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# Courtship of Ducklings by Adult Male Chiloe Wigeon (*Anas sibilatrix*)

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Unlike most birds with seasonal pair bonds, many waterfowl pair much in advance of the next breeding season (Rohwer and Anderson 1988). For example, in Holarctic dabbling ducks (Anatini), courtship and pair formation occur up to 8 months before breeding begins (Hepp and Hair 1983). During the early period of bond formation, males court females and try to

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lead them away from other birds. When females show their preference for one male and rejection of others by giving Inciting displays, temporary associations between males and females are formed. As bonds strengthen, the members of a pair maintain close proximity, synchronize their activities, repel rivals, and perform displays that reinforce the bond (McKinney in press). Pair bonds continue to be tested during spring migration and after arrival on the breeding grounds, although most birds are paired by this time.

Several hypotheses exist to account for the early timing of pair formation in the Northern Hemisphere (reviewed by Rohwer and Anderson 1988). Generally, the balance between benefits from pairing to both sexes and costs to males is of major importance. Although participating in courtship may be energetically costly to females as well as males, females are expected to pair as soon as possible because of the benefits (such as enhanced feeding efficiency) that they receive when paired. Males must balance the benefits of pairing against the costs of mate defense and vigilance, so that the exact timing of pair formation will be determined largely by the male.

Although the courtship displays of most tropical and Southern Hemisphere dabbling ducks have been described (Johnsgard 1965), the timing of courtship and pair formation for these species is poorly documented. In these regions, the timing of pair formation may be influenced by variable or irregular breeding seasons and the lack of seasonal or molt migrations (McKinney 1985, Oring and Sayler in press). In several South American species, including the migratory Chiloe Wigeon (*Anas sibilatrix*), courtship activity has been noted before the end of the breeding season (Weller 1968), but the significance of this exceptionally early courtship is unknown. I found that unpaired males court and form bonds with ducklings as part of a pair formation process in Chiloe Wigeon. I know of no previous descriptions of this behavior in any waterfowl species.

Courtship of ducklings was discovered incidentally during a study of biparental care in Chiloe Wigeon (December through February, 1985–1988; total 500 h of observation) at five locations in southern Argentina within 70 km of San Carlos de Bariloche (41°08'S, 71°15'W) and one location in Buenos Aires province (38°51'S, 60°05'W). Although similar trends in courtship were observed at all six areas, I focused on data from the three main study areas in southern Argentina: Laguna Los Juncos, Estancia San Ramon, and Arroyo Pilcaniyeu (locations and characteristics further described in McKinney and Brewer 1989). Families or courting males with ducklings were observed during 30- to 60-min periods at all times of day using focal animal sampling (Altmann 1974) to record behavioral interactions and the activities of males, females, and ducklings every 30 s. I observed courtship during 14 days (45 h of observation) at Estancia San Ramon, 35 days (102 h) at Arroyo Pilcaniyeu, 19 days (22 h) at Languna Los Juncos, and 25 days (22 h) at the other three locations.

Although individuals were not marked, all 28 pairs of parents and their broods, 15 courting males, and 6 eight-week-old ducklings were identified consistently by morphological features. Intensity and extent of rust coloration on the flanks and under the tail, amount of white on the forehead, and the shape of whitish cheek patches varied in parental adults, and some courting males were identified by unique com-

binations of these characteristics. I identified broods throughout study periods by comparing the size and age of the ducklings, the location of the brood, and the plumage characteristics of parents (both male and female attend broods) with previous information and sketches of both parents (Brewer 1990). Ducklings were assigned to one of seven plumage classes (Ia–c, IIa–c, IIIa; Gollop and Marshall 1954) and assigned to age groups on the basis of data from 15 known-age broods (those first sighted within 1–3 days of hatching). I could determine the sex of ducklings ca. 8 weeks of age (class IIc) from wing patterns (males have darker specula and bright white upper wing coverts) and from the presence of a two-syllable whistle given only by males (method confirmed in captivity for 14 ducklings, pers. obs.). Six ducklings were identified by the unique pattern of down and feathers on their heads and bodies.

