Foot adaptations in four species of Whistling Duck *Dendrocygna*

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Introduction

Adaptations in the foot structure of North American whistling ducks (=tree ducks) were examined using the comparative ratios of tarsus and mid-toe lengths as indicators of foot size (Rylander & Bolen, 1970). The results indicated that Fulvous Whistling Ducks *Dendrocygna bicolor* have proportionately larger feet than Black-bellied Whistling Ducks *D. autumnalis*. We believe this difference in foot size is correlated with the highly aquatic nesting and feeding habits of the Fulvous Whistling Duck.

A second pair of dendrocygnids, the Wandering *D. arcuata* and Plumed *D. eytoni* Whistling Ducks from Australia, were similarly examined to estimate divergence in foot structure. This paper reports these results, makes a brief ecological comparison between the Australian species, and discusses the evolutionary implications of these data with those obtained from the North American species.

Results

Mean lengths of the wings, tarsi, and mid-toes of the two Australian whistling ducks are presented together with measurements for the North American species in Table 1. Culmen length, while otherwise useful for size comparisons, was not used here because of the remarkably short bill length of *D. eytoni*; this feature remains singularly dissimilar from any of the other seven species of dendrocygnids. Hence, using the wing and tarsi data as indicators of overall body size, *D. eytoni* and *D. autumnalis* are shown as the larger birds of each geographical pair, respectively. Body weights also bear out the larger sizes of these species over their respective congeners discussed in this paper (see Bolen, 1964; Frith, 1967), but weight data are not useful for our present analysis.

Ratios comparing the relative wing and tarsal lengths (Table 2) show that the four species are proportionately rather similar (i.e. a wing/tarsus ratio of about 4 for two

Table 1. Comparison of wing, tarsal, and mid-toe lengths (mm) for four species of whistling duck *Dendrocygna*. Ranges shown in parentheses

Species	N	Wing	Tarsus	Mid-toe
D. arcuata	3	214* (196–230)	52·3 (51–55)	65·6 (64–68)
D. eytoni	6	232† (222–242)	59·6 (58–62)	55·8 (55–60)
D. bicolor	28‡	210 (196–225)	55·8 (52–60)	66·6 (64–70)
D. autumnalis	21‡	238 (229–248)	62·3 (58–66)	64·5 (61–68)

* Data from eighty-two males examined by Frith (1967 p. 65).
† Data from fifty-nine males examined by Frith (1967 p. 79).
‡ Data taken from earlier sources as cited in Rylander & Bolen (1970).

Table 2. Proportions among linear dimensions for four species of whistling ducks, *Dendrocygna*. Data calculated from means in Table 1

	Species			
Proportions	*D. arcuata*	*D. eytoni*	*D. bicolor*	*D. autumnalis*
Wing/tarsus	4·1	3·9	3·8	3·8
Wing/toe	3·3	4·2	3·2	3·7
Toe/tarsus	1·3	0·9	1·2	1·0

Table 3. Proportionate sizes for two pairs of sympatric whistling ducks, *Dendrocygna*, based on means and ranges for adult birds shown in Table 1

Feature	Species (=sympatric pairs)	
	D. bicolor/*D. autumnalis*	*D. arcuata*/*D. eytoni*
Wing	0·88 (0·86–0·91)	0·92 (0·88–0·95)
Tarus	0·89 (0·89–0·90)	0·88 (0·88–0·89)
Middle toe	1·03 (1·02–1·04)	1·18 (1·13–1·16)

Australian species and about 3·8 for the two others). However, when mid-toe lengths are introduced into the ratios, these similarities are no longer apparent and the ratios become distorted (e.g. a wing/toe ratio of 3·3 for *D. arcuata v.* 4·2 for *D. eytoni*). This discrepancy prompted still another comparison to determine the relative difference in size between each of the two species in each pair (Table 3). This revealed that *D. arcuata* is about nine-tenths the size of its sympatric congener, *D. eytoni*, and thus parallels the size relationship also occurring between *D. bicolor* and *D. autumnalis*.

In both geographical pairs, then, the smaller species—*D. arcuata* and *D. bicolor*—have proportionately larger feet as measured by mid-toe lengths. We believe these features are adaptations consistent with certain ecological distinctions that can now be briefly considered.

Comparative ecology

D. eytoni: Plumed Whistling Ducks (=Grass or Eyton's Whistling Duck) are found on tropical grasslands throughout much of Australia; no subspecies are recognized.

