

9

Workshop Summary: Courtship and Pairing in Winter

*Michael G. Anderson, Gary R. Hepp,
Frank McKinney, and Myrlyn Owen*

This report offers recommendations for future research on courtship and pairing by waterfowl. We wish to acknowledge the helpful input of the 65 people who attended and contributed to our discussion in Galveston. In particular, D. G. Raveling stimulated several useful exchanges. Several of the topics we discussed also were identified by Raveling et al. (1982). We believe this reflects continuing interest in these subjects from both theoretical and practical points of view.

Interesting Problems for Future Research

Ecological Bases for the Distribution and Spacing of Birds

Most ethologists now believe that animal social behavior evolves as the product of selfish individuals competing in specific ecological settings (Wilson 1975, Brown 1975, Wittenberger 1981, Alcock 1983). Therefore, identifying factors that shape the basic social organization of a species is critical to our understanding of courtship and pair formation as these processes have evolved to meet the needs of individuals operating within specific social systems. Of key importance here is elucidating ecological and phylogenetic factors that shape the distribution and spacing patterns of birds, both geographically and on a micro scale. Knowledge of this habitat "template" is invaluable for identifying important selection pressures and for comparative studies of behavior. For instance, to understand why birds pair when they do, it is necessary to understand why birds flock or remain dispersed: how spacing and agonistic behavior are related to resource distribu-

Waterfowl in Winter. © 1988 University of Minnesota. Edited by Milton W. Weller and published by the University of Minnesota Press, Minneapolis.

tions, predator disturbance, etc.; and the effects of these factors on the costs and benefits of living in different social classes (e.g., paired vs. unpaired).

Studies of factors affecting flocking, philopatry, and distributions of nonbreeding birds also should help managers identify key factors affecting survival that might lead to more enlightened management.

Pairing in Winter

Nearly all northern hemisphere ducks form pairs away from their breeding grounds between midautumn and early spring (Cramp and Simmons 1977, Bellrose 1980). This pattern of winter pairing appears to be unique among migratory North American birds and thus of special interest to all ornithologists. Geese may pair year-round, but the timing and processes involved are not as well known (Ogilvie 1978, Akesson and Raveling 1982, Owen et al. 1987, Black and Owen 1987).

Few general hypotheses have been offered to explain why waterfowl pair in winter (Lack 1968, Wittenberger and Tilson 1980, Shields 1983), and none has been subjected to rigorous testing. Time of pairing also varies greatly among species (e.g., Bezzel 1959, Weller 1965, Paulus 1983, Hepp and Hair 1983), and only a few attempts have been made to assess what determines these temporal differences (Weller 1965, Paulus 1983).

Comparative and experimental studies and theoretical analyses are needed to determine why ducks pair away from the breeding grounds and what influences variation in the timing of pair formation among individuals and among different species. Further descriptive data are needed for many species, preferably from several locations, to enable rigorous comparative tests of current hypotheses.

Better data on pair bond durations for a variety of species also would be valuable. The question of why most swans and geese are perennially monogamous while most ducks form seasonal pair bonds has been addressed from several viewpoints (e.g., Kear 1970, Maynard-Smith 1977). The central question appears to be: What factors tip the scales in favor of prolonged male parental investment in some species, nonparental associations with brood-rearing mates in other species, and early mate desertion, often coupled with extra-pair copulations or rapid serial monogamy, in still others? Studies of such trade-offs in sedentary southern-hemisphere species (e.g., Siegfried 1974; McKinney 1985, 1986) or island forms, some of which switch mates (e.g., Moulton and Weller 1984), might offer especially valuable insights on this question.

Finally, studies of wild, marked birds might reveal details of liaison formations and switches throughout the period of courtship and pair formation that would be important for analyzing the process of social courtship and mate choice (see below).

Because many ducks pair in late autumn and early winter, numerous pair bonds undoubtedly are disrupted by hunting, which continues through January in the southern United States and even later elsewhere (as in portions of Central America and Europe). Goose families and pairs suffer similar disruption, and this may exact short-term reproductive costs (Owen et al. 1987). Shooting essentially prereproductive pairs seems risky at first glance because of probable costs associated with re-pairing. In some species of geese, late shooting may even prevent re-pairing before the breeding season. However, the costs of disruption are largely unquantified. We need imaginative research to determine the effects of mate loss on overwinter survival and subsequent reproductive performance of individuals, especially by geese and early-pairing female ducks.

