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ENERGETICS OF GROWTH FOR BLACK-BELLIED TREE DUCKS

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Ricklefs (1969) postulated that the rate at which food can be processed and utilized is a physiological constraint that limits the growth rates of birds. The brood size of altricial birds is known to be limited by the ability of the adults to feed their young (Lack 1954, Royama 1966, and Ricklefs 1968) but the energy required for their growth is not known. This subject has been much studied in domestic animals (Kleiber and Dougherty 1934, Brody 1945, Hill and Anderson 1958, Scott et al. 1959, and Hijikuro and Morimoto 1969), but has received little attention in wild birds (Stivens 1961, Brisbin 1965, Sugden 1969, Penny and Bailey 1970). This study is an attempt to determine the energy cost for growth in Black-bellied Tree Ducks (*Dendrocygna autumnalis*) and the ecological efficiency of that growth.

The precocial young of the Black-bellied Tree Duck acquire their own food. The amount that a duckling eats should be limited only by its ability to find food. These ducklings are brooded by the adults for a time but begin the energy-demanding process of thermoregulation around the ninth day of age (Cain 1972). Their growth rate is highest between the ages of 4 to 33 days (Cain 1970).

METHODS

Black-bellied Tree Duck eggs were collected in San Patricio County, Texas, transported to the University of Illinois, and incubated at 39°C in a forced-air incubator at 85–90% relative humidity. Ducklings were brooded in these incubators for 48 hr after hatching and then placed in a 10 m × 10 m room at 32–38°C with a 15-hr photoperiod.

Ducklings used in the metabolism and growth determinations were placed in metabolism cages like those described by Owen (1970) but larger, 54 × 43 × 48 cm. They were fed chick startena for 21 days and milo (*Sorghum vulgare*) thereafter. All the food was oven-dried (65°C) to a constant weight. Temperature was kept at 32°C and the photoperiod at 15 hr during the tests, approximately the conditions normally encountered during the nesting season in south Texas. During intervals between tests, the ducklings were fed a mixture of chick startena, milo, and cracked corn. Duckweed, aquatic invertebrates, and small fish (*Gambusia affinis*) were placed in the water pans daily to insure a balanced diet.

At 3-day intervals the ducklings were weighed to the nearest 0.1 g on a triple-beam balance. The unused food and excreta were collected, oven dried, and homogenized with a Waring Blender. Their caloric value was determined with a Parr oxygen bomb calorimeter.

The relationships among photoperiod, temperature, metabolism, and growth were determined by Kendeigh's (1949) method, which involves subtracting the caloric value of the excreta (excretory energy) from the caloric value of the food eaten (gross energy intake). The remainder is the amount used (metabolized energy), and during a period of constant weight (change within ±1.5%) is called existence energy. Productive energy is the amount metabolized above that needed for existence at a particular temperature.

To calculate the existence requirements for the growing ducklings, I plotted the metabolized energy against weight gained. From the resulting regression lines at weekly intervals the existence energy was the metabolized energy with no gain in weight (i.e. $X = 0$). I calculated the energy cost per gram of dry weight increase by multiplying the metabolized energy required per gram of wet weight increase (the slope of the regression line) by the percent of wet weight that was dry weight. This product, divided by the calories per gram of dry matter and multiplied by 100 yielded the productive efficiency.

RESULTS

Body weight. Growth of body weight for 26 ducklings (fig. 1) followed closely my data for more than 100 pen-raised ducklings (Cain 1970). My previous study showed the growth of pen-raised ducklings to resemble that of wild ducklings. The dry weight of 1-day-old ducklings in this study averaged 31.9% of the wet weight and increased to 43.0% at six weeks of age, remaining constant thereafter (table 1). These values are similar to those reported by Sugden (1969) for Lesser Scaup (*Aythya affinis*) ducklings.

Caloric values per gram dry weight of the duck-

TABLE 1. Weights and caloric values of ducklings sacrificed at weekly intervals.

