

Displays and breeding behaviour of captive Ringed Teal *Callonetta leucophrys*

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Observations of captive Ringed Teal allowed several previously undescribed displays to be noted, including specialised displays for maintaining contact, reinforcing the pairbond and biparental care. Males and females gave loud calls during female-only and pair flights that were associated with nest searching. Pair bonds were reinforced by bouts of contact calling when pairs became separated, and mates and family members greeted each other and came together in group displays after aggressive encounters. Males defended their mates throughout the breeding season, including during forced extra-pair copulation attempts. Males did not consistently defend nest boxes. Females defended a nest box only when they physically occupied it, laid eggs in more than one box, and were the only sex to incubate. One pair re-nested when their ducklings were about four weeks old. Both male and female parents performed Distraction Displays and called to ducklings when they became separated from the brood. A preliminary comparison suggests similarities between Ringed Teal and four closely-related species for displays associated with nest searching and pairbond maintenance, including possible homologies for female vocalizations. Differences were noted in male vocalizations, female inciting behaviour, copulatory displays, and family displays, but further information on these species and wild Ringed Teal is needed to investigate possible convergence or phylogenetic influences.

Key Words: Vocalisations, pairbond maintenance, biparental care, homology, comparative study

The biology and behaviour of the Ringed Teal *Callonetta leucophrys*, which breeds in flooded forest areas in parts of Argentina, Paraguay and Brazil (Olrog 1968; Sick 1993), are poorly known, and the systematic position of this species is still uncertain. Skeletal and plumage characteristics suggest that its nearest living relative is probably the Brazilian Teal *Amazonetta brasiliensis* (Johnsgard 1960; Woolfenden 1961; Weller 1968). However, the feather proteins of Ringed Teal resemble those of the genus *Anas* (Brush 1976) and, along with the Brazilian Teal, it has been classified as closer to the dabbling ducks by Bottjer (1983) on the basis of immunoelectrophoretic data. More recently, on the basis of comparative morphology, Livezey (1991) recognized Ringed Teal and Brazilian Teal as sister-genera and separated from both the other former Cairinini and the true dabbling ducks. Data from DNA sequencing of mitochondrial genes suggest that Ringed Teal are grouped with Maned Duck *Chenonetta jubata* and that Brazilian Teal are most closely related to Bronze-winged Duck *Anas (Specularias) specularis* (Johnson 1997; Johnson & Sorenson 1998).

Behavioural data can be useful in solving taxonomic problems and comparative studies of behaviour have been especially valuable in research on waterfowl (Delacour & Mayr 1945; Johnsgard 1965, 1978; Lorenz 1971). Although Delacour (1959) noted behavioural similarities between Ringed Teal

and the pochards (tribe *Aythiini*), Johnsgard (1960, 1965, 1978) noted similarities with *Aix*. Both Delacour and Johnsgard concluded that Ringed Teal should be placed in the monotypic genus *Callonetta* on the basis of its behaviour, but they did not agree on which species were its closest relatives.

Preliminary observations of captive individuals suggested that the published descriptions of behaviour and vocalisations of Ringed Teal were incomplete. The main objective of this study was to document displays and breeding behaviour (especially vocalisations) to supplement previous accounts. Ringed Teal displays were also compared, whenever possible, to those of potential close relatives to begin to examine the behavioural affinities of this species.

Methods

Captive Ringed Teal were observed at Cedar Creek Natural History Area, Bethel, Minnesota, from 19 July to 2 September 1983 and from 16 May to 14 August 1984. In 1983, three full-winged pairs, two full-winged unpaired males, and one pinioned unpaired male Ringed Teal were housed in a flight pen (5 x 18 x 3.6m) with two nest boxes at a height of 2m (described in Brewer 1988). From 25 July to 8 August, 17 Speckled Teal *Anas flavirostris flavirostris* were housed with the Ringed Teal. Very few interspecific interactions were observed. In 1984, five pairs of full-winged Ringed Teal were released into

a large flight pen (55 x 27.5 x 3.6m) described in McKinney (1967). This pen contained six nest boxes spaced evenly around the pen at a height of about 2m (described in Brewer 1988). Also housed in this pen were eight adult, and later ten young, Chiloe Wigeon *A. sibilatrix* and four adult, and later ten young, White-cheeked Pintail *A. bahamensis bahamensis*. Few interactions were observed between these species and the Ringed Teal.

Adult Ringed Teal were marked with coloured plastic nasal saddles (males) or discs (females) for individual identification. A total of fifteen birds was observed, with two pairs, one male and one female observed in both years. The male was unpaired in 1983 and paired in 1984, and the female was paired in both years, but to different males. All birds were at least one year old.

All behavioural interactions were noted on data sheets during 135.5 hours of scheduled observation, mostly during three-hour watches starting just before sunrise when the birds were especially active. Nests were checked every few days during the laying period and only a few times during incubation when females were off their nests. Casual observations were made several times a week outside the breeding season (21 November 1984 to 30 April 1985) on ten birds (two pairs, four unpaired males, one unpaired female and one juvenile female) in an animal holding facility located at the University of Minnesota, St. Paul, Minnesota. Captive Brazilian Teal (pinioned) and

Maned Duck (pinioned) were observed casually at the Wildfowl & Wetlands Trust, Slimbridge, England from 5 September to 12 September 1985. Captive, pinioned North American Wood Duck and Mandarin *Aix galericulata* were observed occasionally at the Como Park Zoo, St. Paul, Minnesota in May 1986.

Recordings of Ringed Teal, Brazilian Teal, Maned Duck and North American Wood Duck were made with a Sony TCM 5000-EV cassette tape recorder. Additional recordings of Ringed Teal were made with a Uher Report-L tape recorder (tape speed of 9.5 cm/s) and a directional microphone. Recordings were analysed with Kay sound spectrographs 6061B and 7800.

An Elmo super 8 sound 10125-XL macro camera was used to film Ringed Teal behaviour at a speed of 18 frames/s and films were analysed with a Timelapse Data Analyser 3420 projector. Film frames were traced to illustrate major changes in movements during displays, including some transitions between movements to indicate their fluidity.

Data were analysed using nonparametric statistical tests due to small sample sizes. Differences in male and female behaviour were analysed using the Wilcoxon matched-pairs signed-ranks test, and associations between post-copulatory displays and copulation success were analysed using the McNemar test (Conover 1980).

Results and Discussion

In this paper, displays (stereotyped behaviour patterns that are specialised as signals; Moynihan 1955) are capitalised, and presented in boldface type when they are described for the first time. Display terminology is that of Johnsgard (1965) and McKinney (1965) unless otherwise noted. Most data on breeding activities are from 1984. In both years, there was limited opportunity to observe unpaired birds. Further details, additional sonagrams and measured call characteristics, and tracings from film are presented in Brewer (1988).

Display repertoires are shaped by phylogenetic, ecological and social influences (McKinney 1975, 1992), and

a comparison of closely-related species can be useful to investigate these factors. The identities of the Ringed Teal's closest relatives are controversial, but four species have been proposed: North American Wood Duck, Mandarin, Maned Duck and Brazilian Teal. Although information on display repertoires is incomplete for several of these species, identification similarities and differences in comparison to the Ringed Teal has been attempted (Table 1). Homologies are tentatively proposed only for female vocalisations, although signalling needs to be associated with breeding in cavities in wooded wetlands, maintenance of long-term pairbonds, and biparental care may explain some display similarities.

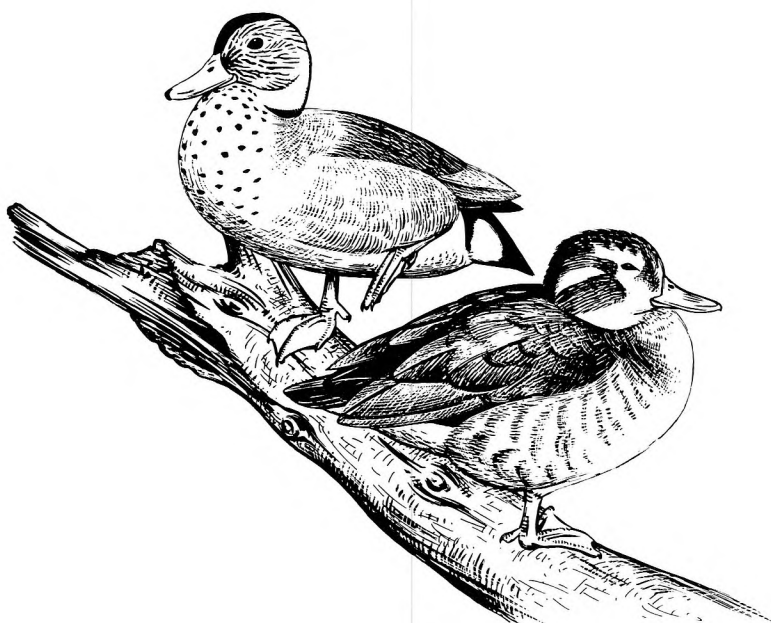


Table 1. Comparison of common Ringed Teal displays to those of proposed close relatives.¹

All known Ringed Teal displays are listed in the first column. Y = display similar to Ringed Teal, N = display present but not similar to Ringed Teal, - = display not present, ? = unknown or uncertain (sonogram not available).

