

Birds and Mammals

8. Ecological Factors Influencing the Social
Systems of Migratory Dabbling Ducks

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DABBLING DUCKS (Anatini) pose several intriguing problems for behavioral ecologists. Why do they differ from most birds in that females, rather than males, are philopatric? Why are they basically monogamous, given that males do not incubate and play no part in brood care in most species? Why does pairing occur in winter, often months before breeding begins, and why are new pair bonds usually formed each year? Why do males of certain species defend breeding territories? In the light of current views on sex-biased dispersal (Greenwood, 1980), mating system evolution (Emlen and Oring, 1977), and pair-bond duration (Rowley, 1983), these characteristics call for evolutionary explanations in terms of phylogenetic, ecological, and behavioral factors.

Several authors have discussed factors that could have led to male-biased dispersal, monogamous mating systems, and winter pairing in waterfowl (Anatidae) in general (Lack, 1968; Wittenberger and Tilson, 1980; Greenwood, 1980, 1983; Oring, 1982). However, there are important variations in morphology and life history within this large family of birds that need to be kept in mind. For example, the factors promoting monogamy in swans and large geese (in which families remain intact for six to nine months and pair bonds tend to be lifelong) may well be different from those promoting monogamy in migratory dabbling ducks (in which parental care lasts only about 1.5 months and new pair bonds typically form each year). Furthermore, even within the Anatini, there may be important differences between the mating systems of sedentary or nomadic species (McKinney, 1985) and those of migratory species. In this broad review, I will focus on key sources of selection that appear to have shaped the social behavior of migratory (primarily Northern Hemisphere) species and their relationship to life-history characteristics distinctive to this group.

KEY FEATURES OF DABBLING DUCK BIOLOGY

Dabbling ducks (including thirty-seven species of *Anas* within the tribe Anatini) are among the most flexible and adaptable members of the family Anatidae. (For reviews of dabbling duck biology see Weiler, 1964; Beilrose, 1976; Cramp and Simmons, 1977; Johnsgard, 1978.) Like most waterfowl,

they are strong fliers. Twenty-two species are wholly or partly migratory (Johnsgard, 1978). In contrast to ducks that feed by diving (pochards, stiff-tails, sea ducks) the elongated body shape and relatively small feet of dabbling ducks equip them well for walking as well as for swimming on the water surface where they obtain most of their food (Raikow, 1973). Consequently nest sites are not necessarily adjacent to wetlands, and females are capable of walking up to several kilometers to lead their newly hatched ducklings to water. Nest sites are usually on the ground, incubation is by females only, and the primary antipredator strategy of nesting females is crypticity. Nevertheless incubating females are very vulnerable to mammalian predators, and studies of remains at fox dens have shown that many are taken on the nest (Sargeant 1972; D. H. Johnson and Sargeant, 1977; Sargeant et al., 1984). Also, the eggs and ducklings of dabbling ducks are often subject to heavy predation (e.g., 50 percent or higher losses of clutches) and females of most species commonly lay replacement clutches (Bellrose, 1976).

Although ducklings are precocial and feed themselves, they do need to be brooded to protect them from cold, they must be led to good feeding areas, and they need to be warned about and protected from predators (e.g., by parental warning calls, escorting to cover, and distraction displays). Parental care is entirely by females in migratory Northern Hemisphere dabbling ducks and, even in certain Southern Hemisphere species in which the male also stays with the brood, it is the female who leads and broods the ducklings. Females remain with their ducklings for forty to sixty days, usually until they can fly (Evans et al., 1952; Oring, 1964a; Ball et al., 1975).

Although migratory dabbling ducks have radiated to occupy diverse wetland habitats and to exploit varied food sources (primarily aquatic plants and invertebrates; Thomas, 1980, 1982; Sugden, 1973; White and James, 1978; Eadie et al., 1979; Swanson et al., 1979; Weller, 1972, 1975; Nudds and Bowlby, 1984), each species has considerable dietary flexibility. This permits seasonal changes in diet, for example in response to temporary flooding (Krapu, 1974) or when birds move from wintering to breeding ranges (Wishart, 1983a). Diet can also change in response to changes in energetic and nutritional needs. Especially significant in this respect is the switch from an omnivorous or vegetarian diet to mainly invertebrate foods by females during the period of egg production (Krapu, 1974, 1979, 1981; Swanson et al., 1979).

Ducks lay large eggs with large yolks and thus eggs are costly to produce. J. R. King (1973) estimated that as much as 52-70 percent of a female's daily energy intake goes toward egg production. Krapu's (1974, 1981) studies in North Dakota have shown that migrant pairs of northern pintail (*Anas acuta*) and mallard (*A. platyrhynchos*) are heavy and fat when they arrive on the breeding grounds. Lipid reserves built up before arrival are used dur-

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TABLE 8.1
Homing rates of dabbling ducks banded on the breeding grounds in North America

	Females				Males				References
	Adult		Juvenile		Adult		Juvenile		
	No. banded	% returned	No. banded	% returned	No. banded	% returned	No. banded	% returned	
Mallard	15	13	20*	5			13*	0	1
	24	42	122*	6					2
	113	46	140	5					3
North American black duck	89	25	289*	2					2
Northern pintail	44	39	115*	13			132*	2	1
Gadwall	16	37	8*	12			9*	0	1
	52	29							4
	33	63	47	6	242	9*	25	4	5
							17*	0	5
Northern shoveler	19	42	12*	8			12*	0	1
	20	15	116	3	19	11*	134	1	6
Blue-winged teal	58	14	30*	0			19*	0	1
	16	0	200*	0					7
American wigeon	21	43							8

SOURCES. 1) Sowis, 1955, 2) Coulter and Miller, 1968, 3) Doty and Lee, 1974; 4) J. M. Gates, 1962, 5) Blohm, 1978, 1979, 6) Poston, 1974; 7) McHenry, 1971; 8) Wishart, 1983b.