Mate Choice

Because many waterfowl, particularly seasonally monogamous ducks, form pairs anew each year away from the breeding grounds, they are an especially attractive group for studies of mate choice. Such choices apparently must be made solely on the bases of phenotypic characteristics of potential mates uncomplicated by variation in breeding territory or habitat quality—a problem that generally complicates studies of mate choice in birds (for reviews, see Bateson 1983). We believe this is a field ripe for progress since little work on modern evolutionary questions of mate choice (e.g., Halliday 1983, Partridge and Halliday 1984) has been done with waterfowl (but see McKinney 1975, Cooke and Davies 1983, Williams 1983).

Studies are needed to test for the occurrence of nonrandom mate choice, the characteristics selected in various species, and the relationship of these criteria to reproductive success. The simple occurrence of nonrandom mate selection has been demonstrated convincingly in only a few species (e.g., wild *Anser caerulescens*, Cooke and Davies 1983; captive *Aythya valisineria*, Bluhm 1985; captive *Anas platyrhynchos*, Williams 1982, K. Holmberg, pers. commun.). This is not a trivial point. Parental investment theory (Trivers 1972) offers specific predictions concerning which sex should be “choosier” in different social systems, but this does not eliminate the possibility that both sexes exercise some degree of mate choice or that other factors might suppress its expression (Partridge and Halliday 1984). For instance, mate choice could be largely masked by strong intrasexual competition for mates, and separation of these two effects is fraught with practical problems. Also the “value” to an individual of any breeding partnership may differ between mates and over the course of a breeding cycle (Anderson 1984). Pair bonds are dynamic, complex relationships, and it is likely that mate assessment continues even after pair formation.

It would be interesting to know which phenotypic characteristics form the bases for mate choice, for both males and females and in a variety of species, and how

selection for these characters might affect reproductive success. Following general suggestions of Trivers (1972), Halliday (1983), and others, we might identify a variety of characteristics (table 9.1) important in mate selection in waterfowl. This list certainly is not exhaustive, but it offers some examples of characteristics that might profitably be tested. Plumage, physical condition, dominance, age, and

Table 9.1 Phenotypic characteristics and selection criteria of possible importance in mate choice by waterfowl

Character selected	Possible selection criteria
Higher fecundity	Female age
Improved social status	Fighting skill, strength, stamina Body size
Parental abilities	Above plus vigilance, attentiveness
Complementarity	Degree of genetic relatedness Previous experience together
Strong reproductive effort	Mutual experience with a breeding area Physical condition (vigor, plumage)
Genetic "quality"	Any phenotypic trait with a genetic basis, additive variance, and high heritability

genetic strain all may be factors affecting mate choice in captive mallards (Klint 1975, 1978, 1980; Cheng et al. 1978, 1979; Goldsmith 1979; Bossema and Kruijt 1982; Williams 1982; K. Holmberg, pers. commun.), but more work is needed to sort out the interrelationships of these factors. Only preliminary studies have been carried out with wild ducks (*Anas americana*, Wishart 1983). Body size may affect mate choice in Canada geese (MacInnes 1966) and snow geese (Ankeny 1977, Cooke and Davies 1983). Large size may be advantageous in increasing clutch size in geese (Cooke and Davis 1983) or social rank in swans (Scott 1981). Links between the characteristic selected and reproductive success will be especially difficult to determine in wild birds but should be attempted in promising situations, such as with sedentary populations. Research combining field studies and captive experiments (e.g., Wishart 1983) seems especially promising.

Process and Functions of Social Courtship

Until about 10 years ago, the functions of courtship were viewed in a rather narrow way. Courtship was shown to synchronize the reproductive condition of mates, to increase the sexual motivation of partners, and to provide reproductive isolation among otherwise similar species (e.g., Tinbergen 1951, Bastock 1967). Questions concerning the strategies and tactics of individuals engaged in courtship only became an issue with the emergence of "selfish-individual" thinking. With a

"good-of-the-species" perspective, getting the right species and sexes together and synchronized seemed sufficient. Now ethologists believe that courtship also may serve many complex functions (Trivers 1972, McKinney 1975, Erickson 1977, Dawkins and Krebs 1978, Alcock 1983, Wittenberger 1983, Krebs and Dawkins 1984). This revolution in approach is based on theoretical expectations and on observations that even simple displays from a complex repertoire may contain more than enough information to assure "correct" choice of mates (Nuechterlein 1981). Consequently, we have reason to suspect that much of social courtship in waterfowl may deal with salesmanship or the assessment of potential mates, generally resulting from the competing self-interests of the individual players involved.

