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Growth and Parental Feeding of
Least Flycatchers in Relation to
Brood Size, Hatching Order and Prey Availability

by

James V. Briskie

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master of Science
in
Department of Zoology

Winnipeg, Manitoba

GROWTH AND PARENTAL FEEDING OF LEAST FLYCATCHERS

IN RELATION TO BROOD SIZE, HATCHING ORDER

AND PREY AVAILABILITY

BY

JAMES V. BRISKIE

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

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For my father and

In memory of my mother

"The mass of men lead lives of quiet desperation. What is called resignation is confirmed desperation. From the desperate city you go into the desperate country, and have to console yourself with the bravery of minks and muskrats. A stereotyped but unconscious despair is concealed even under what are called the games and amusements of mankind. There is no play in them, for this comes after work. But it is a characteristic of wisdom not to do desperate things.

When we consider what, to use the words of the catechism, is the chief end of man, and what are the true necessaries and means of life, it appears as if man had deliberately chosen the common mode of living because they preferred it to any other. Yet they honestly think there is no choice left. But alert and healthy natures remember that the sun rose clear. It is never too late to give up our prejudices. No way of thinking or doing, however ancient, can be trusted without proof. What every body echoes or in silence passes by as true to-day may turn out to be falsehood to-morrow, mere smoke of opinion, which some had trusted for a cloud that would sprinkle fertilizing rain on their fields. What old people say you cannot do you try and find that you can. Old deeds for old people, and new deeds for new. Old people did not know enough once, perchance, to fetch fresh fuel to keep the fire a-going; new people put a little dry wood under a pot, and are whirled round the globe with the speed of birds, in a way to kill old people, as the phrase is...."

Henry David Thoreau, 1854.

CONTENTS

ABSTRACT

The growth and feeding of nestling Least Flycatchers (_Empidonax minimus_) were examined in broods of three, four and five young. Clutches of four were most frequent; however, clutches of five produced the most surviving young. Egg volume increased with laying sequence, decreased with increasing clutch size and was larger in 1985 than in 1984. Incubation was initiated gradually, resulting in asynchronous hatching of the eggs. Nestling growth, based on changes in body mass and tarsus and flattened wings lengths, did not differ with hatching order or brood size. Ectoparasites (Acarina: Macronyssidae) and inclement weather stunted growth and led to brood reduction. Food was more abundant and available earlier in 1985. Clutch size may be limited by nest size. Hatching asynchrony may function as a mechanism to facilitate brood reduction.

Intensity of parental feeding varied with nestling age and brood size. Both sexes delivered food items at equal rates but only the female brooded. Geometrid larvae and chironomids and culicids formed the major components of the diet and were selected in proportions greater than their availability in sweep-net samples.

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INTRODUCTION

It is generally held that an organism is selected to maximize its inclusive fitness by producing the largest number of surviving young possible. Natural selection has produced strategies of egg laying and parental care that maximize an individual's lifetime reproductive success (Williams 1966, Hirshfield and Tinkle 1975, Stearns 1976). Trivers (1972) defined parental investment as "any thing done by the parent for the offspring that increases the offspring's chance of survival while decreasing the parent's ability to invest in other offspring." In birds, any behavior from nest site selection through egg laying, incubation, brooding and feeding of the young is considered parental investment and subject to selective pressures that favor the pattern that enhances fecundity.

The objective of this study is to examine how patterns of parental investment in Least Flycatchers function to maximize this species' lifetime reproductive output. In Chapter I, the limits of clutch size and the function of hatching asynchrony are investigated by comparing the growth and survival of young in relation to hatching order and brood size. Parental feeding and nestling diet are examined in Chapter II.

CHAPTER I

CLUTCH SIZE, EGG SIZE, HATCHING ASYNCHRONY

AND GROWTH IN RELATION TO PREY AVAILABILITY

INTRODUCTION

Birds lay relatively few eggs compared to other oviparous vertebrates. Females seldom lay more than a dozen eggs per clutch, and the range of clutch sizes within a species is even more restricted. Nevertheless, variation does exist and requires an explanation. Clutch size can be determined through selective pressures operating over several generations--the ultimate determinates, or clutch size may result from factors in the immediate environment--the proximate determinants. Food availability, weather, habitat quality, age of the female, population density, year and season have been demonstrated to influence clutch size proximately (see review in Klomp 1970). Clutch size is known to have a high degree of heritability (Perrins and Jones 1974, Ojanen et al. 1979, Furness 1983); however, the selective forces which have determined clutch size continue to be debated.

As formulated by Lack (1947, 1954, 1968), clutch size in birds is determined ultimately by the average maximum number of young which the parents can raise successfully in

a particular region and during a given season. The provisioning of food is probably the most important component of raising offspring. Therefore, clutch size generally reflects the maximum number of young which the parents can feed adequately. The "food-limitation" hypothesis predicts that the most common clutch size should give rise to the most surviving offspring (Lack 1947, Lack and Lack 1951).

Since Lack developed his ideas both complementary and contradictory views have emerged to account for the variety of reproductive strategies seen in nature. From brood-enlargement experiments, it is apparent that some birds can raise extra young without decreasing their offsprings' probability of survival (Vermeer 1963, Harris and Plumb 1965, Bryant 1975). Natural clutch sizes smaller than those that can be reared do not mean necessarily that birds are not maximizing their reproductive output. If an individual that is raising a large brood experiences a lower probability of survival than an individual attending a small brood, then selection will favor clutches smaller than the parent can raise. Clutch size is determined not by the maximum number of young that can be raised at a given breeding attempt but by the maximum number that can be produced over the lifetime of an individual (Williams 1966, Charnov and Krebs 1974). This pattern of breeding effort below the biological potential is considered characteristic of long-lived birds (Stearns 1976). Since passerines and other short-lived

birds have a low probability of breeding again, reproductive effort in these species should be maximized at every breeding attempt (Stearns 1976).