* Captive reared ducklings, released as juveniles

* Twenty-one of twenty-three adult male gadwalls and two adult male northern shovelers that returned were unpaired.

ing the early part of the breeding season, while females are producing the first clutch of eggs and males engage in mate-defense and energetically costly pursuit flights. Females obtain most of the protein required for egg production by feeding on invertebrates, which is extremely time-consuming (Dwyer et al., 1979). Krapu (1981) believes that, in the case of the mallard, protein intake limits clutch size, and lipid reserves provide the energy resources necessary for the female to acquire the protein needed for the initial clutch. Thereafter, lipid reserves are depleted and the ability of females to produce re-nest clutches depends on availability of food on the breeding area. During incubation, females lose weight as they use up lipid reserves and have reduced time available for feeding (Folk et al., 1966; H. J. Harris, 1970; Krapu, 1981; Gatti, 1983).

Like other waterfowl, dabbling ducks have an annual, postbreeding wing-molt, during which the flight feathers are molted simultaneously and the birds are flightless for three or four weeks while the new feathers are growing. An annual flightless period occurs in only a few other bird groups,

mostly aquatic types, such as loons and grebes, that can afford the risks involved (Woolfenden, 1967). The main advantages of a simultaneous rather than a gradual wing-molt are probably related to seasonal partitioning of major time and energy demands in the annual cycle (J. R. King, 1974). In migratory dabbling ducks, activities that require full flying ability coincide with the periods in the year when energy demands are great (migration, breeding, and wintering phases) (Fig. 8.1). The scheduling of the flightless period after the breeding season is probably favored (at least in the Northern Hemisphere) by the high predictability of abundant food and warm weather in the summer months.

Flightless waterfowl are restricted in their mobility and are especially vulnerable to predators (Oring, 1964b; Gilmer et al., 1977). Replacement of the flight feathers is energetically demanding and requires a nutrient-rich diet (Owen, 1980). In many species, there are well-marked seasonal movements to traditional molting places where food and cover are in close proximity (Salomonsen, 1968). Dabbling ducks favor large marshes that provide safety from drought, a rich reliable food supply, emergent vegetation for escape cover, and seclusion from disturbance (Hochbaum, 1944). In many species, however, it is primarily males and those females that have been unsuccessful in their breeding attempts that move to these molting marshes; females that raise broods tend to stay in the breeding area to molt.

In summary, for females of migratory dabbling ducks, reproduction entails a) high risks of predation while at the nest and when escorting ducklings; b) high energetic demands of egg production calling for increased time spent feeding; c) frequent need to produce replacement clutches; d) loss of body weight during incubation associated with reduced time available for feeding. During the annual flightless period, dabbling ducks have special needs for a rich, localized food supply and habitat providing security from predators; females who raise broods may have less ready access to these requirements than males. Also, in some species, the ability of females to reproduce successfully can be influenced by their body condition on arrival at the breeding grounds, which in turn may depend on conditions on the wintering grounds. Therefore the costs and risks of reproduction are inevitably high for females, and males may be expected to behave in ways that tend to reduce these costs and risks for their mates.

FIDELITY TO THE BREEDING AREA

Studies by Sowls (1955) and others (Table 8.1) have documented strong tendencies for female mallard, northern shoveler (*A. clypeata*), North American black duck (*A. rubripes*), gadwall (*A. strepera*), and American wigeon to return to breed in the same area in successive seasons, as long as

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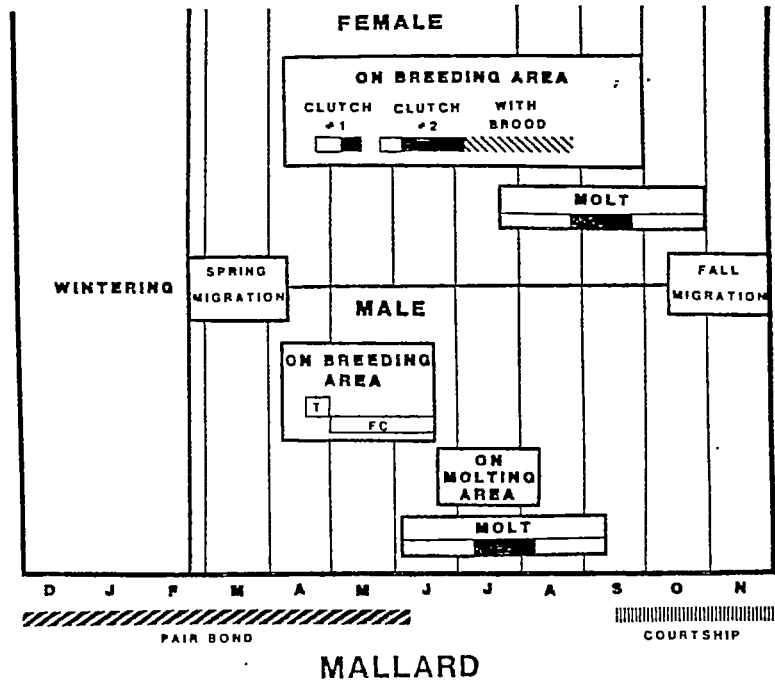