We have a rich information base on waterfowl courtship (e.g., Heinroth 1911, Lorenz 1941, McKinney 1965, Johnsgard 1965) that has proved to be of great taxonomic importance and that still offers many clues for understanding waterfowl social systems. However, we have surprisingly little strong evidence on the function of complex social display (e.g., Laurie-Ahlberg and McKinney 1979). Observations and experiments on marked birds are badly needed to address the goals and tactics of individuals within their social system. We need a fresh look at waterfowl courtship, including an examination of hypotheses concerning mate assessment, conflicts of interest, and evolutionarily stable courtship strategies.

Issues of Perspective and Methodology

In addition to the research topics noted above, we believe that there are several issues of methodology and perspective that require comment or deserve further study.

(1) Studies of wild birds remain critical for gaining insights into selection pressures operating in nature, but expanded use of controlled experiments with captive birds to test many existing ideas will be very helpful and should be encouraged.

(2) As the questions we ask become more sophisticated and difficult to answer, it will be increasingly important to search for populations of birds that are amenable to particular studies. Situations that permit the use of individually marked birds will be invaluable, especially if the population can be followed year-round. At the same time, we sense a growing concern over possibly serious effects of various marking techniques on the behavior of study subjects, especially with regard to potentially subtle discrimination tasks such as mate choice (for finches and doves, see Goforth and Baskett 1965; Burley 1981; Burley et al. 1982; Immelmann et al. 1982). Critical

studies of marker biases should be carried out for a variety of effects on several species.

(3) More deliberate hypothesis-testing approaches would be helpful in this field and are overdue, considering the wealth of behavioral and ecological information available on waterfowl. These tests could occur via observational studies that take advantage of natural experiments, comparative studies, or controlled experiments. Others argue that inductive approaches are still essential to reveal the nature and range of variability in behavior, especially in different habitats. Certainly, basic descriptive data on wintering social behavior are still lacking for many species and are sorely needed for comparative purposes.

(4) Studies designed to examine intraspecific variations in social behavior in relation to geographical location, time, or local habitat conditions are badly needed. We suspect that considerable variability will be found both spatially and temporally, and it would be interesting to discover the causes of such variation. Spacing, agonistic behavior, and time of pairing may be especially interesting to examine in this way. We are hampered in attempts to generalize about social behavior because, for many species, data are available from only a single time and place.

(5) The union of bioenergetic and behavioral approaches has been very productive, and we agree with the conclusion of Raveling et al. (1982) that studies combining these disciplines remain especially promising.

(6) We stand to gain much insight and stimulation for our work by extending our horizons to consider the social systems of tropical and southern hemisphere waterfowl, and other birds in general, when developing research questions about northern hemisphere waterfowl.

(7) It is crucial for progress that we approach even very specific research questions from the broader perspective of the annual cycle of each species. Thus, questions of behavior during nonbreeding periods cannot be viewed in isolation, and important research questions on courtship and pairing in winter become an integral subset of broader questions concerning the evolution of waterfowl social behavior.

LITERATURE CITED

- Akesson, T. R., and D. G. Raveling. 1982. Behaviour associated with seasonal reproduction and long-term monogamy in Canada geese. *Condor* 84:188-196

