

WHY DO NORTHERN MOCKINGBIRDS FEED FRUIT TO THEIR NESTLINGS?

RANDALL BREITWISCH

PETER G. MERRITT

AND

GEORGE H. WHITESIDES

ABSTRACT.—We tested two predictions of Morton's (1973) hypothesis that nestling frugivory becomes profitable as nestlings develop endothermy. Parent Northern Mockingbirds (*Mimus polyglottos*) fed nestlings a mixed diet of animal prey and fruit, mainly arthropods, throughout the 12-day nestling period. Fruit was brought infrequently to nestlings before the seventh day after hatching, by which time the young were largely endothermic. By 10 to 12 days after hatching, nestling diet comprised 30 to 35% fruit. Both predictions, (1) fruit should be fed to nestlings primarily after development of endothermy and (2) the amount of fruit fed should satisfy thermoregulatory needs of older nestlings, were supported. Older nestlings received enough fruit to fulfill most of their thermoregulatory, maintenance, and activity costs. Parent mockingbirds may feed nestlings an optimal mixture of animal protein, for growth, and fruit carbohydrates, for other energetic needs.

The time an altricial passerine spends as a dependent nestling is a dangerous period in its life. Eggs and nestlings often die, owing primarily to predation, starvation, desertion, hatching failure, and adverse weather (Ricklefs 1969), and selection favors brevity of nestling vulnerability (Dawson and Evans 1957, Lack 1968). Nestling diet should reflect selection for a rapid growth rate within developmental constraints and parental foraging abilities. Foods of dependent young characteristically have high protein content: even many birds that are primarily frugivorous as adults typically feed large quantities of insects or other animals to their young (Skutch 1954, 1960, 1969; Morton 1973; Ricklefs 1974; Snow 1976; Wheelwright 1983). The relatively low protein content of fruits (Jenkins 1969, Morton 1973, White 1974) has been thought to be the main reason why they are not the primary food of nestlings (Snow 1962, Snow 1970, Morton 1973). Recent work has challenged this view, suggesting that the low protein content of fruits may nonetheless sustain nestling growth rates; relatively low protein-to-calorie ratios of fruits and the consequent need to deal with these extra calories, rather than the absolute protein content of fruits, may account for the rarity of total frugivory in nestlings (Ricklefs 1976, Foster 1978).

Morton (1973) argued that parent birds have advantages in feeding fruit to nestlings: fruit is often abundant and easy to procure. Furthermore, fruiting by particular species of plants may be highly predictable in certain habitats. He hypothesized that frugivory by altricial

nestlings becomes profitable as nestlings develop endothermy within several days after hatching, because as a nestling becomes endothermic, energy derived from carbohydrate-rich fruit can be used for temperature maintenance. In addition, energy costs of general body maintenance and activity increase concomitantly with the development of nestling endothermy, and carbohydrate and lipid-derived energy may be used to help meet these needs (Foster 1978), leaving protein-rich foods (e.g., arthropods) to support rapid structural growth.

The temporal feeding pattern of nestlings which receive a mixed diet of animals and fruits has been little studied (however, see Bolles 1890 and Wheelwright 1983). Beyond the common observation that fruits are seldom fed to young until a few days after hatching (e.g., Morton 1973, Skutch 1976), few detailed data have been published on the relative and absolute amounts of fruits and animals fed to nestlings in relation to nestling age.

Adult Northern Mockingbirds (*Mimus polyglottos*) eat a mixed diet of animals and fruit (Beal et al. 1916, Howell 1932, Bent 1948). During the 1980 breeding season, Merritt and J. H. Marden noted that parent mockingbirds breeding in southern Florida also fed nestlings a mixed diet. Adult mockingbirds often were seen leaving their territories for several minutes to forage in fruiting trees as far away as a few hundred meters (Merritt 1980). Parent birds often carried fruit to their nestlings. We studied these mockingbirds in order to test two

TABLE 1. Feeding schedule of nestling mockingbirds on the University of Miami campus, 1981.

