Brood care, pair bonds and plumage in southern African Anatini

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In the Holarctic, migrant species of sexually dimorphic Anatini have a bond between male and female breeders that is seasonal only and breaks soon after egg-laying. The male usually deserts his mate and joins other males while undergoing the post-breeding moult. Reports of males of North American ducks accompanying their females with broods are regarded as rare exceptions (Oring, 1964).

According to Kear (1970), pair bonds are of relatively long duration in certain species of sexually monomorphic Anatini, and probably also in a number of near-tropical ones. Weller (1968) noted that those Argentinian species which retain a long pair bond are those in which males commonly attend the broods. A related general comment is that males of monomorphic southern hemisphere anatines regularly accompany their females with broods. However, there is no published account providing quantitative, comparative data on this phenomenon.

This paper summarizes unpublished records and appraises the significance of males accompanying females with their broods in six species of southern African Anatini, viz, African Black Duck Anas sparsa, Cape Teal A. capensis, African Yellowbill A. undulata, Red-billed Teal A. erythrorhyncha, Hottentot Teal A. punctata and Cape Shoveler A. smithii. For these species, there are 360 brood records on file with the African Wildfowl Enquiry. In addition to these data, my own observations cover 435 broods recorded over the last 15 years. The records derive from all parts of southern Africa, taken here as the entire sub-continent south of about 15°S.

The brood records were analysed according to number and age of ducklings, the presence of one or two accompanying adults, and in relation to place and time of breeding (Table 1). Presumably some of the records of two adults in attendance could apply to two females and not necessarily male and female, since in five of the six species only an expert can tell the sexes apart in the field. However, my own records indicate that the incidence of two females accompanying the same brood is rare, and that it is quite in order to regard the two attending adults as male and female parents.

Brood care

It is clear from Table 1 that in the Cape Teal both parents almost invariably accompany their young, and that the male normally remains with the female and the ducklings until they reach flying age. How much longer the pair and parent-young bonds may persist is not known.

The African Black Duck is the only other species, of the five remaining here, in which males have been observed accompanying females with well-grown young. However, the evidence for this is ambiguous, due to the

Table 1. Incidence of male and female parents accompanying broods. Figures in parentheses represent numbers of broods accompanied by both parents, other figures refer to broods accompanied by females only

Species	No. broods and age (in weeks) of ducklings				Total no.
	0–1	1-3	3-5	5-7	broods observed
A. sparsa	11 (2)	9	7	6 (2)	33 (4)
A. capensis	3 (40)	4 (28)	$\frac{1}{(15)}$	2 (13)	10 (96)
A. undulata	98 (10)	89 (4)	57	40	284 (14)
A. erythrorhyncha	18	19	11	7	(24)
A. punctata	(8) 5	(11) 5	(5) 5	2	17
A. smithii	(1) 86	(1) 66	46	27	(2) 225
	(21)	(8)	(4)		(33)

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species' secretive habits, its localized and 'difficult' habitat, and other factors which are responsible for a general paucity of observations and unsatisfactory, incomplete records (Siegfried, 1968). Current work, involving individually marked wild birds, indicates that the African Black Duck has a long-standing or permanent pair bond. It is probable (Siegfried, 1968), that the males temporarily desert their mates with young broods, but remain in the same general area (the permanent home range of the pair) and later rejoin the female.

There is one record of a Cape Teal male moulting wing feathers while accompanying a female with a brood. There are no observations of brood-accompanying males directly helping to care for the young. There are isolated records of brood-accompanying males driving off conspecific males in the Red-billed Teal and the Cape Shoveler, but this behaviour has not been observed in the African Yellowbill and Hottentot Teal. In the Cape Teal brood-accompanying males frequently drive away other males. However, the male's aggressiveness is usually associated with Inciting by the brood female and thus appears to be an expression of sexual behaviour rather than defence of the young. Such parental behaviour as brooding, distraction display, active defence of young and leading them to safety are performed solely by the female. Thus, males which accompany females with broods apparently do so as an extension of the pair bond through the attraction provided by the female, and the presence of the brood itself exerts no extra inducement. Of course the male's attendance could still promote survival of the young through enhanced predator detection.

