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# Whistling-ducks: Zoogeography, Ecology, Anatomy

*Eric G. Bolen and Michael K. Rylander*

The eight species of whistling-ducks, genus *Dendrocygna*, are generally regarded as a clearly defined natural group and are usually placed in a category to themselves, for example, as a subfamily (Dendrocygninae) or tribe (Dendrocygnini). The birds are generally considered to be related closely to the geese and certain ducks, such as the White-backed Duck *Thalassornis leuconotus* (Johnsgard, 1967), but their place among the waterfowl always has been somewhat puzzling.

The whistling-ducks are of interest because of questions raised both with regard to their systematic position and to the ecology of certain highly specialized members. For example, *D. autumnalis* walks gracefully on land, perches on such narrow supports as barbed wire fences, often grazes for food, and nests in tree cavities, sometimes more than 10 meters above the ground!

The number and variety of studies on whistling-ducks (see below) attests to the attention biologists have paid to the group. Such an interest is noteworthy since the whistling-ducks, being only locally hunted as game, have not frequently been the subject of well-subsidized government research projects. Most of the major studies of the group have been prompted by the biological—more than the economic or recreational—interest that the genus commands.

In spite of the attention they have received, there has never been a general review of the genus, although excellent partial reviews may be found in the standard monographs of waterfowl (for example, Phillips, 1922; Delacour, 1954; Palmer, 1976; Johnsgard, 1975; Bellrose, 1976). It seems appropriate, at this time, to assemble and organize the important published and unpublished information on the genus, analyze and interpret the major biological issues pertinent to it, and speculate on promising areas for future study. Our hope was to select material that will be useful to both evolutionary and wildlife biologists. Although we have emphasized the zoogeography and ecology of the group, we have also included a section on anatomy and its relationship to locomotion and feeding, in keeping with what we consider a fortunate trend in monographs of this kind (for example, Tuck, 1972; Stonehouse, 1975; Stemmler, 1955; Johnsgard, 1973).

## *Early Studies of the Whistling-ducks*

The tenth edition of Linnaeus' *Systema Naturae* (1758:127) contains the following terse description for *Anas autumnalis*: "grisea, remigibus cauda ventreque nigris, area alarum fulva albaque."

Thus was established, by convention, the specific name for the Black-bellied Whistling-duck *Dendrocygna autumnalis*, though this was not the first published description of the species, since Linnaeus frequently based his

descriptions on previously published material. Although there is some controversy regarding the basis for Linnaeus' description (see Friedmann, 1947; Hellmayer and Conover, 1948:314), it seems that the descriptions for *autumnalis* and *arborea*, both of which appeared in this edition of the *Systema Naturae*, were based primarily on earlier works by Edwards (1743-1751, *vide* Hellmayer and Conover, 1948:314). Banks (1978) has traced the nomenclatural history of *autumnalis*, and his paper may be referred to for additional details.

The first acknowledged reference to *arborea* is that of Sloane (1725; see Salvadori, 1895:162), making this species the first of the eight whistling-ducks to be described in the scientific literature. The twelfth edition of the *Systema Naturae* (1766:205), appearing eight years after the tenth, contained an original description of *viduata*, based on a specimen from Cartagena, Colombia.

The fourth whistling-duck to be described was *bicolor*, but here some confusion arises because taxonomists have not always been able to agree on which of several brief descriptions published in the early nineteenth century actually referred to *bicolor*. No fewer than six specific names (including *arcuata*) have been applied to this species by competent ornithologists during the last two centuries. The currently accepted name *bicolor* was given to the species in 1816 by Vieillot (1816:136).

The next two whistling-ducks were discovered by Dr. Thomas Horsfield, a Pennsylvania-born physician who practiced medicine and studied natural history in Java, principally from 1811 until 1818 (Stresemann, 1951:134). Horsfield collected specimens that he took to England and later described as *javanica* and *arcuata*, though at first he did not recognize them as two distinct species. Throughout the years these two species have suffered a history of almost hopeless nomenclatural confusion wherein they have been misidentified continually, and frequently referred to by the other's name because authors have quoted seemingly reliable sources in which the birds had been misidentified.

The generic designation *Dendrocygna*, proposed by Swainson (1837), was initially applied only to *arcuata*, *javanica*, and *arborea*. The genus found favor among ornithologists, as the following year *autumnalis* and *viduata* were included in the genus by Eyton (1838). Curiously, the 1838 monograph of anatids by Eyton carried the original description of *eytoni* (p. 111), provided by Gould (who named the bird after Eyton) but assigned to a different genus, *Leptotarsus*. The generic name is appropriate, inasmuch as this terrestrial form does indeed have a thin tarsometatarsus; however, it is interesting that Eyton did not place this species in *Dendrocygna*, even though evidently most whistling-ducks had already been recognized and accepted by Eyton as the well-defined group of birds that we recognize today. It was not until 1844 that *eytoni* was placed in *Dendrocygna*.

Thus, by midcentury, only one species in the genus was left to be discovered and described, and that one, not surprisingly, was *guttata*, about

which so little is known even today. Alfred Russell Wallace, who was forced to leave the Amazon in 1852 because of ill health, sold his Amazon collections to support an expedition to Malaysia. In the Moluccas he collected in 1861 the specimen that was later (1863) referred to as *D. guttata*.

One need only examine the synonymies of the whistling-ducks in Salvadori (1895) to understand the immense problems confronting the taxonomist who attempts to unravel the various conflicting names, descriptions and generic designations in the genus. Frequently an author who cited another author could not tell, on the basis of the description provided, if the two of them were referring to the same species. Eyton's (1838) monograph of the anatids was incomplete, and therefore of limited help in resolving taxonomic problems. Comprehensive treatises such as Salvadori (1895), which made monumental attempts to straighten out the discouraging bibliographic and taxonomic confusion, often required that the compilers re-examine study skins and critically read the published descriptions with the actual skin in hand. Often the meticulous scholarship behind such treatises was impressive (see, for example, the footnote in Salvadori, 1895:153, where he surmises Cuvier's inability to distinguish *arcuata* from *javanica*).

While eighteenth and nineteenth century taxonomists were studying the numerous study skins of whistling-ducks that were being shipped to their museums from all over the world, the biology of these birds also was receiving due attention, and by the beginning of the twentieth century, eggs from all species except *arborea* and *guttata* had been described in the literature (Oates, 1902:157-159). Notes concerning the field biology of the more common species in the genus became more frequent, although those prior to Swainson (1836-1847) and Gosse (1847) were primarily anecdotal and based on casual observations by untrained persons. The first whistling-ducks to be kept in captivity were *arborea* and *autumnalis* (prior to 1750), and by 1857 most of the species had been kept in confinement. A number of their behavioral traits, such as a tendency to keep apart from other anatids, had been noted by several nineteenth century authors who studied captive birds (see Phillips, 1922).

The first anatomist to study the genus *Dendrocygna* in any detail appears to be Shufeldt (1914), who described the skull and postcranial skeleton of *autumnalis*. The nineteenth century avian anatomists, such as Beddard, Furbringer, Gadow, and Garrod made critical and sometimes exhaustive studies that included anatids, but not specifically the whistling-ducks.

Most of the important literature prior to 1920 concerning the natural history of whistling-ducks has been summarized by Phillips (1922). Since then, partial literature reviews and bibliographies have appeared for species when they occur in areas covered by regional handbooks and catalogs, such as Hellmayr and Conover (1948), Palmer (1976), Johnsgard (1975), and Bellrose (1976), for the North American species.

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## DISTRIBUTION AND ZOOGEOGRAPHY

It is a rare place indeed that does not have some representation, if only seasonal, of the family Anatidae. Yet it is common knowledge that some anatids are typical of certain areas while others are not. Flight alone ultimately does not control bird distributions. Factors associated with each species' adaptations and historical development seem more important, and many species show remarkable habitat and distributional correlations. Other species show an equally remarkable tolerance and enjoy diversified habitats the world over. Patterns of avian distribution as illustrated by waterfowl remain a complex facet of faunal geography.

The genus *Dendrocygna*, consisting of eight clearly defined species, is closely aligned with swans and geese (Anserinae) but is sufficiently distinct to warrant tribal distinction (Delacour and Mayr, 1945). Little discussion of the tribe's ecology and zoogeography has followed its taxonomic study.

This chapter first treats the tribe's fossil history and present distribution, proceeds with discussions of ecological and biological relationships, and concludes with an exploration of distributional patterns.

*The Fossil Record*

The earliest fossil record of modern duck and swan taxa is from the Oligocene of Europe; geese date from the same area in the following epoch (Howard, 1950). The only known precursor of recent whistling-ducks is from

a Lower Miocene deposit in South Dakota where Miller (1944:89) recorded *Dendrochen robusta* as "the earliest whistling-duck in the known fossil record." From this find, a complete left humerus, Miller noted that *Dendrochen* tends to connect, morphologically, the geese and modern whistling-ducks; of the modern species, *Dendrochen* most nearly resembles *Dendrocygna bicolor*. [The root forming suffix-*chen* is itself also the basis for a modern genus including the Holarctic blue and snow goose complex. However, Delacour (1954) and others now recognize only a single genus of true geese, *Anser*, into which *Chen* is absorbed. Wetmore (1924) stated that the humeri of *Anser albifrons*, in particular, strongly suggests those of *Dendrocygna*.]

Wetmore (1924) recorded the fossil *Dendrocygna eversa* from the Upper Pliocene of Arizona; after comparing these remains with comparable bones of existing whistling-ducks, he concluded that the fossil represents a species smaller than any of the modern forms. Wetmore also noted the similarity of the Arizona fossil with *D. bicolor*. The single fossil of Old World origin comes from DeVis' (1888) *Dendrocygna validipennis* of Australia's "post Pliocene" deposits in New South Wales.

The available fossil evidence, then, echoes an ancestral North American form and two extinct species of the modern genus from such widespread areas as Australia and Arizona.

There is little, if anything, to be made of these scant records in deciphering the origins of whistling-ducks, although Howard (1950) postulated waterfowl origins in pre-Tertiary Europe. On the other hand, the records do suggest something regarding the magnitude of previous whistling-duck distribution.

*Dendrochen* from South Dakota should not be regarded as an extratropical species, or as a tropical bird that somehow occurred outside of its usual environment. In North America, Tertiary climates were far different from those of today. Chaney (1947) analyzed Tertiary floras and found, both from morphological and taxonomic evidence, that the tropical forests of Central America formerly extended to 50°N latitude in North America. Associated with the vegetational environment, of course, was the faunal response to these conditions, and the faunal history of recent tropical groups once found in the higher American latitudes is indeed rich.

Among birds, Darlington (1957) listed both parrots and trogons as once occurring in North America. A Chachalaca *Ortalis* sp., presently "Neotropical," was also found with *Dendrochen* in the South Dakota deposits. Such evidence led Miller (1944) to note that a change to a cooler, less humid climate in the Pliocene and Pleistocene could have been an important causal factor enforcing a restriction southward of groups that were once more widespread. Moreover, if Howard's (1950) European waterfowl primordium is correct, the whistling-ducks had already radiated widely by the Pliocene. It is not unlikely that whistling-ducks or their immediate fossil ancestors radiated in tropical environments the world over. If they had done so, they

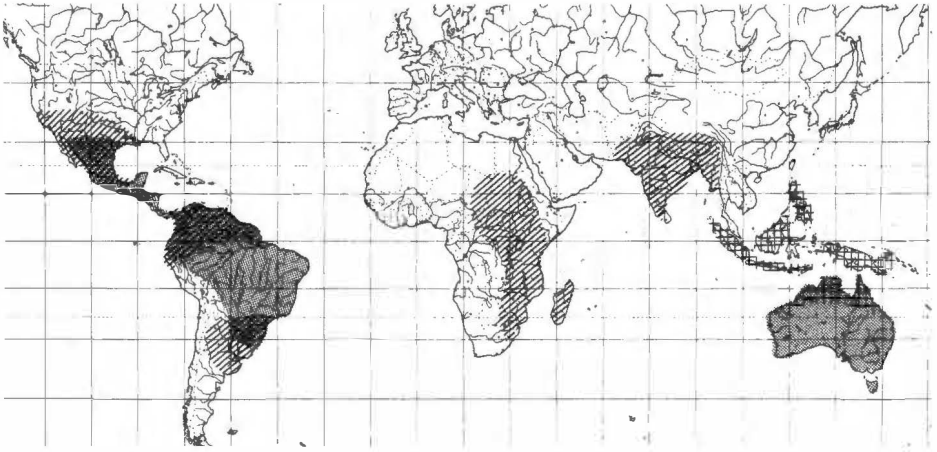


FIG. 1.—Distribution of *D. bicolor* (cross-hatching), *D. arcuata* (double-hatching), *D. autumnalis* (shading, Western Hemisphere), and *D. eytoni* (shading, Australia).

would have occupied many areas well beyond the confines of present tropical regions. However, it is well to recall Mayr's (1946) suggestion that the ancestors of tropical species in the Old and New Worlds were perhaps less tropical than their living descendants.

#### *Present Distribution*

The present distribution of the whistling-ducks encompasses five continents and their major shelf islands (Figs. 1 and 2). The equatorial affinities of the distributions are easily seen, and planimeter readings provide a rough estimate of the actual areas that are geographically tropical or extratropical (Table 1). Of the total whistling-duck range occurring in any major area, only Australia has less than 50 per cent in tropical regions. The "New World" classification, uniting North, Central and South America, follows Reichenow's (1888) suggestion that these areas be combined in zoogeological discussions (see Mayr, 1946:4).

More important, perhaps, is the "use" that whistling-ducks make of tropical areas (Table 1). Only Africa, with its northern tropics engulfed in desert, has a significant departure from total use based on availability, and this area, eleven per cent of the world total, is most likely ecologically unsuitable for significant waterfowl use. We may reasonably conclude that whistling ducks are present throughout the tropics wherever suitable waterfowl environment exists. Moreover, an expansion of the equatorial belt by only five or so degrees would include all but the most peripheral whistling-duck distributions; these distributions occur particularly in the New World species. It is quite apparent that the southern continents figure heavily in tropical climates and hence in the distributions of whistling-ducks.

Species distributions are shown in Figs. 1 and 2. Patterns are discussed later, but for now it can be seen (a) that Fulvous and White-faced Whistling-



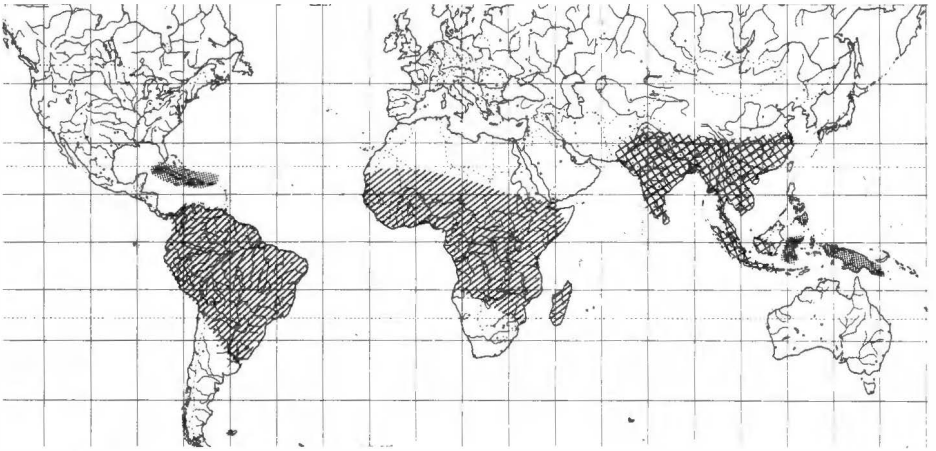


FIG. 2.—Distribution of *D. viduata* (cross-hatching), *D. javanica* (double-hatching), *D. arborea* (shading, W. Indies), and *D. guttata* (shading, E. Indies).

ducks occupy two or more disjunct continents; (b) that Black-bellied and Plumed Whistling-ducks are found on single or connected continents; (c) that Wandering and Indian Whistling-ducks occupy both a continent and major island chains; and finally, (d) that Cuban and Spotted Whistling-ducks are strictly limited to island clusters. The distributions involved are therefore complex.

#### *Bergmann's Rule*

Bergmann's Rule states that northern forms (often species, but among birds more commonly subspecies) of homoiothermic animals have a larger body size than closely related counterparts of southern origin. This cline was originally correlated with decreasing mean temperatures, but more often it is associated with increasing latitude or altitude (Van Tyne and Berger, 1959:359). The concept also has been viewed as having less adaptive significance to climate than insulation and vascularization (Scholander, 1955, 1956). Recently, Le Febvre and Raveling (1967) demonstrated that body size, surface area, and heat loss were adaptively related to the wintering locations of various races of the Canada Goose *Branta canadensis*. Weller (1964) suggested that Bergmann's Rule helps explain the origins of the congeneric Redhead and canvasback ducks, *Aythya* spp.. The following two examples drawn from the subspecies of the Black-bellied and Wandering Whistling-ducks may be considered with regard to Bergmann's Rule.

The Black-bellied Whistling-duck has two well recognized races. Other forms (Friedmann, 1947) are enough in doubt to be omitted here (see Pitelka, 1948); their body sizes, if they indeed represent acceptable subspecies, in no way alter the present discussion. Of the races accepted for discussion, the larger *Dendrocygna a. autumnalis* is found from Panama north to southern Texas, whereas *D. a. discolor*, both smaller and with different breast coloration,

TABLE 1.—Affinities of present whistling-duck distributions to tropic zone. Above: data are means of 10 planimeter readings for the total area of whistling-duck range and the amount of that range lying within the tropic zone; range determinations follow Delacour (1954). Below: distributions calculated on the basis of utilizable habitat within each area.

Land mass	Total area of whistling duck range	Distribution of total area		Percent of total area	
		Tropical	Extratropical	Tropical	Extratropical
Africa	10.35	9.80	0.55	94.7	5.3
Continental Asia	4.20	2.10	2.10	50.0	50.0
East Indies	0.95	0.95	0	100.0	0
Australia	4.13	1.55	2.58	35.6	62.4
New World	10.69	8.18	2.51	76.6	23.4
Total range	30.32	22.58	7.74	74.5	25.5

Land Mass	Total area of Land mass in tropic zone	Distribution of whistling duck range within tropic zone		Per cent	
		Vacant	Occupied	Vacant	Occupied
Africa	12.71	2.91	9.80	20.2	79.8
Continental Asia	2.10	0	2.10	0	100.0
East Indies	0.95	0	0.95	0	100.0
Australia	1.55	0	1.55	0	100.0
New World	8.18	0	8.18	0	100.0
Totals	25.49	2.91	22.58	11.4	88.6

tion, extends south from the Panamanian Isthmus into Brazil and northern Argentina (Fig. 1). A summary of the linear body measurements for these bird appears in Table 2.

