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Morphology and ecology of the southern African whistling ducks (*Dendrocygna*).—The model and analyses Rylander and Bolen (1970) made to demonstrate morphological and ecological differences between the North American whistling ducks *Dendrocygna bicolor* and *D. autumnalis,* prompted me to examine similar adaptations in the southern African whistling ducks, the Fulvous *D. bicolor* and White-faced *D. viduata.* Some morphological differences, especially relative foot size, are noted between the two species, and supplementary data on the birds' breeding ecology are presented.

Table 1 summarizes standard linear dimensions for *bicolor* and *viduata* taken in southern Africa. Because large series of measurements are not available, and in order to keep to a minimum potential errors resulting from workers using different measuring techniques, I have tabulated only data from museum specimens measured by P. A. Clancey of the Durban Museum, South Africa. Although the samples are small, *bicolor* is manifestly the smaller species in all linear dimensions except in length of middle toe. Published data on weights of the two species are too few to permit a meaningful comparison.

Comparing proportions within the linear dimensions of each species and the relative differences in size between the species, Table 2 shows that the ratios are similar in all cases except those involving toe length, and that *bicolor* averages slightly more than 90 percent of the size of *viduata,* again except for the middle toe. Thus *bicolor* has a relatively larger foot than *viduata.* These results agree very

TABLE 1

MEAN DIMENSIONS FOR ADULT FULVOUS AND WHITE-FACED TREE DUCKS[1]

Species	Culmen	Wing	Tarsus	Middle toe (excluding claw)
D. bicolor	46.2 (44–48)	213.8 (203–225)	51.2 (46–53)	65.5 (63–67)
D. viduata	50.3 (46–53)	226.1 (219–240)	53.0 (50–56)	57.1 (54–61)

[1] Measurements in mm. All measurements from Clancey (1967; in litt., 1970). Ranges shown in parentheses. Samples comprised 5 males and 5 females for each species, except middle toe measurements, which derive from 5 female and 2 male *bicolor* and 7 male and 3 female *viduata.*

closely quantitatively with the findings of Rylander and Bolen (1970); North American *bicolor* consistently proved about nine-tenths the size of *autumnalis,* but with a proportionately larger foot.

Rylander and Bolen (1970) related relative foot size in adult *bicolor* and *autumnalis* to the two species' swimming efficiency and nesting habits, *bicolor*'s larger foot being a presumed adaptation to the bird's aquatic feeding and ground nesting habits, as opposed to *autumnalis*'s smaller more dextrous foot being primarily related to arboreal cavity nesting and a relatively less aquatic life. They noted that *autumnalis* seldom frequents deep water, feeding mainly by wading in shallows, whereas *bicolor* spends a large proportion of its time swimming and dabbling for food. In fact *bicolor* is a good diver (see Johnsgard, 1967).

In southern and central Africa *bicolor* and *viduata* often occur sympatrically, and thousands of individuals of the two species are commonly seen residing together at the same place (Dowsett and De Vos, 1965). Some observers have been struck by the apparent similarity of the species' habitat requirements, feeding habits, and social behavior (e.g. Verheyen, 1953), although little detailed information is on record about feeding behavior or food. Preliminary unquantified observations by the writer indicate that in Zululand *bicolor* feeds regularly by diving, but not so *viduata*, which commonly forages on the edges of waters. Further when the two species are seen at rest, *viduata* characteristically presents a more erect body and neck posture than *bicolor*. Frith (1967) noted a similar difference in posture between the Australian whistling ducks *D. eytoni* and *D. arcuata,* and stated that a very distinct ecological segregation exists between these species in their choice of habitat and feeding behavior. *D. eytoni* has the more erect posture and feeds on the edges of waters, meadows, and widely over short-grass plains, whereas *arcuata* favors deep, permanent waters and secures nearly all of its food in water, much of it by diving.

Rylander and Bolen's theory that the relatively smaller more dextrous foot of *autumnalis* might be an advantage to this perching and mainly arboreal nesting duck cannot be applied to *viduata* which, like its sympatric congener in Africa, rarely if ever perches above the ground and always nests in ground cover or over water in matted rank vegetation. Similarly in Australia both *eytoni* and *arcuata* are nonarboreal and are ground nesters.

