

FOOD OF NESTLING PURPLE MARTINS

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Post-fledging survival of young passerine birds appears to be strongly influenced by the quantity of food received while in the nest (Perrins 1965). A number of studies have been done to determine how much nestlings are fed but few (e.g., Royama 1966) have involved the greater part of the nestling period.

Finlay (1971) used mechanically recorded visits to the nest cavity as an index of feeding activity in Purple Martins (*Progne subis*). He assumed that food was brought to the nestlings on each visit. His results showed an increase in visits to the nest cavity with increased brood size, but the increase was not proportional to the number of nestlings involved. Finlay's study raises a number of questions concerning amount of food fed to individual nestlings in broods of various sizes: (1) are parent birds able to maintain constant energy intake by individual nestlings when brood sizes are larger by increasing the proportion of feeding visits to the nest or, (2) can they compensate for a larger brood by bringing either a greater biomass of food per feeding visit or, (3) does the decreased surface-area-to-volume relationship in larger broods enable individuals to maintain themselves sufficiently on a lower biomass of food? I tried to answer these questions in Finlay's study area on the shore of Astotin Lake (53° 40' N, 112° 50' W) in Elk Island National Park, Alberta, where martins were nesting colonially in artificial nest boxes during the summers of 1970 and 1971.

MATERIALS AND METHODS

To answer the above questions I obtained qualitative and quantitative measurements of food brought to nestling Purple Martins and analyzed these data with respect to brood size, age of nestlings, time of day, and season. Unless otherwise stated the test for significance used was Wilcoxon's signed rank test (Steel and Torrie 1960) and the accepted level of significance was $P < .05$.

Nest boxes.—Purple Martins had inhabited the 4 wooden houses used during the study for several years. I built an observation blind behind each house and had easy access by moving a black cloth covering the back of each 18 cm² nesting compartment. A periscope fastened over an opening in this cloth let me view activities without alarming the birds.

Martin population.—Because the colony size was so small all nesting pairs were studied in both years. In 1970 2 of the 4 pairs started laying about 1 week before the others. Nestlings that hatched and survived were rearranged in these 2 nests to give broods of 3 and 2, to match those of the second 2 pairs of martins. In all nests some nestlings died, probably a result of asynchronous hatching—the younger birds apparently could not compete successfully for food. All the nestlings except for 2 in the older brood of 3

young died on the same day at the ages of 23 and 14 days, probably as a result of 3 consecutive cold rainy days.

In 1971 two broods were studied; 1 brood of 2 nestlings that hatched 8 July, and in which 1 nestling died on day 19, and 1 brood of 4 nestlings, which hatched 14 July, and in which 2 nestlings died on day 12. The above deaths were accidentally caused by a food digestion study and resulted in brood sizes 2 and 1.

Food and food value.—The diet of nestlings was determined by collecting food given them from days 2 to 23 post-hatching, using the method of placing a piece of pipe cleaner around the neck of the nestling just tightly enough to prevent swallowing (Orians 1966). After a feeding visit the nestling was immediately removed from the nest and the food forced up to the beak by massaging the throat. Food gathered by this technique was placed in a vial for subsequent weighing and identification. The volume of food collected from each nestling was replaced by an approximately equal volume of food that I caught.

Insects were identified to family with the aid of keys (Jaques 1947, 1951). A determination of the caloric value of the most common insects in the samples representing different families was done (Spice 1972) but results were inconclusive.

Food collection periods.—Collection of food samples at any one nest did not exceed 2 consecutive hours, with at least 4 h intervals between collections. Collection of food terminated when nestlings were about 21 days old; at this age food began slipping past the pipe cleaner, presumably a result of strengthened esophageal musculature. Nestlings were weighed each day at about 18:00.

The birds' activities at the nest were monitored by me over time periods varying from 1 to 3 h. Movements by adult martins in and out of the nest cavity were registered by a mechanically activated event recorder.

Weather.—Data on meteorological conditions were collected at the colony site in both years. Readings of light intensity, wind speed, temperature, and relative humidity were made immediately before and after the observation and collection periods. General weather data were obtained from the Edmonton International Airport, about 48 km from the study area.

RESULTS AND DISCUSSION

Of 956 food samples collected from the nestling martins, 246 were collected between 8 and 29 July 1970 from 4 broods, and 710 samples were collected between 15 July and 11 August 1971 from 2 broods.