Fig. 8.1. The timing of seasonal activities in a pair of mallards. In this hypothetical example, the female lost her first clutch to a predator soon after incubation had started but the replacement clutch hatched successfully. On the breeding area, this male was territorial (T) initially, then made forced copulation (FC) attempts on other females. The periods of body feather molt are indicated in white, wing-molt in black. The representative chronologies for male and female are based on data on North American migratory populations summarized by Bellrose (1976).

they survive and the habitat remains suitable. However, this "homing tendency" is weak in female blue-winged teal (*A. discors*) and greatly influenced by habitat conditions on the breeding grounds in the northern pintail. Although Sows (1955) showed that pintails home well when conditions are suitable for breeding, during periods of severe drought in the North American prairies this species can be nomadic and pioneering (G. S. Hochbaum and Bossenmaier, 1972) and many fly north to the arctic (R. I. Smith, 1970; Calverley and Boag, 1977; Derksen and Eldridge, 1980).

Studies of two species in which females show strong homing tendencies (gadwall and northern shoveler) have revealed that males rarely return to the same breeding area in successive years unless they fail to acquire a mate

during the winter (Table 8.1). Natal philopatry (return of yearlings to the area of their birth) has been documented also in several migratory *Anas* species, and again the tendency is stronger in females than males (Table 8.1).

Dabbling ducks of both sexes are capable of breeding in their first year (Bellrose, 1976), but yearlings weigh less, have reduced lipid reserves in spring, lay smaller clutches, and lag behind older birds both in pairing and laying (Krapu and Doty, 1979; Dean and Skead, 1979; Wishart, 1983a, b). Postfledging mortality rates in the first year of life are high in migratory populations subject to hunting (Boyd, 1962; Cramp and Simmons, 1977), but annual survival is much higher among adults (e.g., 62% for male, 54% for female North American mallards according to Anderson, 1975). Maximum ages for wild mallards are thought to be sixteen to twenty years (Anderson, 1975), and an exceptional individual can live as long as twenty-nine years (Clapp et al., 1982). In summary, birds that survive beyond the first year have many advantages over yearlings, and presumably they stand a better chance of evading predators and producing offspring because of their experience in breeding, molting, and wintering areas.

Female dabbling ducks take the lead in selecting: a) the breeding area; b) the nest-site; c) the places visited by the brood (H. A. Hochbaum, 1944; Sowls, 1955; Poston, 1974; Wishart, 1983a). They are dependent on the area selected as the breeding home range for the food resources they need to produce eggs and to sustain them during incubation; their choice of a safe nest-site can determine their own survival and that of their eggs, and, by their decisions on where to lead their ducklings, they must play a major role in brood survival. In making all of these decisions, females stand to benefit by being in familiar terrain, and it is not surprising that fidelity to the breeding area is strongly developed in female dabbling ducks.

WHY ARE DABBING DUCKS BASICALLY MONOGAMOUS?

All dabbling ducks form pair bonds and monogamy is the general rule. This poses an interesting problem since only females incubate and in most species males do not take part in care of the young. Why then do males restrict their reproductive efforts by practicing monogamy?

The most popular hypothesis is that male-biased sex ratios produce such strong competition among males for access to females that each male is forced to defend a single female (Lack, 1968; Wittenberger and Tilson, 1980). For example, in eight North American species of *Anas*, males comprise 53-63 percent of fall populations (Bellrose, 1976) and similar male-biased ratios have been reported for several Southern Hemisphere species (Caithness and Pengelly, 1973; Dean and Skead, 1977). The main factor producing these imbalances is generally thought to be heavy mortality of females during the breeding season.

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Two aspects of the phenomenon of male-male competition are relevant here. Does a male have any opportunity to breed if he does not obtain a mate, and does a male need to guard one female to ensure that his sperm will compete successfully with sperm from other males? Both factors are probably important in dabbling ducks.

Several studies have shown that some male dabbling ducks (even old, experienced individuals) fail to obtain mates in certain years and arrive on the breeding grounds unpaired (e.g., Poston, 1974; Dwyer, 1974; Blohm, 1978; Humburg et al., 1978; Seymour and Titman, 1978). Some of these males succeed in pairing with reneating females whose pair bonds have broken, but others remain unpaired for the whole breeding season. In the species studied to date, unpaired males apparently continue to court females rather than switching to a promiscuous strategy. Therefore, failure to obtain a mate may well mean that a male has little chance of breeding that season.

Mate-guarding is generally strongly developed in male dabbling ducks, but there are specific variations in the vigor and duration of male defense (Titman and Seymour, 1981; McKinney et al., 1983). As well as closely escorting and remaining watchful, paired males actively threaten other males that show interest in the female and attack males that attempt to copulate with her. Females can be subjected to forced extrapair copulations that lead to sperm competition and, if they occur during the period before and during egg-laying, these inseminations can result in the fertilization of eggs. In species such as the mallard that show moderately strong development of mate-defense behavior, males follow their mates more consistently and closely during the female's fertile period (Goodburn, 1984). Therefore defense of a male's genetic paternity appears to be an important aspect of his monogamous tendencies.

