

CHAPTER 6

PRIMARY AND SECONDARY MALE REPRODUCTIVE STRATEGIES OF DABBLING DUCKS

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ABSTRACT.—Monogamy is the primary mating system in dabbling ducks. Paired males contribute to their mate's breeding effort by (a) protecting the female from predators and disturbance by rival males while she feeds intensively during the period of egg production (probably all *Anas* species), (b) defending a territory within which the female feeds (several species), (c) helping to care for the ducklings (certain southern hemisphere species). Paired males also engage in forced extra-pair copulations (recorded in 21 of 37 *Anas* species to date) and in some species these may be important secondary reproductive strategies. Polygamy does not occur in holarctic species, probably because each male is unable to monopolize more than one female in synchronously breeding populations with male-biased adult sex-ratios, but bigamous behavior has been observed in captives of three southern hemisphere species (Cape Teal, *A. capensis*; Speckled Teal, *A. flavirostris*; White-cheeked Pintail, *A. bahamensis*). Opportunities for males to hold two mates simultaneously may occur in wild populations of such species because extended and/or irregular breeding seasons are likely to produce asynchrony in the breeding and molt schedules of individuals.

INTRODUCTION

In birds with monogamous mating systems, paired individuals are generally considered to have very limited possibilities for increasing their reproductive success by activities unrelated to their pair-bonds. Some instances of intraspecific nest parasitism may prove to benefit paired females by supplementing the eggs they incubate themselves, but this phenomenon has not yet been well documented (Yom-Tov 1980). Opportunistic extra-pair copulations and occasional polygyny have been observed in many species (Gladstone 1979; Oring 1982; Ford 1983; McKinney et al. 1984), but cost-benefit analyses in terms of male fitness have not been made. The prediction by Trivers (1972)—that males of monogamous species can be expected to try to inseminate additional females, without aiding or monopolizing them, and that “mixed male reproductive strategies” will result—seems logical but is still largely untested. There is circumstantial evidence for such mixed strategies in several avian species (Beecher and Beecher 1979; Mineau and Cooke 1979; Fujioka and Yamagishi 1981) and comparative studies of waterfowl (Anatidae) have suggested factors that appear to favor or prohibit their use (McKinney et al. 1983). My purpose here is to review evidence for secondary reproductive strategies in one group of primarily monogamous waterfowl and to suggest some promising lines for future research on such variations on the monogamy theme.

The dabbling ducks (tribe Anatini) comprise one of the most familiar and widely studied groups of birds. As surface-feeding ducks, they feed primarily by dabbling, head-dipping, and up-ending in shallow water. Their food consists of aquatic plants and invertebrates, strained from the water by lamellae on the sides of the

bill. Fresh water is preferred, but some species use brackish lagoons and even sea shores. All spend time swimming but they walk well on land and come ashore to rest. Most nest-sites are on the ground in vegetation, but a few species use tree-holes. In all species incubation is by the female only. Usually ducklings are led, brooded, and protected by the female only, but the male helps in a few species.

The group has representatives on all continents except Antarctica. Most of the 37 living species (now usually placed in the single genus *Anas*) fall clearly into one of 7 sub-groups: mallards, wigams, green-winged teals, pintails, and blue-winged ducks, found in both northern and southern hemispheres; and austral teals and silver teals occurring only in the southern hemisphere. Many geographic races have been distinguished, including 20 forms endemic to islands (Weller 1980). Most species (26) breed primarily in temperate, subarctic or alpine zones, and many of these make extensive seasonal migrations. Of the remaining 11 species breeding in subtropical and/or tropical regions, many are sedentary, but two are nomadic.

With such a worldwide distribution, the members of the genus *Anas* are well suited for comparative, correlational studies involving factors dependent on latitude, geography, climate, and ecology. In this review I stress the importance of factors likely to influence the temporal availability of females, because this is especially relevant to secondary male strategies.

Although much information is available on diverse aspects of the biology of many dabbling ducks (Sowls 1955; Johnsgard 1965, 1978; Frith 1967; Bellrose 1976; Palmer 1976; Cramp and Simmons 1977; Bookhout 1979; Todd 1979; Weller 1980) data on mating systems based on study of wild, marked birds is lacking for most species. Almost all species (and many races) have been kept and bred in zoos and private collections, but few studies on captives have focused on the variations in monogamy that concern us here. The traditional view has been that dabbling ducks are monogamous and little attention has been paid to extra-pair-bond activities of males. Extra-pair copulations have been observed in 21 *Anas* species, but only a few of these species have been studied thoroughly enough to permit speculation on the probable significance of such copulations in enhancing male fitness (reviewed in detail by McKinney et al. 1983). Bigamous behavior has been observed in only three species (all captives) and, because these findings are new, most attention is given to this topic here.

SEASONAL MONOGAMY: THE BASIC *ANAS* MATING SYSTEM

In *Anas* species breeding in temperate and subarctic regions of the northern hemisphere, pair-bonds form on the wintering grounds, usually several months before breeding begins. Pairs migrate northward in spring, the female leading her mate back to the area where she bred in previous seasons. These pair-bonds break during the short breeding season (April–June), usually while the female is incubating. If early clutches are taken by predators, one or several replacement clutches may be laid. The same pair-bond may be retained for these re-nest attempts or mate-switches may occur. New pair-bonds form each winter and it is probably rare for individuals to breed together in successive seasons. Therefore, in these species the basic breeding system is seasonal monogamy and mate-choice has

nothing to do with territory quality. (For reviews of *Anas* breeding behavior see Weller 1964; McKinney 1975a.)

