LOCOMOTOR MECHANISMS IN NORTH AMERICAN DUCKS

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The Anatinae of North America may be divided into two general adaptive types, the dabbling ducks and the diving ducks. The dabbling ducks (Tribe Anatini) are primarily surface feeders, and feed from the bottom only as deep as they can reach by tipping up, without entirely submerging. Thus they feed mainly in shallow, inshore waters. In contrast, the diving ducks (Tribes Aythyini, Mergini, and Oxyurini) feed mainly by diving in deeper offshore waters. The dabbling ducks can walk on land with relative ease, and different species feed there to a greater or lesser extent. The diving ducks, however, walk on land poorly at best, and seldom feed there. The dabblers frequently utilize areas bordered by trees or containing emergent vegetation, where the extent of open water is limited. Their flying abilities are suited to the use of these spatially restricted areas, particularly in taking off and landing. They take off by "rocketing" upward, aided by an initial jump and climbing vertically clear of obstructions. This requires the immediate production of powerful lift forces. Most diving ducks cannot take off in this manner, but must instead use the method called "skittering." They travel across the water surface paddling with their feet and flapping their wings, gaining speed and lift until they are able to rise from the surface. This is adequate for their needs because they usually remain in open water where the necessary space is available. Rocketing and skittering may be compared to the takeoff of helicopters and fixed-wing aircraft respectively. In landing the dabbling ducks are again more proficient. They can fly more slowly than divers and thus drop with greater agility into restricted spaces. Diving ducks typically use a faster, flatter approach and generally land only on water. Weller (1964) describes these movements in some detail.

Several workers have studied the locomotor system of birds by means of quantitative comparisons. The most extensive study is that of Hartman (1961) who measured heart, muscle, and body weights as well as wing and tail areas in many groups. Poole (1938) recorded weights and wing areas for 143 species. Greenwalt (1962) reprinted similar data from several earlier workers. All of these studies contain some data on the Anatidae but are primarily concerned with formulating general principles of dimensional relationships with respect to flight. None concentrates on a single group of birds. Storer (1955) studied weight, wing area, and skeletal proportions in three species of hawks. No comparable study has been done on waterfowl.

This paper will describe certain morphological variations in ducks which are correlated with differences in locomotor abilities. The muscular and

TABLE 1

MEASUREMENTS OF FIFTEEN SPECIES OF NORTH AMERICAN DUCKS

Species	No. of Specimens	Body Weight (gr.)		Wing Area (cm²)		Paddle Area (cm²)	
		Mean	Range	Mean	Range	Mean	Range
Anatini							
Anas cyanoptera	1	320.0		481.7		28.1	
Anas clypeata	2	514.6	457.1–572.0	578.8	566.9–590.6	37.4	36.2–38.6
Anas acuta	2	712.5	625.0–800.0	800.7	701.3–900.1	46.4	45.9–46.8
Anas americana	2	800.4	743.6–857.1	638.5	629.5–647.6	39.7	39.0–40.4
Anas platyrhynchos	5	961.3	828.5–1057.1	869.8	752.0–1018.4	56.9	48.2–64.4
Aythyini							
Aythya affinis	1	665.0		454.4		63.4	
Aythya valisineria	1	910.0		700.8		93.6	
Mergini							
Somateria fischeri	1	1457.1		718.6		67.6	
Somateria spectabilis	2	1700.0	1571.4–1828.5	824.4	748.0–900.7	76.5	74.4–78.5
Somateria mollisima	1	2342.7		1014.9		108.6	
Melanitta perspicillata	5	826.9	614.3–977.0	649.2	517.0–699.7	81.3	72.6–88.9
Melanitta fusca	2	1167.8	1164.0–1171.5	735.4	710.8–760.0	104.1	100.6–107.6
Bucephala albeola	5	396.2	343.2–486.2	326.9	259.2–368.6	47.8	44.6–51.6
Bucephala clangula	3	764.0	618.0–914.2	566.0	499.4–621.0	75.7	59.8–80.6
Oxyurini							
Oxyura jamaicensis	12	520.8	414.3–714.3	325.7	301.2–374.8	65.4	54.5–73.2

skeletal systems are very important in locomotion, and have been discussed elsewhere (Raikow, 1970, 1971). In the present paper I will consider size, shape, and slotting of the wings, and the size of the paddles relative to the behavioral distinction noted above between dabbling and diving ducks.