Day of age	Date	Terr.	Nest ^b	Brood size	Per nestling per hour ^a			
					Animal trips ^c	Fruit trips ^c	Animal volume	Fruit volume
1	7/07	10	2	1	2.25	0.08	7.71	0.42
1	6/23	31	1	2	3.00	0.00	9.35	0.00
2	5/05	30	1	2	2.67	0.08	12.05	0.28
2	7/03	7	1	3	2.72	0.19	12.05	0.76
3	5/30	28	1	4	3.21	0.00	16.44	0.00
3	7/09	10	2	1	3.33	0.08	15.47	0.42
4	6/26	31	1	2	4.88	0.58	26.94	2.19
4	7/05	7	1	3	2.50	0.22	12.34	0.85
5	5/12	10	1	2	3.62	0.50	22.83	2.57
5	5/08	30	1	2	3.54	0.33	25.04	1.84
6	5/09	30	1	2	4.96	0.25	31.50	1.46
7	5/26	27	1	3	3.39	0.44	17.98	2.06
7	6/29	31	1	2	4.08	1.67	22.24	7.25
8	5/21	6	2	3	3.56	1.14	25.49	6.67
8	6/04	28	1	4	2.21	1.17	17.57	7.51
9	5/16	10	1	2	3.04	0.96	18.83	5.76
9	5/28	27	1	3	3.69	0.83	24.40	5.19
10	6/06	28	1	4	3.29	0.85	21.26	4.42
10	4/19	6	1	2	4.08	1.42	27.63	7.48
10	4/05	13	1	2	5.92	2.54	39.80	12.15
11	5/24	6	2	3	3.81	0.78	22.49	4.76
11	5/01	21	1	3	3.17	0.86	19.77	5.16
11	5/14	30	1	2	3.54	1.75	20.26	9.67
12	5/19	10	1	2	3.00	1.58	21.83	10.39
12	6/09	13	2	2	3.38	1.17	20.73	6.43

^a Trips/nestling/h calculated by dividing total trips in that feeding category by (12 × brood size); volume/nestling/h calculated similarly but includes apportionment of unknown food items.

^b Number of nests observed on that territory (broods in two successive nests observed on three territories).

^c Total number of animal trips = 2,501 (2,462 + 3 + 13 + 23); total number of fruit trips = 568 (545 + 23). Invertebrate and fruit trips (23) are counted twice, once in each food category (see Table 2).

predictions of Morton's hypothesis: (1) fruit should be fed to nestlings primarily after the development of endothermy, and (2) the amount of fruit fed should satisfy the thermoregulatory needs of older nestlings. Finally, we asked whether the amount of fruit fed to older nestlings met their maintenance, activity, and thermoregulatory energy costs.

STUDY AREA AND METHODS

We conducted our study on the main campus of the University of Miami, Dade Co., Florida. The mockingbird population was individually color-banded as part of research by Merritt (1984). The data were collected during 300 h apportioned as 25 12-h observation periods (06:00–18:00) on 12 broods of 9 pairs of birds from 5 April to 9 July 1981 (23 of 25 periods between 1 May and 9 July). Because feeding rates varied throughout the day, we observed nests continuously for 12-h periods. Often, we watched birds from a blind 4 to 10 m from the nest. Four broods were monitored for one day each, four broods for two days, three broods for three days, and one brood for four days. Broods sampled two or more days were observed on nonconsecutive days, with one exception. The sample includes observations on broods from 1 to 12 days old (nestlings fledge

at about 12 days of age). The distribution of broods studied was one brood 6 days old (= day 6), three broods each at days 10 and 11, and two broods at each of the 9 remaining days. We knew the age of the young from hatching observations and parental behavior or estimated ± 1 day from nestling body size and feather development. The age of nestlings sampled was significantly correlated with time in the breeding season; more young broods were sampled later in the season ($r_s = -0.44$; $P < 0.05$; $n = 25$). Mean brood size was 2.4 ($n = 12$; see Table 1).

During each 12-h observation period, we recorded every trip to the nest by either parent to the nearest second. Lag times between arrivals and feedings were noted in order to record feeding times accurately. One or more food items were usually delivered to the nestlings on each trip. Food items were identified with the aid of binoculars to general kind (e.g., fruit, insect, spider, lizard) and to particular kind when possible (e.g., species of fruit or taxonomic order of insect). Invertebrate and vertebrate prey lengths were estimated (<0.5, 0.5–1, 1–2, 2–3, 3–4, 4–5, 5–6, 6–7, 7–8, ≥ 8 cm; borderline cases were arbitrarily assigned to the higher class). Length estimates were desirable because of the diversity of insect larvae

fed that differed in cross-sectional area and length. Food could be identified only because mockingbirds in the study area (1) usually nest within 5 m of the ground, (2) often build their nests in sparse foliage, (3) habitually pause one to several seconds on an exposed twig or branch near the nest before feeding, (4) bring food in their bills rather than regurgitate food items to nestlings, and (5) seem nearly oblivious to observers beyond several meters from the nest (however, see Merritt, in press).