*Male courtship activity.*—In general, male courtship of ducklings was similar to male courtship of adult females (Johnsgard 1965; pers. obs.). Males directed four courtship displays at ducklings (Rakoo, Display Shake, Grunt-whistle, and Preen-behind-the-wing; Johnsgard 1965, Brewer 1990) and performed Precopulatory Head-pumping (Johnsgard 1965) near them. Group flights with 1–2 juvenile females and 2–8 adult males, similar to courtship flights described for adult American Wigeon (*Anas americana*; Wishart 1983), occurred late in the study period. I identified the intended receiver of a display by noting the body orientation of the performer (McKinney in press), and I consider here only those displays that were unambiguously directed at ducklings (60 displays were directed at paired females; no unpaired females were present).

For 12 known-age broods, the age at which ducklings were first courted ranged from 9 days (class Ib) to 33 days (class IIa) (mean [±SD] = 21 ± 6.6). The number of displaying males at one location ranged from one to 23, with up to seven males simultaneously courting one or more ducklings. No male parents courted their own ducklings, although most pairs accompanied them until ducklings were at least 6 weeks old. Male ducklings or juveniles did not court females during the study period.

Almost all courtship directed at ducklings (2,800 of 2,810 displays) was performed by adult males judged to be unpaired because they did not associate with an adult female for at least 1 h or exhibit behavior seen when pairs are separated. (Courtship of ducklings did not start until after most broods had hatched, and it was very unlikely that paired males would be away from their own mates for such long periods.) These males increased as a proportion of the local population and in number throughout the breeding season at all study areas. Mean sex ratios (male : female) ranged from 1.26:1 (Arroyo Pilcaniyeu [AP]) and 1.41:1 (Laguna Los Juncos [LLJ]) in December (mean number of adults present = 41 and 47) to 2.13:1
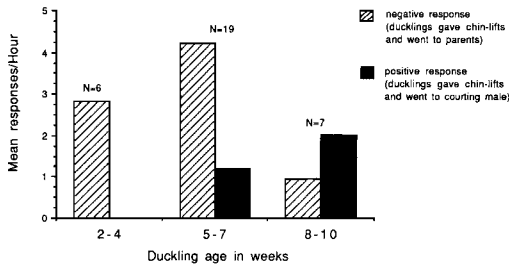
Fig. 1.   Mean responses per hour to courting males by ducklings accompanied by their parents. Number of broods above bars. Number of broods is small for the 2–4 week age group because fewer ducklings of this age received displays; in the 8–10 week age group, few broods were still accompanied by their parents.

(AP) and 3.28:1 (LLJ) ($\bar{x}$ = 47 and 31 adults) in January and 3.0:1 (AP) in February ($\bar{x}$ = 69 adults).

Males directed courtship displays at ducklings of all age classes, but courtship rate (displays per hour) and frequency (percent hour of observation with courtship) increased with duckling age (2–4 weeks: rate = 0.67–2.6, frequency = 13–34%; 5–7 weeks: rate = 7.2–14, frequency = 63–72%; 8–10 weeks: rate = 9.3–15, frequency = 79–95%). In addition, males directed a higher proportion of Preen-behind-the-wing displays (used in pair maintenance) and Pre-copulatory Head-pumping at 8–10-week-old ducklings (29%, $n$ = 234 displays) than at 5–7-week-old ducklings (10%, $n$ = 77).

Although the overall sex ratio of 8-week-old ducklings was approximately 1:1, adult males directed more courtship displays at female ducklings ($n$ = 430 displays) than at male ducklings ($n$ = 56) and were more aggressive towards male ($n$ = 42 aggressive actions) than towards female ducklings ($n$ = 7). Courting males were frequently aggressive to each other (352 threats, 236 chases, and 91 fights in 110 h of observation), as in other wigeon (Wishart 1983), and a greater number of aggressive actions occurred near female ducklings (89 actions near females, 16 near males).

*Responses of ducklings and parents.*—Both male and female parents were generally intolerant of courting males near their ducklings and repeatedly threatened, chased, and pecked them (total 2,060 aggressive actions during 186 h of observation). Some courting males appeared to be tolerated more than others, although these "favored" males did not differ in any obvious way from the other males. Some ducklings of all ages responded negatively to courting males by returning to their parents, running or swimming away from the males, or directing Chin-lifts—a display similar to the Inciting of adult females (Johnsgard 1965)—to their parents (Fig. 1). Some parental aggression ($n$ = 16) occurred after ducklings gave Chin-lifts when the ducklings appeared to be soliciting aid and inciting their parents to threaten and chase courting

males near them. Ducklings also gave Chin-lifts during or after parental aggression to courting males ($n$ = 214 bouts) and during family group displays after aggression ($n$ = 76), similar to family Triumph Ceremonies associated with aggression in geese (Heinroth 1911). Ducklings sometimes gave Distress Calls as they tried to return to their parents, and some dived repeatedly when small groups of males displayed near them.