- Alcock, J. 1983. Animal behavior: an evolutionary approach. 3rd ed. Sinauer Associates, Sunderland, Mass. 722pp
- Anderson, M. G. 1984. Parental investment and pair-bond behavior among canvasback ducks (*Aythya valisineria* Anatidae). Behav. Ecol. Sociobiol. 15:81-90.
- Ankney, C. D. 1977. Male size and mate selection in lesser snow geese. Evol. Theory 3:143-148.
- Bastock, M. 1967. Courtship: an ethological study. Aldine Press, Chicago. 220pp.
- Bateson, P. 1983. Mate choice. Cambridge Univ. Press, Cambridge, Mass. 462pp.
- Bellrose, F. C. 1980. Ducks, geese and swans of North America Stackpole Books, Harrisburg, Pa. 540pp.
- Bezzel, E. 1959. Beitrage zur Biologie der Geschlechter bei Entenvogeln. Anz Ornithol. Ges. Bayern 5:269-356.
- Black, J. M., and M. Owen. 1988. Variations in pair bond and agonistic behaviors in barnacle geese on the wintering grounds. Pages 39-57 in M. W. Weller, ed., Waterfowl in winter Univ. Minnesota Press, Minneapolis.
- Bluhm, C. K. 1985. Mate preferences and mating patterns of canvasback ducks (*Aythya valisineria*). Pages 45-56 in P. A. Gowaty and D. W. Mock, eds. Avian Monogamy. Ornithol. Monogr. 37.
- Bossema, I., and J. P. Kruijt. 1982. Male activity and female mate acceptance in the mallard (*Anas platyrhynchos*) Behav 79:313-324.
- Brown, J. L. 1975. The evolution of behavior. W. W. Norton, New York 761pp.
- Burley, N. 1981. Sex ratio manipulation and selection for attractiveness. Science 211:721-722.
- , G. Krantzberg, and P. Radman. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. Anim. Behav. 30:444-455.
- Cheng, K. M., R. N. Shoffner, R. E. Phillips, and F. B. Lee. 1978. Mate preference in wild and domesticated (game-farm) mallards (*Anas platyrhynchos*). I. Initial preference. Anim. Behav 26:996-1003.
- , ———, ———, and ——— 1979. Mate preference in wild and domesticated (game-farm) mallards: II. Pairing success. Anim. Behav. 27:417-425.
- Cooke, F., and J. C. Davies. 1983. Assortative mating, mate choice and reproductive fitness in snow geese. Pages 279-295 in P. Bateson, ed. Mate choice. Cambridge Univ. Press, Cambridge, Mass 462pp
- Cramp, S., and K. E. L. Simmons, eds. 1977. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 1. Oxford Univ. Press, Oxford. 722pp.
- Dawkins, R., and J. R. Krebs. 1978. Animal signals: information or manipulation. Pages 380-402 in J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Blackwell Scientific Publ., Oxford
- Erickson, C. J. 1977. Sexual affiliation in animals: pair bonds and reproductive strategies. Pages 697-725 in J. B. Hutchinson, ed. Biological determinants of sexual behavior. John Wiley, New York
- Goforth, W. R., and T. S. Baskett. 1965. Effects of experimental color marking on pairing of captive mourning doves. J. Wildl. Manage. 29:543-553.
- Goldsmith, A. R. 1979. Social behaviour, pair formation and the behavioural effects of testosterone in the mallard (*Anas platyrhynchos*). Ph D. Thesis. Univ. Leicester, Leicester. 176pp.
- Halliday, T. R. 1983. The study of mate choice. Pages 3-32 in P. Bateson, ed. Mate choice. Cambridge Univ. Press, Cambridge 462pp.
- Heinroth, O. 1911. Beitrage zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Verh. Int. Ornithol. Kongr. 5:598-702
- Hepp, G. R., and J. D. Hair. 1983. Reproductive behavior and pairing chronology in wintering dabbling ducks. Wilson Bull. 95:675-682.
- Immelmann, K., J. P. Hailman, and J. R. Baylis. 1982. Reputed band attractiveness and sex manipulation in zebra finches. Science 215:422.