DIET OF NESTLINGS

Influence of time of year on diet.—Families of insects contributing more than 1% of the total weight of food collected in either year are listed in Table 1. Relative use of insect families differed between years; for the Nymphalidae this difference was significant (χ^2 , $P < 0.05$) and appeared to reflect both the 7 days' difference in initiation of the nesting season, and the premature deaths of the nestlings on 29 July 1970. In 1971 the study terminated on 11 August, 13 days later than in 1970. The mourning cloak butterfly (*Nymphalis antiopa*) was the species most heavily taken, and as these do not start emerging

TABLE 1
FREQUENCY¹ OF INSECTS BY FAMILIES FED TO NESTLING PURPLE MARTINS AT ELK ISLAND
NATIONAL PARK, ALBERTA

Family	1970 (%)	1971 (%)	Family	1970 (%)	1971 (%)
Aeschnidae	22	27	Coenagrionidae	4	1
Syrphidae	29	17	Muscidae	3	1
Nymphalidae	1	23	Apidae	2	1
Chironomidae	10	4	Cicadellidae	2	1
Siricidae	5	5	Order: Trichoptera	2	1
Formicidae	4	6	Corixidae	2	1
Cerambycidae	5	2	Others	8	6
Libellulidae	1	4			

¹ Based on percentage of total weight collected (1970, 101.2 g wet weight; 1971, 278.7 g wet weight).

as adults much before the first of August (Can. Dept. Agric. 1958) they were not available for the nestlings studied in 1970. The insignificant difference in biomass of aeschnids (dragonflies) taken is not unexpected because premature death of the nestlings in 1970 biased the food samples towards those families containing small insects that are fed to younger nestlings. The difference in the use of syrphids (flower flies) between the 2 years was significant (χ^2 , $P < 0.05$). This seemed to be because syrphid activity is greatly affected by weather conditions. (Under sunny conditions they contributed 24% of diet compared to 3% under cloudy, Spice 1972.) Data from the Edmonton International Airport indicated that 1971 was sunnier (mean hours of sunshine per day 8.7 in 1970 and 12.1 in 1971), drier (total precipitation 11.2 cm in 1970 and 3.1 cm in 1971), and warmer (mean temperature 21.7 C in 1970 and 25.0 C in 1971), so based on weather conditions this difference in use of syrphids between years is not unexpected.

Influence of time of day on diet.—The martins' use of various families of insects depended on the time of day the birds were feeding. Of the 4 insect families taken most frequently, aeschnids were captured throughout the day, chironomids (midges) only in the morning, and nymphalids (butterflies) and syrphids mainly around midday (Spice 1972).

To investigate the relationship between time of day and amount of food supplied to nestlings, the rate at which food was supplied was estimated by averaging the weight of food brought per hour for each hour of the feeding period (Fig. 1). I feel that the fluctuation in amount of food brought to the nestlings was a reflection of begging intensity of nestlings, which seemed to influence the number of feeding trips by adults. Begging intensity was higher