MATERIALS AND METHODS

Measurements were made on forty-five specimens collected in the vicinity of San Francisco Bay, California, and (*Somateria*) Barrow, Alaska. These represent six genera and fifteen species. The wing was spread and pinned down on a sheet of paper, and its outline traced. The outline was then measured with a planimeter to obtain the wing area. In several specimens both wings were measured but gave nearly identical results, so in most cases only one wing was measured and this value was doubled to give the wing area of the specimen (Table 1). The wing was spread so that the leading edge was as nearly as possible perpendicular to the body axis, and the wing extended to the maximum degree possible short of damaging the tissues. This standardized method gave repeatable results, insuring that a comparable measurement was made in each case. This is important since wing area varies continuously with the degree of wing spreading, and comparisons are valid only if a uniform method is used. For this reason I have not attempted to pool my data with those of other authors (noted above) who have also measured wing areas in waterfowl.

Relative wing area is expressed as Buoyancy Index following Hartman (1961). This equals the square root of the wing area divided by the cube root of the body weight.

Paddle area (Table 1) was determined by spreading one foot and pinning it to a piece of paper. The outline was then traced around all four digits and their webbing. The area was measured with a planimeter and doubled to give the paddle area of the specimen. Relative paddle size is expressed as the Paddle Index, which equals the square root of the paddle area divided by the cube root of the body weight. The length of the alula and the areas of wingtip slots were measured on the wing tracings. The primary emarginations were measured on study skins.

RESULTS

Wing Size.—The wing area relative to body weight (Buoyancy Index) is larger in *Anas* than in the diving ducks (Table 2). The highest value for diving ducks equals the lowest value for *Anas*. Other things being equal, the amount of lift produced by a bird is proportional to its wing area. The larger area in *Anas* is one factor providing for the greater lift needed in its special flying abilities as discussed above.

Since the species studied varied considerably in weight (Table 1) it is possible that differences in Buoyancy Index are related merely to body size and not to behavioral differences. It is well known that larger birds tend on the whole to have relatively smaller wings than do smaller birds (Poole, 1938). (See Storer (1955) for an example among hawks.) This follows from the surface-volume relationship, i.e. that area varies as the square of a linear dimension while weight varies as the cube.

TABLE 2

BUOYANCY INDEX AND PADDLE INDEX IN FIFTEEN SPECIES OF NORTH AMERICAN DUCKS

Species	No. of Specimens	Buoyancy Index Mean	Buoyancy Index Range	Paddle Index Mean	Paddle Index Range
		Anatini			
Anas cyanoptera	1	3.20		0.77	
Anas clypeata	2	3.02	2.87–3.16	0.77	0.73–0.81
Anas acuta	2	3.17	2.85–3.50	0.77	0.73–0.80
Anas americana	2	2.73	2.64–2.81	0.48	0.47–0.50
Anas platyrhynchos	5	2.99	2.70–3.24	0.77	0.68–0.86
		Aythyini			
Aythya affinis	1	2.44		0.91	
Aythya valisineria	1	2.73		1.00	
		Mergini			
Somateria fischeri	1	2.36		0.73	
Somateria spectabilis	2	2.40	2.35–2.45	0.73	0.72–0.73
Somateria mollisima	1	2.40		0.79	
Melanitta perspicillata	5	2.72	2.48–3.05	0.97	0.92–1.00
Melanitta fusca	2	2.58	2.53–2.62	0.97	0.95–0.98
Bucephala albeola	5	2.46	2.24–2.67	0.94	0.88–0.96
Bucephala clangula	3	2.65	2.57–2.74	0.95	0.91–0.98
		Oxyurini			
Oxyura jamaicensis	12	2.26	1.96–2.41	1.01	0.92–1.10

The Buoyancy Index equals the square root of wing area divided by the cube root of body weight. The Paddle Index equals the square root of the paddle area divided by the cube root of the body weight.

