FEEDING ECOLOGY AND DEVELOPMENT OF JUVENILE BLACK DUCKS IN MAINE

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ABSTRACT.—Data from 41 juvenile Black Ducks (*Anas rubripes*) collected in the Penobscot River valley of Maine from June through August 1974–76 were used to estimate the proportion of aquatic invertebrates in the prefledging diet and the allometric growth rates of the tarsi, flight muscles, and alimentary system. The proportion of aquatic invertebrates in the diet of downy and partially feathered juveniles averaged 88 and 91% of dry weight, but decreased to 43% for fully feathered young. The most important invertebrate food organisms for juvenile Black Ducks were asellid isopods, molluscs, nymphs of Ephemeroptera and Odonata, and larvae of Coleoptera, Trichoptera, and Diptera. A high proportion of invertebrates was consumed during the period of fastest absolute and relative growth.

Estimation of allometric growth rates with the power formula ($Y = a \cdot X^b$) showed that (1) the legs were relatively large at hatching and developed slowly; (2) the flight muscles, which were relatively small at hatching, grew slowly until the 4-week period preceding fledging, when they increased as the 4.75 power of body weight; and (3) growth of the liver and gizzard was approximately proportional to body weight. The data support Ricklefs' thesis that delayed functional maturity of the wings permits an increase in the overall growth rate of waterfowl. *Received 12 January 1979, accepted 6 August 1979.*

BECAUSE the components of avian reproductive strategy (e.g. nest site, clutch size, mode of development) are interdependent, it is necessary to consider the requirements of the young with those of the parent birds (Cody 1971: 473). The same is true of energy relationships; adults and young must be treated as a single unit during the period of parental care (Ricklefs 1974: 268). These concepts have stimulated increased interest in the growth and energy requirements of young birds (e.g. Ricklefs 1975).

Before such a holistic approach is possible for the Black Duck (*Anas rubripes*) or other waterfowl, additional data must be collected. Information on the food requirements and development of the young is essential. Early reports on the foods used by juvenile waterfowl were based on limited collections (Collias and Collias 1963) or on techniques biased toward the less digestible food items (Swanson and Bartonek 1970). Nevertheless, the importance of aquatic invertebrates for the young of several species of dabbling (Anatini) and diving (Aythyini) ducks has been established (Bartonek and Hickey 1969, Sugden 1973). Limited data available for juvenile Black Ducks suggest that aquatic invertebrates may be an important food (Mendall 1949: 82–83), but the timing and extent of invertebrate use are unknown. The objectives of the present paper are to quantify the proportion of freshwater invertebrates in the diet of juvenile Black Ducks and to describe the allometric growth of the tarsi, wing musculature, and alimentary system.

STUDY AREA AND METHODS

Juvenile Black Ducks were collected in the lower Penobscot River valley, within 55 km of Orono, Maine. Undeveloped areas of the Penobscot valley currently support spruce-fir and maple-beech-birch

forest types (Ferguson and Kingsley 1972). The soils of this area developed in a stony till of variable thickness overlying relatively insoluble Paleozoic rocks (Doyle 1967). As a result, waters of the lakes and ponds are dilute, and total alkalinities rarely exceed 20 ppm (as $CaCO_3$) (Mairs 1966). Approximately 25 beaver ponds and sedge-meadow streams were used as collection sites during the study. These wetlands are classified as Types 3 and 4 (Martin et al. 1953), or as subclasses of deep and shallow marsh associated with seasonal flats, shrub swamps, and bogs (Golet and Larson 1974).

Although I tried to observe a period of feeding activity before each collection (Swanson and Bartonek 1970), this was at times impossible because of low Black Duck densities and poor visibility in Maine wetlands. Of the 41 juveniles collected from June through August 1974–76, 88% contained more than 5 food items in the esophagus and were included in the analysis. Approximately equal numbers ($n = 13$, 12, 11) of downy (class I), partially feathered (class II), and fully feathered (class III) juveniles were collected. The class III sample included both flying and flightless young because flighted juveniles were impossible to distinguish when feeding.