The process of pair formation has not been studied in marked individuals of any wild *Anas* populations, but there are many clues to the basic mechanisms from studies of individually marked captives (Weidmann 1956; Weidmann and Darley 1971; McKinney 1975b; Cheng et al. 1978, 1979; Laurie-Ahlberg and McKinney 1979; Standen 1980; Williams 1983) and from field observations on unmarked birds (Lebret 1961; Wishart 1983). Males intent on pairing approach females and direct courtship displays toward them. Females respond to such males by threatening them, by showing acceptance of them (by performing inciting displays beside them), or by various kinds of behavior that encourage male courtship (e.g., nod-swimming). The adult sex ratio in wintering populations is usually skewed in favor of males (Bellrose et al. 1961), so that competition is intense and some males fail to secure a mate. When a number of males direct courtship toward the same female, "social courtship" results. This usually occurs on water. As well as directing displays at the female and maneuvering to attract and hold her attention, males threaten one another and perform aggressive displays. Chasing and fighting tend to be infrequent, but subordinate males perform appeasement displays (e.g., nod-swim) that seem to enable them to remain in the competition.

The female makes her initial choice from among the males that court her and indicates her preference by performing inciting displays beside the chosen male and threatening other males. When given free choice, females exhibit clear preferences (Cheng et al. 1978) apparently based on behavioral and morphological features (Bossema and Kruijt 1982; Kruijt et al. 1982). Early bonds seem unstable and are likely to be contested by rival males. Switches occur, apparently as a result of the chosen male being displaced by a dominant male which is then accepted by the female. Disputes between well-matched males are settled by fighting.

Pair-bonds are presumably reinforced by displays, by copulations, and by collaboration by mates in rejecting advances of rival males. Males perform characteristic displays directed at the female when mates come together (e.g., belly-preen, preen-dorsal, preen-behind-wing, bridling, and lateral dabbling) and in some species the female may respond with similar displays (e.g., preen-behind-wing). Pair copulations, preceded by mutual head-pumping, occur during the winter several months before egg-laying begins. At this time (e.g., September in Mallards, *Anas platyrhynchos*), gonads are regressed and spermatogenesis is not occurring (Höhn 1947; Johnson 1961, 1966); so apparently these copulations are part of the mate-testing and/or pair-bond-maintaining processes. Mates give combined display performances during encounters with other pairs or with courting males. In some species similar displays are given by both sexes (e.g., rapid chin-lifting in wigeons); more commonly, the female performs inciting while the male adopts a threat posture or swims away (followed by the inciting female) giving turn-back-of-head.

In summary, *Anas* pair-bonding involves expression of individual preferences by males (directing displays at certain females) and females (inciting beside one of the courting males). Acceptance of the male by the female must play an important role in preserving the bond but, when challenged, the male must be able to drive away all rivals, if necessary by fighting. Wittenberger (1979) has termed

this type of mating system "female-defense monogamy," but the implication that males control the system by sequestering a female (Wittenberger and Tilson 1980) is misleading in neglecting the role of females in the process.

Pair-bonds of some tropical and southern hemisphere *Anas* species are suspected to be long-term rather than being formed anew each year (Weller 1968; Kear 1970; Siegfried 1974). Retention or reforming of old bonds may well be more feasible in sedentary populations than in migratory ones, and this tendency might also be favored by natural selection in species where mates cooperate in brood-care and/or where breeding seasons are irregular and of variable duration. Although there are a few records of prolonged bonds in Cape Teal (*A. capensis*; Siegfried et al. 1976) and African Black Duck (*A. sparsa*; McKinney et al. 1978) firm evidence on this point is scarce. I suspect that considerable variation exists in the length of pair-bonds in *Anas* populations with extended and/or irregular breeding seasons. Judging from the occurrence of courtship behavior before each breeding season and/or breeding attempt, bonds are frequently contested and mate-switches are probably common. This is quite different from the situation in swans, geese, and whistling ducks, where pair-bonds are characteristically long-term and often lifelong.

REVIEW OF MALE MATE-SUPPORT ROLES

Paired males appear to contribute to their mate's breeding effort in three ways: (a) by protecting the female directly (probably all *Anas* species), (b) by defending a territory within which the female feeds (several species), and (c) by helping to care for the ducklings (certain southern hemisphere species). Obviously these activities restrict males' abilities to exploit secondary mating options.

Protection of the mate.—Throughout the duration of the pair-bond the male associates closely with his mate most of the time (except when she is at the nest). From the male's point of view, close escorting of his mate is necessary if he is to minimize the chances of (a) losing his mate to another male or (b) having his mate inseminated by other males. The importance of the latter hazard is indicated by the especially close escorting and guarding of females by their mates during the period just before and during egg-laying. It is during this same period that females must increase their intake of invertebrate food for egg-production (Krapu 1979), which necessitates more time spent feeding (Dwyer 1975; Afton 1979; Stewart and Titman 1980; Titman 1981). Ashcroft (1976) has shown for Common Eiders (*Somateria mollissima*) that the vigilant behavior of the male allows the female to feed more efficiently, the male taking over the "lookout" role for both birds, and the same situation probably applies in dabbling ducks.

The role of male vigilance in protecting his mate from surprise attack by predators and from attempts by other males to force copulation is strongly indicated by observations on the behavior of pairs (Seymour and Titman 1978). Mates keep in close vocal contact with one another, giving very quiet calls as they move around together, loud contact calls when separated (decrescendo call, repeated calls). Females respond to alarm calls by their mates by stopping feeding and also becoming alert. Males also call to their mates while the latter are on their nests (Dwyer 1974). In some situations paired males crouch to avoid detection by flying males and move out of sight with the female.