I plotted the weight against the wing area for the forty-five specimens of fifteen species considered in this study, and then connected the outside points for all individuals of each genus to give a polygon for each genus (Fig. 1). It is apparent that at any given body weight, the different genera have different wing areas. In a given weight range *Anas* has the largest wings and *Oxyura* the smallest, the other diving ducks being intermediate. *Somateria* falls outside the weight range of the other genera, yet its wing areas fall almost entirely within the range of *Anas*. Figure 1 shows that the relative wing area *between* genera is independent of body weight, so the correlation between wing area and habits is not an artifact of the surface-volume relationship, but is presumably biologically significant. *Within* a genus, however, wing area does increase with weight in a ratio roughly consistent with that expected from the surface-volume relationship, namely that weight increases more rapidly than area.

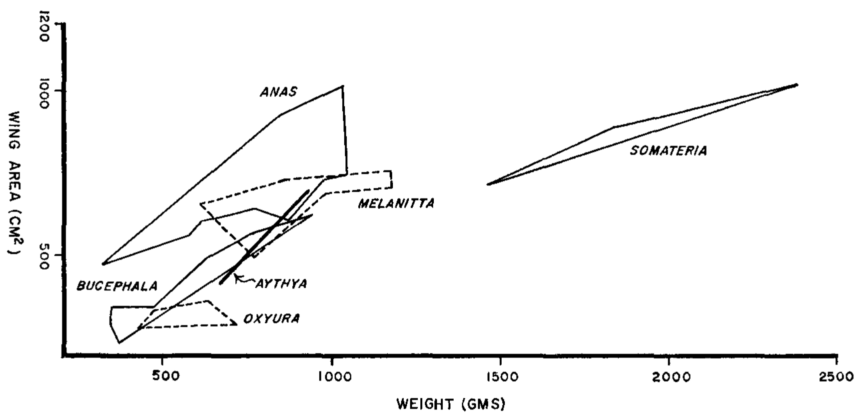

FIG. 1. The weights and wing areas for 45 specimens of 15 species of ducks were plotted, and the outermost points for each genus connected. *Aythya* is represented by a line since only two specimens were measured. The species and number of specimens included here are listed in Table 1. The illustration demonstrates that wing area is not a simple function of weight, but is different in genera with similar weights. The functional significance of the relationship between weight and wing area in the different genera is discussed in the text.

Wing Shape.—The shape of a bird's wing is aerodynamically suited to its method of flight. Savile (1957) recognized four basic wing shapes which have evolved many times in different avian groups. The *slotted soaring wing* and the *high aspect-ratio wing* are characteristic of terrestrial and oceanic soaring birds respectively. The *elliptical wing* is "adapted to operation in confined spaces" (Savile, 1957:224) since it provides high lift and good control under various conditions. It is found in birds which fly through restricted areas in the vegetation of forest or scrub, such as many Passeriformes, Galliformes, Piciformes, and Columbiformes. This wing type commonly has well-developed slotting, which increases lift at low speeds. The *high-speed wing* has a moderately high aspect ratio, a slender elliptical tip, a swept-back leading edge, a lack of tip slots, and other features. It is efficient for relatively direct, rapid flight, but not for slow flight or great maneuverability.

Savile (1957) reported that ducks have a moderately developed high-speed wing. While this is adequate to characterize the subfamily of ducks as a whole, detailed comparison shows that within this group the different genera have subtle differences in wing shape which are of functional importance (Fig. 2). In general, the diving ducks have a more typical high-speed wing, with reduced slotting (discussed below), and a more pointed tip resulting from a relatively straight trailing edge. *Anas* has a more rounded trailing edge, with greater wingtip slotting. Thus its shape more closely approaches the elliptical type