The food from each esophagus was preserved in 75% ETOH in the field, and the carcasses frozen. In the laboratory, I identified the food items using Martin and Barkley (1961), Pennak (1953), and a reference seed collection. The dry weight of each food was measured to the nearest 0.1 mg after drying for 48 h in a convection oven at 50–55°C.

I chose dry weight as the principal measure of food importance in this study because differences in the moisture content of seeds and invertebrates bias volumetric and wet weight data (Sugden 1973), and because dry weight has a more direct nutritional and energetic interpretation. Statistical treatment of food-use data is often difficult; an alternative is to present the results in several formats, each of which reduces certain biases. For this study I calculated food importance as (1) percentage occurrence, (2) aggregate percentage, and (3) aggregate dry weight. Swanson et al. (1974b) reviewed the use of these terms. Aggregate dry weight is the total weight of a food item in a sample of birds divided by the weight of all such food items; aggregate percentage is the proportion of a given food item in each bird averaged over all birds in a sample.

Specimens frozen during the summer were later dissected. The age of each bird was estimated by reference to plumage descriptions (Gollop and Marshall 1954). To quantify juvenile development, I obtained wet weights to the nearest 0.1 g for the gizzard, liver, flight muscles (pectoralis, coracobrachialis, and supracoracoideus), and whole body. I compared the differential growth of organs and tissues with allometric growth constants as described by Ricklefs (1975) and Brody (1945: Ch. 15).

Results and Discussion

Juvenile food use.—The importance of aquatic invertebrates for three age classes of juvenile Black Ducks is summarized in Table 1. Of the three statistics, percentage occurrence is least informative because of the use of both animal and plant foods by nearly all birds. Agreement between the aggregate percentage and aggregate dry weight estimates suggests that the analysis has not been seriously biased by large food volumes in a small number of birds. All three statistics show a transition from consistently high invertebrate consumption in classes I and II to a diet of mixed composition during class III.

The significance of the decline in the aggregate percentage use of invertebrates during class III was tested with a one-way ANOVA. The F-statistic was significant ($F = 9.55$, df = 2,33, $P < 0.001$), and a Student-Newman-Keuls test (Sokal and Rohlf 1969: 239) showed that invertebrate usage by class III young was less ($P < 0.01$) than that of classes I and II; 95% confidence limits for invertebrate consumption were: class I, 83.6–100%; class II, 87.4–100%; and class III, 10.3–80.6%.

Important invertebrate foods consumed by class I birds were Diptera, Trichoptera, and Ephemeroptera (Table 2). The dipterans were larval, pupal, and adult midges (Chironomidae) and mosquitoes (Culicinae). For about 10 days after the ducklings hatched, most of their prey were adult or emerging insects captured at or above the water surface.

Dry weight consumption of trichopteran larvae and ephemeropteran nymphs

TABLE 1. The importance of aquatic invertebrates in the diet of juvenile Black Ducks collected in Maine.

Statistic	Age class		
	Class I (1–18 days) $n = 13$	Class II (19–43 days) $n = 12$	Class III (44–63 days) $n = 11$
Aggregate dry weight	95	84	34
Aggregate percentage	88	91	43
Percentage occurrence	100	100	91

peaked during class I. The mayfly nymphs that were eaten, *Ephemerella, Leptophlebia,* and *Siphlonurus,* frequently had the darkened and developing wing pads indicative of approaching emergence. These were, however, aquatic forms, showing that by 10–12 days of age the downy young fed largely on subsurface organisms. The caddis flies captured were *Banksiola* and *Platycentropus.*

Subsurface foraging was the rule for class II young, and several invertebrate taxa were taken in significant amounts. Mollusca and the isopod *Asellus* contributed nearly half of the total dry weight. During class II, predation on Diptera shifted away from adults and emerging pupae toward the aquatic larvae of Stratiomyiidae (*Odontomyia*) and Tipulidae. Consumption of the gastropod *Gyraulus* and the pelecypod *Pisidium* increased in class II, but the weight data are biased by a high ash content.