Defense of a breeding territory.—Paired males of several *Anas* species defend stretches of water against intruding conspecifics for periods of about one week (Mallard; Dzubin 1969) up to several weeks (Northern Shoveler, *A. clypeata*; Poston 1969; Seymour 1974). Male Mallards hold territories at the beginning of the breeding season while their mates are in pre-laying and laying phases, but Shovelers continue to defend their territories throughout the incubation period. Provision of a secluded area, where females can feed efficiently while protected from interruption by their escorting mates, appears to be an important benefit of territoriality in the Northern Shoveler (McKinney 1973; Seymour 1974; Afton 1979) and probably in certain other territorial species (Gadwall, *A. strepera*; Dwyer 1974; Blue-winged Teal, *A. discors*; Stewart and Titman 1980).

African Black Duck pairs hold territories on rivers and in one study (Ball et al. 1978) territories were maintained throughout the year except for the period of wing-molt. In this case, the river territory could serve all needs of the pair (food for the pair and their ducklings, cover for nest-sites, and safe molting places). There was strong competition for mates and for territories, and only territory-owning pairs bred. Other species living on rivers (Salvadori's Duck, *A. waigiuiensis*; Kear 1975) or shorelines (Crested Duck, *A. specularioides*; Weller 1972) hold similar all-purpose territories. Probably this system is favored in primarily insectivorous species by the need to control an exclusive area that will ensure an adequate food supply for the young in addition to other benefits.

White-cheeked Pintails (*A. bahamensis*) behave territorially, both in the wild and in flight pens, but male intolerance appears to be associated especially with defense of the mate against rival males and it is not clear if territories are important for female feeding seclusion (McKinney and Bruggers 1983). Other *Anas* species are known to be territorial (Brown Teal, *A. aucklandica chlorotis*; Hayes 1981; pers. obs.) but have not been studied intensively.

Some *Anas* species do not establish breeding territories. This is the case in the Northern Pintail (*A. acuta*), a species with large breeding pair ranges that may be economically undefendable (Derrickson 1978). Similarly, Green-winged Teal (*A. crecca*) and Red-billed Pintail (*A. erythrorhyncha*) are non-territorial (McKinney and Stolen 1982; pers. obs. on wild birds). Flight pen observations suggest that the same is true in Speckled Teal (*A. flavirostris*) and Brown Pintail (*A. georgica*).

Assistance in care of ducklings.—Males of all holarctic *Anas* species desert their mates before (or occasionally shortly after) the ducklings hatch and move to safe areas where they undergo the wing-molt. In the southern hemisphere, broods of many species are observed with two adults in attendance and in some cases males appear to assist their mates in protecting their offspring. However, for most southern species, documentation of male brood care in wild broods is poor because (a) the sex of the adults could not be determined (most of these species are monomorphic), (b) it was not known if the second adult was the female's mate, and/or (c) behavioral observations were not made. In some cases, records for broods raised in captivity confirm field reports of biparental attendance but descriptions of behavior observed are scarce.

Based on the fragmentary evidence available, brood care patterns in southern hemisphere species appear to be of three types: (a) male usually present and apparently contributes to protection of ducklings, (b) male usually not present, and (c) male sometimes present (Table 1).

TABLE 1
EVIDENCE ON PARENTAL ROLES IN BROOD-CARE IN SOUTHERN HEMISPHERE *Anas*

Brood-care categories	Number of wild broods seen with		Category based on captives	Reference no.	
	2 adults	1 adult		wild	captives
A. Biparental care usual					
<i>sibilatrix</i>	4		A	1	2, 4
<i>capensis</i>	96	10	A	3, 4	4
<i>specularioides</i>	11		A	1	2
<i>castanea</i>	3		A	4	2
	>50%			5, 6	
<i>aucklandica chlorotis</i>	1		A	4	4, 10
B. Male's presence and/or care variable or uncertain					
<i>flavirostris</i>	3	2	B	1	4
<i>gibberifrons gracilis</i>		usual	A	5	2
<i>a. aucklandica</i>		?		7	
<i>g. georgica</i>	4	1		8, 15	
<i>georgica spinicauda</i>	1		B	1	4
<i>b. bahamensis</i>	5		B	9	4
<i>bahamensis galapagensis</i>		a few		10	
<i>erythrorhyncha</i>	24	55	B	3	4
<i>specularis</i>			A		11
<i>versicolor</i>	occurs		A	12	11, 15
<i>waigiuenis</i>	presumed		A	10	
C. Brood care by female only					
<i>sparsa</i>	4	33		3, 13	
<i>s. superciliosa</i>		usual		10, 4	
<i>u. undulata</i>	14	284		3	
<i>hottentota</i>	2	17	A	3	11
		usual		14	
<i>smithii</i>	33	225		3	
<i>rhynchosotis</i>		usual		5	

Reference numbers: 1. Weller 1975a; 2. Kear 1970; 3. Siegfried 1974; 4. McKinney, unpublished; 5. Frith 1967; 6. F. I. Norman, pers. comm.; 7. Weller 1975b; 8. Weller 1975c; 9. McKinney and Bruggers 1983; 10. Johnsgard 1978; 11. M. Ounsted, pers. comm.; 12. Weller 1967; 13. McKinney et al. 1978; 14. Clark 1969; 15. Todd 1979.