Ringed Teal	Brazilian Teal	North American Wood Duck	Mandarin	Maned Duck	Total Number of displays:		
					Y/Y?	N/N?	-/?
Male displays:							
Flight call	Y?	N	Y?	Y?	3	1	0
Long whistle	Y	N	N	N	1	3	0
Short calls	N	N	N	N	0	4	0
Pre-copulatory:							
Head-bobbing	-	-	Y	Y	2	0	2
Head-jerking	-	-	-	N?	0	1	3
Post-copulatory:							
Long whistle	Y	-	-	-	1	0	3
Alert-beside	-	N	-	N	0	2	2
Female displays:							
Flight call	Y?	Y	Y	N	3	1	0
Houii	Y?	Y	Y	Y	4	0	0
Alarm call	Y	Y	Y	Y	4	0	0
"Inciting":							
Rotary-head-movements	-	N	N	-	0	2	2
Peep calls	-	-	-	-	0	0	4
Soft calls	Y	Y	Y	Y	4	0	0
Displays of both sexes:							
Pre-flight:							
Neck-craning	-	Y	Y	Y	3	0	1
Greeting	N	N	N	N	0	4	0
Post-aggression	N	N	N	N	0	4	0
Distraction display	Y	?	?	Y	2	0	2
Duckling displays:							
Contentment calls	?	Y	Y?	?	2	0	2
Distress calls	?	Y	Y?	?	2	0	2

¹See text for sources of display information.

Pairbond Maintenance

The observations may support Johnsgard (1978) who suggested that this species has strong pairbonds that may be relatively long-lasting. In general, mates remained close to each other and tended to synchronize their activities during the breeding season. The maintenance of the pairbond throughout the brood-rearing period may be important to coordinate parental effort if biparental care increases duckling survival. Strong pairbonds that last throughout the breeding season must also be important in facilitating the coordination between mates during double brooding (Brewer 1989). In addition, two pairs observed after the 1984 breeding season continued to reinforce their bonds.

Data from 1981-1987 on captive individuals show that one pairbond lasted through four breeding seasons, two through three breeding seasons, and two through two breeding seasons. It is not known when during the year pairbonds first formed, but they were present by April at the latest. No extra-pair courtship was observed, and only one instance of mate-switching was documented. In 1984, three days before the mate of an incubating female died, a paired male began to accompany her. The pairbond between this male and his original mate then weakened (pair spent less time together) until she died nine days later, after becoming more male-like in her plumage and less active due to disease (leucocytozoonosis). The condition of the deserted

female and the availability of a recently widowed female probably had a strong influence on the male's decision to switch mates.

Ringed Teal performed several specialised pair maintenance displays throughout the year, some of which are similar to displays given in the same contexts for species in **Table 1**. For example, to synchronise flight take-off and direction, paired individuals usually performed several bouts of **Neck-craning** (Johnsgard 1965), characterised by slow repeated extensions of the neck in the direction of intended flight (**Figure 1**). The slow thrusting of the head in Neck-craning was most similar to the Neck-craning and aiming described for Maned Duck (Kingsford 1986), North American Wood Duck (Heinroth 1910; Bellrose & Holm 1994), and Mandarin (Cramp & Simmons 1977), in contrast to the rapid neck jerks or pointing of the head noted for Brazilian Teal (McKinney 1953; pers. obs.). Lateral **Head Shakes**, like those typical of *Anas* pre-flight displays (Johnsgard 1965), rarely preceded flight, and only before a takeoff from water.

Vocal and other sound signals for maintaining contact are especially well-developed in Ringed Teal, possibly because of its use of heavily wooded, low visibility areas and activity during crepuscular periods (Navas 1977). In general, the fundamental frequencies of Ringed Teal calls are quite low (below 1,500 hertz) as are those of North American Wood Duck (Bellrose & Holm 1994), which may facilitate

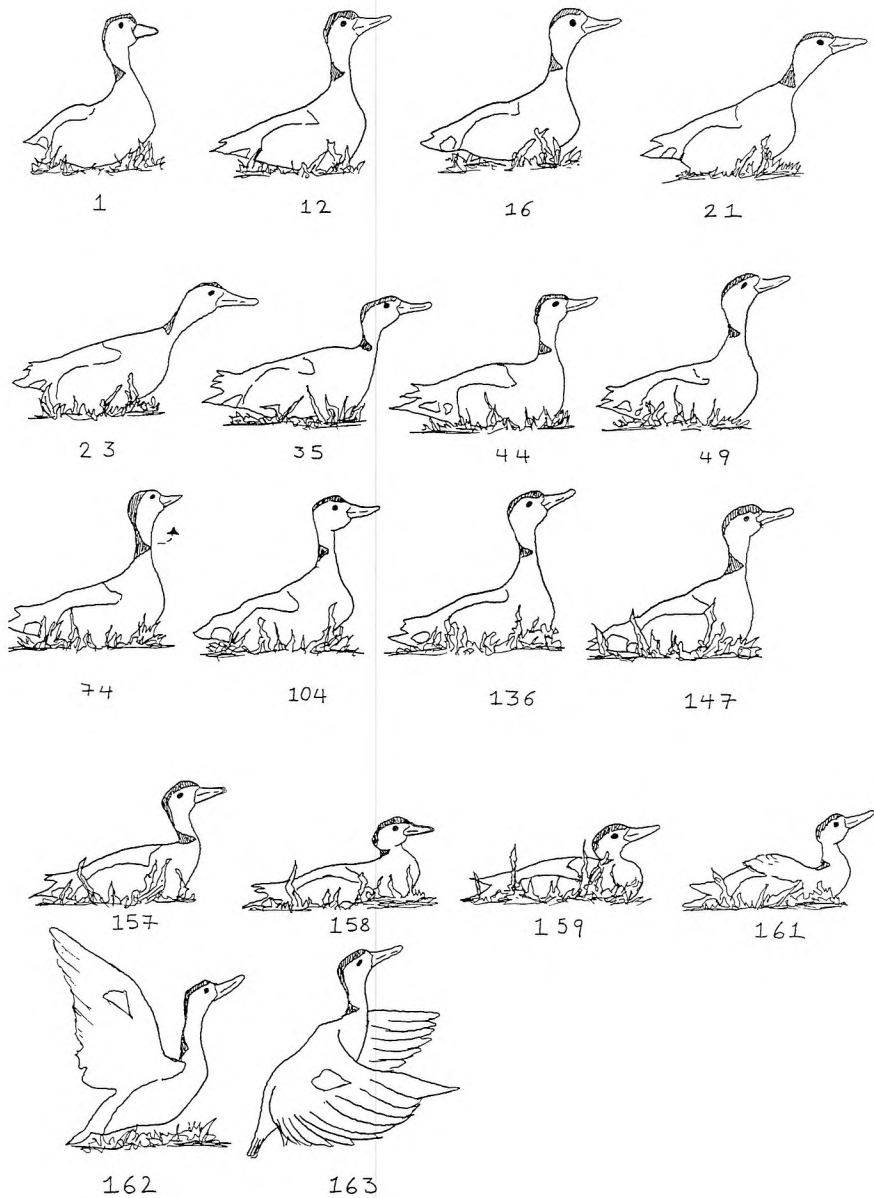


Figure 1. Male Ringed Teal performing pre-flight Neck-crane before flying up to a nest box. Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

sound transmission through dense vegetation. In Ringed Teal, the wings of both sexes whistle in flight (**Figure 2a**; Dudley 1958; Johnsgard 1978), signalling the location of an individual to its mate in densely vegetated areas. Soft nasal **Honks** (**Figure 2b**) were given by four males during Neck-craning ($n=13$), probably enhancing the synchronisation of takeoff by mates. Some Honks were given in very rapid succession so that they formed a continuous "prrrr"; at other times, single Honks were drawn out so that they sounded more like "baaap" (Brewer 1988).

