UNIVERSITY OF ALBERTA

FOOD HABITS OF NESTLING PURPLE MARTINS

BY

© HELENE SPICE

A THESIS

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ABSTRACT

Qualitative and quantitative aspects of the diet of nestling purple martins (Progne subis) were studied during the summers of 1969 through 1971, by collecting food from the nestlings, counting movements of adults in and out of the nest cavity, and recording the number of feeding trips.

Flying insects were the only important components of the diet. Members of the Families Syrphidae, Aeshnidae and Nymphalidae contributed the greatest biomass. Relative rates of consumption of various insect families varied with age of nestlings, time of day, and season.

Weight of food fed to the nestlings at a given age varied with the sex of the parent, probably reflecting differences in brooding behavior and hence feeding rate. Weight of food brought per visit to the nestlings varied with age of the nestlings, sex of adults, and season, but not with brood size.

Feeding rate was not proportional to brood size, therefore nestlings in larger broods received less food per bird per unit of time than nestlings in smaller broods. Lower food intake by nestlings in larger broods was reflected in lower peak nestling weights. Weight of food fed to similar-sized broods was greater during the cool, wet summer of 1970 than during the warm, dry summer of 1971.

The percentage of trips to the nest cavity in which food was carried to the nestlings varied with brood size;

parents of larger broods brought food on a greater percentage of their trips to the nest than parents of smaller broods.

The percentage of time nestlings were brooded also varied with brood size; larger broods were brooded less frequently than smaller broods.

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may my heart always be open to little
birds who are the secrets of living
whatever they sing is better than to know
and if men should not hear them men are old

e e cummings

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INTRODUCTION

Post-fledging survival of young passerine birds appears to be strongly influenced by the quantity of food received while in the nest (Perrins, 1965). The energy value of this food is probably the important factor, thus food quality, as well as quantity, could be important in this regard. Few investigations of food consumption in nestling passerines have directly considered both these aspects of the diet over the entire nestling period. For example, many studies have documented only the relative importance of various prey items brought to the nestlings (Hamilton, 1951; Lack and Owen, 1955; Lockie, 1955; Orians, 1966; Owen, 1956). In other studies only the frequency of feeding visits to the nest by adults have been recorded (Finlay, 1971; Gibb, 1950, 1955; Kendeigh, 1952; Lack and Silva, 1949; Moreau, 1939, 1947; Morehouse and Brewer, 1968; Peterson, 1955).

Although Dunnet (1955), Gibb and Betts (1963), Kluijver (1950, 1961) and Lack and Lack (1951) attempted to determine not only what, but also how much the nestlings were being fed, they did not carry the study over the entire nestling period. Only Royama (1966) analyzed the qualitative and quantitative aspects of the diet over the greater part of the nestling period. He found no clear tendency in the relationship of feeding frequency with brood size in great tits (Parus major), but did find an

inverse relationship between the total weight of food brought per chick per day, and brood size; adults with larger broods brought less biomass of food per feeding trip.

Finlay (1971) used mechanically recorded visits to the nest cavity as an index of feeding activity in purple martins (Progne subis). He assumed that with all such visits food was brought to the nestlings. His results showed an increase in visits to the nest cavity with increased brood size, but like many of the above-cited studies the increase was not proportional to the number of nestlings involved. Finlay's results raise a number of questions concerning the volume of food fed individual nestlings in broods of various sizes: Are parent birds able to keep energy intake of individual nestlings constant when brood sizes are larger by increasing the proportion of feeding visits to the nest, or can they compensate by bringing a greater biomass of food per feeding visit, or more energy-rich food items? Or does the decreased surface-area-to-volume relationship in larger broods sufficiently enable individuals to maintain themselves on a lower energy intake?

I attempted to answer these questions by documenting qualitatively and quantitatively the food brought to nestling purple martins in relation to brood size, age, time of day and season. This study, encompassing the summers of 1969 through 1971, was carried out at the edge of Asto-

tin Lake (53° 40' N, 112° 50' W) in Elk Island National Park, Alberta, where martins were nesting colonially in artificial nest boxes.

MATERIALS AND METHODS

Effective methods and appropriate equipment for observing the birds, collecting food, and mechanically counting the number of passages in and out of the nesting compartments were developed during the summer of 1969. Consequently few data were obtained in that year; none are included in the results.

I. Nesting boxes and blinds

Martin houses that had been inhabited by a colony of purple martins for several years in the same location were used. These houses had nine nesting compartments arranged in tiers of three, and all opening in the same direction. Access to these compartments was possible from behind the house. In 1970, four houses were used; in 1971 this number was reduced to three. Each box was approximately 8 feet off the ground. The backs of the nesting compartments were covered by a black or grey cloth which could be easily displaced from within a blind constructed behind each house, and in which the observer sat (Appendix I). With the aid of a "periscope" (Appendix II) I was able to view activities in each compartment without having to move, and thus avoided alarming the birds. Direct observation of activities in the nesting compartment was necessary to determine the number of visits to the nest that were feeding visits. This arrangement also facilitated the collection of food from the nestlings immediately after they had been fed, and thus ensured that

the collected material represented only one feeding visit.

In 1969 I found the martins harbouring heavy infestations of external parasites (fleas, mites and lice). To eliminate possible variation in intensity of parasite infestation among broods, and also to ease my own distress while in the blind, I attempted to eliminate these nest parasites in 1970 and 1971. To do this nest boxes were fumigated in early spring by covering them with plastic and placing cotton waste soaked in ethyl acetate in each box for 24 hours in 1970, and 3 days in 1971. In neither year were parasites eliminated, but their numbers were reduced from those present in 1969.

II. Clutch manipulations

In 1970 an attempt was made to ensure that nestlings of different broods were of the same age so that the effect of brood size on the quality and quantity of food fed could be evaluated under similar environmental conditions.

To obtain nestlings of equal age, eggs were removed as layed and replaced by plaster of Paris replicas until females of both nesting pairs started brooding. The real eggs were then replaced for incubation, having been kept in unoccupied nesting compartments. After hatching, nestlings were distributed between the pairs to give brood sizes of 2 and 3 nestlings.

No such manipulations were done in 1971.

III. Collection, replacement, preservation and identification of food.

The quality of the diet of nestling purple martins was determined by collecting food fed to the nestlings from day 2 to day 23 post-hatching, using the method of Orians (1966). This involved the use of a piece of pipe cleaner which was placed around the neck of the nestling just tightly enough to prevent swallowing. 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 the nestlings was replaced by an approximately equal volume of food caught by the observer, so that the effect of food collection on the energy received by the nestlings was minimized. This replacement food consisted mainly of members of the order Odonata because they were easy to collect, and were used extensively as food by the martins. Members of the families Coenagrionidae and Syrphidae were fed to younger nestlings, and mainly Libellulidae to older nestlings. Some of this replacement food was fed in the fresh condition, but most after being frozen and then thawed. When frozen material was used, moisture was replaced by my saliva to facilitate consumption of the food by the nestlings.

To simplify food replacement in 1971, after numerous

specimens of two of the major food items (Aeschna canadensis and Nymphalis antiopa) had been collected, I decided to only identify these species and then feed them immediatly to the nestling from which the items was taken. The sex of the aeschnids was also determined. These food items were recorded, and their weight estimated from an average of those previously collected and weighed.

In 1970, after weighing, most food samples were placed in vials containing 70 per cent alcohol and glycerin; however, every fifth sample was frozen shortly after collection for calorific determination. To obtain the weights of the individual families of insects in each food sample from material placed in alcohol, the original weight of the families was calculated by the following formula: $a = \frac{bc}{d}$ where: a= original wet weight of family

b= original wet weight of entire sample

c= weight of family after storage in alcohol

d= weight of entire sample after storage in alcohol

In 1971 the fresh weights of all food samples were measured, samples were then placed in a vial and frozen. Subsequently the samples were thawed, the families of insects separated out, dried, and weighed to determine their relative importance in the nestlings diet.

All insects, except for the smaller moths and a few mutilated specimens were identified to family with the use of the keys of Jaques (1947, 1951).

IV. Collection and observation periods

In 1969 I observed that martin activity generally started between 0430 and 0500 hours, and ended at about 2100 hours. Thus, in 1970, food collection and observation periods were concentrated between 0500 and 0800 hours, 1100 and 1400 hours, and 1800 and 2100 hours. In 1971 the entire feeding day from 0430 to 2030 hours was sampled except for the hours from 0800 to 0900 and 1700 to 1800 hours, because from the 1970 data it was apparent that different families of insects are brought to the nestlings at different times of the day.

Collection of food samples at any one nest did not exceed two hours; all food brought by the adults during this time was collected and replaced with an approximately equal biomass of insects.

To calculate the total amount of food provided to the nestlings it was necessary to know the proportion of visits to the nest cavity in which food was brought. This was accomplished by observing the birds' activities at the nest, over time periods which varied from 1 to 3 hours.

To determine the effect of brood size on the number of movements by adult martins in and out of the nest cavity, a mechanically activated event recorder was used. A micro-switch, placed at the door of the nesting compartment late in incubation, was activated when martins entered or left the nest cavity. They rapidly adapted to the switch, and usually within an hour seemed to accept its

presence.

V. Weather data

Data on meteorological conditions were collected in both years at the site of the colony to investigate the possible effects of weather conditions on the quality and quantity of insects used. Readings of light intensity, measured with an exposure meter directed at the sun, were converted to foot candles by comparison with a photometer; wind speed was estimated with a Dwyer wind meter about 4 feet from the ground; temperature was recorded with a mercury thermometer; and relative humidity was estimated with a sling psychometer. All measurements were made immediately before and after the observation and collection periods.

In 1970 similar daily information was obtained from the park meteorological station about 0.25 miles from the study site.

General weather data used in a comparison of conditions between years were obtained from the Edmonton International Airport, about 30 miles from the study area.

VI. Weighing of nestlings

To determine the effect of brood size on the weight of nestlings, they were weighed every day at about 1800 hours by placing them individually into a plastic sling suspended from a 100-gram Pezola spring scale.

RESULTS AND DISCUSSION

I. Population studied (Table 1)

In 1970 the population studied consisted of four pairs of purple martins, each inhabiting a different nest box. Of the four pairs, two started laying about a week before the other two. The first two pairs hatched seven eggs, but within three days two nestlings died; the surviving nestlings were arranged in broods of three and two. The second two pairs of martins hatched eight eggs, but lost three nestlings within the first few days, and again broods of three and two nestlings were arranged. In all nests the nestlings that died were younger by a day or two than the others, and had not gained any weight since hatching.

All nestlings except for two in an older brood of three, died on the same day at the ages of 23 and 14 days, probably as a result of three consecutive cold and rainy days.

In 1971 two pairs of martins were studied (Table 1); each in different nest boxes. The first pair produced four eggs, three of which hatched (one hatched a day later than the others and died within three days). The second pair produced four eggs, all of which hatched and survived early nestling life.

As a result of a food study (Appendix III), one of the nestlings of the first pair and two of the second

Table 1. Nesting success of the population of purple martins studied.

Year	Broods	No. of eggs		No. nestlings surviving (days)			
		Layed	Hatched	6	12	18	24[1]
1970	Two broods hatched July 6	7	7	3	3	3	2
				2	2	2	0
	Two broods hatched July 16	9	8	3	3	0	0
				2	2	0	0
1971	One brood hatched July 8	4	3	2	2	1	1
	One brood hatched July 14	4	4	4	4	2	2

[1] Nestlings surviving to 24 days fledged.

pair died on the same day when they were 18 and 12 days old respectively.

II. Food of the nestling purple martins

Qualitative aspects

The qualitative aspects of the diet of nestling martins are reflected in a list of the families of insects identified from 956 food samples collected from the nestlings (Appendix IV). Of these, 246 samples were collected between July 8 and 29 in 1970 from four broods of martins, and 710 samples were collected between July 15 and August 11 in 1971 from two broods.

Certain families of insects were more commonly represented than others in the diet of nestling purple martins. The more important, those contributing more than 1 per cent of the total weight consumed in either year, are listed in Table 2.

There were differences in the utilization of the families of insects between years.

This difference was significant (X^2; $p<0.05$) for the Nymphalidae and appeared to reflect the difference in timing of the nesting seasons of the martins. In 1970 laying was a week earlier (July 8) than in 1971 (July 14); furthermore, sampling of nestling food had ceased by July 29 in 1970, but extended to August 11 in 1971. The mourning cloak butterfly (Nymphalis antiopa) was the species in this family contributing by far the most to

Table 2. Utilization, based on percentage of total biomass collected, of various families of insects by nestling purple martins studied at Elk Island National Park, Alberta (Appendix V).

Family	Similar Periods		Total Period	
	1970	1971	1970	1971
Aeschnidae	22	27	21	27
Syrphidae	29	17	31	22
Nymphalidae	1	23	1	25
Chironomidae	10	4	8	3
Siricidae	5	5	5	4
Formicidae	4	6	4	6
Cerambycidae	5	2	4	1
Libellulidae	1	4	3	4
Coenagrionidae	4	1	4	1
Muscidae	3	1	5	1
Apidae	2	1	3	1
Cicadellidae	2	1	2	1
O. Trichoptera	2	1	2	1
Corixidae	2	1	2	1

the nestlings. They begin to appear in the food samples about the first of August, which is when they are reported to commence emerging as adults (Canadian Department of Agriculture, 1958). Thus, because sampling in 1970 ended before this species was readily available, it was not surprising that the Family Nymphalidae was poorly represented in the samples of that year.

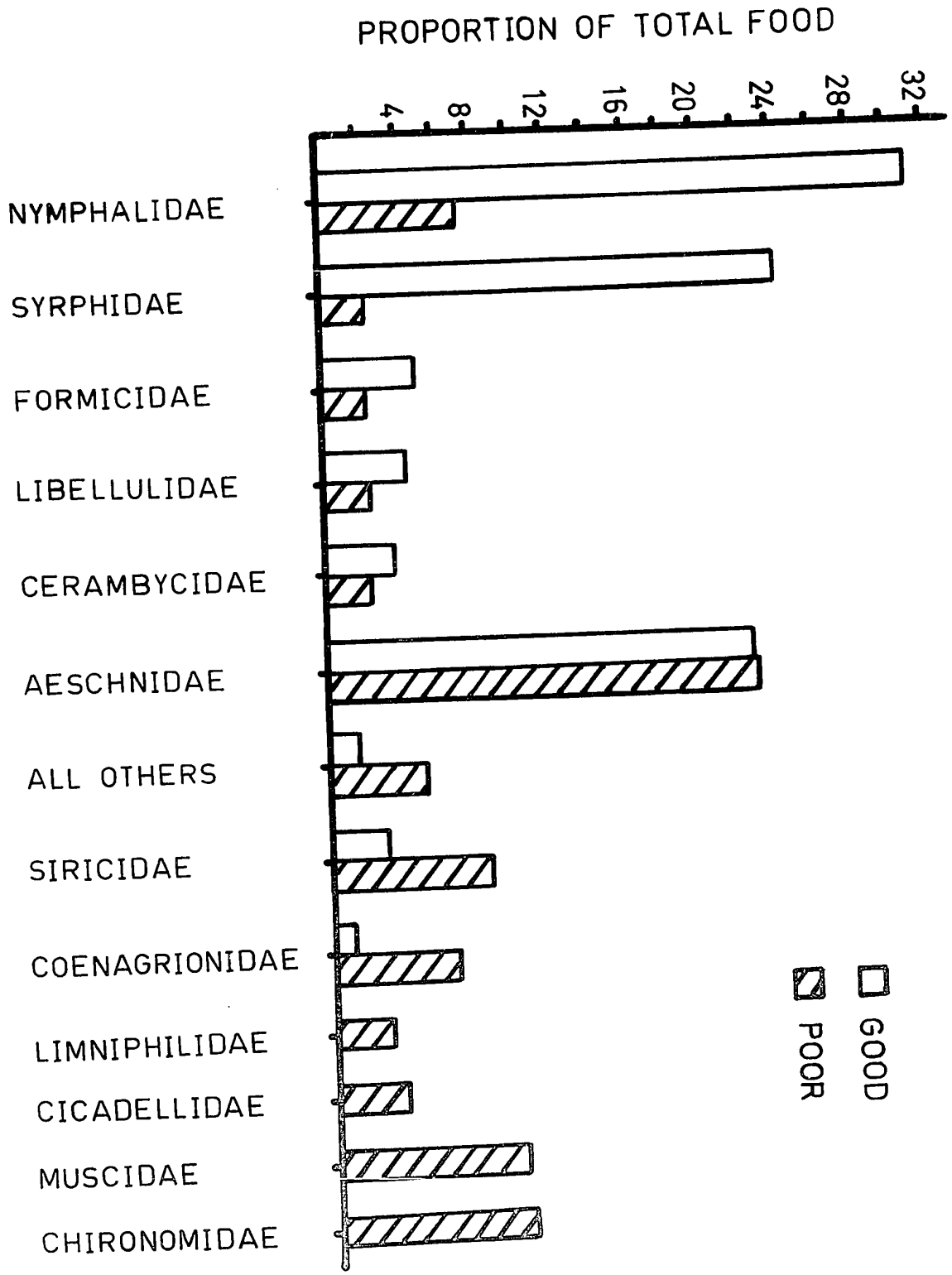
Although not statistically significant, there was a difference in the biomass of aeschnids used in the two years. This was probably related to the age of the nestlings being sampled. The early death of the nestlings in 1970 meant that the food samples were biased towards those families which were fed at an earlier age, and which contained smaller items (Figure 4; p.25). Thus larger items such as the aeschnids would not have been as well represented in the samples that year.