Age in weeks	N	Wet weight (gram)	Dry weight (gram)	Percent dry weight	Caloric value (kcal/gram) dry weight	Caloric value (kcal/gram) wet weight
pipped	3	30.8	9.8	31.9	6.0	1.9
2	4	45.0	11.2	24.9	5.5	1.4
3	5	59.8	19.7	33.0	4.8	1.6
4	1	85.6	29.5	34.5	5.4	1.9
5	1	166.6	62.6	37.6	5.6	2.1
6	1	257.0	110.4	43.0	5.7	2.4
7	1	405.5	167.1	41.2	5.6	2.1
9	1	440.0	184.4	41.9	5.3	2.2

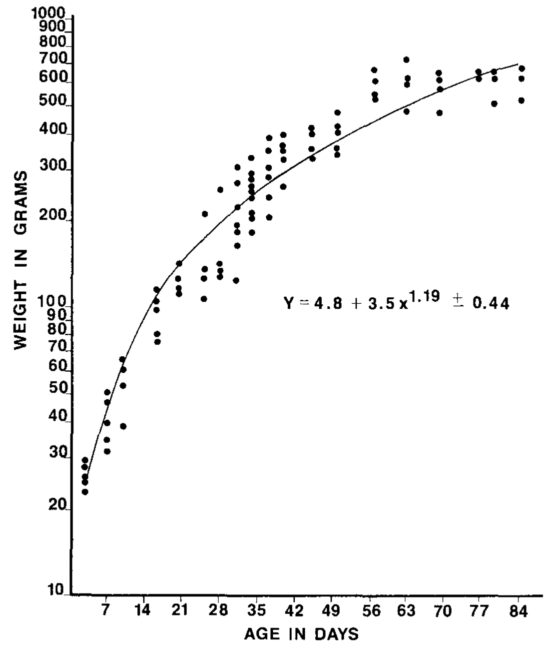

FIGURE 1. Growth of ducklings in terms of wet weight at daily intervals for the first 84 days. Least squares non-linear regression provided the line.

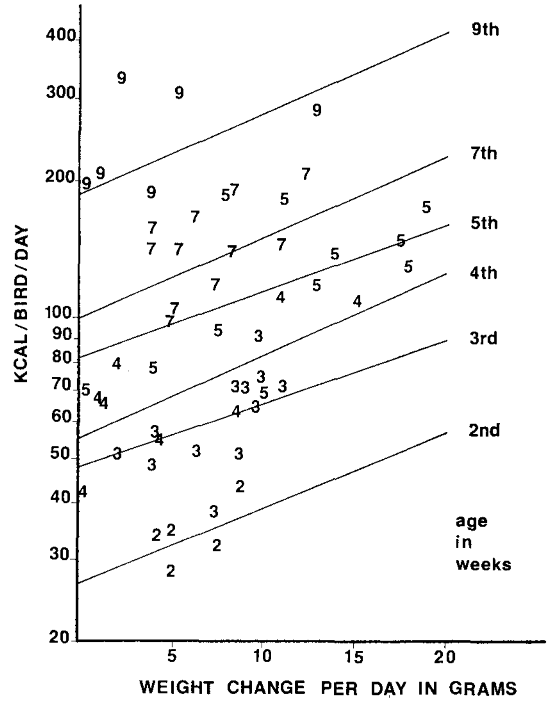

FIGURE 2. Linear relationships between metabolized energy and changes in wet weight for the growing ducklings.

lings' carcasses decreased from 6.0 kcals at hatching to 5.5 kcals at two weeks and remained fairly constant thereafter (table 1). This decrease is probably due to the metabolism of the yolk that is absorbed at hatching (Kear 1965).

The caloric value of the ducklings per gram of wet weight increased slightly with age, probably a result of fat deposits (Sugden and Harris 1972, Ricklefs 1974). The difference between sexes for the growth rate, dry weight, and caloric values were not significant, so all values reported here include both sexes.

Energy consumption. Gross energy intake increased with age during the nine weeks studied (table 2) and was significantly different at weekly intervals except between three and four weeks. Adults at the same temperature and photoperiod consumed significantly less energy. This difference reflects the productive and existence energy demands for the ducklings as compared with only existence energy needed by the adults.

Energy lost in excreta increased through the fourth week. The caloric value of the excreta increased significantly from 3.6 kcals/g for ducklings less than 31 days of age to 4.2 kcals/g after 31 days. Total excretory energy, however, declined after the fourth week (table 2) as the utilization coefficient increased.

Total metabolized energy increased throughout the nine weeks of growth (table 2). The metabolized energy averaged 0.64 kcals/g/day for 2-week-old ducklings and decreased to 0.37 kcals/g/day for the 9-week-old ducklings. This decrease in metabolism on a per-gram basis may be due to the decrease in the growth rate as the ducklings aged and to the lower metabolic rate normally seen in larger birds (Kendeigh 1970).