Relative volumes of food items were estimated on a scale of 1 to 5 within fruit, invertebrate, and vertebrate prey categories. For animal prey, volume was estimated per unit length. Using volume and length estimates for animal prey and volume estimates for fruit, we calculated total volume of animal prey and fruit fed per nestling per day. We then divided these totals by $(12 \times \text{brood size})$ to yield values of food volume per nestling per hour. We apportioned unknown food items between animal and fruit categories based upon each parent's percentages of known food items delivered. Then, for each parent, unknown food items were assigned the mean relative volumes of known animal and fruit items fed by each parental sex to young at that age (i.e., broods were pooled by parental sex for each day of nestling age). We were frequently unable to observe feedings to individual nestlings and for analyses assumed equal feeding, dividing total feedings equally among all brood members.

Nestling growth and cloacal temperatures were recorded in the field each morning from 15 May to 4 July 1980 by Y. Oniki and Merritt (unpubl.). The growth constant, K (Ricklefs 1967), was calculated using the mean growth rate of 20 nestlings that were seen on or near their natal territories at least 13 days after fledging. We used K to estimate the age of physiological endothermy (Dunn 1975). Cloacal temperatures were obtained from 14 of these nestlings. Temperatures were measured to 0.1°C with a Bailey temperature probe within 2 min after the nestlings were removed from the nest. We follow Ricklefs and Hainsworth (1968) and Dunn (1976) in converting these data via the equation: endothermic response of nestling = $((T_n - T_{am}) / (T_{ad} - T_{am})) (100)$, where T_n = nestling cloacal temperature, T_{am} = ambient temperature, and T_{ad} = adult body temperature (42°C). The converted temperature data were used as a second measure of the development of endothermy. In addition, we recorded all brooding bouts in the 1981 study, and these data were used as a third measure.

We employed the Spearman rank correlation coefficient in our analyses (Sokal and Rohlf

TABLE 2. Total number of trips to the nest by parent mockingbirds.

Food item	Number of trips	Percent of all trips
Invertebrates ^a	2,462	67.5
Invertebrates and fruits	23	0.6
Invertebrates and limestone bits or snail shells	3	0.1
Reptiles ^b	13	0.4
Subtotal	2,501	68.6
Fruits ^c	545	14.9
Subtotal	3,046	83.5
Limestone bits or snail shells	4	0.1
Unidentified food	524	14.4
Food brought but not fed	14	0.4
Subtotal	3,588	98.4
Trip without food	58	1.6
Total	3,646	100.0

^a Primarily arthropods (spp. of Odonata, Orthoptera, Coleoptera, Lepidoptera, Hymenoptera; spiders).

^b *Anolis carolinensis*, *distichus* and/or *sagrei*.

^c *Bischofia javanica*, *Clusia rosea*, *Eugenia uniflora*, *Ficus* spp., *Guaiaacum sanctum*, *Manilkara zapota*, palm spp., among others.

1981:607). Number of broods observed for each day of nestling age was small, and this statistic efficiently yet conservatively uses these data.

RESULTS

COMPOSITION OF NESTLING DIET

We observed parent mockingbirds making a total of 3,646 trips to the nest (Table 2). In 3,588 trips, the birds carried material in their bills. Overall, 82.1% of all feeding trips with identified food items (2,501 of 3,046) brought animal matter, and 99.5% of this subtotal (2,488 of 2,501) were trips with invertebrates. These figures were not independent of nestling age. Nestlings one to six days old were fed almost exclusively animal matter, predominantly insects and spiders. The amount of fruit fed increased dramatically in the mid-nestling period and leveled off at 30–35% of total trips/nestling/h for days 10 to 12 (Fig. 1, Table 1).