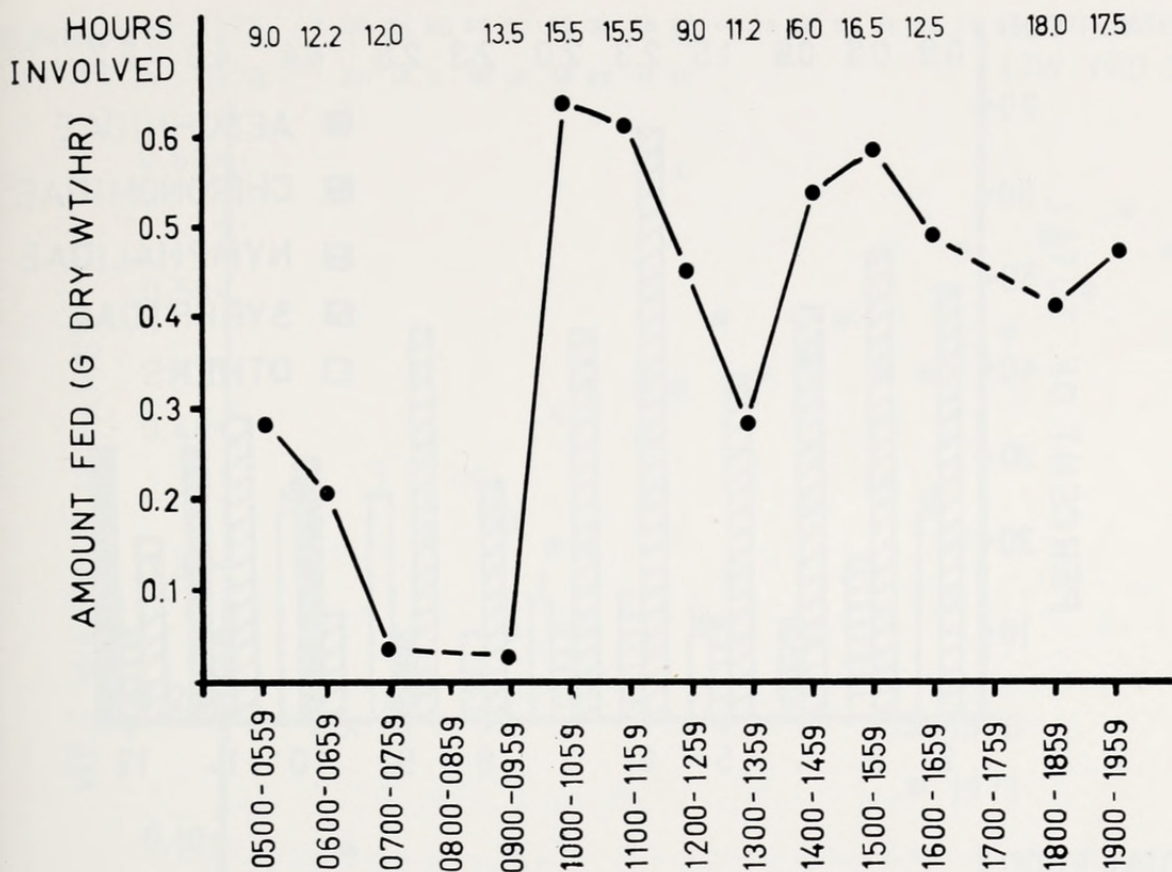


FIG. 1. Rate of feeding of nestling Purple Martins expressed as mean biomass (g dry weight) fed per hour. Data from 1971. Hours involved indicate the hours the author spent collecting food from nestlings at that time of day in 1971.

in the morning, declined after a feeding period, and cycled in this manner throughout the day. The degree of fluctuation may reflect both the availability of food and the hunger of the adults themselves.

Influence of nestling age on diet.—The relative use of various insect families over the nestling period in 1971 is shown in Fig. 2. The size of the insects used in these families (along with their availability) could account for changes in use with age: syrphids <2 cm long, aeschnids and nymphalids <3 cm long.

Role of parents in supplying food.—As nestling age increased, parental feeding increased, and for awhile most of this activity was performed by the male. However, as the need to brood the young decreased, the female provided more food and the male's proportion of feedings was reduced correspondingly (Spice 1972).

EFFECTS OF BROOD SIZE

Visits to nest.—A nonproportional increase of adult visits to the nest with increasing brood size has been generally found (Moreau 1939, 1947; Lack