Several studies have shown stunted growth and presumably lower survival with larger brood sizes (e.g., Gibb 1950, Lack and Lack 1951, Lack et al. 1957, Ricklefs 1968, Hussell 1972, Murphy 1983). Experimentally enlarged broods generally produced fewer surviving young (Rice and Kenyon 1962, Perrins 1964, 1965, Ward 1965, Askenmo 1977) or more young that weighed less at fledging (Nelson 1964, Schifferli 1978, Cronmiller and Thompson 1980). This suggests that many birds lay clutches which produce the greatest number of surviving young.

Apart from parental feeding abilities, predation has been considered to influence the evolution of clutch size. As larger broods are more conspicuous and therefore subject to greater rates of predation, small clutches should be advantageous when many nests are depredated (Skutch 1949, Lack 1949). As a result of lesser predation, small clutches on average survive to produce more young than larger clutches (Lack 1949). When failed clutches can be replaced, smaller clutches permit an earlier start at lower energetic cost (Slagsvold 1984).

If food supply fluctuates unpredictably over the breeding season, then the adjustment of clutch size to the pre-

vailing resources cannot be determined precisely at laying. Under these circumstances, asynchronous hatching of the eggs and the resulting inequality in offspring size are viewed as adaptations to facilitate brood reduction by starvation (Lack 1947, 1954, 1968). If food supplies decline, the selective feeding of the oldest and largest young, at the expense of younger siblings, ensures that at least some of the brood survive to reproductive age (Lack 1947, Ingram 1959). When food is abundant all members of a brood can be fed adequately with little or no detriment to the youngest nestlings. Clutch size and asynchronous hatching, therefore, are viewed as evolved traits that enable a bird to maximize its reproductive output.

In addition to the "brood-reduction" hypothesis, four other mechanisms have been suggested as selection pressures favoring hatching asynchrony. In the "egg-insurance" hypothesis, a female lays more eggs than she can likely raise. This insures against the inviability of part of the clutch. Asynchrony creates a weight hierarchy that facilitates the rapid elimination of some young should all of the young hatch. However, this function of asynchrony has been generally applied to some seabirds, gulls, raptors and pelicans where the full clutch is rarely raised and brood reduction occurs regardless of food supply (Dorward 1962, Stinson 1979, Parsons 1975, Cash 1985, Hebert 1985).

The "peak-demand reduction" hypothesis views hatching asynchrony as a mechanism to prevent peak feeding demands of individual nestlings from coinciding (Hussell 1972). It is at this peak period that parental abilities reach their limits. By staggering the ages of the brood this bottleneck in provisioning can be reduced.

The "nest-predation" hypothesis suggests that when predation rates are high, increased hatching synchrony minimizes predation on nestlings (Clark and Wilson 1981). As nestlings are generally more conspicuous and preyed upon more than are clutches, selection should favor extending the relative proportion of the nesting period in which only eggs are in the nest. However, the greater rate of predation necessary to favor complete synchrony are seldom realized. In most situations, the optimal strategy is to initiate incubation on the penultimate egg and hatch the eggs slightly asynchronously. Brood reduction is viewed as a necessary consequence of hatching asynchrony and not an adaptation for it.

Finally, the "sibling-rivalry reduction" hypothesis emphasizes the role that initial asymmetries, due to hatching spread, play in establishing intrabrood dominance hierarchies (Hahn 1981, Nuechterlein 1981). The efficiency with which "pecking-orders" can be created and maintained in an asynchronous brood reduces intrabrood aggression and minimizes energetically wasteful competition in the allocation

of parental attention.   Under this hypothesis the advantage of hatching early is not so much a head start in growth but rather the benefits obtained by securing a higher position in the dominance hierarchy (Nuechterlein 1981).

In Chapter I,   I examine the patterns of hatching and growth in a population of Least Flycatchers that nests at relatively high densities in the dune-ridge forest, Delta Marsh, Manitoba.   This density is supported by seemingly su- perabundant food, in the form of large emergences of midges (Diptera: Chironomidae) (Busby and Sealy 1979, Biermann and Sealy 1982, Sealy 1980a, Guinan 1985).   I test two hypoth- eses in Chapter I. First, Least Flycatchers should maximize their reproductive fitness by laying clutches which produce the greatest number of surviving young.   The most frequent clutch size should yield the largest number of young and this clutch size should be larger than that of adjacent re- gions where food presumably is less abundant.   Second, nes- tlings' growth should be constant regardless of the order in which they hatch.   Detrimental effects of hatching order on last-hatched nestlings, even when food is abundant, would suggest that hatching asynchrony is maladaptive and another explanation must be sought.   No effect of hatching sequence on growth and survival would agree with the predictions of the "brood-reduction" hypothesis, but would not necessarily rule out alternative explanations.

MATERIALS AND METHODS

Study Area

The study was conducted during the breeding seasons of 1984 and 1985 in the forested dune-ridge that separates Lake Manitoba from the Delta Marsh, Manitoba, on the properties of the University of Manitoba Field Station, and the adjacent Portage Country Club (50° 11' N, 98° 19' W). The vegetation of the study area was described by MacKenzie (1982). Aerial photographs and a map of the area are shown in Goossen (1978) and Sealy (1980b). The study area extended approximately 3.0 km, from the Assiniboine River Diversion west to Cram Creek.

