SOCIAL ORGANIZATION IN RUDDY AND MACCOA DUCKS

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SEVEN taxa of stiff-tailed ducks (tribe Oxyurini) are recognized here as comprising the genus *Oxyura*. Two taxa occur in the Northern Hemisphere, the remaining five are found in the Southern Hemisphere. This paper describes broad features of the ecology and behavior of the Northern and Southern Hemisphere taxa, with attention focused on contrasting the North American Ruddy Duck (*O. j. jamaicensis*) with the African Maccoa Duck (*O. maccoa*). Differences in mating and spacing systems are examined and are interpreted in relation to likely key pressures of selection that are believed to have shaped the evolution of specific social organizations and communication processes. This comparative approach permits provisional identification of the adaptive significance of the distinctiveness manifest in the displays and plumage features of the two species.

MATERIALS

This paper follows Woolfenden (1961) and Weller (1968) on *Nomonyx* vs. *Oxyura*, and deals with the following taxa: Genus *Oxyura*—*O. jamaicensis*, Ruddy Duck; *O. j. jamaicensis*, North American Ruddy Duck; *O. j. andina*, Colombian Ruddy Duck; *O. j. ferruginea*, Peruvian Ruddy Duck; *O. leucocephala*, White-headed Duck; *O. maccoa*, Maccoa Duck; *O. vittata*, Argentine Ruddy Duck; and *O. australis*, Australian Blue-billed Duck.

I have studied the ecology and behavior of wild *maccoa* for 17 years in southern Africa (Siegfried 1968, 1969a, 1969b, 1970, Siegfried and van der Merwe 1975). During December 1970–September 1971 I studied wild nominate *jamaicensis* wintering in the southern and eastern USA, and breeding in Manitoba, Canada (Siegfried 1972, 1973a, 1973b, 1973c, 1973d, MS). I saw wild *australis* breeding during August 1974 at Perth in Australia. *O. leucocephala*, *ferruginea*, and *vittata* I know only from captive birds at the Wildfowl Trust, Slimbridge, and in collections elsewhere. I have not seen *andina*.

In summary, my knowledge of *maccoa* and nominate *jamaicensis*, both in the wild and in captivity, is reasonably comprehensive. The main elements of the ecology and ritualized behavior patterns of *australis* have been documented (Johnsgard 1965, 1966, 1967; Braithwaite and Frith 1969 and references therein cited). Much less is known about *leucocephala* (Bauer and Glutz 1969, Matthews and Evans 1974) and *vittata*, *ferruginea*, and *andina* are poorly known (Johnsgard 1965, 1967; Weller 1968).

DISTRIBUTION AND ANNUAL CYCLE

The seven taxa comprising *Oxyura* are essentially geographically allopatric, occurring mainly within the warm-temperate climate zones of

North and South America, Europe and Asia, Africa and Australia (Delacour 1959). The Southern Hemisphere species occur permanently dispersed throughout their ranges. All suitable habitat usually has resident breeding populations. Nonresident populations appear to undertake seasonally regular, short-distance movements, and irregular long-distance dispersal in response to changing water conditions and other environmental pressures. These birds tend to form flocks on the larger permanent waters during the nonbreeding dry season (Frith 1967, Clark 1974). In contrast, the two Northern Hemisphere forms (nominate *jamaicensis* and *leucocephala*) embrace predominantly migratory populations, moving north over long distances and dispersing to exploit seasonally available habitat for breeding in late spring. In winter these birds form large flocks locally in the southern parts of their ranges. Relatively small, permanently resident, breeding populations occur in these southern regions (Phillips 1926, Bauer and Glutz 1969).

The broad ecological requirements, in terms of habitat, appear to be similar for all species. The birds are almost exclusively aquatic, doing all their feeding in water. They tend to use predominantly permanent wetlands in open grassland and semiarid country. Such preferred waters usually support rich concentrations of invertebrate benthos. The birds all are specialist divers, feeding by straining mainly invertebrates from the muddy ooze overlying the bottoms of ponds, swamps, shallow lakes, sheltered lagoons, and bays. Breeding birds are dependent on stands of new-grown emergent vegetation, mainly rushes and sedges, in which they build their nests. In all species the sexual cycles tend to be regular, and in both hemispheres breeding seasons peak in late spring and summer. The egg-laying seasons of the southern species are longer than in the migratory populations of the northern forms, whose sexually active males have a relatively shorter period for inseminating receptive females successfully (Hochbaum 1944, Braithwaite and Frith 1969).