The Cape Shoveler, Hottentot Teal and African Yellowbill males do not regularly accompany their mates with broods. The Red-billed Teal occupies a position intermediate between these three species and the Cape Teal. In the African Yellowbill and to a greater extent in the Cape Shoveler it is evident that some males do continue, for a limited time, to associate with their mates while their ducklings are young; the incidence of this behaviour appears to be more frequent in these species than in their North American counterparts, the Mallard *A. platyrhynchos* and Northern Shoveler *A. clypeata* (cf. Oring, 1964).

In the Red-billed Teal and Cape Shoveler (the two species with sufficient data for comparison) the parental male's presence appears to be of no advantage to the size of the brood (Table 2); which tends to bear out the contention that in these species selection for the

Table 2.	Mean brood size in relation to age and parental accompaniment. Figures
	in parentheses represent broods
	accompanied by both parents, other
	figures refer to broods accompanied by
	females only. Sample sizes are given in
	Table 1

Species	Mean brood size in relation to age (in weeks)			
	0-1	1-3		
A. erythrorhyncha	7·16 (7·12)	6·42 (5·10)		
A. smithii	7·00 (6·72)	5·12 (4·42)		

male's attendance has operated mainly for reasons other than increased survival and success of the brood *per se*. Broods hatched early in the season were no more often attended by males than late-hatched ones, but this conclusion is based on inadequate data. The data were insufficient to compare the incidence of male attendance in different geographical areas of breeding. Such comparisons, particularly in the Red-billed Teal, might contribute much towards understanding how and why the male's behaviour varies.

Ecological synopsis

Before exploring whether relationships between parent and young can be correlated with morphological and behavioural characters of the various species, it is necessary to report certain ecological features of fundamental importance as selective pressures shaping the species. Synoptical accounts are set out below, based on personal observations supplemented by information taken from the literature. They are substantially correct in outlining the generalized condition applicable to each species, and should be regarded as no more than that. The accounts are compiled from (a) data collected in those parts of the natural range of a species in which it is most numerous, and (b) from populations which are not, or very little, affected by man-made changes to the environment. The main artificial factor, which has a considerable bearing on the ecology of southern African waterfowl, is the everincreasing multitude of water storage and irrigation schemes; these are most developed in the Republic of South Africa. However, there are still extensive areas of southern Africa which contain pristine wetlands and their populations of waterfowl. The biologist cannot evaluate the survival value nor interpret properly the evolutionary significance of an animal's behavioural (or other) adaptations without recourse to a study of the natural condition. Moreover, recently it has become clear that features of social behaviour can vary considerably within a species, with different populations showing adaptive modifications most effectively appropriate to the ecological circumstances under which they live (Crook, 1970; Watts & Stokes, 1972).

African Black Duck

Temperate zone. Localized and nowhere numerous. Inhabits perennial rivers and streams. Sedentary with a permanent home range. Usually in pairs and never congregates into large groups. A regular, annual, seasonal breeder. Social courtship reduced.

Cape Teal

Temperate zone. Locally common. Most typically inhabits alkaline waters of shortlived nature in arid areas. Nomadic, with long-distance movements. Usually in pairs and small parties, occasionally forms flocks of 100 or more. Irregular opportunistic breeder; breeding varying with erratic and sporadic rainfall. Social courtship occurs.

African Yellowbill

Temperate zone. Wildspread and numerous. Found on most waters including floodplains, lakes, *vleis* and largerivers in relatively well-watered regions. Resident, with local short-distance movements. Usually in pairs and small parties, though often encountered in flocks of a hundred or more. A regular, annual seasonal breeder. Social courtship occurs.

Red-billed Teal

Mainly tropical zone. Widespread and very numerous—the most numerous of the Anatini in southern Africa. Found on most waters, but especially flood-plains and lagoons in relatively well-watered regions. Mainly resident, with local short-distance movements. Also partly nomadic populations with extensive long-distance dispersal in the dry season. Usually in pairs, or small parties, but often encountered in flocks of a thousand or more. A regular, annual, seasonal breeder in well-watered areas of regular rainfall. Social courtship occurs.