Weather

Weather data were obtained from the Environment Canada meteorological station located on the study area. Mean monthly temperature and precipitation during this study are summarized in Table 1. In general, 1984 was typical of summers in this region while 1985 was abnormally cool in June and wet in August.

Nesting Density and Breeding Chronology

The first two km of the dune-ridge forest, beginning at the Assiniboine River Diversion, was searched repeatedly throughout the breeding seasons to locate Least Flycatcher

Table 1. Summary of weather conditions on the study area during the breeding seasons of 1984 and 1985.

Year	Month	Mean temperature (C)		Total precipitation (mm)	General conditions
		Maximum	Minimum		
1984	May	15.6	3.9	29.2	cool and wet
	June	23.6	11.3	92.0	warm and wet
	July	26.0	12.5	33.4	warm and dry
	August	26.8	12.8	42.2	warm and damp
1985	May	18.0	5.0	31.5	warm and dry
	June	18.6	7.3	55.8	cool and damp
	July	24.5	10.8	22.6	warm and dry
	August	20.6	9.3	119.5	cool and wet

nests. From this area (approximately 16 ha) the nesting density was calculated. Nesting attempts initiated 15 days after the first clutch initiation attempt are excluded from the analysis since early renests could not be distinguished readily from late first-nesting attempts. As the number of nests located increased as I gained experience, nesting density is an approximation of the minimum density.

Nests were numbered with flagging tape and visited frequently to monitor their progress. Clutch initiation is the day the first egg was laid. For nests found during incubation the day of initiation was determined by back-dating from the day of hatching of the first young based on an incubation period of 14 days (mean 13.9, range 12-18, N=66). The incubation period is the time from clutch completion to the day the first young hatched. An allowance of one day was made for each day of laying although occasionally laying was delayed by a day. Nests that contained nestlings when found were back-dated from the day they fledged based on a nestling phase of 15 days (mean 15.2, range 13-19, N=36). The nestling phase is the period from when the first young hatched to when the last nestling fledged. Seventeen clutches from 1984 and 30 clutches from 1985 could not be dated accurately.

Clutch Size

Clutch sizes were determined in nests visited during laying or within the first five days after clutches were completed. Although clutch size might be under-estimated due to partial clutch loss during laying or early in incubation, observations of nests monitored closely during this period indicate the error is small. Of 106 nests visited daily during laying only five (4.7%) experienced partial clutch loss while 26 (24.8%) were completely removed.

Four nests parasitized by Brown-headed Cowbirds (Molothrus ater) in 1985 are excluded from the analysis since they are known to remove hosts' eggs. Least Flycatchers accept cowbird eggs (Rothstein 1975, pers. obs.) thus, clutches probably were not altered by egg ejection.

To compare clutch size between the study area and adjacent regions, mean clutch size was calculated from nests reported to the Prairie Nest Records Scheme (P. N. R. S.) deposited at the Manitoba Museum of Man and Nature. Only records which indicated two or more visits were used.

Nesting Success

Not all nests were located prior to clutch initiation (Table 2). A direct calculation using all nests over-estimates nest success since breeding attempts that failed early would be under-represented (Mayfield 1961, 1975). To avoid

Table 2. Proportions of active nests of the Least Flycatcher found at different stages of the nesting cycle, Delta Marsh, Manitoba. Data for 1984 and 1985 combined. Sample sizes are given in parentheses.

Nesting stage	Percent nests found		
	1984	1985	Total
Before laying complete	74.3(78)	57.4(85)[a]	64.4(163)
Early incubation (<5 d)	8.6(9)	10.8(16)[b]	9.9(25)
Late incubation (>5 d)	3.8(4)	6.8(10)	5.5(14)
Unknown stage of incubation	9.5(10)	18.2(27)	14.6(37)
Nestlings	3.8(4)	6.8(10)	5.5(14)
Total	100.0(105)	100.0(148)	100.0(253)

[a] Includes one nest parasitized by Brown-headed Cowbird.
[b] Includes three nests parasitized by Brown-headed Cowbirds.

this bias only nests found before clutch completion were analysed.

I disturbed many nests by visiting them frequently. Bart (1977) and Mead and Morton (1985) found human visitations increased nest failures, however, other workers have reported little or no effect (Nolan 1963, Willis 1973, Nilsson et al.1985). My visits to Least Flycatcher nests generally lasted only a few s. In most instances the adults returned to the nest before I had left the area. Nests were not visited when a predator was noticed near the nest. Weighing and measuring the nestlings created greater disturbances. However, predation rates at these intensively-visited nests (percent depredated: 22.7) differed little from nests checked infrequently (percent depredated: 27.9; x^2 =.089, d.f.=1, p>.05).

In 1985, some broods were augmented experimentally (see section on Growth). These nests were excluded from the analysis of brood size at fledging. As no nest was sacrificed in its entirety, all nests were included in the calculation of nesting success. A successful nest is one that fledged at least one young.

Post-fledging survival was estimated by recapture frequencies of banded nestlings known to have fledged. Only birds recaptured from 12 to 35 days after leaving the nest were analysed. Data from both years were combined with

banding recaptures from 1981-1983 (S. G. Sealy, unpubl. data).

