ECOLOGICAL AND ANATOMICAL ADAPTATIONS OF NORTH AMERICAN TREE DUCKS[1]

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Current views of adaptive radiation are heavily weighted with ecological and anatomical evidence. Among birds such evidence is described for various taxa of oscines (Beecher, 1953), Cuculidae (Berger, 1952), Anatidae (Goodman and Fisher, 1962), Scolopacidae (Rylander, 1965; 1969), and, most notably, Darwin's finches (Lack, 1947).

A growing accumulation of behavioral data has also been incorporated into the modern concepts of evolution. Kear (1967) tested several species of ducklings for their reactions to a visual cliff. She found a general tendency for cavity-nesting species to react about equally between the shallow and deep sides of the cliff, but ground-nesting species preferred the shallow side. As the powers of the ducklings' depth perception probably do not vary between species, Kear held the responses of the cavity-nesters as an advantageous compromise between a tendency to avoid severe falls and the need to jump from the nest after hatching.

Gottlieb's (1968) experiments suggest that the maternal call of female ducks functions as the selective portion of the audiovisual perceptual mechanism for species-recognition among ducklings in the nest. The strength of the ducklings' perception was unrelated to each species' nesting habits (ground vs. cavity nests), but Gottlieb found a species-specific behavioral response among ducklings exposed to audio stimulation in confined nesting boxes. Attempts to leave the nesting box were absent or weak in the ground-nesting species, whereas in cavity-nesters the ducklings quickly departed.

This suggests to us that mechanical adaptations for climbing may prevail among ducklings of cavity-nesting species. Moreover an important selective mechanism is apparently exerted at the time such ducklings leave their nest locations. Our consideration of the tree ducks (*Dendrocygna*) develops anatomical comparisons between two partially sympatric species in North America, the Fulvous (*D. bicolor*) and Black-bellied Tree Duck (*D. autumnalis*). Their respective habits, particularly nesting and duckling egress from the nest site, and the presumed anatomical adaptations peculiar to each, are foremost in our comparisons.

NOMENCLATURE

A confusing and probably unnecessary situation clouds the taxonomic designation of Fulvous and Black-bellied Tree Ducks. We wish to clarify

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the existing situation and to remark on the position followed in this paper.

FULVOUS TREE DUCK—The current A.O.U. Check-list (1957) recognizes two races: *Dendrocygna bicolor helva* for the United States and central Mexico and *D. b. bicolor* for the remaining range of the species (South America, southern Asia, and Africa). This racial division is based solely on a bill width of more (*bicolor*) or less (*helva*) than 20 mm (Friedmann, 1947). We prefer to follow Delacour (1954: 42) and others who recognize no valid subspecies throughout this bird's remarkable worldwide distribution.

BLACK-BELLIED TREE DUCK—The current A.O.U. Check list (1957) recognizes two North American races based on Friedmann's (1947) review: *Dendrocygna autumnalis fulgens* from southern Texas and northeastern Mexico and *D. a. lucida* from south-central Mexico, Central America to Panama, and the infrequent records from Arizona (Brown, 1906; Vorhies, 1945) and California (Bryant, 1914). The South American (Venezuela to Northern Argentina) form is the distinctively gray-breasted *D. a. discolor*. If this system is followed, the fourth and nominate race, *D. a. autumnalis*, is by elimination found only in the West Indies.

We again defer to Delacour (1954: 47) and, particularly, to Hellmayr and Conover (1948: 314–316) who share the opinion that no racial difference exists in the Black-bellied Tree Ducks found north of Panama. Texas birds handled in this and other studies (cf. Bolen, 1964; McDaniel et al., 1966; Bolen and Forsyth, 1967; Bolen 1967a; 1967b) have exhibited as much variation in belly coloration as Friedmann (1947) ascribes to his "races." Hence, we recognize only *D. a. discolor* and *D. a. autumnalis* as valid races of the Black-bellied Tree Duck. The data presented in this paper thus refer to *D. a. autumnalis* from southern Texas.

LABORATORY MATERIALS AND FIELD DATA

Hatching and posthatching juveniles were obtained from both wild and penned stock in Louisiana (*bicolor*) and southern Texas (*autumnalis*). Only known-age birds were selected for study. These were frozen or preserved in alcohol for dissection and measurement at Texas Tech University, Lubbock. Weights and linear measurements of freshly collected adults of both species were taken at the Welder Wildlife Foundation, Sinton, Texas. Growth data for living Black-bellied Tree Ducks were collected from juveniles hatched and raised at Texas A&I University, Kingsville, Texas, and from wild broods of known age captured near Mathis, Texas.

Field data for the Black-bellied Tree Duck originated from a larger study (Bolen, 1967a) of this species in southern Texas and from observations of Fulvous Tree Ducks in both Louisiana and Texas during 1962–1967 inclusive.

The following specimens were dissected under low magnification: *D. autumnalis*, piped (2), 1-day-old (2), 7-day-old (2), *D. bicolor*, 1-day-old (2), 7-day-old (4). All muscles were subject to unequal shrinkage by the preservative, but apparently this shrinkage did not adversely affect the comparisons except in small muscles.

For example, the biceps femoris was significantly wider and thicker in a 1-day *autumnalis* than in a 1-day-old *bicolor*, both before and after the specimens were embalmed.

Interdigital webs (between digits II and III) were carefully removed from juveniles and adults, placed between microscopic slides, and the scales per mm^2 counted under low magnification with an eyepiece micrometer.

Description of Muscles

The following description of the thigh musculature of a 1-day-old *autumnalis* applies also to the musculature of a 7-day-old *autumnalis*, and 1-day-old and 7-day-old *bicolor*, with the exceptions noted below (Variations in Musculature).

M. sartorius arises from the last dorsal vertebra and the anterior end of the ilium. The origin is fused with the origin of m. iliotibialis. M. sartorius inserts on the proximal end of the tibia.