I have observed wild broods of Cape Teal, Chestnut Teal (*A. castanea*), and Brown Teal and noted several kinds of male care. In all cases, males were extremely watchful and alert for predators, spending most of the time in head-erect postures while the ducklings fed. Male Chestnut Teal also gave warning calls, escorted lagging ducklings, and attacked hovering birds of prey. Male Crested Ducks, Bronze-winged Ducks (*A. specularis*), and Chiloe Wigeon (*A. sibilatrix*) are noted for their attentiveness to broods, and probably they provide similar kinds of protection. Most of these species have not been intensively studied in the field, and it is not known whether broods are especially vulnerable to predation. In the Cape Teal, this seems likely to be the case, because open habitats devoid of emergent cover are commonly used.

Two parents are not usually seen with broods of African Black Duck, African Yellowbill (*A. undulata*), Hottentot Teal (*A. hottentota*), Cape Shoveler (*A. smithii*), and Australasian Shoveler (*A. rhynchosotis*). In two marked pairs of African Black Ducks, the female alone led their ducklings all day. At night, however, they joined the male at favored roosting places on their river territories, and it is possible that males help protect their broods from nocturnal predators.

In five southern species (Speckled Teal, Brown Pintail, White-checked Pintail,

Red-billed Pintail, and Grey Teal, *A. gibberifrons*) the relationship of males to their broods is poorly understood. Some broods are accompanied by two adults, others by just one. In some cases observers disagree on which is the typical pattern for the species. Active participation by males in care of ducklings has not been described. No intensive studies of wild broods have been made, but I have watched captives of the first four species and noted less interest by escorting males in the ducklings than was typical in Chestnut Teal and Cape Teal.

Three factors might contribute to the impression of "partial male attendance" in these species. First, the need for male participation in brood care could vary in different parts of the species' range (e.g., in relation to availability of escape cover or predator densities). Second, the accompanying male may be interested primarily in the female rather than the brood (e.g., maintaining his pair-bond for future breeding attempts, as suggested by Siegfried 1974). Third, males might be adopting a bet-hedging strategy, either escorting their broods (mate-holding and/or protecting ducklings) or deserting for an alternate mate when circumstances favor it.

BENEFITS OF MONOGAMY TO MALES AND FEMALES

By pairing with a single female, a male can protect his genetic paternity and minimize the risk of cuckoldry. The importance of this factor in dabbling ducks is shown by (a) the increased vigilance of males while their females are fertile and (b) active defense of the female against males attempting to force copulation (p. 76). A male also stands to enhance his own reproductive success by providing vigilance, warning, and defense for his mate. Male vigilance during the fertile period is probably universal in *Anas*, but thereafter desertion of the female may occur at various stages (e.g., early, middle, or late incubation in holarctic species).

Females stand to benefit in various ways from having a male escort (protection from harassing males and predators), but the extent to which males contribute to their mate's breeding efforts is likely to change during the course of the breeding season. Anderson (1984a) has measured such changes in the Canvasback (*Aythya valisineria*), and there are probably many parallels with dabbling ducks. The interests of males and females are likely to coincide in promoting strong mate-defense by males during the pre-laying and laying phases. For males this is the crucial time for protection of paternal investment; for females it is a risky time when nest-sites are being selected, and when intensive feeding is needed to produce eggs. Later, during the incubation period, males are likely to have conflicts of interest. If the male remains in close contact with the incubating female, he will be in a good position to fertilize the eggs in her re-nest clutches, if these are required. On the other hand, the payoff may be greater if he deserts his mate and proceeds to a molting site in preparation for the wing-molt (e.g., if the earliest males to molt have advantages in successful migration, wintering or pairing). Alternatively, males may have opportunities to engage in secondary reproductive strategies. In regions where breeding is possible over an extended period, males may be better off staying with the same female throughout the brood-rearing period and keeping the same mate for subsequent breeding attempts. Here again, the interests of both partners (though not identical) may lead to persistence of the bond.

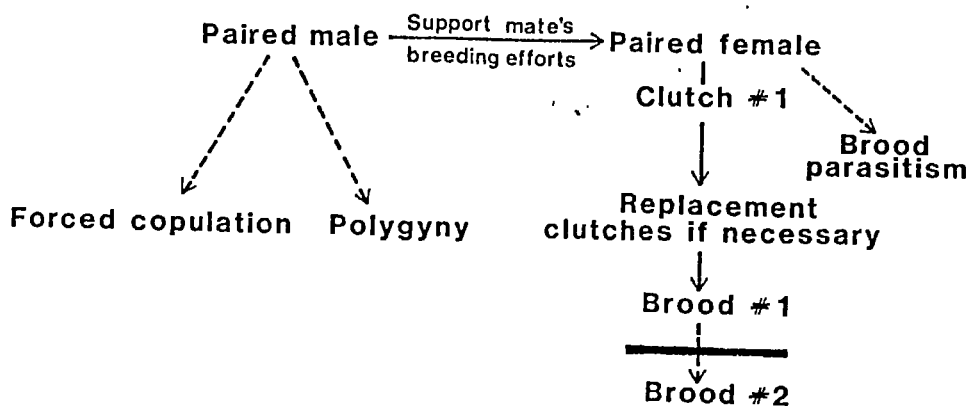


FIG. 1. Primary (solid lines) and secondary (dashed lines) breeding options theoretically available to *Anas* species. Two broods require a lengthy breeding season usually impossible in holarctic species.