Egg Size

Maximum egg length (L) and greatest breadth (B) were measured to the nearest 0.05 mm with sliding calipers. Egg volume was calculated using the formula given by Hoyt (1979): Volume= $0.51LB^2$. All eggs in a clutch were assumed to have the same shape. Daily visits permitted the laying order to be determined. Each egg was numbered and then measured when the clutches of three, four, and five were complete.

Initiation of Incubation

Nests were watched during laying to determine when incubation began. Observation bouts of one-half hour were made on nests that contained one, two, three, and four eggs. Only watches on nests with four-egg clutches were analysed. Additional watches were made the day after clutches were completed.

Observations were divided proportionately between the late morning (1000-1200 h), late afternoon (1430-1630 h) and evening (1900-2100 h). In all, 30 nests were observed for a total of 37.5 h. A given nest was watched during 1 to 8 observation bouts, and 21 of the 30 nests were observed for 1

h or less.   Observations were made from approximately 20-25
m through binoculars, and the total time of parental atten-
dance was recorded to the nearest s.   A bird positioned deep
in the nest was assumed to be contacting the eggs.   Nest
watches were avoided during inclement weather so as not to
record females sheltering but not contacting the eggs (Hus-
sell 1972).

Eggs were held to the cheek to determine whether incu-
bation had begun.   In most cases eggs were easily classified
as warm or cold.   The few considered luke-warm were recorded
as cold.

In 1985, Least Flycatcher nests were checked at night
during laying by R. Barclay and his assistants.   With his
permission the preliminary results are presented here.

Hatching Asynchrony

The hatching spread, or interval from the hatch of the
first to the last young, was determined by visiting nests
4-10 hours prior to and during hatching.   Nestlings still
wet were considered to have hatched within the last hour. A
nestling found hatched between visits but with dry down was
recorded as having hatched half-way between the two visits.
Occasionally two nestlings had hatched since a previous vis-
it.   Here, one nestling was typically wet while the other
was dry.   Under these circumstances the nestlings were aged

according to the criteria above. Only nests in which the hatching of the first and last young could be determined accurately were used.

Growth

Upon hatching, nestlings' tarsi and wings were marked with non-toxic felt marks for individual recognition. Marks were renewed when needed.   The day the first nestling hatched is day zero.   Young in broods of three, four, and five were measured every 48 h ($\pm$ 1 h) to 10 days post-hatching.   Measurements refer to the time from when the first nestling hatched. As a result of asynchronous hatching some broods still contained an egg at 48 hrs.   Only broods in which the entire hatching order was known are analysed.

In 1985 nestlings were transferred among 12 nests to increase the sample of broods of five.   Nestlings were transferred immediately after hatching and placed in other nests so that the normal sequence of hatching asynchrony was maintained as closely as possible. Because of the asynchrony between nests, the transfer of nestlings was opportunistic and the effects of differences in egg size could not always be preserved.   Usually only one nestling was transferred.   All nestlings were accepted by their foster parents.

Nestling mass (to nearest 0.1 g) was recorded using a triple-beam balance from 24-30 June 1984, and an Ohaus digital scale for the remainder of 1984 and all of 1985. Nestlings were handled prior to weighing to induce defecation. Tarsus and flattened wing lengths were measured to the nearest 0.1 mm with sliding calipers and (or) a ruler to 1 mm. After approximately eight days the flattened wing included the unsheathing primaries (see Appendix I). All nestlings were banded at 8-10 days with numbered U.S. Fish and Wildlife Service aluminum bands and one colored plastic leg band identifying the bird as a hatching-year individual.

Analysis of Growth

Growth curves were fitted to the mean mass and mean tarsus length of nestlings by non-linear regression. The Richards model was selected for its flexibility in providing a close fit (Richards 1959). In its integrated form the Richards equation is written as;

$$W = A \ (\ 1 \ + \ b \ e^{-kt})^{\frac{1}{1-m}} \qquad (1)$$

where;

W = size at time t

A = asymptotic size

b = time-scale constant

k = growth-rate constant

m = curve-shape constant

Different shapes of growth curves are due to differences in $\underline{m}$. This constant determines the proportion of the final size at which an inflection point occurs.   When $\underline{m}=2$ equation (1) reduces to the familiar Pearl-Verhulst logistic model with the inflection point occurring when $\underline{W}$ is 50% of the asymptote.   Values of 1 and 2/3 give the Gompertz and von Bertalanffy curves, with inflection points at 37 and 30% of the asymptote, respectively.   When $\underline{m}=0$, the non-sigmoidal, monomolecular equation results.   Thus, $\underline{m}>0$ defines a family of sigmoidal curves with the inflection points at ever increasing proportions of the asymptote.

The growth-rate constant, $\underline{k}$, determines the spread of the curve along the time axis.   It expresses the rate at which the value of some function of $\underline{W}$ changes.   The constant is specific for each curve type depending on $\underline{m}$ (Richards 1959).   For comparative purposes, $\underline{k}$ is the most meaningful biologically (but not the only meaningful parameter) as it represents the rate at which the mass or some other measure of growth changes over time.

The time-scale constant $\underline{b}$ reflects the choice of the zero of time.   It can be eliminated from the equation by adjusting the time scale.   When time is measured from the point of inflection $\underline{b}$ becomes unity (Richards 1959).   In this study $\underline{b}$ becomes biologically relevant as it marks the spread of hatching times from the first hatch.