A size gradation separates the Wandering Whistling-duck into three distinctive races. Linear data are shown in Table 2. Note that these distributions are largely in the Southern hemisphere and, accordingly, the cline in body size extends to the south. The relationships are less clear inasmuch as the smallest form, *Dendrocygna arcuata pygmaea*, is found eastward (New Britain and Fiji Islands) of the other races. Nevertheless, the largest race occurs farthest from the Equator. The intermediate size *D. a. arcuata* is found on the large island chains north and west of Australia. Curiously, Delacour (1954) finds that within *arcuata*, birds in the Celebes and the Lesser Sunda Islands are very slightly larger than the more northerly—that is, birds nearer to and north of the Equator—and western members of the same race. On New Caledonia, the former population is now presumed extinct (Frith, 1967:68). Miles (1964) reported recent observations of *pygmaea* in the Fijis where the introduced mongoose (*Viverridae*) apparently exterminated the previous population; otherwise, *pygmaea* is found on, and is perhaps restricted to, New Britain.

Distribution maps for the Wandering Whistling-duck and its races sometimes represent its distribution imperfectly. A marked contrast between the maps appearing in Delacour (1954:33) and Frith (1967:68), for example, illustrates the problem. Frith (1967:xix) addresses the matter: "The most recent comprehensive work that includes Australian waterfowl (Delacour,

TABLE 2—Above: comparison of body dimensions for subspecies of the Black-bellied Whistling-duck (data in millimeters from the sources indicated); samples sizes in parentheses when specified by authorities. Below: comparison of body dimensions for subspecies of the Wandering Whistling-duck (data in millimeters from the source indicated); sample sizes not specified.

Measurement	<i>Dendrocygna autumnalis</i>									
	<i>autumnalis</i>				<i>discolor</i>					
	Bolen 1964 (N=21)		Delacour 1954:48		Bourne 1979 (N=160)		Delacour 1954:49		Phillips 1922:163	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Total length	498.1	471-507			467.7	449-493				
Wing	237.9	229-248		217-246	241.6	227-259		210-232	230	
Tarsus	62.2	58-66		52-65	51.5	47-59		51-59	55	
Culmen	53.1	49-56		43-53				40-48	48	

Structure	<i>Dendrocygna arcuata</i>					
	<i>australis</i>		<i>arcuata</i>		<i>pygmaea</i>	
	Delacour 1954:39		Delacour 1954:39		Delacour 1954:41	
Wing	200-222		180-203		173-183	
Tarsus	44-48		43-45			
Culmen	42-48.5		42-48		40.5-43.5	

1954:64) gives several misleading ideas of their distribution, because the author was forced to rely solely on published records . . ." Because of Frith's extensive experience in Australia, we have utilized his map for the Wandering Whistling-duck in the construction of Fig. 1; otherwise, the ranges in other distribution maps we present were adopted from Delacour (1954) as we are unaware of similar discrepancies for the ranges of other species of whistling-ducks. Frith (1967:69) found this species most abundant on the tropical northern coast between the Kimberley Ranges in the west and Rockhampton in the east; stragglers are occasionally present in New South Wales and South Australia. Hence, the Wandering Whistling-duck is more locally distributed in the Australian tropics than may be generally recognized.

The three races of the Wandering Whistling-duck are *D. a. arcuata*, to the north, *D. a. australis*, in Australia and New Guinea, and *D. a. pygmaea*, on New Britain and the Fiji Islands. Because the larger races are found as the distance from the Equator increases, this species thus follows Bergmann's rule.

In the Black-bellied Whistling-duck, the southern subspecies ranges as far south (Argentina) in latitude as the northern race does to the north of the Equator (Texas), yet birds from the southern extreme show no corresponding increase in body size. Historically, the evolution of a larger race must be tentatively considered a relatively recent event. Such evidence suggests that the basic stock of this species was first established in the New World in South America. Once dispersed northward, the Isthmus of Panama or an oceanic gap apparently provided a barrier inhibiting further genetic exchange. The larger northern race thereafter developed.

The east-west gradient of the medium and smaller-sized Wandering Whistling-ducks, superimposed on the general north-south pattern, complicates matters. We tentatively suggest that the intermediate race has replaced a former and widespread distribution of *pygmaea* in the Java-Philippine Island complex. The still smaller race then interrupted this sequence leaving isolated populations of *pygmaea* scattered eastward into the small islands of its present distribution. If so, the Wandering Whistling-duck seemingly developed from stock originally located in the large, equatorial islands of the southeast Asian coastline.

This line of biological evidence suggests that the Black-bellied and Wandering Whistling-ducks, at least, are of distinct tropical origins; large subspecies of each species today radiate from an equatorial locus in their respective distributions.

#### *Breeding Chronology in North America*

Late nesting perhaps reflects geographic origins among closely related birds. However, we must limit much of our discussion to North America because adequate data from other regions are lacking. Nesting dates for the Fulvous Whistling-duck in Louisiana extend from late May well into August. Meanley and Meanley's (1959) earliest nesting record is 25 May; McCartney (1963) back-dated a Louisiana nest to 27 May.

Bent (1925:278) lists the following dates of nest initiation, with the sample size shown in parentheses: California, 28 April to 13 July (23) and 7-25 June (12); for Texas, 16 May to 10 September (9) and 16 June to 12 July (4).

Hatching dates from wild clutches artificially incubated by John J. Lynch (*in* McCartney, 1963) in Louisiana are as follows: June (fourth week), three clutches; July (first week), one clutch; July (second week), six clutches; July (third week), seven clutches; July (fourth week), two clutches; August (third week), one clutch.

Assuming an incubation period of approximately 25 to 28 days, the rates of nest initiation for the above clutches include late May through late July. Cottam and Glazener (1959) present no specific nesting chronologies for Fulvous Whistling-ducks, but they found 17 nests in late summer; the birds first arrived at the nesting area in June and reached a peak number of more than 100 by mid-July. Some hens in Lynch's captive flock produced a few eggs as late as October; most, however, had laid by mid-August. McCartney (1963:80) says, ". . . (the birds) begin nesting in Louisiana about the final week of May. Although by early June virtually all of them are on the breeding grounds, the entire population. . . may not begin to breed this early. The nesting season extends until late August."

Bent (1925:272) lists, for Texas, 3 May to 18 October (16 nests) and 20 June to 14 July (8) as dates of nesting for the Black-bellied Whistling-duck. Our unpublished data show nest initiation extending from an average (three years) beginning date of 5 May to 20 August based on back-dating 111 clutches. The nesting season in southern Texas averaged 109 days in length;

no two-week period contributed more than 23 per cent of the total number of nests initiated. About 62 per cent of the nests were started by 1 July; 92 per cent were started prior to the first week of August.

Necropsied specimens provide additional data for nesting chronologies. Female Black-bellied Whistling-ducks examined May through August all showed advanced ovarian development, and many contained fully shelled eggs. Known hatching dates and estimations of brood ages further corroborated the previously reported nesting season's length although brood ages include only nests containing eggs that actually hatched. Hatching dates extended, on the average, from 28 June to 10 September whereas back-dating broods estimated this period to be 19 June to 28 August. Cottam and Glazener (1959) reported at least one brood hatched after September 15.

The foregoing data clearly indicate that the North American whistling-ducks not only nest well into summer but also that the nesting period often extends for three months or more. Some renesting records have undoubtedly been included in the chronologies, but these certainly do not alter the definite late nesting trend. The length of the nesting season has in fact suggested to some authorities (see Bent, 1925; Johnson and Barlow, 1971) that the whistling-ducks annually produce two broods. Current field study has failed to support this point of view, and the two North American whistling-ducks, at least, should be considered single-brooded species.

Does late nesting in whistling-ducks indicate a southern, if not tropical origin? Weller (1964:98) suggested that it does for the Redhead Duck: "If Baker (1908) is correct in stating that single-brooded north tropical anatids tend to nest later than do temperate species, then the later nesting season of the Redhead may indicate a more southerly origin (than that of the Canvas-back)."

Birds nesting in temperate latitudes have a relatively short period in which they may successfully rear young; those nesting nearer the Equator are not similarly limited by adverse temperatures. Presumably, as Weller (1964) noted, no selective pressures toward early breeding occur in southern environments. The nesting environment of northern waterfowl contains selective forces that have presumably shortened the nesting season to a relatively short period beginning with warming temperatures in spring. Sows (1955:90), for example, concluded that low spring temperatures delayed the beginning of the nesting season of ducks in Manitoba.

The termination of the nesting season is presumably adapted to the survival of broods faced with winter weather. Cool weather would seem to be especially important for the survival of whistling-ducks in temperate zones. Johnstone (1957) commented that the young thrive only if the temperature is moderate. Data provided by Beer (1964) also illustrate the susceptibility of the whistling-ducks to cold: 38 per cent of the whistling-ducks at Slimbridge, England, died during severe winter cold whereas 21 per cent died during normal winter weather. In comparison, the taxonomically related tribe of geese and swans (Anserini) had respective mortalities of one and two

per cent under the same conditions. Interestingly, Beer observed that the feet of whistling-ducks seem particularly susceptible to frostbite. At Slimbridge, England, the smallest species of the whistling-ducks *D. javanica* is placed in heated winter quarters whereas some of the larger species are normally left free to roam the grounds (Bolen, 1978).

A reasonable conclusion, therefore, is that whistling-ducks have limited tolerance to cold, and that their lengthy nesting season is primarily an adaptation to the longer periods of warm weather.

A long nesting season, including "late-nesting," seems to be particularly valuable for birds in low latitudes. Tropical birds may adapt in other ways (in addition to those related to temperature) to keep their nesting season safely in phase with seasonal changes. Frith (1959) has shown such relationships between rainfall and the reproductive period for several species of Australian ducks. More recently Frith (1967:75) says of the Wandering Whistling-duck in Australia, that ". . .the volume of the testes, an indication of sexual activity in the male. . .closely parallels the water-level as it rises and falls." Cottam and Glazener (1959) pointed out that southern Texas waterbirds, including both Fulvous and Black-bellied Whistling-ducks, seem adapted to the sudden availability of nesting habitat caused by heavy rains and surface runoff and begin building nests at this time. Hence, birds such as the whistling-ducks have a long period in which to take advantage of a particularly favorable set of conditions.

Extensive periods of reproduction are thus regarded as a characteristic adaptation of birds having a southern origin. The whistling-ducks nesting in North America, and probably elsewhere, seemingly fit well into this general pattern of development.

### *The Fixity of Distribution*

Mayr's statement (1946:5)—"Instead of thinking of fixed regions, it is necessary to think of fluid faunas"—remains well taken. The whistling-duck distributions in North America, omitted from Mayr's discussion, are of interest from the standpoint of both zoogeography and ecology. We have already mentioned the problem of using range maps for species found elsewhere; the difficulties arise largely from exclusive reliance on inadequate published records and from inexperience with birds of foreign lands, a problem emphasized by Frith (1967).

The ranges of both the Fulvous and Black-bellied Whistling-ducks include most of North and Middle America (Fig. 1.), but we will restrict our comments to the United States because data are insufficient to expand the discussion further. The Fulvous Whistling-duck has ventured to areas far removed from its former distribution. Jones (1966) cites the winter of 1955-56 as the time when Fulvous Whistling-ducks were considered well-established winter residents rather than stragglers on the eastern seaboard.

The Fulvous Whistling-duck has been known to nest for some time in Lower California (Shields, 1899; Barnhart, 1901; Bryant, 1914a; Dickey and

van Rossem, 1923) and Texas (Dresser, 1866; Merrill, 1878; Griscom and Crosby, 1925). Nevada records stem largely from Washoe Lake (Linsdale, 1936, 1951; Alcorn, 1941, 1946; Gullion, 1951). In Louisiana, where the Fulvous has been recorded at least since 1892 (Beyer, 1900), nesting records were entirely lacking (Oberholser, 1938) until Lynch (1943) recorded his discoveries of 1939. Thereafter, Lowery (1955) and Meanley and Meanley (1959) added other records. Then, in the mid-1950's, a dispersal began. By 1961, Newman and Andrle (1961) were able to cite records from Florida, North and South Carolina, and Virginia. They say (p. 8) that "the movement seems to have been picking up force . . . so that one can now find wintering flocks more easily in the South Atlantic States than in Louisiana . . ." Enough so, in fact, that Chamberlain (1961:14-15) believed it "almost certain that this sampling was but a small fraction of those that moved northward." Sykes (1961) wrote of the whistling-duck "invasion" into coastal Virginia. A year later, Baird (1963:6) added New Jersey, Rhode Island, and New Brunswick, prompting his conclusion that "clearly here is a species on the move, for these records are not of single birds but of flocks . . ." Biaggi and Rolle (1961) recorded a flock of Fulvous Whistling-ducks in Puerto Rico during the winter of 1960, and two birds were recently shot during Maine's hunting season (G. W. Davis, personal communication). A host of additional records could be cited.

Thereafter, a second phase appeared in what already was a dramatic range expansion: Fulvous Whistling-ducks headed inland to the Great Lakes region. These and the coastal records are shown in Fig. 3, adapted from Baird (1963).

Published accounts of the range of the Black-bellied Whistling-duck in the United States include "lower Rio Grande Valley and irregularly to Corpus Christi" (Bent, 1925:272), "visit Texas" (Kortright, 1942:375), "from the border of Texas (south)" (Delacour, 1954:74), "common on the Lower Rio Grande" (Phillips, 1922:158), and "not uncommon in suitable places along the Lower Rio Grande" (Sennett, 1878:62). Dresser (1866:42) adds that the species is "found occasionally near Matamoras during the summer" on the Mexican side of the Rio Grande at Brownsville. We conclude from these observations that Black-bellied Whistling-ducks formerly nested in the lower Rio Grande Valley and only infrequently extended north of this drainage. Some range maps indeed fix the Rio Grande River as the northern limit of this bird's distribution (see Kortright, 1942:376).

Our records from several more northerly areas (Nueces, Kleberg, Live Oak, and San Patricio counties) indicate a recent, although limited, expansion of breeding distribution (see also Delacour, 1964:329; Oberholser, 1974:148). Artificial lakes have apparently influenced this expansion. The most notable breeding population occurs at Lake Corpus Christi (Lake Mathis on earlier maps) in Live Oak and San Patricio counties. The numbers of Black-bellied Whistling-ducks in this area presently exceed the nesting population in the Rio Grande Valley.

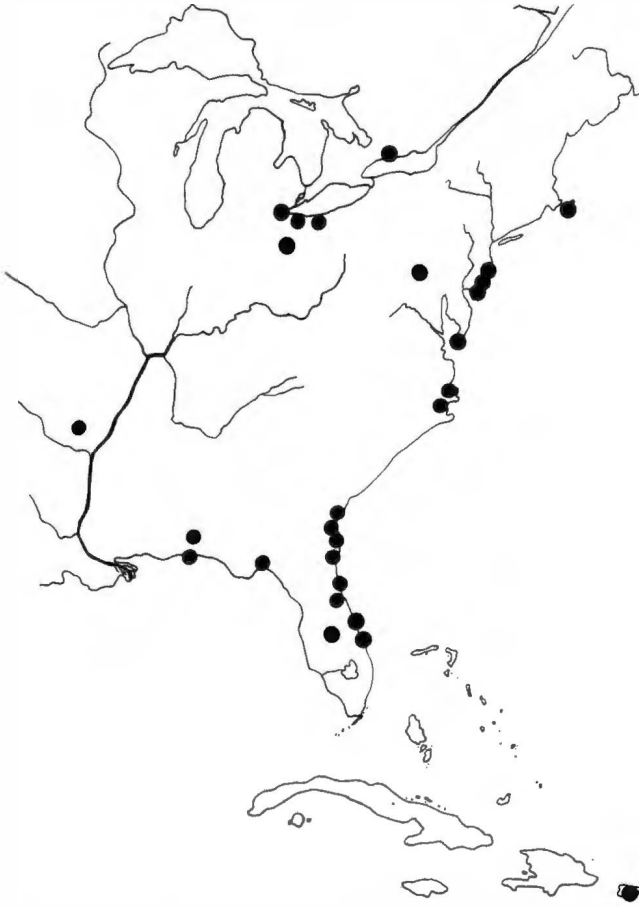


FIG. 3.—Sightings (in part) of Fulvous Whistling-duck, 1955 to 1980.

At the Welder Wildlife Foundation, near Sinton, Texas, the late Clarence Cottam told us that Black-bellied Whistling-ducks nested on the Foundation's lakes in the late 1950's (Cottam and Glazener, 1959). His searches of museum collections, however, failed to turn up specimens of the species even though the Welder vicinity was investigated many years before. Hancock (1887), for example, makes no mention of the Black-bellied Whistling-duck in the Corpus Christi region although many other species of ducks are named in his checklist. Evidently the small, natural lakes have not attracted the birds until recently; these are highly susceptible to drought and may be quite dry for some time. Wet years, in contrast, seemingly aid range extension. Meitzen (1963) noted the influx of marsh and waterbirds, whistling-ducks among them, eastward into Calhoun and Refugio counties during and following the wet year of 1957. Lamm (1948) likewise remarked about the dispersal of White-faced Whistling-ducks during Brazil's rainy season.



There are some references to expanded range that may be inaccurate, or at least improbable, especially when breeding status is implied. Friedmann (1947) included Louisiana in the range of the species, but Lowery (1974; 179) reported the recovery in Louisiana of a single Black-bellied Whistling-duck banded near Sinton, Texas. We question the observation of a “. . .gunner (who) told me that this bird is common during the winter” at Galveston (Dresser, 1866:42).

The White-faced Whistling-duck's range includes both South America and Africa, sympatric with much of the Fulvous Whistling-duck's distribution in these continents. Sightings in the West Indies are rare and “possibly of accidental occurrence” (Wetmore and Swales, 1931). The northern limit of its distribution in the New World is likely in Costa Rica, where Griscom (1933) recorded six specimens as from an “outlying colony” and not unlike those from South America. Slud (1980) reported it “with some frequency” during the wet season, and occasionally during the dry season in northwestern Costa Rica.

Despite the disjunct distribution of White-faced Whistling-ducks in Africa and South America, no valid racial separation is recognized. Friedmann (1947) examined an extensive series of specimens and concluded that although the South American birds were slightly larger in their average size (especially tarsal and toe measurements), the overlap with African birds was too great to justify racial separation. Furthermore, the designation of the race, *D. v. personata*, proposed in 1854 by Hartlaub (*in* Friedmann, 1947) on the basis of an interrupted black throat band in the African birds, is not acceptable; the plumage of South American specimens also includes this aberration within and between the sexes.

Clark (1974) reviewed the status of White-faced Whistling-ducks in southern Africa, noting the expansion of the birds' range in the Transvaal, Zululand, Natal and the Orange Free State (but not in Western Cape Province). Earlier records, dating to 1906 and the following three decades, described the species as rare or as an irregular visitor. Water projects (storage dams and sewage effluent ponds) were credited for the range expansion; White-faced Whistling-ducks were more successful in establishing resident breeding populations than Fulvous Whistling-ducks (Clark, *op cit.*). The extensive rice fields and marshlands of northern Nigeria attracted thousands of birds; they fed there at night, but not exclusively, as Serle (1943) also saw flocks of White-faced Whistling-ducks feeding on newly tilled farmland during the daytime.