Mate-guarding by males also provides benefits to female waterfowl. By minimizing disturbance by predators and rival males, a male can enhance his mate's feeding efficiency. Such feeding enhancement has been demonstrated in eider ducks (*Somateria mollissima*) (Ashcroft, 1976; Spurr and Milne, 1976), shelducks (*Tadorna tadorna*) (I. J. Patterson, 1977), swans (*Cygnus columbianus bewickii*) (D. K. Scott, 1980), geese (*Branta canadensis*) (McLandress and Raveling, 1981), and goldeneyes (*Bucephala clangula*) (Alton and Saylor, 1982). Time budget studies indicate that mate-guarding occurs in many species of dabbling ducks during the period of egg production (Dwyer, 1975; Seymour and Titman, 1978; Alton, 1979; G. R. Stewart and Titman, 1980; Titman, 1981). Males of some dabbling duck species also defend breeding territories within which their mates feed during the incubation period.

Therefore, males stand to benefit from defending individual females by ensuring that they will have an opportunity to breed and by protecting their

genetic paternity. Females also benefit by having a male consort during their fertile periods because this coincides with the period when they must spend extra time feeding for egg production, and male vigilance and protective behavior can enhance their feeding efficiency. If males are contributing essential support for their mate's breeding effort, perhaps females really control dabbling duck mating systems by forcing males to be monogamous? Some light can be thrown on this question by examining the ways in which males engage in secondary reproductive strategies.

SECONDARY MALE REPRODUCTIVE STRATEGIES

As well as maintaining a pair bond with one female, male dabbling ducks attempt to copulate forcibly with other females. This behavior has been recorded in twenty-one species of *Anas* and, at least in well-studied species such as the mallard and northern pintail, forced copulation appears to be a secondary reproductive strategy of paired males (see McKinney et al., 1983 for review of this and other hypotheses). Experiments with captive mallards have shown that females can store sperm for up to seventeen days (Elder and Weller, 1954) and that eggs can be fertilized by sperm delivered during forced copulations (Burns et al., 1980). Forced copulation attempts are directed mainly at females during their fertile periods. As well as defending their mates and attempting to prevent forced copulations, paired males have also been seen to force copulation on their own mates after the latter have been assaulted. Such behavior suggests an antidote insemination strategy. Therefore some (perhaps many) dabbling duck species appear to have "mixed male reproductive strategies" of the type predicted by Trivers (1972): monogamy as the primary strategy, promiscuity as a secondary strategy.

Similar mixed strategies have been reported for bank swallows (*Riparia riparia*) (Beecher and Beecher, 1979), snow geese (*Anser caerulescens*) (Mineau and Cooke, 1979), cattle egrets (*Bubulcus ibis*) (Fujioka and Yamagishi, 1981), and lesser scaup (*Aythya affinis*) (Afton, 1985). Extrapair copulations have been observed in primarily monogamous species of birds in many families but the forced nature of these copulations is especially obvious in waterfowl (Gladstone, 1979; Ford 1983; McKinney et al., 1984). One factor that may have favored the evolution of forced copulation strategies in waterfowl is the presence of an intromittent organ (phallus). This structure is probably primarily an adaptation to aquatic life; most anatids copulate while the pair is swimming on the water surface.

As well as attempting forced copulations, paired males of several species have been observed to direct courtship displays toward other females. This behavior occurs during the early stages of pair-formation while bonds are still tentative (e.g., Wishart, 1983a), and may continue into the breeding

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season in species such as the green-winged teal (*A. crecca*) (McKinney and Stolen, 1982). In the mallard, although many pair bonds remain intact or reform for renesting attempts within the same breeding season, mate switches sometimes occur (Humburg et al., 1978; Ohde et al., 1983), producing serial monogamy. Therefore, extrapair courtship is probably associated with tendencies for paired males to assess alternative mates.

Opportunities for males to hold more than one mate simultaneously are rare in migratory dabbling ducks because of male-biased sex ratios. Wishart's (1983a) observations on pair formation in the American wigeon (*A. americana*) suggest that persistent courtship and aggression among rival males prevent bigamous relationships from developing. In species where females have a strong tendency to return to the same place to breed, it is difficult to imagine how polygynous bonds could persist after the birds leave their wintering areas in spring. Each male can follow only one female back to her breeding home range.

The importance of these factors in preventing polygyny in migratory dabbling ducks is supported by a study in which the sex ratio was experimentally altered. Ohde et al. (1983) showed that some wild mallard males were capable of pairing simultaneously with two females when males were removed from, and extra females released into, a local breeding population in Iowa. Bigamous behavior has also been documented in captives of three Southern Hemisphere *Anas* species (Cape teal *A. capensis*, white-cheeked pintail *A. bahamensis*, and speckled teal *A. flavirostris*) (Stolen and McKinney, 1983; McKinney and Bruggers, 1983; McKinney, 1985), and perhaps such behavior occurs at times in wild populations of these species where it is favored by local conditions. In some parts of their range these species may have extended and/or irregular breeding seasons that could produce unusual operational sex ratios. Some sedentary populations offer more opportunities for extrapair liaisons (e.g., African black ducks *A. sparsa*; McKinney et al., 1978), and some may nest in small colonies (e.g., speckled teal in nestholes of monk parakeets *Myopsitta monarca*; Weller, 1967) where the proximity of females could facilitate bigamy. These possibilities remain to be investigated in the field.