When pairs became separated, male Ringed Teal gave **Long Whistles** (**Figure 2c**; represented as "wheee-ooo" by Johnsgard 1965), Honks, Meow Calls, and **Short Whistles** (**Figure 2a**), singly or in various combinations. Extended bouts of Long Whistles were given by paired males during the first few days of the mate's incubation period and, in three cases, during the first few days after a mate had died. Unpaired males also gave Long Whistles, probably to advertise their position. Long Whistles began with a head shake (**Figure 3**), then the call was given as the bill was tossed vertically upward and the tail and wings were raised to show the white patches near the tail. The Long Whistle of the male Ringed Teal is most similar in form to the pure tone whistle of the male Brazilian Teal (**Figure 4a**), although it is lower in frequency, and is not as wheezy as similar *Aix* (Cramp &

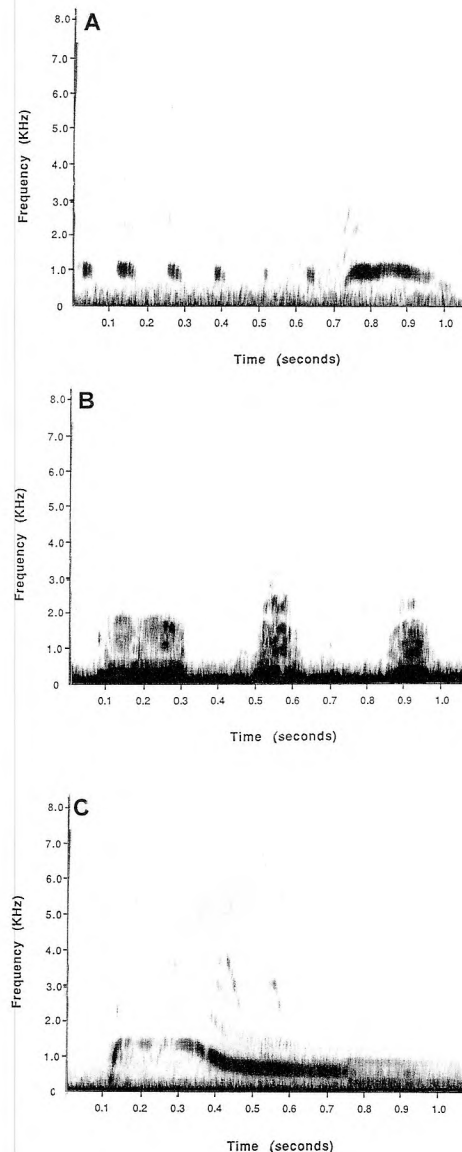


Figure 2. Wing Whistles (short, repeated sounds in A) may help to keep pairs in contact. Male Ringed Teal give Honks (B), Long Whistles (C), and Short Whistles (prolonged sound in A) when separated from their mates and in other contexts.

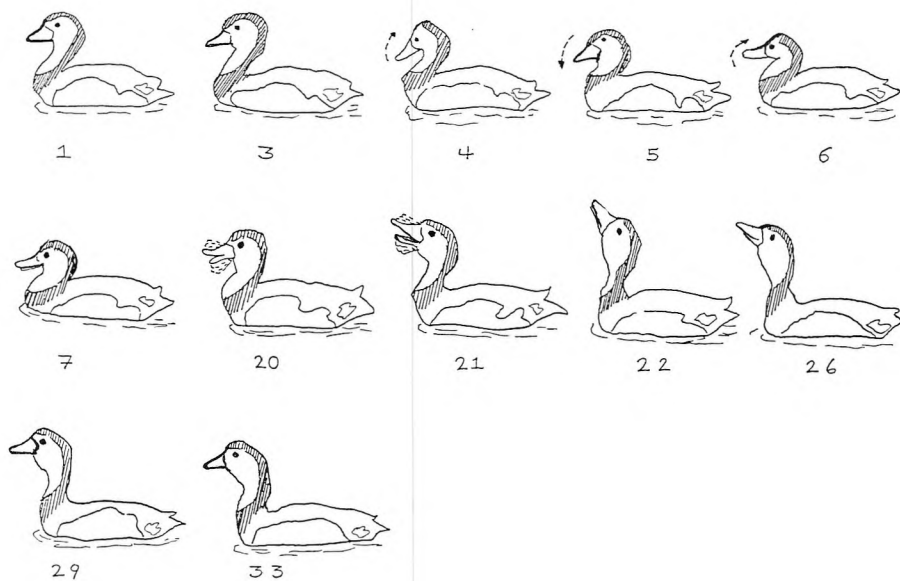


Figure 3. Male Ringed Teal performing a Long Whistle. Numbers indicate film frames used for tracing from film exposed at 18 frames per second. Dashed arrows and outlines indicate directions of bill movements. Long Whistle call was given in frames 7 through 29.

Simmons 1977; Bellrose & Holm 1994) and Maned Duck (Frith 1967) calls. The head toss, which is a conspicuous component of the Ringed Teal Long Whistle, is similar to that accompanying the male **Burp** of the North American Wood Duck (Korschgen & Frederickson 1976; Bellrose & Holm 1994).

Meow Calls resembled the "meow" of a domestic cat, and were given from an alert posture, with the neck slightly extended and the bill open (Figure 5; described by Heinroth 1911). Short Whistles appeared to be modified Long Whistles, although during the display, there was no preceding head shake and the bill toss was more rapid (Figure 6). The range of call duration was 0.3-0.45

seconds for Short Whistles and 0.4-1.1 seconds for Long Whistles (Brewer 1988).

In general, shorter calls used in similar contexts are more whistled or wheezy and at higher frequencies in Brazilian Teal (Figure 4b), Mandarin (Cramp & Simmons 1977), North American Wood Duck (Bellrose & Holm 1994), and Maned Duck (Marchant & Higgins 1990; pers. obs.).

Female Ringed Teal gave **Houii** calls (Figure 7a; represented as "hou-eeee" by Johnsgard 1960) when their mates were out of sight. The female Houii call began with a head shake, then the female raised her head upward and gave the call as she brought her head

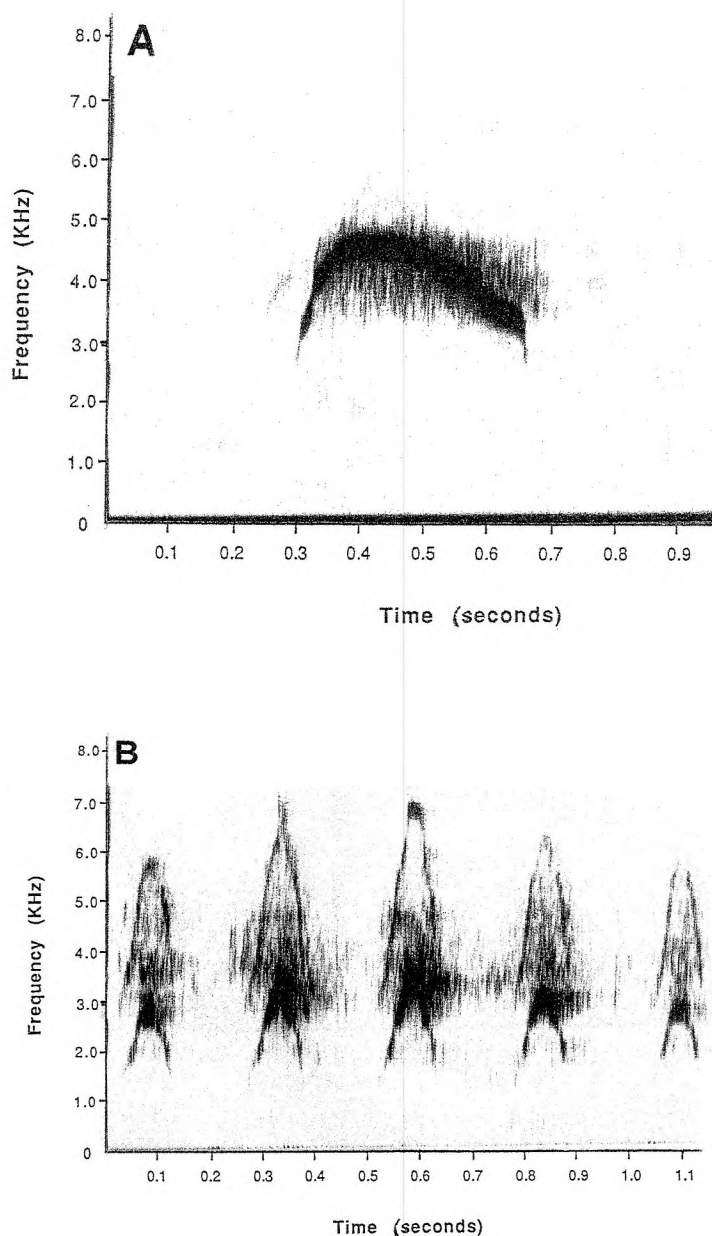


Figure 4. The loud whistle of the male Brazilian Teal (A) is most similar to that of male Ringed Teal. However, short calls of Brazilian Teal (B) are quite different from calls given in similar contexts by male Ringed Teal.

