Socially induced suppression of breeding plumage in the Maccoa Duck

W. R. SIEGFRIED

Introduction

In species of ducks (subfamily Anatinae) in which males have special bright breeding plumages the annual acquisition and loss of plumages are believed to be regulated by 'fixed' celestial factors such as photoperiodism (Murton & Westwood 1977). In the Maccoa Duck *Oxyura maccoa*, post-breeding males normally lose their bright colours (cobalt blue beak, black head, and chestnut body) and acquire annually a dull female-like dress (blackish beak, grey-brown head and body). This dull dress normally lasts 4–5 months, and it is not strictly a homologue of the 'eclipse' found in *Anas* spp. (Siegfried 1968a, 1970).

Male Maccoa in full or partial dull dress have been observed in all months of the year at many localities in southern Africa, in spite of a fairly strict regimen of seasonal breeding in certain regions (Clark 1964, 1974; Siegfried 1969). Why should particular males be in dull dress and what is their status during the breeding season? It is postulated that at least some of these males are either adult (older than two years) or younger non-breeders, and it is possible that their dull dress reflects subordinate status induced through social behaviour. The evidence for this was gathered in the south-western Cape, South Africa, in the mid-1960's and embraced observations involving artificially raised, captive birds. The birds were kept in out-door enclosures with ponds fringed by natural vegetation, and given an *ad lib.* supply of artificial food (high-protein poultry mash).

Results

In a group of a female and four males kept together since time of hatching, one male first developed a full breeding dress when two years old. This male harassed the other males which failed to develop fully bright dress for a further year, during which they were associated with the dominant bird whose dress altered seasonally between bright and dull. The dominant bird wore bright plumage for seven months of the year. At the end of the three-year period the dominant male was removed, resulting in one of the remaining males becoming dominant. This three-year-old male, then, for the first time, assumed a bright dress and in the subsequent nine months underwent normal seasonal changes in plumage (Siegfried 1968a). Five years after hatching the two remaining males had not yet assumed a bright dress.

A female and four males, aged between three and four years, all having previously undergone the normal sequence of seasonal plumage changes (bright to dull) were introduced together into an enclosure (10 x 12 m) containing one pond. At the time of introduction all four males were in bright dress. Within four weeks one male completely dominated the others, which began losing their bright colours. During the following eighteen months the subordinate males remained in dull dress with blackish beaks, whereas the dominant male's dress alternated seasonally between bright and dull. The female, the dominant male, and one of the other males were then, during the non-breeding season, transferred to a larger (3X) enclosure with two ponds. With the onset of the breeding season both males assumed fully bright dress which they retained for the rest of the season. Each male tended to keep to his own pond. At the end of the breeding season, each male assumed a dull plumage. At the start of the following breeding season one of the males came relatively quickly (within one month) into bright dress and commenced to harry the second bird which showed signs of new breeding plumage. The latter individual took three months to develop full bright plumage.

A three-year-old male and a female were kept together for two years. The male's dress underwent normal changes, and the female laid fertile eggs during the two breeding seasons. She was then removed and, subsequently, during two years the lone male underwent normal changes of dress. A pair of aggressive and highly territorial Black Duck *Anas sparsa* (Siegfried 1968b) were then introduced into the enclosure. The female Black Duck dominated the male Maccoa, chasing him on sight. The Maccoa prematurely lost his bright

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dress and became somewhat secretive, hiding in the vegetation and seldom venturing on to the larger of the two ponds that formerly had served as his main arena for performing displays. He had unrestricted access to food, but failed to acquire a bright plumage during his six months of association with the Black Duck. When the Black Duck pair were removed, the male Maccoa changed into a bright dress almost immediately, three months out of phase with the normal onset of such plumage.

Finally, all yearling males have an adult-sized penis, and females lay eggs in their first year. Elsewhere (Siegfried 1968a, 1970) I have reported on young males deferring bright dress until about two years old. Apparently, however, this deferred maturity is not invariable, since a male raised and kept in isolation developed partial breeding dress when one year old.