Hottentot Teal

Tropical zone. Localized and nowhere numerous. Found mainly on permanent sheltered waters, but also floodplains in relatively well-watered regions. Resident, with local short-distance movements. Usually in pairs and small parties. A regular, annual, seasonal breeder. Social courtship occurs.

Cape Shoveler

Temperate zone. Locally common and numerous. Inhabits most typically shallow, seasonal *vleis* in areas of dependable rainfall. Suspected migrant with long-distance movements, though part of the population is resident. Usually in pairs and small parties, though often encountered in flocks of a hundred or more. A regular, annual, seasonal breeder. Social courtship occurs.

Pair-bond

The point made by Weller (1968), that the *Anas* males which commonly accompany females with broods are those which have relatively long lasting pair-bonds, only applies here to the Cape Teal. The African Black Duck's riverine habitat provides peculiar condition; a sedentary, anti-social way of life coupled with a long-standing or permanent pair-bond are the species' main behavioural adaptations (Siegfried, 1968). The male usually does not accompany his female with the brood.

Although much of southern Africa is either arid or semi-arid, receiving irregular and unpredictable rains, there are only two anatids typical of these areas—the Cape Teal and the Cape Shelduck *Tadorna cana*. The rest of the waterfowl community tends to be concentrated in the better-watered areas of either the tropical or temperate zones (Siegfried, 1970). In the Cape Teal it is assumed that the long-standing pair-bond is related (though not exclusively so) to the species' need to take advantage of unpredictable breeding opportunities. Non-breeding Cape Teal, paired as well as unpaired birds, gather together on more permanent waters where they take part in social courtship the whole year round. Not only are new pair bonds formed but existing ones are continually tested and reinforced, maintaining the birds in an almost constant state of synchronized readiness for breeding. It is necessary for the members of a pair to travel together and to be ready to establish territory and initiate nesting early in response to the erratic presence of short-lived habitat. This does not, however, entirely explain why the pair bond remains intact once incubation has started.

On a basis of species counts alone, in southern Africa generally, there are at least four times as many potential predators on waterfowl nests than there are in most of the Holarctic region. In the arid and semi-arid areas Cape Teal often construct their nests in a minimum of cover. In addition to predators, flash flooding or rapid drying up of breeding water commonly contribute to the destruction of eggs and ducklings. The Cape Teal, to realize its maximum reproductive potential, must be ready not only to nest early, but, if unsuccessful, to make repeated attempts at breeding and the short-lived habitat may not permit time for renewed courtship, re-pairing and establishment of territory following on nest or brood destruction. The pale grey plumages of adults and downy young blend well with the brine-encrusted saline pans, devoid of emergent cover, which are preferred breeding habitat. Broods are perhaps relatively more vulnerable to predators when feeding along these open shorelines, and the presence of both parents probably improves detection of predators and enhances survival of the young.

In the African Yellowbill social courtship and pair formation tend to occur seasonally (Rowan, 1963). This is more especially true in the Cape Shoveler (Siegfried, 1965). However, casual observations give the impression that the incidence of these behaviour patterns is considerably less compressed in time and less intense in rate of performance than in their northern counterparts, the Mallard and the Northern Shoveler. In the southern species there is opportunity for repeated social courtship and breeding over a relatively extended period.

The prolonged pair-bond appears to be better developed in the Cape Shoveler than in the African Yellowbill (Table 1). Generally, in the food-specialist Shovelers a mated male needs to expend much time and energy in establishing and defending a discrete, exclusive territory to provide his mate with the opportunity to feed unhindered, for building up energy reserves for egg laying and incubation (Seymour, 1971; personal observation). It stands to reason that energy and time savings will accrue to those Shovelers which are already paired when attempting to replace clutches.