Although the situation is still unknown in *andina*, it is reasonably certain that the males of all members of *Oxyura* acquire annually a dull, femalelike, nonbreeding plumage. This condition is now definitely known to occur in six of the seven congeners. The dull dress normally lasts about 5 months, and is not strictly a homologue of the "eclipse" found in *Anas* spp. (Siegfried 1968, 1970). In the Northern Hemisphere species males in nonbreeding plumage retain white face-masks. In the Southern Hemisphere species the heads of males in nonbreeding dress resemble those of females. The females of all seven congeners are rather uniform in appearance.

With onset of breeding, all males acquire bright blue beaks, chestnut bodies, and in the southern forms uniformly black heads, and in the

northern forms black heads with white masks. An exception is *andina*, in which breeding males have white face masks spotted with black or black heads spotted white. This plumage pattern appears to be intermediate between those of typical Northern and Southern Hemisphere taxa. In nominate *jamaicensis* breeding males have white undertail coverts. In *ferruginea* and in all other southern taxa breeding males have brown undertail feathers. In all taxa the heads of juvenile males resemble those of females.

Social Organization

Mating and spacing systems are major constituents comprising a species' social organization. The functioning of these systems depends on effective and efficient communication between members of the social group. Each species' communication system has its own species characteristics, involving signaling devices resorting in morphological and acoustical features and display movements.

Abundant evidence now favors the general conclusion that distinctive features in the communication systems of different species, and in some cases different populations of the same species, have evolved in association with a host of interrelated adaptations in response to a variety of environmental selection pressures (Crook 1964, 1970; Orians 1971). In *Oxyura* males generally many signals seem to be adapted to communication in dense emergent vegetation (Johnsgard 1965, Siegfried and van der Merwe 1975).

The main elements of the ritualized behavior patterns within *Oxyura* have been described by Johnsgard (1965, 1966, 1967, 1968), who emphasized the taxonomic implications attending differences between the species' display repertoires. Johnsgard (1968) advocated the following classification: a northern group comprising *jamaicensis* and *leucocephala*, a southern group of *australis* and *vittata*, and *maccoa* as a link between the two groups. Matthews and Evans (1974) suggested that *leucocephala* has more in common with the southern group, particularly *australis*. From a detailed study of the displays of *maccoa*, Siegfried and van der Merwe (1975) concluded that *maccoa*, *australis*, and *vittata* constitute a more or less homogeneous Southern Hemisphere group, distinct from *leucocephala* and nominate *jamaicensis*.

It is possible now to go one step further and attempt to correlate specific behavioral and morphological features with differences in environmental factors and social systems. Current knowledge restricts the exercise to nominate *jamaicensis* and *maccoa*, but there are hints that some of the correlations pertaining to these forms may be effective in the broader arena of Northern vs. Southern Hemisphere *Oxyura*.

NOMINATE *JAMAICENSIS* AND *MACCOA* COMPARED

The conclusions reported here are based on observations of individually marked birds of both species breeding in the wild.

In *maccoa* breeding males are strongly territorial, advertising and defending their presence in discrete areas with fixed boundaries embracing open water and stands of emergent vegetation. Individual territories are relatively large and can extend 80 m along the frontage of a more or less uniform stand of emergent cover. Territorial males are highly intolerant of all other males at all times, and territory owners display aggressively to rivals many tens of meters away. Females move through the territories for purposes of feeding and for selecting nesting habitat and/or fittest males. Promiscuity occurs and no social courtship or pair bond exists in the normally accepted sense. A successful territorial male can have one or more females nesting in his territory. A sexually active male, whether territorial or not, will copulate with any female who responds cooperatively to his courtship displays. Rape apparently is unusual, and generally females behave aggressively towards males. The territorial male does not attend the female(s) when she is off the nest and takes no part in the rearing of the young. The incubating female does not restrict her feeding to the male's territory containing the nest. Females with broods wander freely.