Trip totals alone were not the best indicators of total volume of animal matter fed to nestlings (Fig. 1); parents sometimes carried more than one food item. Also, larger animal items were fed to older nestlings, as is reflected in the animal volume data in Figure 1B. The rapid increase from days 1 to 6 in volume of animal matter is not as apparent from animal trip data (Fig. 1A). Also, the difference in animal volume fed to very young nestlings versus nestlings within a few days of fledging is not reflected in the corresponding trip data. Animal volume/nestling/h was correlated with nestling age (Spearman rank correlation: $r_s =$

0.51; $P < 0.05$; $n = 25$). The correlation of animal trips/nestling/h with nestling age was nearly significant ($r_s = 0.32$; $P > 0.05$; $n = 25$).

The amount of fruit fed to nestlings also increased markedly during the latter half of the nestling period, both as the number of trips with fruit and fruit volume/nestling/h (Spearman rank correlations for trips: $r_s = 0.83$; $P < 0.05$; $n = 25$ broods; volume: $r_s = 0.83$; $P < 0.05$; $n = 25$). Number of fruit trips/nestling/h was positively correlated with hour of day from 06:00 to 18:00 ($r_s = 0.70$; $P < 0.05$; $n = 12$). The number of trips with animal matter/nestling/h was negatively correlated with hour of day ($r_s = -0.61$; $P < 0.05$; $n = 12$), but total number of trips/nestling/h was not ($r_s = -0.05$; $P > 0.05$; $n = 12$). Neither animal volume nor fruit volume/nestling/h was correlated with brood size ($r_s = 0.02$ for animal volume and $r_s = 0.04$ for fruit volume; for each, $P > 0.05$; $n = 25$).

NESTLING TEMPERATURES AND BROODING SCHEDULE

Using Oniki and Merritt's (unpubl.) value of 0.492 for the growth constant K , we estimated the age of physiological endothermy as 7.0 days via Dunn's (1975) correlation between K and the age of physiological endothermy for 22 altricial species. Cloacal temperatures indicated an increase in endothermic capability during the first several days after hatching. Nestlings five days old appeared as able to maintain temperatures as older nestlings (Fig. 2).

Young were brooded almost entirely by females (97.1%, $n = 310$ bouts). The mean number of brooding bouts/h was negatively correlated with nestling age ($r_s = -0.82$; $P < 0.05$; $n = 25$) and decreased sharply after day 6 (Fig. 3). This finding supports the relationship between total time spent brooding/day and age of nestlings in indicating that young of that age have a greater endothermic capability than before.

DISCUSSION

Our data supported the first prediction from Morton's hypothesis, since mockingbirds fed almost no fruit until after their young were largely endothermic. Most fruit was fed after day 6, increasing markedly over days 7–9. Foster (1978) suggested that nestlings of frugivorous birds are not fed fruit for the first few days after hatching because parents may lack the behavioral flexibility to feed smaller fruits than they themselves consume. Adult mockingbirds eat very small fruits and pulp from large fruits, so the question of behavioral flexibility and fruit size is irrelevant here. Size of

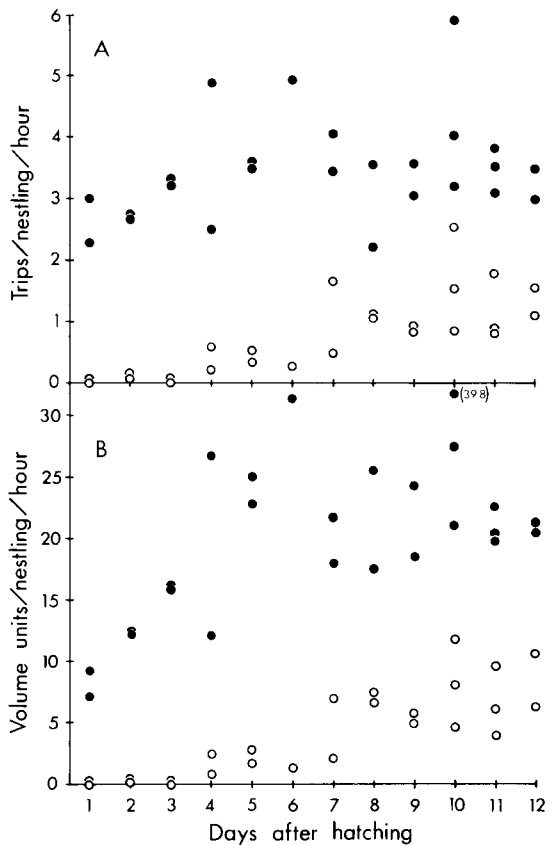


FIGURE 1. Food delivery to nestling mockingbirds: A) trips with food, and B) food volume units delivered to nestlings in relation to nestling age. Solid circles = animal prey, open circles = fruits.