Mean mass and tarsus length were fitted by nonlinear regression according to the procedure outlined by Marquardt (1963). Starting values of $\underline{b}$ and $\underline{k}$ were selected and the curve fitted when iterations converged or when convergence was assumed. The $\underline{m}$ value was held constant for each fitting procedure. Various $\underline{m}$ values were then substituted until the residual variance was minimized. The $\underline{k}$ and $\underline{b}$ values used to compare treatment groups were those obtained with the $\underline{m}$ value that minimized variance. The fitting procedure provided estimates of standard error (S.E.) for the regression coefficients for each data set. Growth in relation to hatching order and brood size was compared by fitting the same $\underline{m}$ value in each treatment as it is difficult to interpret differences in $\underline{k}$ derived from curves of differing forms (Richards 1959). Although this may increase the residual variances in some instances (that is, result in a poorer fit), the magnitude of the difference was negligible compared to the errors that resulted from forcing a fit to the nearest standard growth curve (e.g. logistic). To avoid errors associated with over-testing, the growth-rate constants were compared between treatments by Tukey's least significant difference T-test for multiple comparisons. The harmonic mean was used when sample sizes were not equal (Winkler and Hays 1975).

In all analyses mean data were used to avoid the problems associated with residual autocorrelation in fitting curvilinear functions to growth data of individuals (see

White and Ratti 1977, White and Brisbin 1980, Zach et al. 1984 for examples of these difficulties). As observations are not independent from one period to the next, autocorrelation can result when growth data are collected by following the same individuals. For example, a nestling underweight at time t will have a greater than random probability of being underweight at time $t+1$. By using the mean value this problem is circumvented since on average some nestlings will be greater and some less than the true mean.

Proper growth curve fitting requires an appropriate asymptote to be used. The asymptotic mass of Least Flycatchers was obtained by mist-netting free-flying young that had fledged from nests studied earlier. Only masses obtained from birds greater than 12 days post-fledging were used in the analysis, since prior to this time young still depend upon the adults. After approximately 12 days the young become independent and move widely across the study area (S. G. Sealy, unpubl. data). For both years combined, 41 fledglings of known age, hatching order, and brood size were recaptured. Sample sizes are small in some categories; however, no significant differences in mass were found with either hatching order or brood size (two-way ANOVA: $F=0.73$, d.f.$=4,29$, $p=0.58$ and $F=0.16$, d.f.$=2,29$, $p=0.85$, for hatching order and brood size, respectively). Therefore, all data were combined to calculate the asymptotic mass.

The tarsus length of recaptured fledglings was not recorded consistently. Therefore, tarsus length was measured on 25 Least Flycatcher adults (20 male, 5 female, both sexes analysed together) in the University of Manitoba Museum of Zoology collection (UMMZ nos. 2188-2193, 2195-2214) to determine the asymptotic mean.

The distribution of flattened wing lengths in fledgling recaptures (Figure 1) suggests a bimodal distribution indicative of sexual dimorphism by this early age. Nestlings were not sexed, so it was not known which asymptotic value would have been the most appropriate in a sigmoidal function. Thus, growth of the wing was fitted by linear regression. Mean values were log transformed to linearize the data.

Arthropod Sampling

Arthropod abundance where Least Flycatchers foraged was estimated using a sweep-net technique similar to that described by Busby (1978). A standard 37-cm, wire-frame net was swept 40 times in 180° arcs through the vegetation at heights ranging from approximately 0.5 to 5.0 m. No area was sampled twice.

Arthropod abundance was monitored in one area throughout the breeding season. Every five days, weather permitting, three sweep samples were taken within the same one-ha

Figure 1. Frequency distribution of flattened wing
lengths of Least Flycatcher fledglings
recaptured at least 12 days after they
left their nests.

Number of individuals (y-axis)

Flattened wing length (mm) (x-axis)
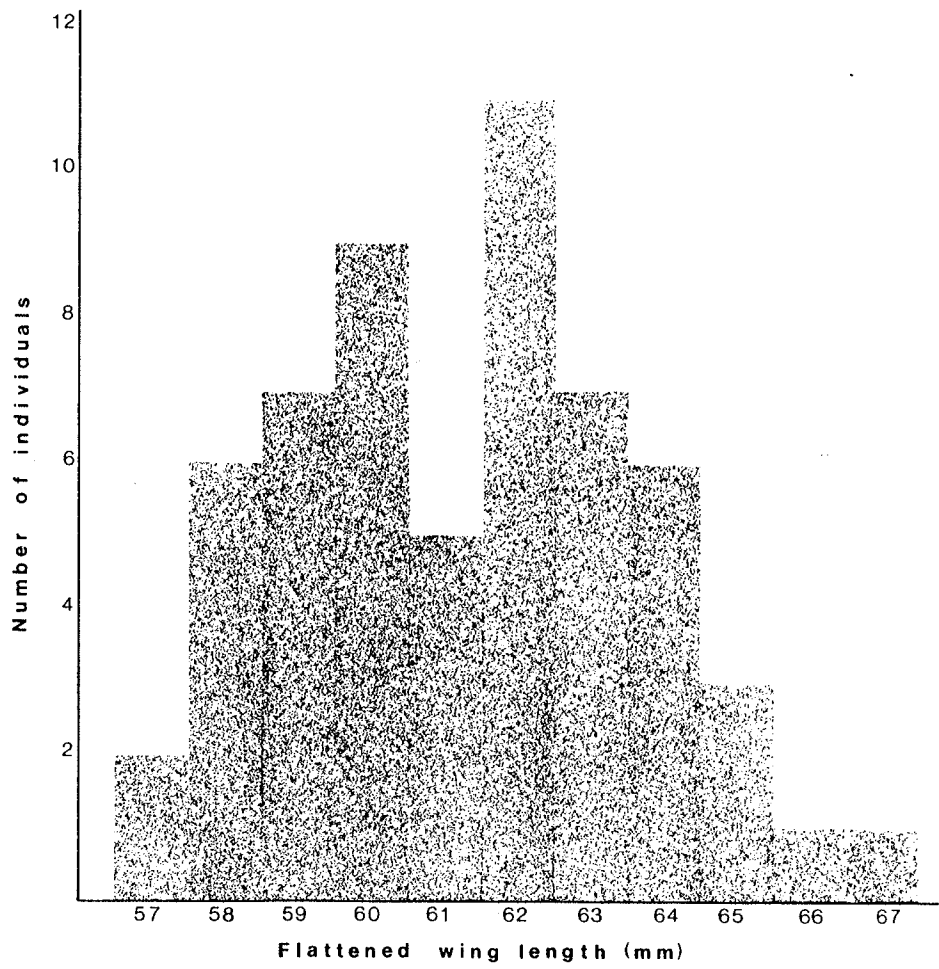
portion of the ridge (approximately in the center of the study area). Sampling occurred in the morning (0700-0800 h), afternoon (1300-1400 h), and evening (1800-1900 h). Samples were frozen, then preserved in alcohol, and the taxa were sorted and counted. The results, when averaged, gave an estimate of the relative abundance for that sampling day. Because of the large numbers of chironomids in some periods, arthropod abundance was estimated by subsampling each sweep.