Discussion

During the breeding season male Maccoa are territorial, advertising their presence in, and defending, discrete areas. Territorial males are very aggressive and intolerant of other males. Promiscuity occurs and there is no social courtship or pair-bond in the normally accepted sense (Siegfried 1976). This system is 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 in. Generally there are more males than there are nesting territories, and males holding relatively inferior territories are ignored by females. There is a surplus of males over females, and mature males not unusually fail to find even marginal territories that are untenanted and consequently do not breed (Siegfried 1976). It is likely that a special bright breeding dress has evolved in males in response to seasonal competition for territories and mates. Presumably a bright dress assists a territorial male in advertising his dominant status for as long as it is advantageous for him to do so.

Territory holders invariably are males in bright dress. Non-territorial males in bright dress will display sexually to females if given the opportunity to do so, as also will dull plumaged males, including yearlings, but they rarely perform displays directing aggression at territorial males. The cobalt blue beak is believed to be a major device used in signalling aggression (Siegfried & v. d. Merwe 1975). A change in beak colour was the first change to occur in the loss of bright dress in those captive males which were subjected to intra- and inter-specific harassment and domination. Subordinates never developed a fully bright blue beak. Relatively prolonged retention of a bright dress, or elements thereof, presumably would be advantageous to dominant males in maintaining their status (Balthazart 1983).

Apparently, certain males do not acquire a fully bright dress, because they are too young and/or low in the social order. Their chances of holding breeding territory, in competition with older higher ranking males, and obtaining a mate at the same time, are slight. This theory will, however, not apply unless by attempting to breed and competing against superior males, the individual itself suffers increased mortality and the deferred competitor ultimately leaves more progeny. For polygynous species, Lack (1960) advanced the thesis that young males by deferring breeding and by retaining a cryptic juvenile plumage gain advantage to themselves by decreasing risk of predation. However, the implication that bright plumage and attendant display automatically increase risk of predation cannot be assumed as a matter of course. In 20 pinioned male Maccoa Duck, kept for six years in a 15 ha enclosure with numerous large natural ponds, four dominant, bright plumaged, territorial males suffered no predation during the breeding seasons, but ground and aerial predators took low-ranking, dull (3 out of 5) and bright plumaged (6 out of 11) non-territorial adult males. The territory holders occupied the best emergent cover and their harassing actions forced subordinate birds into presumably vulnerable positions in marginal cover in and out of the water. In this context, bright plumaged subordinate birds might be more susceptible than dull birds.

It seems likely that enhanced freedom from predation cannot be invoked as the only possible advantage of suppression or assumption of a bright dress. It is suggested that Maccoa males by wearing a dull dress, both in and out of the breeding season, reduce intra-specific aggression by signalling (to males and females) non-competitive low social status when unpredictable shortages of habitat occur. If all low ranking

males adopted bright dress during the breeding season they conceivably would experience more persecution by territorial males, and would still be unable to breed because of the high level of competition. Since social courtship and pair-bonding are non-existent, and because the female's nesting, and the availability of suitable nesting cover, are seasonal, it would be presumably disadvantageous for males to wear bright dress and to expend energy on territorial behaviour much before the females are ready to select nesting territories and mates. Bright dress could be especially disadvantageous after the breeding season when areas of water decrease and food supplies become concentrated locally, forcing the birds to aggregate – a frequent but irregularly occurring phenomenon in the Maccoa Duck's annual cycle. This could explain why a proportion of the adult male Maccoa Duck's population can always be found in dull plumage.

Finally, it is not known whether, in Maccoa males younger than two years, deferment of bright dress occurs in the absence of social domination. It appears clear, however, that social behaviour can be of direct and over-riding importance in regulating the acquisition and loss of bright dress at least in captive males.

Summary

Captive male Maccoa Ducks *Oxyura maccoa* failed to develop normally bright breeding plumage when subjected to harassment and domination by socially higher-ranking males. Subordinate males wore a dull female-like dress. The significance of this is discussed in relation to the species' social system.

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W. R. Siegfried, FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa.