Dominance in wintering Anatinae: potential effects on clutch size and time of nesting

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In many avian species, females breeding for the first time nest later (Coulson 1966; Pinkowski 1977; Zwickel 1977; Nolan 1978) and have smaller clutches (Lack 1966; Klomp 1970) than older, more experienced females. These phenomena have also been reported in the Anatinae (Heusmann 1975; Krapu and Doty 1979; Armbruster 1982; Baillie and Milne 1982). Lack (1968) proposed that young females find it harder to procure food, thereby inhibiting formation of eggs, and causing delays in nesting and smaller clutch sizes. Wynne-Edwards (1962), however, attributed the later nesting of first-time breeders to their inability to compete successfully with experienced individuals for breeding sites. Hannon *et al.* (1982) supported Wynne-Edwards' (1962) hypothesis by indicating that nesting of yearling Blue Grouse *Dendragapus obscurus*, was delayed through social interactions with adult females during the breeding season. Delayed sexual maturity of first-time breeders could also be responsible for these events, but some evidence indicates that young females, provided with equal access to resources (i.e. food and nest sites), are capable of reproductive efforts similar to adults (Batt & Prince 1978; Zwickel 1980). I propose that delayed nesting and reduced clutch size of female Anatinae breeding for the first time may be caused by social factors, occurring outside the breeding season, which affect development of nutrient reserves.

North American ducks establish pair bonds each year on wintering grounds or during spring migration, usually with different mates (McKinney 1965; Palmer 1976). Waterfowl breeding for the first time pair later than adults (McKinney 1965; Spurr & Milne 1976). Younger males are less competitive than adults for mates because of slower plumage development (McKinney 1970) and differences in reproductive display (Dane & Van der Kloot 1964; Korschgen & Fredrickson 1976). Other factors, such as intensity of courtship activity (Bossema & Kruijt 1982) and condition of individuals (Wishart 1979), that influence pair bond formation, may also be age-related. Although these studies have focused on differential pairing activity of male age classes, the same pattern also should be true for females. In some passerines, for example, older females arrive at breeding areas earlier, pair earlier and nest earlier than yearlings (Nolan 1978).

Timing of pair bond formation is important because paired waterfowl have advantages over unpaired individuals of a population. In autumn and winter, paired dabbling ducks *Tribe Anatini* of both sexes are dominant to unpaired conspecifics, and paired females participate in aggression less frequently than unpaired females because they are protected by their mates (Hepp 1982). For low-ranking male Shelducks *Tadorna tadorna*, dominance status improves after establishment of pair bonds (Patterson 1977). There is even some evidence that paired Gadwall *Anas strepera* are found in better wintering habitats than unpaired Gadwall (Paulus 1980). In addition, Ashcroft (1976) reported that increased closeness of pair members improved the foraging rate (food items/min) of female Eiders *Somateria mollissima*. If a female's mate was close, aggression involving the female occurred less often than if the mate was more distant or absent; hence, feeding efficiency increased. The ability of female Eiders to forage undisturbed and to establish nutrient reserves is extremely important in preparation for breeding, because reserves are used not only for development of clutches but also to provide the sole energy for incubation (Milne 1974).

Even though there are costs (i.e. attraction of mates and intrasexual competition) to establishing and maintaining pair bonds, early pair formation is beneficial to wintering ducks because of preferential access to resources resulting from the superior dominance rank of paired individuals. If resources are limited in winter (Fretwell 1972), then dominant individuals should fare better than subordinates. In some passerines, dominants have greater access to food (Craig *et al.* 1982), lose less weight during periods of food restriction (Baker &

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Fox 1978), and have greater overwinter survival (Kikkawa 1980).

Timing of pair bond formation consequently influences subsequent productivity of an individual. Because of their subordinate status, yearling or subadult members of a population may not be able to collect the nutrient reserves necessary for optimal breeding. Accumulation of nutrient reserves (lipids and proteins) by female waterfowl prior to nesting is essential for optimal reproductive success. Factors adversely affecting acquisition of food and subsequent development of nutrient reserves by females will delay time of laying (Perrins 1970) and reduce clutch size (Ryder 1970).

In some species of ducks, formation of lipid reserves is the most critical factor because protein demands, generally, are satisfied by foraging at the breeding areas. Lipid reserves of female dabbling ducks, for example, contribute greatly to lipid requirements of the initial clutch and provide the energy needed by females foraging for protein-rich invertebrates (Krapu 1979, 1981). Krapu and Doty (1979) reported that lipid content of adult Mallards *Anas platyrhynchos* was 24% greater than among yearlings; yearling Mallards began nesting later than adults and clutch sizes were smaller. Females of other species (e.g. Eiders), however, depend entirely on endogenous reserves for all energy expended during nesting (Korschgen 1977). Females attempting to nest without sufficient lipid and protein reserves often desert their nests before hatching or sometimes die of starvation. Baillie and Milne (1982) suggest that poor breeding performance of young Eiders is related to size of reserves that individuals are able to accumulate before nesting.

It is clear that development of sufficient nutrient reserves by female waterfowl before nesting is critically important for optimal reproductive success. Factors inhibiting formation of these reserves will delay nesting and reduce clutch size. First-time breeders pair later and, therefore, are subordinate to early-pairing adults. Younger females nest later and have smaller clutches than adults. I suggest that behavioural dominance from pairing mediates development of nutrient reserves in wintering Anatinae and, hence, is an important factor affecting time of nesting and clutch size of females.

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