairbonds (Johnsgard 1965; Kear 1970; Weller 1968). In geese and swans, frequent Triumph Ceremonies promote the pairbond and signal aggression, which enhances the dominance status of pairs and families in winter flocks (Fischer 1965; Raveling 1970, Radesater 1974; Scott 1980a,b; Akesson & Raveling 1982; Black & Owen 1988). Pairbonds are reinforced in Falcated Duck, Gadwall, and the northern wigeon by mutual pair palavers (Triumph Ceremonies) similar to those of geese that include aggressive components, female Chin-lifting and Inciting, and single or repeated Chin-lifts by males, with Slow or multisyllabic Fast Whistles (Lorenz & von de Wall 1960; Lorenz 1971; Cramp & Simmons 1977; Wishart 1983). In Chiloe Wigeon, loud, frequent, and prolonged Triumph Ceremonies were performed throughout the year in response to the presence of other wigeon, after aggressive encounters, and as a greeting display between mates. Chiloe Wigeon males, however, only gave Rakoo Calls, apparently homologous to the slow, 2 to 3 syllable whistles of American and Eurasian Wigeon (Cramp & Simmons 1977; Wishart 1983) and the Burp calls of Gadwall and Falcated Duck (Lorenz & von de Wall 1960; Cramp & Simmons 1977). The loud Rakoo Call was less wheezy than the corresponding calls of the other species, presumably due to the much larger tracheal bulla in male Chiloe Wigeon (Phillips 1923; Johnsgard 1971), which also probably contributes to the low, buzzy boom heard at close range during Triumph Ceremonies. Male Chiloe Wigeon did not Chin-lift during Triumph Ceremonies, and only gave calls corresponding to Fast Whistles (Pic Calls) during Bill-flipping bouts. The presence of

strong, long-term pairbonds and biparental care in Chiloe Wigeon may have selected for louder, more specialized Triumph Ceremonies in this species.

In addition to Triumph Ceremonies and female Inciting, pre-flight displays, male and female calls, and courtship displays appear to keep mates in close contact, synchronize their activities, and reinforce pairbonds. Males of all three wigeon species, Gadwall, and Falcated Duck call repeatedly when females are out of sight (e.g. on the nest during incubation), but female Decrescendo Calls, used as contact calls in Gadwall and Falcated Duck (Lorenz & von de Wall 1960; Cramp & Simmons 1977), are rare in all three wigeon (Johnsgard 1965; Cramp & Simmons 1977; Wishart 1983; this study). Male wigeon appear to be especially active in keeping in contact with their mates, possibly related to their greater role in vigilance during feeding on land. Female Chiloe Wigeon tended to rely on their mates for defence, and actively maintained pairbonds by frequently Chin-lifting near their mates when conspecifics were near the pair. Frequent Inciting of the Australian Wood Duck is thought to be associated with a high level of competition for food during grazing on land, as occurs in geese (Kingsford 1986; McKinney 1992), and Chin-lifting and Inciting by female Chiloe Wigeon may reflect a convergent strategy. Frequent Chin-lifting by female Chiloe Wigeon was also likely influenced by the need for protection from harassment by other males during the frequent FEPC attempts seen in this species.

There are several records of males accompanying females and broods in American and Eurasian Wigeon (McClanahan 1942; Dementiev & Gladkov 1967; Cramp & Simmons 1977; Wishart 1983), but this behaviour is rare and male defence of ducklings has not been reported. In contrast, both female and male Chiloe Wigeon regularly accompanied broods, escorted and defended ducklings (including giving alarm calls), and called to reunite separated ducklings. Male Chiloe Wigeon showed strong interest in ducklings by escorting ducklings in broods other than their own in captivity, as noted by Heinroth (1911). Adoption of wigeon ducklings was common in captivity, but was not recorded as frequently in wild birds (**Table 1**).

Kingsford (1986; 1990a,b) noted similarities between the Australian Wood Duck and geese, including long-term pairbonds and biparental care, that he believed were related to a grazing lifestyle. Grazing on land is common for adult American and Eurasian Wigeon, but these species do not spend much time grazing on land with broods and their parental care displays vary little from those of the Gadwall and Falcated Duck (**Table 2**). In contrast, grazing on land is common in Chiloe Wigeon families (Brewer 1990), as in geese (summarized by Owen & Black 1990 and Krapu & Reinecke 1992). Female parental care displays of Chiloe Wigeon are similar to those of its close relatives (**Table 2**), but male, duckling, and family displays of Chiloe Wigeon show convergence with the behaviour of other biparental grazers.

Family bonds were strong in Chiloe Wigeon and both ducklings and parents played active roles in maintaining and reinforcing bonds. Chiloe Wigeon ducklings, like Canada Geese *Branta canadensis* (Black & Barrow 1985), gave Chin-lifts to their parents at an early age. Ducklings greeted their parents and one another, and this behaviour probably promoted brood cohesion that appears to be important in giving protection from predators in exposed habitats (grazing on land). The development of greeting calls (Peeps) into Honks and Trills, precursors of adult Honks and Rakoo Calls respectively, was similar to the connections between greeting calls and Triumph Ceremonies noted by Fischer (1965) in Greylag Geese *Anser anser*. Male Chiloe Wigeon performed Triumph Ceremonies in response to duckling and female Chin-lifts, and were aggressive to wigeon and other birds near the brood when ducklings Chin-lifted. Ducklings frequently participated in family Triumph Ceremonies, and they tended to give more Chin-lifts to their male parent. In geese and swans, family Triumph Ceremonies

maintain prolonged family bonds, and families and young birds receive important benefits from remaining together (Black & Owen 1989; Scott 1980b; 1984; Bregnballe & Madsen 1990; Fox *et al.* 1995). Triumph Ceremonies in Chiloe Wigeon may play a similar role, including allowing ducklings to feed with fewer interruptions.

Duckling Chin-lifting and family Triumph Ceremonies have not been seen in the two northern wigeon or Falcated Duck. Gadwall ducklings are reported to Chin-lift when excited, possibly as a form of family Triumph Ceremony (Lorenz 1971). In general, the behaviour of ducklings has not been well-studied, and it is difficult to make meaningful comparisons.

In conclusion, many displays appear to be homologous among the three wigeon and their closest relatives, but distinctive features of the wigeon appear to be adaptations to their grazing lifestyle. Display specializations of Chiloe Wigeon are associated with biparental care and strong family bonds, suggesting convergence with the family structure of geese. Several topics for future research can be suggested as a result of this study. The presence of long-term pairbonds in Chiloe Wigeon is strongly suspected but needs to be documented. More information on adult courtship is needed to examine why the Grunt-whistle display has been retained by the Chiloe Wigeon. The relatively high frequency of forced extra-pair copulation attempts in Chiloe Wigeon compared to the northern wigeon needs investigation in wild birds, and the occurrence of multiple paternity of broods (likely to be rare because of strong mate-guarding) needs to be determined. Additional phylogenetic studies of the dabbling ducks are needed to clarify whether Chiloe Wigeon displays represent the ancestral condition in the wigeon group or whether they are recently developed specializations.

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