fruits did not preclude parents feeding fruits to young nestlings. Small fruits and small bits of pulp from large fallen ripe fruits were available throughout the study and were fed to nestlings. Furthermore, some frugivorous species which feed their young mixed diets indeed feed fruit to very young nestlings; Wheelwright (1983) found that young Resplendent Quetzals (*Pharomachrus mocinno*) were fed large whole fruits as early as the second day after hatching.

We did not measure the abundance of fruits or insects during this study. Questions of seasonal abundance of food supplies remain, in view of the significant correlation between time in breeding season and age of nestlings observed. A wide variety of ripe fruits is common in southern Florida suburban habitats throughout spring and summer months (Breitwisch 1977: 188–190), and this was true for the university campus in 1981; we think that the seasonal availability of fruit was unlikely to change markedly during this study. We have no information on the abundance of insects from April to July. Our interpretation of re-

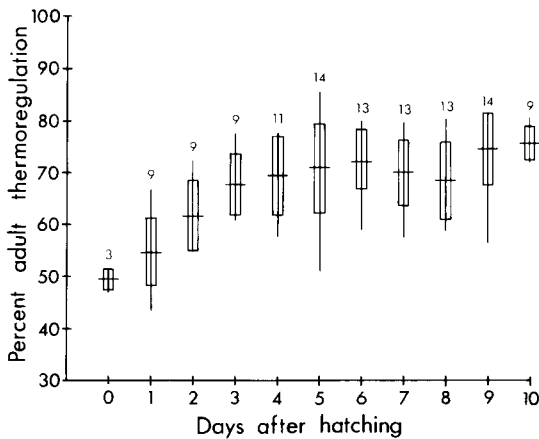


FIGURE 2. Endothermic response of nestling mockingbirds in relation to nestling age (see text for calculation). The mean, standard deviation and range are shown.

sults could be confounded by increased insect availability with time, yet we observed nestlings six days old or younger as early as the first week of May, and arthropods were almost their sole food.

Growth rate, nestling cloacal temperatures, and brooding times suggest that mockingbirds attain a well-developed endothermic capability by the midpoint of nestling life, consistent with other altricial passerines of their size (Ricklefs 1974, Dunn 1975). Most investigations of the development of physiological endothermy in altricial nestlings are based on laboratory studies of solitary nestlings (however, see Dunn 1976, Marsh 1979, Clark and Balda 1981). Laboratory studies indicate an inability to maintain high body temperatures at early ages. Dunn (1975) distinguished between "physiological" and "effective" endothermy. Nestlings of species whose broods are typically greater than one probably are effectively endothermic earlier than these laboratory data suggest (Royama 1966; Ricklefs 1974, Dunn 1975, 1976; Marsh 1979; Clark and Balda 1981). Similarly, mockingbird nestling temperatures and brooding times suggest effective endothermy perhaps one to two days earlier than indicated by our calculation of physiological endothermy based upon the growth constant. Development of endothermy and cessation of brooding have also been found associated in Bank Swallows (*Riparia riparia*; Beyer 1938, Marsh 1979), Rufous-winged Sparrows (*Aimophila carpalis*; Austin and Ricklefs 1977), and White-crowned Sparrows (*Zonotrichia leucophrys*; Morton and Carey 1971).