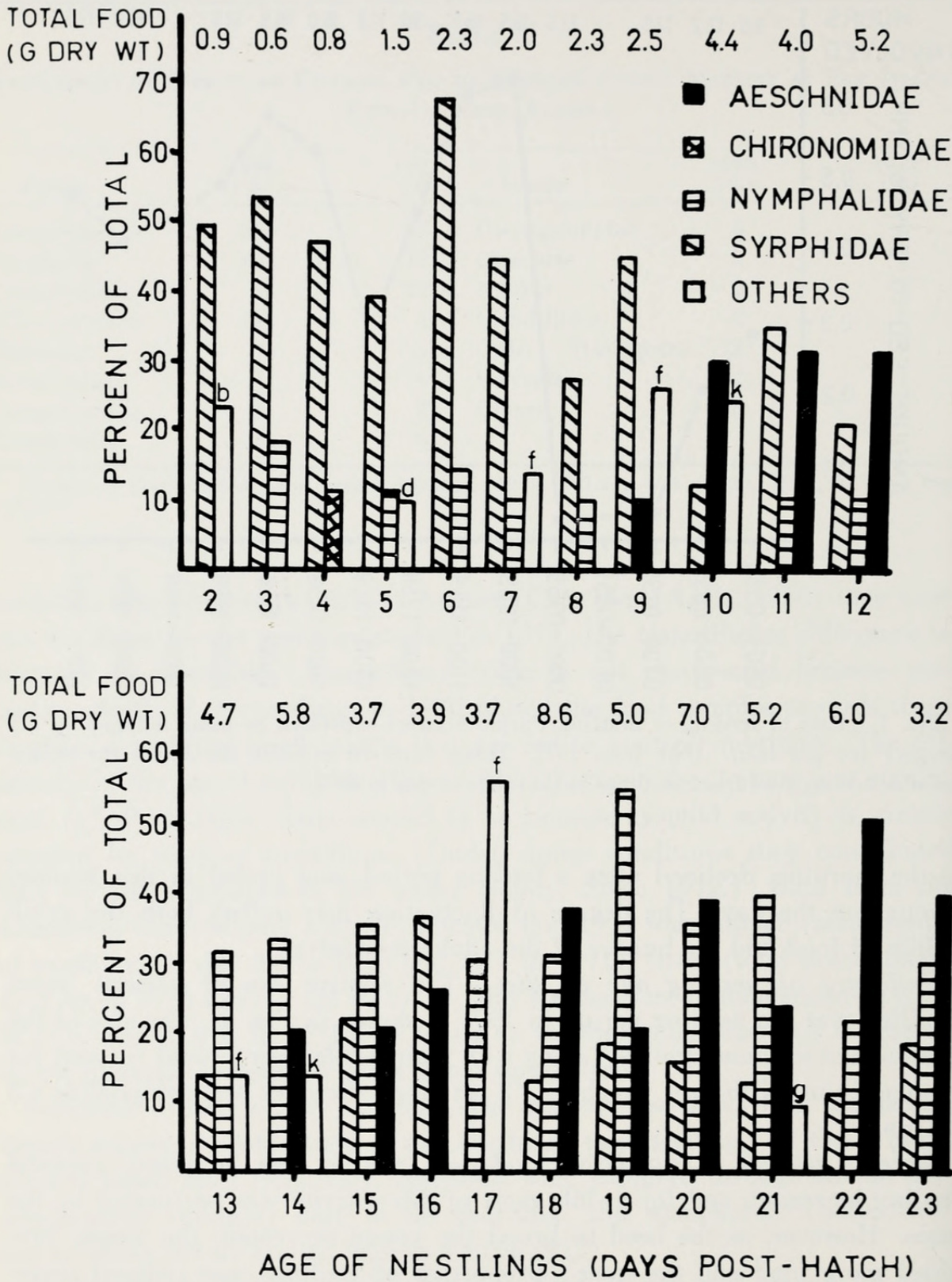


FIG. 2. Use of insect families in relation to age of nestling Purple Martins expressed as % of total food collected for that age. Only those families contributing 10% or more of the weight of food gathered at a specific age are figured. Key to letters above bars: b, Asilidae; d, Coenagrionidae; f, Formicidae; g, Libellulidae; k, Siricidae.

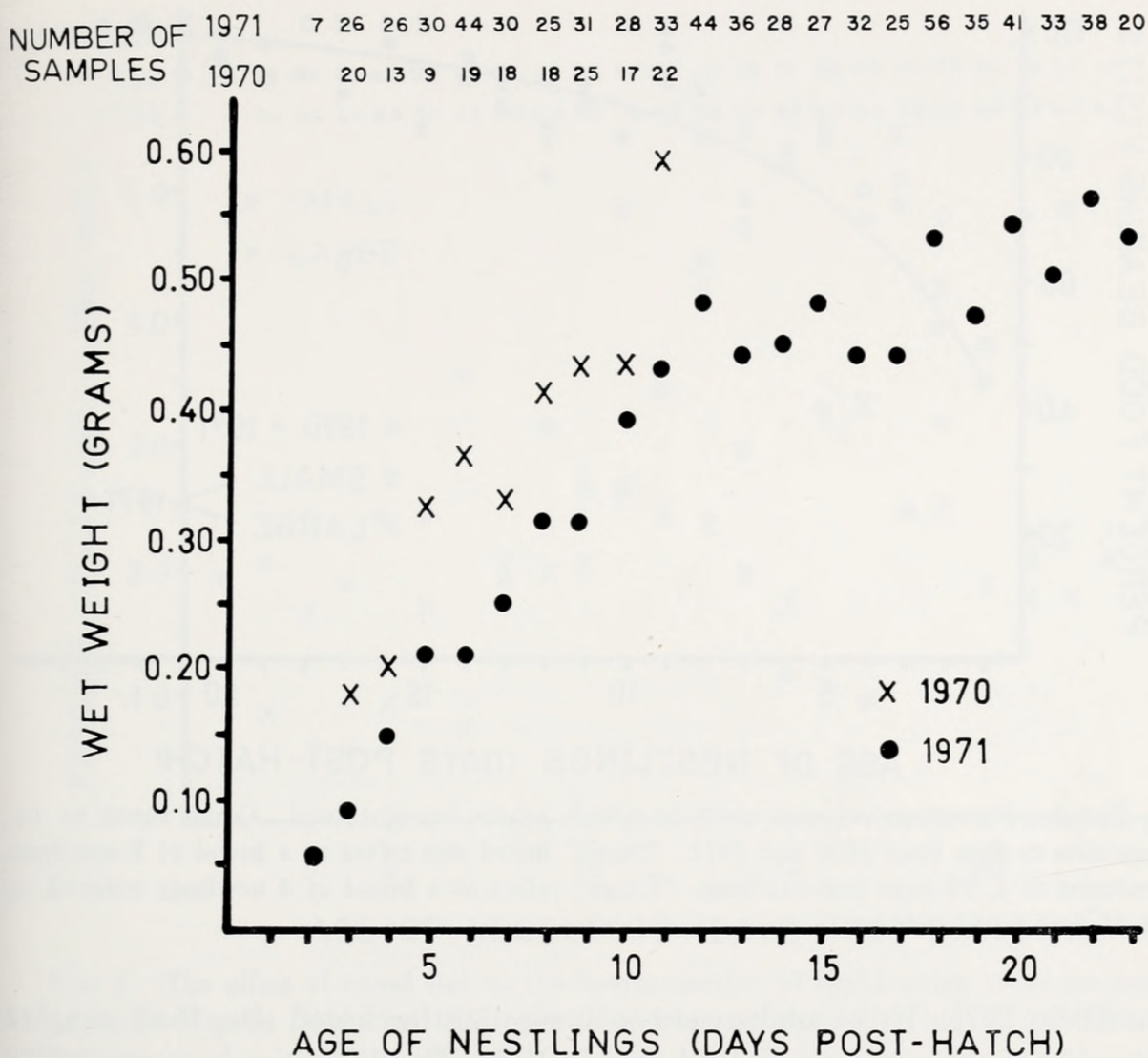


FIG. 3. Mean weight of food samples brought to nestlings by adults throughout the nestling period. Mean brood size in 1970 = 2.5; in 1971 = 3.0.

and Silva 1949; Kendeigh 1952; Gibb 1950, 1955; Morehouse and Brewer 1968; Finlay 1971). However, the assumption that nestlings belonging to larger broods receive less food does not necessarily follow. Adults having larger broods could compensate in several ways to meet their nestlings' energy requirements.