In the African Yellowbill, as in the Mallard, feeding is less specialized, the breeding female ranges more widely. and, consequently, the male's role is less important in ensuring opportunities for the female to feed. In the African Yellowbill, and in the Mallard, a proportion of all 'rape-flights' (McKinney, 1965) appear to be initiated by re-nesting females which have been deserted by their mates; the rape-flight culminates in fertilization of the eggs. Rape is rare in Shovelers (McKinney, 1970).

If the preceding arguments are correct in their claims for advantages accruing through extended pair-bonds, what of the opposite? Why are the bonds in the African Yellowbill, Cape Shoveler and Hottentot Teal not as durable as in the Cape Teal? What factors are involved in the termination of the bond? According to Sibley (1957), the males of northern hemisphere Anatini desert their mates early in the cycle because their bright plumage might increase the risk of danger to their females and progeny by drawing the attention of predators. This explanation cannot be invoked for the dull-plumaged, monomorphic southern species. For northern species, Selander (1966) suggested spatial separation of the sexes as a mechanism ensuring adequate food resources for the young. In the north food is abundantly available for a relatively short time. In northern Anatini, selection has operated in numerous ways to both shorten and maximize the reproductive effort: clutches are larger, incubation periods are shorter and growth rates of ducklings are faster than in their southern counterparts (Kear, 1973). Under these conditions, the suggestions made by Sibley and Selander are plausible, and, in addition, selection would favour early termination of the pair-bond so that the annual moult, as an extra-energy demanding process, occurred in the sexes at different times and places before migration.

In those parts of well-watered southern Africa which receive predictable rains the whole reproductive cycle, from start of social courtship through to fledging of the brood, and post-breeding moult, occupies a longer period and the individual's breeding cycle proceeds at a slower rate than in the Holarctic. There are, of course, seasonal periods of food abundance and scarcity, but the extremes of northern climates are absent. Productivity even during the most favourable time of the year is well below that found in the north. Thus, there is relatively less food available at the same time to parents and young in the south, and Selander's (1966) suggestion could apply here as well. However, it seems more likely that selection favours early onset of moult in males, since social courtship commences as soon as the moult is over and because those males which are first ready to commence the new cycle of social courtship will be those which have moulted early. These males presumably have an advantage in obtaining mates; and there is no evidence to suggest that males and females ever occupy separate geographical areas, as is the case in 'wintering' populations of certain Holarctic migrants.

The ecological condition is different for the Cape Teal. The ephemeral breeding habitat can be extremely productive. Presumably, this allows the male to stay with the female and brood and to exercise his final advantage, in terms of his genetic contribution, by enhancing survival of brood, and/or giving him an edge for future breeding attempts. Interestingly, the Cape Teal's incubation period is shorter than those of the other southern African Anatini. The longest belongs to the African Black Duck, which lays the smallest clutch of all, and whose habitat is considered to be relatively poor in producing food (Siegfried, 1968).

So far discussion has focussed on the Cape Teal, African Yellowbill and Cape Shoveler. Besides being the best known of the six species, they represent fairly clear-cut examples of species which have either a long or a short pair bond. Relatively little is known about the Hottentot Teal. The Red-billed Teal has been left until last, because it does not fit neatly into one of the two categories of pair bonding considered thus far. The data assembled (Table 1) clearly indicate that certain birds maintain a long bond and others a short one. Based on casual observations, it appears that broods are accompanied most often by both parents when they occur on waters from which other Red-billed Teal are absent. Using the ecological premise applied to the other species, the Red-billed Teal condition can be explained only if considerable segments of the population are exposed to, and respond to, different environmental pressures. There is ample evidence from ringed birds (Winterbottom, 1964) to indicate that Red-billed Teal wander extensively in the arid and semi-arid areas, where they also breed. Presumably these birds would be subjected to ecological pressures similar to those prevailing on the Cape Teal. It is not known, however, to what extent they comprise a

group distinct from the main population inhabiting the well-watered tropical areas. Conceivably, there might be variable behaviour in the same individuals under different environmental conditions.