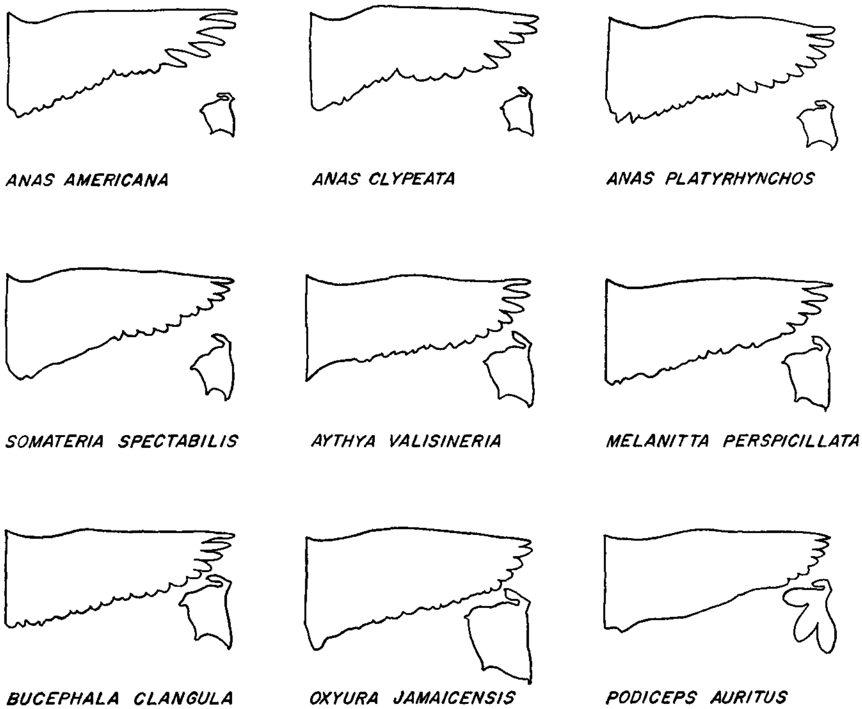

FIG. 2. Outline tracings of the wings and paddles of eight representative species of ducks and a grebe. The drawings are adjusted to equal wing lengths, so that the relative size of wing and paddle may be directly compared between species. The evolution of diving habits is accompanied by an increased paddle size, and by a more pointed, less slotted wing. *Anas americana* and *Oxyura jamaicensis* illustrate extremes of these features in dabbling and diving ducks respectively. The wing of *Oxyura* more closely resembles that of a grebe (*Podiceps*) than that of a dabbling duck (*Anas*).

than does that of divers, especially when the wing is extended, as during take-off. In level flight the wing is less fully extended, so that the ends of the primaries converge to close the slots, and the wing presents a more pointed appearance.

Wing Slotting.—Wing slots are devices which increase lift and lower the minimum flight speed by delaying stalling. Their aerodynamic characteristics are described by Savile (1957) and Jack (1953). Avian wing slots occur along the leading edge and at the wing tip. The leading-edge slot is formed when the alula is lifted away from the wing. In order to compare the size of the leading-edge slot between species I measured the length of the alula and divided this by the total wing length, from shoulder to tip, and by the standard

TABLE 3

RELATIVE LENGTH OF THE ALULA IN FIFTEEN SPECIES OF NORTH AMERICAN DUCKS

	Alula/Total Wing Length			Alula/Standard Wing Length		
Species	Mean	Range	No. of Specimens	Mean	Range	No. of Speci-mens
		Anatini				
Anas cyanoptera	0.24		1	0.35		1
Anas clypeata	0.23		1	0.32		1
Anas acuta	0.21	0.19–0.23	2	0.31	0.29–0.33	2
Anas americana	0.22		1	0.29		1
Anas platyrhynchos	0.24	0.21–0.27	5	0.33	0.32–0.35	4
		Aythyini				
Aythya affinis	0.23		1	0.34		1
Aythya valisineria	0.24		1	0.36		1
		Mergini				
Somateria fischeri	0.24		1	0.32		1
Somateria spectabilis	0.22		1	0.33		1
Somateria mollisima	0.27		1	0.36		1
Melanitta perspicillata	0.22	0.20–0.25	5	0.32	0.31–0.33	5
Melanitta fusca	0.23	0.23–0.23	2	0.33		1
Bucephala albeola	0.24	0.22–0.29	4	0.36	0.34–0.38	4
Bucephala clangula	0.23	0.22–0.24	2	0.33	0.32–0.35	3
		Oxyurini				
Oxyura jamaicensis	0.24	0.19–0.28	9	0.38	0.32–0.43	12

Total Wing Length is measured from shoulder to wing tip; Standard Wing Length is measured from wrist to wing tip.

measurement of wing length, from wrist to tip (Table 3). Measured either way the length of the leading-edge slot varies but little between species. Thus it does not seem to be functionally significant in the different flying abilities of dabbling and diving ducks. The scoters (*Melanitta*) have the peculiar habit of holding the alula extended while diving (Brooks, 1945), possibly as a diving plane. This habit is not associated with any change in length of the alula (Table 3).