The difference between the two years in use of certain other families, such as syrphids, chironomids and muscids, seemed to be related to meteorological conditions, which also differed considerably between the two nesting seasons (Table 3). From these data 1971 was sunnier, drier and warmer. To determine whether certain families were utilized more than others under these conditions, the percentages contributed by various insect families to the diet in "good" and "poor" light conditions were compared (Figure 1). Good light conditions, encountered when a photometer registered more than 3500 foot candles, were associated with periods of bright

Table 3. A summary of weather conditions during the nestling periods for purple martins in 1970 and 1971. Data from Edmonton International Airport.

Weather conditions	1970 July 8-29	1971 July 14- Aug. 9
Completely sunny days (%)	0	52
Completely cloudy days (%)	15	11
Partially cloudy days (%)	85	37
Days on which rain fell (%)	50	19
Total percipitation (inches)	4.40	1.22
Mean maximum temperature (°F)	71.4	76.7
Mean minimum temperature (°F)	50.5	52.0
Mean hours of sunshine per day	8.7	12.1

Figure 1. A comparison of the relative utilization of insect families by purple martins feeding under good and poor light conditions. Expressed as a percentage of the total food collected under that light condtion. (Light condtions considered good when photometer indicated more than 3500 foot candles, poor light when less than 500 foot candles.) Data from 1970 and 1971. Total weight of food collected under good light conditions 51.27 grams wet weight; under poor light conditions 11.82.


PROPORTION OF TOTAL FOOD
4
8
12
16
20
24
28
32
NYMPHALIDAE
SYRPHIDAE
FORMICIDAE
LIBELLULIDAE
CERAMBYCIDAE
AESCHNIDAE
ALL OTHERS
SIRICIDAE
COENAGRIONIDAE
LIMNIPHILIDAE
CICADELLIDAE
MUSCIDAE
CHIRONOMIDAE
POOR
GOOD

sunlight; whereas poor conditions were encountered when light readings fell to less than 500 foot candles, and were associated with days of heavy cloud, early mornings and late evenings. The data presented in Figure 1 were collected when conditions were either completely cloudy or completely sunny. By limiting the data in this way, I knew what the light conditions were when the food samples were taken by the adult martins.

There was a significant difference (X^2; $p<0.05$) between the two years in the utilization of syrphids. Nymphalids and syrphids were the major items in the diet of nestling martins on sunny days (Figure 1). In the absence of nymphalids from the diet in 1970 it is not surprising that syrphids were relatively more important in that year, being the major items taken during brighter periods of weather. Correlated with the generally poor light conditions in 1970, there was a greater utilization of forms such as chironomids, muscids, and coenagrionids.

If the nutritional value of a dietary item is based only on biomass, one must assume a constant calorific value per unit weight. A study done on the calorific value of insects (Cummins and Wuycheck, 1971) indicates that this assumption is not valid, and therefore the calorific values of samples from different families of insects were determined. These data for the most heavily utilized families in terms of biomass are shown in Table 4 (p. 30). In 1970 the caloric content (small calories) of the

biomass of each insect family collected from food samples of nestling purple martins was: Syrphidae 15,500, and Aeschnidae 13,000; in 1971: Syrphidae 9,000, Aeschnidae 16,000, and Nymphalidae 14,500. In spite of differences in calorific values, the relative nutritional contribution of these families to the diet of the nestling martins remained the same as when based on biomass alone.

The species composition of the food brought to nestling martins at Elk Island National Park differed from that reported in the literature for fledged purple martins. Beal (1918) analysed the contents of stomachs from martins that had been collected from February to September inclusive in the United States and Canada. He found the food to be entirely animal matter; the major components of the diet were: hymenopterans 23 (per cent), dipterans 16, odonatans 15, hemipterans 15, coleopterans 13, and lepidopterans 9. The last were taken in August and September and, except for one butterfly, all were moths.

Johnston (1965) analysed the contents of stomachs from 34 purple martins collected between April and August in Kansas. He found that coleopterans, dipterans, hymenopterans and hemipterans were the most important, but that their relative importance changed with the season. Odonatans contributed, at most, 1 per cent of the food items found in the stomachs, as did syrphids

and lepidopterans until August when the latter rose to 14 per cent. The lepidopterans were not identified as butterflies or moths.

These differences probably reflect the different locations in which the birds were feeding. The colony I studied was adjacent to a lake which probably explains a greater use of insects having aquatic stages in their life cycle; whereas in the other studies the birds were probably collected from a diversity of habitats so that this bias would not appear in their results. Furthermore, the period of time over which these birds were collected for the analysis of their stomach contents differed, as did the age of martins from which the samples were taken.

The discriminatory powers of purple martins were apparent in the selection of only one sex of certain prey insects. Beal (1918) found that of the 11 honey bees eaten, all were drones. I recorded 7 honey bees in food samples of nestling martins and all were males.

Beal (1918:5) recorded the presence of "a bit of mollusk shell" in the food analyzed. Mollusc shell was found in 3.3 per cent of all food samples collected in this study. This material could function as either grit or as a source of calcium, or both. Johnston (1965:8) did not record mollusc shell but did note the presence of plant parts, but in May only. He suggested that these plant parts were "probably injested while the birds were carrying cut leaves to their nests...." I usually found

plant material associated with mollusc shell, but occassionally alone, as in the husks of sun flower seeds (Helianthus annuus) and the seeds of bur-reed (Sparganium sp.). Thus Johnston's explanation that plant parts were only accidentaly injested may not be true in that martins in this study deliberately brought seeds, or parts thereof to their young; the adults may have used these items as well.

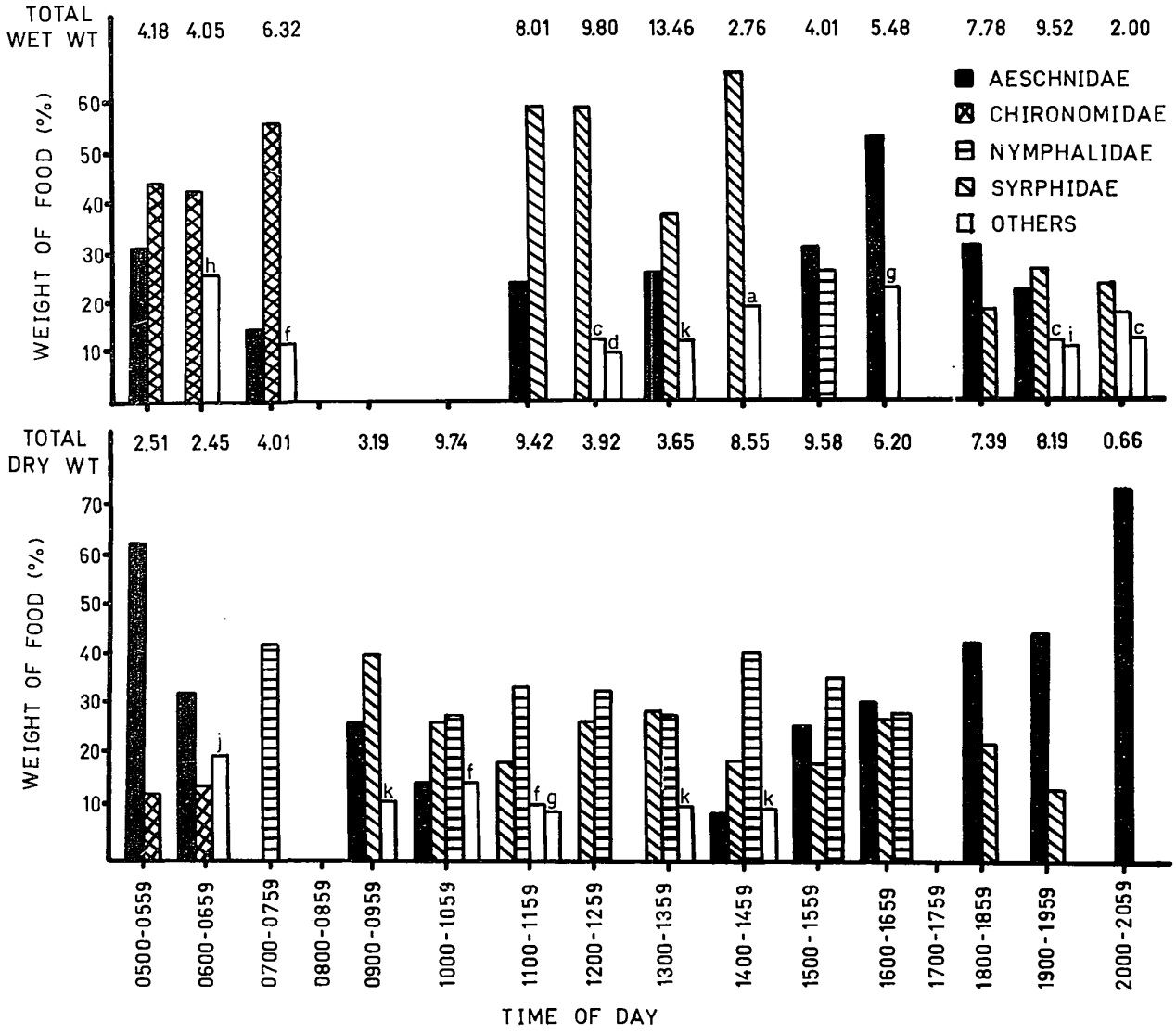
Beal (1918:2) stated that "they [swallows] do not eat Lepidoptera... extensively, either larval or adult." My results disagree with this statement, as lepidopterans, in particular Nymphalis antiopa, were a major food item for the nestlings in 1971.

Wade (1966) stated, with no data to support his claim, that purple martins eat large numbers of mosquitoes, thus making them a very beneficial bird to have around the home. Kale (1967:11), having reviewed the scientific and popular ornithological literature, concluded that "Mosquitoes are a negligable item in the diet of the purple martin.". The results of this study support Kale's conclusion. Although mosquitoes were supplied to the nestlings, in neither year did they comprise more than 1 per cent of their diet.

The utilization of the various families of insects by purple martins depended on the time of day the martins were feeding (Figure 2). Of the four insect families utilized most heavily, aeschnids were taken throughout

Figure 2. Utilization of insect families by nestling purple martins expressed as per cent of total food collected during a given hour. Only those families contributing 10 per cent or more to the weight of food gathered are figured.
Key to letters above bars:

a.	Apidae	g.	Libellulidae
b.	Asilidae	h.	Limnephilidae
c.	Cerambycidae	i.	Muscidae
d.	Coenagrionidae	j.	Noctuidae
e.	Dytiscidae	k.	Siricidae
f.	Formicidae		


TOTAL WET WT
4.18 4.05 6.32 8.01 9.80 13.46 2.76 4.01 5.48 7.78 9.52 2.00
WEIGHT OF FOOD (%)
AESCHNIDAE
CHIRONOMIDAE
NYMPHALIDAE
SYRPHIDAE
OTHERS
TOTAL DRY WT
2.51 2.45 4.01 3.19 9.74 9.42 3.92 3.65 8.55 9.58 6.20 7.39 8.19 0.66
WEIGHT OF FOOD (%)
0500-0559
0600-0659
0700-0759
0800-0859
0900-0959
1000-1059
1100-1159
1200-1259
1300-1359
1400-1459
1500-1559
1600-1659
1700-1759
1800-1859
1900-1959
2000-2059
TIME OF DAY

the day; chironomids, only in the morning; nymphalids and syrphids were taken mainly around midday. The other families recorded were extensively used only at certain times, and possibly reflected sporadic periods of increased availablility. The formicids, for example, which are known to have mating flights at certain times of the year (Goetsch, 1957) were used only sporadically. Martins apparently take advantage of these swarms when they are available, which increased the relative utilization of this family on particular days.