SECONDARY REPRODUCTIVE STRATEGIES COMBINED WITH MONOGAMY

In addition to collaborating with their mating partners in jointly raising ducklings, both male and female dabbling ducks have other reproductive options (Fig. 1). For females, the major option would seem to be brood parasitism, laying in the nests of other birds. Although both inter- and intraspecific brood parasitism occur in a number of waterfowl (Weller 1959; Payne 1977; Yom-Tov 1980), this behavior appears to be rare in most species of dabbling ducks. Most *Anas* species place their nests on the ground, in vegetation, often far from water, and nests tend to be widely dispersed. Brood parasitism is common in waterfowl that nest over water (pochards, stiff-tails) or in tree-holes (perching ducks, whistling ducks), presumably because nests are more concentrated and easily located. Among dabbling ducks, it may be common only in a few species that frequently use tree-holes as nest-sites (e.g., Chestnut Teal; Norman 1982).

In most parts of the northern hemisphere, there is not sufficient time for female dabbling ducks to rear two broods each year and the annual cycle of these species is geared at most to producing several replacement clutches and rearing a single brood. In many tropical and southern hemisphere species, breeding can occur over a much longer period and double-broodedness seems to occur when conditions are favorable (Braithwaite, 1976b).

For males two possibilities exist for secondary reproductive strategies: extra-pair copulation and polygyny.

Forced copulation. — Dabbling ducks are well known for the occurrence of forced copulation (FC). Males vigorously chase females in aerial pursuits, females are overpowered and mounted (on land or water) and, especially when many males participate, the female's mate may be unable to prevent forced insemination. FC has been recorded in 21 *Anas* species, and probably it occurs in all but a few members of the group. (The only species in which it has been looked for and *not* found is the African Black Duck.) Evidence indicating that FC is a secondary reproductive strategy of paired males in certain *Anas* species has been reviewed in detail elsewhere (McKinney et al. 1983) and will be summarized only briefly here. The key points are:

1. Eggs can be fertilized by insemination during FC (Burns et al. 1980).
2. In all species studied intensively, FCs are performed primarily by paired males; unpaired males court females and try to obtain mates.
3. In the best studied holarctic species, FCs occur during the period when eggs are being fertilized, and in captive Mallards FC attempts were directed primarily at females in pre-laying and laying condition (Cheng et al. 1982).
4. Paired males usually defend their mates by attacking males that attempt FC.
5. Paired males may force copulation with their own mates. This often occurs shortly after their mates have been subjected to FC, suggesting an antidote insemination strategy.
6. Experiments using artificial insemination and genetic plumage markers in Mallards have shown that (a) the second of two competing inseminations 6 h apart overlays the former insemination and is 70% more potent, (2) there is an insemination "window" within 1 h of oviposition when the next egg in the clutch is fertilized (Cheng et al. 1983). The extent to which males time their copulations to take advantage of these temporal factors influencing sperm competition is not known.

The proportion of eggs in wild clutches that are fertilized by males other than the female's mate has not been determined for any *Anas* species. Also, judging from the frequency with which it is observed, FC is probably more important as an insemination technique in some species (Mallard, Northern Pintail) than in others (Northern Shoveler). In species such as the Northern Pintail, paired males undoubtedly spend time and energy seeking FC opportunities, and the concept of a "mixed male strategy" (Trivers 1972) is appropriate. In species such as the Northern Shoveler, where males defend a breeding territory and spend most of their time guarding it, FC is probably an option that males exploit only occasionally when the opportunity presents itself.

Polygyny. — There appears to be no firm evidence that polygyny occurs in wild populations of any holarctic *Anas* species, although successive monogamy can occur within one season (Humburg et al. 1978) and instances of bigamy have occurred when sex-ratios were experimentally altered in favor of females (Ohde et al. 1983). Typically these species have skewed sex-ratios, with a preponderance of males (Bellrose et al. 1961) and it is unlikely that a male could hold more than one mate at a time in unmanipulated populations. Recently, however, we have observed instances of bigamy in three southern hemisphere species under flight pen conditions. No such behavior occurred in three holarctic species (Mallard, Northern Shoveler, Green-winged Teal) breeding in the same pens in other years.

Bigamous relationships developed in 1981 and 1982 in groups of three pairs of Speckled Teal in a flight pen (27.5 m × 55.0 m × 3.6 m high). These birds were bred from stock obtained from aviculturists in the USA and they appeared to be typical representatives of the Chilean race (*Anas f. flavirostris*). The same male was involved in both years, but the females were different. The events were carefully documented in 1982 (Fig. 2).

During May and early June, male W was strongly paired to female W (as were the Y and R pairs). Pair W copulated regularly and male W also made many FC attempts on female Y, which was in wing-molt much of this time and especially vulnerable. On 19 June male W suddenly broke up the Y pair by dominating