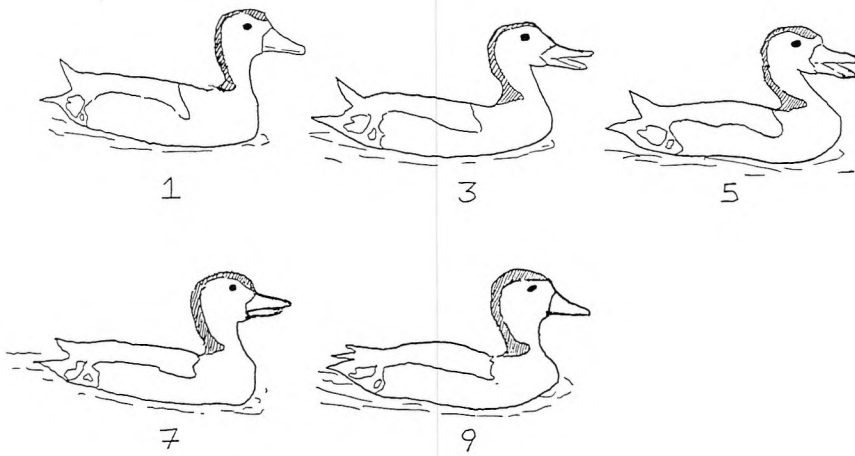


Figure 5. Male Ringed Teal performing a Meow Call. Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

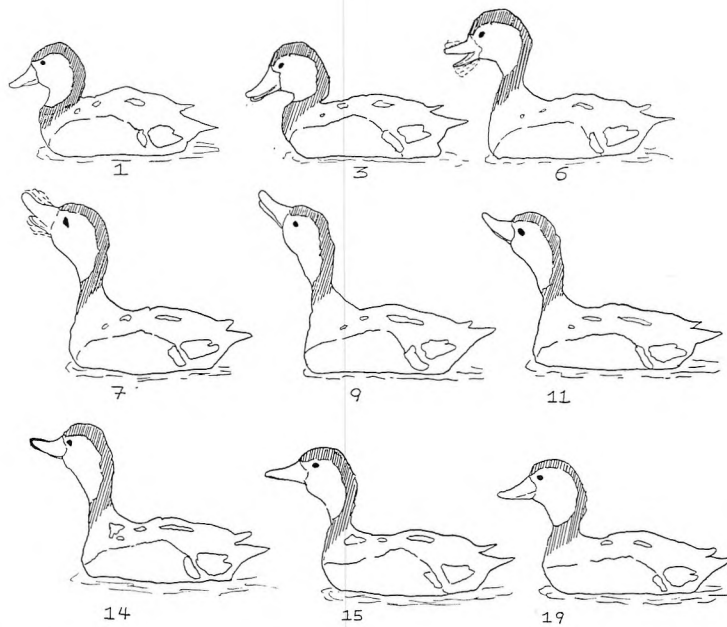


Figure 6. Male Ringed Teal performing a Short Whistle. Numbers indicate film frames used for tracing from film exposed at 18 frames per second. Dashed lines indicate directions of bill movements. Short Whistle Call was given in frames 3 through 15.

forward and pointed her bill downward (pictured in Johnsgard 1965). The loud Houii of female Ringed Teal, with its complex harmonics, appears to be homologous to the contact calls of female North American Wood Duck (**Figure 8a**; coquette call pictured in Bellrose & Holm 1994), Maned Duck (**Figure 8b**; Frith 1967; Marchant & Higgins 1990), and Mandarin (descriptions by Heinroth 1911; Lorenz 1971; Cramp & Simmons 1977; pers. obs.). In addition, the calls of both *Aix* species are given with a head movement similar to that of Ringed Teal. The loud quacks given by female Brazilian Teal are quite different and much more like the calls of *Anas* species (Heinroth 1911; Phillips 1923; Delacour & Mayr 1945).

Sometimes when members of a pair were separated, each member of the pair called alternately until the pair was reunited. These call bouts included from two calls (one Long Whistle and one Houii Call) to a total of nine calls (four Long Whistles and five Houii Calls). Females initiated 96 of 150 call bouts overall when mates became separated in the pen, and initiated significantly more call bouts than males [Wilcoxon's matched pairs test=19, $P<0.05$]. Males and females did not always strictly alternate their calls during a call bout; sometimes one individual called two or three times before the mate called back. This resulted in 66 of 150 call bouts with unequal numbers of female and male calls. Two of three females in 1983 and two of five

females in 1984 called more often than their mates in call bouts.

Several other displays of Ringed Teal apparently functioned in pairbond maintenance. **Preen-behind-the-wing** (Johnsgard 1960), a typical pair maintenance display, was performed by one male, flashing the white wing patch and speculum broadside to his feeding mate when another pair was nearby. When mates reunited after a separation, they sometimes directed **Rotary-head-movements** (**Figure 9**) towards each other. These rapid and repeated chin-lifting movements, with a forward component, were accompanied by **Peep Calls** (**Figure 7b**; represented as "tet-tet-tet" by Johnsgard 1965) in females and sometimes by Honks in males. Rotary-head-movements given in this situation appeared to have a bond-reinforcing function, as they were given when no other birds were nearby and were neither preceded nor followed by aggression to other birds. Male and female North American Wood Duck greet each other with Bill-jerks (Bellrose & Holm 1994), and male Mandarin also perform Bill-jerks on rejoining the female during incubation (Cramp & Simmons 1977). Brazilian Teal mates flick their bills up and down, similar to Bill-jerks, when near each other after a separation (pers. obs.). The head movements of these three species differ from Rotary-head-movements of Ringed Teal in that they lack the forward head movement. Paired Maned Ducks perform a different greeting ritual