In the 5–7 and 8–10 week age categories, some ducklings still escorted by their parents responded positively to courting males by going towards them and giving Chin-lifts (Fig. 1), just as paired adult females do to their mates (Lorenz 1951–1953). Up to five ducklings showed a preference for certain courting males, although no males were able to defend associations with more than one duckling for longer than 3–7 days. These males had no distinguishing physical features.

To test the observed differences in duckling behavior by age, each brood in an age group was scored as positive or negative based on whether ducklings responded overall more positively or more negatively towards males when they were in that age class. Using these data, responses were found to depend on age ($G_{adj}$ = 9.982, df = 2, $P$ < 0.01; 2–4 weeks old: $n$ = 16 broods; 5–7 weeks: $n$ = 16; 8–10 weeks: $n$ = 5). At Arroyo Pilcaniyeu, where all three age classes were observed, negative responses per hour decreased with age (4.8, 3.7, 1.1) while positive responses increased in frequency (0, 1.6, 1.8).

*Formation of bonds between adult males and ducklings.*— As ducklings began to remain with courting males and give Chin-lifts beside them, bonds began to form between unpaired adult males and 6–8-week-old ducklings (class IIb–IIc). Activities of ducklings accompanied by a courting male or by a male parent did not differ significantly (Mann-Whitney test, $n_1$ = 9 male-duckling "pairs," $n_2$ = 10 families, $P$ > 0.05), but courting males spent significantly more time feeding (Mann-Whitney test, $n$ = 9, $n_2$ = 10, $T$ = 111, $P$ < 0.05) and less time alert ($T_1$ = −3.6, $P$ < 0.001) or engaged in aggressive interactions ($T_1$ = −3.008, $P$ < 0.002) than male parents that accompanied ducklings in age class IIc. Bonds between ducklings and their parents began to break when ducklings left their parents and spent time with courting males, and when parents were unable to keep their ducklings close to them due to the almost constant intrusion of courting males. In areas with fewer courting males, bonds between parents and ducklings did not break until ducklings were 9–11 weeks old, which suggests that the presence of courting males was an important factor in the timing of family break-up (Brewer 1990).

Almost all "pairs" including known-sex ducklings were composed of adult males and female ducklings, and they behaved similarly to adult pairs of ducks (e.g. Common Goldeneyes, *Bucephala clangula*; Afton and Sayler 1982). Both individuals defended their

partner against other adults and ducklings, associated closely, and gave pair-reinforcing displays (Preen-behind-the-wing by male adults, Chin-lifts by ducklings) and pair palavers similar to those of adult pairs of Chiloe Wigeon (Johnsgard 1965). Ducklings escorted by males also gave Chin-lifts to incite aid ($n$ = 62 bouts) and after intruding males were chased away ($n$ = 112). One male copulated once with the female juvenile that he was accompanying (only the male gave pre- and post-copulatory displays).

Although several adult males accompanied and defended male ducklings, only twice was a male duckling (class IIc) escorted for an entire 1-h watch. Younger male ducklings (class IIc) behaved like female ducklings when adult males accompanied them, but class IIIa and juvenile males tended to avoid adult males. As the breeding season progressed, female ducklings and juveniles were conspicuously accompanied by adult males, and male ducklings and juveniles typically spent time alone or with other male ducklings.

Information on the persistence of adult male-female duckling "pairs" was limited to 15 cases in which I could identify the male—and in some cases the duckling—by plumage. Eleven "pairs" remained together for an entire 1-h focal animal sample, four for at least 2–3 days, one for at least 16 days, and one for at least 22 days. Additional adult male-female duckling or adult male-juvenile female "pairs" that could not be identified consistently were common at all study sites late in the breeding season, when almost no adult pairs were present.