Therefore, male dabbling ducks can diverge from strict monogamy in at least three ways: by seeking forced extrapair copulations, by switching mates during a breeding season (serial monogamy), and by attempting to hold two mates simultaneously (bigamy). Forced copulations have been observed in many species and, at least in migratory species, this appears to be the main way in which paired males can supplement the reproductive effort they invest in their mates. However, promiscuous activities inevitably compete with mate-guarding and mate-support activities. The ways in which males resolve these conflicts can be instructive in revealing the importance of male mate-support roles in certain species.

THE TIMING OF PAIR FORMATION

In the Northern Hemisphere, pair formation in migratory dabbling ducks occurs during the fall, winter, and/or spring months while the birds are in flocks away from the breeding grounds. The chronology of pairing varies greatly among the seven best-studied North American species (Paulus, 1983; Hepp and Hair, 1983, 1984); for example, gadwall pair early in the winter (October-November) while green-winged teal delay pairing until February-March. This means that most pairs of these two species form eight and three months respectively before the next breeding season begins. Why does pairing occur so early?

Observations on courtship and pairing behavior in urban mallards (Weidmann, 1956; Leuret, 1961) and other *Anas* species (Johnsgard, 1960a, b, 1965; von de Wall, 1965; McKinney et al., 1978; Soutiere et al., 1972; Wishart, 1983a, b; Hepp and Hair, 1983) combined with analytical and experimental work with captives (Weidmann and Darley, 1971; McKinney, 1975; Laurie-Ahlberg and McKinney, 1979; Dervieux and Tamisier, 1979; Cheng et al., 1978, 1979; Standen, 1980; Bossema and Kruijt, 1982; Kruijt et al., 1982; D. M. Williams, 1982, 1983) indicate that pair formation includes the following steps:

1. Early in the pairing season, some individuals of both sexes show interest in one another by associating and performing displays (usually while swimming). Male attention-getting displays are highly directional, specifying a particular target female. Responsive females stimulate male courtship by giving calls and swimming jerkily (nod-swimming). "Social courtship" results when several males court one female. Courted females indicate preferences for certain males by swimming after them while threatening other males (a ritualized performance called "inciting"). A favored male responds by moving ahead of the female, showing her the back of his head as though "leading" her away from the group. Many early liaisons formed in this way are tentative and temporary, both sexes frequently switching attention to different individuals.

2. As the pairing season advances, some birds become firmly paired: mates are almost always together, their daily activities are synchronized, and both repel rival males. However, as the proportion of unpaired females in the population dwindles, courtship and competition among males increase in intensity. There is evidence for North American black ducks (Stotts and Davis, 1960), gadwall (Blohm, 1982), and American wigeon (Wishart, 1983b) that older males obtain mates earlier than yearlings.

3. When all females are paired, the remaining unpaired males continue to try to secure mates by courting paired females. Courtship and the testing of bonds continue during spring migration and after arrival on the breeding

grounds. Some unpaired males may eventually pair with reneating females whose pair bonds have already broken, but others remain unpaired (Humburg et al., 1978; Blohm, 1978).

As Lack (1968) pointed out, this pattern suggests that pairing early is advantageous for males because of the male-biased sex ratios in duck populations. Males that delay may fail to obtain a mate and forfeit an opportunity to breed that year. However, although competition between males for mates may be a key factor promoting male courtship during winter, bonds cannot form unless females respond. Are there advantages to females in pairing early?

A major consequence of pairing three to eight months before breeding begins is that individuals have a long time in which to test potential mates and make final decisions with care. Several studies indicate that males as well as females are selective in their choice of mate (reviewed by D. M. Williams, 1983). Males direct their courtship to specific females and females make their selection from those males that actively court them (Kruijt et al., 1982). Mate-choice experiments on captive mallards suggest that females favor high-ranking males with undamaged plumage (D. M. Williams, 1982, 1983).

There are several ways in which females could be assessing a male's competence as a breeding partner. Copulations occur during winter, starting months before males are producing sperm (Höhn, 1947). Although males may initiate precopulatory signals, females determine whether and when mounting will occur by assuming the prone posture. Therefore, females have the opportunity to test male competence in achieving intromission as part of the process of mate assessment. Wishart (1983a, b) suggests that female American wigeon are assessing males on the basis of their performance in mate-guarding and pair-bond maintenance during winter, because these characteristics are likely to reflect their efficiency as breeding partners. There is a rich field for further research on mate-selection processes in these ducks that form pairs away from the breeding grounds.

In addition to advantages of early pairing associated with mate choice, dabbling ducks may benefit from being paired while they are on the wintering grounds. The gadwall is one of the earliest species to pair (October-November) but one of the latest to begin breeding (May-June) and Paulus (1983) has suggested that early pairing is advantageous to individuals in enhancing their access to food resources on the wintering grounds. In contrast to most Northern Hemisphere *Anas*, gadwall feed primarily on leafy vegetation and algae, relatively poor quality foods requiring a high investment of time spent feeding (Paulus, 1982). Paulus (1983) has shown that paired birds dominate unpaired birds, giving the former greater access to preferred feeding areas. Unpaired male gadwall spent more time in locomotion than paired birds (Paulus, 1984), probably in part because of movements related

to food search. Hepp and Hair (1984) present further evidence that paired birds are dominant in wintering flocks of dabbling ducks.