M. iliotibialis 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 posterior. It is tendinous centrally in its distal one-fourth and inserts on the tibial cartilage. In *autumnalis* m. iliotibialis appeared to fuse more with m. sartorius, semitendinosus and piriformis pars caudofemoralis than in *bicolor*.

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

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

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

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

M. semitendinosus arises from the first three or four caudal vertebrae. It fuses at its origin with m. piriformis caudofemoralis and is connected to a varying degree with the flexor muscles of the crus by means of tendinous fibers. It inserts on the posterior surface of the tibiotarsus at its proximal end.

M. accessorius was absent.

M. semimembranosus arises from the ventrolateral surface of the ischium, passes medial to m. piriformis caudofemoralis, and inserts on the postero-medial surface of the tibiotarsus, medial to the insertion of m. semitendinosus. These two muscles are fused at their insertions.

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.

M. ambiens is an exceptionally wide muscle which 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.

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.

M. obturator externus arises from the margin of the ilio-ischiadic foramen and inserts proximally on the femur.

M. adductor longus 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.

M. femorotibialis externus has two heads. The proximal head arises from the lateral surface of the femur, near the insertion of m. iliotrochantericus 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.

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

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.

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

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.

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 posterolateral surface of the femur, at the distal end of this bone. Pars iliofemoralis arises from the posterolateral edge of the ilium and ischium, by means of several poorly-defined heads, fuses with pars caudofemoralis, and inserts as described above.

VARIATIONS IN MUSCULATURE

Although *autumnalis* averaged smaller than *bicolor* at hatching and larger a few days later, some pipped *autumnalis* were larger than older *bicolor*. These exceptions probably indicate either inaccurate determination of age or exceptional variation in duckling size in the same brood. The musculature tends to vary proportionally with the size of the specimen as well as with age; hence a comparison of the *actual* sizes of muscles of one species with the muscles of the other is not particularly useful in studying adaptation in these two species. This index is suitable only for comparisons between homologous muscles in closely related species that do not differ greatly and is not generally correct for comparisons of muscles.

TABLE 1

MEAN LINEAR MEASUREMENTS (MM) FOR ADULT FULVOUS AND BLACK-BELLIED TREE
DUCKS[1]

Species	No.	Culmen	Wing	Tarsus	Middle toe
D. bicolor	28[2]	46.6	210.5	55.8	66.6
		(44.0–48.5)	(196.0–225.0)	(52.0–60.0)	(64.0–70.0)
D. autumnalis	21[3]	53.1	238.0	62.3	64.5
		(49.0–56.0)	(229.0–248.0)	(58.0–66.5)	(61.5–68.5)

[1] Data from Friedmann (1947) and Bolen (1964). Ranges shown in parenthesis.
[2] 14 males and 14 females in sample.
[3] 11 males and 10 females in sample.

If we compare the *relative* size of certain muscles—that is, the size relative to bones or other muscles in the same specimen—we have a reliable index that might be useful in explaining functional differences between the two species. For example in both species piriformis pars caudofemoralis increases in size during the first 7 days, as might be expected. It was not possible to correlate the size of this muscle with age or species because of intraspecific variation in both species at all ages. Yet in all ducklings of equal body size, the size of this muscle relative to the thigh musculature in the same specimen was greater in *autumnalis*. Other muscles that were larger in *autumnalis* when compared in this way include the following: iliotrochantericus posterior, iliotrochantericus anterior, semitendinosus, adductor longus (possibly, although difficult to measure), biceps femoris and piriformis pars caudofemoralis (1-day-old ducklings only).

OTHER MORPHOLOGICAL COMPARISONS

We collected linear measurements from published data for adults of both species (Table 1). Except for winglength, these include only measurements of nonfeathered features; middle toe measurements exclude the claw. Friedmann's (1947) data were taken from museum specimens, whereas each of the *autumnalis* were measured while still fresh. We acknowledge that slight and probably insignificant discrepancies may exist because of possible shrinkage among the museum materials.

The linear comparisons developed a point of interest. They show *autumnalis* to be the larger species in every respect except middle toe length.

We then tested various ratios to compare the proportions that exist within the adults of each species. These ratios, shown in Table 2, were much alike in every case where middle toe length was not involved. This suggested a further comparison to determine the relative difference in size between the two species (Table 3). Here *bicolor* consistently proved

TABLE 2
PROPORTIONS AMONG LINEAR DIMENSIONS FOR ADULT FULVOUS AND BLACK-BELLIED TREE DUCKS[1]

	Species	
Proportions	*D. bicolor*	*D. autumnalis*
Wing/culmen	4.51	4.48
Tarsus/culmen	1.19	1.17
Wing/tarsus	3.77	3.82
Wing/toe	3.16	3.68
Toe/culmen	1.42	1.21
Toe/tarsus	1.19	1.03

[1] Data calculated from means in Table 1.

about nine-tenths the size of *autumnalis*, again with the exception of the middle toe. The latter relationship further demonstrated that the smaller species had a proportionately larger foot than adult *autumnalis*.

A small sample of young tree ducks was measured similarly but wing-length was not included (Table 4). We did not have ducklings of similar age in all cases, but even so, those available suggested that no meaningful differences in linear dimensions separated the two species. Additional measurements of living *autumnalis* ducklings from as many as 50 known-age individuals were no different from the sample we measured under laboratory conditions. We have no additional measurements for *bicolor* ducklings. Proportions developed from the laboratory measurements, shown in Table 5, fail to exhibit any species differences including those involving middle toe lengths.

We also measured the web scales from adult and juvenile *autumnalis* and adult and juvenile *bicolor* (Figures 1 and 2). Although the sample was too small to compare statistically, there appears to be a difference in web scale size between both juveniles and adults of each species. *D. bicolor* appears to have larger scales than *autumnalis*, but the scales of the same foot of the same individual vary considerably and it is therefore difficult to compare specimens reliably. To standardize measurements the

TABLE 3
PROPORTIONATE SIZE OF THE FULVOUS TREE DUCK TO THE BLACK-BELLIED TREE DUCK[1]

Feature	Ratio = *D. bicolor*/*D. autumnalis*
Culmen	0.88 (0.87–0.90)
Wing	0.88 (0.86–0.91)
Tarsus	0.89 (0.89–0.90)
Middle toe	1.03 (1.02–1.04)

[1] Based on means and ranges for adult birds shown in Table 1.