RESULTS

Nesting Density and Breeding Chronology

Breeding densities at Delta Marsh are some of the highest reported for a number of insectivorous passerines, including the Least Flycatcher (Table 3, MacKenzie et al. 1982). Only MacQueen (1950) reported a higher nesting density of Least Flycatchers than that of the present study. His estimate, however, was based on a more restricted area.

Least Flycatchers nest throughout the dune-ridge forest, although nests were concentrated along the southern half of the ridge (Figures 2 and 3). Nests on the north side of the study area were typically located in the more exposed subcanopy of mature green ash (Fraxinus pennsylvanica), Manitoba maple (Acer negundo) and peach-leaved willow (Salix amygdaloides) stands. Nests on the south half become increasingly sheltered by dense stands of sapling maples and sandbar willows (S. interior, see Appendix II for a summary of Least Flycatcher nest-site characteristics).

Table 3. Geographical variation in Least Flycatcher nesting densities.

Location	Density (pairs/ha)	Source
Manitoba	4.4	This study, 1984
Manitoba	4.9	This study, 1985
Manitoba	5.7	MacKenzie et al. (1982)
Minnesota	1.4[a]	Breckenridge (1956)
Michigan	1.9[a]	Walkinshaw (1966)
Michigan	1.2-6.5[a]	MacQueen (1950)
Wisconsin	4.3[a]	Rogers (1977)

[a] Converted to density per ha.

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Figure 2.   Distribution of Least Flycatcher nests in
            the dune-ridge forest, Delta Marsh, Mani-
            toba, 1984.   Location of nests indicated
            by open circles.   Semicircles indicate two
            nests in same location.   Each square re-
            presents one 100-m^2 "cell"   (map from Mac-
            Kenzie 1979).

DELTA   MARSH
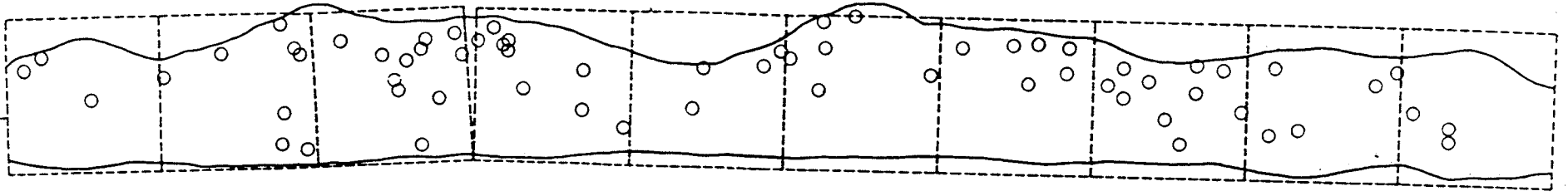
LAKE   MANITOBA
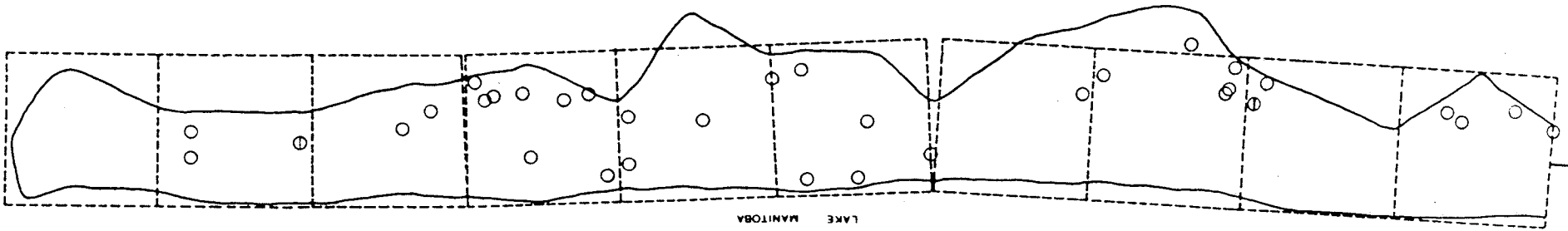
DELTA   MARSH

LAKE   MANITOBA

N

Figure 3. Distribution of Least Flycatcher nests in
the dune-ridge forest, 1985. See Figure 2
for explanation of symbols.