Wingtip slots are formed by the spaces between the separated tips of the primaries. They are usually accentuated by emargination of the feathers. The size and shape of the slots depends on the length of the emarginated segment, the depth of the emargination, and the shape of the proximal end of the slot. I measured the length of the emargination of the outer primary and divided this value by the wing length (Table 4). There is a slight increase in

TABLE 4

MEASUREMENTS OF WINGTIP SLOTS IN FIFTEEN SPECIES OF NORTH AMERICAN DUCKS

Species	Emarginated Segment/Wing Length			Wingtip Slot Area/Wing Area		
	Mean	Range	No. of Specimens	Mean	Range	No. of Specimens
		Anatini				
Anas cyanoptera	0.14	0.13–0.15	5	0.023		1
Anas clypeata	0.16	0.15–0.17	5	0.027		1
Anas acuta	0.14	0.12–0.15	5	0.021	0.021–0.021	2
Anas americana	0.16	0.15–0.16	5	0.053	0.030–0.075	2
Anas platyrhynchos	0.16	0.14–0.17	5	0.031	0.022–0.040	5
		Aythyini				
Aythya affinis	0.12	0.11–0.13	5	0.022		1
Aythya valisineria	0.15	0.12–0.18	5	0.026		1
		Mergini				
Somateria fischeri	0.16	0.15–0.18	3	0.014		1
Somateria spectabilis	0.15	0.13–0.17	5	0.009	0.006–0.011	2
Somateria mollisima	0.17	0.15–0.18	5	0.024		1
Melanitta perspicillata	0.24	0.22–0.27	5	0.021	0.006–0.033	5
Melanitta fusca	0.16		1	0.014	0.009–0.018	2
Bucephala albeola	0.16	0.14–0.18	5	0.008	0.004–0.010	4
Bucephala clangula	0.18	0.15–0.20	5	0.030	0.018–0.037	3
		Oxyurini				
Oxyura jamaicensis	0.15	0.12–0.17	5	0.010	0.003–0.017	12

Melanitta perspicillata, but the difference is small. In general there is no pattern of increased emargination in any genus or tribe. In contrast to this there are great differences in the depth of the emarginated region (Fig. 3). It is very deep in *Anas*, thus forming well defined slots. In divers the emarginated portion is more shallow, though varying between genera (Fig. 3). Furthermore among divers the emargination may be nearly or entirely obliterated in worn plumage, a condition which I did not note in *Anas*.

In an attempt to quantify the somewhat subjective impression of differences in depth of emargination, I measured the area of the slots as shown on the wing tracings. This was divided by the wing area to give a measurement of relative wingtip slot area (Table 4). A complete division between dabblers and divers was not found, but the largest slot areas are in some species of *Anas*, while some divers have considerably smaller slot areas. This is most marked in the smaller species, *Bucephala albeola* and *Oxyura jamaicensis.*