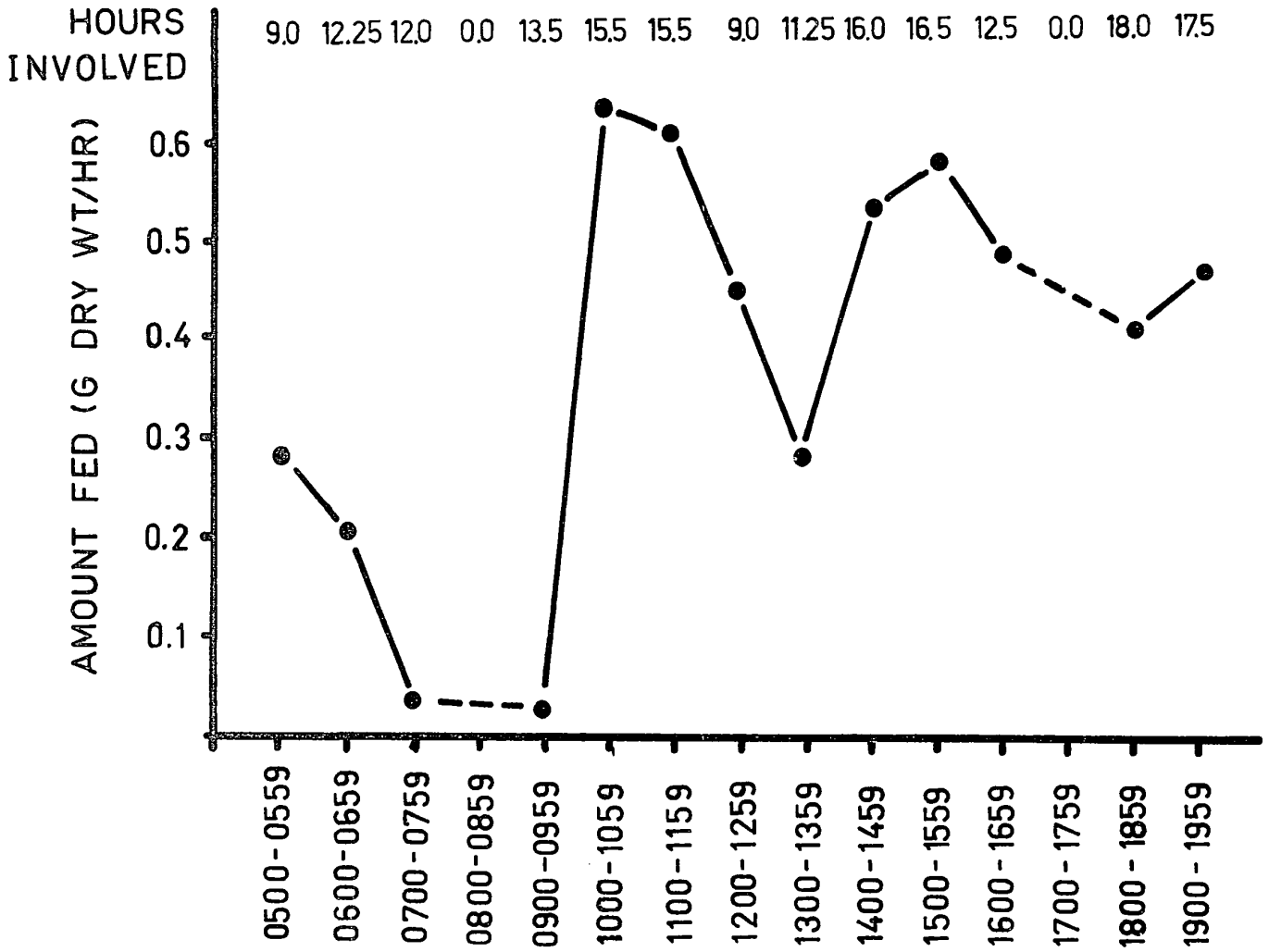
Whether the utilization of the various families of insects can be explained in terms of availability or preference is not known, as no data were obtained on the relative availability of the various families at specific times of the day. Nevertheless, generalizations on the periodicity of flight by certain families of insects can be made (Lewis and Taylor, 1965). Syrphids and nymphalids have normal activity curves that peak about midday, whereas odonatans are active throughout the day. The activity curves for chironomids is skewed away from maximum light. If these generalizations are applied to this study it appears that both availability and preference were involved. The early morning use of chironomids possibly reflected a greater availability of this family at that time of day. Use of syrphids and nymphalids seemed to be influenced by both availability, as the utilization curve followed generally the presumed availability curve, and

preference, as utilization continued in the presumed equal availability of aeschnids. The use of the latter fell during midday when nymphalids and syrphids became available.

While collecting food from the nestlings it seemed that the amount of food supplied to the nestlings was related to the time of day. To investigate this relationship, the rate at which food biomass was supplied to the nestlings throughout the day was estimated by averaging the weight of food brought per hour for each hour of the feeding period (Figure 3).

The fluctuations in food supplied probably reflected the energy requirements of the nestlings. In the early morning begging intensity was probably high because nestlings were hungry, causing adults to feed them at the expense of their own body reserves. As food requirements of nestlings were met, begging intensity would decrease. This was reflected in the rapid decline in amount of food brought to the nestlings between 0700 and 0800 hours. Presumably the adults were attending to their own needs at this time. With low food intake between 0700 and 1000 hours the hunger of the young probably increased as did begging intensity; thus when feeding of the nestlings resumed it was at an even higher level than earlier, probably because the adults were satiated and may not have been consuming part of the food as they possibly were in the early morning. When satiated by 1200 hours the nest-

Figure 3. Rate of feeding nestling purple martins expressed as mean biomass (grams dry weight) fed per hour. Data from 1971. Hours involved indicate the number of hours spent collecting food at that time of day.


HOURS INVOLVED
9.0 12.25 12.0 0.0 13.5 15.5 15.5 9.0 11.25 16.0 16.5 12.5 0.0 18.0 17.5
AMOUNT FED (G DRY WT/HR)
0.6
0.5
0.4
0.3
0.2
0.1
0500-0559
0600-0659
0700-0759
0800-0859
0900-0959
1000-1059
1100-1159
1200-1259
1300-1359
1400-1459
1500-1559
1600-1659
1700-1759
1800-1859
1900-1959

ling's begging activity declined and they were fed at decreasing frequency for two hours. This period was followed by another increase in food intake and then a decline and a third increase between 1700 and 1800 hours. The decline in the extent of fluctuations in food intake as the day progressed probably reflected a greater overlap in feeding of nestlings and adults.

The utilization of members of specific insect families over the nestling period was also investigated. Only data for 1971 were used (Figure 4) because in 1970 sample size was too small for meaningful results.

From day 2 through day 9 post-hatching, syrphids made up the greatest weight of food consumed by nestling purple martins. By day 9 aeschnids began to appear in the diet, and at day 10 assumed an importance that continued until day 23. Nymphalids were consumed throughout the nestling period, but became a major item at day 13, and continued as such until the end of the study at day 23.

Because of differences in the sizes of insects, members of certain families seemed to be fed at only certain ages, for example, nymphalids after day 2, but the large Nymphalis antiopa only after day 11; the medium sized libellulids only after day 5; the largest forms, aeschnids and siricids only after day 8, and the large heavily chitinized cerambycids only after day 10. Observational evidence supported the conclusion that

Figure 4. Utilization of insect families in relation to age of nestling purple martins expressed as per cent of total food collected for that age. Only those families contributing 10 per cent or more of the weight of food gathered at a specific age are figured. Refer to Figure 3 for dey to letters above bars.

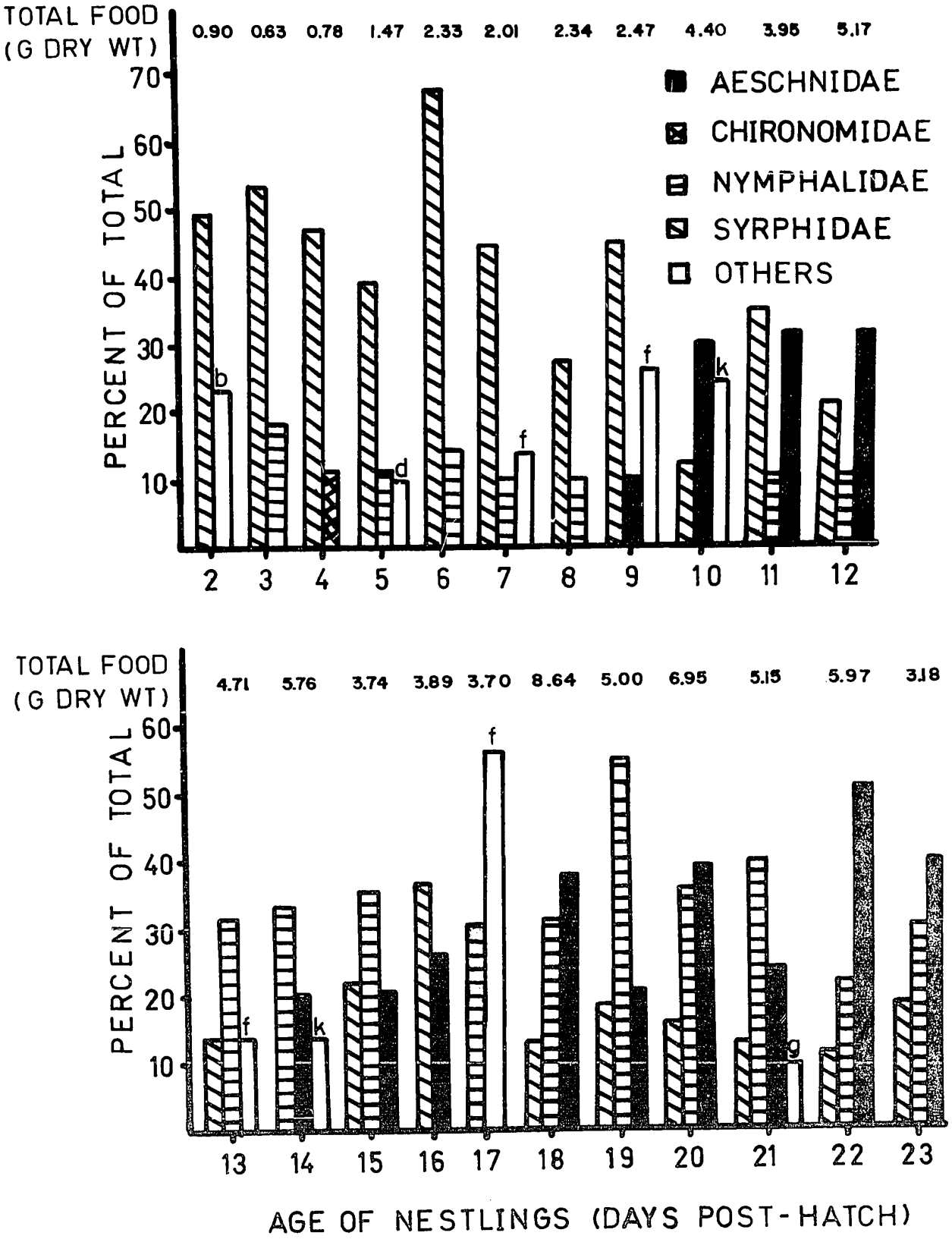
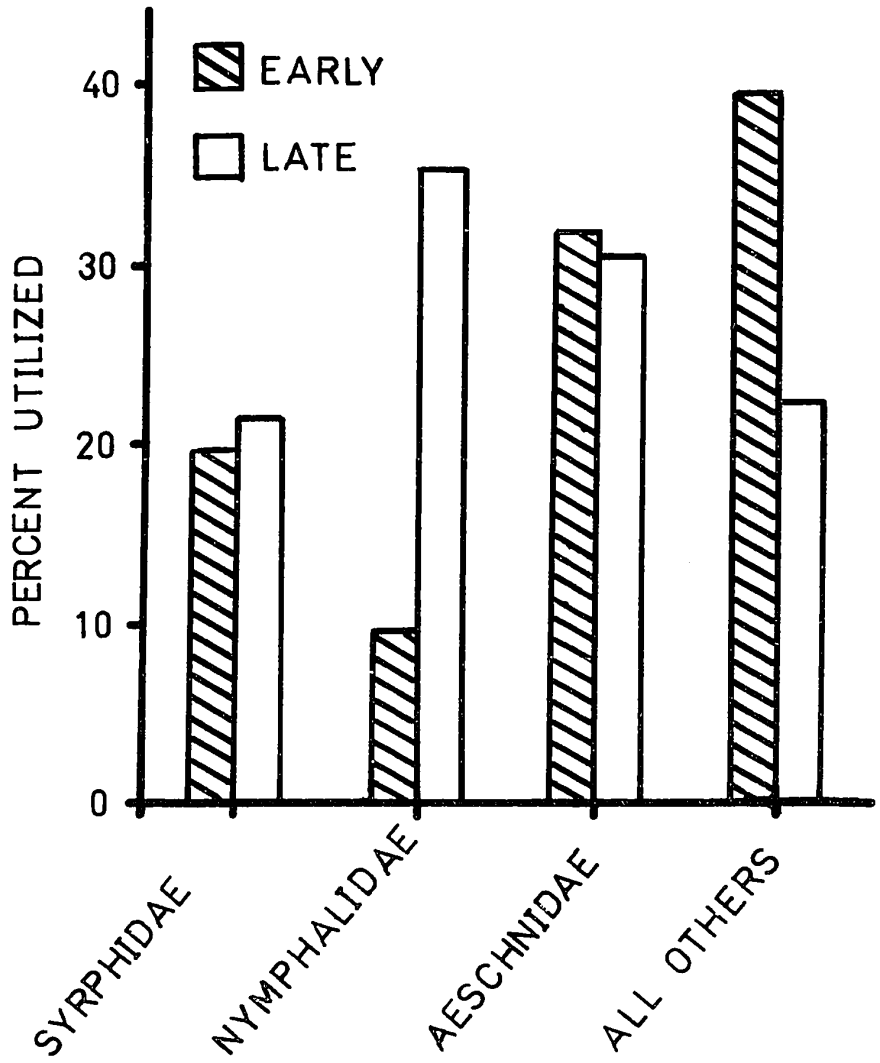

TOTAL FOOD
(G DRY WT)
0.90 0.63 0.78 1.47 2.33 2.01 2.34 2.47 4.40 3.95 5.17
AESCHNIDAE
CHIRONOMIDAE
NYMPHALIDAE
SYRPHIDAE
OTHERS
PERCENT OF TOTAL
70
60
50
40
30
20
10
b
d
f
f
k
2 3 4 5 6 7 8 9 10 11 12
TOTAL FOOD
(G DRY WT)
4.71 5.76 3.74 3.89 3.70 8.64 5.00 6.95 5.15 5.97 3.18
PERCENT OF TOTAL
60
50
40
30
20
10
f
k
f
g
13 14 15 16 17 18 19 20 21 22 23
AGE OF NESTLINGS (DAYS POST-HATCH)

Figure 5. The influence of date of hatching on the families of insects used as food by nestling purple martins. "Early" clutch hatched July 8, 1971, and "Late" clutch hatched July 14, 1971.


EARLY
LATE
PERCENT UTILIZED
40
30
20
10
0
SYRPHIDAE
NYMPHALIDAE
AESCHNIDAE
ALL OTHERS

and 596 syrphids, in which the sex was determined, females outnumbered males. The ratio fed among aeschnids was 1:1.3 and 1:1.1 in early and late broods repectively; for syrphids these ratios were 1:8.2 and 1:5.8. The differences in ratios between early and late broods were not statistically significant. A reliable estimate of the sex ratio of nymphalids for each brood was not possible because of an inadequate sample size. Such differences in sex ratios could affect the quality of the diet through one sex being of more energy value per unit of biomass than the other (Table 4). Among the nymphalids, males have registered a higher caloric value than females, whereas among the syrphids this situation is reversed. The caloric value of males and females among the aeschnids was about equal. If the total caloric value of the biomass fed from each family is calculated for the brood hatched July 8, 1971, the order of importance from a caloric standpoint was: Nymphalidae, Syrphidae, and Aeschnidae. Therefore these data did not change the order of importance of these three families, based on biomass alone (Table 2).