DELTA MARSH
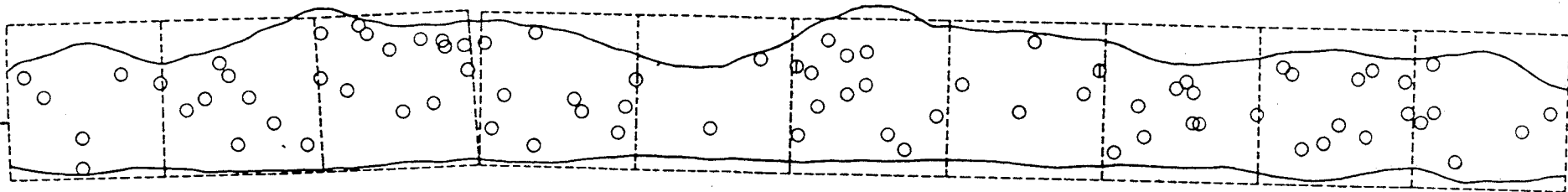
LAKE MANITOBA

DELTA MARSH
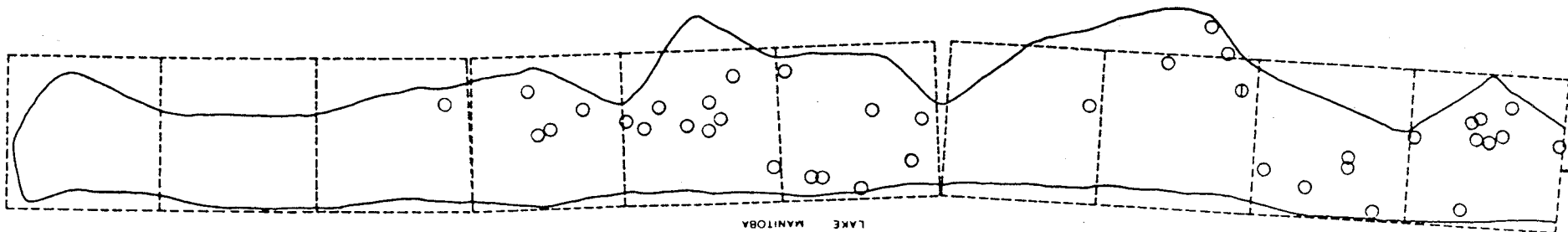
LAKE MANITOBA

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The breeding chronology of the Least Flycatcher in the dune-ridge forest is presented in Table 4. Clutch initiations began earlier and continued longer in 1985. The last nesting attempt in 1985 began on 23 July, two weeks later than the last nesting attempt in 1984. In both years the first-nesting attempts were concentrated within the first two weeks of the clutch initiation period (Figure 4). Nests started after this period were likely renests of nesting attempts that had failed earlier.

Double-brooding was recorded at two nests with marked females in 1985. Seven and eight days elapsed between the fledging of the last young in the first brood and the laying of the first egg in the second clutch, respectively. At one nest both adults remained paired for the second brood. Two young fledged from one second nest, but the other was depredated shortly before the young hatched.

Clutch size

Clutches ranged from two to five eggs; clutches of four eggs were the most common. Clutch size decreased significantly later in the season (two-way ANOVA: $F=8.54$, d.f.$=5,142$, $p<.001$, Table 5) but did not vary between the years ($F=0.79$, d.f.$=1,142$, $p=.38$). Smaller clutches of renests probably accounted for most of the seasonal decline although a few first nests contained only three eggs. Clutches of five were restricted to early nesting attempts.

Table 4. Breeding chronology of the Least Flycatcher in the dune-ridge forest, Delta Marsh, Manitoba. Data for 1984 and 1985 combined.

	1984	1985
Total clutches initiated	105	148
Date first nest constructed	29 May	26 May[1]
Date first clutch initiated	3 June	29 May
Date last clutch initiated	9 July	23 July
Clutch initiation period (d)	37	56
Date first nest fledged	2 July	1 July
Date last nest fledged	7 August	16 August

[1] Least Flycatcher seen carrying nesting material 23 May (K. A. Hobson, pers. comm.)

Figure 4.   Frequency distribution of clutch initiation
            (solid bars) and realized fledging dates
            (open bars) of the Least Flycatcher in the
            dune-ridge forest, Delta Marsh. Arrows
            indicate dates of clutch initiation for
            known double broods in 1985.