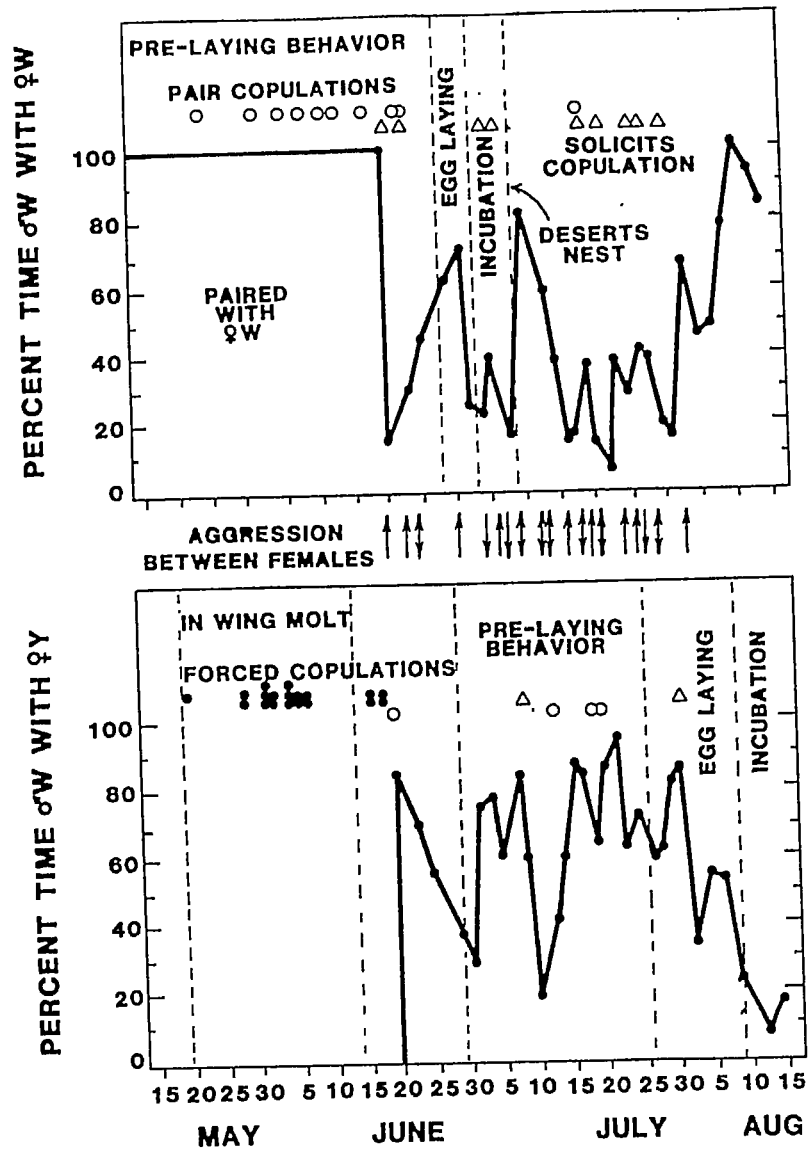


FIG. 2. Bigamous behavior of captive Speckled Teal male W with primary female W (above) and secondary female Y (below) in 1982. ● forced copulation attempts; △ pair copulations initiated by female; ○ pair copulations, initiator uncertain.

male Y and keeping him away from female Y. Female Y accepted male W as a mate and they were seen to perform a pair copulation. (Pair copulations are preceded by pre-copulatory displays and occur only when the female is willing.) On subsequent days, male W divided his time between the two females, repeatedly driving off male Y whenever he came close to female Y. Male W succeeded in maintaining this bigamous relationship for almost two months.

The proportion of time male W spent with each female changed at various times during the study period. He spent more time with female W while she was

egg-laying, less time with her when she began to incubate, and again more time with her when she deserted her nest. Conversely, male W spent more time with female Y while she was in pre-laying and early laying phases, and less when she was incubating.

The two females showed frequent hostility toward one another, threatening, chasing, and at times fighting. Each female tried to monopolize male W, actively following him and inciting beside him. During periods when female W was being neglected, she initiated pre-copulatory behavior and actively solicited copulation from male W. Similar solicitation was also noted by female Y on two occasions; in both cases, this happened on days when male W was showing renewed interest in female W. We interpret this behavior as a mate-holding tactic. This is supported by the fact that female W gave such solicitations during her incubation period, a time when females are not expected to show any interest in copulation.

Very similar sequences of events occurred in cases of bigamy observed in Cape Teal (3 pairs of wild-caught birds in a flight pen measuring 27.5 m × 27.5 m × 3.6 m) (Stolen and McKinney 1983) and White-cheeked Pintail (3 pairs, probably the Caribbean race *A. b. bahamensis*, in the same pen as the Speckled Teal study) (McKinney and Bruggers 1983). In all cases, a paired male suddenly switched from making FC attempts on a second paired female to courting her and dominating her mate. Copulation solicitation and rivalry between females similar to that observed in Speckled Teal occurred in the Cape Teal.

These three species differ from holarctic dabbling ducks in having extended breeding seasons. Both in the wild and in captivity Cape Teal engage in year-round courtship (Johnsgard 1965; pers. obs.), and in many parts of the range breeding is irregular in response to unpredictable rains (Siegfried 1974; Winterbottom 1974; Dean 1978). Speckled Teal also have year-round courtship (von de Wall 1965; Standen 1976), and at least in parts of their range the breeding season is extended and possibly two broods are reared (Johnson 1965). In the southern Bahamas White-cheeked Pintails breed over a long period (McKinney and Bruggers 1983).

With extended and/or irregular breeding seasons, multiple broods are possible, and pronounced asynchrony in the reproductive condition of individuals within local populations is likely. A factor that could be very important here is the timing of the wing-molt. Flight feathers need to be replaced about once per year and waterfowl achieve this by a simultaneous molt after which flight is impossible for 3 or 4 weeks. In species with regular annual cycles the wing-molt occurs immediately after the breeding season (Bellrose 1976; Cramp and Simmons 1977) but with extended and/or irregular breeding seasons some individuals may be flightless while others are breeding (Braithwaite 1976b; Dean 1978). In some species, parents can become flightless while brood-rearing (e.g., Cape Teal; pers. obs.), but otherwise the wing-molt is temporally separated from breeding activities and flightless females offer no immediate reproductive possibilities for males.