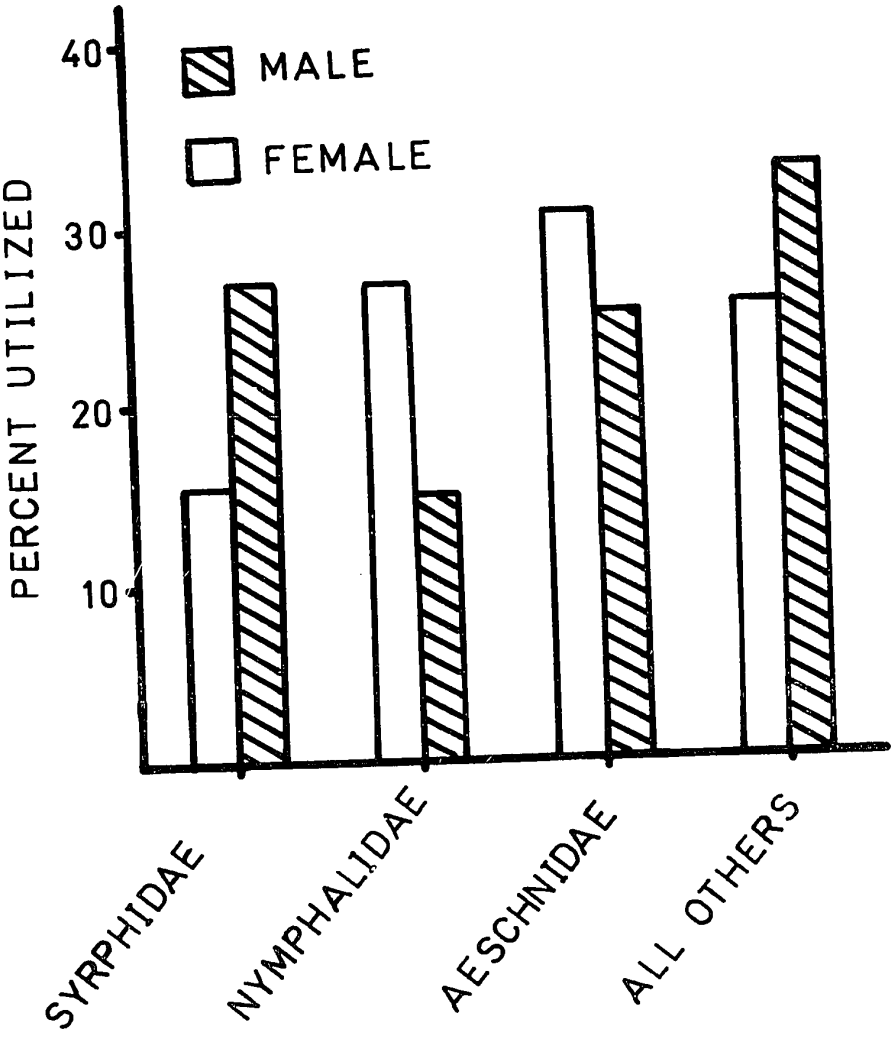
Another variable affecting the type of insect food brought to the nestling was the sex of the adult martin involved. Male and female martins brought a similar biomass of each family, or group of families, fed to the nestlings when the entire nestling period was considered (Figure 6). However, there seemed to be a tendency for

Table 4. Caloric content of males and females from each of three insect families most utilized by purple martins. Data from 1971.

Family	No. indiv. tested	Mean cal/gm dry wt.[1]	Brood hatched July 8			Brood hatched July 14		
			Grams provided dry wt.	Caloric equiv.	Total cal for brood	Grams provided dry wt.	Caloric equiv.	Total cal for brood
Nymphalidae								
♂	7	6438	1.66[2]	10661	21045	8.05[2]	51826	102299
♀	7	6270	1.66	10383		8.05	50474	
Aeschnidae								
♂	5	6110	4.66	28491	63797	4.21	25729	53062
♀	5	6027	5.86	35306		4.54	27333	
Syrphidae								
♂	40	5146	0.75	3833	38281	1.45	7446	54427
♀	30	5615	6.14	34448		8.37	46981	

[1] Mean based on 2-5 sample runs.
[2] Sex ratio of nymphalids assumed equal.

Figure 6. A comparison of the nature of food brought to nestling purple martins by adult males and females. Data from 1971.


40
30
20
10
PERCENT UTILIZED
MALE
FEMALE
SYRPHIDAE
NYMPHALIDAE
AESCHNIDAE
ALL OTHERS

males to provide syrphids and "all others" more extensively, whereas females provided more nymphalids and aeschnids. The differences may reflect the different roles of the male and female in feeding the nestlings with age (Figure 7). As age increased feeding was more intense, and for awhile most of this activity was done by the male. However, as the necessity of the female to brood decreased, her role as a provider of food increased and there was a corresponding decrease in the role of the male. As a result the male fed a greater percentage of food characteristic of early-aged young, such as syrphids and "all others", and a lesser percentage of the food characteristically brought to older nestlings, such as nymphalids and aeschnids.

Quantitative aspects

The relationship between number of visits to the nest and brood size in this study was proportional to the number of nestlings in the brood (Figure 8). This is in contrast to the results of many others, including Finlay (1971) who reported a nonproportional increase of visits with increased brood size in purple martins. Furthermore, he found no difference in the curves for brood size two compared to three. Data from my study demonstrated a significantly greater number of passages in and out of the nest cavity per hour for a brood of three nestlings than for two nestlings. This could be assumed

Figure 7. Amount of time spent by the male in feeding nestling purple martins, expressed as a percentage of total visits. Data from 1971. Curve drawn by inspection.

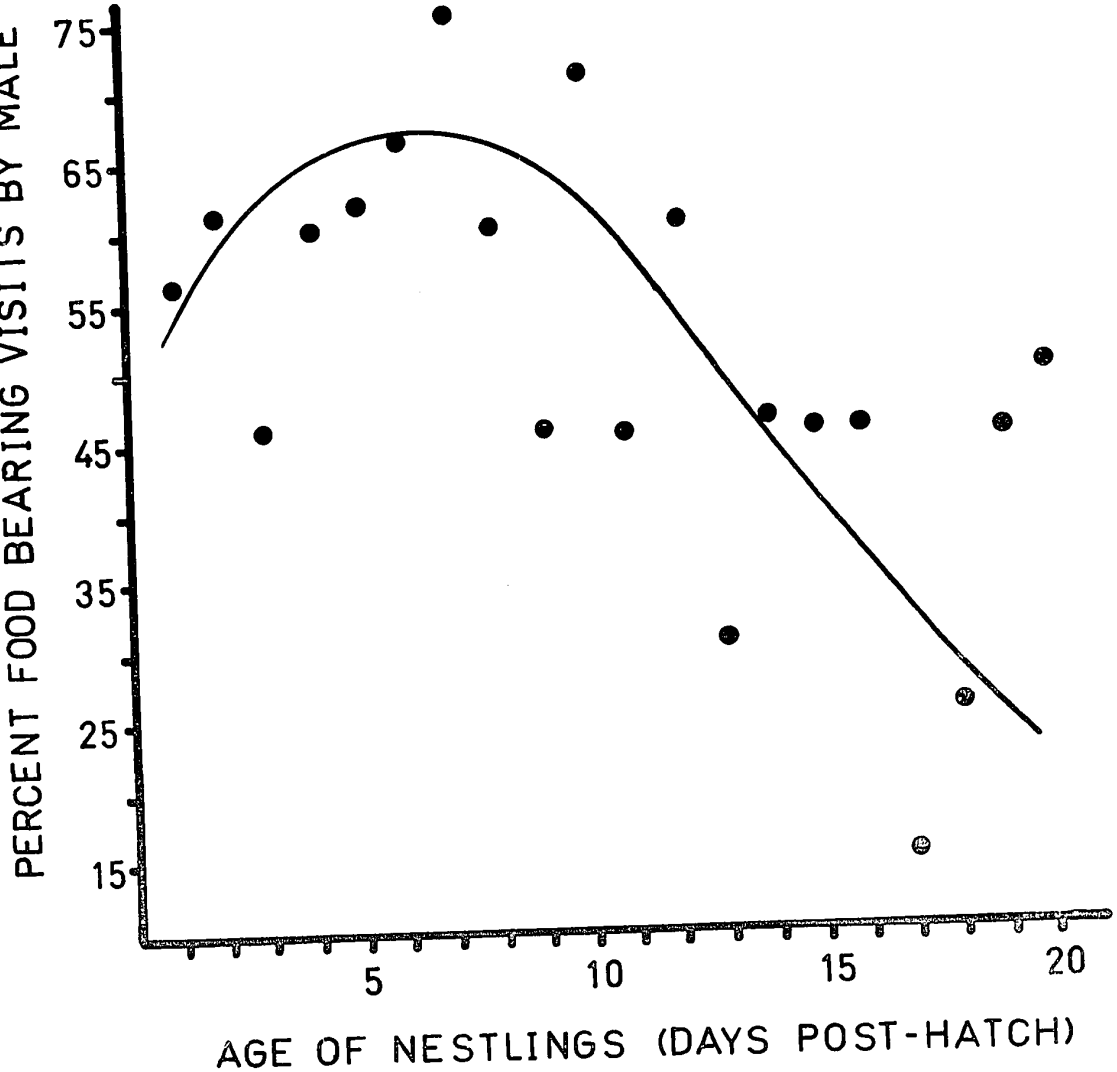
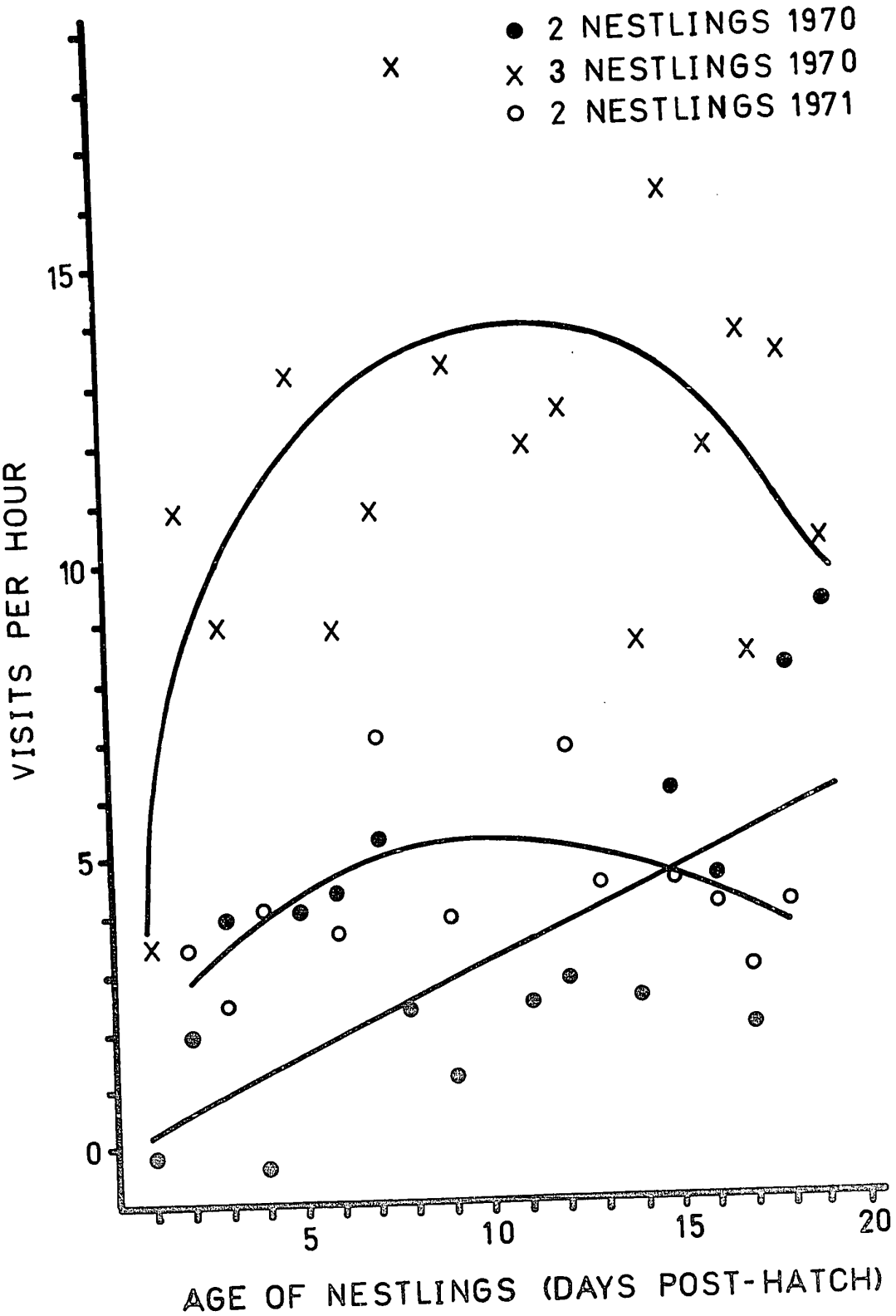

PERCENT FOOD BEARING VISITS BY MALE
75
65
55
45
35
25
15
5
10
15
20
AGE OF NESTLINGS (DAYS POST-HATCH)

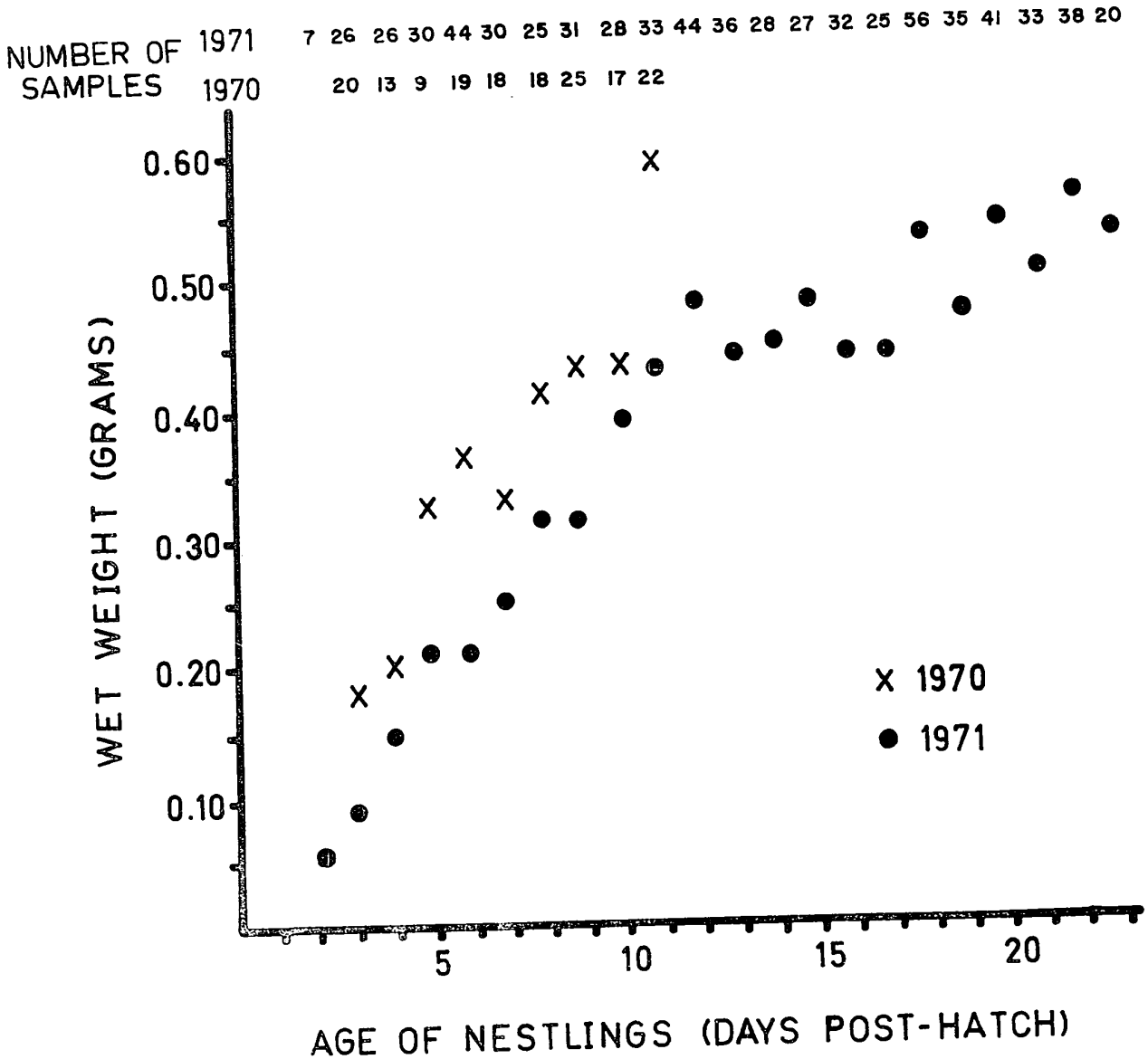
Figure 8. The effect of brood size on the number of visits per hour to the nest by adult purple martins, excluding cold, rainy or windy days. Curves drawn by inspection.