Range expansions similar to those of the Fulvous and Black-bellied Whistling-ducks are not without precedent among other waterfowl. Mendall (1958:20) says of the Ring-necked Duck *Aythya collaris*: “There has been a series of expansions from locally established groups which first appeared considerably east of the former range.” Pioneering tendencies and the loss of breeding habitat were suggested causes of the movement. Newly formed favorable habitat may likewise expand distributions. Hochbaum (1946:407)

says, "When new water areas are created there is a response on the part of certain ducks which come to nest at these new places. We see this in the new refuge marshes (and elsewhere), where ducks moved into areas with which they could have had no previous experience."

Pioneering, indifferent of existing range conditions, may help us understand discontinuous distributions. Not long ago the Gadwall *Anas strepera* ventured far eastward of its usual breeding grounds; the nesting populations now established on Long Island and in Maryland are certainly the result of successful pioneering (Hochbaum, 1955:230).

Based on homing data, Sowls (1955:42) suggested that juveniles are more likely to populate new areas than are adults. He noted that fewer young birds return to their natal origins than do adults with previous nesting experience; differential survival rates, however, may somewhat bias these data. Secondly, adult birds return first to the breeding grounds, and when the younger birds subsequently arrive, internal population pressures might force the latter to nest elsewhere.

That young birds are frequently pioneers may be related to the fall and winter Fulvous Whistling-duck records from the Atlantic seaboard. Two ideas seem plausible. Following the breeding season, populations would be at their yearly peak with young birds in the majority, and such a population build-up might account for the fall and winter dispersal of Fulvous Whistling-ducks (Baird, 1963). In addition, the restlessness that flying young-of-the-year seem to exhibit may explain the widespread wanderings of juvenile ducks preceding their first migratory flight (Hochbaum, 1955:144) and also an expansion of their range. Jones (1966) simply believes that the Fulvous Whistling-duck is an "aggressive species" that colonizes new areas.

The Louisiana Fulvous Whistling-duck population evidently started with similar off-season visits; only much later did nesting occur. Beyer *et al.* (1907:321) remarked, "Though a native of tropical and subtropical America, this species has been observed in Louisiana, not as might have been expected, in summer, but in fall and winter." Years later, the Fulvous Whistling-duck was still considered a "regular winter visitor" (Anon., 1931). It appears then, that winter visits, like those now occurring in the eastern United States, represent a step that precedes summer flights and breeding. If so, an Atlantic Coast "tradition" among Fulvous Whistling-ducks may be unfolding.

As an interesting sidelight, the Fulvous Whistling-duck's winter range has recently extended as far south as Guatemala (Tashian, 1953) and Costa Rica (Slud, 1980).

There is no reason to suppose that pioneering has not, in some ways, accounted for range expansion, but it is far easier to list what appear to be unsuccessful pioneering attempts than to propose what has allowed others to be successful. Some of these, for the Fulvous Whistling-Duck, are Iowa (Roberts, 1932), Florida (Sprunt, 1940), and Utah (Bear River Refuge files). Black-bellied Whistling-ducks have been reported from Arizona (Brown,

1906; Vorhies, 1945), California (Bryant, 1914b) and Illinois (Moyer, 1931). Lacey (1911) noted a Black-bellied Whistling-duck near Kerrville, Texas, well north of the Coastal Bend counties.

Cain (1973), studying the metabolic rates of Black-bellied Whistling-ducks, believed that the northward distribution of this species may be limited by low temperatures that decrease the amount of energy available for successful reproduction. Approximately 125 kcal/bird-day is required for the production of a single egg, and his calculations suggest that Dallas, Texas, would represent the extreme northern limit for reproductive success. However, a decrease of 2.5°C in the average monthly temperature in May (at Dallas), would offset the energy available for successful breeding at that latitude. The species' northernmost breeding range in North America thus remains some 375 air-miles to the south of Dallas, in the general vicinity of Corpus Christi, Texas.

The creation of specialized habitat may have in part provided a stepping stone for increasing whistling-duck distributions. The first time the Fulvous Whistling-duck populated Louisiana is unknown, but it apparently coincided closely enough with the beginning of rice husbandry for Lynch (1943:101-102) to state that "it is not impossible that rice culture made possible the extension of the nesting range of this bird into Louisiana, since most of this region had been prairie prior to cultivation." The rice belt of Texas seemingly had the same effect. Carroll (1930:202) writes that "the northward movement of (this) duck in Texas, having nearly forsaken their old habits in the Rio Grande Valley and breeding regularly now not a great distance west of Houston, where fifteen or twenty years ago they were practically unknown . . ." is likely associated with the area's rice industry. Carroll (1932) later published a note discussing this hypothesis more fully. Arkansas' rice fields may have attracted the flocks observed near Lonoke (Meanley and Neff, 1953; Baird, 1963). Wetmore (1919) associated Fulvous Whistling-ducks with the rice fields of the Sacramento Valley in California. In Louisiana, rice phenology and maturation governs much of the birds' movements and nesting ecology (Hasbrouck, 1944; Meanley and Meanley, 1959).

The intimate associations of Fulvous Whistling-ducks with rice culture are undoubtedly of significance both to dispersal and the expansion of breeding range.

We may now ask if there is something about the whistling-duck *per se* that has encouraged these movements, or whether some external factors, in addition to those already discussed, presently exist which might allow any southern bird to expand northward. Dorf (1960:359) writes, "In the animal world many southern types of both birds and mammals have been extending their habitat ranges northward as a result of the warming trend 'of recent times'." He cites the Cardinal *Richmondia cardinalis*, Tufted Titmouse *Parus bicolor*, and Blue-winged Warbler *Vermivora pinus* as examples of birds that have moved northward in the United States as a consequence of the warming trend. He predicts that this trend might continue over much of

the Northern Hemisphere for two or three hundred years. Mayr (1946) suggested that temperate zone groups can perhaps become more easily adapted to tropical climates than can tropical birds to a temperate climate. A tropical group of waterfowl such as *Dendrocygna* may provide instructive illustrations.

### *Distributional Patterns*

When referring to intercontinental discontinuous distributional patterns of birds, few authors fail to mention the Fulvous Whistling-duck. Numerous texts could be cited, but Phillips' (1922:129) remarks seem especially apt: "No other known bird has a range so remarkable as this one, for it occurs unaltered in four distinct zoological regions. Even the boldest of the hair-splitting systematists must, we think, admit that there are not visible differences among the specimens from California, Argentina, East Africa, and India." However, Peters (1931), and later Friedmann (1947), maintained that the North American birds constitute a valid subspecies. According to them, a narrow bill (less than 20 millimeters) reliably separates these from all other populations. Little support for this subspecific distinction has followed (Delacour, 1954:42), and no subspecific status is given to Fulvous Whistling-ducks in our discussion. Knowlton (1909:193) reported an earlier contention that the Fulvous Whistling-ducks might have three races, but thoughtfully added ". . . it is as difficult to explain the geographical distribution of three as of one." He and Sclater (1864) also reported rumors that slaves introduced Fulvous Whistling-ducks, as pets, into the New World, but there is no evidence to support this contention.

The White-faced Whistling-duck also has a widely disjunct distribution without exhibiting significant geographic variation (Fig. 2). Hence, both the Fulvous and White-faced Whistling-ducks seem appropriate subjects for a discussion of discontinuous continental distributions among the *Dendrocygna*.

Two hypotheses, which are not mutually exclusive, may account for the discontinuous distributions of whistling-ducks: either the birds have expanded by surmounting oceanic barriers, or they have been restricted to their present ranges from an earlier, widespread distribution. In either case, the resulting isolation in the current distribution has not initiated clear racial distinctions.

Mayr (1946) included both the White-faced and Fulvous Whistling-ducks in a discussion of the Pantropical Element (groups that are more or less restricted to the tropics, but are found in both the Old and New World). He notes that the ranges of both species obscure the origin of their group and feels (p. 34) ". . . reasonably certain that transoceanic flight" is the answer that explains the distributions of these whistling-ducks. In describing the affinities of South American and African faunas, Moreau (1966) also suggested that both species made a direct oceanic crossing even though neither are regarded as long-distance fliers. Friedmann (1947) concurs, but he adds

that such dispersals may have been passive, with storms perhaps driving the birds to their present locations. Some recent evidence of Fulvous Whistling-ducks resting in the Sargassos Seas lends credence to the idea that whistling-ducks may undertake transoceanic flights (Watson 1967). McCartney (1963:116) also suggested that Fulvous Whistling-ducks cross stretches of salt water; he postulates routes of about 60 miles length across the Gulf between Louisiana and central Mexico.

Intercontinental dispersal, if of recent occurrence, also satisfied the genetic homogeneity of the respective White-faced and Fulvous Whistling-duck populations. If the restriction idea is accepted, an extraordinarily slow rate of evolutionary development must be accepted unless subsequent genetic infusions occurred by transoceanic dispersals.

According to the restrictions theory, the present distributions are the southern remnants of continuous, high-latitude northern populations. As the northern areas cooled, these populations retreated south; and inasmuch as the continental land masses become more water-isolated southward, the birds were then divided among the continents of their present range.

Island patterns, as well as intercontinental patterns, also are represented among whistling-ducks. The Cuban Whistling-duck is resident in the Bahamas, Greater Antilles, the northern Antilles, and casual elsewhere in the West Indies. No definite mainland records for North America are known (Johnsgard, 1975:52). Danforth (1929) listed the Cuban Whistling-duck as abundant in certain marshes in Hispaniola but less so elsewhere. Cuban Whistling-ducks were considered the most common duck in Haiti but of uncertain status in the Dominican Republic (Wetmore and Swales, 1931). Northrop (1891) also found it abundant on Andros Island in the Bahamas.

Whereas their carcasses were once sold in the markets of Cuba (Cory, 1892), our recent inquiries among ornithologists familiar with Caribbean birds have repeatedly indicated that Cuban Whistling-ducks are today uncommon or even rare. Overshooting may account for their diminished populations.

That the two species of whistling-ducks regarded by Delacour and Mayr (1946:11) as primitive—*D. arborea* and *D. guttata*—should also enjoy only limited, insular distributions fits well with the idea that more advanced forms gradually replace older ones. The latter may remain as small, often relict populations near the perimeter of an earlier and larger distribution. The distributions of the Cuban and Spotted Whistling-Ducks accordingly suggest a radial pattern of distribution that perhaps developed coincident with constriction to the modern tropics; they remain as distributional relicts, widely separated east and west, from a presumed center of whistling-duck origin.

Some behavioral evidence supports the suggestion that the island-dwelling Cuban Whistling-duck is closely related to the continental Black-bellied Whistling-duck. Johnsgard (1965:23) notes the similarity of the copulatory displays between these species. This and some similarities in wing plumage

suggest that the Cuban species shared an ancestor in common with the Black-bellied Whistling-duck prior to its insular isolation.

Some island species may be short lived, as these birds often lose the genetic adaptability to compete successfully with the continental invaders. Presumably the competition is even keener when the invaders are closely related forms. Fulvous Whistling-ducks have recently visited Puerto Rico (Biaggi and Rolle, 1961); Wetmore (1938) and Struthers (1923) also recorded the Black-bellied Whistling-duck on the same island. The presence of well entrenched species on the continents adjacent to the East Indies is somewhat similar. From present distributions (Fig. 2) it is seen that the Indian and Spotted Whistling-ducks are about complementary in their island distributions. The Wandering Whistling-duck overlaps much of both, but it does not enter the continental range of the Indian Whistling-duck. Weller (*in* Delacour, 1964:117) further noted that the Wandering Whistling-duck occurs on those islands and continents where the Fulvous Whistling-duck is absent.

Off-shore islands and island chains, whether oceanic or continental, are all within present whistling-duck distributions. Sri Lanka (Ceylon), Madagascar, the East and West Indies, and the Philippines all have representatives of the whistling-duck tribe; most of these are continental species. New Zealand is seemingly remote enough from Australia, or has insufficient optimal habitat, to prevent whistling-duck dispersal, whereas there are no such barriers to colonization in the Fiji Islands.

The suggestion arises that radiation to island habitats occurred quite some time ago. Contact between island and continental species is common, but niche segregation has apparently evolved to the point where the island-dwelling whistling-ducks are protectively isolated. More, of course, needs to be learned about the ecology of the island species in relation to those of the continents. It also appears that dispersal has been largely a one-way route—from continent to adjacent island with little, if any, return to the mainland by the island forms. Interesting exceptions occur on Madagascar and Sri Lanka where each island lacks an endemic island species of whistling-duck similar to the situation in Cuba (*arborea*) or the East Indies (*guttata*).

#### COMPARATIVE ECOLOGY

##### *Black-bellied Whistling-duck*

The Black-bellied Whistling-duck is exclusively a New World species. Its range includes both North and South America, but ecological data for the species south of Mexico are quite limited. Thus, nesting food habits, etc., for the southern race, *D. a. discolor*, are essentially unknown, although these may not differ greatly from the northern race. Bolen (1964) has published weight and linear measurements for *D. a. autumnalis* and Bourne (1979) has done likewise for the southern race, *D. a. discolor*.

Black-bellied Whistling-ducks are particularly adept in arboreal environments. Their facility for perching in trees is most evident during the nesting

season when the adults search for cavities. Climbing behavior is exhibited by newly hatched ducklings on exit from the nest cavity. The leg musculature in the ducklings is demonstrably unlike that of a sympatric congener, the Fulvous Whistling-duck, that nests on the ground (Rylander and Bolen, 1970; Rylander, 1975). We have on many occasions witnessed adult Black-bellied Whistling-ducks adroitly perched on phone wires, wire fences, and similar perches.

Whereas aviculturists have long noted that the Black-bellied Whistling-duck, and others of the tribe so far as is known, maintain long pair bonds, the maintenance of year-to-year pair bonds for this species has only recently been documented under field conditions. These data were obtained primarily by capturing and banding each member of a nesting pair and subsequently recapturing them together one or more years later (Bolen, 1971). Of the seven instances of known year-to-year mate retention, six pairs were recaptured together on nests one year after they were initially recorded as nesting pairs and thus represent, minimally, two consecutive years of pair-bond maintenance. One other record at hand concerns a pair that was initially captured in 1966 and again in 1968 and 1969; in this instance, the pair-bond was maintained for at least four consecutive years. Mortality between nesting seasons, of course, lessens opportunities for recovering an intact pair a second time and presumably accounts for the occurrence of one member of a banded pair later found with an unbanded mate. Delnicki (personal communication) banded 106 pairs of Black-bellied Whistling-ducks incubating in nest boxes. Of these, he later found two occurrences where both members of each pair acquired new mates even though their former mates still were living. Both of the remated pairs nested successfully in the season before they acquired new mates. According to Cooke *et al.* (1981), "divorce" is equally rare in snow geese (*Anser caerulescens*), and its occurrence does not seem related to previous reproductive success or failure.

Bolen and McCamant (1977) compiled dynamic life tables for the species using band recoveries and recapture data for birds returning to nest a second year. These data indicate that Black-bellied Whistling-ducks experience an annual mortality rate of 46 to 52 per cent, and that females may suffer slightly higher, but statistically insignificant, mortality than males.

Homing tendencies for each of the sexes are thus about as equal as might be expected in a species with year-to-year pair-bond tenure (see Sowls, 1955:40-41, for details of homing phenomena in surface-feeding ducks, *Anas*). Males are as faithful as females in their annual return to nesting areas utilized the year before. The composition of the flock in spring further reflects the balance of this population parameter. Sex ratios for adult Black-bellied Whistling-ducks captured with a cannon-net represent a statistical distribution of 50 per cent for each sex (Table 3).

Courtship in the Black-bellied Whistling-duck is an inconspicuous ritual; precopulatory behavior is probably derived from drinking movements (Johnsgard, 1965:24). Post-copulatory behavior is more obvious, but less so

TABLE 3.—Summary of sex ratio information for Black-bellied Whistling-ducks in south Texas. All data statistically represent a 50:50 distribution ( $P < 0.05$ ). Adapted from Bolen (1970).

Determination	No. males	No. females	Per cent males
Primary (fertilization)	226	209	51.9
Secondary (hatching)	172	165	51.0
Tertiary (juvenile)	12	10	54.6
Quaternary (adults)	327	304	51.8

than for the Fulvous Whistling-duck; the mates stand side-by-side and prominently display their necks in a deeply S-shaped stance, but the conspicuous wing-lifting of the Fulvous Whistling-duck is seldom observed.

Nesting in Texas begins late in April and extends into September. The nesting season is thus lengthy and, as shown in Table 4, does not have a pronounced peak period of nest initiation. Selective forces that foster peaks in waterfowl nesting in more temperate latitudes—presumably the advent of fall weather too adverse for duckling survival in nests begun late in the season—are understandably lacking in the tropically distributed Black-bellied Whistling-duck. That nesting begins relatively late in the long period of mild weather in south Texas (growing season 283 days for the region) supports Weller's (1964) suggestion that no selective pressure(s) toward early breeding occurs in the south because of the relatively long period suitable for rearing broods.

Nests for this species are most often located in natural cavities in a variety of trees at varying distances from water (Delnicki and Bolen, 1975). Live oak *Quercus virginiana* is highly utilized because of the relatively large number of trees with suitable cavities; ebony *Pithecellobium flexicaule* is also locally important in this respect. Both live oak and ebony are of durable wood and are long lived, thus insuring the greatest possibility of year-to-year availability of cavities for repeated utilization of homing Black-bellied Whistling-ducks. Less durable trees may rapidly deteriorate; Erskine (1961) reported that six per cent of the cavities used by Buffleheads *Bucephala albeola* were no longer suitable or available the following year. Delnicki and Bolen (1975) determined that one suitable cavity was available as a nesting site for every 19 acres of ebony or live oak savannah. As with Wood Ducks *Aix sponsa*, the cavity-nesting habits of Black-bellied Whistling-ducks lend themselves to a nest box management program that materially reduces nest predation (Bolen, 1967a). McCamant and Bolen (1979) summarized 12 years of nest box utilization, finding that more than 80 per cent of the nest boxes were utilized and that 75 per cent of the incubated nests produced ducklings. Because of "dump nesting" (see following) and abandonment without incubation, only 28 per cent of all nests ( $N = 746$ ) hatched ducklings along with a corresponding reduction in the percentage of hatched eggs (Table 5).

An unknown proportion of the Black-bellied Whistling-duck population choose to nest on the ground. The sites of ground nests are as varied as those for tree cavities (for example, distance from water), but they are generally



TABLE 4.—*Periods of nest initiation for the Black-bellied Whistling-duck in south Texas, 1963-65.*<sup>a</sup>

Date	Semimonthly numbers of nests started by years			Semimonthly numbers and per cent for all years			Accum. %
	1963	1964	1965	Numbers	Mean	Per cent	
April 15—30	0	0	1	1	0.3	1	1
May 1—15	0	2	3	5	1.7	5	6
16—31	7	10	9	26	8.7	23	29
June 1—15	6	6	14	26	8.7	23	52
16—30	5	0	6	11	3.7	10	62
July 1—15	10	4	4	18	6.0	16	78
16—31	4	6	5	15	5.0	14	92
August 1—15	1	1	3	5	1.7	5	97
16—31	2	1	1	4	1.3	3	100
Totals	35	30	46	111	37.1	100	

<sup>a</sup>Field work in 1962 was limited to June, July, and August. Of eight nests dated in 1962, one was initiated 1—15 June; three, 16—30 June; two, 1—15 July; two, 16—31 July; and none in August.

well concealed under an overstory of brush. Whether or not this habit is passed on from one generation of ground-nesting birds to the next remains unknown.