The displays of the breeding male are geared primarily to advertise the territory holder and his status and to attract and hold a female. Included in the male's repertoire of ritualized behavior patterns are two main and quite different displays: the independent vibrating trumpet call (IVTC) and the vibrating trumpet call (VTC). The IVTC is used in advertising the status of the territory holder, and the VTC in courting a female. Both displays, but especially VTC, are characterized by rather slowly executed body actions and vocalizations. A territorial male displays to either a single male or to a single female. Normally, the male has to contend with only one bird at a time and has extended opportunities for repeating displays in a most precise way. Orientation of the signaler's body and the position of his beak are important: in IVTC the male faces, and presents his beak full on to the rival; in VTC the male's body is lateral to the female, and his beak points downwards into the water. The bright cobalt dorsal surface of the beak appears to be an important device for reinforcing threat postures (Siegfried and van der Merwe 1975).

The species' territorial and promiscuous systems are believed to be advantageous to individual males because they obtain most mates that way, and to females because many would otherwise not obtain mates

with territories suitable for nesting. Generally there are more males than there are breeding territories, and females ignore males holding relatively inferior territories. Males also outnumber females, and not all mature males find even marginal territories that are untenanted and consequently do not breed (Clark 1964, Siegfried MS). Males compete for territories at the start of every breeding season and generally come into breeding condition ahead of females. Individual males can remain sexually active and territorial for at least 4 months. Males probably evolved their bright breeding dress and special displays in response to seasonal competition for territories and mates. In some regions in certain years, when nesting cover is very reduced and at a premium, many females may nest and/or dump eggs and lay parasitically in nests of conspecifics and other species. I have recorded as many as eight nests (all with eggs) at one particular time in the territory of one individual male. Apparently the size of the breeding population is determined on the breeding grounds.

In North American *jamaicensis* breeding males are not territorial. Individuals do not restrict their activities to discrete areas with fixed boundaries but tend to move around in search of females, and to follow them in their selection of breeding sites. Social courtship occurs, though in structure and execution it differs from the *Gesellschaftsspiel* (Heinroth 1911) typical of many *Anas* spp. in which several males continually crowd around and display to a female. Moreover in migratory anatines social courtship occurs on the wintering grounds and paired birds travel together north to breed, whereas in migratory *jamaicensis* most social courtship begins on the breeding grounds.

The newly arrived birds (the males normally a week or so ahead of the females) first congregate and court on the larger waters, from which they disperse to the small ponds used for nesting. Relatively few males (rarely more than six), positioned at varying distances from the swimming female, display simultaneously to her while interacting aggressively among themselves. The female lacks a classical inciting display and apparently indicates her preference for a particular male and accepts his approaches by responding with relatively less aggression and by staying closer to him. Nonpreferred males are threatened overtly and occasionally come under attack by females whose partners also seem to be stimulated into responding aggressively. Males that have been interacting aggressively in the presence of a female can be loafing amicably side by side minutes later. Pair bonding occurs, but is a much looser arrangement than between the partners in most anatines and *Aythya* spp. There seems to be no greeting behavior between associating male and female. Usually one particular male mates with only one particular female, but he will continue to court other females as long as he is sexually active and will

copulate with them if given the opportunity to do so. Females generally behave aggressively towards males.

The male tends to stay close to this mate before and during the laying phase of her cycle. A sexually active and/or mated male tolerates other males at relatively close distance, but their presence appears to stimulate the male into displaying sexually to a female if she is nearby, and aggressively to males. Individual males continue displaying to females and other males throughout the period April–July, after which they undergo molt. The area defended by the male usually extends about 3 m around the female, on or off the nest. The male normally takes no part in the rearing of the young.