Our data also support the prediction that the amount of fruit fed to older nestlings is suffi-

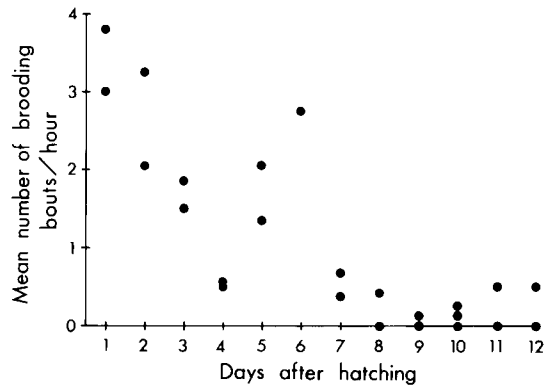


FIGURE 3. Brooding schedule of parent mockingbirds in relation to nestling age. Two of the three nests sampled at day 11 showed no brooding.

cient to satisfy their maintenance energy needs. Thermoregulatory costs for altricial nestlings are relatively low compared with energy used in general body maintenance (=existence energy) and activity energy (Westerterp 1973; Dunn 1975, 1980). Ricklefs (1974:252) provided a pair of metabolic cost curves for a "hypothetical" starling-sized (*Sturnus vulgaris*) altricial passerine. Since adult mockingbirds weigh about 70% of the adult weight of starlings (ca. 50 vs. 70 g), the following calculation is conservative. The costs of maintenance energy for Ricklefs' hypothetical nestlings at about 75% of adult weight (the proportion of adult weight at which mockingbirds fledge) were approximately 63 kJ/day. The estimate of maintenance energy costs for a 37.5-g passerine (75% of adult mockingbird weight) using King's (1974) equation is 66.5 kJ/day. Nestling mockingbirds between 10 and 12 days old received about 75 volume units of fruit daily (Fig. 1B). Figs (*Ficus* spp.) were the most commonly fed fruits (45.3% of all trips with fruit). In our assignment of relative volumes of fruit, a *Ficus aurea* or *F. benjamina* fruit received a value of 5. Thus, 75 volume units are equivalent to 15 fig fruits, each of which weighs ca. 2 g. The energetic contents per 100 g fresh weight of five other species of fig fruits were 218 kJ (*Ficus carica*, Leung 1968), 234 kJ (*F. platyphylla*, Leung 1968), 335 kJ (*F. insipida*, Morrison 1980), 209 kJ (*F. ovalis*, Herbst 1983), and 377 kJ (*F. contitifolia*, Jordano 1983). Using the mean of these values (275 kJ/100 g fresh wt.) as an estimate of the energetic content of figs eaten in southern Florida, 30 g of fig fruits fed to an older nestling mockingbird contained 82 kJ, 15.5–19 kJ more than the nestling's maintenance needs. Not all of the energy contained in fruit is available to nestlings: some is tied

up in structural carbohydrate (e.g., exocarp, pulp fiber, seeds), that is not metabolized. Nonetheless, our data suggest that older nestlings received enough fruit to meet most or all of their maintenance energy needs.

Nestling activity costs additional energy, some of which may be supplied by fruit carbohydrates. Older starling nestlings expend ca. 25 kJ/day for activity and between 4 and 8 kJ/day for thermoregulation (Westerterp 1973), for a total expenditure for maintenance, activity and thermoregulation of 92 to 96 kJ/day. This total should be less for mockingbirds because they weigh less than starlings, and again, fruit provides enough energy to meet most of these costs. Newly hatched mockingbirds, however, have lower maintenance costs and these must be met by energy derived from animal foods in the first several days after hatching.

Energy could also be supplied by the breakdown of lipids, which yield more than twice as much energy as carbohydrates per unit weight (Paine 1971), but lipids and carbohydrates are undoubtedly digested, absorbed, transported, and metabolized at different rates. Some insects, e.g., many larval forms and orthopteran, contain large amounts of lipids. Some fruits, e.g., palms and lauraceous species, likewise are rich in fats (Leung 1968). In general, however, fruits contain about as little fat as insects (both <5% wet weight), but higher percentages of carbohydrates and water (Leung 1968). If insects high in lipids and water are easy to find and capture, there may be fewer advantages in supplying fruits to young, although it is not clear that the young would necessarily benefit directly from an increased supply of protein (Ricklefs 1976, Foster 1978). Would mockingbirds offer their nestlings substantially fewer fruits when large insects (e.g., beetle larvae) are markedly more available?

Fruit may also supply the water needs of nestlings. Midday ambient temperatures during the study period were as high as 32–34°C, and nestlings probably were under some heat stress. If fruit is important as a source of water, it should be fed in increasingly greater quantities as temperature rises during the day. The significant correlation between time of day and fruit trips/nestling/h agrees with this prediction. The same prediction arises, however, if carbohydrates from fruit are used for thermoregulatory maintenance primarily through the night and early morning hours.