TABLE 4

LINEAR MEASUREMENTS (MM) FOR FULVOUS AND BLACK-BELLIED TREE DUCK DUCKLINGS[1]

Age (days)	No.	Culmen	Tarsus	Middle toe
D. autumnalis				
1	2	14.7–15.3	20.0–22.5	21.5–23.5
3	2	15.6–15.8	21.0–22.3	21.0–22.3
5	3	16.5–18.5	20.9–22.5	20.9–24.7
D. bicolor				
Hatching	1	12.2	16.9	18.6
3	4	15.7–16.9	20.5–22.0	21.1–24.1
7	1	15.7	20.6	23.6
8	1	16.7	21.3	22.7

[1] Measurements from laboratory specimens.

posterior edge of the web between digits II and III of the right foot were compared, yet even then the variation resulting from unequal shrinkage and possible uneven contraction of epidermal muscles in the foot made comparisons difficult.

The average size of the webs in juvenile *bicolor* was larger than in juvenile *autumnalis*, although we did not attempt to measure the surface area for each species. A slight difference in shape is evident between the claws of the juveniles of the two species, those of *autumnalis* being slightly more decurved (Figure 3).

NESTING HABITS

The pronounced strength of cavity-nesting among *autumnalis* was determined from 199 nest histories compiled in southern Texas. Of these, 93

TABLE 5

PROPORTIONS AMONG LINEAR MEASUREMENTS FOR KNOWN-AGE FULVOUS AND BLACK-BELLIED TREE DUCK DUCKLINGS[1]

	Proportion					
	Tarsus/culmen		Toe/culmen		Toe/tarsus	
Age in days	D. bicolor	D. autumnalis	D. bicolor	D. autumnalis	D. bicolor	D. autumnalis
Hatching	1.38	–	1.52	–	1.12	–
1	–	1.36–1.46	–	1.46–1.53	–	1.05–1.07
3	1.31–1.33	1.36–1.43	1.33–1.43	1.33–1.43	1.00–1.14	1.00–1.00
5	–	1.13–1.36	–	1.13–1.46	–	1.00–1.15
7	1.31	–	1.50	–	1.15	–
8	1.28	–	1.36	–	1.07	–

[1] Data from Table 4. Compare with appropriate ratios for adults in Table 2.
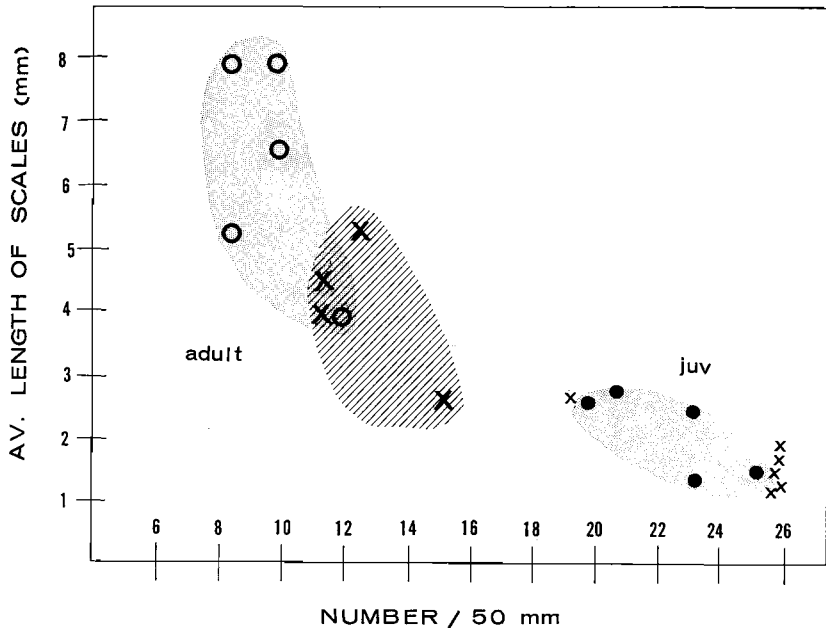
Figure 1.   Size of web scales along posterior border between digits II and III.
X, adult *D. autumnalis*; x, juv. *D. autumnalis*; ○, adult *D. bicolor*; ●, juv. *D. bicolor*.

per cent were in nesting boxes (cf. Bolen, 1967b) or tree cavities. The
balance were in buildings (6 nests) or on the ground (7 nests). The
rarity of ground nests for *autumnalis* is also reflected in the observations
of R. J. Fleetwood (pers. comm.) at Santa Ana National Wildlife Refuge,
Texas. He reports a single known instance of a ground nest at the refuge
during the 7 years of his residence, during which *autumnalis* nested con-
sistently in tree cavities or nesting boxes.