Biomass of food.—One way to compensate would be for the parents of larger broods to bring food samples of relatively greater biomass. To investigate this, the mean weight of each food sample brought per visit was compared with increasing age of nestlings (Fig. 3). In both years mean weight of food brought per feeding trip increased with age; thus the adults were compensating for size of nestlings. However, the data do not indicate a compensation for brood size. The mean values for 1970 were significantly higher than in 1971, but the average brood size in 1970 was 2.5 nestlings compared

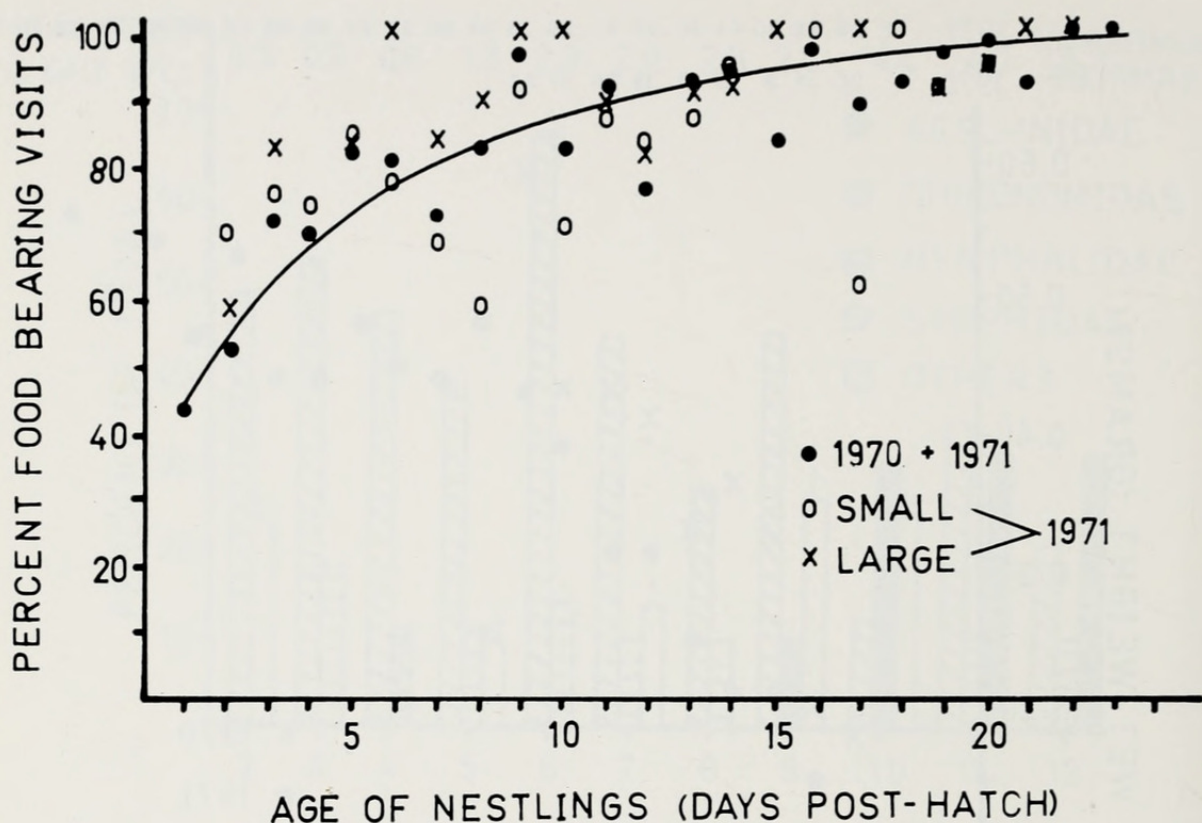


FIG. 4. Percentage of nest visits in which adults brought food. Curve fitted by inspection to data from 1970 and 1971. "Small" brood size refers to a brood of 2 nestlings reduced to 1, 19 days post-hatching. "Large" refers to a brood of 4 nestlings reduced to 2, 12 days post-hatching.

to 3.0 in 1971. If the adults were compensating for brood size, food samples should have been heavier in 1971 than in 1970. The difference in mean weight of food samples between the years probably reflected weather conditions, which in 1970 were cooler and cloudier. This was correlated with a greater diversity of prey items in the diet, the majority of these also being smaller items. Two possibilities exist: smaller prey items are coated with more saliva by the adult, thereby increasing the average wet weight recorded per collected sample; or, the adults were collecting a greater total weight of food material per feeding trip when prey items were small in size.

Brood size related to weight of food brought per feeding trip was also investigated using the 1971 data. There was no significant difference in the weights of food samples brought to the 2 broods. Royama's (1966) results differed from mine in that he found average weight of prey brought per feeding trip was heavier among tits feeding smaller broods. This he explained by saying that begging intensity in smaller broods was less and thus gave adults time to select larger prey items. This difference between species may reflect the fact that whereas tits usually bring but one food item per trip, martins frequently bring more than one.