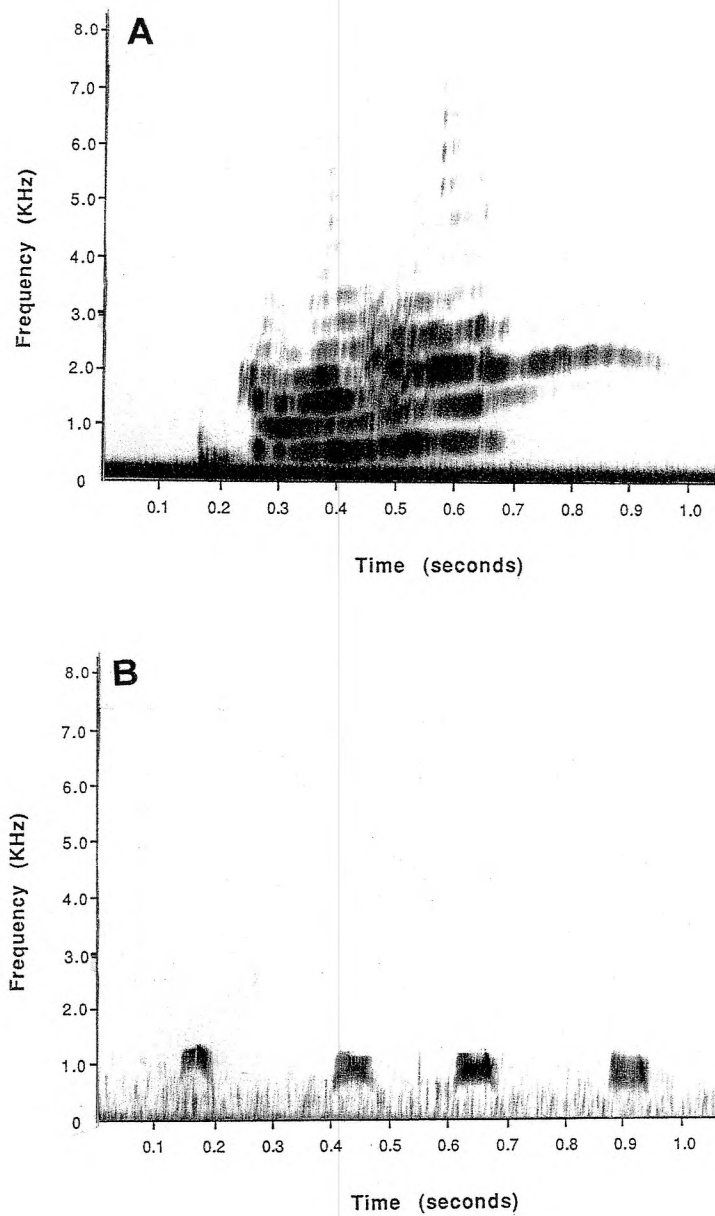
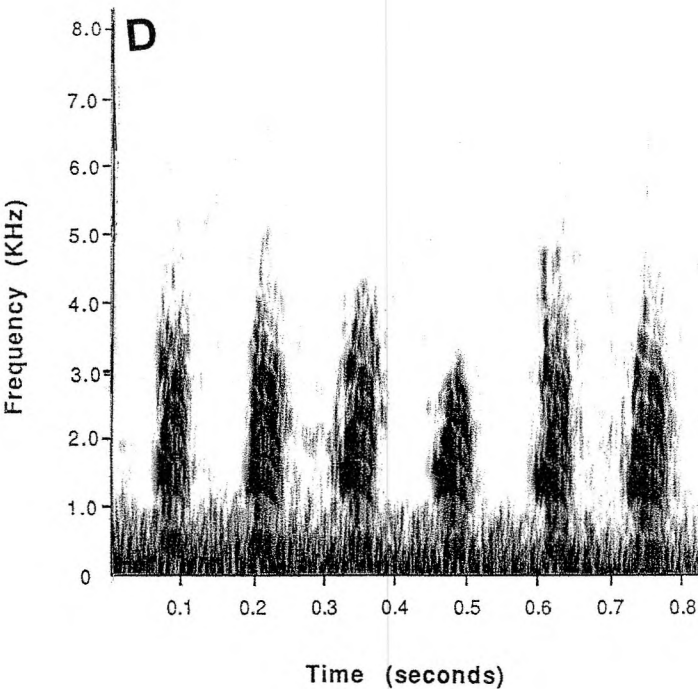
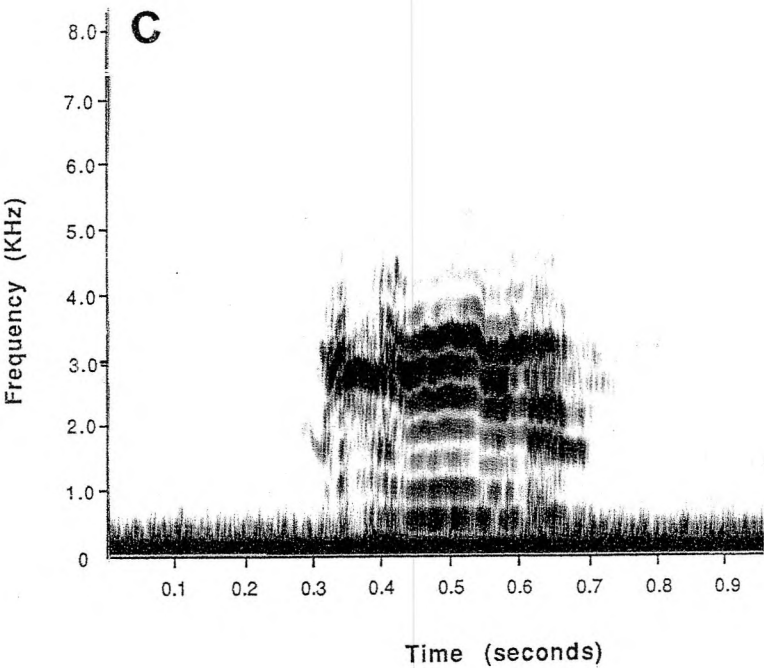


Figure 7. Female Ringed Teal give Houii (A) and Peep Calls (B) in several contexts. Gee Calls (C - see over) are given during nest-prospecting flights and Loud Calls (D - see over) are given as an alarm and to call ducklings.



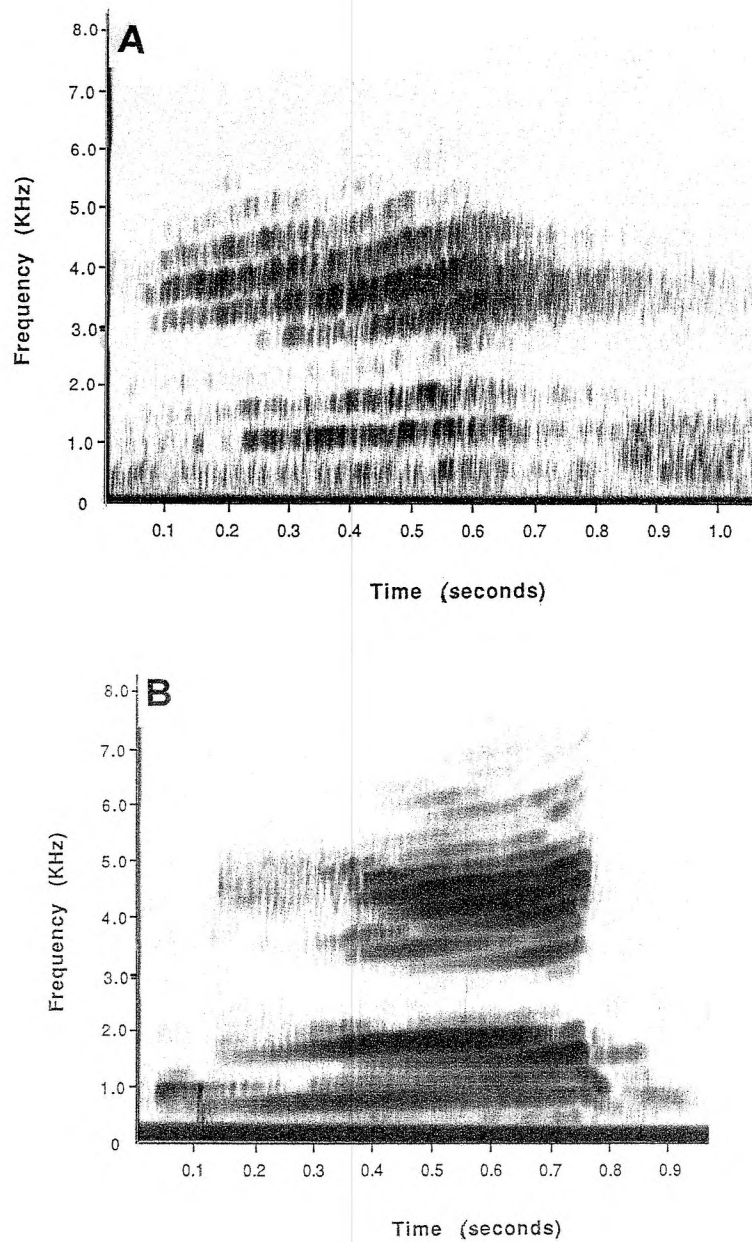
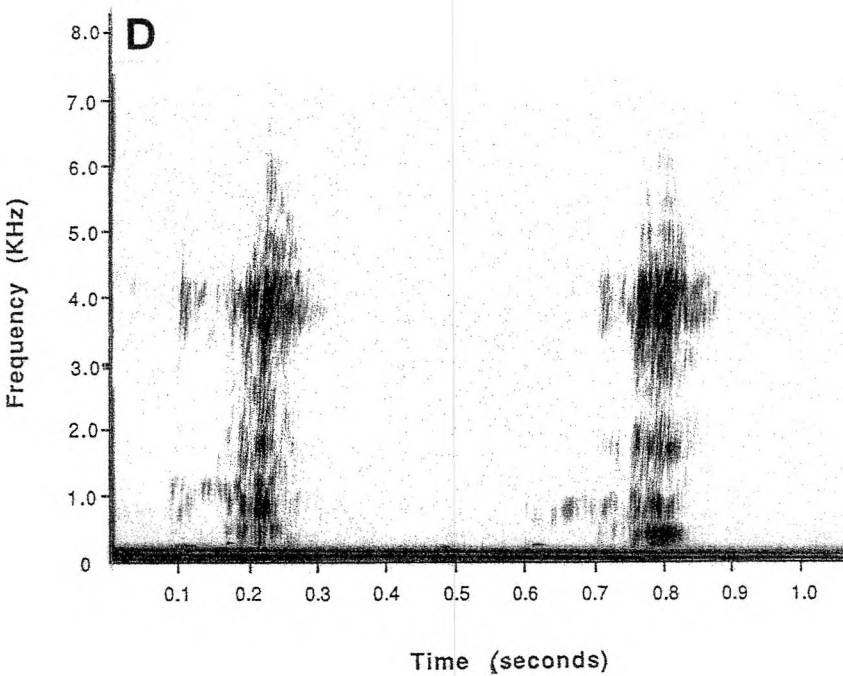
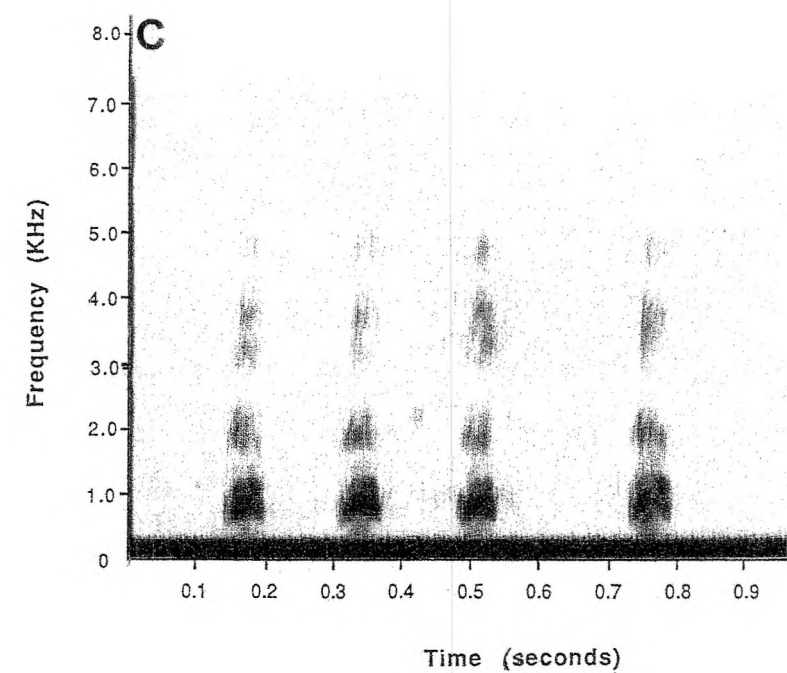