If fruits were fed to nestlings primarily to supply water, fleshy fruits should be preferred to oily, less fleshy species. Some parents nevertheless fed both fleshy and oily fruits to their nestlings. Our data do not enable us to con-

vincingly distinguish the relative importance of water, lipid, and carbohydrate content of fruits.

Fruits fed by parent mockingbirds may also provide necessary vitamins and minerals. Some fruits contain large amounts of these nutrients; figs, for instance, contain high levels of calcium (Jenkins 1969). Little is yet known about these aspects of the nutritional needs of wild birds (Ricklefs 1976, Robbins 1983) or the nutritional contents of non-cultivated fruits (Foster 1978).

The amount of fruit fed to nestling birds is thought to be limited in part by the increased predation resulting from retarded growth and protraction of the nestling period (Snow 1970, Morton 1973, White 1974). Oilbirds (*Steatornis caripensis*), Bearded Bellbirds (*Procnias averano*), and euphonias (*Euphonia* spp.) are wholly frugivorous; their young are fed only fruit and have exceedingly long nestling periods for altricial birds of their size (Snow 1962, Snow 1970, Morton 1973, White 1974). Yet, a mixed diet for nestlings in which fruits largely supply maintenance energy does not necessarily lengthen the nestling period (Foster 1978). Ricklefs (1976) found that nestlings of a variety of species fed mixed diets did not grow more slowly than comparable species fed only animal matter.

We conclude that parent mockingbirds may feed their nestlings an optimal mixture of animal protein for growth and fruit carbohydrates for maintenance. Any markedly different mixture of fruits and animals might lengthen the nestling period or result in fewer nestlings being raised.

ACKNOWLEDGMENTS

We dedicate this paper to Oscar T. Owre, Maytag Professor of Ornithology Emeritus in the Department of Biology at the University of Miami. R. P. Balda, T. H. Fleming, V. L. Hages, J. C. Lee, E. S. Morton, O. T. Owre, K. D. Waddington, N. T. Wheelwright, and S. C. White-Schuler commented on versions of the manuscript. We thank T. H. Fleming, S. M. Green, L. H. Herbst, P. Myers, P. J. Regal, and T. L. Taigen for discussion of ideas. Field observations by A. L. Kippenhan, J. H. Marden, and Y. Oniki were helpful. Funds were provided to Merritt for research on mockingbirds from the Tropical Audubon Society, the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and the University of Miami Department of Biology. This paper is contribution No. 81 from the University of Miami Department of Biology Program in Ecology, Behavior, and Tropical Biology.

LITERATURE CITED

- AUSTIN, G. T., AND R. E. RICKLEFS. 1977. Growth and development of the Rufous-winged Sparrow (*Aimophila carpalis*). *Condor* 79:37–50.
- BEAL, F. E. L., W. L. MCATEE, AND E. P. KALMBACH. 1916. Common birds of southeastern United States