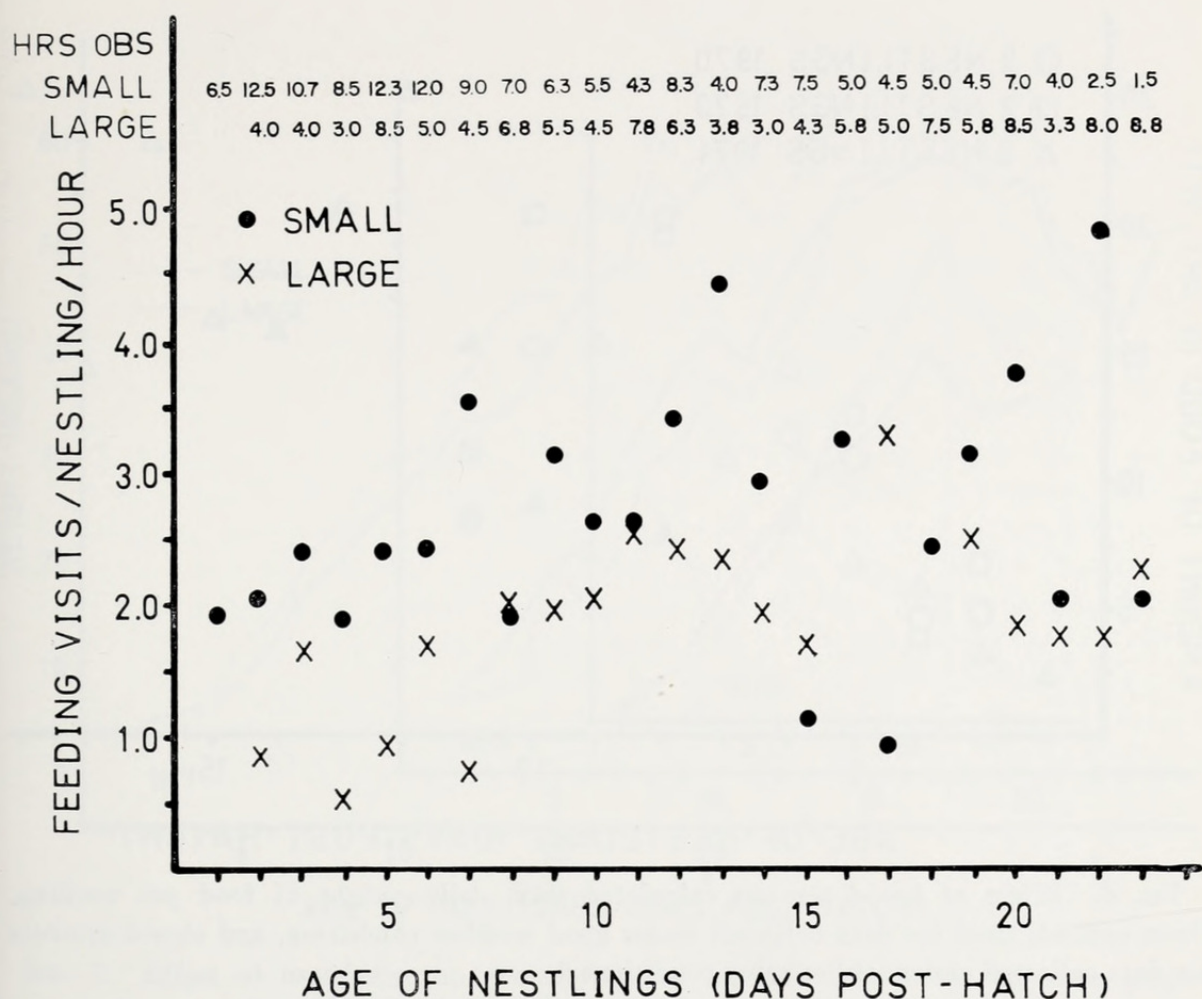


FIG. 5. The effect of brood size on the hourly number of food-bearing visits per nestling Purple Martin. Data from 1971. (See Fig. 4 for explanation of "small" and "large" broods.)

Frequency of feeding trips.—Adults could also compensate for a larger brood by increasing feeding frequency. Figure 4 shows that the percentage of food bearing visits, regardless of brood size, increased with the nestlings' age. Figure 4 also reveals that adults feeding larger broods carried food on a significantly greater percentage of trips to the nest. This factor has not been considered by many workers who have assumed that all trips to the nest cavity by adults are equal to, or proportionately equal to, the number of food bearing trips.

To determine if this method of compensation gave an individual nestling of the larger brood the same number of actual feedings as those given an individual of the smaller brood, the number of times nestlings were fed per hour was investigated in the 2 broods of different size in 1971 (Fig. 5). Nestlings in the smaller brood were fed significantly more often than were those in the larger brood. Similar results were seen in the data from 1970, but sample size was such that values could only be determined up to day 12.