In contrast *bicolor* selects marshes and rice fields for its nests in Louisi-
ana (Lynch, 1943; Meanley and Meanley, 1959; Meanley, 1959; Mc-
Cartney, 1963) and California (Shields, 1899; Barnhart, 1901; Bryant,
1914; Wetmore, 1919; Dickey and Van Rossem, 1923). Shields saw
bicolor perched in trees near Tulare Lake, California, but found no
evidence of cavity nesting. Nests in dense aquatic vegetation, "almost
invariably over water," are reported for *bicolor* in Texas (Cottam and
Glazener, 1959) whereas *autumnalis* uses tree cavities in the same area
(Bolen, MS). We suspect that the cavity nests attributed to *bicolor* in
southern Texas (Burrows, *in* Bent, 1925: 274) were actually those of
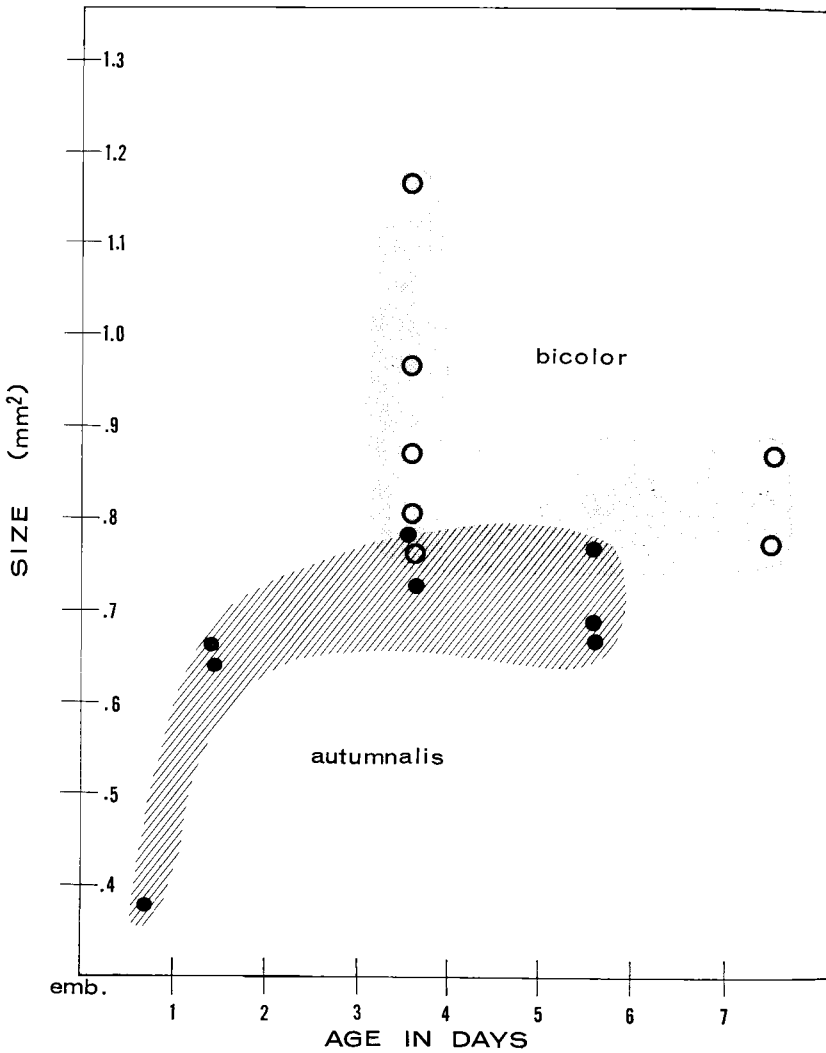*autumnalis*; only the eggs, and not the incubating birds, were the basis

Figure 2. Differences in web scale size along posterior border between digits II and III based on area of web scales. ◯, *D. bicolor*; ●, *D. autumnalis*.

of Burrows' conclusion. Carroll (1930, 1932) noted the relationship between rice culture (i.e. flooded fields) and the incidence of *bicolor* in Texas as did Meanley and Neff (1953) and Baird (1963) in Arkansas.

We believe that these diverse nesting habits are related to the anatomical features we have described respectively for *bicolor* and *autumnalis*.
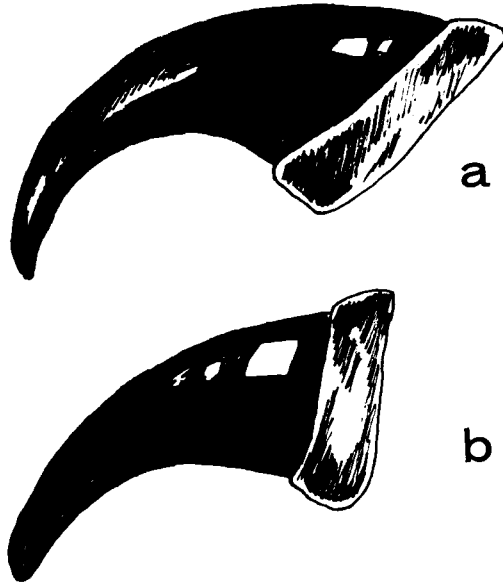
Figure 3. Middle toe claws of juvenile (a) *D. autumnalis* and (b) *D. bicolor* showing greater curvature in *autumnalis*.

DISCUSSION

As previously pointed out, mm. iliotrochantericus anterior and posterior and the flexors of the thigh are relatively larger in *autumnalis* than in *bicolor*. The smaller size of juvenile *autumnalis* and their relatively larger flexors may be related to this species' arboreal nesting habits, because the ability of the duckling to ascend the inner wall of the nesting cavity is certainly a function of the duckling's weight and the strength of its flexors. An explanation for the relatively larger mm. iliotrochantericus anterior and posterior is not so apparent as these muscles extend the leg. Conceivably a duckling scrambling up a vertical surface would require rapid extension of the hind limb between thrusts, that is, when the limb is raised preparatory to flexion.