2 NESTLINGS 1970
3 NESTLINGS 1970
2 NESTLINGS 1971
VISITS PER HOUR
0
5
10
15
5
10
15
20
AGE OF NESTLINGS (DAYS POST-HATCH)

to indicate that the respective broods were receiving a similar number of visits per individual per unit time. The level of activity registered at the nest entrance for a brood size of three was close to that recorded by Finlay (1971), however, the same activity for birds with brood size two was much lower in this study than in his. Unfortunately I had no data from a brood size of four to compare with his, and therefore individuals in such broods may have been receiving fewer visits relative to those in smaller broods. This was supported by observational data alone for brood sizes four and two. However, the assumption that nestlings were receiving less food if they belonged to a larger brood size does not necessarily follow, because adults having a larger brood size could have compensated in several ways to meet the added energy requirements of their nestlings.

One way to compensate would be for the adults of larger broods to bring food samples of greater biomass relative to food samples brought to smaller broods. To consider this, I investigated the mean weight of food sample brought at each visit with increasing age of nestlings (Figure 9). The results showed that the mean weight of food brought per feeding trip increased with age in both years. The curves showed a rapid increase from 0.05 to 0.45 grams by the time nestlings have reached 10 to 12 days of age. Thereafter weight of food brought increased much more slowly to a level of about 0.55 grams by the

Figure 9. Mean weight of food samples brought to nestling purple martins by the adults throughout the nestling period.


NUMBER OF SAMPLES
1971
1970
7 26 26 30 44 30 25 31 28 33 44 36 28 27 32 25 56 35 41 33 38 20
20 13 9 19 18 18 25 17 22
0.60
0.50
0.40
0.30
0.20
0.10
WET WEIGHT (GRAMS)
5
10
15
20
AGE OF NESTLINGS (DAYS POST-HATCH)
X 1970
● 1971

time nestlings reached the age of 23 days. Therefore the adults were compensating for age of nestlings, however the data do not indicate a compensation for brood size. The mean values for 1970 were significantly higher (Wilcoxon's signed rank test on the median values) than in 1971, but the average brood size in 1970 was 2.5 nestlings compared to 3.0 in 1971. If the adults were compensating for brood size, food samples should be heavier in 1971 relative to 1970. The differences between the two years probably reflected weather conditions. Weather conditions in 1970 were cooler and duller, and this was correlated with a greater diversity of prey items in the diet, the majority also being smaller. Two possibilities exist: smaller prey items are coated by more saliva from the adult, thereby increasing the average wet weight recorded per collected sample; or purple martins were collecting a greater total weight of food material per feeding trip when prey items were small rather than large.

The increased weight of food sample with increased age of nestling agrees with the data of Royama (1966) who found that among great tits there was a tendency for the average weight of food brought to the nestlings to increase up to between day 10 and 15. However, he found that the weight then decreased until fledging, which my data did not show. Among the martins the weight of food continued to increase but the frequency of feeding trips apparently decreased (Figures 8 and 13; and Finlay, 1971) as fledging

approached. This too may have resulted in less food being fed to the nestlings as they approached fledging.

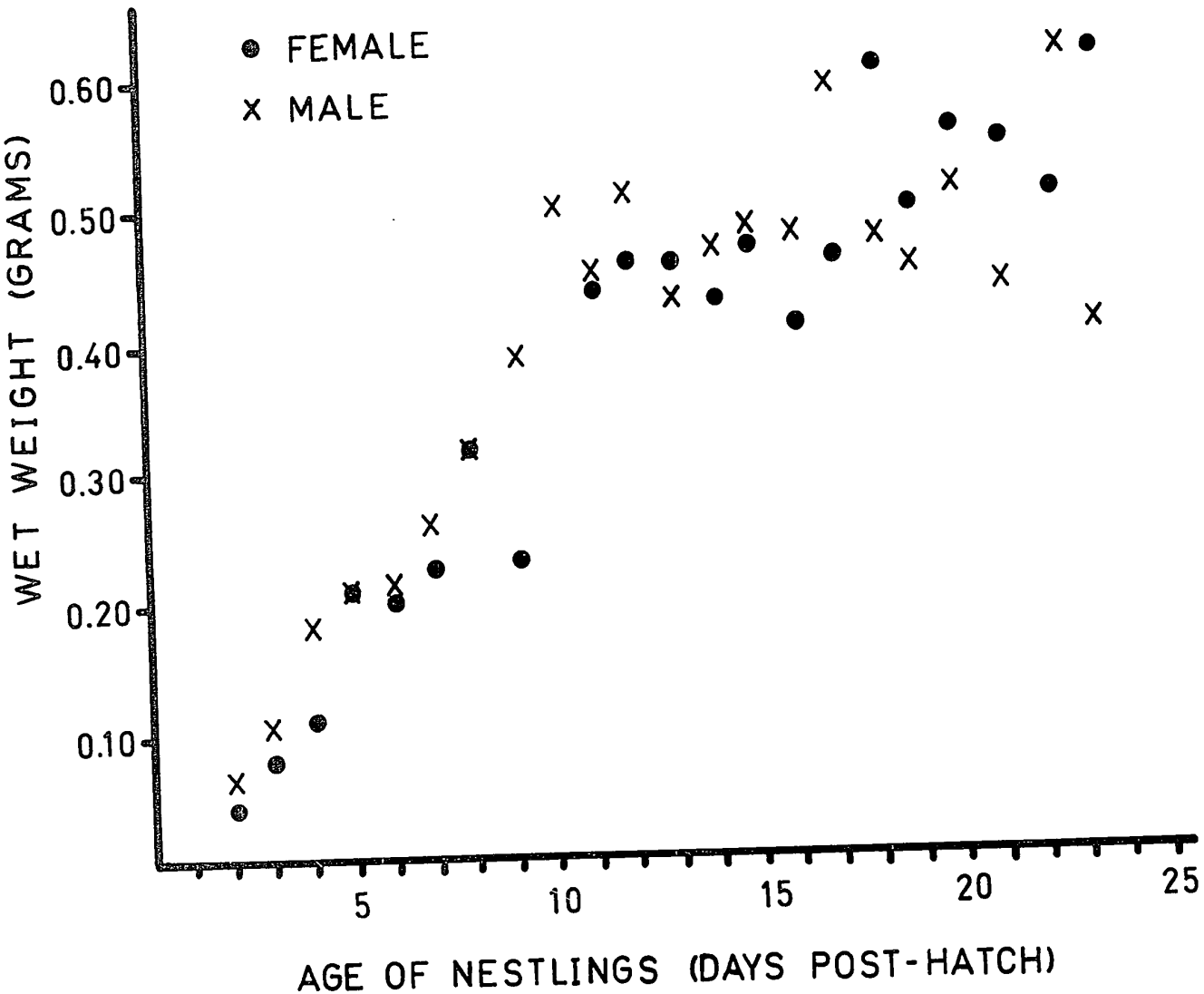
The influence of brood size on the weight of food brought per feeding trip was investigated using the data from 1971. Two broods were studied: one brood of two nestlings which hatched July 8, and in which one nestling died on day 19, and one brood of four nestlings, which hatched July 14, and in which two nestlings died on day 12. Wilcoxon's signed rank test indicated no significant difference in the weight of food sample brought between the two 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. Furthermore, the higher the frequency of feeding trips the smaller was the weight of food sample. This he explained on the basis of stimuli received from begging young. With a small brood the amount of begging is correspondingly small and as a result the stimulus to bring food is weaker, so that the adults do not bring food until they encounter a large prey item, thus saving energy. In a larger brood size the begging intensity is high, the stimulus to bring food is stronger, so that any size of prey is enough to stimulate the parent to bring it to the nest. One would not expect this to occur in martins, for unlike tits they usually bring more than one item to the nest at a time, so that for martins with a larger brood size it would be energetically more efficient for the

adults to bring a large number of small items, thus making the weight of sample approximately equal to that of a single larger item. The small size of the tit's beak probably prevents it from doing likewise.

These same data were separated to compare the mean weight of food samples brought per feeding trip by males and females (Figure 10). Until day 17 post-hatching, males brought significantly (Wilcoxon's signed rank test) heavier weights of food per feeding trip than did females. After day 17 the converse was true, the reason for this switch could not be determined.

Another way for martins with larger broods to provide energy levels comparable to those in smaller broods would be to utilize insects having a higher caloric value. The two broods in 1971 were compared and it appeared that this did not occur. This can be seen if Figure 5 in which the food of the early (2 nestlings) and late (4 nestlings) broods are compared in relation to the caloric values of the different families shown (Table 4). Syrphids and aeschnids were used about equally by each brood so they were disregarded. Nymphalids were used more by the larger brood, and "all others" by the smaller. Thus the only way the individuals of the larger brood could have received more energy than the smaller brood was for the latter to have been caloricly inferior to the former. This was not likely, as the most prevalent insects in this category were formicids, siricids, libellulids, chironomids and

Figure 10. The influence of sex of adult on the mean weight of food sample brought to nestling purple martins. Data for 1971.


FEMALE
MALE
WET WEIGHT (GRAMS)
0.60
0.50
0.40
0.30
0.20
0.10
5
10
15
20
25
AGE OF NESTLINGS (DAYS POST-HATCH)

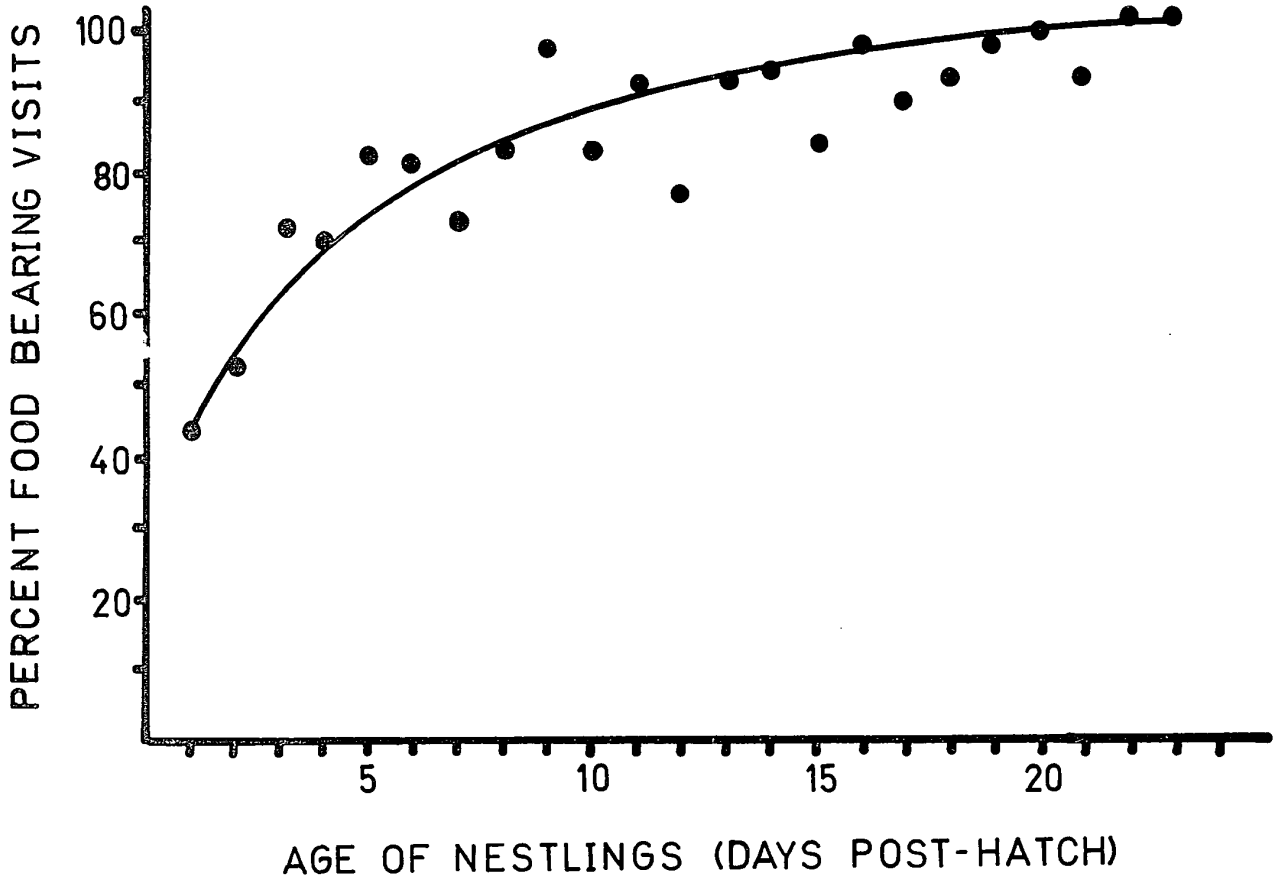
cerambycids, all of which, with the exception of libellulids, had caloric values about equal to that of Nymphalids (Appendix VI).

Adults could also have compensated by increasing the frequency of feeding visits. The data on percentage of visits that were feeding visits were obtained by observation and appear in Figure 11. The percentage of visits in which food was brought to the nestlings changed with their age. The percentage increased most rapidly from day 1, when 45 per cent were food bearing, to day 6 when about 80 per cent were food bearing. It then rose more slowly until day 22 when virtually 100 per cent of the visits involved the bringing of food.

During early stages of nestling life, movements in and out of the nest cavity which were not feeding trips usually involved the return of the female to brood after having departed when the male had entered to feed the nestlings and brood them briefly. This pattern of movements by the adults was characteristic during good weather conditions. When cold conditions prevailed (<15°C) the female often did not leave the nest cavity when the male entered.

