

- LORENZ, F. W. 1950. Onset and duration of fertility in turkeys. *Poult. Sci.* 29: 20-26.
- MCCARTNEY, M. G. 1951. The physiology of reproduction in turkeys: 2. Degree and duration of fertility and hatchability in broody and non-broody pullets. *Poult. Sci.* 30: 663-667.
- SHUGART, G. W. 1988. Uterovaginal sperm-storage glands in sixteen species with comments on morphological differences. *Auk* 105: 379-385.
- VAN DRIMMLEN, G. C. 1946. "Sperm nests" in the oviduct of the domestic hen. *J. South African Vet. Med. Assoc.* 17: 42-52.

Received 3 April 1989, accepted 14 August 1989.

Age-related Pair Bonding by Male Eurasian Wigeons in Relation to Courtship Activity

JUAN A. AMAT

Estación Biológica de Doñana, Apartado 1056, E-41013 Sevilla, Spain

Mate choice by ducks occurs during a communal courtship in which several males display to a single female. For most ducks, pair formation occurs months before breeding, and pair bonds generally last a single season. By pairing early, female ducks may increase their ability to breed early and lay large clutches (Rohwer and Anderson 1988). *Parental investment theory* (Trivers 1972) predicts that females should be the "choosier" sex in these species (Wishart 1983, Rohwer and Anderson 1988, but see Afton and Sayler 1982). Male qualities important in acquiring mates include age, courtship behavior, plumage color, size, and body condition (e.g. Wishart 1983).

Young male ducks pair later than do adults (Wishart 1983, Hepp 1986, McKinney 1986). Given that the sex-ratio is male biased in most duck populations (Bellrose et al. 1961, Campredon 1983, Wishart 1983), the later a male pairs, the greater the probability of remaining unpaired. Because young males often develop alternate plumage later than adults (McKinney 1965, Weller 1965, Wishart 1985), the probability of remaining unpaired should be greater for the younger cohort. Indeed, Blohm (1982) and Wishart (1983) found that adult male Gadwalls (*Anas strepera*) and American Wigeons (*A. americana*) paired more frequently than yearling males. Wishart (1983) suggested that energetic constraints would affect pairing chronology (see also Afton and Sayler 1982, Brodsky and Weatherhead 1985), and Blohm (1982) speculated that age-related differences in neuroendocrine development, plumage growth, or courtship behavior (see also Bruggers and Jackson 1981) conferred a competitive advantage to older males. Although adult dabbling ducks predominate in pair bonds, it has not been shown whether this is actually due to female choice, as Blohm (1982) suggested. I present evidence that in a dabbling duck species male age per se is not a criterion used by females when choosing a mate during courtship.

During the winters of 1986/1987-1988/1989, I observed communal courtships of Eurasian Wigeons (*A. penelope*) in the Marismas (marshes) of the Guadalquivir, southwestern Spain. I noted the number and age (yearling or adult) of participating males. Yearling

males can be distinguished from adults under field conditions because their greater upper wing-coverts are gray, which contrasts with the white of adults (Cramp and Simmons 1977).

On 20 February 1987 and 17 February 1989, I recorded the pairing status of male Eurasian Wigeons. I chose those dates because by mid-February most females are paired (pers. obs.). I randomly positioned a telescope and began to count males from right to left, recording whether or not the first 50 adult and 50 yearling males I watched were paired. Individuals were categorized as paired if they were close to, synchronized activities with, and defended females, or if females incited males (Afton and Sayler 1982, Hepp and Hair 1984).

The sex ratio of Eurasian Wigeons wintering in the Marismas was 100 males to 88 females, and the age ratio of males was 100 adults to 109 yearlings (Campredon 1983). Although there are annual differences in age ratio of wintering Eurasian Wigeon populations, differences were small (usually <10%; Campredon 1983).

I found no annual differences (*G*-test, $P > 0.05$) in the pairing frequency of males according to age, and therefore I pooled data. By late February, adult males were paired in 84 of 100 cases. Yearlings were paired in 25 of 100 cases. The difference in the pairing frequency by both categories of wigeon males is highly significant ($\chi^2 = 37.3$, $P < 0.001$) if pairing frequency is adjusted for male age ratio in the wintering population.

I recorded the composition of 27 communal courtships and found that 18.3% of the male ($n = 115$) participants were yearlings. Assuming that males pair according to frequency of participation in communal courtships, there is no difference ($\chi^2 = 1.6$, $P > 0.05$) in the frequency of occurrence of adult and yearling males in pair bonds. Consequently, I conclude that male age was not a criterion used by wigeon females when they chose mates.

Female dabbling ducks mainly choose mates according to male behavioral dominance (Brodsky et al. 1988). Females paired to a dominant male foraged

undisturbed for longer periods or with increasing efficiency, because their mates reduced interference from unpaired males (Ashcroft 1976, Spurr and Milne 1976, Afton and Saylor 1982, Paulus 1983). This may be particularly important for the Eurasian Wigeon, as it requires long undisturbed feeding periods to satisfy daily energy requirements (Mayhew 1988).