The coefficient of utilization increased sharply after the fourth week (table 2), indicating a more efficient use of the energy consumed. The ducklings begin to grow contour feathers rapidly between the fourth and fifth weeks (Cain 1970) and no doubt gain some insulation from this added feather layer.

Existence metabolism. Regression analysis of the relationship between metabolism and weight gain at

TABLE 2. Gross energy intake, excretory and metabolized energy, and the utilization coefficients of ducklings at weekly intervals with ±2 standard errors.

Age in weeks	N	Weight in grams	Gross energy intake (kcal/bird/day)		Excretory energy (kcal/bird/day)		Metabolized energy (kcal/bird/day)		Coefficient of utilization	
2	6	54.0	49.8	7.2	15.4	2.5	34.5	4.6	69.3	4.0
3	14	109.0	93.1	12.0	31.1	4.9	62.0	7.6	66.7	2.0
4	8	148·7	115.3	25.4	40.2	8.0	75.1	17.7	64.7	2.0
5	13	198.9	150.4	22.0	32.2	7.7	118.3	19.7	78.2	5.2
6	15	275.0	195.6	25.7	35.1	5.5	160.5	19.9	82.9	2.0
7	12	379.8	172.3	29.6	30·2	2.4	142.0	17.0	85.8	0.6
9	8	576.5	242.2	47.2	26.3	5.1	215.9	41.8	88.8	1.0
Adult	8	684.7	125.5	15.5	16.8	2.8	108.7	17.3	86.5	1.0

TABLE 3. Linear regression equations, ±2 standard error, for metabolism versus weight gain at weekly intervals with the F values and the degrees of freedom to compare the regression coefficients and elevation between weeks.

Age in weeks	Equations	SE	Significance of coefficient F =	Significance of coefficient (df)	Significance of elevation F =	Significance of elevation (df)
2	$Y = 26.9 + 1.5 \times$	8.0				
			0.11	(1,16)	20.17	(1,17)
3	$Y = 47.7 + 2.1 \times$	25.0				
			0.89	(1,18)	6.97	(1,19)
4	$Y = 55.8 + 3.5 \times$	33.6				
			0.02	(1,17)	5.03	(1,18)
5	$Y = 84.5 + 3.8 \times$	72.2				
			0.56	(1,27)	6.57	(1,28)
7	$Y = 101.1 + 6.3 \times$	54.6				
			0.88	(1,16)	21.81	(1,17)
9	$Y = 187.7 + 11.4 \times$	68.3				

weekly intervals (fig. 2) indicates a constant relationship between the different age ducklings. There is no significant difference between the regression coefficients (table 3) for adjacent weeks or widely separated weeks. The differences in elevation of the lines are significant and reflect the increased metabolism required for the larger ducklings.

As the body weight increased with age the existence energy also increased (table 4). The calculated existence energy from the regression equations (where $X = 0$) is similar to that observed from a small number of specimens that did not change weight during a 3-day period. The energy requirement per gram of wet weight decreased as expected with increasing body size (table 4).

Productive energy. Productive energy increased both absolutely and relatively to the metabolized energy during the first six weeks (table 5). The ducklings' growth rate is greatest during this period (fig. 1) and decreases afterwards, until the peak body weight is attained around 17 weeks (Cain 1970). This trend has been reported for Lesser Scaup (Sugden 1969).

The energetic cost to produce one gram of dry weight is calculated by multiplying the slope of the regression lines (i.e. the cost of wet weight production) by a factor that relates dry weight to wet weight (table 5). The caloric value per gram of dry weight (table 2), divided by this calculated cost to produce one gram of dry weight equals the productive efficiency (table 5).

Productive efficiency decreased with age for the tree ducks. Brisbin (1965) reported a similar decrease in the growth efficiency for Herring Gull (*Larus argentatus*) chicks, and attributed it to an increasing cost of maintaining respiration associated with increasing biomass and muscular activity.

The production of biomass, in terms of kcals, relative to the productive energy available was calculated for weekly intervals (table 6). During the 4th–6th weeks period the caloric cost per gram increased considerably and then decreased through the ninth week. This increase cost per gram is probably related to the emergence of contour feathers during the fourth through sixth week (Cain 1970), a considerable energetic load on the ducklings. The efficiency of biomass production increased after the 6th week (table 6), probably due to the lessened energetic cost of feather production.

Ecological growth efficiency. To calculate ecological growth efficiency for Black-bellied Tree Ducks, I divided the biomass increment by metabolized energy because the latter more closely represents energy removed from the environment than does gross energy intake (i.e. "food" of Brisbin 1965).