Several factors may influence the relatively low percentage of food-bearing trips while the nestlings were young. The biomass of the naked nestlings was small, thus heat loss was proportionately greater at an earlier age. Even though males brooded in the absence of the female,

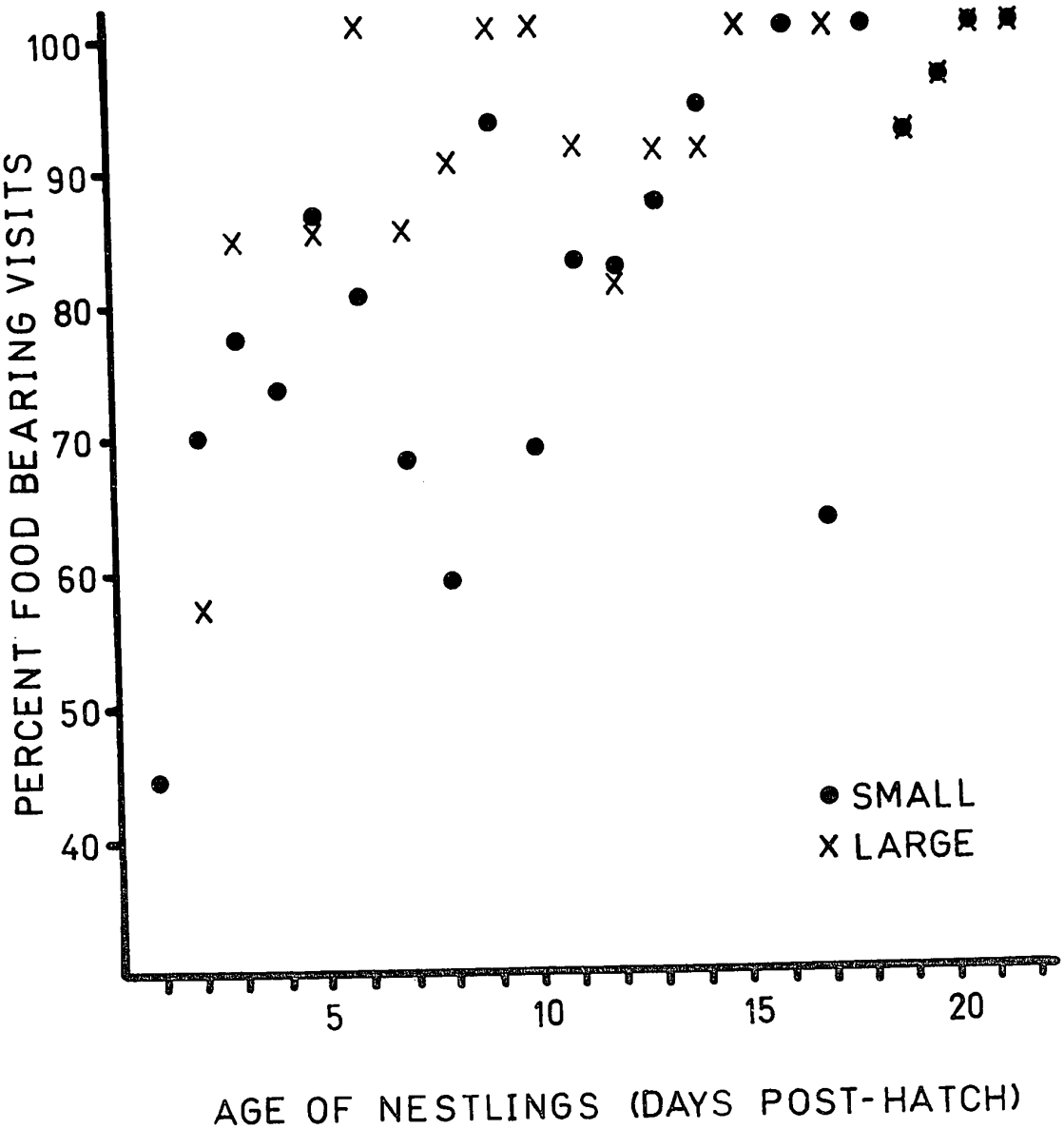
Figure 11. Percentage of visits to the nest by adult purple martins that are food bearing visits. Data from 1971. Curve fitted by inspection.


PERCENT FOOD BEARING VISITS
100
80
60
40
20
5
10
15
20
AGE OF NESTLINGS (DAYS POST-HATCH)

they tended to leave the nest cavity before the return of the females. Further, the absence of a brood patch made brooding activity by males less effective than by females. Thus the sooner the female returned to the nest the lower the heat loss by the nestlings. Also, young nestlings required less absolute weight of food, so females did not need to contribute to feeding at this time. Since females spent more time brooding, any time away from the nest was probably spent feeding themselves. As the nestlings grew older their biomass increased so that proportionate heat loss decreased and also they attained homeothermy through the insulative properties of the developing plumage, but they required more absolute weight of food. As a consequence brooding was less important than feeding as the nestling period progressed. This would appear to explain the increase in percentage of trips to the nest cavity that brought in food. As the female was gradually relieved of the necessity of brooding the young, her activity in feeding them increased, and that of the male decreased (Figure 7). These findings agree with those reported by Kluijver (1950) and Royama (1966) for great tits. Presumably this differential role in feeding activity would function in equalizing the energy expended by each parent over the nestling season.

These data of percentage of visits that were feeding visits, were compared for the different brood sizes (Figure 12). Among adults feeding larger broods, a significantly

Figure 12. The effect of brood size on the percentage of visits to the nest by adult purple martins that are food-bearing visits. "Small" brood size refers to a brood of 2 nestlings that was reduced to 1, 19 days post-hatching. "Large" refers to a brood of 4 nestlings that was reduced to 2, 12 days post-hatching. Data from 1971.

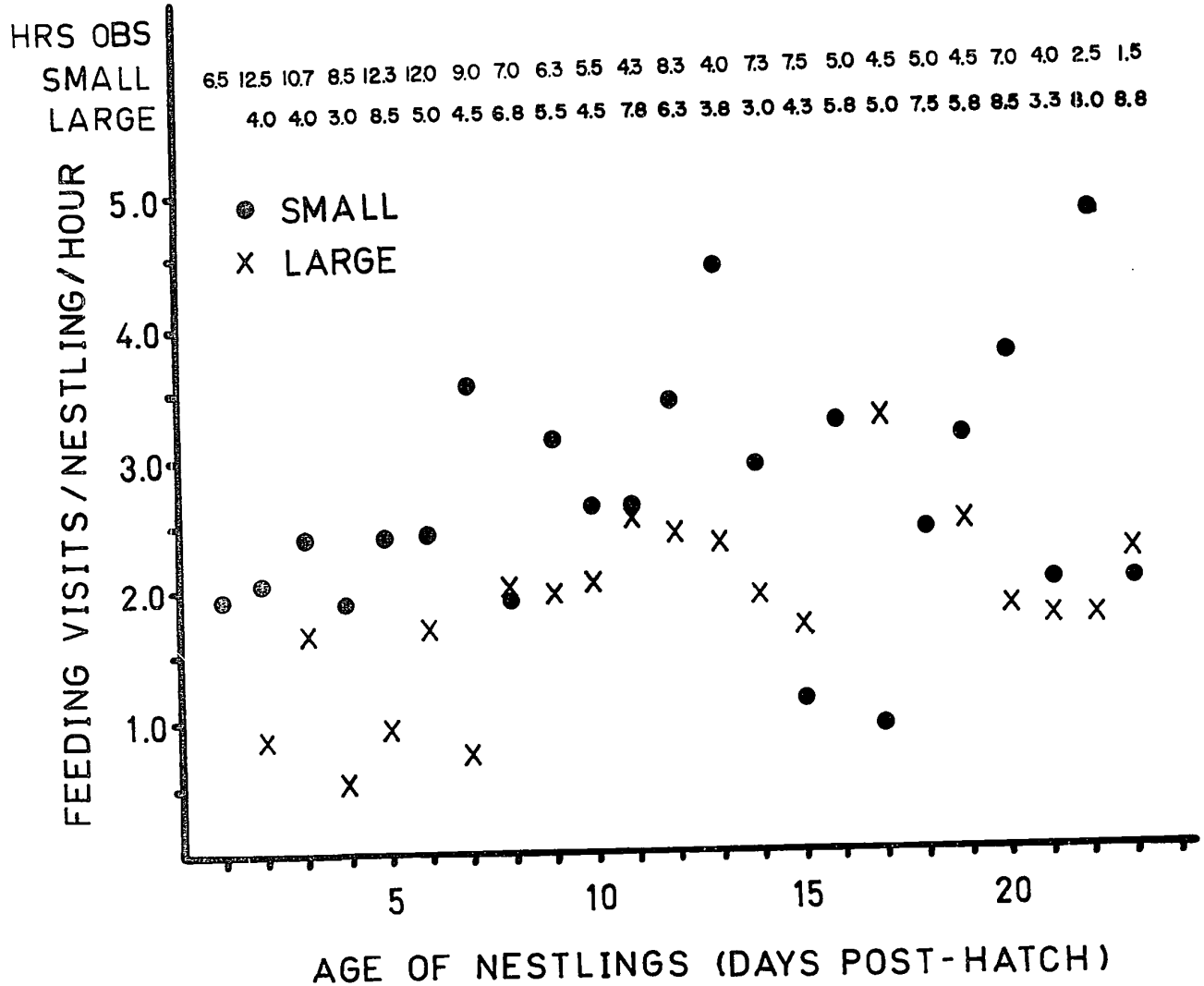

100
90
80
70
60
50
40
PERCENT FOOD BEARING VISITS
5
10
15
20
AGE OF NESTLINGS (DAYS POST-HATCH)
SMALL
LARGE

greater percentage of their trips to the nest involved the carrying of food (Wilcoxon's signed rank test). This factor has not been considered by many workers who have assumed that trips to the nest cavity by adults are equal to, or proportionately equal to, the number of food bearing trips. This study indicates that this assumption is not valid, and that adults of larger broods may compensate by increasing the percentage of trips which are actually food bearing trips.

To determine if this method of compensation could result in the individual nestlings of a larger brood receiving the same number of actual feeding trips as those of a smaller brood, the number of times nestlings were fed per hour was investigated in broods of different sizes using data from 1971 (Figure 13). Nestlings in smaller broods were fed significantly (Wilcoxon's signed rank test) more often than were those in larger broods. Similar results were seen in the data from 1970, but sample size was such that values could only be determined up to day 12. These data showed that nestlings of a smaller brood size received more food on an individual basis than those in larger broods.

Thus the total weight of food injested per nestling per day should vary with brood size. Knowing the mean weight of food brought to the nest with each trip throughout the nestling period, and knowing the number of such trips per unit of time for broods of different sizes, it

Figure 13. The effect of brood size on the number of food bearing visits per nestling purple martin per hour. Data from 1971. (See Figure 12 for explanation of "small" and "large" broods.)


HRS OBS
SMALL
LARGE
6.5 12.5 10.7 8.5 12.3 12.0 9.0 7.0 6.3 5.5 4.3 8.3 4.0 7.3 7.5 5.0 4.5 5.0 4.5 7.0 4.0 2.5 1.5
4.0 4.0 3.0 8.5 5.0 4.5 6.8 5.5 4.5 7.8 6.3 3.8 3.0 4.3 5.8 5.0 7.5 5.8 8.5 3.3 8.0 8.8
SMALL
LARGE
FEEDING VISITS / NESTLING / HOUR
1.0
2.0
3.0
4.0
5.0
5
10
15
20
AGE OF NESTLINGS (DAYS POST-HATCH)

is possible to calculate the total food intake of the different brood sizes (Figure 14).

The total weight of food supplied in 1970 was significantly higher than in 1971 (Wilcoxon's signed rank test). This probably is a result of weather conditions which in 1970 were generally colder than in 1971 (Table 3), so that presumably the nestlings of this year would require more food.

Apparently food intake of nestlings, per unit time, increased with age to about day 13, and then leveled out (Figure 14). Results beyond day 18 were not obtained because at this age nestlings began coming to the door to receive food and the adults were able to feed without activating the recorder.

Knowing the weight of food brought to the nestlings and the approximate caloric content of the food they were consuming, it was possible to calculate the energy provided on a daily basis (Figure 15). The calories supplied increased rapidly until day 12, and then became variable for the remainder of the nestling period considered. The highest daily value calculated being about 60,000 calories for a nestling 12 days old.

Theoretically nestlings from smaller broods which were receiving more food per unit of time than nestlings from larger broods, would show different growth curves than nestlings from larger broods. Such seemed to be the case in the data for 1970 (Figure 16) and for 1971 (Figure

Figure 14. Effect of brood size on the calculated total weight of food per day per nestling. Open symbols used for data under good weather conditions, and closed under cold or rainy conditions.

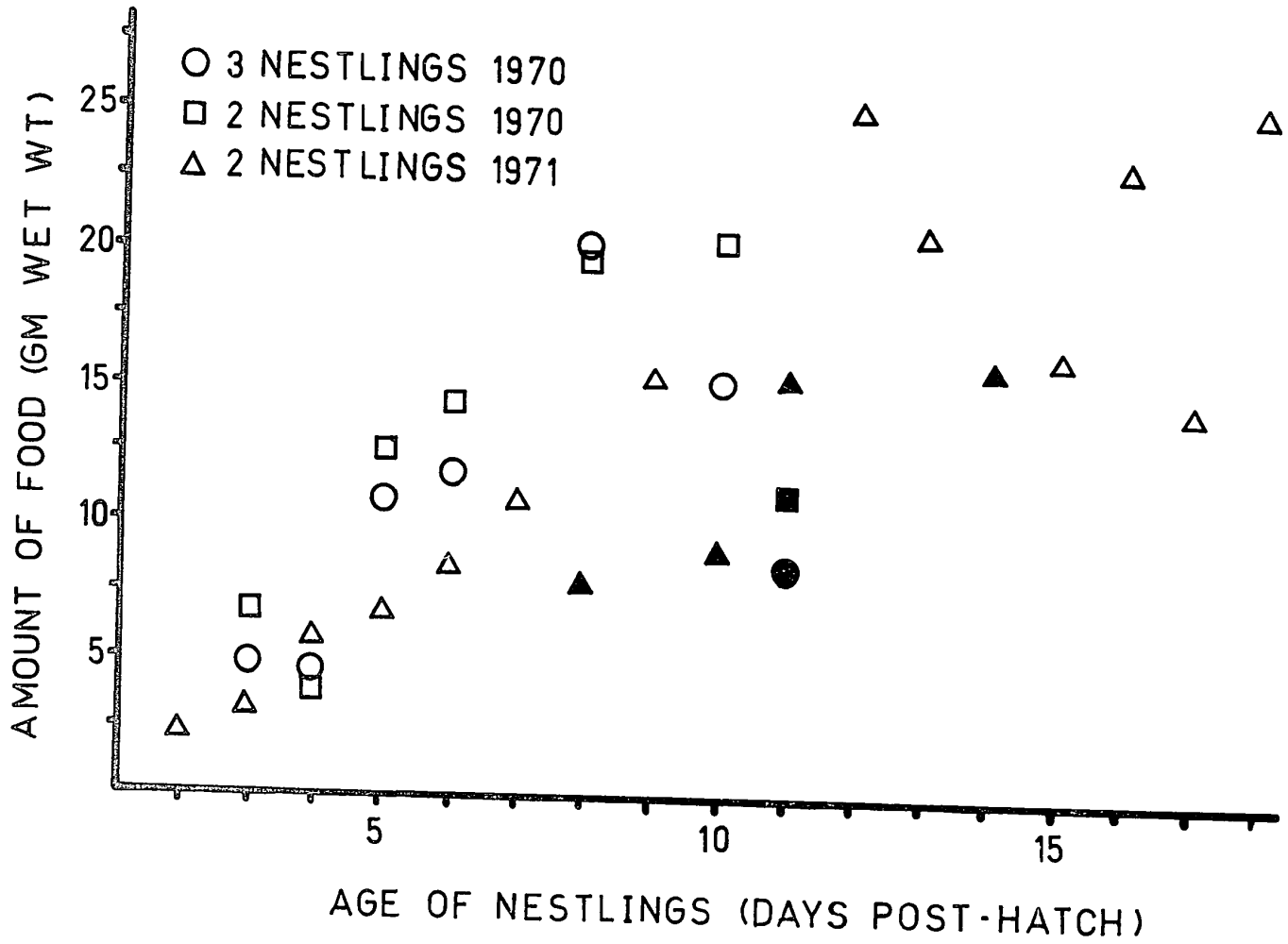

3 NESTLINGS 1970
2 NESTLINGS 1970
2 NESTLINGS 1971
AMOUNT OF FOOD (GM WET WT)
25
20
15
10
5
5
10
15
AGE OF NESTLINGS (DAYS POST-HATCH)

Figure 15. Calculated values of calories supplied with age to individual nestling purple martins from a brood size of 2. Data from 1971.