Figure 8. Contact calls of female North American Wood Duck (A) and Maned Duck (B) are similar to those of female Ringed Teal. Inciting calls of Maned Duck (C - see over) and Brazilian Teal (D - see over) are more similar to the Loud Calls that female Ringed Teal give in different contexts.



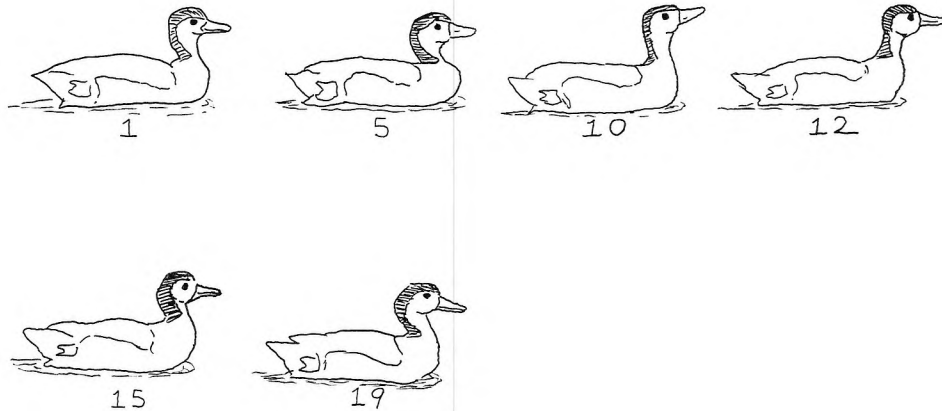


Figure 9. Male Ringed Teal greeting his mate with Rotary-head-movements as he rejoins her. Numbers indicate film frames used for tracing from film exposed at 18 frames per second.

that includes Drinking and Head-pumping when pairs reunite (Kingsford 1986).

Nest Prospecting

One of the first events of the pre-laying period in 1984 was the occurrence of extended flights, in which the female or pair flew around the pen several times. In late April, paired females were not joined by their mates on these flights, and they gave from one to three **Gee Calls** (Figure 7c) just before or as they alighted. Females gave at least one Gee Call during almost all female-only flights (76 of 82 flights), and two females gave two-three calls (during three of 18 and 16 of 35 flights). Some of the flights were followed by visits to nest boxes within one minute of the end of the

flight (mean=32%±12; n=3 females and 79 flights). Because Gee Calls were usually given as the female was alighting, they probably functioned in contact between mates, rather than to attract the attention of predators, as has been suggested for Persistent Quacking in *Anas* species (McKinney *et al.* 1990). During female-only flights, the male watched the female and often gave a series of Honks, which increased in volume when the female was farthest away from him. It is possible that female-only flights early in the breeding season may have reflected a lack of male motivation, because males consistently accompanied females on flights soon after females began to inspect nest boxes.

Beginning in early May in 1984, both mates regularly made extended pair

flights together. The number of pair flights decreased as soon as the female began laying. One pair nested a second time, and pair flights were seen again just before and during the first few days of laying. Females gave Gee Calls during 151 of 266 pair flights, and males gave Short Whistles during 39 of these flights. Many pair flights were not accompanied by calls (108 of 266) and in general, females called much more frequently than males during flights. Most pair flights were followed by visits to nest boxes by either or both individuals within one minute after the flight (mean=82%±15 of flights; n=4 pairs and 266 flights). Both members of two pairs usually visited nest boxes together (23 of 30 visits), but two other females most frequently visited nest boxes alone after their mates accompanied them on flights (31 of 53 visits). After three flights, when mates did not land near each other, they gave alternating calls (Long Whistle and Houii) until the pairs were reunited.

Pair nest search flights have been described for North American Wood Duck (Heinroth 1910; Bellrose & Holm 1994), Mandarin (Heinroth 1911; Cramp & Simmons 1977) and Maned Duck (Kingsford 1986; Marchant & Higgins 1990). Females and sometimes males of these species give short calls during nest search flights, near a nest site, or as the pair leaves, but no loud male calls have been noted in flight or as the pair lands after the flight, unless the pair has become separated. Both male and female Ringed Teal gave loud calls

during some nest prospecting flights, especially just before or as they were alighting. This suggests that the calls given during nest search flights function in maintaining contact in the wooded habitats of Ringed Teal, and may be related to the presence of a strong, long-term pairbond (lacking in *Aix*, which also inhabit wooded habitats).

The calls given in flight by female Ringed Teal (Gee Calls) resemble the calls that North American Wood Duck females give before alighting (high intensity hawk call; Bellrose & Holm 1994) and that female Mandarins give in flight ('ack' calls; Cramp & Simmons 1977). Female Maned Duck are said to give repeated clucks during nest-searching (Marchant & Higgins 1990). Phillips (1923) describes a grunt-like quack for startled female Brazilian Teal in flight. The Short Whistles that male Ringed Teal gave during nest searching, although loud calls, may be similar to the male Maned Duck call given in flight (Frith 1967), the brief whistled "wriick" or "hwick" call given in flight by the male Mandarin (Cramp & Simmons 1977), and the whistle given during flight by male Brazilian Teal (Phillips 1923). Short Whistles are less harmonically complex than the nest searching call of the male North American Wood Duck (Bellrose & Holm 1994).

Nest box inspections occurred when both males and females flew directly, from the ground or water below, up to the top or front ledge of the box.

Usually a pair went together to a nest box, then the male remained alert on top of the box while the female went inside. When a male went to a nest box alone ($n = 100$ visits), he frequently gave Honks from the top of the box until his mate joined him there ($n=43$ call bouts by six males). Males also gave Meow Calls ($n=5$ by three males) and Short Whistles ($n=4$ by four males) from the top of a nest box when the female was in sight but not on or in the nest box. Overall, males gave at least one type of call during 47% of visits to nest boxes when their mates did not accompany them ($n=6$ males).

Four male Ringed Teal were recorded entering unoccupied nest boxes ($n=9, 17, 4, 11$) for very brief periods. Males went into nest boxes when their mates were nearby, immediately after the mate or another female had left the box, or when a box was occupied by a female. Two males entered nest boxes occupied by their mates ($n=1$ and four visits), with one visit occurring during a re-nesting attempt. All four males entered nest boxes occupied by a female other than their mate (total 17 visits), and two males entered nest boxes when a female was incubating ($n=5$ and three visits to two females). Males that visited incubating females never spent more than a few minutes in the nest box at any stage before broods hatched, so the suggestion made by Johnsgard (1978) that males share in incubation cannot be supported.

Eight additional brief visits by males were not associated with female nest box visits or occupation.