The first appreciable use of seeds from aquatic plants occurred during class II. None of the genera identified was taken in large amounts, and all of the seeds were from the production of previous years. Aggregate percentage (43%) is a better estimate of invertebrate use by class III juveniles than is aggregate dry weight (34%), because the dry weight figure was biased by the ingestion of 4 g of *Nuphar* seeds by a single duckling.

Only Mendall (1949: 82–83) has published data on the foods of juvenile Black Ducks. He examined 11 class I young collected in freshwater marshes and estimated invertebrate use at 67% by volume through about 10 days of age with a rapid decline thereafter. In my study most of the diet of class I and class II birds, and 40% of that of class III birds, consisted of invertebrate animals. Nearly all plant foods of the prefledging period were seeds; few vegetative parts were consumed with the exception of small amounts of *Lemna* and *Spirodela.*

The waterfowl literature suggests that juvenile Black Ducks are intermediate in their dependence on invertebrate foods. Juvenile Gadwall (*Anas strepera*) and American Wigeon (*A. americana*) consume invertebrates for only about 2 weeks (Sugden 1973), whereas the Lesser Scaup (*Aythya affinis*) (Bartonek and Murdy 1970) and goldeneyes (*Bucephala clangula, B. islandica*) (Palmer 1976) are almost exclusively invertebrate predators. Other species of the intermediate group include the Pintail (*Anas acuta*) (Sugden 1973), Mallard (*A. platyrhynchos*) (Chura 1961), and Redhead (*Aythya americana*) and Canvasback (*A. valisineria*) (Bartonek and Hickey 1969). The latter species consume invertebrates during a large but variable portion of the flightless period and then shift to a diet that is generally vegetarian in freshwater habitats.

Additional qualitative comparisons can be made with other species and habitats. Collias and Collias (1963) showed that most juvenile waterfowl can strain the larger Cladocera from water. During the present study no trace of Cladocera was found

TABLE 2. Summary of food items from three age classes of juvenile Black Ducks collected in Maine.

Food item		% occurrence			% dry weight		
Scientific name	Common name	Class I $n = 13$	Class II $n = 12$	Class III $n = 11$	Class I $n = 13$	Class II $n = 12$	Class III $n = 11$
Animal material		100	100	91	95	84	34
Crustacea							
Isopoda *Asellus*	Aquatic sowbugs	23	75	18	4	21	2
Amphipoda *Hyalella*	Freshwater scuds		58			tr[a]	
Insecta							
Ephemeroptera	Mayflies (N,A)[b]	54	58	18	59	1	tr
Odonata	Odonates (N,A)	31	50	64	3	4	6
Anisoptera	Dragonflies	23	50	27	2	3	3
Zygoptera	Damselflies	15	8	55	1	tr	3
Hemiptera	Aquatic bugs (N,A)	15	25	45	1	tr	2
Trichoptera	Caddis flies (L,P,A)	38	58	27	14	6	1
Coleoptera	Beetles (L,A)	23	25	45	tr	11	1
Hydrophilidae	Water scavengers		25	27		10	tr
Dytiscidae	Diving beetles	8	17	18	tr	tr	
Others		15	17	18	tr	tr	1
Diptera	Flies (L,P,A)	85	58	36	4	9	tr
Culicidae	Mosquitoes	62			3		
Chironomidae	Midges	31	8	27	1		
Others			50	18		9	tr
Mollusca	Snails, clams	38	25	27	2	24	6
Miscellaneous		46	50	45	8	8	16
Plant material		62	58	91	5	16	66
Seeds		62	58	91	5	14	63
Carex, Eleocharis, Nuphar, Sparganium	Sedge, spikerush, pond lily, burreed						
Vegetation			17	18		2	3
Lemna, Spirodela	Duckweed						

[a] tr = less than 0.5%.
[b] N = nymphs, L = larvae, P =pupae, A = adults.