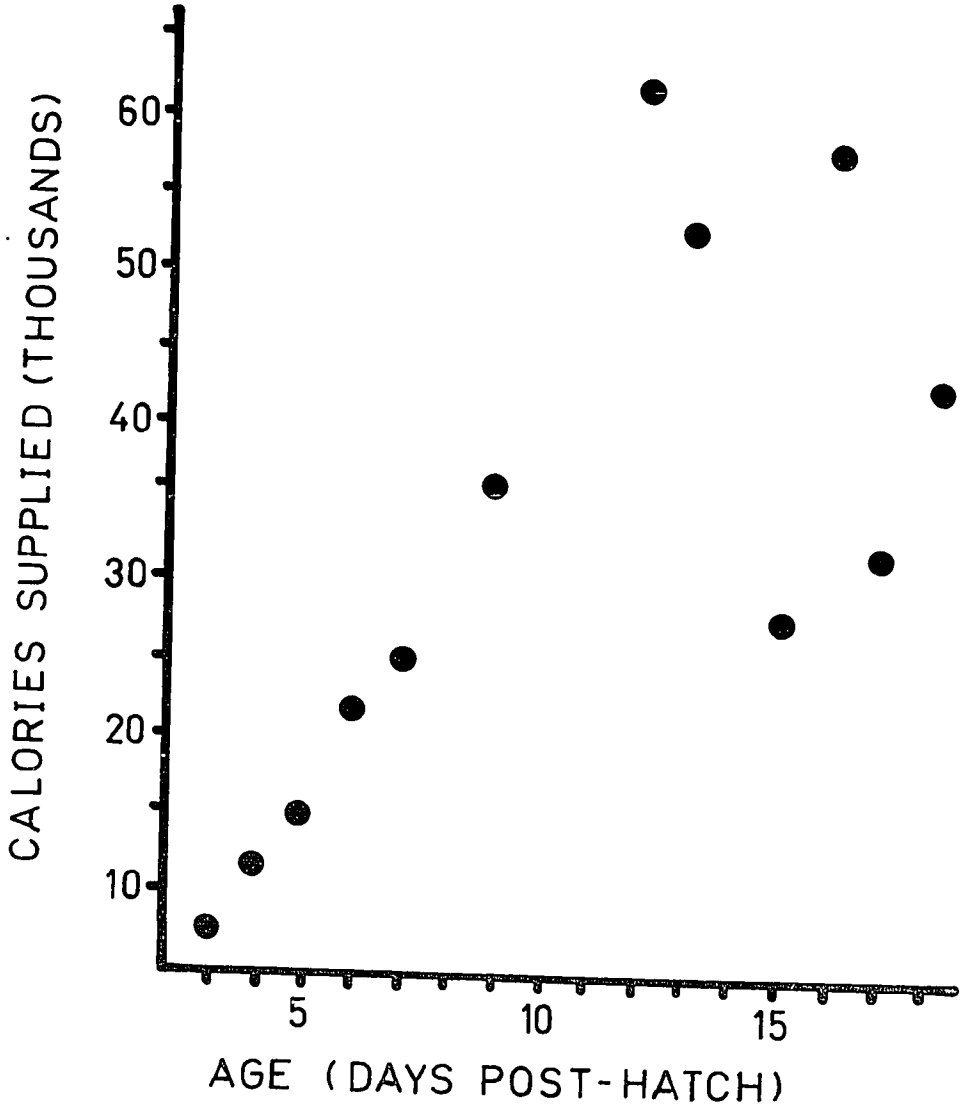

CALORIES SUPPLIED (THOUSANDS)
60
50
40
30
20
10
5
10
15
AGE (DAYS POST-HATCH)

Figure 16. The effect of brood size on the growth curves of the brood, for 4 broods in 1970. Both broods on the same graph hatched the same day. "Small" broods had 2 nestlings, and "Large" had 3.

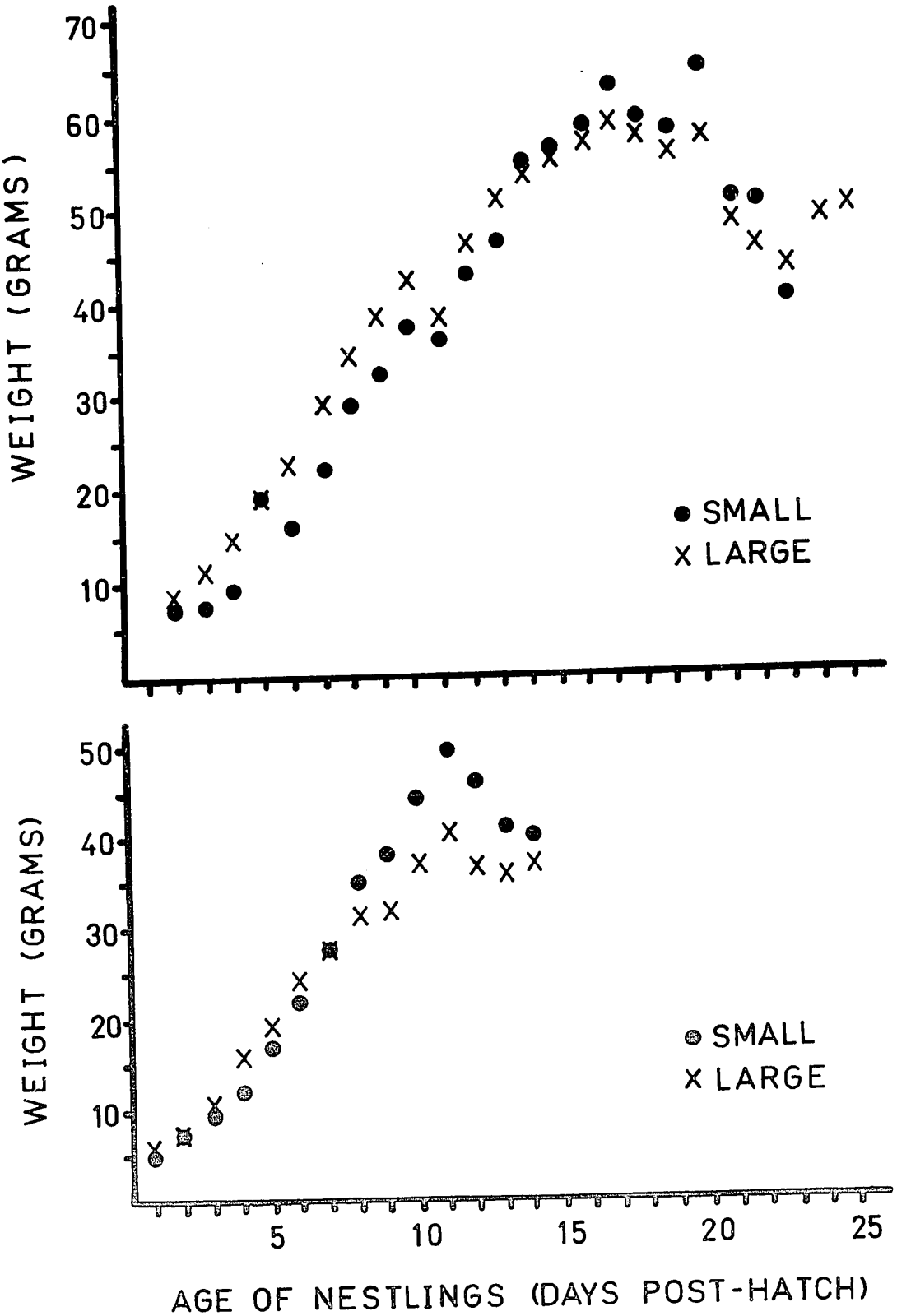
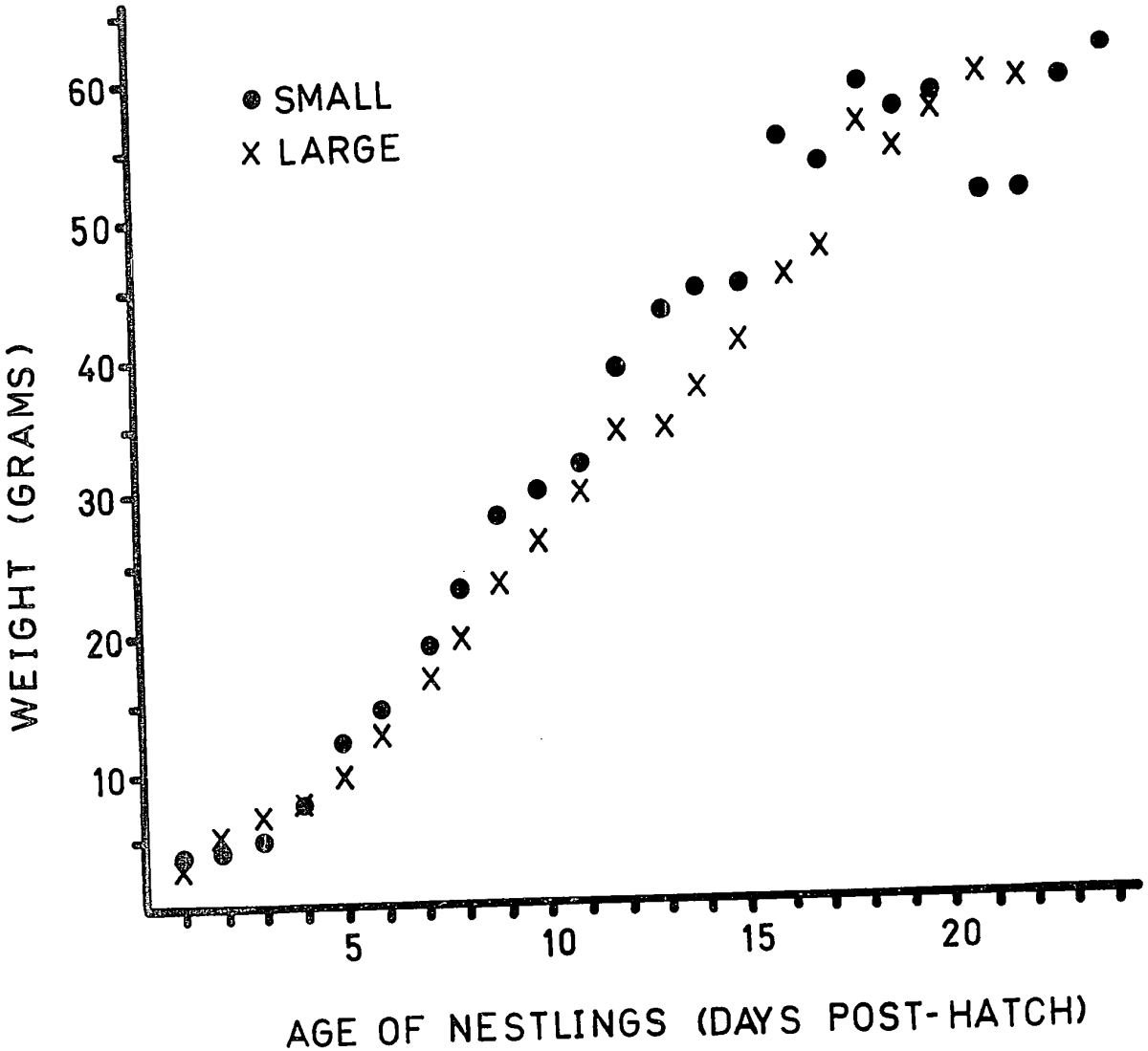

WEIGHT (GRAMS)
70
60
50
40
30
20
10
SMALL
LARGE
WEIGHT (GRAMS)
50
40
30
20
10
SMALL
LARGE
5
10
15
20
25
AGE OF NESTLINGS (DAYS POST-HATCH)

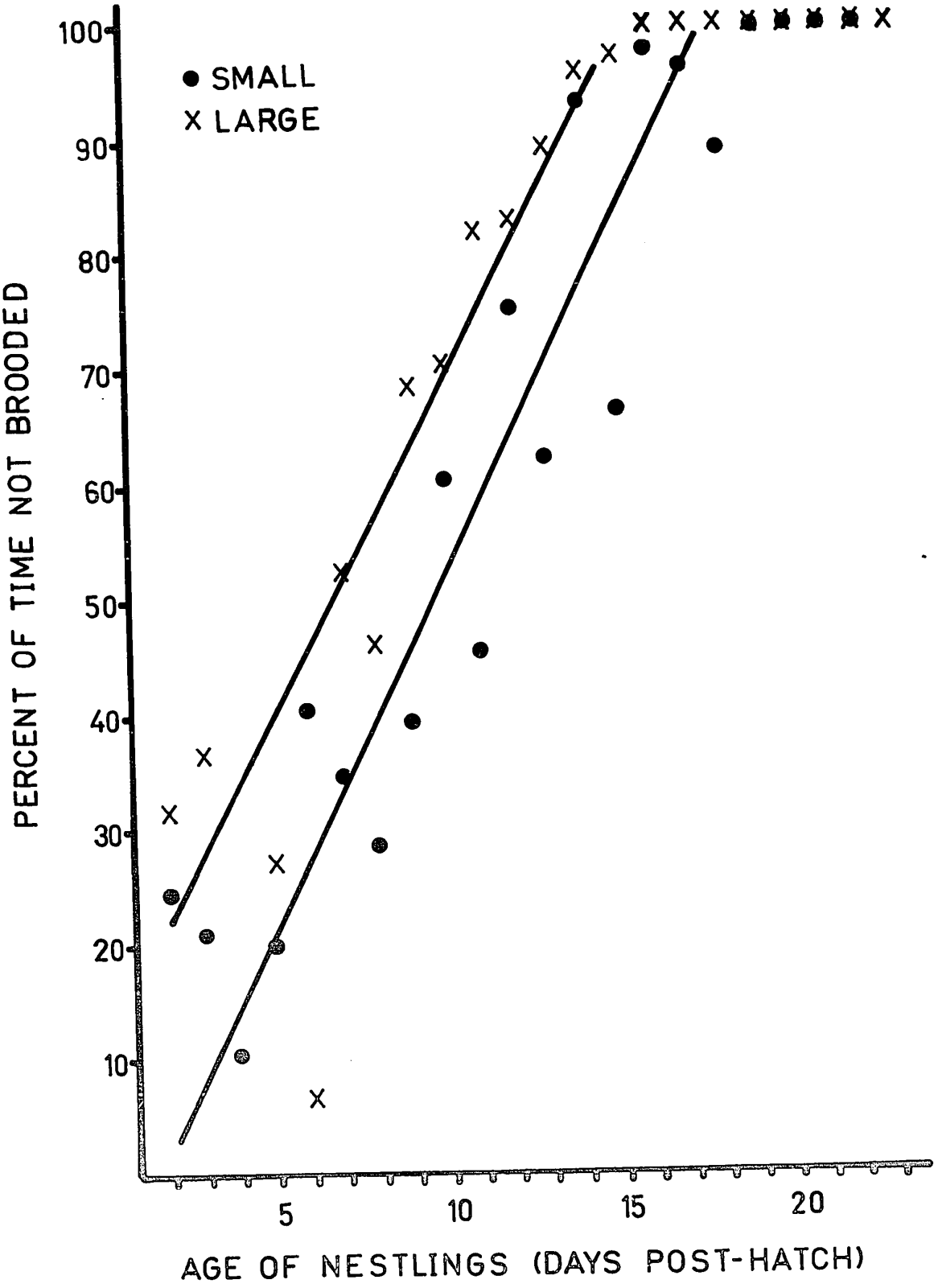
Figure 17. The effect of brood size on the growth curves of the brood, for 2 broods in 1971. The "small" brood hatched 6 days later than the "large". (See Figure 12 for explanation of "small" and "large" broods.)


SMALL
LARGE
WEIGHT (GRAMS)
60
50
40
30
20
10
5
10
15
20
AGE OF NESTLINGS (DAYS POST-HATCH)

17). In all cases the smallest broods attained the greatest average weight. The difference was not apparent early in nestling life in 1970. This can probably be explained through differential energy drain in different sized broods. Heat loss among nestlings of larger broods should be less because of the surface-area-to-volume relationship, and thus larger brood sizes would be particularly advantageous during a colder season, such as 1970. However, when homeothermy is attained by the nestling, a large brood size ceased to be an advantage, and at this time (about day 13) the curves reversed their orientation with nestlings from smaller broods being heavier than those of a larger brood.