Nests are placed on the ground in the shelter of tall grass or a bush, and often at a mile or more from water. Lavery (1967) observed that the daily feeding routine started in the late afternoon when, at first, the birds walk or graze near roosting sites, then fly to feeding areas elsewhere. Plumed Whistling Ducks feed mainly on land, selecting foods heavily dominated by grasses. They will dive when wounded, but they do not otherwise exhibit this behaviour. Plumed Whistling Ducks perch rarely and awkwardly. Likewise, they are slow and awkward swimmers, whereas on land, the birds walk long distances gracefully (Frith, 1967 p. 80).

D. arcuata: there are three races of this species, differing in size, present in Australia, Indonesia, and the Philippines. The largest of these, *D. a. australis*, frequents the more permanent freshwater lagoons of tropical Australia.

The nest of the Wandering Whistling Duck (=Water Whistling Duck) is a sheltered, grass-lined depression on the ground often far from water; the species makes little or no use of tree perches. They feed entirely in water taking small amounts of animal matter in addition to various parts of aquatic plants; their foods are secured by expert and constant diving. Frith (1967 p. 66) once watched several thousand Wandering Whistling Ducks froth the water to a boil as they swam and dove for food. It is primarily in this respect—a utilization of aquatic foods in relatively deep water—that the Wandering Whistling Duck remains ecologically separated from the Plumed Whistling Duck throughout their sympatric ranges in Australia (Frith, 1967 p. 88). Wandering Whistling Ducks exhibit a nearly horizontal posture and thus are unlike the vertically oriented posture of Plumed Whistling Ducks (Rylander & Bolen, 1974a).

Evolutionary considerations

The foregoing comparisons show that *D. arcuata* possesses (a) a foot size disproportionately larger than its sympatric congener and (b) feeding behaviour that is distinctively aquatic and, as such, quite dissimilar from that of *D. eytoni*. Moreover, these same distinctions are also found in a pair of dendrocygnids *D. autumnalis* and *D. bicolor* sympatric in North America.

That such duplication in morphological and ecological features occurs in two geographical pairs of whistling ducks suggests an instance of parallel evolution. However, we believe this is best explained in the case of the two rather cursorial species of each pair, *D. autumnalis* and *D. eytoni*. The similarities between the highly aquatic species, *D. arcuata* and *D. bicolor*, more likely indicate a common and rather immediate genetic ancestry; they are perhaps best considered as super-species, as suggested by many additional similarities in their plumage

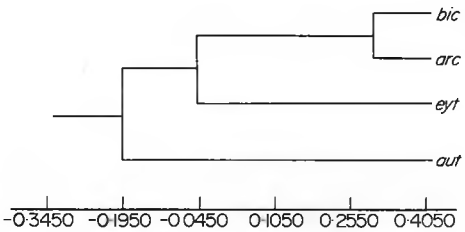

Figure 1. Correlation phenogram of four species of *Dendrocygna* based on NT–SYS computer analysis of thirty-five seemingly non-adaptive features (e.g. downy plumage pattern, threat displays, etc.). The computer program is adopted from the concept of numerical taxonomy as developed by Sokal & Sneath (1963). Note that *D. eytoni* is more nearly related in the correlation to *D. bicolor* and *D. arcuata* even though its foot adaptations and ecology closely resemble *D. autumnalis*. Scale shows units of correlation.

(*cf.* Delacour & Mayr, 1945) and their nearly contiguous distributions across southern Asia.

The case for parallel evolution gains strong support using numerical taxonomy, as developed by Sokal & Sneath (1963). Each of thirty-five presumably non-adaptive features for each species was coded for computer analysis using the standard NT-SYS program. The resulting phenogram, direct from the computer printout, shows that *D. eytoni*, the cursorial Australian species, is more closely related to the aquatic species, *D. bicolor* and *D. arcuata* than to the New World cursorial species, *D. autumnalis* (Figure 1). Hence, the cursorial habits and similarities of foot structure of *D. eytoni* and *D. autumnalis* may have evolved independently in each of two pairs of whistling ducks on opposite sides of the world. The associated similarities of gait and feeding adaptations are fully discussed elsewhere (Rylander & Bolen, 1974a, 1974b).

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Summary

A comparison of the mid-toe and tarsus proportions for two geographical pairs of whistling ducks *Dendrocygna* spp. shows that each pair contains one member with disproportionately larger feet. These species, *D. bicolor* and *D. arcuata*, have highly aquatic habits whereas the other members of each pair (*D. autumnalis* and *D. eytoni* respectively) are far less aquatic and exhibit cursorial habits. In the latter case, the similarities in foot sizes suggest an instance of parallel evolution that is strongly supported by phenetic analysis of other characteristics.

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