Clutch size for the species averages 13.4 eggs ( $N = 58$  nests) and may vary between nine and 18 eggs (Bolen 1967*b*). However, calculation of mean clutch size for Black-bellied Whistling-ducks is complicated by their propensity to lay compound clutches or "dump nests." Clutches of unusually large sizes, far in excess of the physiological capabilities of a single hen, are commonplace. The most notable of these is the extreme of 101 eggs laid in a single nest box (Delnicki *et al.*, 1976). Nonetheless, many of the compound clutches are successfully incubated by a single pair of birds. On the other hand, the percentage of eggs that hatch decreases as the size of the clutch increases since the hen's inability to cover properly the entire clutch staggers the development of the incubating eggs and hatching is thus quite asynchronous. The subject of nest parasitism is more fully discussed by Weller (1959) but the evolutionary implications of this trait in Black-bellied Whistling-ducks remain, in our judgment, an enigma.

The incubation period averages 28 days, based on our field work, but this time period may not represent exactly the incubation period under ideal field conditions. The date that the clutch is complete and the date of hatching are often difficult to obtain for an adequate series of nests under field conditions. Moreover, individual variation adds to the problem. Breckenridge (1956) suggests that the six-day variation he found in Wood Duck incubation periods resulted from individual differences among each hen's attentiveness to her clutch; some hens were off the nest more than others and the period's length varied accordingly. Because both male and female Black-bellied Whistling-ducks alternately incubate, the amount of individual variation is doubled per nest. Finally, interruptions during incubation may affect determination of the incubation period. Stotts and Davis (1960) support this

TABLE 5.—Summary of nest box utilization, nest success, and hatched eggs for Black-bellied Whistling-ducks, 1964–75, inclusive. Data adjusted for nest and eggs experimentally removed for other purposes. Adapted from McCamant and Bolen (1979).

No. boxes available	No. boxes used	% used	Research effort	
			No. visits	Visits/box
622	506	81.4	8,494	13.7

No. nests	No. incubated nests	No. successful nests	%Successful	
			All nests	Incubated nests
746	279	210	28.2	75.3

No. eggs			%Hatching	
All nests	Incubated nests	Hatched	All nests	Incubated nests
21,982	8,868	4,276	19.5	48.2

view with data indicating that longer incubation periods occurred when Black Duck *Anas rubripes* hens were repeatedly flushed from their nests. Delacour (1954:47) and Johnstone (1957) list 27 and 26 days, respectively, as the incubation period for Black-bellied Whistling-ducks raised under captive or semicaptive conditions.

Renesting—the production of a replacement clutch following the loss of the initial clutch—proceeds in Black-bellied Whistling-ducks without a change in mates. This behavior is consistent with the long pair-bonds maintained by the species. Delnicki and Bolen (1976) found that at least 19 per cent of pairs whose first nest they “destroyed” produced second nests the same breeding season. The persistence of renesting in this species was indicated when the second clutch of the season was likewise removed from two pairs who subsequently renested a second time (that is, their third clutch of the year). The distances between first nests and renests were not significantly different from the year-to-year locations of first nests by the same pair. Unfortunately, renesting has not been studied in any other species of whistling-duck.

Bolen and Smith (1979) recorded the attentiveness of a pair of incubating Black-bellied Whistling-ducks for eight days using a telemetric monitoring system (see Smith and Bolen, 1979). The division of labor in this pair was equal, with each sex contributing about 42 per cent of the incubation; the nest was unattended for 16 per cent of the period. Interestingly, the day-to-day regime showed that one sex dominated incubation during a 24-hour period, followed by the dominance of the other bird for the next 24 hours; this regime alternated daily but balanced evenly in each sex’s overall attentiveness throughout the period of study. Rylander *et al.* (1980) examined skin tissues for differences, if any, between the amount of vascularization of male and female birds during incubation; no evidence of dimorphism was found. The abdominal skin of each sex was highly vascularized with essentially the

TABLE 6.—Summary of foods for the Black-bellied Whistling-duck in southern Texas. Adapted from Bolen and Forsyth (1967).

Item	Per cent volume <sup>a</sup>	Per cent frequency <sup>b</sup>
<i>Cynodon dactylon</i>	29.5	45.5
<i>Sorghum vulgare</i>	48.3	31.8
<i>Echinochloa</i> sp.	5.7	18.2
<i>Polygonum</i> sp.	0.6	27.3
<i>Heteranthera liebmanni</i>	13.2	22.7
<i>Zea mays</i>	2.0	4.5
Mollusca	5.0	36.4
Insecta	3.0	22.7

<sup>a</sup>Data shown here combine foods from stomachs and crops.

<sup>b</sup>Data from stomachs only.

same degree of development although neither showed the defeathered areas known as incubation patches that are common in incubating passerines. As one might therefore predict, each sex of incubating bird also provided equal amounts of thermoregulation during their respective periods of attentiveness (Bolen and Smith, 1979). McCamant and Bolen (1977) found that surviving adults of either sex will not continue incubation alone when their mates are lost.

Black-bellied Whistling-duck nests are not lined with down, a trait Delacour (1954:31) attributes to all of the eight species of *Dendrocygna*. Johnsgard (1961) believes this may be associated with the male's role in incubation, thus making it unnecessary to have down for insulation.

Bent (1925:270) describes the eggs of Black-bellied Whistling-ducks as ovate or short ovate with the white to creamy white shell finely pitted or glossy and smooth. The eggs we examined were finely pitted when fresh and unincubated but they became smooth and glossy as incubation progressed. They are in general quite similar to the white eggs of domestic poultry. Measurements taken in the field of 538 eggs averaged 52.7 millimeters long ( $S_d = 3.08$ ) and 38.9 in width ( $S_d = 1.96$ ).

Food habits of the Black-bellied Whistling-duck in southern Texas reflect a highly vegetative diet (Bolen and Forsyth, 1967). By volume, 92 per cent of the items from 22 stomachs and 11 crops were plant material, principally cultivated grain sorghum *Sorghum vulgare* and Bermudagrass *Cynodon dactylon* (Table 6). Other food plants included smartweeds *Polygonum* sp., millets *Echinochloa* sp., and water stargrass *Heteranthera liebmanni*. All plant foods consisted only of seeds and did not include leaves, stems, or other vegetative structures. Animal foods (eight per cent by volume) consisted of insects and mollusks with the snail *Physa anatina* of some importance. Similarly, a sample of 30 adults from Guyana contained 97 per cent plant materials (Bourne, 1981). The animal foods in these birds were limited to aquatic insects and snails although two contained small tadpoles of the marine toad *Bufo marinus*. Food habits for the species change with the advance of the growing season. In Texas, there is an initial period following

the birds' spring arrival when stockyard grains are utilized; this is followed by Bermudagrass in May and the seeds of aquatic plants in summer. Stubble flights to sorghum fields occur in the early autumn.

In Venezuela, Bruzual and Bruzual (1983) analyzed the stomach contents of 13 Black-bellied Whistling-ducks and found that plant material comprised 99 per cent by volume. The principle species were *Oryza sativa*, *Echinochloa colonum*, and *Cyperus palustris* in frequency; and *O. sativa* and *Cyperus rotundus* in volume. In Guyana, the southern race of Black-bellied Whistling-ducks in season feeds extensively in cultivated rice fields, allegedly reducing yields in the harvest. However, Bourne and Osborne (1978) found that depredation was less than two per cent and that cost estimates of the crop losses were not of a magnitude to consider the species a serious economic pest. Their study also determined that the birds ingested 20 grams of ungerminated rice seed per feeding and the feeding activities peaked during the nighttime at 20:00 and 03:00. Newly sown, flooded rice fields were used for feeding, whereas dry-sown fields were selected for daytime maintenance activities.

External parasitism has been studied by McDaniel *et al.* (1966), who noted the presence of six arthropods, including mallophagans and acarinids. Endoparasites found in Black-bellied Whistling-ducks include cestodes, nematodes, trematodes, an acanthocephalan and a nasal mite (George and Bolen 1975). Overall, 47 per cent of the 90 birds examined harbored helminth parasites; juveniles were more heavily parasitized than adults but no correlation existed between the parasite loads and the physical condition of the host. Such light parasite loads may reflect the food habits of the host, since their primary reliance on plant foods, described above, may preclude high rates of infection. In comparison, Lavery (1970) determined the extent of endoparasitism in the two Australian species, one which frequently eats mollusks and the other which feeds as a dry-land grazer. He found that the infection rates for intestinal helminths were 87 per cent and seven per cent, respectively.

Brood ecology has not been studied adequately for any species of whistling-duck, although Cain (1970) described the growth and plumage development in juvenile Black-bellied Whistling-ducks. Flight is attained between 56 to 63 days and the juvenile plumage is complete at 10 to 13 weeks, with the first annual plumage present by the 34 to 35th week. Regarding brood mortality, Bolen (1967b) suggested that more ducklings are lost early in life than later, and that broods are not greatly reduced after this early period of duckling mortality. Further, a small sampling of broods indicated that those accompanied by only one parent (assuming the permanent loss of the other parent) were of smaller size than similarly aged broods accompanied by both parents (7.7 ducklings of flying-age versus 9.7 ducklings, respectively). Bolen and Beecham (1970) noted that juvenile Black-bellied Whistling-ducks apparently do not rely heavily on animal foods as do some other species of waterfowl; although the crops of a 21-day-old brood

contained insects from 17 families as well as spiders and other invertebrates, the total animal matter in these and the crops of a 35-day-old brood did not exceed nine per cent. In Guyana, Bourne (1981) found that juveniles consumed little more than 10 per cent animal foods by volume; young apple snails *Pomacea* sp. dominated these materials. However, the animal foods in two ducklings of unspecified age reached 54 per cent by volume, dominated by spiders and trace amounts of shorefly *Scatella stagnalis* larvae and pupae. The movements, survival, and other facets of brood ecology remain among the more important gaps in our knowledge of the entire whistling-duck group.

### *Fulvous Whistling-duck*

Fulvous Whistling-ducks seldom, if ever, perch, and they typically nest in clumps of marsh grasses or similar vegetation rather than in tree cavities. Older literature (see Bent, 1925) reporting nests of this species in tree cavities is almost certainly in error, especially where Fulvous Whistling-ducks are sympatric with other cavity-nesting waterfowl. In these cases, the eggs of one species may have been mistaken for those of the other. Rylander and Bolen (1970) have shown that the leg musculature in ducklings of this species is unlike that of a cavity-nesting congener. In particular, the feet of Fulvous Whistling-ducks are larger in proportion to their tarsi length, suggesting a strong adaptation for aquatic rather than arboreal movements.

Pair-bond tenure under field conditions is not well documented for this species, although aviculturists have noted long-term pairing in captive birds and the male's role with incubation (Delacour, 1954:32). Flickinger (1975) collected a male Fulvous Whistling-duck incubating a 13-egg clutch in a rice field near El Campo, Texas, thus confirming this trait in wild birds.

Spring sex ratios, homing tendencies, and other details of Fulvous Whistling-duck populations prior to the onset of nesting are unknown.

Courtship behavior, as in other species of whistling-ducks, is ill defined (Johnsgard, 1965:17). However, the postcopulatory display of Fulvous Whistling Ducks is especially showy. Immediately following copulation, the male dismounts and stands side-by-side with the female in shallow water; both then stand erect facing the same direction and tread in a splashing "step-dance" while uplifting their outer wings. The birds' necks are deeply curved into an "S" so that the bill touches the breast plumage throughout the display. The posturing is such that one mate is the mirror image of the other partner. Meanley and Meanley (1958) published fine photographs of a pair of Fulvous Whistling-ducks in full postcopulatory display.

Data of sufficient quality and quantity currently do not exist to delineate the nesting chronology of the Fulvous Whistling-duck. However, the nesting season in the United States is lengthy. Barnhart (1901) found a "full clutch" on 28 April and other nests in May; June seems the month of peak nesting activity in California. Fulvous Whistling-ducks seem highly adaptable to changing environmental conditions within the broad framework of an oth-

erwise suitable nesting season. Cottam and Glazener (1959) emphasized the role of late season rainfall and the attendant vegetational response in the nesting chronology of Fulvous Whistling-ducks and other waterbirds in south Texas. In particular, Lynch (1943) noted that the species nests late in the summer, usually in late July, probably because the maturing rice offers adequate nesting cover then. Meanley and Meanley (1959) reported that nesting began in mid-May, "or as soon thereafter as the rice is high enough to provide nesting cover," and extended into August.

Where it exists, rice *Oryza sativa* culture is important to the ecology of the Fulvous Whistling-duck. Lynch (1943) suggested that rice culture fostered the extension of the breeding range of this bird into Louisiana since much of the area had been unbroken prairie prior to rice cultivation. Meanley and Meanley (1959) plotted the spring movements of the birds from the freshwater marshes along the coast into the rice-belt areas when the rice plants reached 20 to 25 centimeters in height; by April, when the rice was 30 or more in height, the population had extended into most of the rice-producing areas. For nest cover, rice mixed with heavy infestations of weeds, *Echinochloa* sp., *Paspalum* sp., *Cyperus* sp., *Polygonum* sp. and others, are preferred over pure stands of rice whereas rice plants more often make up the actual material used in nest construction (Meanley and Meanley, 1959). The nests are almost always located over water in dense vegetation, even in the absence of rice (Cottam and Glazener, 1959).

Populations of Fulvous Whistling-ducks in Texas declined rapidly during the 1960's from exposure to pesticides of the chlorinated hydrocarbon group (Flickinger and King, 1972). These insecticides, principally aldrin and dieldrin, were applied to rice seed to attack the river water weevil *Lissorhoptrus oryzophilus*, but their residual effects caused drastic reduction in the breeding populations of Fulvous Whistling-ducks. More recently, however, the ban on these insecticides resulted in the recovery of the Gulf Coast population; Flickinger *et al.* (1977) reported an aerial census of about 17,000 Fulvous Whistling-ducks in the rice-belt counties of Texas and Louisiana in 1975.

An experiment using hand-reared, color-marked Fulvous Whistling-ducks released into wild flocks in Texas found that the birds moved eastward in late summer and southward later in the year (Flickinger *et al.*, 1973). Some birds were still in the Texas-Louisiana rice belt in November whereas at least one other had traveled to Veracruz, Mexico by October; the latter observation supports the assumption that the Gulf Coast population of Fulvous Whistling-ducks may winter in southern Mexico.

Nesting densities are not well known from large samples but Meanley and Meanley (1959) found 20 and 13 pairs per 5 square miles, respectively, in two areas in Louisiana where the species seemed particularly abundant.

Clutch sizes from a single hen vary from 10 to 15 eggs with an average of 13 per nest (Lynch, 1943). Like Black-bellied Whistling-ducks, Fulvous Whistling-ducks also engage in nest parasitism so that eggs from several

TABLE 7.—Summary of foods for the Fulvous Whistling-duck in Louisiana. Adapted from Meanley and Meanley (1959).

Item	Spring		Autumn	
	Dry-planted rice <sup>a</sup>	Water-planted rice <sup>b</sup>	Mature rice <sup>c</sup>	Mature rice <sup>d</sup>
<i>Fimbrystilis</i> sp.	65			
<i>Paspalum</i> sp.	25		50	30
<i>Eleocharis</i> sp.	10			
<i>Cyperus rotundus</i>			30	
<i>Echinochloa</i> sp.			20	45
<i>Brasenia schreberi</i>		11		
<i>Oryza sativa</i>	trace	78		15
Misc. plant materials		11		10

<sup>a</sup>Percentage frequency from droppings.

<sup>b</sup>Percentage volume from stomachs.

<sup>c</sup>Percentage volume from stomachs and crops.

<sup>d</sup>Percentage frequency from droppings.

hens are placed in a single nest, thus confounding efforts to determine clutch size of individual birds under field conditions. Barnhart (1901) found 62 eggs in one such nest and reported hearing of nests with as many as 100 eggs. Shields (1899) found Fulvous Whistling-duck eggs in the nest of Red-heads *Aythya americana* in California, thus indicating that nest parasitism is interspecific as well. The incubation period in captive birds is 26 days (Johnstone, 1957), although some variations undoubtedly exist.

Bent (1925:275) describes the eggs as bluntly ovate, short ovate, or oval and white to buffy white, often stained with deep shades of buff, and 54.5 by 40.7 millimeters ( $N = 212$ ) in size. Based on our field work, we emphasize that the eggs of the Fulvous Whistling-duck are blunter and obviously more buffy in color than the more ovate and white eggs of the Black-bellied Whistling-duck, a comparison that should help resolve confusion regarding the cavity-nesting habits sometimes attributed to Fulvous Whistling-ducks.

The food habits of Fulvous Whistling-ducks (Table 7), known primarily from studies in Louisiana, only partially reflect their utilization of rice fields. Rice seeds made up 78 per cent of the contents of 15 birds collected in April and May whereas watershield *Brasenia schreberi* comprised 11 per cent of the foods (Imler, in Meanley and Meanley, 1959). However, agricultural practices have much to do with the amount of rice ingested by Fulvous Whistling-ducks; water-planted seed is more readily utilized than seeds in dry fields that are drill planted (see Bourne and Osborne, 1978). Accordingly, in the spring, Fulvous Whistling-ducks ingest large amounts of weed seeds such as *Fimbrystilis* sp. where rice seed is dry planted; they take only trace amounts of rice in these areas. Furthermore, rice is not a major food in the fall when numerous weed species produce seeds just above the waterline. Details of Fulvous Whistling-ducks' food habits in Louisiana are set out in Table 4.

In coastal South Carolina, Landers and Johnson (1976) reported a diet of 74 per cent grasses, primarily *Panicum dichotomiflorum*. The seeds of eight

plants were exclusively utilized by Fulvous Whistling-ducks, being absent in the crops of other waterfowl collected in the same area. The birds' diet in South Carolina was much like those elsewhere in its pre-1955 distribution range in North America, suggesting that these similarities, in part, accounted for the species' successful range expansion in the eastern seaboard states.

Bruzual and Bruzual (1983) found that plant material constituted 99 per cent by volume of the food consumed by 21 Fulvous Whistling-ducks in Venezuela. The most frequent species in the stomach contents they analyzed were *Oryza sativa*, *Echinochloa colonum*, and *O. perennis*. The species that contributed most by volume were *O. sativa*, *Cyperus articulatus*, and *C. rotundus*.

Virtually nothing is known of brood sizes or other aspects of brood ecology in this species of whistling-duck. Meanley and Meanley (1959) followed the plumage development of a single bird (female) raised in captivity: at 35 days, quills on the wings and tail appeared; at 40 days the juvenile plumage appeared and was about completed by 60 days, save for ectrices and remiges and a remnant of a downy cheek stripe; initial flying occurred at 63 days.