No field studies have been made on Cape Teal, Speckled Teal, or White-cheeked Pintail with the objective of relating breeding seasons, gonad condition, and the timing of wing-molts. However, the studies by Frith (1959), Braithwaite and Frith (1969) and Braithwaite (1976a, b) provide such information for four Australasian *Anas* species. Chestnut Teal, Australasian Shoveler, and Australasian Black Duck

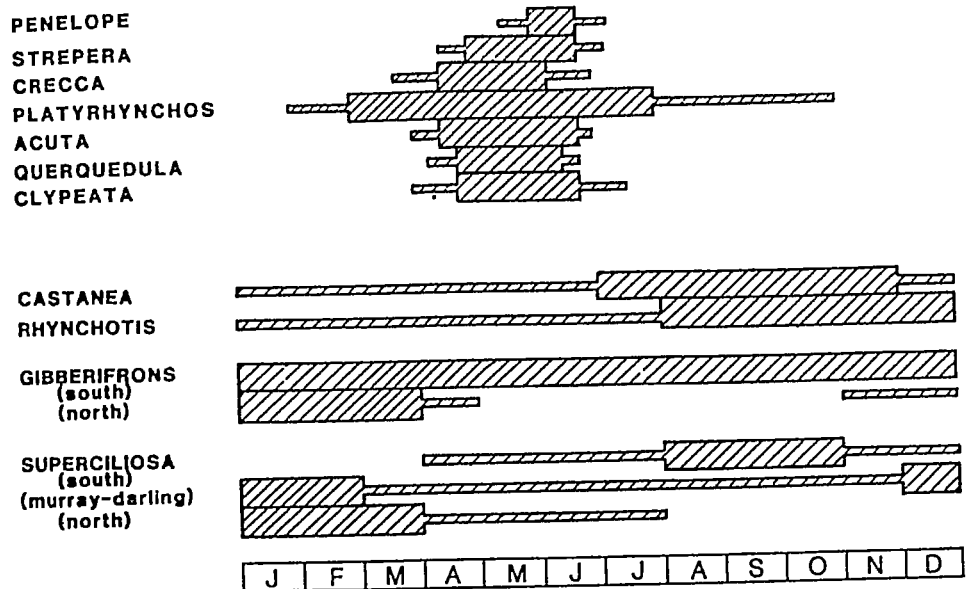


FIG. 3. Egg-laying seasons of seven holarctic and four Australasian *Anas* species (from Cramp and Simmons 1977; Braithwaite 1976a).

(*A. superciliosa*) tend to have regular annual breeding seasons, but Grey Teal breed at any time of year when conditions are favorable (Fig. 3). In all four species, breeding may be inhibited during periods of drought, and there are regional variations within species in the months when most breeding can be expected. The Grey Teal is an ecological counterpart of the Cape Teal in Africa, both being adapted to arid country through nomadism and irregular breeding. Braithwaite (1976a, b) has shown that the gonad cycle of Grey Teal is largely under environmental control (rather than photoperiodic and endogenous as in regular, annual breeders), and both sexes are capable of rapid gonad growth in response to rainfall, rising water levels, and the associated flush of aquatic food. If conditions remain favorable, some birds can raise two broods before molting. Therefore, in Grey Teal populations there is likely to be more marked asynchrony in the timing of breeding and molting than occurs in holarctic species with a short, regular, annual breeding season followed by a regular post-breeding molt (Fig. 3).

In addition to the wing-molt period, *Anas* females are "unavailable" for fertilization by males while they are incubating and brood-rearing, but females may be able to begin egg production again shortly after losing a clutch or brood. Therefore, at any one time, in a species with extended breeding seasons, a local population (e.g., of Grey Teal) might include some females that are fertilizable (pre-laying, laying or in the reneest interval) and others that are not (incubating, brood-tending, post-breeding, molting). This could produce wide variation in operational sex-ratios (i.e., "the average ratio of fertilizable females to sexually active males at any given time": Emlen and Oring 1977) and males are likely to have more varied options than are open to males of holarctic species (Fig. 4).

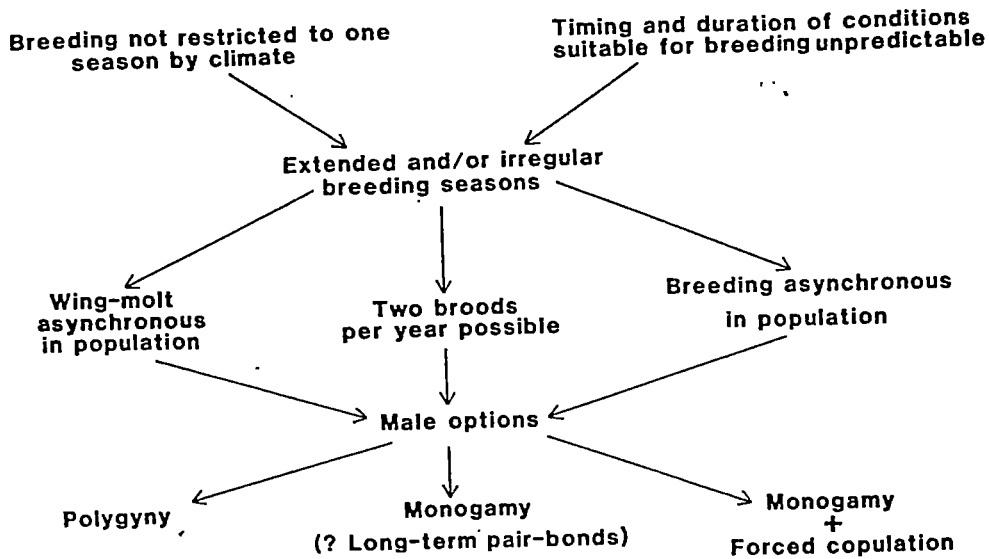


FIG. 4. Predicted male breeding options in southern hemisphere *Anas* species.