in the Black Ducks examined. Perhaps a density threshold must be reached before Cladocera are an efficient food source, and this density rarely occurs in Maine wetlands. The contribution of chironomids to the diet of juvenile Black Ducks was also less than that reported for several other species. Chironomid larvae and adults provided 30% (volume) of the diet of prefledging Mallards (Chura 1961: 126) and 15% (dry weight) of the diet of juvenile Pintails (Sugden 1973: 21). Ruddy Ducks (*Oxyura jamaicensis*) are efficient at straining pond sediments, and the food of 18 young contained 73% (volume) chironomids (Siegfried 1973: 1,294). Although chironomids and culicids were a significant part of the diet of class I Black Ducks, they contributed only a trace to the total prefledging intake. Either chironomid densities are low in Maine marshes, or the peaty substrate makes their location by foraging Black Ducks difficult.

Factors affecting food use.—The data from Table 2 illustrate several of the factors (Swanson et al. 1974a) that affect food use in waterfowl. Those discussed here include the ecology of invertebrate prey and the behavioral maturation and pattern of growth of ducklings.

Invertebrate distribution, mobility, and life history all affected juvenile food use. Sampling of aquatic invertebrates in a series of Maine wetlands (Reinecke 1977) showed that the large mayfly nymphs eaten by class I ducklings were abundant, and

TABLE 3. Estimated proximate analysis of the diet of three age classes of juvenile Black Ducks.

Age class (n)	Proximate nutrients								
	% dry wt					% ash-free dry wt			
	Ash	Fat	Crude protein	NFE[a]	Crude fiber	Fat	Crude protein	NFE	Crude fiber
Class I (13)	12.7	10.6	49.3	19.9	7.5	12.1	56.5	22.8	8.6
Class II (12)	28.5	6.2	34.6	17.0	13.7	8.7	48.4	23.7	19.2
Class III (11)	8.7	4.8	25.8	38.1	22.6	5.3	28.3	41.7	24.7

[a] Nitrogen-free extract.

presumably available, in streamside wetlands but not in ponds. Strong swimming organisms (e.g. Hemiptera and adult Coleoptera) were recorded as food items less frequently than crawling or sedentary forms (e.g. Ephemeroptera, Trichoptera, Isopoda, Mollusca) (Table 2). The emergence of aquatic insects can affect food availability and stimulate waterfowl foraging activity (Swanson 1977). In this study, most of the mayfly nymphs captured by the ducklings had enlarged and darkened wing pads; similar nymphs observed in the field were moving into shallow water to ascend vegetation and emerge.

Behavioral development affected duckling food use by limiting potential foraging substrates. Field studies of juvenile waterfowl (Sugden 1973) indicate that generalized surface feeding predominates until at age class Ib, approximately 12 days, there is a transition to subsurface straining. Although behavioral observations were not made in my study, analysis of the food samples suggested a similar relationship. Early class I ducklings captured arachnids, homopterans, and emerging chironomids at or above the water surface; all other age classes obtained subsurface invertebrates.

The pattern of juvenile growth was also related to the quantity and quality of food consumed. Although the protein requirement for growth in captive waterfowl is high (18–22%) (Scott 1973), the dietary protein ingested by juvenile Black Ducks in natural habitats exceeded this level (Table 3). The estimates in Table 3 were calculated from the dry weight data of Table 2 and proximate analyses in Reinecke (1977) and Driver et al. (1974). Except for the large proportion of ash in the class II dry matter diet, the estimates are nearly identical for classes I and II and indicate that the protein intake was approximately 100% over the requirement. If it is assumed that crude fiber is unavailable to waterfowl (Mattocks 1971), then the caloric content of the diet of class I, II, and III birds was 5.27, 4.53, and 3.80 kcal/g ash-free dry matter. As shown in a later section, the time of greatest relative and absolute weight gains coincides with the period of high invertebrate and protein intake during classes I and II. Thus, the invertebrate diet of juvenile Black Ducks offers not only high protein content but also high caloric density and digestibility at a time when weight-specific metabolic rate (Sugden and Harris 1972) and growth rate are highest. Rapid growth presumably is advantageous for juvenile Black Ducks because of their high postnatal mortality (Reed 1975).