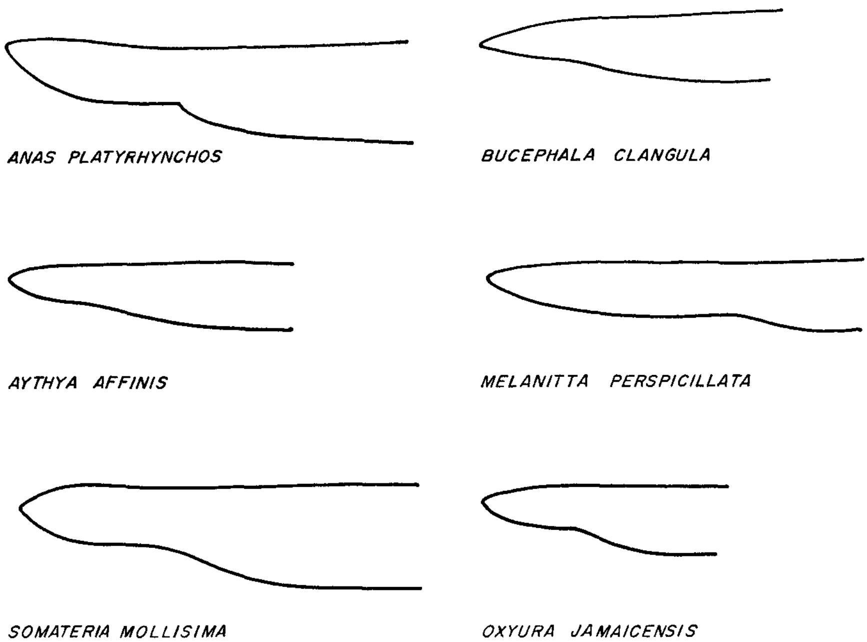

FIG. 3. Outline tracings of the distal end of the outer primary in six species of ducks. One species of each genus studied is included. All are from fresh plumaged birds. The efficiency of wingtip slots depends upon the depth of the emargination, and on the shape of the proximal end of the emarginated region of the feather. This region is deepest in *Anas*, and shallower in diving ducks. The transition from emarginated to unemarginated regions is abrupt in *Anas*, but more gradual in diving ducks. The emarginated region is unusually long in *Melanitta perspicillata.*

Anas cyanoptera and *A. clypeata* are in the same weight range as these diving species, but have more than twice the wingtip slot area. The largest slots were in *Anas americana,* which also has the smallest wings in its genus (Table 2) among the species studied. Possibly the increased slot area compensates for this to some extent.

In *Anas* the transition from emarginated to unemarginated regions is abrupt, so that the proximal end of the slot is U-shaped. In contrast the transition in divers is more gradual, giving a more V-shaped slot. The latter condition denotes a less efficient slotting mechanism (Savile, 1957).

Paddle Area.—Ducks are propelled through the water by the use of their feet, though dabblers and eiders may use the wings as an aid in diving. The main propulsive structure is thus the paddle, by which I mean the second through fourth digits and their webbing, plus the hallux, whose surface area is slightly increased in diving ducks by having an enlarged lobe. The Paddle Index indicates the surface area of the paddles relative to body weight. Table 2 shows that in most divers the surface area of the paddles is relatively larger than in *Anas*, which is of obvious functional significance in increasing the efficiency of swimming and diving. It results primarily from a lengthening of the second through fourth digits and a corresponding increase in web area. The progressive evolution of this feature in the tribe Oxyurini has been discussed previously (Raikow, 1970).

DISCUSSION

Ecological isolation in *Anas* is accomplished largely by differences in feeding habits and correlated structural specializations of the head and bodily proportions. Differences in feeding behavior which reduce interspecific competition have not been studied in detail, but some broad differences are obvious. For example, the long-necked Pintail (*Anas acuta*) can feed from the bottom in deeper water than other species, the Shoveler (*A. clypeata*) is specialized for straining food through its well-developed lamellae, etc. (Kortwright, 1942; Lack, 1971). Most such differences are not reflected in the locomotor features considered here. A large deviation from the generally similar measurements in the five species of *Anas* studied is the relatively small paddle in the Am. Widgeon (*A. americana*) (Table 2). This is correlated with the fact that the Am. Widgeon is the most terrestrial species studied, a good deal of its feeding being done by grazing. Kortwright (1942) says that "they are active on land, where they trot about and graze like little geese." The smaller paddle is clearly an adaptation to agility on land. Reduced foot size is characteristic of cursorial forms, e.g. the Secretarybird (*Sagittarius serpentarius*) has toes only one-fifth as long as those of most hawks (Welty, 1964).

The diving ducks as a group have smaller wings and larger paddles than do the dabbling ducks. The larger wings of dabblers, together with their more elliptical shape and increased slotting, are adapted to the use of small bodies of water, and inshore areas of larger bodies which may be spatially broken up by surrounding or emergent vegetation. This type of wing is aerodynamically suited to permit their habit of rocketing upward from these areas where a long clear distance for a running start may be absent. This relationship between wing type and habitat was pointed out by Savile (1957:218) who, however, did not document his statement. The paddle size in ducks is for each species a compromise between the optimally small paddle best suited for walking on land, and at the other extreme, the optimally large paddle best suited for aquatic locomotion.

Among the diving ducks studied two genera deserve special mention. The eiders (*Somateria*) alone among the divers, lack an enlarged paddle (Table 2). Its relative size is comparable to that of *Anas*, although a lobed hallux is present. This implies that eiders are less efficient divers than other members of the Mergini. Little is known about their underwater actions, but Humphrey (1958) reports that they use their wings underwater like Anatini, a sign that foot propulsion alone is not adequate. The eiders are ground nesters and walk efficiently on land, so the *Anas*-like paddle size is clearly adaptive. The wing size of eiders is reduced as in other divers (Table 2), which is correlated with the open waters which they frequent.