Obviously the biomechanics in this study cannot be studied satisfactorily without motion picture analysis. This was not feasible in the present study, but we may make certain *a priori* statements regarding the locomotor behavior in question. These statements, expressed in terms of a mechanical model, may serve as a theoretical basis for additional studies that incorporate a detailed analysis of the duckling's egress from the nesting cavity. While the following model necessarily utilizes several arbitrary
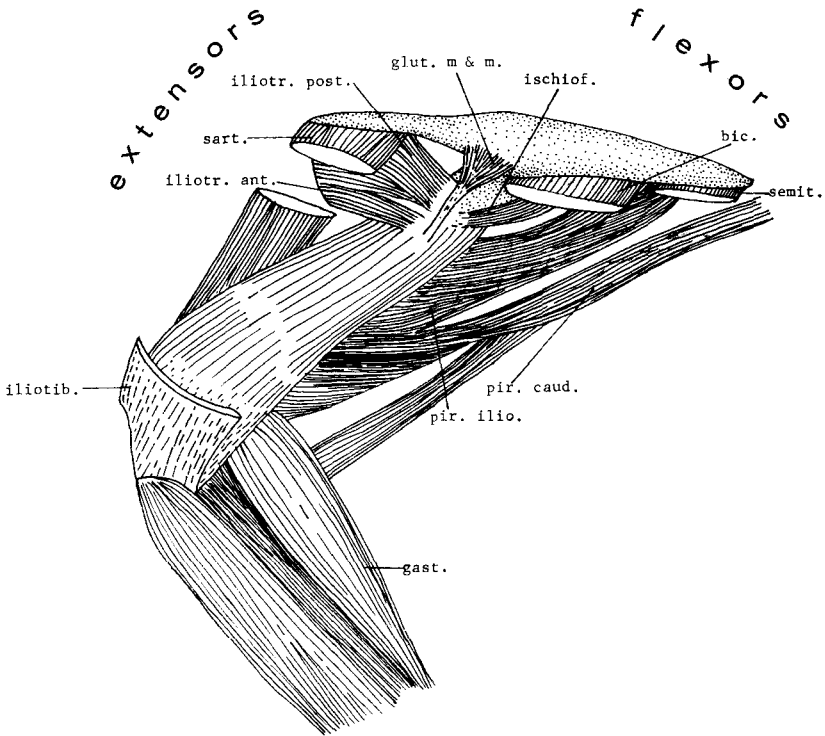
Figure 4. Deep thigh musculature of 3-day-old *D. autumnalis*, lateral view;
iliotib. = iliotibialis; iliotr. ant. = iliotrochantericus antericus; sart. = sartorius;
iliotr. post. = iliotrochantericus posterior; glut. m & m. = gluteus medius et minimus;
ischiof. = ischiofemoralis; bic. = biceps femoris; semit. = semitendinosus; pir.
caud. = piriformis pars caudofemoralis; pir. ilio. = piriformis pars iliofemoralis;
gast. = gastrocnemius.

values, we believe that, from a theoretical standpoint, it describes relation-
ships that have a high probability of proving valid when the locomotor
behavior of this species is analyzed in detail.

The extensors (cf. Figures 4 and 5) in *autumnalis* are larger perhaps
because of the need to rotate the leg forward very rapidly while climbing.
At the moment one leg is being thrust forward in order to gain a new
foothold, the other foot is sustaining the weight of the duckling. It would
seem advantageous, therefore, to develop as great a facility for rapid
forward thrusting as possible.

Because we are dealing with angular acceleration of the femur around
a pivot (the acetabulum), to estimate the torque involved for angular
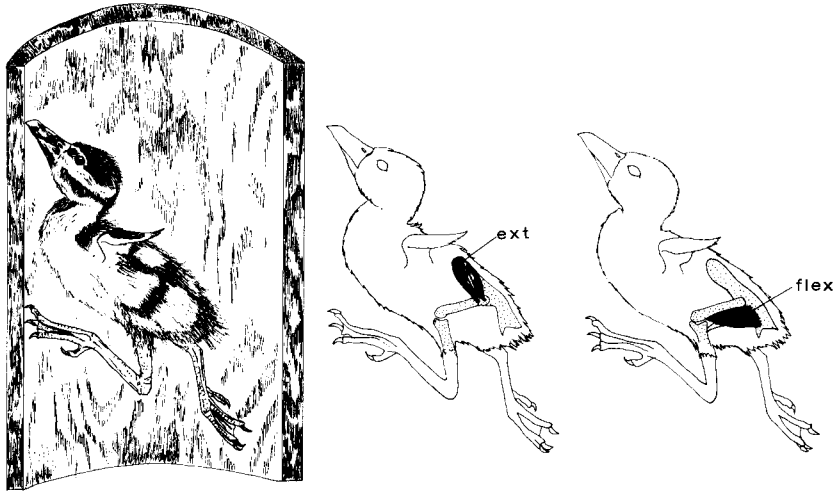rotation one must consider the force (of the muscle) and the moment

Figure 5. Presumed posture of juvenile *D. autumnalis* during climb from nesting cavity, showing relationship between the extensors (ext) and flexors (flex) employed in lifting the bird.

arm. The forces developed by the mm. iliotrochanterici are presumably proportional to some degree with their size, but to attempt to determine the exact relationship is not feasible.

Figure 6 is based on Figure 5 and shows that the extensors exert a force (f) on the femur and that the resulting torque (fd) is responsible for rotating the hindlimb around the acetabulum. To effect an increased angular acceleration it is necessary to increase either f or d or both. Likewise, the more we increase d (i.e. a more distal insertion of the extensor on the femur), the less force (f) will be required for the same torque. Two related species, such as the tree ducks considered here, have, with regard to their hind limb extensors, the same moment arm (d) and presumably different capabilities for exerting forces (f) on the femur with these muscles; hence we would expect variation in torque and potential for angular acceleration. Although we might expect similar differences in muscle size if m. iliotrochantericus inserted more distally (i.e. if d is increased), the mechanical advantages of increasing d might make the differences in force necessary for angular acceleration less critical. Suppose, for instance, that the optimal angular velocity for climbing in these ducklings is three radians per second. Given the mechanical advantage of, say $d = 6$ mm (rather than $d = 1$ mm, which is the case of the ducklings), it might be possible, considering the weight
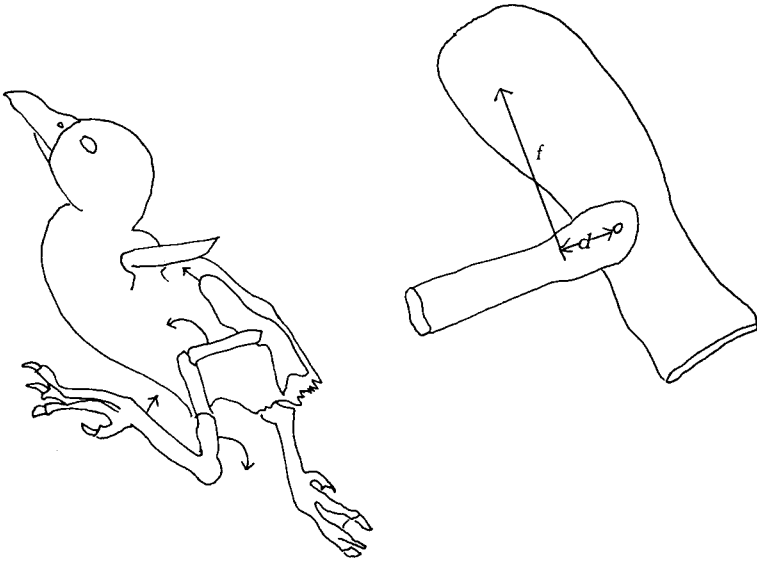
Figure 6. Model illustrating forces involved in lifting duckling up cavity wall. Arrows on left figure indicate directions of rotation. Right hand figure shows anterior pelvis and proximal femur on left side; f = force exterted by iliotrochantericus; d = distance between acetabulum and insertion of iliotrochantericus.