- in relation to agriculture. U.S. Dep. Agric. Farmers' Bull. 755.
- BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Natl. Mus. Bull. 195.
- BEYER, L. K. 1938. The nest life of the Bank Swallow. Wilson Bull. 50:122-137.
- BOLLES, F. 1890. Young Cedarbirds and Great Crested Flycatchers in captivity. Auk 7:290.
- BREITWISCH, R. J. 1977. The ecology and behavior of the Red-bellied Woodpecker, *Centurus carolinus* (Linnaeus) (Aves: Picidae), in south Florida. M.S. thesis, Univ. of Miami, Coral Gables, FL.
- CLARK, L., AND R. P. BALDA. 1981. The development of effective endothermy and homeothermy by nestling Piñon Jays. Auk 98:615-619.
- DAWSON, W. R., AND F. C. EVANS. 1957. Relation of growth and development to temperature regulation in nestling Field and Chipping sparrows. Physiol. Zool. 30:315-327.
- DUNN, E. H. 1975. The timing of endothermy in the development of altricial birds. Condor 77:288-293.
- DUNN, E. H. 1976. The relationship between brood size and age of effective homeothermy in nestling House Wrens. Wilson Bull. 88:478-482.
- DUNN, E. H. 1980. On the variability in energy allocation of nestling birds. Auk 97:19-27.
- FOSTER, M. S. 1978. Total frugivory in tropical passerines: a reappraisal. Trop. Ecol. 19:131-154.
- HERBST, L. H. 1983. Nutritional analyses of the wet season diet of *Carollia perspicillata* (Chiroptera: Phyllostomidae) in Parque Nacional Santa Rosa, Costa Rica. M.S. thesis, Univ. of Miami, Coral Gables, FL.
- HOWELL, A. H. 1932. Florida bird life. Coward-McCann, New York.
- JENKINS, R. 1969. Ecology of three species of Saltators in Costa Rica with special reference to their frugivorous diet. Ph.D. diss., Harvard Univ., Cambridge, MA.
- JORDANO, P. 1983. Fig-seed predation and dispersal by birds. Biotropica 15:38-41.
- KING, J. R. 1974. Seasonal allocation of time and energy resources in birds, p. 4-70. In R. A. Paynter [ed.], Avian energetics. Publ. Nuttall Ornithol. Club No. 15.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- LEUNG, W.-T. W. 1968. Food composition tables for use in Africa. FAO-HEW, Public Health Service, Bethesda, MD.
- MARSH, R. L. 1979. Development of endothermy in nestling Bank Swallows (*Riparia riparia*). Physiol. Zool. 52:340-353.
- MERRITT, P. G. 1980. Group foraging by mockingbirds in a Florida strangler fig. Auk 97:869-872.
- MERRITT, P. G. 1984. Song function and the evolution of song repertoires in the Northern Mockingbird, *Mimus polyglottos*. Ph.D. diss., Univ. of Miami, Coral Gables, FL.
- MERRITT, P. G. In press. Observer recognition by the Northern Mockingbird. J. Field Ornithol.
- MORRISON, D. W. 1980. Efficiency of food utilization by fruit bats. Oecologia 45:270-273.
- MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. Am. Nat. 107:8-22.
- MORTON, M. L., AND C. CAREY. 1971. Growth and development of endothermy in the mountain White-crowned Sparrow (*Zonotrichia leucophrys*). Physiol. Zool. 44:177-189.
- PAINE, R. T. 1971. The measurement and application of the calorie to ecological problems. Annu. Rev. Ecol. Syst. 2:145-164.
- RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978-983.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian. Contrib. Zool. 9:1-48.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds, p. 152-297. In R. A. Paynter [ed.], Avian energetics. Publ. Nuttall Ornithol. Club No. 15.
- RICKLEFS, R. E. 1976. Growth rates of birds in the humid New World tropics. Ibis 118:179-207.
- RICKLEFS, R. E., AND F. R. HAINSWORTH. 1968. Temperature regulation in nestling Cactus Wrens: the development of homeothermy. Condor 70:121-127.
- ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York.
- ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. Ibis 108:313-347.
- SKUTCH, A. F. 1954. Life histories of Central American birds. Pac. Coast Avifauna 31:1-448.
- SKUTCH, A. F. 1960. Life histories of Central American birds. Vol. 2. Pac. Coast Avifauna 34:1-593.
- SKUTCH, A. F. 1969. Life histories of Central American birds. Vol. 3. Pac. Coast Avifauna 35:1-580.
- SKUTCH, A. F. 1976. Parent birds and their young. Univ. of Texas Press, Austin.
- SNOW, B. K. 1970. A field study of the Bearded Bellbird in Trinidad. Ibis 112:299-329.
- SNOW, D. W. 1962. The natural history of the Oilbird, *Steatornis caripensis*, in Trinidad, W. I. Part 2. Population, breeding ecology and food. Zoologica 47:199-221.
- SNOW, D. W. 1976. The web of adaptation. Quadrangle, New York.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. Freeman, San Francisco.
- WESTERTEP, K. 1973. The energy budget of the nestling Starling (*Sturnus vulgaris*): a field study. Ardea 61:137-158.
- WHEELWRIGHT, N. T. 1983. Fruits and the ecology of Resplendent Quetzals. Auk 100:286-301.
- WHITE, S. C. 1974. Ecological aspects of growth and nutrition in tropical fruit-eating birds. Ph.D. diss., Univ. of Pennsylvania, Philadelphia.

Department of Biology, University of Miami, Coral Gables, Florida 33124. Received 27 November 1982. Final acceptance 21 October 1983.