Copulatory Behaviour

Pair copulations ($n=55$) were recorded during the pre-laying and laying periods. They took place away from other birds and usually when other pairs were feeding or loafing. A copulation was judged to be successful if the male curled his tail around the female's tail and thrust as though intromission was occurring. Success was "unknown" when no thrust was observed, and copulations were judged "unsuccessful" when the male mounted but there was no tail bend nor thrust. Pairs separated immediately after 18 successful copulations ($n=35$), but after 17 successful copulations, the pair remained coupled end-to-end for 1-10 seconds, presumably with the male phallus still inside the female cloaca ($n=3$ pairs).

Males attempted to initiate copulations by **Head-bobbing** ($n=46$ display bouts for seven males) and Head-jerking ($n=20$ display bouts for three males). Head-bobbing (described as "dipping movements of the bill" by Johnsgard 1960) consisted of slow and repeated extensions of the head and bill straight out from the front of the body, or pointed slightly downward. Head-bobbing was similar to the slow Head-pumps described for Maned Duck (Frith 1967; Kingsford 1986) and Mandarin (Bruggers & Jackson 1981).

Some Ringed Teal males also performed exaggerated pre-diving movements that have been termed Head-jerking, while approaching their mate or swimming around her before attempting a copulation. **Head-jerking** was similar to the pre-diving movements described for other waterfowl (McKinney 1965), in which the bird swims forward with exaggerated rapid head jerks (forward and backward horizontal movements) and the tips of the primaries are cocked up. This display was never followed by diving, and appeared to be a pre-copulatory display. Pre-diving movements have been noted for some Anatini before copulation (eg African Black Duck *Anas sparsa*; McKinney *et al.* 1978), but these movements were followed by diving or crash-diving before copulation. Kingsford (1986) once saw crash-diving in male Maned Duck during the middle of a pre-copulatory display but a copulation did not follow; this is the only description of movements similar to the Ringed Teal Head-jerking described for the species reviewed here. No male pre-copulatory Head-pumping, the typical pre-copulatory display of Anatini, was observed, and males did not dip the bill in the water as described for North American Wood Duck (Korschgen & Frederickson 1976), Brazilian Teal (Johnsgard 1965), and also Maned Duck (Kingsford 1986).

Males initiated most copulations (53 of 60; Wilcoxon's matched pairs test=21, $P<0.01$), but females initiated seven copulations by assuming the

prone position and holding it for several seconds before their mate gave any pre-copulatory displays. However, only the three sequences initiated by a re-esting female led to successful copulations. The prone posture was not maintained for extended periods as occurs in *Aix* (Lorenz 1971; Korschgen & Frederickson 1976). Female Brazilian Teal perform Head-pumping (Johnsgard 1960) and female Maned Duck sometimes perform Head-dipping (Marchant & Higgins 1990) before copulations.

Two females did not adopt a prone posture before a total of nine copulations. Seven of these copulations proceeded without any obvious female resistance, but two cases appeared to be examples of forced pair copulations. In one case, a male attempted to mount his mate as he pecked at her back and the back of her head, and she pecked at her mate. The second case appeared to be associated with a second nesting attempt by a pair with 11-day-old ducklings. On 8 August 1984, the male approached his mate then proceeded to mount and copulate with her although she did not adopt the prone posture and threatened the male as he mounted her. This copulation was successful and the pair remained attached for about three seconds after the male thrust was seen. No male post-copulatory displays were given. On 10 August, the same pair was nest-prospecting and the female was briefly in a nest box. On 11 August, a successful pair copulation was observed. One other pair

began reneesting before their brood had fledged, and copulations were first noted on 3 August 1984 (Brewer 1989).

The majority of copulations observed to completion were successful (39 of 55; $n=6$ males), and a male post-copulatory display was given after all but two successful copulations. There was a significant association between post-copulatory displays and copulation success ($\chi^2_1=9.94$, $P<0.005$). An **Alert-beside** posture, with the neck stretched upward and head held high with the bill horizontal, was the most numerous and most common male post-copulatory display ($n=35$ displays for seven males), and was performed after 20 successful and 15 unsuccessful copulations. The presence of the Alert-beside posture was not consistently associated with the success of the copulation ($\chi^2_1=0.47$, n.s.). No consistent orientation of Alert-beside toward the female was noted.

As described by Johnsgard (1965), a single Long Whistle was also given by males broadside to their mates as a post-copulatory display ($n=17$ displays for 5 males). Long Whistles were given only after successful copulations, and there was a significant association between the two ($\chi^2_1=22$, $P<0.001$). Facing the female in a motionless posture with the tail lifted, described by Johnsgard (1960), and male post-copulatory bathing were each noted once in this study.

Specific display postures accompanied by a loud call are common in Anatini post-copulatory displays

(McKinney 1975; Johnsgard 1978), but postures (eg Bridling) that accompany the call were absent in Ringed Teal. Male North American Wood Duck face the mate after copulation, but swim away from the female before doing so (Korschgen & Frederickson 1976), and male Maned Duck have been noted to swim around and away from the female with the tail raised (pictured in Johnsgard 1965). Male Brazilian Teal give a whistling call from a posture similar to that adopted by Blue-winged Ducks (McKinney 1970). Male Mandarins (Bruggers & Jackson 1981), North American Wood Ducks (Bellrose & Holm 1994), and male Maned Ducks (Kingsford 1986) also perform Turn-back-of-head as a post-copulatory display. Thus, the post-copulatory displays of Ringed Teal differ in some ways from those of all four species in **Table 1**.

Nine attempted forced extra-pair copulations (FEPCs), similar to those reported for other duck species by McKinney *et al.* (1983), were observed during the 1984 breeding season. Forced extra-pair copulations have not been described previously for Ringed Teal. FEPC attempts were made by four different paired males on two paired females, when the male's own mate was laying ($n=8$) or before his mate had started to lay ($n=1$). All nine FEPCs were directed at laying females. None of the FEPC attempts appeared to be successful and no post-copulatory displays were observed. In three of the nine attempts, one or two males

were near the female in addition to her mate and the male attempting FEPC; in one instance, two males attempted FEPC in quick succession. All FEPC attempts were similar: the male rushed at the female, mounted her while grasping the back of her neck (she was not in the prone position), and attempted intromission.

Females always responded by trying to swim away, but never flew or dived when approached. During one FEPC attempt, the female gave a Houii call, her mate answered with a Long Whistle, and then he flew over and defended her. In every case, the male defended his mate by threatening, chasing, pecking at, and lunging at the male attempting the FEPC, effectively knocking him off the female and driving him away. Males also threatened and drove off other males that were nearby when an FEPC attempt was made on the mate. One male attempted FEPC while his female was in a nest box; in the other instances, males left their mates to attempt FEPC, and their mates followed but then remained at some distance from the FEPC attempt. Forced extra-pair copulations, although infrequent and unsuccessful in this study, may be a viable secondary male reproductive strategy (McKinney *et al.* 1983) in the wild. The strong mate defence that is associated with the strong pairbonds of this species may be important during forced extra-pair copulation attempts for protecting male paternity, reducing female injury, and minimising the female's time and ener-

gy losses during a physically stressful period, as suggested by McKinney & Evarts (1998).

Laying Behaviour

Dates of first egg-laying for 1984 were 24, 26 May and 1, 20 June (only one egg was laid during the study period in 1983). Because females laid eggs in more than one box and spent short periods of time in nest boxes on the days when eggs were laid, there was an uncertainty about laying schedules of individual females in relation to observed copulations. The earliest pair copulations were observed 20 days prior to the first laying date; most were observed a few days before the first date of laying. Pair copulations continued until at least one week after the last date of egg laying for one female that never incubated a clutch; for incubating females ($n=3$ females and four nesting attempts), the last copulations were observed two days before the start of incubation.

Most visits to nest boxes during the prospecting phase occurred in the early morning and in several cases, nest box checks showed that eggs were laid in the early morning. Males accompanied their mates to the nest box, then either remained perched on the box, flew to a nearby perch, or flew to the pond and began feeding. Females spent up to 78 minutes in a nest box during laying visits. Males gave repeated Long Whistle, Meow Calls, or Honks while their mates were in the nest box. Similar to other species in **Table 1**, individual nest

boxes were not treated consistently as defendable resources by males (Brown 1964), and this may facilitate parasitic laying by females. Females visited, and laid eggs in, more than one box during the laying period. In five cases, more than one female laid in the same box on one day. Three eggs were laid in one female's nest box after incubation had started, as indicated by the hatch dates of the ducklings. It is not known whether Ringed Teal lay in more than one nest in the wild, but the use of the communal nests of Monk Parakeets *Myiopsitta monachus* and nest cavities of other parrot and parakeet species for breeding (Phillips 1923; Navas 1977) could facilitate this behaviour.