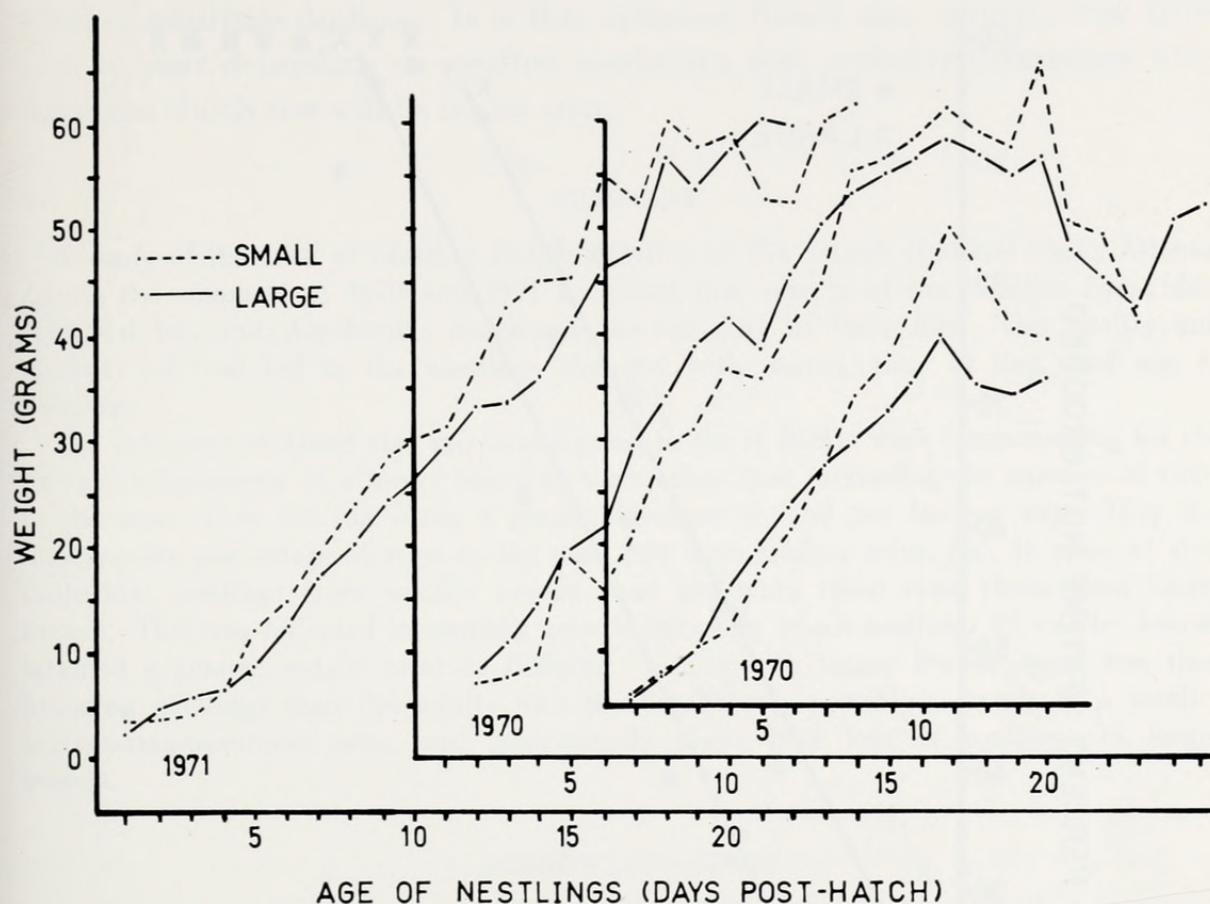


FIG. 7. Effect of brood size on growth curves. In 1970 broods on the same graph hatched the same day. In 1971 the "small" brood hatched 6 days later than the "large." "Small" broods had 2 nestlings and "large" had 3.

to-volume relationship, and thus until homeothermy is attained, a larger brood size would be advantageous during a colder season, such as 1970.

Brooding activity.—It has been suggested that, because the surface-area-to-volume ratio is greater for smaller broods, individuals in small broods lose more heat and therefore require more food to maintain themselves than do nestlings of a larger brood size (Royama 1966). It seems possible that increased brooding activity of adults could compensate for this to some extent. Amount of time spent not brooding by females with small and large broods was analyzed for 1971 (Fig. 8). The percentage of time nestlings were brooded decreased with age to day 16 or 17, after which females ceased brooding. Slopes of regression lines were similar for both brood sizes, however, percent of time spent brooding the larger brood was significantly less than that spent brooding the smaller. Royama (1966) found a similar situation among Great Tits (*Parus major*). This suggests that the parents do reduce heat loss by their nestlings through brooding behavior. This observation has general implications for clutch size. Adults with a small brood can more