It has been suggested that, because the surface-to-volume ratio is greater for smaller broods, they lose more heat and therefore require more food to maintain themselves than nestlings of a larger brood size (Royama, 1966). It would seem possible, however, that the brooding activity of the adults could compensate for this to some extent at least. The amount of time spent brooding by females with small and large broods was analyzed for 1971 (Figure 18). The percentage of time the nestlings were brooded decreased with age to day 16 or 17, after which no brooding was performed. The slopes of the regression lines were similar for both brood sizes, however the percentage of time spent brooding the large brood was significantly less than that spent brooding the smaller. Royama (1966) found a similar

Figure 18. The effect of brood size on the percentage of time nestling purple martins are not brooded throughout the nestling period. Data for 1971. (See Figure 12 for explanation of "small" and "large" broods.)


100
90
80
70
60
50
40
30
20
10
● SMALL
X LARGE
PERCENT OF TIME NOT BROODED
5
10
15
20
AGE OF NESTLINGS (DAYS POST-HATCH)

situation among great tits. This suggests that the parents attempted to compensate for heat loss through brooding behavior. This result has general implications for clutch size. When brood size is small, rather than large, adults can more easily provide their young with food, and at the same time, provide the intensive brooding that is required. As brood size increases, and the surface-area-to-volume relationship decrases, heat loss decreases. Thus, although adults must spend more time feeding the young, they can accomplish this by spending less time brooding. However, at a certain brood size, for any one year, the ability of the adults to feed and brood the young at appropriate levels must reach an optimum; beyond this brood size the survival of nestlings will decline. It is this optimum brood size under average annual weather conditions which probably determines the most common clutch size for the area and the species of nidicolous bird considered. This conclusion was supported by the fact that, in this study, as brood size increased the weight of the individual nestling decreased. Lack (1948a) and Lack, Gibb and Owen (1957) have shown similar results, and Perrins (1965) has shown that lowered nestling weight was correlated with lowered post-fledging survival of young.

CONCLUSION

A documentation of the food habits of nestling purple martins at Elk Island National Park for the summers of 1970 and 1971, indicated that the families Syrphidae and Aeschnidae provided the greatest biomass to the diet of both years. The time at which the birds nested appeared to be important in determining the relative importance of most insect families, particularly the Nymphalidae, which made an important contribution to the diet in 1971 when the nesting season was later than usual. Weather conditions also seemed to have a great effect on the quality and quantity of food fed to the nestlings. Cloudy, rainy weather resulted in a greater variety of smaller prey items being fed than during sunny weather.

The utilization of various insect families changed with time of day. In general syrphids and nymphalids were more important from late morning to early evening, whereas aeschnids were taken more extensively during the early morning and evening. The biomass of insects supplied to the nestlings also varied with the time of day.

Age of the nestlings affected the utilization of the various insect families. The smaller syrphids were most heavily utilized during early nestling life, whereas aeschnids and nymphalids became more important later on.

There was a difference in the brooding behavior of the male and female; males spent much less time brood-

ing. This fact was reflected in a difference in the weight of food brought to the nestlings by the two sexes over the nestling period.

The average weight of food brought per trip to the brood varied with the age of the nestlings. It increased from about 0.08 grams on day 1 to 0.45 by day 10 or 11, after which there was a gradual increase to about 0.55 grams at day 23. Males seemed to bring a larger weight of food per trip than did females. The weight of food did not appear to change with brood size, but did change with season.

Brood size influenced the number of movements in and out of the nest cavity by the parents. Larger brood sizes were reflected in larger numbers of movements which, however, were not proportional to the number of nestlings in the brood. Thus nestlings in larger broods received less feeding trips per individual, as well as less biomass of food per individual per unit of time. This fact is apparent in the growth curves for individuals. Nestlings from smaller broods consistently reached a higher peak weight than those from larger broods, even when the difference was only one nestling. Season also affected the total wet biomass fed per individual; when weather conditions were wetter and cooler more food may have been supplied to the nestlings.

The percentage of trips to the nest cavity in which food was carried to the nestlings varied with brood size.

Parents of larger broods brought in food on a greater percentage of their trips to the nest than did parents of smaller broods. In general the percentage of trips to the nest cavity that were feeding trips increased from about 45 at day 1 to 80 by about day 8 or 9, and then rose slowly to 100 by day 23.

The percentage of time the nestlings were brooded also varied with brood size, so that broods of a larger size were brooded less frequently than those of a smaller size.

In summary, the quality of food changed with the time of day, season and age, but probably not with brood size; and the quantity of food changed with time of day, season, age and brood size.

Although sample size was small and the data obtained were too few from which to draw definite conclusions to all the questions posed, interesting trends are revealed, which in most cases are supported by a similar study by Royama (1966) on nestling tits, and are probably valid.

A number of questions were raised which could not be dealt with in this study, such as the following: Does assimilative efficiency vary with the family of insect consumed? Does it change with the age of the nestlings? What are the energy requirements of the nestlings and how do they change with temperature? What is the optimum weight of fledging for a nestling purple martin? To what extent is an increased brood size advantageous in regulating heat loss? To what extent can the brooding of the adults reduce heat loss in a small brood?

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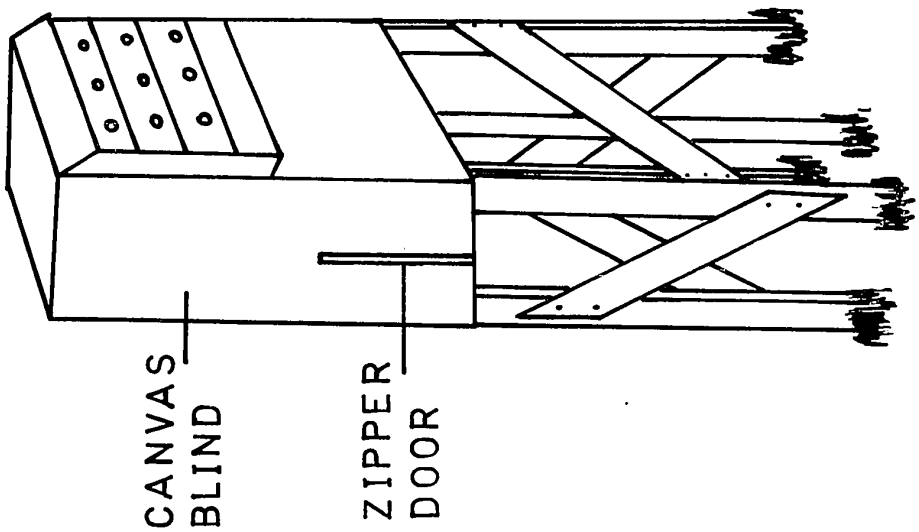
Appendix I Diagram of nest box and blind.

Appendix II Back of nest box (blind removed) showing curtains covering back of nesting compartments and "periscope".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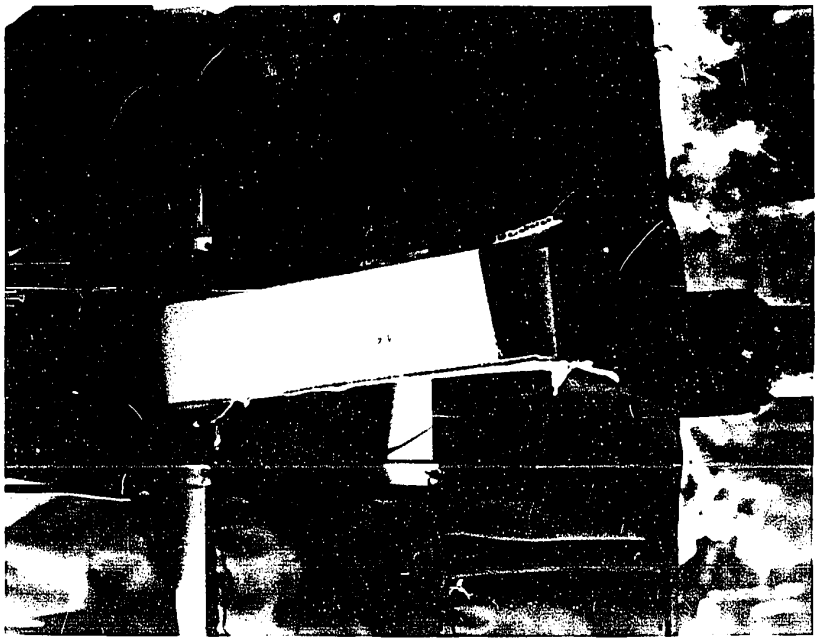

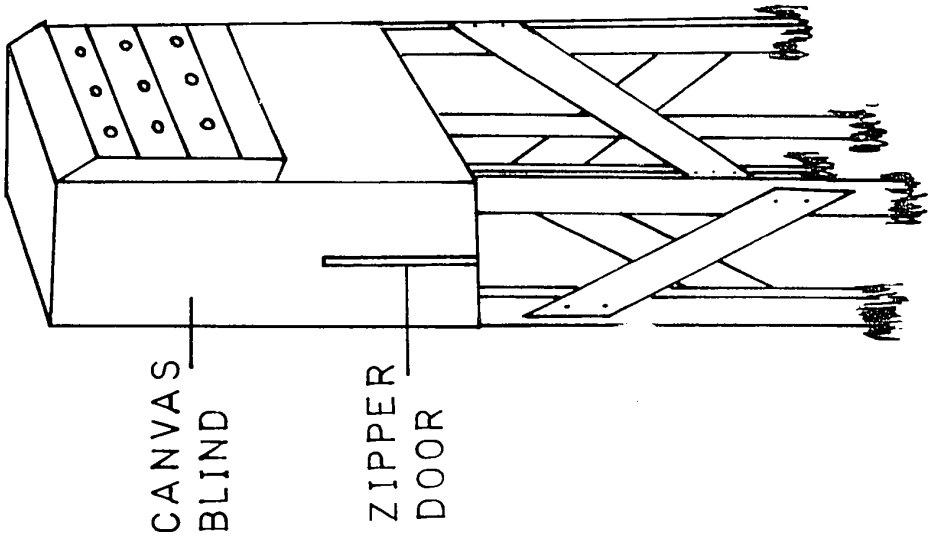
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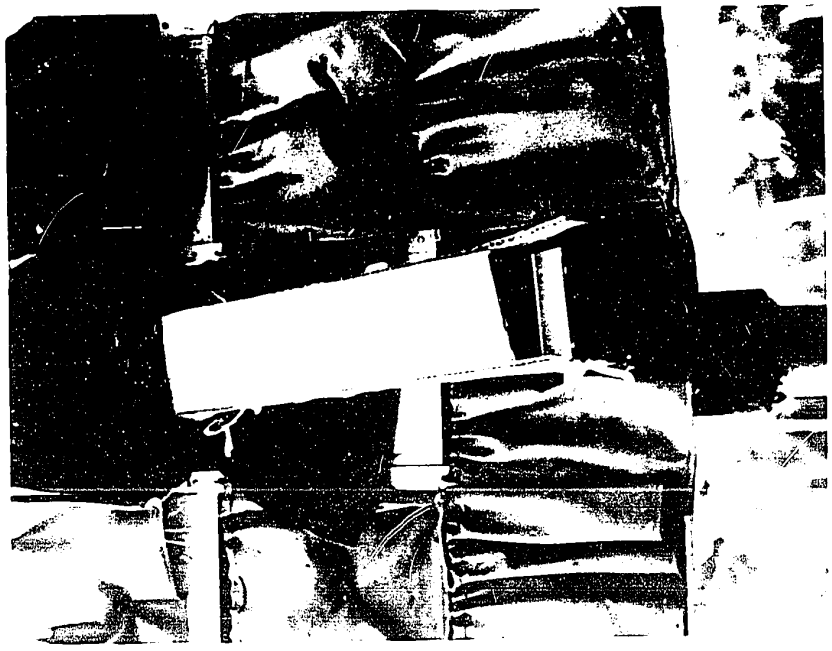

Appendix III

It was thought desirable in 1971 to determine the efficiency of assimilation of energy supplied in the food. The method used was to take half of the nestlings out of each nest box each morning before any feeding activity had occurred, and place them in a small box on top of a hand-warmer (to maintain their body temperature). They were fed every half hour for a period of 1-2 hours, and all feces passed within this time were collected. Food items tested were those which were found to be important during the summer of 1970 ie. syrphids, odonatans (libellulids later in nestling life, because of the inability to catch enough aeschnids, and coenagrionids early in nestling life when the nestlings could not handle larger prey items), and chironomids. These were alternated every four days, with the fourth day item being a family which, although not as important as the others, contributed to the food of the nestlings. For these items coleopterans, lepidopterans and formicids were used.

Ants were fed because hymenopterans contributed a significant amount of food to the nestlings in 1970. However flying ants, ichneumonids and siricids, the items used by the martins, could not be obtained in large quantities. The fact that they might be toxic to the nestlings because of the presence of formic acid was considered, but since they naturally fed on flying ants, and other birds regularly eat ants from ant hills, ie. flickers (Colaptes

sp.), it was assumed no harm would result. However, shortly after feeding the ants to the nestlings, it became apparent that they were in fact toxic, and within three hours all nestlings involved had died.

Many fecal samples had been obtained previously, so that information on assimilation appeared attainable, but upon closer analysis of the fecal samples it became apparent that nestlings must be retaining food from the previous day, as evidence of families not fed were seen up to the third fecal sample the next morning.

If this type of experiment is contemplated in the future it must be carried out in the laboratory, where nestlings can be fed entirely one type of insect for a day or more to ensure that the feces are composed only of the remains of what was fed.

Appendix IV Families of insects identified in the food of nestling purple martins, based on 956 food samples taken in 1970 and 1971.

Order	Family
Coleoptera	Carabidae
	Cerambycidae
	Chrysomelidae
	Curculionidae
	Dytiscidae
	Gyrinidae
	Pselaphidae
	Scarabaeidae
	Staphylinidae
Diptera	Asilidae
	Bombyliidae
	Cecidomyidae
	Chironomidae
	Culicidae
	Dolichopidae
	Empidae
	Ephydridae
	Muscidae
	Mycetophilidae
	Otitidae
	Pipunculidae
	Phoridae
Diptera (cont'd)	Simuliidae
	Stratiomyidae
	Syrphidae
	Tabanidae
	Tachinidae
	Therevidae
	Tipulidae
	Trupaneidae
Ephemeroptera	Siphlonuridae
Hemiptera	Anthocoridae
	Corixidae
	Gerridae
	Lygaeidae
	Miridae
	Nabidae
	Notonectidae
	Saldidae
Homoptera	Aphididae
	Cicadellidae

Order	Family
Hymenoptera	Apidae
	Bombidae
	Braconidae
	Eurytomidae
	Formicidae
	Ichneumonidae
	Siricidae
	Tenthredinidae
	Vespidae
Lepidoptera	Geometridae
	Hesperiidae
	Lasiocampidae
	Noctuidae
	Nymphalidae
	Tineidae
Neuroptera	Chrysopidae
Odonata	Aeschnidae
	Coenagrionidae
	Libellulidae
Orthoptera	Tettigidae
Plecoptera	Perlidae
Trichoptera	Leptoceridae
	Limnephilidae

Appendix V

The times of day at which food was intensively collected differed between the two years. The data were therefore analysed in two ways; on the basis of similar periods in both years, and for the total period in both years.

Appendix VI Caloric value of some of the insect families of lesser importance in the diet of nestling purple martins.

Family	No. indiv. tested	Energy value (cal/g dry wt)
Chironomidae	370	5800
Formicidae	18	6300
Libellulidae	6	5100
Siricidae	2	6700