#### *Cuban Whistling-duck*

This is the largest of the eight species of whistling-ducks. Its plumage superficially resembles the Spotted Whistling-duck but actually differs in that the flank spots of the Cuban Whistling-duck are somewhat irregular in shape and they do not appear linearly arranged along the side of the body. Johnsgard (1965:23) believes that the species is an island-dwelling but highly modified form sharing a common lineage with the Black-bellied Whistling-duck; similarities in the pattern of the wing plumage suggested this relationship.

The postcopulatory behavior is similar to that of the Black-bellied Whistling-duck, which again suggests close phylogenetic lineage between these two species. They hybridize readily in captivity; the behavioral sequence following copulation has been described by Bolen and Rylander (1973). The multisyllable call of the Cuban Whistling-duck, although not often uttered, is not unlike the Black-bellied Whistling-ducks' shrill whistle.

Wetmore and Swales (1931) reported that the birds were easy to shoot and that survivors from the first volley usually returned to give the gunner a second opportunity. This behavior may reflect a long pair-bond, as described for Black-bellied Whistling-ducks (see Bolen, 1971); that is, when one member of a pair is shot, the other circles about its fallen mate, presenting the hunter with still another shooting opportunity.

Almost nothing is known of the Cuban Whistling-duck's field ecology. David (1941) reported that breeding occurs in June and July and that the clutch size is about nine eggs, whereas Wetmore and Swales (1931) cited laying in January and the appearance of the young in March. Little else appears in the literature, and the political conditions in Cuba in recent



TABLE 8.—Comparative proportions among linear dimensions for three closely related species of *Dendrocygna*. *D. bicolor* and *D. javanica* are sympatric in India; *D. arcuata* occurs in Australia and much of the East Indies north to the Philippines. Adapted from Bolen and Rylander (1975).

Ratio	<i>D. arcuata</i>	<i>D. bicolor</i> <sup>a</sup>	<i>D. javanica</i>
Wing/tarsus	4.1	3.8 (4.1)	4.1
Wing/toe	3.3	3.2 (3.3)	3.1
Toe/tarsus	1.3	1.2 (1.3)	1.3

<sup>a</sup>Values in parenthesis are from Siegfried (1973).

decades have not fostered research on the Cuban Whistling-duck in its name-sake homeland. Moreover, research on this species will likely be severely limited for some time to come.

### *Indian Whistling-duck*

The Indian Whistling-duck is the smallest of the eight species of *Dendrocygna*. Its range encompasses much of "British India," the landmass now including Pakistan and the Indochina peninsula, as well as mainland China and much of the East Indies (but apparently only the western portion of Borneo). Indian Whistling-ducks are by far the most common waterfowl in the provinces of northern Thailand; they concentrate in vast numbers in swamps and woodland ponds during the dry months and spread to marshlands and rice fields in the rainy season (Deignan, 1945). Amstutz (1973) listed the species as very common from January to May, in flocks reaching 300 birds near Rangoon, Burma. There are no recognized subspecies.

The species is one of the least known of the group. Field studies of its ecology are wanting, and we rely primarily on the accounts of general works for our discussion. Except for size, it resembles both the Fulvous and Wandering Whistling-ducks, yet it seemingly exhibits ecological traits dissimilar from those of others of the group. Ripley (1945) emphasized that the super-species consisting of *D. bicolor* and *D. arcuata* nicely bracket *D. javanica* (see Table 8), thus posing an interesting phylogeographical problem that has remained unresolved.

Ali (1969:40) and Ali and Ripley (1968:138) report the species as perching freely yet diving and walking with ease. Acknowledging its walking abilities, Henry (1955:411) further noted that the species' "true home" is in the water where it dives at least 6-8 feet . . . both in play and for food." Abdulali (1965) observed the simultaneous dive of several thousand Indian Whistling-ducks at the Alipore Zoo in Calcutta, perhaps in response to the passage overhead of a predatory bird. Bolen and Rylander (1975) found a similarity in the toe/tarsus ratios between the Indian and Fulvous Whistling-ducks, suggesting that their respective swimming abilities and other movements in water may be alike (Table 8); much of the ecological isolation between these species—sympatric in India—presumably occurs in the choice of foods secured by each species.

In flight, the smaller Indian Whistling-duck is less rapid and direct than the larger Fulvous Whistling-duck and shows a fluttering "unducklike" manner in its movement (Abdulali, 1958).

Indian Whistling-ducks display a remarkable variety of nesting habits. Whistler (1949:523) referred to nests on the ground or in slightly elevated masses of dense vegetation, in a tree cavity or the abandoned nests of crows and kites, or between the boughs. Ali and Ripley (1968:139) cite Whistler's data (but add old heron nests to these of crows and kites), noting that nests at ground level bordering jheels are fairly substantial pads of leaves, rushes, and grass.

The foods of the Indian Whistling-duck are not documented by quantitative studies from any portion of its range. However, Dharmakumarsinhji (n.d., p. 100) reported that fish and insects are secured by upending or diving, thus supporting the hypothesis that Indian Whistling-ducks' foods separate this species ecologically from the similarly adapted (in diving and swimming) Fulvous Whistling-duck. Plant materials may be preferred in Sri Lanka (Ceylon), but Henry (1955:411) cites that large quantities of mollusks are eaten and Baker (1908:103) found large quantities of freshwater snails in the birds he examined. Ali (1969:40) reported worms, snails, fish, and even frogs and other animal materials in addition to shoots and grain. Grazing habits, ". . .like a goose. . .," are also attributed to Indian Whistling-ducks (Ali and Ripley, 1968:139). It seems clear, then, that the food habits of the Indian Whistling-duck embrace a variety of behavioral mechanisms, such as diving and grazing, and an unusual variety of materials.

Knowledge of this species' breeding biology is indeed meager. Data for clutch sizes are likely derived from avicultural sources (see Delacour, 1954), but indicate that this species lays fewer eggs than do others of the genus. Sets of five to eight eggs (Bolen, 1973), usually eight (Riley 1938:39) or 10 to 12 (Hume and Marshall 1881:113), or commonly 10 with a maximum of 17 (Ali and Riley 1968:139), seem to characterize the range of normal clutch sizes. The incubation period is variously reported as 25 days (Dharmakumarsinhji, n.d., p. 100) to "probably 30 days" Delacour (1954:44). Both sexes are thought to share incubation duties.

Hume and Marshall (1881:116) were among the first to write about waterfowl that carry their young from the nest, and they cited two personal observations where ducklings of Indian Whistling-ducks were transported in the claws of their parents. Such anecdotes—including conveyance in the parent's bills—appear occasionally in the scientific literature. However, most authorities have consistently observed that ducklings, particularly those of cavity-nesting species, jump unassisted from the nest in response to the parents' calls from below. Nonetheless, a review of this intriguing subject (Johnsgard and Kear, 1968) suggests that parental transport of ducklings should not be quickly dismissed as a possible occasional behavior among some species.

*Spotted Whistling-duck*

This species, restricted to the East Indies, is the least known of the whistling-ducks. Nonetheless, Spotted Whistling-ducks are the commonest and most widespread duck in New Guinea where it favors "grassy waters" (Rand and Gilliard, 1967: 53). Its ecology has not been studied in the field, with only observations from avicultural collections available for comment, and even these are scanty.

Superficially, Spotted Whistling-ducks resemble Cuban Whistling-ducks (another island-isolated species). Both species have plumage patterns quite unlike the other species, but the Spotted Whistling-duck's white flank "spots" are rounder and linearly arranged. Additionally, our visits to the Wildfowl Trust indicate that captive Spotted Whistling-ducks are far more inquisitive of humans than are Cuban Whistling-ducks, a behavioral trait regularly noted by Geoffrey V. T. Matthews (personal communication). Spotted Whistling-ducks rush across even large pens to "visit" humans, nibbling and chattering through the wire, whereas Cuban Whistling-ducks remain quietly at a distance when similarly confronted.

Delacour (1954:35) cited observations of nests in tree cavities, but detailed descriptions of nests have not been published. Rand and Gilliard (1967: 53), for example, note that their nests are "said to be in a hole in a tree; eggs undescribed." Spotted Whistling-ducks commonly perch in trees, roosting there overnight, and may be more arboreal in their habits than any of the whistling-duck group. Little more may be said of the Spotted Whistling-duck other than to emphasize the challenging studies that await an adventurous field ecologist.

*White-faced Whistling-duck*

The breeding season for White-faced Whistling-ducks in southern Africa seems limited to the austral mid-summer, a period when rainfall can be expected (Clark, 1976). Breeding records, compiled from clutches, broods, and examination of collected birds, show that 78 per cent (122 of 157 records) of the nesting activities occurred in January and February. Lamm (1948) saw large flocks on brackish marshes in Brazil from mid-September to April that later dispersed during the rainy season.

White-faced Whistling-ducks in much of Africa show an interesting delineation of breeding chronology when compared with Fulvous Whistling-ducks. Both species utilize essentially the same nesting habitat, but Fulvous Whistling-ducks nest mainly during the dry season following the rainy period; in contrast, nesting activities for the latter species coincide with the vast flooding that follows the rainy period, an adaptation apparently consistent with their feeding behavior (Siegfried, 1973), and not unlike similar breeding adaptations among certain Australian ducks (see Frith, 1959; Braithwaite, 1974). In South Africa, however, this relationship is less evident, presumably because of the availability of permanent water in reservoirs and other man-made installations.

Nesting sites for this species are somewhat variable, although most are located in long grass within 45 meters of water. Other nests were located over 1 to 1.5 meters of water in cattail *Typha* sp. or sedges *Carex*; a single instance of a nest situated in the fork of a willow *Salix* sp. 2.5 meters above water also was cited by Clark (1976). All of the ground nests were well hidden, and those over water had partial canopies of living vegetation that added to their concealment. Serle (1943) described 11 nests that were shallow, circular depressions in the ground about 240 millimeters across the rim and 45 deep; wisps of dry grass were the only nesting materials. These nests were concealed in rank vegetation either near marshland or in the short grass of fallow farmland, with some of the latter 400 meters from water.

Clutch size varies from seven to thirteen eggs with a mean of 10.5 for the 19 nests reported by Clark (1976); Serle (1943) reported clutches of 10 to 12 eggs. Dump nesting occurs, as Clark (*op. cit.*) cited a clutch of 16 eggs separable into groups of two sizes and another where four eggs were added to a nest within 24 hours. In one instance, an egg (presumably from a Fulvous Whistling-duck) was added to a clutch after incubation was underway, thus demonstrating occasional interaction between these species in the form of nest parasitism. Delacour (1954:45) reports that the incubation period is 28 to 30 days, but does not cite supporting field data. Moreau and Moreau (1940) hatched White-faced Whistling-duck eggs under a foster mother; the eggs hatched at 32 days and the young flew at the end of three months. An average of nearly seven ducklings was recorded for 106 broods of ages varying from downy young to about two months (Clark, *op. cit.*). Brooding duties are assumed by both parents.

More information is known about the feeding behavior of White-faced Whistling-ducks than about the actual foods they ingest. Both Mitchell (1957) and Delacour (1954:46) remarked that adults dive skillfully but Siegfried (1973) seldom observed this behavior in ducklings. Siegfried's comparison of linear measurements and their ratios between White-faced and Fulvous Whistling-ducks revealed the relatively smaller foot size of the White-faced Whistling-duck. This suggests that the White-faced Whistling-duck is less aquatic in its habits, including feeding, and that the two species are ecologically isolated, in part, by manifestation of this adaptation wherever they occur sympatrically. In body posture, the White-faced Whistling-duck is erect and straight necked, again suggesting that their niche is unlike that of the more horizontal-bodied Fulvous Whistling-duck; this relationship exists in other species where sympatry occurs (see Rylander and Bolen, 1974b).

In his comparative study of feeding ecology among filter-feeding waterfowl in africa, Douthwaite (1977) found that White-faced Whistling-ducks employed the widest range of feeding techniques among the species he studied; they usually fed in shallow water and preferred to walk or stand instead of swimming. Diving was not common, and grazing was even more rare.

Douthwaite (1977) examined 34 crops of White-faced Whistling-ducks from the Kafue Flats of southern Zambia. Seeds and fruits constituted 92 per cent of the diet in this sample, and rhizomes 8 per cent; no invertebrates were included in the diet. Older literature, summarized by Phillips (1922:123), indicated that a wide variety of foods may be utilized, such as insects, mollusks, crustaceans, various seeds including rice, and occasionally fish. These records also mention an instance where White-faced Whistling-ducks sought small invertebrates on freshly exposed tidal flats on the coast of Liberia. Clearly, the study of food habits of this species requires the seasonal examination of stomachs from both adults and ducklings.

In Venezuela, the ecology of the White-faced Whistling-duck was studied intensively for several years by Gomez (Gomez and Rylander, 1982), who also analyzed the stomach contents, determined the composition and caloric values of body tissue and eggs, and calculated the approximate metabolic values for maintenance.

Gomez found that White-faced Whistling-ducks in Venezuela eat mostly vegetal matter, especially tubercles, and that the type of food eaten is correlated with the phenology of the plants. Seed consumption increases as the rainy season progresses, and the largest number of grasses is consumed during the dry season. Consumption of insects is highest during the rainy season when they are most abundant and when the diversity and quantity of vegetal matter is lowest. A major factor determining the type of food ingested appears to be food availability rather than food preference, but during the breeding season animal matter may be selected because of increased protein requirements.

Males predominate and the populations of both sexes depend to some extent on human disturbance. In some cases, such as the building of dikes, this disturbance favors the ducks.

The principal regulator of the nesting cycle appears to be the rains. Pair formation coincides with the beginning of the rainy season and nest building and egg laying follows. The nest is a small depression made from grass, predominantly *Sporoborus*.

The typical clutch size for these birds is eight to 12. The principal predator of whistling-duck eggs appears to be a Caracara, *Polyborus plancus*. Foxes, storks, and the tegu (*Tupinambus*) are important predators of the young.

Bruzual and Bruzual (1983) also studied the food habits of this species in Venezuela and analyzed the contents of 67 stomachs. They reported that plant material comprised 93 per cent of food volume. The most frequent species in the diet were *Cyperus palustris* and *Echinochloa colonum*. The most important plant species by volume were *Oryza sativa*, *Cyperus rotundus*, and *O. perennis*. These investigators found that rice consumption was less in the White-faced Whistling-duck than in either the Black-bellied or Fulvous Whistling-duck. They suggested that the hunting season for the

White-faced Whistling-duck be closed after harvest and the fields inundated with water to permit this species to feed on *O. perennis* and *C. rotundus*, two weeds that comprise about two-thirds of this species' diet.

### *Plumed Whistling-duck*

The Plumed Whistling-duck is restricted to the tropical grasslands of Australia. On its flanks it possesses striking lanceolate plumes that are buff with black margins. There are no recognized subspecies. Lavery (1965) proposed that *D. eytoni* be referred to as the "Grass Whistling-duck" instead of Eyton's or the Plumed Whistling-duck, but the last name is already widely utilized in the literature and emphasizes the unique flank plumage that characterizes the species.

Plumed Whistling-ducks are not tree dwellers, and perch only rarely, and then, very awkwardly. On land they walk long distances gracefully but are slow and awkward swimmers (Frith, 1967:80). Rylander and Bolen (1974b) and Bolen and Rylander (1974) noted the similarities of posture, gait, and foot adaptations between the Plumed and Black-bellied Whistling-ducks and proposed that these two species may represent the first description of convergent evolution in the Anatidae.

Flocks of Plumed Whistling-ducks are clearly composed of mated pairs throughout the year, probably indicating a life-long pair bond (Frith, 1967:85). Nests are placed on the ground in scrapes under the shelter of long grass or shrubs; they are often one to two or more kilometers from the nearest water (d'Ombrain, 1945a, 1945b).

Australian waterfowl of many species respond to heavy rainfall and/or the rising waters that follow (that is, the wet season). Their response, in many cases, is both remarkable and dramatic (see Frith, 1959). Others, including the two Australian whistling-ducks, while showing less synamic responses, are nonetheless adapted to breeding during the wet season of the annual climatic cycle in Australia. For the Plumed Whistling-duck, the onset of the wet season initially induces dispersion, often extensive, to inland area where water has filled the shallow swamps and meadows utilized as breeding habitat. February and March are the months of greatest breeding activity in Queensland and the Northern Territory in most years, but variations in the season (either exceptionally wet or dry) alter the breeding chronology or even the proportion of the population that breeds (Frith, 1967:86).

Frith (1967:87) measured nine clutches of eight to 14 eggs and listed the incubation period as 28 days with the male sharing incubation duties. D'Ombrain (1945b) found that a captive pair of Plumed Whistling-ducks exchanged incubation shifts every 24 hours, between 6 and 7 PM; their eggs were also laid in the evening between 5:45 and 7:30 PM, not unlike the laying times for Black-bellied Whistling-ducks. Hersloff *et al.* (1974) suggested that the deposition of eggs in the evening may be an adaptation for nocturnal activities, namely that gravid hens do not carry fully shelled eggs during active periods (that is, nocturnal feeding).

TABLE 9.—Comparative diets (percentage volume) of whistling-ducks in northern Queensland, Australia. Adapted from Lavery (1971).

Items by family	Plumed Whistling-Duck	Wandering Whistling-Duck'
Nymphaeaceae	0.6	72.8
Gentianaceae	0.3	10.5
Polygonaceae	6.2	1.1
Gramineae	83.7	1.2
Others	9.2	14.2

'0.2 per cent animal matter is excluded from these data; none occurred in the diet of the Plumed Whistling-duck.

The food habits of the Plumed Whistling-duck are quite different from its sympatric relative, the Wandering Whistling-duck (Table 9). Plumed Whistling-ducks feed mainly on land, taking predominantly grasses. Their daily feeding routine starts in the late afternoon when they walk and graze near their roosting sites, then fly to feeding areas on grasslands elsewhere (Lavery, 1967). Lavery (1970) found that sedges were the major food items for Plumed Whistling-ducks during the wet season and that grasses dominated the diet during the dry season; their preference for plant foods instead of animal matter enhances the low (seven per cent) rate of helminth parasitism in this species. Although the bill of this species is singularly shorter than any of the other species in the genus, no known adaptive significance has been established for this physical feature. Likewise, the highly fimbriated lateral margin on the anterior process of the tongue is peculiar, but its function does not seem clearly related to the existing knowledge of the species' food habits (Rylander and Bolen, 1973).

#### *Wandering Whistling-duck*

Lavery (1965) proposed that this species be recognized as the "Water Whistling-duck," in keeping with its habitat preferences, instead of the Red or Wandering Whistling-duck, but again, we have chosen the name most frequently used in the older literature. Nevertheless, Wandering Whistling-ducks swim and dive actively in the deeper, more permanent fresh-water lagoons and swamps in contrast with the more mesic habitat already described for the Plumed Whistling-duck. The similarities of gaits, posture, and toe/tarsus ratios between the Wandering and Fulvous Whistling-ducks reflect the aquatic habits of each (Rylander and Bolen, 1974*b*; Bolen and Rylander, 1974) and provide anatomical support for the ecological preferences Frith (1967) and others have described for the Australian species of whistling-ducks.