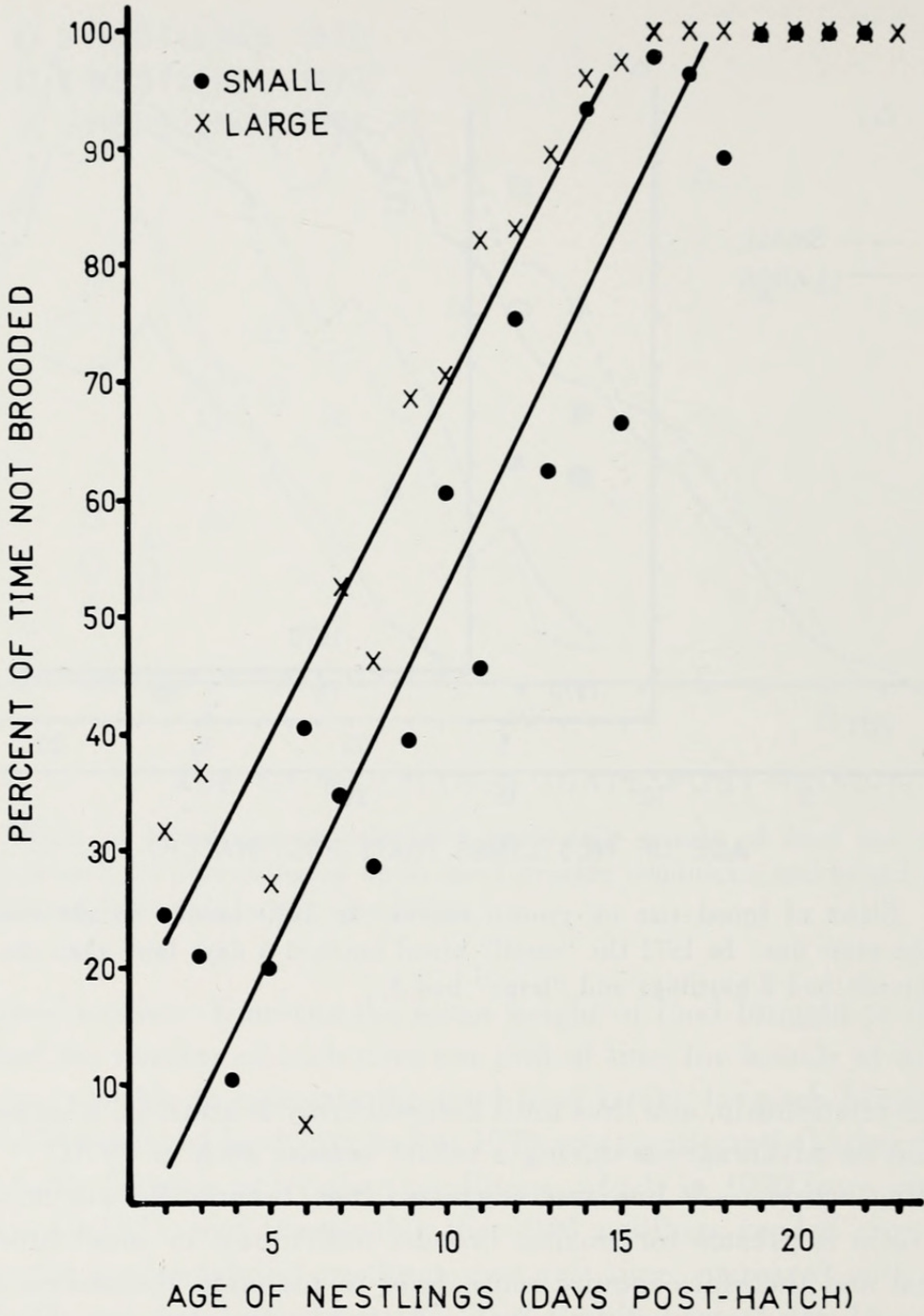


FIG. 8. Brood size related to percentage of time nestling Purple Martins were not brooded throughout the nestling period. Data from 1971. Regression lines: Large, $Y = 8.9 + 5.8X$; Small, $Y = -10.1 + 6.1X$.

easily provide them with food and intensive brooding. As brood size increases, and the surface-area-to-volume relationship decreases, heat loss by nestlings decreases. Thus, although adults must spend more time feeding young in large broods they can accomplish this by spending less time brooding. Hence, for any particular year there is an optimum brood size that permits adults to feed and brood the young with greatest success; beyond this brood size sur-

vival of nestlings declines. It is this optimum brood size, which varies from year to year depending on weather conditions that probably determines what the mean clutch size will be for an area.

SUMMARY

A study of the food of nestling Purple Martins at Elk Island National Park, Alberta, during the summers of 1970 and 1971 indicated that insects of the families Syrphidae, Nymphalidae, and Aeschnidae comprised the majority of their diet. The quality and quantity of food fed to the nestlings changed with season, time of day, and age of nestlings.

The influence of brood size was investigated to see if adults were compensating for the energy requirements of a larger brood in ways other than increasing the number of visits to the nest. They did not bring a greater biomass of food per feeding trip. They did increase the percentage of trips to the nest that were feeding trips, but, in spite of this, individual nestlings from smaller broods were fed more often than those from larger broods. This was reflected in nestling growth curves in which nestlings of smaller broods attained a greater weight prior to fledging. Adults with larger broods spent less time brooding nestlings than did adults with smaller broods, possibly a result of a smaller surface-area-to-volume ratio, and consequently lesser heat loss by nestlings in larger broods.

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