My results indicate that, although adult male Eurasian Wigeons pair more frequently than yearlings, differential pairing is due to decisions made by the males regarding whether or not to participate in communal courtships, and pairing is not due to differential choice by females. Such decisions might be dictated by the magnitude of interindividual differences in attributes important in determining dominance status (Amat 1986) and would be affected by costs related to mating (see Daly 1978, Wishart 1983, Hepp 1986, Rohwer and Anderson 1988).

In contrast, Afton and Saylor (1982) never observed subadult Common Goldeneye (*Bucephala clangula*) males to be paired, in spite of frequent participation of subadult males in communal courtships. Thus, criteria used by female ducks in choosing mates vary among species, presumably in response to the type of benefit that they gain when pairing (cf. Rohwer and Anderson 1988).

I was supported by funds from the Comisión Asesora de Investigación Científica y Técnica (grant to F. Braza). Alan D. Afton, Eduardo Aguilera, and an anonymous referee provided constructive criticism on earlier drafts of the manuscript.

LITERATURE CITED

- AFTON, A. D., & R. D. SAYLER. 1982. Social courtship and pairbonding of Common Goldeneyes, *Bucephala clangula*, wintering in Minnesota. *Can. Field-Nat.* 96: 295-300.
- AMAT, J. A. 1986. A possible significance of the occurrence of chin-spots in male ducks. *Gerfaut* 76: 31-35.
- ASHCROFT, R. E. 1976. A function of the pairbond in the Common Eider. *Wildfowl* 27: 101-105.
- BELLROSE, F. C., T. G. SCOTT, A. S. HAWKINS, & J. B. LOW. 1961. Sex ratios and age ratios in North American ducks. *Illinois Nat. Hist. Surv. Bull.* 27: 391-474.
- BLOHM, R. J. 1982. Differential occurrence of yearling and adult male Gadwalls in pair bonds. *Auk* 99: 378-379.
- BRODSKY, L. M., C. D. ANKNEY, & D. G. DENNIS. 1988. The influence of male dominance on social interactions in Black Ducks and Mallards. *Anim. Behav.* 36: 1371-1378.
- , & P. J. WEATHERHEAD. 1985. Time and energy constraints on courtship in wintering American Black Ducks. *Condor* 87: 33-36.
- BRUGGERS, R., & W. B. JACKSON. 1981. Age-related differences in reproductive behaviour of male Mandarin Ducks. *Bird Study* 28: 107-114.
- CAMPREDON, P. 1983. Sexe et âge-ratios chez le Canard siffleur *Anas penelope* L. en période hivernale en Europe de l'Ouest. *Rev. Ecol. (Terre Vie)* 37: 117-128.
- CRAMP, S., & K. E. L. SIMMONS (Eds.). 1977. The birds of the western Palearctic, vol. 1. Oxford, Oxford Univ. Press.
- DALY, M. 1978. The cost of mating. *Am. Nat.* 112: 771-774.
- HEPP, G. H. 1986. Effects of body weight and age on the time of pairing of American Black Ducks. *Auk* 103: 477-484.
- , & J. D. HAIR. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. *Condor* 86: 251-257.
- MAYHEW, P. W. 1988. The daily energy intake of European Wigeon in winter. *Ornis Scandinavica* 19: 217-223.
- MCKINNEY, F. 1965. Spacing and chasing in breeding ducks. *Wildfowl Trust Annu. Rep.* 16: 92-106.
- . 1986. Ecological factors influencing the social systems of migratory dabbling ducks. Pp. 153-171 in *Ecological aspects of social evolution* (D. I. Rubenstein and R. W. Wrangham, Eds.). Princeton, Princeton Univ. Press.
- PAULUS, S. L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. *Auk* 100: 947-952.
- ROHWER, F. C., & M. G. ANDERSON. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. Pp. 187-221 in *Current ornithology*, vol. 5 (R. F. Johnston, Ed.). New York, Plenum Publ. Corp.
- SPURR, E., & H. MILNE. 1976. Adaptive significance of autumn pair formation in the Common Eider *Somateria mollissima* (L.). *Ornis Scandinavica* 7: 85-89.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136-179 in *Sexual selection and the descent of man, 1871-1971* (B. Campbell, Ed.). Chicago, Aldine Publ. Co.
- WELLER, M. W. 1965. Chronology of pair formation in some Nearctic *Aythya* (Anatidae). *Auk* 82: 227-235.
- WISHART, R. A. 1983. Pairing chronology and mate selection in the American Wigeon (*Anas americana*). *Can. J. Zool.* 61: 1733-1743.
- . 1985. Moulting chronology of American Wigeon, *Anas americana*, in relation to reproduction. *Can. Field-Nat.* 99: 172-178.

Received 3 April 1989, accepted 17 August 1989.