The ecological growth efficiency increased through the first seven weeks of growth (table 7) and declined

TABLE 4. Existence metabolism at weekly intervals for Black-bellied Tree Ducks.

Age in weeks	Weight	Existence metabolism (EM) kcal/bird/day Calculated[a]	N[b]	Observed[c]	kcal/g/day
2	54.0	26.9	1	27.4	0.50
3	109.0	47.7	2	43.2	0.44
4	119.7	55.8	3	59.1	0.46
5	166.9	84.5	2	88.9	0.50
6	277.0	96.8	2	92.2	0.35
7	340.8	101.1	3	123.0	0.30
9	586.5	187.7	1	177.6	0.32
adult	684.7		8	108.7	0.16

[a] From the regression equation where $X = 0$.
[b] Sample size of observed ducklings and adults.
[c] From ducklings not changing body weight during a metabolic trial.

TABLE 5. Productive energy and the energy cost to produce one gram of dry weight.

Age in weeks	N	Productive energy (PE) kcal/bird/day	PE/ME	Factor to convert dry to wet wt.[a]	Kcal/g/cost of dry wt. increase (factor X b^2)[b]	Productive efficiency
2	6	7.5	21.8	4.01	6.0	91.6
3	14	14.3	23.1	3.03	6.4	74.8
4	8	19.3	25.7	2.89	10.0	54.1
5	13	33.7	28.5	2.66	10.0	54.7
6	15	63.7	39.7	2.32	14.3	39.6
7	12	40.9	28.8	2.42	15.3	37.0
9	8	27.2	13.0	2.38	27.2	19.6

[a] Determined by dividing the percent of dry weight (table 2) into unity (1).
[b] Slope of regression equations (table 4), the energy to gain 1 gram wet weight.

TABLE 6. Efficiency of productive energy available and the cost to produce one gram of wet weight for the ducklings at weekly intervals.

Age in weeks	N	Productive metabolism per week	Dry weight increase per week	Biomass[a] increase in kcals	Efficiency
2	6	53.2	–	–	–
3	14	100.0	8.5	47.6	0.47
4	8	156.1	12.6	70.5	0.45
5	13	236.6	18.9	105.8	0.41
6	15	445.9	32.7	183.1	0.41
7	12	286.4	43.2	241.9	0.84
9	8	280.8	41.0	229.6	0.81

[a] This value is obtained by multiplying the dry weight increase by 5.6 kcal/g, the average for dry material.

TABLE 7. Ecological growth efficiency, calculated by dividing the kcals of biomass increase per week by the metabolized energy required for that week's growth.

Age in weeks	N	Dry weight increase	Metabolized energy kcal/ bird/ week	(kcals) Biomass increment	Ecological growth efficiency
0–2	6	7.68	483	43.0	9.0
2–3	14	8.50	434	47.6	11.0
3–4	8	12.60	525	70.5	13.0
4–5	13	18.90	828	105.8	13.0
5–6	15	32.70	1123	183.1	16.0
6–7	12	43.20	994	241.9	23.0
7–9	8	82.00[a]	1510	459.2	15.0
adult	8	–	761	–	0.0

[a] This is a two-week period.

thereafter. The increase from approximately 9% for the first two weeks of growth to 24% during the 6th–7th weeks is not unexpected because of the increased metabolic efficiency (table 2) and the rapid growth of the ducklings through the first seven weeks. Further decline in the ecological growth efficiency supports Brisbin's (1965) prediction that the efficiency will decrease as growth ceases at the adult size.

DISCUSSION

A complex relationship exists among existence energy, productive energy, and weight increase during the growth period. Up to the fourth week of growth, much of the metabolized energy is required for existence as evidenced by the low ratio of productive energy to metabolized energy (table 5). During this early period, the ducklings are small-bodied and covered only with natal down. Temperature regulation for these ducklings, which is complete about the 12th day after hatching (Cain 1972), would require a considerable expenditure of energy until the body is covered by the contour feathers.

Production of the contour feathers probably requires much energy from the growing ducklings. Cain (1970) showed a lag in the growth of young Black-bellied Tree Ducks during the fourth week, when the contour feathers emerge. Penny and Bailey (1970) showed the same trend in the growth of young Black Ducks (*Anas rubripes*) and the American Coot (*Fulica americana*) during the third week of growth.