Juvenile growth.—Age and weight data for juvenile Black Ducks were taken from Penney and Bailey (1970), Smart (1965), and the present study, and fitted with three sigmoid curves using the graphical method of Ricklefs (1967). Visual evaluation indicated that the best fit was obtained with a Gompertz equation,
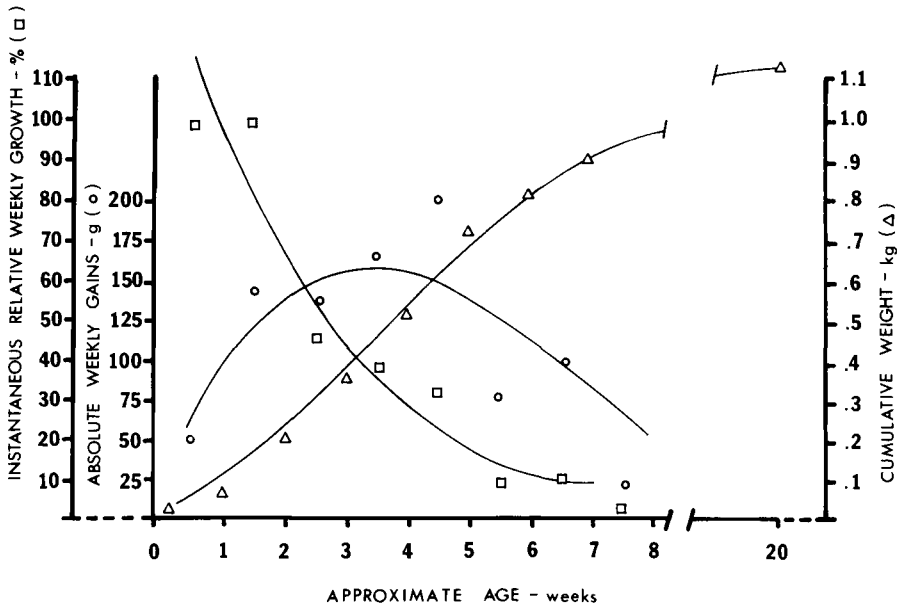
$$W = 1,125 \cdot e^{-e^{-0.394 \cdot (T-3.22)}}$$

Fig. 1. The pattern of growth in juvenile Black Ducks illustrated with empirical data and curves derived from a Gompertz equation.

where W = weight (g), e = base of natural logarithms, and T = time (wks). Figure 1 illustrates the cumulative, instantaneous relative $(\log_{10}W_{i+1} - \log_{10}W_i)/(T_{i+1} - T_i)$ and absolute weekly $(W_{i+1} - W_i)/(T_{i+1} - T_i)$ growth of juvenile Black Ducks with empirical data and predictions from the Gompertz equation. The model provided a reasonable first approximation; some of the residual variation may have been the result of pooling data for the sexes. Departures of the data points from the cumulative weight curve near the inflection suggest that the data deviate somewhat toward a logistic model. The growth constant for juvenile Black Ducks (0.394) was identical to the value (0.057) calculated by Ricklefs (1973: 183) for Mallards when the time scale for the Black Duck data was converted from weeks to days.

Data from the dissection of juveniles were used to explore the relationships between growth of body weight and growth of tissues and organs. The model for the analyses of allometric relationships was the parabolic or power formula,

$$Y = a \cdot X^b$$

and its logarithmic transformation

$$\log_{10} Y = \log_{10}a + b \cdot \log_{10}X,$$

where Y = tissue weight (g), X = body weight (g), and a and b are constants. Figures 2A–C illustrate log-log plots of tarsal length and pectoral muscle, gizzard, and liver wet weight against body weight. Lack of specimens between 400 and 500 g provided a convenient but arbitrary breaking point in the curves to compare the slopes (b), which I computed using linear regression on data transformed to common logarithms. For each set of data points, b is interpreted as the exponential rate at which tissue weight increases with body weight.