of the limb to be rotated, to increase the angular velocity with relatively little noticeable increase in muscle size in most cases.

During the climbing movement the complex movements of the limb components are abbreviated in Figure 6. Although the proper pelvic orientation may be maintained in part by the extensors, most likely the combined actions of several muscles are more important in this process. A careful examination of all limb muscles did not reveal noticeable differences between the two species, except with regard to the iliotrochanteric muscles.

In its original form the model overestimated the importance of the iliotrochanteric muscles in maintaining a correct orientation of the pelvis during ascension. It would be difficult to determine the extent to which certain muscles helped maintain the climbing posture, and whereas the original model is inadequate because it does not take into account the action of more distal muscles in maintaining orientation, it partially describes the actions of the thigh muscles. The hypothesis is as follows:

The posture indicated in the model (Figure 7) represents the stage of the ascent in which the duckling gains a minimal mechanical advantage from torque. In the condition indicated the axis between the acetabulum and the point where the foot contacts the wall is horizontal. In order to climb in this position, the muscles must theoretically exert a greater force than in other positions, if we do not take momentum into consideration.
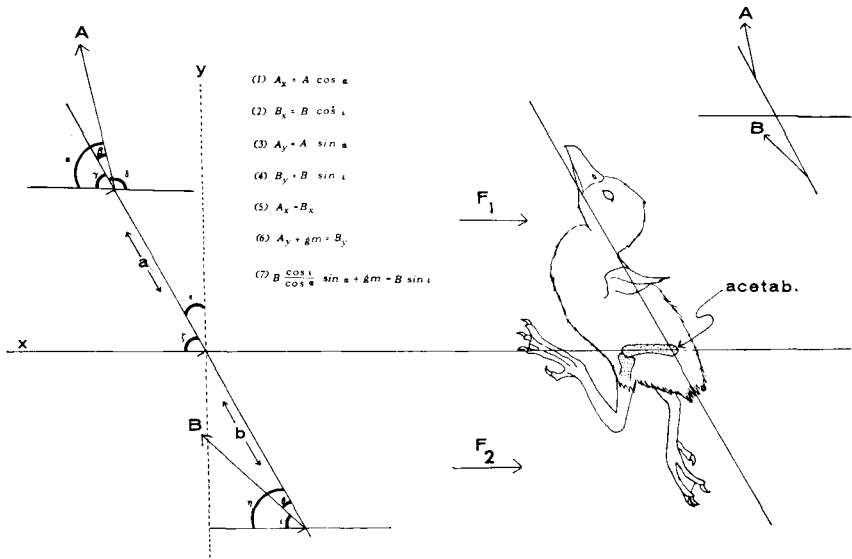
Figure 7. Model showing biomechanics of juvenile *D. autumnalis.* F_1 and F_2 are forces acting around the fulcrum (acetabulum) to maintain posture. A = force exerted by extensors of thigh; B = force exerted by flexors; a = distance along synsacrum between acetabulum and origin of iliotrochantericus anterior and posterior (extensors); b = distance along synsacrum between acetabulum and origin of flexors.

In order to prevent "tipping" backwards, which would result if only the flexors were contracted, the following condition must be satisfied:

$$A_x \sin \gamma = B_x \sin \eta$$

or, more conveniently,

$$Aa \cos \alpha \sin \gamma = Bb \cos \iota \sin \eta.$$

If we assume a reasonable degree of correlation between muscle size and function, the ratio, A/B, which is significantly greater in *autumnalis* than in *bicolor*, is related to the condition above in the following way:

$$\frac{A}{B} = \left(\frac{b}{a}\right)\left(\frac{\cos \iota \sin \eta}{\cos \alpha \sin \gamma}\right).$$

It follows that

$$\frac{A}{B} = \left(\frac{b}{a}\right)^3 \quad \text{when} \quad \zeta = 60°, \quad \beta = 5°, \quad \iota = 25°;$$

hence, $A = 3B$. This implies that in order to maintain the position we have adopted in our model, the force exerted by m. iliotrochantericus anterior and posterior must be approximately three times the force exerted by the flexors. This appears to be a conservative estimate, since the insertion is very close to the acetabulum, which gives a mechanical disadvantage not accounted for in the model.