The displays of the breeding male are geared primarily to function in social courtship and pair bonding behavior. The male's main (most frequent) display is bubbling (see Johnsgard 1965), which functions in both male:male and male:female interactions. In an aggressive response, the male faces his rival while performing bubbling. In courting, a bubbling male orientates his body laterally to the female. In a group of courting birds of more than one male, the males typically display rapidly alternating forms of bubbling in accordance with constantly and suddenly changing aggressive and sexual responses. In this competitive situation, conceivably it could be advantageous for a male to posture in ways that can be altered with a minimum of time and effort to signal different intentions. Bubbling embraces less emphasis on vocalizations and the display's body movements are performed faster than in IVTC or VTC of *maccoa*. In this connection, in nominate *jamaicensis* the male has a large tracheal air sac that is inflatable during bouts of displays. This special air sac might be kept fully or semi-inflated, thus facilitating rapid response in production of vocalizations when necessary. In contrast, in *maccoa, australis,* and *vittata,* males have a simple trachea and during certain displays the whole neck is inflated by air drawn relatively slowly into the oesophagus and trachea.

Hays (*in* Cornwell and Bartonek 1963) first reported that the Ruddy Duck's blue beak is important in signaling aggression. I agree with this, and suggest that in lateral bubbling the male's white cheek patches should be investigated in relation to possible appeasement of the female's relatively high level of aggression. This could be important in social courtship situations in which the males have to make rapid and sudden changes involving full-frontal and laterally orientated bubbling. Be this as it may, in the social courtship situation it is crucial for the male to be able to attract and to hold the attention of a female. In this context, the male's tail-flash display (see Johnsgard 1965), in which the male exposes his white undertail while swimming in front of the female, apparently func-

tions to hold the female's attention and to elicit a following response away from rivals. *O. maccoa* males lack the tail-flash, but do have a leading swim (with tail down) that they use in leading a responsive female into the emergent cover of their territory (Siegfried and van der Merwe 1975).

Although local conditions may vary, the North American prairies as a whole appear to provide a seasonally regular abundance of suitable habitat for breeding *jamaicensis*. Even in drought years sufficient habitat seems available to accommodate successful breeding by the migratory population, which has virtually half a continent to disperse over (see Smith 1971, Henny et al. 1972). In this connection the *jamaicensis* population is much smaller than those of most other migratory Anatidae in North America (Martinson et al. 1968). In many of these species it is not unusual during years of drought for the birds to form nonbreeding flocks in spring and summer (Leitch 1964). I know of no published accounts for similar behavior in migratory *jamaicensis*. There appears to be no large and readily observable nonbreeding population of males, and, unlike *maccoa*, males do not compete for breeding habitat, which appears superabundant. I believe that the size of the breeding population is largely determined on the wintering grounds.

The absence of typical territorial behavior and the presence of social courtship and loose pair bonding in migratory *jamaicensis* is believed to be advantageous to males because these systems provide them with best chances of obtaining mates and to females because fit monogamous mates offer them best chances of maximizing their reproductive effort. Given a breeding range within which nesting cover and food are not limiting, if suitable breeding ponds are patchily distributed and their availability subject to temporal change it would be advantageous to the female to be mobile and perhaps not to share resources with others. Females in shifting around would disperse over the available breeding habitat. In this connection, the constant presence of a preferred mate, as an instant inseminator and aid in protection against unmated males and predators, would be advantageous. For a male it would be advantageous to follow a female around. It would be relatively disadvantageous for a male to set up and remain in a fixed territory, as so doing would presumably decrease his chances of obtaining a mate. This appears to be the condition for and situation in migratory *jamaicensis* on the northern prairie breeding grounds.

NORTHERN VERSUS SOUTHERN HEMISPHERE *OXYURA* GROUPS

I believe that at least some of the correlations between environmental factors and behavioral features as they apply to *maccoa* and migratory

jamaicensis respectively constitute indirect evidence for the adaptive significance of the distinctiveness manifest in the displays and plumage features of the two taxa. These correlations may be extended tentatively to a comparison between all Northern vs. Southern Hemisphere taxa of *Oxyura*.