Plumage

According to Weller (1968), in southern anatids a sexually monomorphic (and usually dull) plumage is owned by those forms which show a tendency towards permanent pairing, an extended period of courtship, reduced migration, and the absence of an 'eclipse' plumage in males. Among southern African Anatini, the Cape Shoveler is the only species with permanent sexual dimorphism in plumage; it also is the only species in which apparently a major segment of the population performs regular migration (Siegfried, 1965). Thus in this case sexual dimorphism in plumage appears to be correlated with migration, and casual observations suggest that the species' social courtship is more strictly seasonal and commences later in the year than that of the resident African Yellowbill in the same geographical area. Since the two species differ little in their local breeding peaks, the Yellowbill a few weeks ahead of the Shoveler (Rowan, 1963; Siegfried, 1965), it stands to reason that the Cape Shoveler has a relatively shorter pair bond before initiating nesting. Thus if tenure of pair-bond is to be measured from time of first pairing to time of first nesting then the Cape Shoveler fits Weller's (1968) proposition that: 'in fact, strongly migratory segments of duck populations at any latitude may be less prone toward permanent pairing'. The fact that in the Cape Shoveler pair-bond may endure well into and beyond incubation seems of lesser importance in relation to the development of sexual dimorphism. What does seem to be critical, and common to regular migrants, at all latitudes, is that their annual time and energy budgets permit only relatively compressed bouts of courtship tending to be restricted to a short season. Tamisier's (1972) studies on European Teal Anas crecca on their wintering grounds point to the need for individuals to balance time spent on courtship against the energy expenditure and predation risks involved; the birds spent relatively little time on courtship, which occurred mainly towards the end of the wintering period.

In the southern African Anatini, taken as a group, courtship commences a new cycle as soon as breeding and the annual moult are completed; and the ecological conditions

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permit a relatively extended period of social courtship, and probably the formation of longer-lasting pair-bonds, prior to actual breeding. The striking male plumage features of northern birds apparently evolved primarily in response to intense competition for mates, in the relative absence of opposing selection pressures. Conceivably in response to predation, the dull-plumaged Red-billed Teal and Cape Teal are reported to have reduced and simplified their postures and vocalizations in courtship displays (Kaltenhäuser, 1971), and the African Yellowbill and Black Duck tend to perform their courtship activities after sunset (personal observation). It seems likely that sexual dimorphism or monomorphism in plumage will be understood fully only when more is known about time/energy budgets and predation pressures. It is suggested that for many dimorphic Anatinithe food and feeding situation affords a short period of intense, elaborate social courtship. In monomorphic forms, predation pressure is heavier and a lower but more sustained level of food permits a longer period for more frequent, less intense, less elaborate social courtship. Males of southern hemisphere anatines at high latitudes, with relatively short periods of high productivity, tend, as in northern migrants, to have bright plumage; this applies to certain species of Anasin southern Australia, New Zealand and South America.

It is possible to invoke the same ecological correlates in seeking to explain the evolution of reduced sexual dimorphism and simplified social courtship displays in certain isolated island races derived from mainland Anas stocks. An essentially ecological explanation would differ quite radically from the hypothesis developed by Sibley (1957) and advanced further by Johnsgard (1960, 1963, 1965). These authors claimed that conspicuous male plumages are present in those northern Anatini which occur together, and were evolved specifically as a mechanism to avoid hybridization. In presenting their case both authors stressed the island situation in a sort of inverted argument; that since insular populations are separated from closely related species, the chances of hybrid matings are minimal and hence selection for bright male plumage is relaxed. However, more recent studies of Anas species have failed to produce evidence that male plumage brightness is a reinforcer for preventing hybridization (Johnsgard, 1967). In addition, those races of Anas. (e.g. Greenland Mallard A.p. conboschas) which inhabit islands with ecological extremes tend to retain bright plumage in males.

Sibley (1957) explained the lack of sexual dimorphism in many southern hemisphere Anatini by speculating that these species were ecologically segregated to a greater degree than species in the north, resulting in decreased chances for hybridization. This argument does not fit the facts, as pointed out by Siegfried (1965) and Weller (1968). In contradistinction to Sibley and Johnsgard, it is submitted that in most northern anatines enhanced sexual selection, as an ecological effect, is primarily responsible for favouring conspicuous male plumage, and that these bright plumages mainly function epigamically (attracting and stimulating females) and intrasexually (competing with conspecific males) in social courtship. It is logical to assume that in the species of Anatini occurring together, selection for isolating mechanisms basically resorts to vocalizations and postural displays (rather than bright colours) per se), since these signals can be made effective as and when necessary. Most morphological characters, on the other hand, also comprise other adaptations.