- Johnsgard, P. A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca, N.Y. 378pp.
- Kear, J. 1970. The adaptive radiation of parental care in waterfowl. Pages 357-392 in J. H. Cook, ed. Social behaviour in birds and mammals. Academic Press, London.
- Klint, T. 1975. Sexual imprinting in the context of species recognition in female mallards. Z. Tierpsychol. 38:385-392.
- . 1978. Significance of mother and sibling experience for mating preferences in the mallard (*Anas platyrhynchos* L.). Z. Tierpsychol. 47:50-60.
- . 1980. Influence of male nuptial plumage on mate selection in the female mallard (*Anas platyrhynchos*). Anim. Behav. 28:1230-1238.
- Krebs, J. R., and R. Dawkins. 1984. Animal signals: mind-reading and manipulation. Pages 380-402 in J. R. Krebs and N. B. Davies, eds. Behavioural ecology—an evolutionary approach. 2nd ed. Blackwell Scientific Publ., Oxford.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., London. 409pp.
- Laurie-Ahlberg, C. C., and F. McKinney. 1979. The nod-swim display of male green-winged teal (*Anas crecca*). Anim. Behav. 27:165-172.
- Lorenz, K. 1941. Vergleichende Bewegungstudien an Anatinen. J. Ornithol. 89:194-294.
- MacInnes, C. D. 1966. Population behavior of eastern arctic Canada geese. J. Wildl. Manage. 30:536-553.
- Maynard-Smith, J. 1977. Parental investment: a prospective analysis. Anim. Behav. 25:1-9.
- McKinney, F. 1965. The courtship movements of Anatidae. Behav. 25:120-220.
- . 1975. The evolution of duck displays. Pages 331-357 in G. Baerends, C. Beer, and A. Manning, eds. Function and evolution in behaviour. Clarendon Press, Oxford.
- . 1985. Primary and secondary male reproductive strategies of dabbling ducks. Pages 68-82 in P. A. Gowaty and D. W. Mock, eds. Avian monogamy. Ornithol. Monogr. 37.
- . 1986. Ecological factors in the evolution of social behavior of dabbling ducks. Pages 153-171 in D. I. Rubenstein and R. W. Wrangham, eds. Ecological aspects of social evolution. 551 pp.
- Moulton, D. W., and M. W. Weller. 1984. Biology and conservation of the Laysan duck (*Anas laysanensis*). Condor 86:105-117.
- Nuechterlein, G. L. 1981. Variations and multiple functions of the advertising display of western grebes. Behav. 76:289-317.
- Ogilvie, M. A. 1978. Wild geese. Buteo Books, Vermillion, S.D. 350pp.
- Owen, M., J. M. Black, and H. Liber. 1988. Pair bond duration and timing of its formation in barnacle geese (*Branta leucopsis*). Pages 23-38 in M. W. Weller, ed. Waterfowl in winter. Univ. Minnesota Press, Minneapolis.
- Partridge, L., and T. R. Halliday. 1984. Mating patterns and mate choice. Pages 222-250 in J. R. Krebs and N. B. Davies, eds. Behavioral ecology: an evolutionary approach. Sinauer Associates, Sunderland, Mass.
- Paulus, S. L. 1983. Dominance relations, resource use, and pairing chronology of gadwalls in winter. Auk 100:947-952.
- Raveling, D. G., A. D. Afton, W. C. Alexander, M. G. Anderson, R. O. Bailey, D. F. McKinney, R. D. Saylor, R. D. Titman, and R. A. Wishart. 1982. Report of the social behavior discussion group. Pages 26-33 in M. G. Anderson and B. D. J. Batt, eds. Workshop on the ecology of wintering waterfowl. Delta Waterfowl Research Station, Portage la Prairie, Man.
- Scott, D. K. 1981. Social behaviour of *Cygnus columbianus bewickii*. Pages 211-225 in Proc. 2nd Int. Swan Symposium. Int. Waterfowl Res. Bureau, Slimbridge, U.K.
- Shields, W. M. 1983. Optimal inbreeding and the evolution of philopatry. Pages 132-159 in I. R. Swingland and P. J. Greenwood, eds. The ecology of animal movement. Clarendon Press, Oxford.
- Siegried, W. R. 1974. Brood care, pair bonds and plumage in southern African Anatini. Wildfowl 25:33-40.

- Tinbergen, N. 1951. *The study of instinct*. Clarendon Press, Oxford. 228pp.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in B. Campbell, ed. *Sexual selection and the descent of man, 1871-1971*. Aldine Press, Chicago.
- Weller, M. W. 1965. Chronology of pair formation in some nearctic *Aythya* (Anatidae). *Auk* 82:227-235.
- Williams, D. M. 1982. Agonistic behaviour and mate selection in the mallard (*Anas platyrhynchos*). Ph.D. Thesis, Univ. Leicester, Leicester. 243pp
- . 1983. Mate choice in the mallard. Pages 297-309 in P. Bateson, ed. *Mate choice*. Cambridge Univ. Press, Cambridge.
- Wilson, E. O. 1975. *Sociobiology, the new synthesis*. Belknap Press, Cambridge, Mass. 697pp.
- Wishart, R. A. 1983. Pairing chronology and mate selection in the American wigeon (*Anas americana*). *Can. J. Zool.* 61:1733-1743.
- Wittenberger, J. F. 1981. *Animal social behavior*. Duxbury Press, Boston, Mass. 722pp
- . 1983. Tactics of mate choice. Pages 435-447 in P. Bateson, ed. *Mate choice*. Cambridge Univ. Press, Cambridge, Mass.
- , and R. L. Tilson. 1980. The evolution of monogamy: hypotheses and evidence. *Ann. Rev. Ecol. Syst.* 11:197-232.