I believe that the bigamous tendencies shown by our captive Cape Teal, Speckled Teal, and White-cheeked Pintails reflect bet-hedging strategies in males of these species. For example, a male might be able to take a second mate while his first is incubating. If his primary mate succeeds in bringing off a brood, he may return to her and assist in brood-care. If the primary mate loses her clutch or brood and does not initiate another breeding attempt promptly, the male could switch to a second mate if the latter is close to egg-laying condition. Females are especially vulnerable to desertion while in wing-molt, but then so are males. African Black Ducks associate with partners other than their mates while the latter are molting and such liaisons could lead to mate-switches (McKinney et al. 1978).

Little is known about sex-ratios in southern hemisphere dabbling ducks. Data for adults and juveniles of African Yellowbill and Red-billed Teal in birds trapped for banding (Dean and Skead 1977) and for Grey Teal, Australasian Black Duck, and Australasian Shoveler from hunters' bags (Braithwaite and Norman 1974, 1976, 1977) are either skewed in favor of males (similar to ratios in northern hemisphere species) or show no significant difference. However, these findings may have little relevance to the operational sex-ratio. It is the availability of fertilizable females at different stages in the breeding season that is expected to influence the potential for polygyny.

The important influence that degree of synchrony among the individuals in a breeding population is likely to have on mating systems is now widely recognized (Maynard Smith 1977) but few studies have documented such effects (Wunderle 1984). As Wells (1977) has pointed out, in regard to anuran amphibia, it is essential to distinguish between the "breeding season" of a species, the "breeding period" of local populations, and the "breeding histories" of individuals. To understand the mating system, we need to focus on individuals and their reproductive efforts over their lifetimes. Intensive studies of marked birds are required to assess

whether multiple mates are economically defensible (i.e., the "environmental potential for polygyny": Emlen and Oring 1977) and to determine the extent to which individual males can exploit this potential.

COMPARISON WITH OTHER AVIAN MATING SYSTEMS

Female-defense polygyny appears to be a relatively rare type of mating system in birds (Oring 1982). It is known in rheas, tinamous, and some pheasants, but in various ways all of these are different from what we have observed in *Anas*. Emlen and Oring (1977) expect female-defense polygyny to evolve when females clump for reasons other than reproduction (e.g., safety, localized resources) and the females in a harem are expected to cooperate. It is possible that an element of "resource-defense" is involved in some *Anas* species. For example, Speckled Teal are reported to use cavities in nests of the Monk Parakeet (*Myiopsitta monachus*) as nest-holes in eastern Argentina (Weller 1967), and this could produce clumping that would allow a male to maintain bonds with two or more females simultaneously. Cape Teal nest on the ground but may prefer nesting on islands (Winterbottom 1974), which could result in similar clumping of females. Nothing is known about patterns of nest dispersion in wild White-cheeked Pintails.

Among other waterfowl, polygynous behavior has been described in one population of the Comb Duck (*Sarkidiornis melanotos*), a member of the perching duck group (tribe Cairinini) with races in tropical Africa and South America. Siegfried (1979) observed males of the African race defending territories, advertising for mates from tree-top perches, and holding harems of up to four females. Females nest in tree-holes and Siegfried suggests that the distribution of suitable cavities is important in attracting females to certain territories. He observed males competing for females, and females competed with each other for cavities. Unmated males apparently clustered around harems and tried to court or make FC attempts on females in the harem.

Possibly other members of the perching duck group also have polygynous systems. All are hole-nesters, which could produce clumping of females, and most are tropical and have extended breeding seasons.

Forced copulation is apparently a widespread phenomenon, not only in *Anas* but also in other waterfowl tribes. In certain holarctic species it appears to be a secondary male insemination strategy but our observations on bigamy in three southern hemisphere species suggest that in addition to an insemination function, males might be using FC to establish relationships with females as a prelude to taking them as secondary mates. On the other hand, Siegfried's (1979) description of FC activities in Comb Ducks suggests that an "alternative mating strategy" (Dawkins 1980; Rubenstein 1980) might be involved here, subordinate unpaired males adopting a sneaking strategy. Studies of marked birds in the wild are needed to establish whether this is the case.

CONCLUSIONS

1. Monogamy is the primary mating system in holarctic dabbling ducks probably because each male is unable to monopolize more than one female in synchronously breeding populations with adult sex-ratios skewed in favor of males.

2. The environmental potential for polygyny (EPP) is expected to be relatively higher in many southern hemisphere *Anas* populations, which have extended breeding seasons and asynchrony in breeding and wing molt.
3. Bigamous tendencies observed in males of three southern hemisphere species in captivity suggest that males of these species can exploit this EPP.
4. The behavior of female Cape Teal and Speckled Teal involved in bigamous relationships indicate strong rivalry for monopolization of the male, and suggest a competitive female-defense polygyny system.
5. Forced copulation appears to be the only secondary reproductive strategy available to males of holarctic species; in southern hemisphere species FC can occur as well as polygyny and the two options may be intimately related.
6. Field studies on marked birds of southern hemisphere species are needed to test these ideas.

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