To lift the duckling in this position, the following additional conditions must be satisfied:

$$Ay + \text{mass} = By.$$

If

$$A \cos \alpha = B \cos \iota$$

and

$$A \sin \alpha + 50 \text{ gm} = B \sin \eta,$$

Then

$$A = B \frac{\cos \iota}{\cos \alpha}.$$

It follows that

$$\frac{A}{B} = \frac{60 \text{ gms f}}{30 \text{ gms f}} = 2.$$

Hence, in order to satisfy these conditions, the force exerted by m. iliotrochantericus must be at least twice the magnitude of that exerted by the flexors. If we calculate the forces by substituting in the equations other values that fall within the range of variation indicated by our measurements, we obtain a ratio of A/B which is always at least 2.0. This results even when we choose values that give a maximum mechanical advantage to *autumnalis*, viz., the weight of the smallest duckling in our collection and the bone lengths that give the greatest mechanical advantage with regard to leverage. It follows from the model that in order to climb out of the nesting cavity a duckling depends to a large degree on the forces exerted by mm. iliotrochantericus anterior and posterior.

This analysis does not preclude the possibility that *bicolor* may also be able to climb out of a nesting cavity, but does suggest that the physical differences between *autumnalis* and *bicolor* are important factors in explaining their nesting behavior. The implication also arises that the climbing adaptations of downy *autumnalis* do not preclude ground nesting and the successful departure of ducklings hatched in ground nests. Kear (1967) found that *autumnalis* ducklings choose the shallow side of a visual cliff about 80 per cent of the time. Our field studies uncovered *autumnalis* ground nests only rarely, but when these hatched, the ducklings ably departed for the nearest surface water in a manner not unlike the young of a typical ground-nesting species.

Climbing adaptations perhaps similar to those of *autumnalis* presumably occur in other cavity-nesting waterfowl. Bolen and Cain (1968) described a mixed clutch of *autumnalis* and Wood Duck (*Aix sponsa*) eggs. At hatching, all the ducklings of both species successfully left the nesting box with the Wood Duck hen. This suggests that the audio cues stimulating departure may not be species-specific between cavity-nesting waterfowl. The survival value for all ducklings of cavity-nesting species that hatch in an interspecific parasitic nest thus seems obvious. The appropriate climbing adaptations, presumably similar to those we have proposed, must of course accompany whatever behavioral features may exist in cavity-nesting species.

An incorrect, but popularly held belief is that the ducklings of cavity-nesting waterfowl utilize "wing hooks" when ascending the cavity's interior wall. These observations refer to the claw present on digit I or, sometimes,

on digits I and II. Our measurements of the digit I claw from five *autumnalis* and five *bicolor* ducklings fell between 1.1 mm and 2.1 mm; these did not vary significantly between the two species. The claws are curved in both species. We feel that neither the length nor the shape of the digital claws in *autumnalis* or *bicolor* ducklings suggests any advantage to either a cavity- or a ground-nesting duck. The digital claws in these species are surely no more than an anatomical vestige (cf. Fisher, 1940) lacking any relationship with the egress of ducklings from any sort of nest.

It may be possible in the future to construct a mechanical model that estimates the mechanical advantage in swimming provided by the larger foot of *bicolor* (Table 3), or the advantage, if any, afforded in climbing or perching by the relatively smaller foot and the smaller web-scales of *autumnalis* (Figure 2). We have on several occasions seen *autumnalis* sitting on such tenuous perches as strands of wire fence, loops of Spanish moss (*Tillandsia usneoides*), and, once, on telephone lines. Such dexterity presumably is the result of a foot adapted to arboreal habits. Lawrence (*in* Bent, 1925: 271) noted that *autumnalis* seldom frequents deep water and instead prefers wading in shallow lake edges. He suggests this trait "may be from the fear of the numerous alligators that usually infest the lagoons." We doubt this conclusion, but we nonetheless support the accuracy of shallow-water behavior for *autumnalis*. By contrast, *bicolor* is a swimming species, spending a large proportion of its time dabbling (rather than wading) for food. We have never seen *bicolor* in trees or even perched above the ground. Meanley (1959) says "in three summers of study (in Louisiana) I never saw a Fulvous Tree Duck alight in a tree or even on a stub in a pond."

We accept middle toe length as a valid index to overall foot size, as shown earlier in Table 3. Moreover, peculiarities in foot structure (size, shape, etc.) are held as adaptive features. Bendell and Elliott (1966) suggest that differences in foot and leg size between two species of grouse chicks of the same age may be related to their respective efficiencies in forest and open environments. Dalacour and Mayr (1945) correctly noted the uselessness of a lobed fourth toe as a taxonomic feature for the Anatidae; this structure is adaptively related to the diving behavior of several waterfowl groups. Because the proportions developed in Table 5 for both *autumnalis* and *bicolor* ducklings do not show important differences, we conclude that any adaptive significances in foot size are not visibly present at the duckling stage of life. In this regard, it is interesting that both species of tree ducks rear their young in a similar manner and, when available, in similar habitat. Both male and female adults attend

the broods in a manner not unlike the true geese (*Anser and Branta*). The young of both species are prone to dive when threatened in open water or sparse cover; whereas the *autumnalis* adults tending broods often fly to escape imminent danger, the adult *bicolor* may dive with their broods. It appears, then, that a foot size conducive to maximum swimming efficiency is important to the survival of both *bicolor* and *autumnalis* ducklings, while for the adults, this feature is more fully developed only in *bicolor*. Conversely, the relatively smaller, more dexterous foot in adult *autumnalis* is a presumed adaptation primarily concerned with arboreal nesting.

SUMMARY

Physical adaptations among two species of North American tree ducks (*Dendrocygna*) are suggested from a study of muscle size and linear measurements of *D. bicolor* and *D. autumnalis*. These species differ particularly in their nesting ecology.

The thigh and leg muscles of ducklings are described from laboratory dissections. Intra- and interspecific variations in the musculature are noted. Other morphological comparisons included relative foot size for both adults and ducklings, the frequency and number of web scales, and the claw length and shape for ducklings. Data collected in this study are assessed in relation to a review of each species' nesting habits and general behavior.