Benefits of having paired status while on the wintering grounds are likely to be especially significant for females. The constant presence of a vigilant male escort can enhance a female's access to localized food sources (as in gadwall), protect her from disturbance by courting males, and give her warning of surprise attack by predators. Advantages of these kinds in enhancing the feeding efficiency of females have been demonstrated in a number of waterfowl but until very recently most attention has been given to the period of egg production in the case of dabbling ducks.

Excepting the gadwall discussed above, specific differences in pairing chronology among *Anas* species remain to be explained. A delay in pairing until later in winter could be related to age or body condition, as in the case of yearling males that weigh less and lag behind older individuals in assumption of breeding plumage (e.g., American wigeon; Wishart, 1983b). Also, energetic constraints related to body size, dietary needs, habitats, and climatic conditions could have important influences on pairing chronology. The costs of courtship and mate-guarding may be too high for some species during the early part of the winter (e.g., green-winged teal; Tarnisier, 1972). Cost-benefit analysis for different species is another fruitful field for future research.

In summary, males of migratory dabbling ducks are expected to benefit by securing a mate early in the pairing season because of male-biased sex ratios in wintering populations. Both sexes, but especially females, probably benefit from having several months in which to test prospective mates and make their final decisions on breeding partners. Females stand to benefit from having a mate while on the wintering grounds because the male's vigilance and protection allow her to feed more efficiently, and paired birds dominate single birds giving them greater access to preferred feeding sites. The pattern of pairing chronology observed in each species is likely to be influenced especially by energetic and social requirements associated with specific differences in feeding ecology and winter habitats. Within each species, key factors promoting pair formation are different for males and females. Although males compete, often strenuously, to monopolize individual females, females also play active roles in mate selection.

WHY DO MALES DESERT THEIR MATES AND PAIR ANEW EACH YEAR?

Advantages of retaining, or reuniting with, the same mate have been demonstrated in several long-lived bird species (reviewed by Rowley, 1983) and, in view of the benefits that dabbling ducks appear to derive from being

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paired, it is necessary to explain why a pattern of re-pairing each year has evolved in this group.

The annual breakup of pair bonds in migratory Northern Hemisphere species is well documented. In the fourteen holarctic species concerned, females are observed alone with their broods (Bellrose, 1976; Cramp and Simmons, 1977; Gilmer et al., 1977). Since males of many species leave the breeding grounds weeks ahead of brood-tending females, mates could repair only if individuals return to the same wintering areas. There is evidence that several sea ducks do renew their pair bonds in successive seasons by meeting on traditional wintering areas (Savard, 1985), but this has not been documented in dabbling ducks. One study of marked mallards demonstrated that mates can reunite (probably before leaving the breeding area) and return to breed in the same area in subsequent years (Dwyer et al., 1973), but this is thought to be a rare occurrence.

Several hypotheses have been proposed to account for male desertion. C. G. Sibley (1957) and Kear (1970) suggested that the male's presence may be disadvantageous in betraying the nest-site. At least for dabbling ducks, this is not a very convincing idea because males rarely go near the nest, and in any case it would not apply to such species as the northern shoveler in which males remain conspicuously on territory throughout incubation (Poston, 1974; Seymour, 1974). The possibility that males leave to reduce competition for food with the female and ducklings (Selander, 1966; Salomonsen, 1968) is difficult to envisage as a product of individual selection. Dabbling duck broods are highly mobile, their food resources are not usually economically defendable, and it is unlikely that an individual male's departure could benefit his own family in respect to the food available to them. Moreover, there is evidence that males of two species (blue-winged teal and northern shoveler) may not leave the breeding area after pair bonds break (McHenry, 1971; DuBow, 1985).

As pointed out by Bellrose et al. (1961), early departure from the breeding area has several potential advantages for males that are not open to brood-tending females. In particular, males have the option of moving to a molting site that provides a rich, assured food supply and greater safety from predators than they would have if they stayed on the breeding areas (Oring, 1964a, b; Salomonsen, 1968; Fredrickson and Drobney, 1979; Prince and Gordon, in press). Males can begin wing-molt a month or more before brood-tending females, which generally delay molt until the ducklings fledge (Oring, 1964a; Gilmer et al., 1977). Thus males have more time to recover from the energetic costs of renewing the flight feathers, to accumulate reserves for migration to the wintering areas, and (especially in species that pair early) to attain body condition that permits expenditure of time and energy in courtship and competition for mates.

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In summary, in Northern Hemisphere migratory species of dabbling ducks with short, regular breeding seasons pair bonds break annually because males desert their mates while the latter are incubating. Likely benefits of desertion for males are ability to move to favorable areas for the wing-molt, and early completion of the wing-molt in preparation for migration to the wintering areas and subsequent competition for mates for the next breeding season. Opportunities for mates to reunite for subsequent breeding seasons are limited because of early departure of males from the breeding grounds and presumed difficulties of finding old mates on wintering areas. In general, evidence on the ultimate factors causing male desertion and the rarity of re-pairing is circumstantial and further studies of marked pairs on the breeding grounds are needed.

WHY ARE SOME SPECIES TERRITORIAL?