The Ruddy Duck (*Oxyura jamaicensis*) has the relatively smallest wings of the fifteen species studied. In shape they most nearly conform to Savile's (1957) characterization of the high-speed type, being small, pointed, and minimally slotted. Bent (1925:158) comments on the "grebelike" nature of the flight, swimming, and diving habits of Ruddy Ducks. Figure 2 shows that the wing shape in Ruddy Ducks is more like that of a grebe that that of a dabbling duck. Ruddy Ducks have the relatively largest paddles of all species studied except *Aythya valisineria* (Table 2). While they swim excellently, both on the surface and beneath it, they are clumsy and incompetent on land, being unable to walk more than a few steps (Kortwright, 1942: 369). This is in part due to the posterior placement of the feet and their specialized musculoskeletal system (Raikow, 1970), but the very large paddles undoubtedly add to their clumsiness on land. The Ruddy Duck represents an extreme in a spectrum of specialized conditions illustrated by the species investigated in this study.

It is believed that the diving ducks evolved from dabbling ducks, i.e. that the common ancestor of present-day dabblers and divers closely resembled the former. Thus the differences between the two represent primitive conditions in the dabblers and derived conditions in the divers. The divers are not a monophyletic group, however (Delacour and Mayr, 1945), rather it is probable that the three tribes of divers studied here arose separately from the Anatini and evolved into divers independently of one another. The similarity of their modifications is a result of parallel evolution. Nevertheless, while the general pattern is similar in each case, the details vary. Each character has diverged from the primitive condition to different degrees in different groups. Relative paddle size, for example, has not increased at all in *Somateria*, but has increased from a lesser to a greater degree in the other diving genera studied. The same is true of the reduction of wing area and slotting, and conversion to a more pointed wing shape. In each species a particular combination of characters is thus in a sense a visible reflection of its ecological niche.

SUMMARY

The relationship between locomotor morphology and feeding ecology was studied in fifteen species of North American ducks. Two general adaptive types are recognized. Dabbling ducks (Anatini) feed on the surface, seldom dive, walk and feed on land, feed in shallow, inshore waters, and take off from restricted areas by rocketing upward. Diving ducks (Aythyini, Mergini, Oxyurini) feed underwater by diving, walk on land poorly if at all, feed in open, offshore waters, and take off by running along the surface. These ecological differences are correlated with morphological differences.

Dabbling ducks have the largest wing areas relative to body weight, the most rounded wings, and the best developed wingtip slotting. This improves their ability to land and take off from spatially restricted areas. They have the relatively smallest paddles, which is correlated with their lesser aquatic adaptations but giving them greater agility in walking on land. The smallest paddles are in *Anas americana*, the most terrestrial of the species studied.

Diving ducks have smaller, more pointed, less slotted wings. These are adequate for rapid, direct flight, but inadequate for a rocketing take-off, thus limiting these birds to more open waters. They have the relatively largest paddles, however, in relation to their efficient diving abilities. The Ruddy Duck (*Oxyura jamaicensis*) is a superb diver but helpless on land. Its structural characteristics reflect this condition. Eiders, the most cursorial diving ducks studied, have paddle areas comparable to those of dabbling ducks. Similarities in the different tribes of separately derived diving ducks are due to parallel evolution in relation to similar adaptive specializations.

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NEW LIFE MEMBER

Dr. Clait E. Braun, of Fort Collins, Colorado, has recently become a Life Member of The Wilson Ornithological Society. He holds degrees from Kansas State University, University of Montana, and Colorado State University, and is currently a Research Biologist for the Colorado Division of Game, Fish and Parks. Besides the Wilson Society Dr. Braun also belongs to the AOU, the Cooper Society, The Wildlife Society, American Society for Mammalogists and Sigma Xi. He is a recognized authority on the White-tailed Ptarmigan (our picture shows him holding one in winter plumage) and has also published work on the Blue Grouse and the Band-tailed Pigeon. Some members of the Society will remember him as the leader of the high country field trip following the 1970 Meeting in Fort Collins. Dr. Braun is married with one daughter, and lists photography, and stamp and coin collecting as his hobbies.