Wandering Whistling-ducks feed entirely in the water, dabbling in the shallows or diving with ease to depths of 10 feet. They often feed at night and flocks sometimes fly several miles to larger lagoons (Frith, 1967:72). In the Northern Territory, Frith (*op. cit.*) reports that waterlilies (seeds, buds, and leaf parts of *Nymphaea* sp.), grasses (seeds of aquatic species including *Paspalum*, *Oryza*, and *Echinochloa*) and various sedges were present in

volumes of 30, 42, and 17 per cent, respectively, with the balance consisting of a variety of other plants. However, gizzard contents vary with locale, and other samples from Australia include major components of various Gentianeaceae and club rush *Scirpus littoralis*. The rapid habitat changes that follow the Australian rainfall regime contribute materially to these differences in diet. Lavery (1970) thus noted that Wandering Whistling-ducks in northern Queensland were 87 per cent parasitized with intestinal helminths, a response to their dietary intake of freshwater gastropod mollusks. Mosquitoes, too, may be locally important foods of Wandering Whistling-ducks. The crop of an adult male collected near the Ross River in Australia contained 500 mosquito larvae and 487 pupae (Marks and Lavery, 1959).

Wandering Whistling-ducks, perhaps more so than Plumed Whistling-ducks, respond to rainfall as a proximate factor for breeding. Lavery (1970) presented correlations between rainfall patterns in Queensland with the enlargement of male and female gonads and the initiation of clutches for Wandering Whistling-ducks; these data include the reduction of breeding activities during the severe drought of 1961. Development of *Echinochloa* seedheads, a major food of the ducklings, followed the rainfall regime and likely represents the ultimate factor in the breeding chronology of this species.

The nest of this species is not unlike that of the Plumed Whistling-duck: scrapes in the ground under vegetative shelter and often some distance from water. Only meager clutch data exist for Wandering Whistling-ducks, but Delacour (1954:38) reports that six to 15 eggs represent the range of clutches he examined, and reproductive success, measured by brood sizes, was 44 per cent. Both sexes, presumably as with all other species of the genus, share incubation and brooding duties.

#### MORPHOLOGY

We have followed the nomenclature of Howard (1929), with a few noted exceptions, for the skeletal system, and the nomenclature and numbering system of George and Berger (1966), for the musculature. We have added, in parentheses, some common synonyms, particularly names used by Goodman and Fisher (1962), as a matter of convenience, as the latter study is likely to be referred to in comparing the feeding musculature of *Dendrocygna* with that of other anatids.

It is widely recognized that the classification and naming of avian muscles is highly controversial and that contemporary anatomists often use entirely different systems of nomenclature (compare, for instance, the nomenclature of George and Berger, 1966; and Goodman and Fisher, 1962). In following George and Berger, we are not necessarily adopting their viewpoints regarding myological classification, but rather providing, we hope, a quick reference to the literature and synonyms. It seems inadvisable to add still another "tentative" classification and nomenclature to the distressingly complex and often confusing current situation.



### *The Skeletal System*

In the skeletal system of whistling-ducks, the feeding apparatus, pelvic girdle, and hind limb are most readily correlated with specific functions. The following discussion is based on studies by Rylander and Bolen (1970, 1974a, 1974b) which may be consulted for additional details.

The most obvious adaptations in the feeding apparatus are in the maxilla, which is broader at the tip in *bicolor* and *arcuata* than in *autumnalis* and *eytoni*. This expansion is accompanied by a larger buccal cavity in the first two species, which may be correlated with a more highly refined straining apparatus in these two predominantly aquatic feeders. The nail at the tip of the maxilla is large in these two species, but it is not clear if this represents a genetic adaptation for more efficient straining, or whether the feeding behavior in *autumnalis* and *eytoni* has worn (through abrasion) what might have otherwise been nails equal in size to those of *bicolor* and *arcuata*.

The maxillary bone is thicker in the two terrestrial species, and the ceratohyal bone, which is perhaps correlated with the straining mechanism since part of the tongue musculature attaches to it, is relatively wider in the two aquatic species.

The skull of all dendrocygnids is noted for the vaulted cranium and the infraorbital bar, but there is no apparent relationship between these features and the behavioral or ecological traits that are shared by the members of the genus.

The postcranial skeleton appears to be correlated with the species' characteristic locomotor behavior, at least in the case of *autumnalis*, *eytoni*, *arcuata*, and *bicolor*. In particular, the anatomical adaptations reported by Raikow (1970) for diving ducks can be demonstrated in *bicolor* and *arcuata*: the legs are attached more laterally, the ilioischiatric foramen is relatively larger and the tarsometatarsus thicker (Figs. 4, 5). The larger ilioischiatric fenestra may indicate a more highly developed m. ischiofemoralis, which originates from this location and which flexes the femur during swimming. Presumably it is relatively larger in species which depend on diving to obtain food. The relatively larger tarsometatarsi suggest larger flexors and extensors of the foot, also probably important in swimming. In addition, a longer tarsometatarsus in *autumnalis* and *eytoni* could have evolved as an adaptation to walking.

It is possible that the other four species can be classified on the basis of their pelvis as to the degree to which they are adapted for swimming and diving, but the adaptive significance of these characters in their case is not as clear. These other species may be more generalized in form, that is, specialized neither for walking nor for diving.

With these reservations in mind, we may tentatively group, on the basis of their skeletons, *guttata* and *javanica* with the diving species, and *arborea* with the walking species. *D. viduata* was not possible to classify in this regard, as its structural characteristics are intermediate between the two groups.

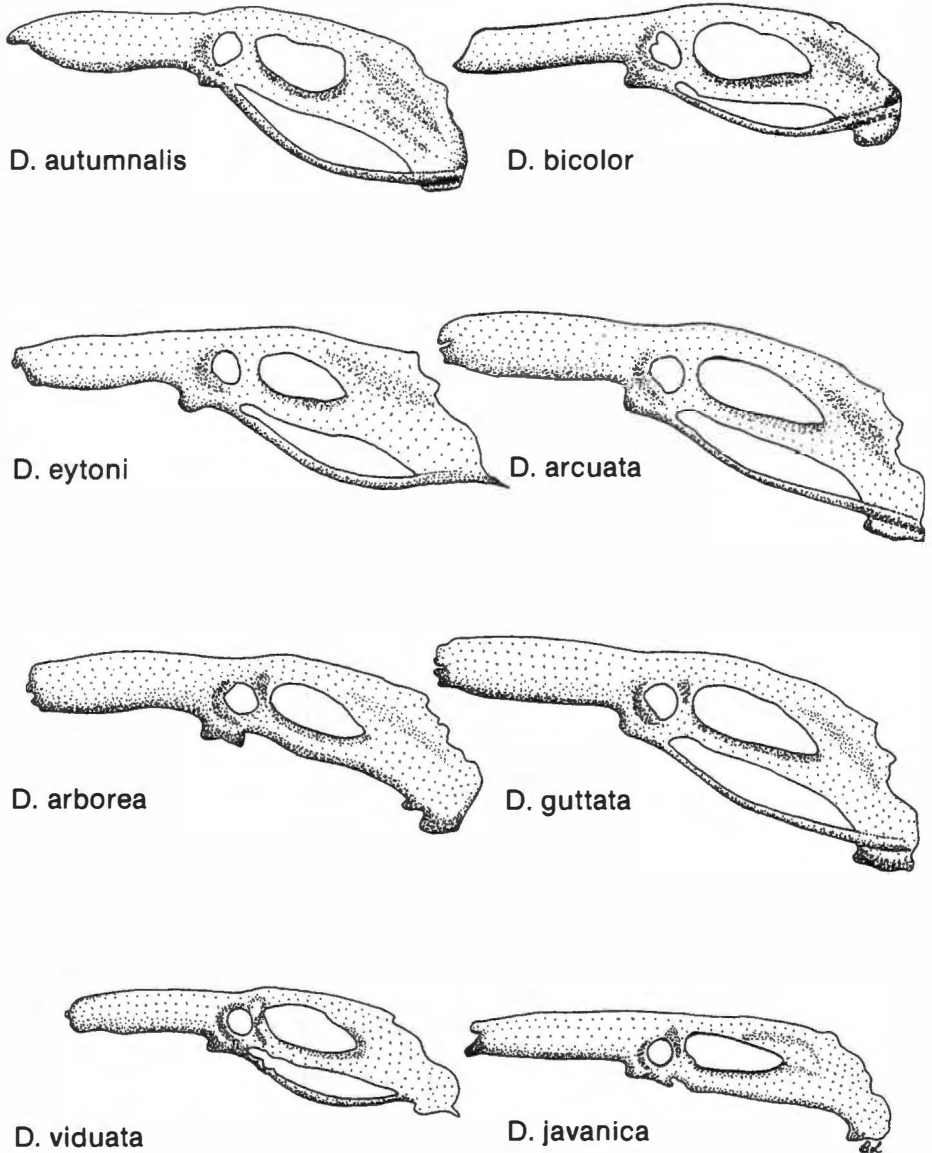


FIG. 4.—The pelvis in the eight species of *Dendrocygna*, view laterally, and showing a relatively larger ilioischiatric fenestra in *D. bicolor* and *D. arcuata* than in *D. autumnalis* and *D. eytoni*. The other four species appear to be intermediate in form.

In the presumed aquatic group *bicolor*, *arcuata*, *guttata*, and *javanica* the synsacrum was not measurably narrower between the acetabulae, nor was the postacetabular ilium elongated, as Raikow (1970) reported for other species specialized for swimming.

Other postcranial adaptations in the skeleton can be demonstrated in the foot of *autumnalis*, which is smaller than in *bicolor* (Rylander and Bolen,

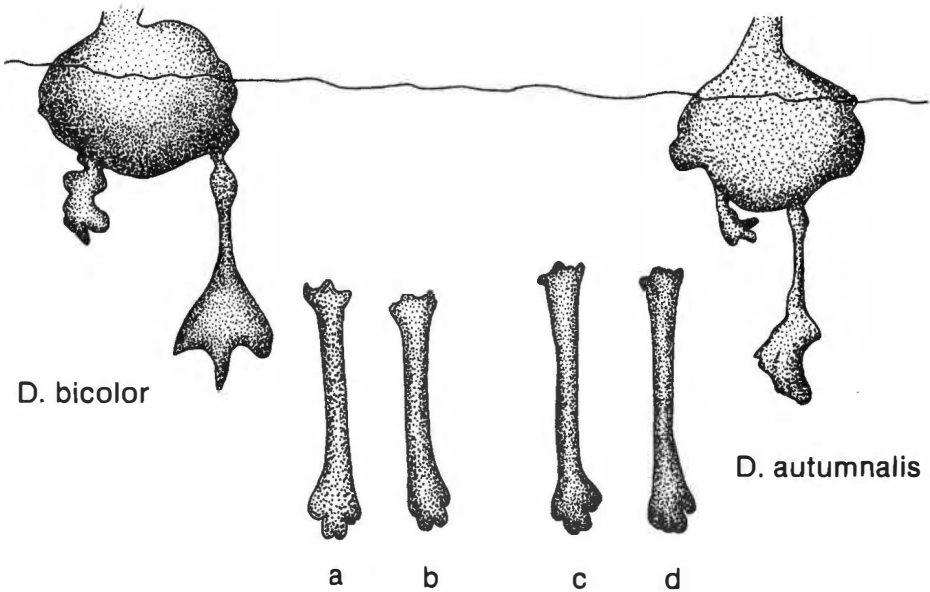


FIG. 5.—Swimming postures of *D. bicolor* and *D. autumnalis*. Note that the former species has larger feet and more laterally positioned legs. The tarsometatarsus in *D. autumnalis* (c) and *D. eytoni* (d) is relatively longer than in *D. bicolor* (a) and *D. arcuata* (b). The figures of the swimming ducks were made from photographs taken of birds in a large aquarium. The tarsometatarsi were drawn using a camera lucida.

1970). A larger foot could be an adaptation for swimming, as could a smaller foot for walking.

### The Muscular System

At least two specimens each of *autumnalis*, *bicolor*, *viduata*, *arcuata*, and *eytoni* were dissected and intraspecific variation was noted. For some of the small muscles, especially in the tongue, a weak stain was applied to the surface before the muscles were separated under a dissection microscope (Wild M-5). The stain (Bock and Shear 1972) consists of 1 g. iodine, 2 g. potassium iodide, dissolved in 100 ml. distilled H<sub>2</sub>O. Drawings of the smaller structures, such as the tongue and jaw musculature, were made using a Wild Stereomicroscope and drawing tube.

In this chapter we have described the origins and insertions of the muscles of the feeding apparatus and upper hind limb, noted interspecific differences in musculature, and commented on the significance of the muscles when the musculature suggests functional relationships that are unique to the genus or to a species within the genus.

### Muscles of the Jaw (Figs. 6, 7, 8)

1. M. depressor mandibulae originates from an extensive area on the posterolateral (parietal) surface of the skull, and inserts on the retroarticular process of the mandible. This muscle appeared typical in every way.

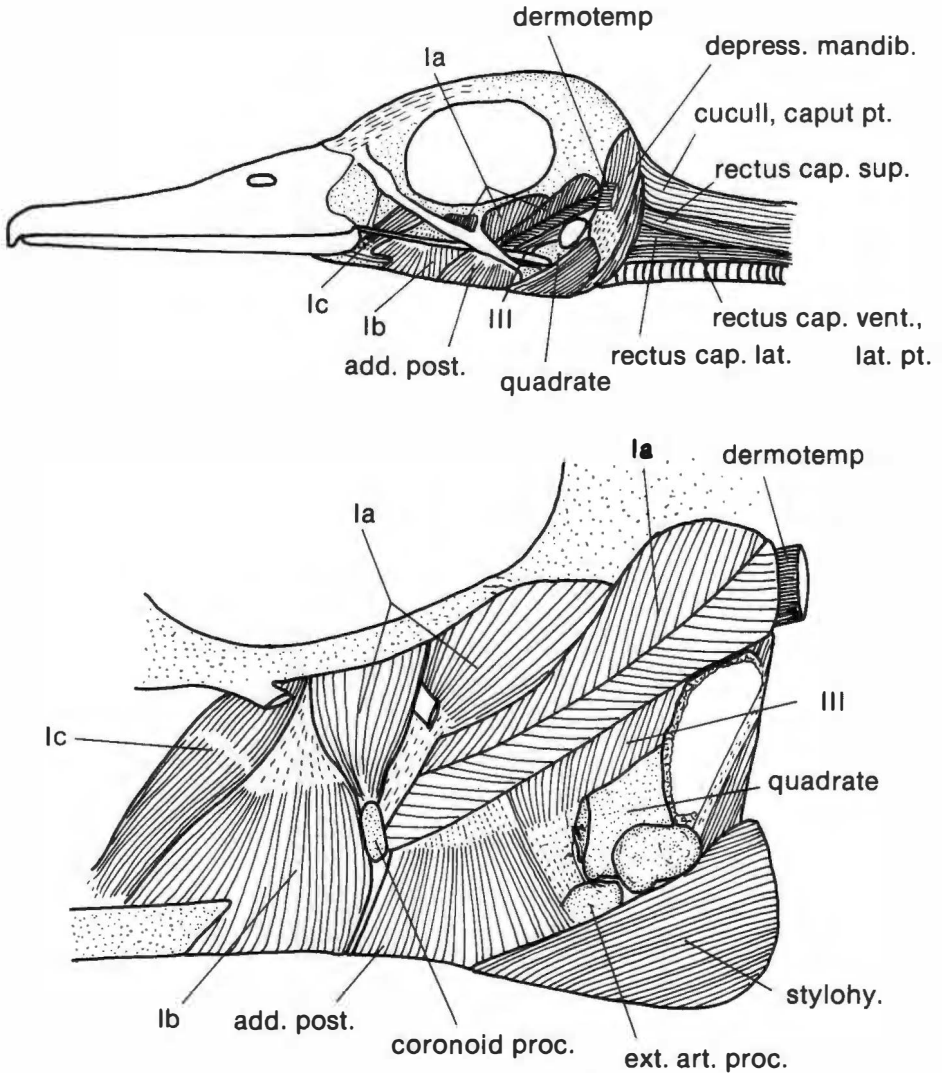


FIG. 6.—Superficial (top) and deep (bottom) jaw musculature in the White-faced Whistling-duck. The following abbreviations are for Figs. 6, 7 and 8. *la*, *lb*, *lc*, *III*, divisions of *m. adductor mandibulae* (see text); *add. post.*, *m. adductor mandibulae*, pars posterior; *ceratogloss.*, *m. ceratoglossus*; *ceratohy.*, *m. ceratohyoideus*; *cucull., caput pt.*, *m. cucullaris*, caput; *depress. mand.*, *m. depressor mandibulae*; *dermotemp.*, *m. dermotemporalis* (= *m. cucullaris*, part); *ext. art. proc.*, external articular process; *geniohy.*, *m. geniohyoideus*; *hyogloss. obl.*, *m. hyoglossus obliquus*; *hyogloss. rect.*, *m. hyoglossus rectus*; *intermand. dors.*, *m. intermandibularis dorsalis* (= *m. mylohyoideus*); *intermand. vent.*, *m. intermandibularis ventralis* (= *m. mylohyoideus*); *pteryg. dors.*, *m. pterygoideus dorsalis*; *pteryg. vent.*, *m. pterygoideus ventralis*; *rectus cap. lat.*, *m. rectus capitis lateralis*; *rectus cap. sup.*, *m. rectus capitis superior*; *rectus cap. vent. lat. pt.*, *m. rectus capitis ventralis*, pars lateralis; *serpihy.*, *m. serpihyoideus*; *stylohy.*, *m. stylohyoideus*; *thyrohy.*, *m. thyrohyoideus*.

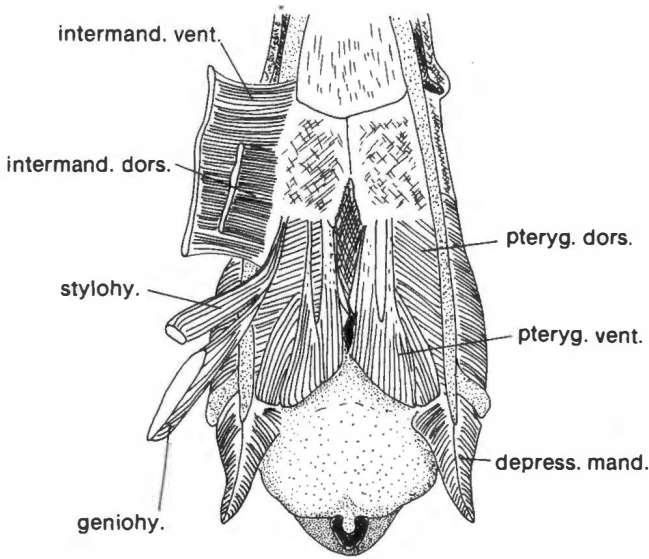


FIG. 7.—Ventral view of the musculature of the head of the White-faced Whistling-duck. Abbreviations as in Fig. 6.