One female initiated a second breeding attempt in the same season, the first egg being laid 34 days after her first brood hatched (Brewer 1989). Two earlier cases of double-brooding were recorded in 1981, second clutches being started when first broods were three to four weeks old (Jeff Burns, pers. comm.).

Incubation and Nest Exodus

When females remained in nest boxes for extended periods and did not add to their clutches, this signalled the start of incubation. For two females, incubation lasted for 26 and 27 days, incubating 12 and 15 eggs respectively. A female that nested twice in one season incubated clutches of eight and seven eggs for 25 days each. The unusually large clutches of 12 and 15 resulted from several females laying in

a nest. Clutches for pairs breeding in isolated pens were incubated for 24, 25, and 25 days with six, seven, and eight eggs in each clutch respectively. Nests were lined with several inches of white to light gray down, the first down being added several days before incubation began.

Incubating females took recesses in very early or mid-morning and in late afternoon, and were escorted by their mates while they fed intensively. When a female left the nest box, she joined her mate immediately and often both birds greeted each other with Rotary-head-movements. During incubation, the male mate preened, slept, or fed near or on the nest box, unless avoiding an approaching individual or pair.

In all four broods, eggs were pipped for about 24 hours and the ducklings remained in the nest box for a similar length of time, losing their down sheaths and drying off while the female brooded them. Two broods were observed leaving the nest box in mid-to-late morning when in each case the female called to her brood from below the nest box with **Loud Calls** (Figure 7d). The male also stood below the box, close to the female, and after all of the ducklings emerged, the pair and brood moved together into the water. Further details are presented in Brewer (1989).

Aggressive Interactions

Generally, paired birds of both sexes showed little tolerance toward nearby conspecific males, females or pairs, and threatening, chasing, and pecking

were common activities among the captives. Males defended their mates very closely throughout the pre-laying and laying periods, and when females were feeding during incubation recesses. In one instance, during the takeover of a new mate, the female with the weakening pairbond threatened and chased the new female away from the male, suggesting that she was defending the original pairbond.

Rotary-head-movements were given by pairs as a threat to other birds and this display was sometimes followed by chasing (n=4 for three females; n=9 for four males), or by threatening with the bill open and the head low (**Open-bill Threat**) (n=1 for females; n=2 for two males), as in other waterfowl (eg Cramp & Simmons 1977). Males also returned to their mates and performed Rotary-head-movements after threatening or chasing other birds (n=11 for four males). Bouts of Rotary-head-movements given by Ringed Teal after aggressive encounters were similar to "pair palavers" of North American Wood Duck (Heinroth 1910; Bellrose & Holm 1994) and Brazilian Teal (pers. obs.), in which both members of a pair lift their heads up and down and give rapid calls during or after an aggressive encounter. Ducklings as young as 17 days old also gave Open-bill Threats in response to the close proximity of other ducks or humans. Preen-behind-the-wing was not noted as a threat display toward other males as reported by Johnsgard (1960).

In situations where ritualised **Inciting** displays occur in other ducks (eg Cramp & Simmons 1977), females directed Rotary-head-movements with Peep Calls towards the mate when other individuals or pairs were in close proximity. Although this display was not common (n=17), it was sometimes followed by Open-bill Threats (n=6), chase (n=1), or swim-off (n=1), or aggression by the male only (n=6) or pair (n=2). The soft, peeping calls given by Ringed Teal and the rotary movements of the head differ from displays given in similar situations by other species in **Table 1**. Loud calls are given during inciting displays in the North American Wood Duck (Bellrose & Holm 1994), Mandarin (Cramp & Simmons 1977), Maned Duck (**Figure 8c**), and Brazilian Teal (**Figure 8d**). These calls resemble the Loud Calls that female Ringed Teal gave in threatening situations and when calling ducklings, but do not resemble the Soft Calls (Peep Calls) given by Ringed Teal females during pair maintenance displays. The Peep Calls of female Ringed Teal are similar to the Soft Calls given by the other species when feeding and when accompanying ducklings. The head movements that accompany Inciting in Maned Duck and Brazilian Teal are like those of many *Anas* females rather than Ringed Teal, and the more vertical head movements (Bill-jerks) given by *Aix* females lack the forward, circular motion of Ringed Teal Rotary-head-movements.

During the laying period, pairs visited a variety of boxes and when more

than one pair was at a nest box, threats and pecks were given by all birds attempting to occupy any part of the nest box. Males swam-off (followed as if chasing) other males or pairs near the nest box where their mates were located at the time. Females inspecting, laying, or incubating inside nest boxes vigorously drove out both male and female intruders. Once a female was incubating, her mate spent most of his time on or near the mate's box, but no longer attempted to drive away intruders. Instead, males flew away from the nest boxes when approached, sometimes giving an Open-bill Threat before doing so.

Alarm Calls

Males gave Long Whistles, Honks, and Meow Calls, and females gave Houii Calls and Loud Calls in response to a disturbance such as approaching aerial predators or humans. These calls were given from elevated perches, or as birds swam away from the shore or flew. Similar calls are used in alarm situations by both sexes of other species in **Table 1**.

Family Activities

Biparental care and strong family cohesion were characteristic of Ringed Teal broods (Brewer 1989). Usually the female led the brood, giving soft Peep Calls almost constantly, especially when there was a disturbance. Loud Calls and Houii Calls were given by the female when the ducklings became

separated from her by more than about one metre. Ducklings gave **Contentment Calls** (Kear 1968) as they fed, swam, or rested near either parent and **Distress Calls** (Kear 1968) when they became separated from both parents. Female parents responded to duckling Distress Calls by both going to the duckling and giving Houii Calls ($n=2$); male parents responded by going to the duckling and occasionally giving Long Whistles ($n=2$). Ducklings gave Rotary-head-movements when reunited with each other or with either or both of their parents ($n=20$).

Both parents defended the ducklings against conspecifics and other ducks by threatening, chasing and pecking (Brewer 1988, 1989). After defence by either parent, ducklings (or whole family groups) sometimes gave Rotary-head-movements when ducklings returned to the parent ($n=11$). In response to potential danger, such as a large bird flying low over the pen, ducklings dived or hid in cover. Ducklings feigned death when handled by a person, relaxing their muscles and allowing themselves to be manipulated much like the behaviour described for adult female ducks taken by foxes (Sargeant & Eberhard 1975).

Male parents responded with loud Honks, females gave Loud Calls, and both parents gave Open-bill Threats with repeated **Hisses** when a family was approached closely by a person. Hisses were given with an Open-bill Threat posture, with the tail feathers fanned and wings slightly lowered off

the back, exposing the white wing patches (pictured in Brewer 1988). One female frequently gave hoarse, grating croaks in bouts with Hisses and Open-bill Threats when she and her brood were approached closely in a small pen. Both parents also performed typical **Distraction Displays** in response to a person near the brood (n=2 pairs). In this display, parents mimicked a bird with broken wings by flapping their wings half-open as they moved together along the ground, away from the ducklings and the person (pictured in Brewer 1989).

Biparental care has been described for Maned Duck (Kingsford 1986, 1990) and noted for Brazilian Teal (Phillips 1923). Both Maned Duck and Brazilian Teal parents also perform Distraction Displays like those described here for Ringed Teal, but greeting displays or goose-like Triumph Ceremonies associated with brood defence have not been described for either of these species. Family cohesion in Ringed Teal appeared to be strong, with Rotary-head-movements probably important in maintaining family bonds. Duckling displays have not been described for the species in **Table 1**, except for duckling vocalisations of North American Wood Duck (Gottlieb 1974; Bellrose & Holm 1994) and reference to the similarity between the two *Aix* species (Cramp & Simmons 1977). The forms of Distress and Contentment Calls from sonagrams are very similar for Ringed Teal and North American Wood Duck ducklings, and more information

on ducklings of other species would be useful.

Summary

There are some similarities, but many differences, in the displays of these species compared to Ringed Teal, and it is difficult to identify homologies. Female Ringed Teal calls were similar to those of almost all proposed close relatives, except for calls given during Inciting, indicating that these displays may be homologous (**Table 1**). Although Ringed Teal male flight calls appeared to be similar to those of three of the four species, few similarities were present for any other Ringed Teal male displays. Greeting and post-aggression displays were present in all species compared, but all were different from those of Ringed Teal (**Table 1**). A number of uncertainties remain due to a lack of detailed display information, including sonagrams. Further work on this interesting group of species, and more information on the use of displays by wild Ringed Teal will be needed to complement new phylogenetic data if we are to determine the true affinities of this unique species.

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