In southern Africa *viduata* and *bicolor* with broods have been observed sharing the same habitat. As far as is known, both species care for their young in a similar

TABLE 2

PROPORTIONS WITHIN LINEAR DIMENSIONS OF ADULT FULVOUS AND WHITE-FACED TREE DUCKS AND THE RELATIVE DIFFERENCES IN SIZE BETWEEN THE TWO SPECIES[1]

Ratio	*D. bicolor*	*D. viduata*	*D. bicolor/viduata*	
Wing/culmen	4.62	4.45	Culmen	0.92
Tarsus/culmen	1.11	1.05	Wing	0.94
Wing/tarsus	4.12	4.27	Tarsus	0.97
Wing/toe	3.26	3.96	Toe	1.15
Toe/culmen	1.42	1.13		
Toe/tarsus	1.28	1.08		

[1] All data based on means in Table 1.

way and frequently select similar "nursery" habitat. However my observations indicate that *bicolor* ducklings find much of their food by diving, and *viduata* rarely so. In this connection it is pertinent to refer to the breeding seasons of *bicolor* and *viduata* in southern Africa. In compiling Table 3, I have drawn on data given by Benson (1963) and unpublished information on file with the African Wildfowl Enquiry and the South African Ornithological Society's nest record scheme, which provided the bulk of the records. Table 3 shows that a broad but clear, difference in breeding periodicity between the two species holds for all territories except South Africa. Essentially the difference is a dry/wet season one, with *bicolor* breeding mainly during the dry season (April to September) and *viduata* in the rainy months (October to March). The same difference in the annual breeding cycle operates in the Congo as well. In Katanga Verheyen (1953) found that *bicolor* normally nests during the dry season and molts between September and November, whereas *viduata* nests during the rains and molts in April and May.

A point that must be taken into account when attempting to explain why the seemingly more aquatic *bicolor* breeds during the dry season (and not the rainy period) is that, in most of the bigger southern African floodplains (e.g., the Kafue Flats in Zambia) peak flood occurs normally well after the rains have ended, and flood waters only begin to recede in June. Possibly the difference in breeding is related to the ecological availability of food to both adults and ducklings of the two species. Interestingly, the White-backed Duck, *Thalassornis leuconotus,* another accomplished diver (and regarded as a member of the Dendrocygnini), also breeds mainly during the dry season (Benson, 1963). However the factor(s) responsible for initiating breeding in *viduata* and *bicolor* have not yet been identified nor are there nearly enough breeding records from any one particular locality to attempt an analysis of the ducks' response to environmental factors influencing breeding.

Ruwet (1964a), in proposing that the annual activity cycles of *bicolor* and *viduata* in the Congo were controlled by physionomical changes in the environment, pointed out that ecological segregation in breeding periodicity could be expected to break down under artificial conditions such as might be provided by man-made and main-

TABLE 3

NUMBER OF BREEDING RECORDS BY MONTHS[1] OF FULVOUS AND WHITE-FACED TREE DUCKS IN SOUTHERN AFRICA

	J	F	M	A	M	J	J	A	S	O	N	D
D. viduata												
Malawi	—	2	4	—	—	—	—	—	—	—	—	—
Zambia	3	14	4	1	1	1	—	—	—	—	—	—
Rhodesia and Botswana	6	7	5	1	1	—	—	—	1	3	4	3
South Africa	16	7	4	2	—	—	—	—	—	—	1	5
D. bicolor												
Malawi	—	—	—	—	—	3	1	1	—	—	—	—
Zambia	—	1	2	1	1	—	1	2	—	—	—	—
Rhodesia and Botswana	—	—	—	1	3	2	1	2	1	—	—	—
South Africa	7	6	7	2	—	1	2	—	—	—	—	2

[1] Broods and egg sets have been adjusted to months in which clutches were completed.

tained waters. This would seem partly to underlie the absence of marked breeding isolation in South Africa. The South African records are mostly from artificial waters and, secondly, mainly from the Transvaal highveld and the Durban area, which lie within the southern fringe of both species' natural ranges.

Finally, what are the origins and evolutionary significance of the different breeding cycles shown by the closely related and sympatric *bicolor* and *viduata*? Ruwet (1964b), in attempting to explain the situation in the Congo, proposed the hypothesis that *viduata* and *bicolor* evolved first in separate geographical areas, without presenting any notable ecological and ethological divergences. On coming into contact with one another, the species avoided competition for the exploitation and occupation of the same habitat by evolving their ecologically isolated breeding cycles. In this manner each species exploits the same habitat in the same way, but at different times. Alternatively, Ruwet (1964b) suggested that at first the two forms had their respective centers of distribution to the north and south of the equator; that is to say, in regions where the alternation of seasons is inversed. After having colonized the area of the other form in the opposite hemisphere, each species retained its annual breeding cycle, true to its original hemisphere. This explanation can only be valid for regions where the two forms are equally common and likely to be in competition. If, for instance, a southern form colonized an area north of the equator it could conserve its natural cycle if it found itself in a place already entirely occupied by a form with a similar ecology, or else, if nothing else opposed it, it would adapt to local climatic conditions.

The significance of the morphological differences presented here adds support to preliminary observations of differences in feeding behavior between adult *bicolor* and *viduata* and also their young, which make it likely that the two species are, in fact, adapted to employ different methods of feeding and consequently are ecologically isolated. The need for further study of the whistling ducks, and the interesting problems they present, is obvious. The Dendrocygnini constitute a relatively poorly-known group within the otherwise well-studied Anatidae.

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