2. *M. adductor mandibulae* is complex and highly variable. A tough fascial covering lies between the skin and most of *m. adductor mandibulae*, particularly the Ia portion. This fascia lies superficial to the postorbital ligament to which it is rather tightly fused. When this fascia is removed, the underlying Ia is exposed. The anterior part of Ia, in some specimens, has come to lie superficial to this flat tendon, and furthermore this anterior part is usually divided into a rostral and a caudal portion by the caudal branch of the postorbital ligament. When these two portions of the anterior part of Ia are removed, it can be seen that the underlying flat tendon is sometimes continuous caudally with the tendon that partially covers the posterior part of Ia (the top part of a "T", and is usually continuous rostrally with the superficial tendinous covering of Ib and to a slight extent, the covering of Ic, also). (This flat tendon was not continuous in one individual each of a Mallard, Pintail, and Snow Goose that were dissected.)

Since the bipartite anterior part of Ia lies superficial to this tendon, many of its fibers originate from this tendon. In some specimens there was a tendinous covering on the portion that lies caudal to the postorbital ligament (caudal branch). This tendon covers the muscle near its insertion, and fuses with the more deeply situated extensive tendinous covering that was referred to above (the top of the "T"). It is, however, a separate tendon, and inserts on the coronoid process of the mandible more superficially than the insertion of the tendon from the posterior part of Ia.

When all of Ia is removed (including all of the tendinous "T"), the thick fascia (tendon?) covering II laterally is exposed. Also, *m. adductor mandibu-*

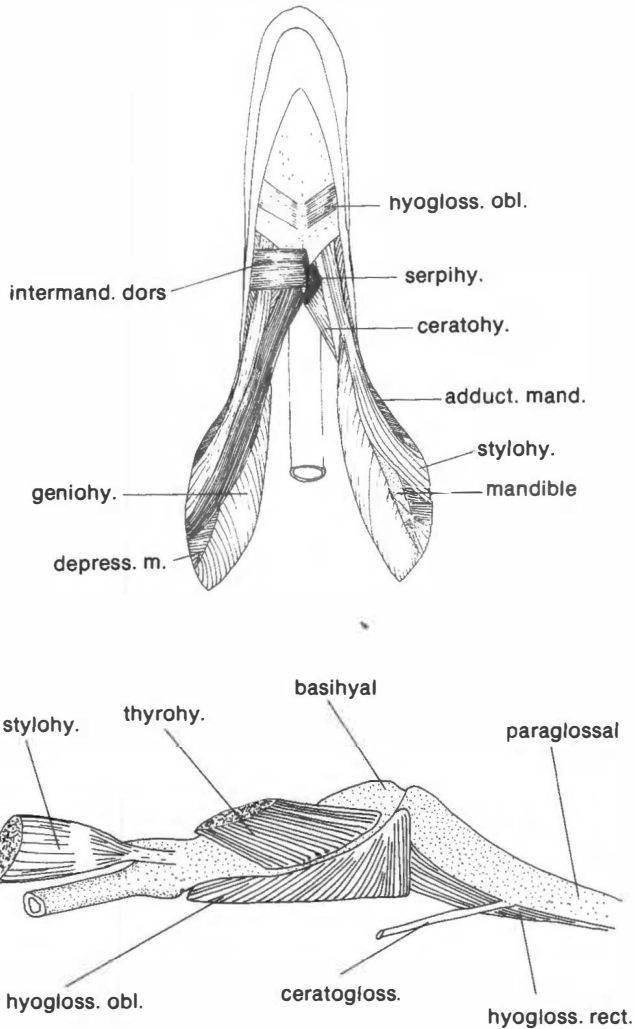


FIG. 8.—Ventral view of the jaw musculature (top) and lateral view of the tongue musculature (bottom) in the White-faced Whistling-duck. Abbreviations as in Fig. 6.

lae posterior and III can be seen. The fibers between III and Ia are slightly fused.

Dissection of three one-day-old Black-bellied Whistling-ducks revealed that the subdivisions of Ia described above were distinctly formed by that age.

Pars superficialis (=m. adductor mandibulae externus, superficialis; I) can be divided into three parts. Ia originates from the temporal fossa that is on the squamosal bone, not the temporal fossa as indicated on the duck skull by Howard (1929), which is the origin of the m. depressor mandibulae. It inserts on the lateral coronoid process of the mandible. Ib, a fan-shaped muscle, arises internally and ventrally from the osseous orbital bar and inserts

laterally on the lower jaw, rostral to the lateral coronoid process. It originates rostrally from the postorbital process (=osseous orbital bar) and inserts laterally on the lower jaw, rostral to the insertion of Ib.

*Pars profundus* (=m. adductor mandibulae externus, profundus; III) originates from the lateral surface of the otic and orbital processes of the quadrate bone and adjacent squamosal bone (caudal to the origin of m. adductor mandibulae posterior). It inserts on the external articular process of the mandible.

*Pars medialis* (=m. adductor mandibulae externus, medialis; II) originates ventrally from the postorbital process and adjacent part of the temporal fossa and inserts dorsally on the lower jaw, rostral to the lateral coronoid process.

*Pars posterior* (=m. adductor mandibulae posterior) arises from the orbital process of the quadrate (by a strong tendon at the tip) and inserts laterally on the lower jaw, rostral to the external articular process. The inserting fibers cannot easily be separated from those of m. adductor mandibulae externus, profundus; in addition, the muscle fibers cannot always be easily separated from the underlying m. pseudotemporalis profundus. The degree of tendinous covering varied among individuals.

3. *M. pseudotemporalis superficialis* originates from the posterior wall of the orbit. It inserts medially on the lower jaw, rostral to the lateral coronoid process. The mandibular ramus of the trigeminal nerve partly separates this muscle from m. pseudotemporalis profundus, and a sheet of fascia partly separates this muscle from m. adductor mandibulae, medialis. No significant variation was noted among specimens.

4. *M. pseudotemporalis profundus* arises from the anterior surface of the orbital process of the quadrate and inserts on the dorsal edge and medial surface of the mandible.

5. *M. pterygoideus ventralis* is not divisible into a superficial and deep layer in *Dendrocygna* (see George and Berger 1966: 248). The single layer has two parts: *pars lateralis* which originates from the internal articular process of the mandible and inserts in the tissue lining the upper jaw internally, at about the level of the coronoid process; and *pars medialis*, which is larger than *pars lateralis*, arises more medially from the internal articular process and inserts ventrally on the palatine bone. The two muscles are fused near their origins.

6. *M. pterygoideus dorsalis, pars lateralis* originates medially from the lower jaw, anterior to the internal articular process, and inserts on the caudal part of the wing of the palatine. *Pars medialis* originates from the internal articular process and adjacent medial surface of the lower jaw. It inserts dorsolaterally on the pterygoid bone. Authors differ in their interpretations of this and the previous muscle with regard to the end of the muscle that should be designated as the origin. We are here following Goodman and Fisher (1962).

7. *M. protractor quadratus* originates from the caudal and ventral part of the orbit and adjacent part of the skull. The fibers at the origin extend ven-

trally to an area rostral to the mandibular foramen and insert on the body and part of the orbital process of the quadrate bone.

8. *M. protractor pterygoideus* arises from the interorbital septum and adjacent wall of the orbit and inserts caudally on the pterygoid.

*Muscles of the Tongue, Larynx, and Trachea (Figs. 7, 8)*

1. *M. mylohyoideus* (= *m. intermandibularis ventralis* and *m. intermandibularis dorsalis*) has a ventral layer (*m. intermandibularis ventralis*) that originates from the medial surface of the mandible and inserts on the midline raphe on which the corresponding muscle of the other side inserts. This layer covers the dorsal layer (*m. intermandibularis dorsalis*), which has a similar origin and insertion just dorsal to the ventral layer. In some specimens the two layers were separated by a substantial layer of fat. The dorsal layer is about 5 millimeters wide and the ventral layer about 15 millimeters wide. The caudal borders of the two layers generally approximate each other, although the ventral mylohyoid extends a few millimeters more posteriorly. The rostral fibers of *m. serpihyoideus* and *m. stylohyoideus* lie deep (dorsal) to the dorsal layer of *m. mylohyoideus*.

2. *M. serpihyoideus* is here considered to be any muscle originating from the posterior part of the mandible and inserting ventrally on the midline raphe. In this sense, part of it would therefore correspond to *m. mylohyoideus*, which originates more anteriorly from the mandible and which inserts on the midline raphe. In the anatids examined, *m. mylohyoideus* consists of two parts—a broader ventral part and a narrower dorsal part. The serpihyoid can also be divided into two parts which correspond in some ways to the two parts of the mylohyoid. The dorsal part is much more massive than the ventral part, and originates chiefly from the posterolateral surface of the mandible, where it is covered to a varying degree by the origin of *m. stylohyoideus*. There are also fibers which arise from the ventral edge of the mandible and the adjacent medial surface. The dorsal serpihyoid inserts along the midline raphe ventral to the broad diagonal tendon that separates it from the dorsal mylohyoid, and many of its inserting fibers are fused to this tendon. The ventral serpihyoid is a delicate strip of muscle about 2 millimeters wide that originates from the ventral edge of the mandible, just posterior to the point where the dorsal serpihyoid passes over the edge of the mandible and is partially covered by this muscle. The ventral serpihyoid follows the posterior border of the dorsal serpihyoid for about a fifth of its length, then begins to course more medially through the masses of gular fat to insert on the midline raphe near the posterior edge of the ventral mylohyoid. Relatively few muscle fibers actually reach the mylohyoid, and the insertion appears to be a very thin tendon that fuses with its opposite and with the ventral mylohyoid fibers and associated midline flat tendon that connects the two ventral mylohyoid muscles. Since the serpihyoid distinguishes itself as a dorsal and ventral part only at its insertion (that is, the two parts are separated by the dorsal mylohyoid and diagonal tendon), it



thereby differs from the two parts of the mylohyoid which are distinguishable, even at hatching, by both dorsal and ventral origins and insertions. Some authors designate the origin and insertion of this muscle in the opposite way.

3. *M. stylohyoideus* originates from the lateral surface of the mandible at its posterior end and follows the serpihyoid along its dorsal and lateral border until the level of the dorsal mylohyoid. At this point it passes over the lateral surface of the ceratohyal. It inserts dorsally on the basihyal, at the basihyal/ceratohyal articulation (only on the ceratohyal in several ducklings that were dissected). It first passes deep to the dorsal layer of *m. mylohyoideus*. There is a variable degree of fusion between the fibers of this and *m. serpihyoideus*. This insertion differs from that reported by Goodman and Fisher (1962) who describe a ventral insertion.

In *Dendrocygna*, the origin is typically not covered by *m. depressor mandibulae*, as Goodman and Fisher (1962:127) noted was characteristic of all the species they examined except *B. canadensis*, *B. nigricans*, *C. dolor*, *D. autumnalis* and *C. hybrida*. Several specimens of *Dendrocygna* (several species) which we examined did, however, show a small amount of covering of the stylohyoid by the inserting fibers of the depressor mandibulae. Also, in no specimens did we find the insertion of the stylohyoid on the ventral surface of the basihyal bone, as they reported for all their specimens (p. 127).

4. *M. geniohyoideus* arises from the medial surface of the mandible, dorsal to the origin of *m. mylohyoideus*. It inserts on the distal part of the ceratobranchial and the entire epibranchial.

5. *M. genioglossus* was not present.

6. *M. ceratohyoideus* originates on the ceratobranchial and epibranchial and inserts on the basihyal. This muscle can sometimes be separated into two partially overlapping parts: a posteroventral part, the larger of the two, originating more distally on the ceratobranchial; and an anterodorsal part. Some of the fibers of the latter part insert on the basihyal.

7. *M. ceratoglossus* originates on the ceratohyoideus and inserts on the lateral edge of the paraglossal. The long tendon of insertion passes beneath a tendinous sheath at the level of *m. mylohyoideus dorsalis*.

8. *M. hyoglossus obliquus* is a paired muscle that originates from the basihyal and inserts on the dorsolateral part of the paraglossal at its caudal end.

9. *M. hyoglossus anterior* originates caudally on the paraglossal, on its ventrolateral side, with a small slip sometimes from the inserting tendon of *m. ceratoglossus*; it sends its tendon of insertion rostrally to insert on the cartilaginous paraglossal and surrounding tissue of the tongue. Only one head of origin was found.

10. *M. meroglossus* was not present.

11. *M. dermoglossus* was not present (see George and Berger, 1966:260-261).

12. *M. depressor glossus* was not present (see George and Berger, 1966:p. 261).

13. *M. thyrohyoideus* originates laterally on the cricoid cartilage and inserts dorsally on the basihyal, anterior to the insertion of *m. stylohyoideus*. We could not distinguish a more medially situated muscle that could be identified as *m. thyroglossus*.

14. *M. tracheohyoideus* originates on the trachea and inserts on the basihyal and ceratohyal. George and Berger (1966:262-263) should be consulted regarding the nomenclatural problems associated with muscles referred to by this name.

15. *M. sternohyoideus* was not found and probably does not exist in *Dendrocygna*.

16. *M. sternotrachealis* originates on the sternum, near the articulation with the coracoid bone, and inserts on the trachea near the tracheal bifurcation, caudal to the insertion of *m. ypsilotrachealis*.

17. *M. ypsilotrachealis* arises from the furcula and adjacent sternum and inserts on the trachea.

18. *M. thyroarytenoideus* originates dorsally from the cricoid and inserts dorsolaterally on the arytenoid.

19. *M. constrictor glottidis* is deep to the thyroarytenoideus. It originates from the dorsolateral edge of the cricoid and inserts laterally on the arytenoid. Its fibers run perpendicular to those of *m. thyroarytenoideus*.

We found no measurable differences in the jaw and hyoid musculature among the species dissected. It is possible that precise measurements of muscles in large numbers of birds of the same age and sex would reveal significant differences which could be correlated with differences in behavior, but we believe that a study of the skeleton offers more promise for functional interpretation than does the muscular system, to a large extent because bone size is more reliably quantified than muscle size.

Goodman and Fisher (1962) did not discuss the variation of musculature within *Dendrocygna*, as they were concerned mainly with larger morphological differences between diverse groups of waterfowl. Also, it was not clear from their monograph how many specimens of *D. autumnalis* they completely dissected. We are unable to interpret their description of a tendinous "inverted T" for the raphe of Ia. The only difference we found between our observations and theirs with regard to Ia was our observation that Ia extends ventrally to the supræmatic process, rather than two or three millimeters dorsal to it (p. 95).

There were minor differences in the attachments of *m. serpihyoideus* and *m. stylohyoideus* as reported by Goodman and Fisher (1962) and us; these differences are noted in the muscle descriptions.

A more or less diamond-shaped tendon lies superficial to the basihyal. The dorsal intermandibularis and hyoglossus obliquus attach firmly to the midline of this tendon on its ventral surface and *m. serpihyoideus* attaches to its dorsal surface. In fact, the tendon may be regarded as the tendinous origin of part of *m. hyoglossus obliquus* as its fibers generally parallel those of the muscle. In *Anas* it was observed that this tendon gave rise to a super-

ficial tendinous covering of *m. hyoglossus obliquus* as well, but a superficial tendinous covering on *Dendrocygna* was rarely found, and in those cases was very slight. The fibers of *m. serpihyoideus* meet the tendon at an angle, which would appear to place tension on the tendon in an inefficient manner. On the other hand, the attachment of *m. serpihyoideus* to a second tendon that rests on the surface of the thyrohyal and basihyal may be secure enough to make the strain on the oblique fibers of the ventral tendon of insertion of minor importance.

We agree with Goodman and Fisher (1962:178), who interpret *autumnalis* as a "functional intermediate between the grazers and strainers." This conclusion seems to apply to its congeners as well, though one objective of the present study was to look for variation within *Dendrocygna* that might suggest adaptive radiation wherein some species are more suited for straining and others for grazing. As noted above, however, we do not feel confident that the minor interspecific variations in musculature we observed were significant enough to allow conclusions to be drawn in this regard.

#### *Muscles of the Pelvic Appendage*

1. *M. sartorius* arises from the last dorsal vertebra and the anterior end of the anterior iliac crest. The origin is fused posteriorly with the origin of *m. iliobtibialis*. *M. sartorius* inserts on the proximal end of the tibia.

2. *M. iliobtibialis* arises by an aponeurosis from the anterior iliac crest and most of the posterior iliac crest. The proximal one-fifth of this muscle is aponeurotic centrally. It fuses anteriorly with *m. sartorius* and posteriorly with *m. semitendinosus* and spreads as a thin sheet of muscle over most of the lateral surface of the thigh, where it is fused to a varying degree with the underlying *m. femorotibialis externus*. It is tendinous centrally in its distal one-fourth and inserts on the tibial cartilage. In *autumnalis*, *m. iliobtibialis* appeared to fuse more with *m. sartorius*, *semitendinosus* and *piriformis pars caudofemoralis* than in *bicolor*.

3. *M. iliobtrochantericus posterior* arises from most of the anterior iliac fossa and is well-developed in both species. Anteriorly, this muscle fuses with *m. iliobtrochantericus anterior*. The ventral border of *m. iliobtrochantericus posterior* is superficial to the dorsal border of *m. iliobtrochantericus anterior*. It inserts on the proximal end of the femur.

4. *M. iliobtrochantericus anterior* arises from the anterolateral and ventrolateral edge of the ilium. Near its origin it fuses with *m. iliobtrochantericus posterior* and inserts on the femur just distal to the insertion of that muscle.

5. *M. iliobtrochantericus medius* arises from the ventrolateral edge of the ilium, posterior to the origin of *m. iliobtrochantericus anterior*, with which it is partially fused. It inserts on the femur just proximal to the insertion of *m. iliobtrochantericus anterior*.

6. *M. gluteus medius et minimus* is a thin, triangular-shaped muscle lying deep to *m. iliobtibialis*. It arises from the dorsal surface of the ilium, between the origins of *m. biceps femoris* and *m. iliobtrochantericus posterior*. It

becomes tendinous in the distal one-half of the muscle and inserts on the lateral surface of the femur, proximal to the origin of *m. femorotibialis externus* and caudal to the insertion of *m. ilirotrochantericus anterior*.

7. *M. femorotibialis externus* has two heads. The proximal head arises from the lateral surface of the femur, near the insertion of *m. ilirotrochantericus anterior* and is fused to a great extent with *m. femorotibialis medius*. The more medially situated distal head arises from the posterolateral surface of the femur and fuses distally with the proximal head. This muscle inserts on the patellar ligament.

8. *M. femorotibialis medius* arises from the anterior surface of the femur and inserts on the patellar ligament.

9. *M. femorotibialis internus* arises from the distal two-thirds of the posteromedial surface of the femur and inserts tendinously on the proximal end of the tibiotarsus.

10. *M. biceps femoris* arises from the anterior one-half of the posterior iliac crest. The muscle become ligamentous distally, sends tendinous fibers to *m. gastrocnemius externus*, and passes through the biceps loop to insert on the lateral surface of the fibula.

11. *M. semitendinosus* arises from the first three or four caudal vertebrae. It fuses slightly at its origin with *m. piriformis pars iliofemoralis* and is connected to a varying degree with the flexor muscles of the crus by means of tendinous fibers. It inserts on the medial surface of the tibiotarsus at its proximal end. *M. accessorius* was absent.