Finally, Weller (1968) suggested that loss of the 'eclipse' plumage in Neotropical Anatini might be due to the irregularity of breeding seasons, and that birds constantly in breeding plumage have an advantage in being ready to pair at short notice whenever environmental conditions permit. From the foregoing accounts it is clear that Weller's mould does not accommodate the southern African species, the majority of which are regular seasonal breeders, but, nevertheless, have no eclipse. The eclipse can be regarded as a special cryptic plumage, increasing chances of survival of moulting males which are normally brightly coloured. Predators and other factors, induce moderation and compromise selection for brightness. Thus, the males in a particular population will be as conspicuous as is advantageous within the confines of particular ecological limits. If selection for brightness proceeded from an original state of dull plumage (whether the same as that of the female or not) and went no further than a point beyond which it would be disadvantageous to go, then that bright plumage would always be worn since at no time would it be especially disadvantageous to the individual. If, however, the degree of brightness is such that its continued presence is disadvantageous to the individual during its most vulnerable period (the moult), then selection for a special cryptic plumage for that period could be expected. In this regard, the shovelers present an interesting case. There are four species, the Northern Shoveler, Cape Shoveler, Australian and New

Zealand Shoveler *Anas rhynchotis* and Red Shoveler *A. platalea*, with male plumage ranging from most bright in the Northern Shoveler to least bright in the Cape Shoveler. The Northern Shoveler has an eclipse; the Cape Shoveler lacks a special eclipse and is permanently brighter than the female. The Australian and New Zealand Shoveler is considerably brighter than the Cape Shoveler and has an eclipse plumage (Frith, 1967).

In concluding this discussion, much of which is speculative, it is desirable to emphasize the modern view (e.g. Crook, 1970; Orians, 1971) that ecological factors are intrinsic in determining the evolution of mating and spacing systems of animals. In the final analysis, it is likely that food and feeding ecology, with attendant energy budgeting, will prove of fundamental importance to our understanding of social systems in the Anatini. Study of the ecological origins of waterfowl behaviour has been neglected; and these studies are needed as much as the psychological and phylogenetical ones.

Acknowledgments

Some of the concepts developed in this paper have resulted from extensive opportunities I have had to observe wild waterfowl in southern and northern hemisphere continents of the old and new worlds. I am grateful to the following bodies for financial support. The Frank M. Chapman Fund, American Museum of Natural History: the Wildlife Management Institute and the Delta Waterfowl Research Station; the South African Council for Scientific and Industrial Research; the University of Cape Town; the University of Minnesota; the Fitz-Patrick Memorial Trust; and the Cape Provincial Department of Nature Conservation. For helpful information, I thank A. Clark, P. G. H. Frost, D. F. McKinney, A. J. Tree and E. A. Zaloumis.

Summary

The incidence of males accompanying females with broods is compared in six Anas species: African Black Duck A. sparsa, Cape Teal A. capensis, African Yellowbill A. undulata, Redbilled Teal A. erythrorhyncha, Hottentot Teal A. punctata and Cape Shoveler A. smithii. Males accompany females with broods in those species which have extended pair-bonds. Length of pairbond is influenced by ecological factors which shape a species' social behaviour as well as features of its morphology. It is suggested that plumage brightness in males evolved as a result of sexual selection. In migratory forms the ecological conditions, regulating time and energy budgets, afford a relatively short period for elaborate, intense social courtship. Regular migrants have sexually dimorphic plumage. Most residents and nomads are monomorphic: this is attributed to heavier predation pressure and a lower but more evenly sustained productivity of food, permitting a relatively extended period for less intense, less elaborate social courtship.

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A group of Cape Teal Anas capensis displaying.

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