The conclusion that *bicolor* nests in ground cover whereas *autumnalis* nests primarily in tree cavities suggested a mathematical model examining the adaptations of duckling leg muscles to each species' nesting habits. The model proposes a mechanical climbing advantage in the duckling musculature of the cavity-nesting *autumnalis*. Another selective advantage presumably lies in the relatively smaller, but more numerous web scales of young *autumnalis*, which may enhance traction during their vertical ascent inside a cavity nest. A relatively larger foot in *bicolor* seems related to this species' swimming and nesting habits; this difference is

especially pronounced in the adult foot as determined from ratios involving middle toe lengths for each species.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, fifth Ed. Baltimore, Amer. Ornithol. Union.

BAIRD, J. 1963. The changing seasons. Audubon Field Notes, 17: 6–8.

BARNHART, F. S. 1901. Evolution in the breeding habits of the Fulvous Tree Duck. Condor, 3: 67–68.

BEECHER, W. J. 1953. A phylogeny of the oscines. Auk, 70: 270–333.

BENDELL, J. F., AND P. W. ELLIOTT. 1966. Habitat selection in Blue Grouse. Condor, 68: 431–446.

BENT, A. C. 1925. Life histories of North American wild fowl. U. S. Natl. Mus., Bull. 130.

BERGER, A. J. 1952. A comparative functional morphology of the pelvic appendage in three genera of Cuculidae. Amer. Midl. Naturalist, 47: 513–605.

BOLEN, E. G. 1964. Weights and linear measurements of Black-bellied Tree Ducks. Texas J. Sci., 16: 257–260.

BOLEN, E. G. 1967a. The ecology of the Black-bellied Tree Duck in southern Texas. Unpublished Ph.D. dissertation, Logan, Utah State Univ.

BOLEN, E. G. 1967b. Nesting boxes for Black-bellied Tree Ducks. J. Wildl. Mgmt., 31: 794–797.

BOLEN, E. G., AND B. W. CAIN. 1968. Mixed Wood Duck-Tree Duck clutch in South Texas. Condor, 70: 389–390.

BOLEN, E. G., AND B. J. FORSYTH. 1967. Foods of the Black-bellied Tree Duck in South Texas. Wilson Bull., 79: 43–49.

BROWN, H. 1906. The Water Turkey and Tree Ducks near Tucson, Arizona. Auk, 23: 217–218.

BRYANT, H. 1914. Occurrence of Black-bellied Tree Ducks in California. Condor, 16: 94.

CARROLL, J. J. 1930. Breeding of the American White Pelican in the Texas coast. Condor, 32: 202–204.

CARROLL, J. J. 1932. A change in the distribution of the Fulvous Tree Duck in Texas. Auk, 49: 343–344.

COTTAM, C., AND W. C. GLAZENER. 1959. Late nesting of water birds in South Texas. Trans. North Amer. Wildl. Conf., 24: 382–395.

DELACOUR, J. 1954. The waterfowl of the world, vol. 1. London, Country Life, Ltd.

DELACOUR, J., AND E. MAYR. 1945. The family Anatidae. Wilson Bull., 57: 3–55.

DICKEY, D. R., AND A. J. VAN ROSSEM. 1923. The Fulvous Tree Ducks of Buena Vista Lake. Condor, 25: 39–50.

FISHER, H. I. 1940. The occurrence of vestigial claws on the wings of birds. Amer. Midl. Naturalist, 23: 234–243.

FRIEDMANN, H. 1947. Geographic variations of the Black-bellied, Fulvous and White-faced Tree Ducks. Condor, 49: 189–195.

GOODMAN, D. C., AND H. I. FISHER. 1962. Functional anatomy of the feeding apparatus in waterfowl (Aves: Anatidae). Carbondale, Southern Illinois Univ. Press.

GOTTLIEB, G. 1968. Species recognition in ground-nesting and hole-nesting duck-lings. Ecology, 49: 87–95.

HELLMAYR, C., AND B. CONOVER. 1948. Catalogue of birds of the Americas and the adjacent islands. Field Mus. Nat. Hist., Zool. Ser., vol. 13, part 1, no. 2.

KEAR, J. 1967. Experiments with young nidifugous birds on a visual cliff. Wildfowl Trust, 18th Ann. Rept.: 122–124.

LACK, D. 1947. Darwin's finches, an essay on the general biological theory of evolution. Cambridge, England, Cambridge Univ. Press.

LYNCH, J. J. 1943. Fulvous Tree Duck in Louisiana. Auk, 60: 100–102.

McCARTNEY, R. B. 1963. The Fulvous Tree Duck in Louisiana. New Orleans, Louisiana Wildl. and Fisheries Comm.

McDANIEL, B., D. TUFF, AND E. BOLEN. 1966. External parasites of the Black-bellied Tree Duck and other dendrocygnids. Wilson Bull., 78: 462–468.

MEANLEY, B. 1959. The North American tree duck. Atlantic Naturalist, 14: 182–184.

MEANLEY, B., AND A. MEANLEY. 1959. Observations on the Fulvous Tree Duck in Louisiana. Wilson Bull., 71: 33–45.

MEANLEY, B., AND J. A. NEFF. 1953. Bird notes from the Grand Prairie of Arkansas. Wilson Bull., 65: 200–201.

RYLANDER, M. K. 1965. A comparative study of the anatomy and physiology of *Erolia* and *Ereunetes* (Family Scolopacidae). Unpublished Ph.D. dissertation, New Orleans, Tulane Univ.

RYLANDER, M. K. 1969. Bemerkungen zur Beckenplexusvariation bei Regenpfeifern, Strandläufern und Verwandten. Anatomischer Anzeiger, in press.

SHIELDS, A. M. 1899. Nesting of the Fulvous Tree Duck. Bull. Cooper Ornithol. Club (presently Condor), 1: 9–11.

VORHIES, C. 1945. Black-bellied Tree Ducks in Arizona. Condor, 47: 82.

WETMORE, A. 1919. Bird records from the Sacramento Valley, California. Condor, 21: 73–74.

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