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PAIR-FORMATION MECHANISMS IN *ANAS* (ANATIDAE) AND RELATED GENERA

Although the " courtship " behaviour of waterfowl has attracted widespread interest and has been the subject of several major papers (e.g. Heinroth 1911, Lorenz 1951–1953), the actual means by which pairs are formed in most species of waterfowl remains unknown. We may conclude by inference that the females of most species of ducks must actively " select " their mates, for the elaborate male displays and plumage patterns present in the group can only be reconciled in terms of sexual selection. In addition, any observer of waterfowl will soon realize that it is the males which actively " court " the females, and that the females often behave in a passive or even antagonistic fashion towards them.

Since males of different species of related waterfowl have different plumages and different combinations and elaborations of homologous display patterns (Lorenz 1951–1953), it appears that these plumages and displays function both as species-specific signals which tend to prevent hybridization (Sibley 1957), and as the probable basis for individual mate selection by females (see Johnsgard 1960). And yet, during actual instances of courtship when all the unmated males repeatedly perform the same displays towards the available females it is often hard to conceive the means by which mate selection actually operates. One must hypothesize that on the basis of minor differences in display and/or plumage characteristics a certain male is singled out by the female from the potential mates and is somehow " notified " of her choice. However, most display descriptions stress male, rather than female, signals, no doubt because they are the more conspicuous and elaborate. Since the mechanism of mate selection is of fundamental importance in terms of isolating mechanisms and sexual selection, I have given some attention to this problem as it concerns the waterfowl group with which I am most familiar, namely, the Anatinae and, in particular, the genus *Anas*.

I began my studies with the Mallard *Anas p. platyrhynchos* and its nearest relatives (Johnsgard 1959, 1960), and concluded that mate selection is probably effected by a rather complex pattern of behaviour which normally involves at least three birds (one female and two or more males). In this activity, the female " incites " (see Lorenz 1951–1953) one male (the " chosen " one) against the other male or males. The former male's response, during early stages of pair formation, is not to attack the indicated bird; but rather he swims rapidly ahead of the inciting female and turns the back of his head towards her. I have termed this type of head orientation, when used in this special situation, " Leading ", although the same kind of head orientation also occurs in certain other situations (such as after " Nod-swimming "; see Lorenz 1951–1953). In his studies on the Mallard, Weidmann (1956) also considered inciting by the female to play an important role in pair formation, which he believed to be a very gradual process in this species. I have concluded that repeated instances of Leading-and-inciting between two birds slowly effects a loose pair bond, which may be strengthened through mutual behaviour such as copulation, " mock " preening, and ritualized drinking.

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When I was given the opportunity to study waterfowl behaviour at the Wildfowl Trust, I decided to investigate as many species of Anatinae as possible, to determine the extent to which this combination of Leading-and-inciting occurs and presumably serves the same function in pair formation as in the Mallard. I was pleased and rather astonished to find that exactly homologous behaviour occurs in practically every species of *Anas* that I was able closely to observe displaying sexually. These included *Anas strepera*, *A. falcata*, *A. formosa*, *A. flavirostris*, *A. capensis*, *A. castanea*, *A. gibberifrons*, *A. luzonica*, *A. poecilorhyncha*, *A. superciliosa*, *A. platyrhynchos*, *A. rubripes*, *A. undulata*, *A. georgica*, *A. acuta*, *A. bahamensis*, *A. erythrorhyncha*, *A. versicolor*, *A. punctata*, *A. querquedula*, *A. discors*, *A. cyanoptera*, *A. smithi*, and *A. clypeata*. In fact, the only species of *Anas* for which I was able to ascertain with confidence that this pattern does not occur, is the African Black Duck *Anas sparsa* in which the male's invariable head-pumping reaction to female inciting is very much like that of shelducks (*Tadorna*) and some perching ducks (*Cairina*). In the wigeons (*Anas americana*, *A. penelope* and *A. sibilatrix*) males often turn-the-back-of-the-head to females which are not inciting; but when the females begin to incite, the males tend to turn towards the female and perform chin-lifting movements towards her. In addition, slightly modified but certainly homologous behavioural patterns of inciting and turning-the-back-of-the-head occur in the adjacent tribes of Cairinini (*Aix*, *Amazonetta*) and Aythyini (all *Netta* species and most if not all *Aythya* species). It is even possible that the outwardly similar display patterns of eiders (*Somateria mollissima*, *S. spectabilis*), goldeneyes (*Bucephala*) and mergansers (*Mergus*) are homologous in origin and identical in function to those of *Anas*.