Apart from humid-arid cycles, the geology and climate of the low-lying warm-temperate landmasses of the Southern Hemisphere have involved a core of stability and permanence throughout the Pleistocene, in marked contrast to the dramatic glacial vicissitudes that prevailed in the Holarctic (see Vuilleumier 1971 and references therein). In North America, for instance, the northern prairies were covered by ice as recently as 10,000–15,000 years ago (Lemke et al. 1965). With the retreat of the ice and glacial lakes, a vast new region became available for colonization by mainly migratory forms of many species. These populations took advantage of highly productive, seasonal habitats for relatively enhanced reproductive output. In exploiting the superabundance of wetlands, migratory populations of *jamaicensis* and *leucocephala* (in the Palaearctic) appear to have been exposed to similar environmental pressures. Both species appear to be restricted to limited winter quarters, conceivably setting an upper limit to the migratory breeding populations at levels well below the normal carrying capacity of the breeding grounds. Social courtship occurs and male territorial behavior is absent or reduced in both species (see Matthews and Evans 1974 for *leucocephala*). For the time being, the possibility should not be discounted that in the social organization of migratory *jamaicensis* former systems involving promiscuity and territoriality are in the process of phasing out, and that an incipient form of pair bonding is currently developing.

In semiarid southern Africa at least, suitable breeding habitat for *maccoa* is limited. This I believe has promoted the evolution of promiscuity and the species' territorial behavior. Those parts of Africa, Australia, and South America that are inhabited by *Oxyura* are, on balance, semiarid. In short, the general conditions applying to *maccoa* could apply as well to *australis*, and possibly to *vittata* and *ferruginea* also. *O. maccoa, australis,* and *vittata* apparently show closer affinities to each other in their displays than either one does to *jamaicensis* or *leucocephala*.

According to Johnsgard (1965: 322), "It is reasonably certain that the South American forms *andina* and *ferruginea* should be considered as southern montane populations of the North American ruddy duck which have progressively lost their white cheek markings and have become larger." I am skeptical about the reasoning and implied certainty of this statement. Unlike Africa and Australia, where apparently no large scale ecological barriers have existed to prevent effectively at least

a degree of gene flow within continental populations of *maccoa* and *australis* respectively, South America is bisected by the Andean mountain range, which attained its present position during the Plio-Pleistocene (Childs and Beebe 1963, Putzer 1969). Although narrow sympatry between *ferruginea* and *vittata* is reported to occur now (Johnsgard 1965), this appears to be a relatively recent phenomenon in terms of the region's climatic and geological histories. In short it seems justified to regard *ferruginea* as having evolved independently as a result of ecological (= geographical) separation from *vittata*. If one accepts that the juvenile males' plumage pattern (femalelike head), which is common to all taxa in *Oxyura*, is closest to the ancestral plumage of the group, and if one were to consider the similar nonbreeding plumages (femalelike head) shared by adult males in *maccoa, australis, vittata,* and *ferruginea* as representative of a "primitive" condition and the different nonbreeding plumage (white head) of the male of nominate *jamaicensis* as secondarily developed, then nominate *jamaicensis* might be regarded as more advanced than *ferruginea*. Thus, and in contradistinction to Johnsgard (1965), for the present I believe the best interpretation to be that *ferruginea* is a relatively long-established austral species, with *andina* as a likely semispecies (i.e. an intermediate form in the speciation process). *O. j. andina* is distributed over those parts of the Colombian Cordilleras known to have been influenced by glaciation during the Pleistocene (see Vuilleumier 1971, Mercer 1972). Thus it might be that the plumage and behavior (unknown at present) of *andina* could be best explained in terms of relatively recent glacial events. Studies are needed particularly of the behavior of *ferruginea* and *andina* and the relationships between social and ecological pressures of selection affecting these taxa and *leucocephala*.

SUMMARY

Broad features of the plumage, behavior, and ecology of Northern and Southern Hemisphere taxa of stiff-tailed ducks (*Oxyura* spp.) are outlined, with attention focused on contrasting the North American Ruddy Duck (*O. j. jamaicensis*) with the southern African Maccoa Duck (*O. maccoa*). Differences in mating and spacing systems are examined and are interpreted in relation to likely key pressures of selection that are believed to have shaped the evolution of specific social organizations and

communication processes. This comparative approach permits provisional identification of the adaptive significance of the distinctiveness manifest in the displays and plumage features of the two species.

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