Most dabbling ducks engage in aerial pursuits at certain stages of the breeding cycle. These pursuits are related to at least four different phenomena: pair formation, forced copulation, mate defense, and territory defense (Dzubin, 1969; Titman and Seymour, 1981; McKinney et al., 1983). Flights associated with pair formation and forced copulation usually involve several (or many) males pursuing a single female, but they can be distinguished by the behavior of the participants. If pair formation is the objective, the males give courtship calls and postures, and the flight proceeds at a leisurely pace; if the males' goal is forced copulation, they are silent, the pursuit is rapid, and the female makes energetic attempts to escape. Mate defense is indicated when chases are closely associated with rivalry between males for mates or copulations. Territory defense is indicated when a paired male chases conspecific pairs as well as single birds, if his pursuits are brief and he returns to his starting point, and if he initiates chases whether his mate is present or not.

Typically a territorial male's "waiting area" (Dzubin, 1955) (also called the "core area," Poston 1974 or "activity center," Dwyer, 1974) is on a wetland (a pond, cluster of ponds, or stretch of shoreline) where he waits for his mate while she is at the nest. Most of his pursuit flights start from here, but in highly territorial species encounters involving threatening and fighting also occur on boundary zones between neighboring territories.

The occurrence, degree, and duration of territorial aggression vary greatly among dabbling ducks and there are several hypotheses on the factors selecting for this behavior (reviewed by Wishart, 1983b). The main proposals are that territoriality a) ensures a male's exclusive access to his mate; b) ensures protection of a food source; or c) reduces nest predation. Underlying recent discussions of these ideas are the assumptions that territory defense entails costs and risks to males, that these are offset by benefits

to males, and that attention should be given to the economic defendability of resources crucial to reproduction (J. L. Brown, 1964; Davies, 1978).

There are two aspects to the idea that territoriality ensures a male's exclusive access to his mate. First, by defending a territory a male might be able to reduce the risk of other males copulating with his mate. By spreading out, breeding pairs tend to reduce the number of males in the vicinity of each female, and by driving out trespassing males each territory-owner could minimize the risk of being cuckolded. Male intolerance toward conspecific males during the prelaying, laying, and at least the early incubation phases have been noted in many *Anas* species, especially during the peak period of mate-guarding (e.g., Titman, 1983 for mallard). However, territorial males usually direct most of their pursuits at the females of intruding pairs, which suggests that the objective is to expel pairs (e.g., Dwyer, 1974 for gadwall).

Secondly, establishment of the male's "waiting area" as a rendezvous place to which his mate flies when she leaves the nest could be important in allowing the male to monitor the progress of his mate's nesting attempt. If the clutch is taken by predators, the male's continued use of the core area will favor maintenance of the pair bond for re-nest attempts. However, it seems that this result could be achieved by site tenacity without defense of the area.

If territoriality provides protection for food resources, the benefits are likely to be greatest for the female during egg production and, in some species, during incubation. In migratory species of *Anas* there is no evidence that food for the ducklings is important. Territories are not defended during the brood-rearing period and broods are so mobile that they often move away from the nesting territory.

In one species, the northern shoveler, territory defense usually continues throughout the incubation period (Seymour, 1974; Poston, 1974) and there is evidence that females are dependent on food obtained on the territory to enable them to survive. Afton (1979) has shown that females feed most of the time they are off the nest during incubation, the proportion of time spent feeding increases as incubation proceeds, and in one instance a female deserted her nest after her mate was killed, apparently because harassment by a new territorial male prevented her from feeding. Afton (1980) attributes the female shoveler's dependence on food resources during incubation to the small body size of this species. Male blue-winged teal (Stewart and Titman, 1980) and American wigeon (Wishart, 1983a, b) are also territorial late into incubation, apparently with similar benefits for females.

The view that the main function of the chasing activities of male dabbling ducks on the breeding grounds is to disperse nests and reduce the risk of predation on eggs was formerly widely held (Hammond and Mann, 1956; Tinbergen, 1957; R. I. Smith, 1968; McKinney, 1965). But this hypothesis has not been critically tested and recent studies suggest that high-quality

protective cover and security from mammalian predators are more important to females in influencing the choice of the site than is the distance from other duck nests. High densities of nests have been found on many predator-free islands (Duebber et al., 1983; Lokemoen et al., 1984) and by planting high-quality nesting cover and controlling predators Duebber and Lokemoen (1980) were able to produce high concentrations of nests on experimental plots in farmland areas. While chasing activities could be influencing nest dispersion under certain circumstances, the effects may be incidental. Perhaps male chases can be explained more simply in terms of mate-guarding and protection of a feeding area for the female rather than as products of selection for a nest-spacing mechanism.

Many factors probably influence the incidence and characteristics of territorial behavior in each species as well as the individual variations observed within species. Specific differences in body size, diet, and feeding methods must be of fundamental importance in determining the home range requirements of breeding birds (Nudds and Ankney, 1982). The spatial and temporal distribution of food resources and the stability of preferred wetland types evidently influence the mobility of breeding pairs and the defendability of feeding areas. For example, in the northern pintail, breeding pairs exploit dispersed and ephemeral wetlands and territoriality is probably not an option for such species (Derrickson, 1978). Within a species, males tend to hold their territories longer in the early part of the breeding season than they do late in the season (Bellrose, 1976). Presumably these variations result from individual decisions by males under the influence of conflicting interests and varying environmental conditions.