12. *M. piriformis, pars caudofemoralis* arises by means of a posterior head from the pygostyle and an anterior head from two or three caudal vertebrae. *Pars caudofemoralis* fuses with *m. piriformis, pars iliofemoralis*, near its insertion and inserts in common with this muscle on the posterior surface of the femur. *Pars iliofemoralis* arises by means of several poorly defined heads from the posterolateral edge of the ilium and ischium. It fuses with *pars caudofemoralis* and inserts as described above.

13. *M. ischiofemoralis* arises from the lateral surface of the ischium and inserts on the posterolateral surface of the femur near the proximal end of the bone.

14. *M. semimembranosus* arises from the ventrolateral surface of the ischium, passes medial to *m. piriformis caudofemoralis*, and inserts on the posteromedial surface of the tibiotarsus. *M. semimembranosus* and *m. semitendinosus* fuse at their insertions.

15. *M. adductor longus et brevis* arises from the ventrolateral edge of the ischium and inserts on the posterolateral surface of the femur lateral to the origin of *m. femorotibialis internus*.

16. *M. obturator externus*, which is much smaller than *m. obturator internus*, arises from the anterior margin of the obturator foramen and inserts proximally on the femur, distal and posterior to the insertion of *m. obturator externus*.

17. *M. obturator internus* arises from the inner surface of the ischium and pubis. The tendon of insertion passes through the obturator foramen and inserts proximally on the lateral surface of the femur.

18. *M. iliacus* arises from the ventral margin of the ilium, immediately anterior to the acetabulum, and inserts on the medial surface of the femur at the proximal end of this bone.

19. *M. ambiens* arises from the pectineal process, passes through the cartilage on the anterior part of the femur-tibiotarsal joint, and inserts in the fascia associated with the flexor muscles of the crus.

### *Comments on Locomotion*

The principal types of locomotion in which differences would be expected among whistling-ducks are swimming and walking. There is no reason to suspect detectable differences in flight. The anatomical bases for differences in walking and swimming have been referred to in the section on the skeleto-muscular system. We here discuss the results of a photographic analysis of walking and swimming among captive whistling-ducks.

The relationship between the pelvic girdle and climbing in the young *autumnalis* has already been referred to (page 23), and a mechanical model for this locomotor behavior has been proposed (Rylander and Bolen, 1970). Motion pictures were not available to test the model with sufficient precision.

Motion pictures of diving *bicolor* and *autumnalis* illustrate a fundamental difference in mode of diving, that of *autumnalis* being awkward as this species alternates the legs during the swim strokes; and that of *bicolor* being more like an acknowledged expert diver, the Ruddy Duck *Oxyura jamaicensis*, which moves both legs together. The theoretical mechanical advantage of moving both legs together is based on the assumption that less energy is wasted in nonproductive bobbing in the case of swimming, and non-productive lateral movement in the case of diving.

We have not been satisfied with the application of the motion picture analysis approach to walking in the whistling-ducks. As mentioned earlier, differences in gait, while detectable subjectively, appeared to be most reliably measured only in terms of the difference in posture during the gait (Fig. 9). These differences in posture were to some extent functions of differences in the angles of the leg joints, a large angle at the knee, for instance, tending to make the duck assume a more upright posture. Also, the angles at the joints which differed when birds of different postures were standing would be expected to change in different ways when the birds walked. Thus, a record of the angle changes in the joints during walking may tell us more about the posture than the gait *per se*, though obviously it is meaningless to consider gait or posture alone.

Thus, we have been unable to devise the appropriate mechanical model to link the structure of the whistling-ducks to their differences in gait. There is

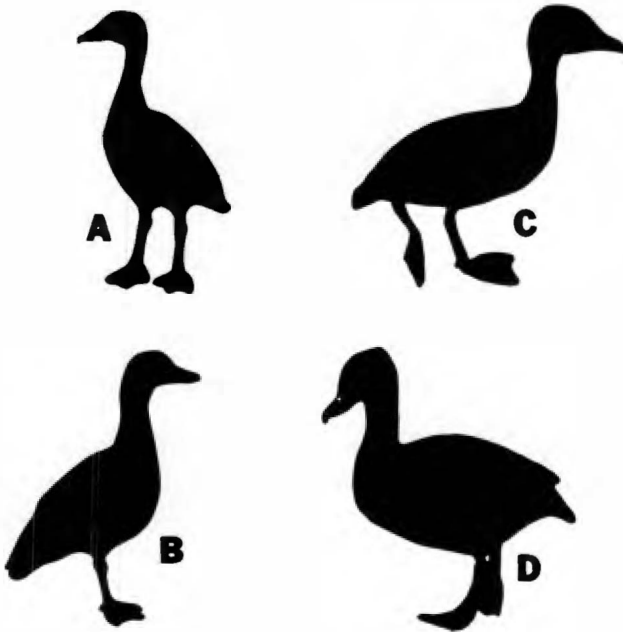


FIG. 9.—Standing postures of the Black-bellied Whistling-duck (A), Plumed Whistling-duck (B), Fulvous Whistling-duck (C), and Wandering Whistling-duck (D). Note the more upright posture in A and B, the two species that are more adapted for walking on land.

the possibility that in spite of differences in the pelvic girdle, *bicolor* is able under certain circumstances to assume the posture of *autumnalis*, and hence to show the same angles and angle changes in the joints during locomotion.

The only differences we have been able to observe in the dendrocygnid hind limb musculature are in the ilioprochanteric muscles, which are relatively larger in hatching *autumnalis* than in hatching *bicolor* (Rylander and Bolen, 1970). This relatively large muscle is apparently correlated with the nesting habits of the species. A model of climbing in that study relates m. ilioprochanteric anterior and posterior to the maintenance of a proper climbing posture as the *autumnalis* ducklings climb up the inner wall of the nesting cavity on the day of hatching. This activity does not occur in *bicolor*, which does not nest in trees. That m. ilioprochanteric posterior does indeed protect the femur (the action postulated by the climbing model) was demonstrated experimentally by removing m. sartorius, m. ilioprochanteric anterior and m. iliopropatellaris in an anesthetized one-day-old hatchery chick and subsequently electrically stimulating the remaining posterior ilioprochanteric muscle (Rylander, 1975).

#### *The Integumentary System*

The parts of the integument that are of special interest in the whistling-ducks appear to be the epidermal covering of the maxilla, the tongue and lamellae, the covering of the tarsus, the web scales, and the claws.

The epidermal covering of the maxilla has been examined in four whistling ducks (Rylander and Bolen, 1974a) and was found to be thicker in two species (*autumnalis* and *eytoni*), which feed on tough terrestrial vegetation, than in two other species (*bicolor* and *arcuata*) which feed mostly on aquatic vegetation. It is possible that a histological examination of the two ecologically distinct groups may reveal differences in the number and distribution of Gandry's and Herbst's corpuscles, which have been associated with feeding behavior.

The length of the maxillary lamellae has been correlated with the reported feeding behaviors of *bicolor* and *arcuata*, which have longer lamella (presumably for more efficient straining) than *autumnalis* and *eytoni*, the two land dwelling forms (Rylander and Bolen, 1974a). The same reservations should be applied to the interpretation of lamellae length as to sensory corpuscles on the bill: species that are almost genetically identical in this respect could develop lamellae of different lengths under different feeding conditions. The nail at the tip of the maxilla, which was larger in the more aquatic *bicolor* and *arcuata*, appears to show considerable wear in *autumnalis* and *eytoni*, and it is unclear how much nail reduction in the latter two species is caused by wear. On the other hand, a close examination reveals that some parts of the nail (for example, posterior regions) that suffer very little from abrasion during feeding, also seem to be better developed in the two aquatic forms.

The lower part of the tarsus is reticulated rather than scutellated in whistling-ducks—a consistent character that helps define them as a group. We do not know the significance of this epidermal character. The adjacent web scales are, however, correlated with the feeding habitats, in that *bicolor* and *arcuata* have fewer (but larger) scales per unit areas than *autumnalis* and *eytoni*. It would be helpful to know precisely the surface area of the feet of these four species, as well as the total number of web scales in each foot. Larger and fewer web scales per unit area might be an advantage to a swimming duck because such a web would presumably require less effort (energy) to keep it inflexible and stable during the swim stroke.

Two other specialized epidermal structures have been demonstrated. Young *autumnalis* have strongly decurved claws (Rylander and Bolen, 1970), evidently adaptations for climbing out of the nesting cavity on the day of hatching; and *eytoni* shows considerable development of the lateral hair-like processes that are ordinarily found rather sparsely on the tongues of ducks (Rylander and Bolen, 1973). We can attribute no specific function to such a specialized tongue.

Finally, there is histological evidence for incubation patches in both male and female incubating White-faced Whistling-ducks (Rylander *et al.*, 1980).

### *The Nervous System*

A consideration of the relationship between behavior and the structure of the nervous system had led to the search for measurements in the nervous

system that might be correlated with the specialized behaviors of the terrestrial whistling-ducks, for example walking, perching, feeding at night, *etc.* (Rylander and Bolen, 1974a). Within the vestibular apparatus it was shown that the semicircular canals were longer in *autumnalis*, which is probably more adept at perching on narrow structures, than in *bicolor*, *arcuata*, and *eytoni*. To obtain what were considered meaningful measurements, the canals were opened and their length measured by inserting a human hair. The lengths of the canals were related to the size of the basitemporal plate (assumed to be a conservative structure within the genus) in order to obtain an expression that indicated the relative development of the semicircular canals. The assumption is that a longer semicircular canal provides greater sensitivity to disturbances in equilibrium, presumably more critical in perching birds. Obviously such an interpretation must remain tentative until the physiological relationship between canal length and capacity for maintaining equilibrium is established.

The differences in relative size of the optic lobes of the whistling-ducks (Rylander and Bolen, 1974a) must be interpreted cautiously, since a comparison of gross size does not take into account density and types of neurons, neuronal circuits, brain chemistry, and the like which influence performance in the central nervous system (Rylander, 1978). Nonetheless, it is of interest that *autumnalis* and *eytoni*, the two terrestrial species, have relatively larger optic lobes (Rylander and Bolen, 1974a), and such development may constitute an adaption to the terrestrial habitat, since a bird on land may require keener senses of sight than one generally restricted to an aquatic habitat. The suggestion that the size of brain parts may be correlated with behavior in birds has been entertained by a number of authors, such as Cobb (1964), who looked at the problem in a number of species, including a duck (Mallard). He suggested that the relatively large optic lobes in the Mallard are correlated with nocturnal feeding habits.

We believe that a more fruitful area for identifying neuroanatomical correlates of behavior is the retina. In spite of some difficulties in interpreting the proportions of rods and cones in the retina in terms of visual acuity under poorly illuminated conditions (such as at night), classic studies (see Walls, 1942) have demonstrated a predominance of rods in nocturnal species such as owls. It is reasonable to assume that rods are responsible for the superb night vision in owls, but we cannot be certain if slight variations in the proportion of rods in closely related species, such as ducks, are related to differences in ability to see at night. On the other hand, a predominance of rods in *autumnalis* (Wells *et al.*, 1975), which feeds more at night than a duck such as the Mallard, suggests that the number of rods are, in fact, an indicator of the ability of whistling-ducks to see at night.

A microscopic examination of the retinas of *autumnalis*, *bicolor*, *eytoni*, and *arcuata* showed no significant differences in number or proportion of rods (Womack *et al.*, 1977), but in all four of these species the number of rods per unit area, as well as the percentage of rods (as compared to cones),



was larger than in the Mallard (Womack *et al.*, 1977; Hersloff *et al.*, 1974; Wells *et al.*, 1975). A reasonable conclusion is that the four whistling-ducks, while not differing among themselves in scotopic sensitivity, are all more capable in this regard than the Mallard.

In an attempt to establish a relationship between the retinal histology and the visual sensitivity in ducks, Hersloff *et al.* (1974) and Wells *et al.* (1975) conducted a series of experiments designed to measure the visual adaptation curves of the Mallard and the Black-bellied Whistling-duck. In addition to testing the "duplicity theory" of vision in ducks, which has been previously tested in pigeons (Blough, 1956), these experimenters were interested in relating visual adaptation curves to the ecology and retinal histology of the subjects being tested. The test of the duplicity theory in *autumnalis* may have provided some support for the theory, if the premise is accepted that a plateau in the visual adaptation curves indicates a duplex retina. On the other hand, the comparative experiments between the Black-bellied Whistling-duck and the Mallard do not indicate a significant difference with regard to visual sensitivity, though, rather curiously, the former species showed a break in the scotopic curve interpreted as characteristic of a duplex retina) whereas the latter species lacked this break (having a plateau, instead). Readers who wish to consider the theoretical aspects of these results should consult Hersloff *et al.* (1974) and Wells *et al.* (1975) where the topic is discussed at length. In spite of a number of mechanisms which need to be understood regarding the relationship between rods and scotopic vision, it appears that a study of retinas in whistling-ducks, when done in conjunction with perception studies, can yield meaningful results that may eventually enhance our understanding of the species' ecology.

#### *Other Morphological Features*

We conclude this chapter on the morphology of whistling-ducks by mentioning two observations, the significance of which is not altogether clear. One concerns the cerebral axis, which makes a more acute angle in *bicolor* and *arcuata*, the two aquatic forms, than in *autumnalis* and *eytoni*, the two terrestrial forms (Rylander and Bolen 1974a). The shape of the posterior part of the skull, and therefore the position of the foramen magnum and the angle of the cerebral axis, may actually be a function of the extent of muscle attachment. Goodman and Fisher (1962: 178) demonstrated a "relatively wide and high skull" in six species of waterfowl, including the Black-bellied Whistling-duck, which they classified as grazers. If such reasoning is extended to the four species of whistling-ducks treated here, one would conclude, on the basis of cerebral angle, that *autumnalis* and *eytoni* are better adapted for grazing than are the other two species.

The second morphological feature which separates these four whistling ducks into two groups is the position of the nares, which are more proximally located in the two terrestrial forms, *autumnalis* and *eytoni*. Whether a greater distance from the tip of the bill is an adaptation for grazing (the

nasal epithelium is better protected from injury?) is an open question. Perhaps more distally positioned nostrils constitute an adaptation for swimming and diving.

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APPENDIX.—Presumably all eight species of whistling-ducks were derived from a single ancestral species. At least two contrasting observations are of interest with regard to the evolution of the genus: the apparent evolutionary tendency towards convergence of characters, such as in *autumnalis* and *eytoni*; and the remarkable uniformity in plumage among widely separated populations of the same species, such as *bicolor* and *viduata*. Although we have strong reservations that a phenetic analysis of the whistling-ducks can resolve the question of which species are most closely related, we undertook such an analysis for the four best known species, and constructed a phenogram (Fig. 10) based on the 35 characters listed below. The extent to which this phenogram reflects the evolutionary history of these species depends, of course, on how conservative the characters actually are, and it may not be possible to do more than make rough guesses about this at the present time.

Character	Dendrocygna			
	<i>bicolor</i>	<i>arcuata</i>	<i>autumnalis</i>	<i>eytoni</i>
1. Short tarsus to midtoe ratio	yes	yes	no	no
2. Flared pelvis	yes	yes	no	no
3. Curved femur	yes	yes	no	no
4. Vertical posture	no	no	yes	yes
5. Horizontal posture	yes	yes	no	no
6. Walking gait	no	no	yes	yes
7. Nail shape	a	a	b	b
8. Lamellae number	a	a	b	b
9. Bill area	a	a	b	b
10. Bill epidermis	a	a	b	b
11. Feeding behavior	dive	dive	graze	graze
12. Upper bill cavity	a	a	b	b
13. Nares near bill tip	no	no	yes	yes
14. Lamellae shape	a	a	b	b
15. Neck muscles	a	a	b	b
16. Equilibrium (auditory lobe)	a	a	b	b
17. Equilibrium (semicircular canal)	a	a	b	a
18. Cerebral axis	a	a	b	a
19. Sides of maxilla parallel	a	a	b	b
20. Size of paraglossal	a	a	b	b
21. Size of ceratohyal	a	a	b	b
22. Integument lining of maxilla	a	a	b	a
23. Forehead-bill profile	a	a	b	a
24. Optic tectum	a	a	b	b
25. Semilunar ganglion	a	a	a	b

## APPENDIX 1.—Continued.

Character	Dendrocygna			
	<i>bicolor</i>	<i>arcuata</i>	<i>autumnalis</i>	<i>eytoni</i>
1. Plume development	moderate	moderate	none	long
2. Tongue structure	normal	normal	normal	unique
3. Spotted bill	no	no	no	yes
4. Multi-colored bill (3 or more)	no	no	yes	no
5. White on wing	no	no	yes	no
6. Patch on wing	no	yes	yes	no
7. Feet gray	yes	yes	no	no
8. Neck striated	yes	no	no	no
9. Markings distinct on downy plumage	no	moderate	very	very
10. Downy with bands (not spots)	a	a	b	c
11. Downy plumage base color yellow	no	no	yes	no
12. Tail length	short (58)	short (57)	long (85)	long (88)
13. Iris color	dark	dark	dark	yellow
14. Bill length (relative)	long	long	long	short
15. Wing size	235	222	246	245
16. Abdominal markings	no	no	yes	yes
17. Specialized primaries	no	yes	no	no
18. Tail coverts white-buff	yes	yes	no	yes
19. Eye ring	no	no	yes	no
20. Spotted breast	no	yes	no	no
21. Voice	a	b	c	b
22. Occipital	distinct	distinct	no	distinct
23. Black neck stripe	yes	yes	yes	no
24. Post-copulatory display	extensive	extensive	moderate	extensive
25. Body feathers with spotted tips	no	no	no	yes
26. Threat posture	a	b	c	b
27. Mutual nibbling	no	yes	no	yes
28. Tracheal structure	a	a	b	a
29. Nocturnal behavior	2	2	b	a
30. Egg color	a	a	b	b
31. Egg size	53 × 41	51 × 37	52 × 38	48 × 36
32. Nest in trees	no	no	yes	no
33. Nest over water	yes	no	no	no
34. Perch commonly	no	no	yes	no
35. Nests far from water with some regularity	no	yes	yes	yes

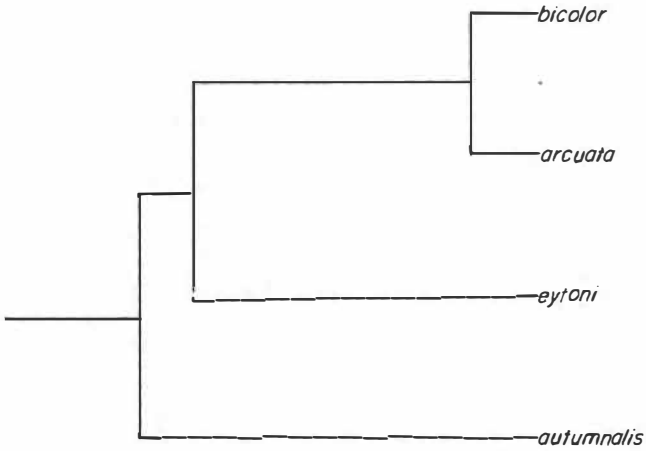


FIG. 10.—Phenogram of *D. bicolor*, *D. arcuata*, *D. eytoni* and *D. autumnalis*, based on characters listed in the Appendix above.