The contour feathers add insulation to the ducklings and enable them to use more of the metabolized energy for productive purposes (table 5). This increased percentage of productive energy may then contribute to the faster growth rate through the sixth week.

The advantage to the ducklings in being precocial, limited only by their ability to gather their own food, may be offset by the increased energy lost until their contour feathers develop. The efficiency of biomass production after the sixth week (table 6) may be the physiological constraint, as suggested by Ricklefs (1969) that limits the growth rate of Black-bellied Tree Ducks. The question now is, why is the development of contour feathers delayed until the fourth week of growth?

SUMMARY

Twenty-six Black-bellied Tree ducklings were placed in metabolism cages to determine the energy cost of growth, productive energy, existence energy and the ecological growth efficiency. Total metabolized energy increased during the 9-wk growth period. The metabolized energy averaged 0.64 kcals/g/day for 2-wk old ducklings and decreased to 0.37 kcals/g/day by the ninth week. The coefficient of utilization increased sharply after the fourth week, indicating a more efficient use of the consumed energy. Existence energy increased with age and body weight. The existence energy per gram of wet weight decreased with age. Productive energy increased during the first six weeks of growth, the period of rapid growth and feather development. The energetic cost per gram of weight produced increased through this same period and was attributed to feather production. The productive efficiency decreased as weight approached the adult level.

Ecological growth efficiency increased from 9% for the first two weeks of growth, to 24% during the 7th week. The development of the contour feathers during the 4th week probably reduces the energetic loss to the ducklings' surroundings via heat transfer and allows more tissue development per energy unit consumed.

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PROLONGED PARENTAL CARE IN THE SOOTY TERN AND BROWN NODDY

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Ashmole and Tovar (1968) reviewed and discussed prolonged parental care of young in birds, with special attention to the Laridae. They suggested that "those birds whose methods of obtaining food require great skill should have a considerable period of post-fledging parental feeding of the young." Dunn (1972) and Orians (1969) found that adult Sandwich Terns (*Thalasseus sandvicensis*) and Brown Pelicans (*Pelecanus occidentalis*), respectively, capture prey on more dives than immature birds.

Sooty Terns (*Sterna fuscata*) and Brown Noddies (*Anous stolidus*) capture fish and squid at the ocean's surface (Watson 1908, Ashmole and Ashmole 1967), and this presumably requires "great skill" in the sense of Ashmole and Tovar. Indeed, Ashmole (1963) suggested that juvenile Sooty Terns on Ascension Island first leave the island with their parents, although his only evidence was that adults and juveniles often flew together over the island during the breeding season. A similar contention regarding Royal Terns (*Thalasseus maximus*) is much better documented (Ashmole and Tovar 1968). Ashmole (1963) also reported that young Sooty Terns on Ascension Island "remain on or near the breeding ground for a week or so after they can first fly."

I present here information indicating some degree of parental care of fledged Sooty Tern and Brown Noddy young on Manana or Rabbit Island, Hawaii.

In 1971, I observed, over a 24-hr period, a quadrat containing the nest sites of nine marked Sooty Tern young that had been fledged for about a week. I began the watch at 14:45; none of the juveniles was within the quadrat or visible anywhere from my blind. At 16:15, one of the marked young flew into the quadrat, and by 19:00 all of the nine marked young were within the quadrat. All remained until 06:00, and each was fed by at least one parent during the night. The first juvenile flew away from the quadrat between 06:00 and 07:00 the next morning, and all were out of my sight when I ended the watch at 14:45 that afternoon. Sooty Tern young do not gather in large groups away from the nest sites on Manana, and many juveniles can be seen flying offshore the island shortly after the chicks begin to fledge. The fledged Sooty Tern young in my quadrat apparently were spending the day at sea, but returning to the nest sites at night to be fed by their parents.

In addition, I observed three Sooty Tern young on Manana 15 days after they could fly, and one young 21 days after it could fly. All four of the juveniles appeared in good shape and eventually left the island.

In 1971, all the Brown Noddy young that survived predation by herons during the first two weeks after hatching were fledged by the end of August. I counted 1,335 juveniles on Manana in the daytime on 23 October, and 20 in the daytime on 27 November. Many more than 20 juveniles (at least hundreds) were on Manana the night of 27 November, and many were emitting a high, whispering call associated with the soliciting of food from parents. I observed one juvenile being fed. I heard the same call on the night of 11 December, although no Brown Noddies were on Manana during the daytime. I did not hear the call on the night of 28 December.