In summary, while male interests may be served directly in minimizing the risk of cuckoldry and in helping to maintain the pair bond for re-nest attempts, these benefits are insufficient to account for the behavior of the most highly territorial species. In the latter, territory defense is more likely an important component of indirect male parental investment through protection of a secure feeding area for the female during egg production and, to varying degrees, incubation.

DISCUSSION

The studies reviewed here have shown that for female dabbling ducks reproduction entails high risks of predation, high costs of egg production, and energetic stress during incubation. One important consequence, as Greenwood (1980, 1983) pointed out for Anatidae in general, is that return to a familiar breeding place has great advantages for females, and these advantages provide a convincing explanation for the occurrence of female philopatry in this group of birds. Another consequence, less widely recognized, is that female dabbling ducks receive support from their mates in the form of

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vigilance and protection from disturbance while they feed. Therefore, although males are emancipated from incubation, and in most species brood-rearing, their indirect parental investment may be crucial for female reproductive success.

The requirements of breeding females for male support appear to be key factors promoting primarily monogamous mating systems in dabbling ducks. In species where females require male protection during critical periods of the annual cycle (in wintering flocks, while producing eggs, during incubation), male contributions cannot be shared and polygyny is rarely an option open to males. Monogamy is also favored because of benefits to males associated with male-biased sex ratios. By maintaining a pair bond with a single female, a male can be assured of a breeding partner, and by attending her closely he can protect his genetic paternity. However, although the interests of females and males in maintaining exclusive pair bonds do coincide closely at certain times (notably during the female's fertile period while she is forming eggs) the female's requirements appear to be of primary importance in influencing the timing of pairing (e.g., in gadwall) and the duration of pair bonds and male territory defense (e.g., in northern shoveler).

In migratory dabbling ducks with short regular breeding seasons, the partitioning of the annual cycle into three distinct phases—breeding, molting, and wintering—has profound influences on relationships between males and females. Within each species, food and habitat requirements differ at each stage, and in some cases they are different for each sex. The resulting conflicts of interest between males and females are fundamental to the pattern of seasonal pair bonding in which each sex can influence the behavior of the other in various ways.

In winter, females are the limiting sex and they appear to be largely in control of the process of pairing. By their responses to male courtship and their expressions of mate preferences, they probably have the last word in deciding which male they will lead back to the breeding grounds. For males, courtship is not merely a matter of monopolizing one female by keeping other males away from her. They must also practice salesmanship to gain female acceptance through the vigor of their displays, the constancy of their attention, and the demonstration of their competence as effective escorts. There is no evidence that a male can force an unwilling female to pair with him.

After the pair arrives on the breeding grounds, the female remains largely in control of the activities of the pair during selection of the breeding area and nest-site. Male mate-guarding and enhancement of the female's feeding efficiency are especially important during the prelaying and laying phases. Once the female begins to incubate, her need for mate support may or may not persist. In some species females appear to be very dependent on it, but

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in others they seem able to do without it. In any event, this is the stage at which males can take the initiative in reducing their mate support, attempting forced copulations, and eventually deserting.

Unlike swans and geese, in which biparental brood care is the rule and families remain intact throughout the following winter, male dabbling ducks have the option of deserting their mates during the incubation period. It is possible that some bonds remain intact or re-form, especially in sedentary populations of certain tropical and Southern Hemisphere species, but in migratory species of *Anas*, male desertion seems to be usual. In view of the time and energy required to obtain mates and the probability that well-adjusted partners would benefit by maintaining their bonds from year to year, the occurrence of male desertion needs to be explained.

Two factors favoring male desertion in migratory dabbling ducks are: 1) absence of any further opportunities to breed during the current season and 2) advantages of proceeding with the molt. In Northern Hemisphere species with short breeding seasons, fertilizable females are no longer available after the last re-nest clutches are laid and unsuccessful females leave the breeding areas. At the same time, males may benefit in several ways by proceeding with the molt. In contrast to their mates, who must remain on the breeding area until their ducklings fledge, males may be able to move to a favorable molting site that provides greater safety and a more assured food supply than they would have by remaining on the breeding area. They can also save time by going into wing-molt early and building up their body condition in preparation for fall migration, the stresses of winter, and the costly process of competing for mates.

It is unfortunate that by labeling mating systems according to their basis in "resource-defense" or "mate-defense" many authors have decided to classify migratory dabbling ducks in the "mate-defense" category. This label can be misleading because it tends to imply that monogamy is imposed by males on females. In fact, the question of which sex "controls" these mating systems is not yet settled. Probably the manipulative power changes hands at certain key stages in the annual cycle, and even within the migratory *Anas* species there can be important differences between species.

SUMMARY

Evidence on the high costs of reproduction for females, male-biased sex ratios, competition among males for mates, advantages of early pairing, female philopatry, male mate-support, requirements of birds in wing-molt, and benefits of male desertion is substantial but the causal links between these phenomena are inferred rather than proven. If the interpretation proposed here is correct, however, it suggests that females have a controlling

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influence on pairing and on the behavior of males in the early part of the breeding season but as the female's need for male mate-support wanes, the male can determine if and when the bond is to be broken. Use of the term "mate-defense monogamy" in categorizing the mating system of this group should not carry the overly simple implication that monogamy is imposed on females by the monopolizing activities of males.