During the first 3 weeks of life the pectoral muscles weighed about 1% of body
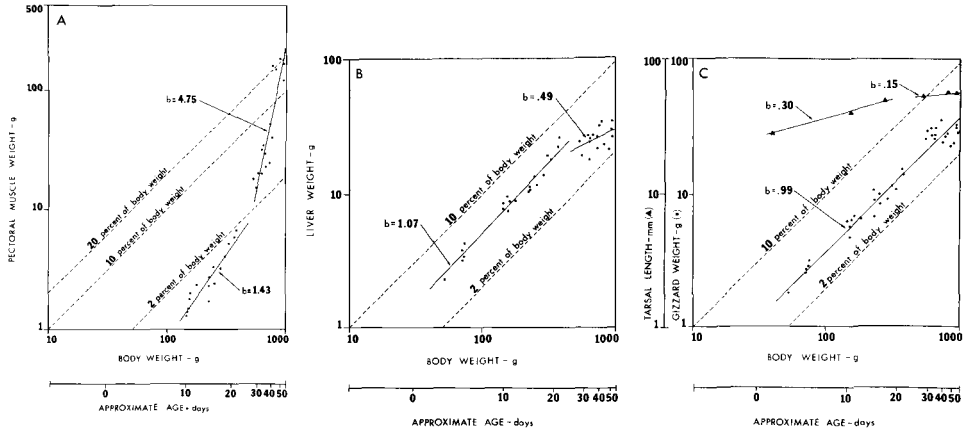
Fig. 2. **A**. the allometric relationship of pectoral muscle weight to body weight in juvenile Black Ducks; **B**. the allometric relationship of liver weight to body weight in juvenile Black Ducks; **C**. the allometric relationships of gizzard weight to body weight in juvenile Black Ducks, and of tarsal length to body weight in juvenile Mallards [Mallard data from Greenwood (1974)].

weight (Fig. 2A). A transition from nonfunctional to functional flight muscles occurred during the second half of the prefledging period. For juveniles under 500 g, the pectoral muscles grew as the 1.43 power of body weight. At this rate it would require many weeks for the flight muscles to reach 22% of body weight, as occurs in adult females (Reinecke 1977). During the last 30 days of development, the flight muscles grew as the 4.75 power of body weight, gaining about 180 g of tissue while increasing from 2 to 20% of body weight.

Growth of alimentary systems was less variable. Liver weight in the youngest birds was 5% initially, grew for 3 weeks as the 1.07 power of body weight, and then slowed as the adult size of 2.6% of body weight was approached (Fig. 2B). Gizzard weight remained essentially proportional to body weight throughout the flightless period (Fig. 2C).

Tarsal measurements were not recorded for juvenile Black Ducks; the data analyzed were taken from Greenwood's (1974) work with Mallards. Mallards and Black Ducks are known to be similar in both growth rates (see above) and in adult body proportions (Palmer 1976). Two phases of growth were apparent (Fig. 2C); in the first, tarsal length increased at the rate expected ($b = 0.3$) from dimensional considerations, and in the second, the rate of growth slowed as adult size was attained.

The impressive feature of juvenile development is the relationship between the growth of the flight muscles and that of the legs (tarsi). Assuming the Mallard data are relevant, the length of the tarsi at hatching was already 50% of adult size at a time when body weight was only 3% of adult weight. For 3 weeks the tarsi grew with the 0.3 power of body weight, and thereafter more slowly. Early maturation of the legs was also reported by Kushlan (1977) for the White Ibis (*Eudocimus albus*) and is probably true for most precocial species that depend on their own mobility for food gathering and escape from predators. The delayed flight capability of the Black Duck contrasts with the rapid development of the wing muscles during the first week of life in terrestrial precocial species such as the Willow Ptarmigan (*Lagopus lagopus*) (Aulie 1976).

Ricklefs has suggested that maturity of tissue function is inversely related to growth rate (1973: 177), and that the Anatidae have growth rates that are variable but faster than other precocial species of equal weight (e.g. Galliformes) (1973: 190). The fastest growing juvenile birds are terrestrial altricial species characterized by immaturity of function in both the front and hind limbs. The data from my study are consistent with Ricklefs' thesis that immaturity of function in the front limbs permits an increased overall growth rate in the anatids.

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