I believe that unpaired adult male Chiloe Wigeon direct courtship displays at ducklings as part of a pair formation process and that some females form bonds with males at an exceptionally early age. To explain this early courtship and "pair" formation, it is appropriate to consider the costs and benefits to individuals (Rohwer and Anderson 1988). Young females may benefit by being "paired" because the males escorting them drove away other males and were sometimes vigilant, although less so than parental males. Before ducklings accepted courting males, however, they were sometimes endangered by separation from their families and were also interrupted during feeding or resting periods. Adult males seemed to incur costs by performing displays, by being chased by other males and parents, and by being vigilant and defending exclusive access to a duckling. Males may benefit by pairing early if they are more likely to obtain a mate, and if they expend less energy or gain other benefits as "paired" rather than courting males. Parents incurred costs as they defended the cohesion of the family unit, but may benefit by promoting "pair" formation between their ducklings and high-quality courting males. In many ways, the breaking of bonds between parents and their ducklings by courting males was similar to the attempt of unpaired males to break bonds between paired adults, with

ducklings and possibly parents influencing the outcome.

Other factors are necessary to explain why courtship and bond formation occur so early in Chiloe Wigeon and to determine if the adult sex ratio is particularly important. The adult sex ratio was highly biased toward males in my study populations. Sex ratios were considerably higher than those noted for northern dabbling ducks, which range from 1.22:1 to 1.56:1 (Bellrose et al. 1961). More information is needed on sex and age ratios in Chiloe Wigeon, and on mortality factors (such as predation and energy stress that may be greater on females) that are likely to affect the sex ratio (Bellrose et al. 1961).

The operational sex ratio (Emlen and Oring 1977) may be further skewed in favor of males in Chiloe Wigeon because of the presence of long-term pair bonds. Data from both wild (Weller 1968, Brewer 1990) and captive birds (Heinroth 1911, Kear 1970, Brewer 1990) suggest that long-term pair bonds are characteristic of this species. If population and operational sex ratios are highly male-biased, and if birds remain in long-term bonds with little mate-switching, few females except young of the year will be unpaired. Intense competition for these females could force males to begin courting them at the duckling stage in order to obtain a mate, even though courtship and pairing with ducklings may be costly.

Further observations lead me to suspect that many yearling males molt before or soon after arriving on the breeding grounds, try to establish pair bonds by courting ducklings, and then breed in their second year when the female has matured. Observations of groups of molting Chiloe Wigeon early in the breeding season in southern Argentina (Weller 1975; J. Fjeldsa pers. comm.; pers. obs.) and the unworn plumage of courting males, which was often different from that of male parents, support this idea. First-year males differ in their plumage from older birds in American Wigeon (Wishart 1983) and some male Eurasian Wigeon (*A. penelope*) delay breeding until their second year (Cramp and Simmons 1977). Data on the ages and life histories of courting male Chiloe Wigeon are needed to confirm this hypothesis.

More extensive data on sex ratios, adult pair-bond durations, and the identities of courting males are needed to test the hypothesis that extreme male-male competition for mates results in courtship and pairing with ducklings. Ultimately, costs and benefits should be measured in terms of time, energy, and future reproductive success for adult males and young females that have paired. The presence of long-term pair bonds, highly skewed sex ratios, and delayed breeding suggested here for Chiloe Wigeon may be unique to this species. Careful observation of other little-known Southern Hemisphere waterfowl, however, may reveal other variations on the social systems typical of their northern relatives.

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# An Interspecific Relationship Between Egg Size and Clutch Size in Birds

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Individual birds should be selected to rear broods that maximize lifetime reproductive success (Lack 1968, Williams 1966). In many species, clutch size may be limited by the number of offspring that parents can feed (Lack 1968, see review *in* Partridge 1990). However, Lack (1967) considered that precocial species laying large clutches should be limited instead by food availability to the laying female. Then, assuming nutrient limitation, any increase in clutch size could

be compensated by decreased egg size. Therefore, Lack (1967) considered that such nutrient limited species would likely show trade-offs between clutch size and egg size. Smith and Fretwell (1974) also considered that this trade-off was most likely in species that lay large clutches without parental care. Lack (1967) tested his hypothesis on wildfowl and found that species that laid larger clutches also laid smaller eggs. Although recently called into question (Rohwer 1988),