That such behaviour occurs in so many species suggests its fundamental significance, and indicates that correct species recognition must be achieved *before* this behavioural pattern is elicited if hybridization is to be prevented, because males of virtually any species of *Anas* will react in the same fashion to an inciting female. Additional and somewhat indirect evidence for the importance of Leading-and-inciting in pair formation is the fact that I have observed these patterns to be present in undiminished intensity and unchanged form in the Kerguelen Pintail *Anas acuta eatoni*, Hawaiian Mallard *A. platyrhynchos wyvilliana* and South Georgia Pintail *A. g. georgica*, even though these island forms exhibit a deterioration of male plumage patterns and other courtship displays.

Lorenz (1951–1953) has described how ritualized, or " mock ", preening is used as a sexual display by males in many species of *Anas*, as well as by the Wood Duck *Aix sponsa* and Mandarin Duck *Aix galericulata*. He did not, however, mention that this behaviour is used as a sexual display by females and as a mutual display between the sexes, especially among paired birds. McKinney (1953) observed ritualized or displacement preening behind the wing, on the back, and behind the slightly raised wing in many species of *Anas*, Aythyini, and Cairinini. Preening behind the slightly raised wing is frequently used as a threat display, and preening on the back is primarily a precopulatory display; but I have recorded ritualized preening behind the wing as a sexual or mutual display in numerous species, including several not mentioned by McKinney. The following list combines my own and McKinney's observations: *Tadorna tadorna* (♂ & ♀), *Sarkidiornis melanotos* (♂), *Aix galericulata* (♂ & ♀), *Aix sponsa* (♂), *Amazonetta brasiliensis* (♂), " *Lophonetta* " (=*Anas*) *cristata* (♀), *Anas sibilatrix* (♂ & ♀), *A. americana* (♂), *A. penelope* (♂ & ♀), *A. falcata* (♂ & ♀), *A. strepera* (♂ & ♀), *A. formosa* (♂), *A. crecca* (♂ & ♀), *A. flavirostris* (♂ & ♀), *A. gibberifrons* (♂), *A. castanea* (♂), *A. luzonica* (♂), *A. poecilorhyncha* (♂), *A. platyrhynchos* (♂ & ♀), *A. rubripes* (♂ & ♀), *A. acuta* (♂ & ♀), *A. georgica* (♂), *A. bahamensis* (♂ & ♀), *A. erythrorhyncha* (♂), *A. versicolor* (♂), *A. querquedula* (♂ & ♀), *A. platalea* (♂ & ♀), *Netta rufina* (♂ & ♀), *N. erythropthalma* (♂ & ♀), *N. peposaca* (♂ & ♀), *Aythya americana* (♂ & ♀), *A. collaris* (♂ & ♀), *A. australis* (♂), *A. nyroca* (♂ & ♀), *A. baeri* (♂ & ♀), *A. fuligula* (♂ & ♀), *A. novae-seelandiae* (♀), *A. marila* (♂ & ♀), and *A. affinis* (♂ & ♀).

It is of interest that all these species possess metallic or white wing specula which are exhibited during the display, often producing a " flash effect " which lasts only for a fraction of a second. Most species precede the preening display with ritualized drinking. It thus appears that many species use ritualized preening behind the wing as a sexual display during pair formation and as a mutual display after pairs are formed, presumably serving to maintain the pair bond. Mutual preening on the back and sometimes behind the wing is also utilized as a precopulatory display in some species of *Anas* (*capensis*, *angustirostris*), in most if not all species of *Netta* and *Aythya*, and also in *Melanitta*, *Bucephala*, and *Mergus*.

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