Number of nests

1984
N=88

1985
N=118

5   15   25   5   15   25   4   14
June   July   August

Date of clutch initiation
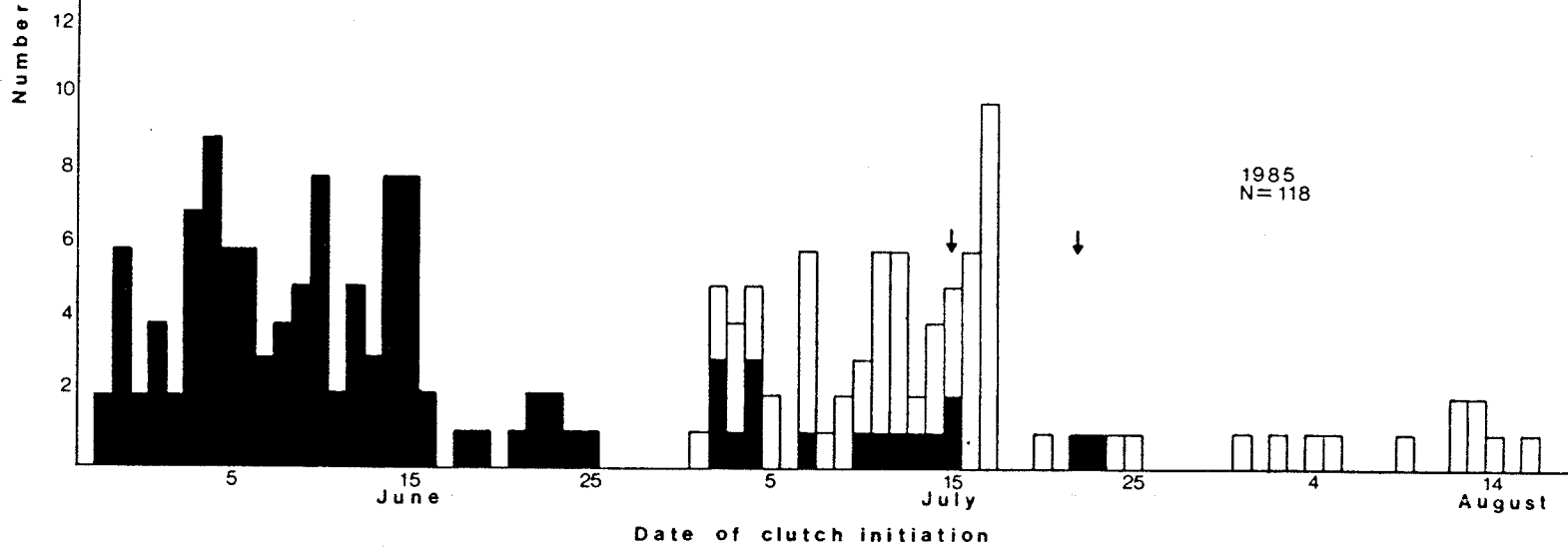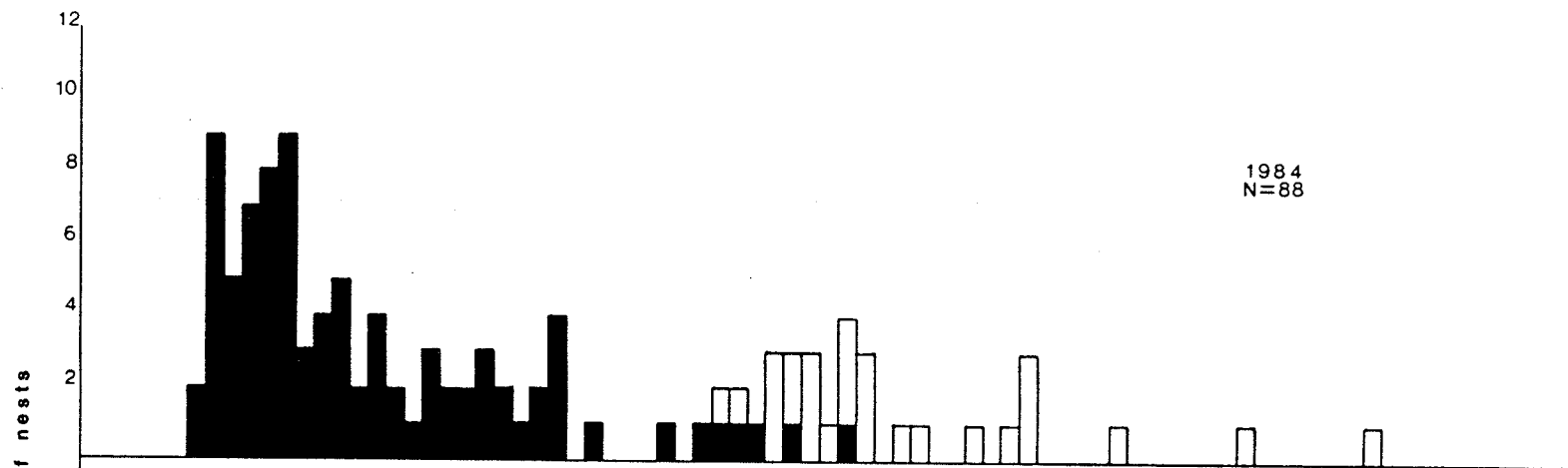
Table 5. Least Flycatcher clutch sizes, dune-ridge forest, Delta Marsh, Manitoba. Data for 1984 and 1985 combined.

Date of clutch initiation	Clutch size				Mean clutch size ($\pm$ S.E.)
	2	3	4	5	
29 May-2 June	0	0	10	2	4.17$\pm$0.11
3 June-12 June	0	3	72	8	4.06$\pm$0.04
13 June-22 June	0	9	21	2	3.78$\pm$0.10
23 June-2 July	0	3	10	0	3.77$\pm$0.12
3 July-12 July	1	3	3	0	3.29$\pm$0.29
>13 July	0	3	2	0	3.40$\pm$0.24
Total	1	21	118	12	3.93$\pm$0.05

A single clutch of two eggs was laid by a female in 1984 which had earlier incubated a clutch of four addled eggs beyond the normal incubation period (see Table 6). The two double-brooded females laid four-egg clutches followed by three- and four-egg clutches, respectively.

The mean clutch size calculated from nests reported to the P. N. R. S. (3.89+0.08, N=35) is not significantly lower from that found on the study area (one-tailed t-test: t=0.44, d.f.=185, p>..05).

Nesting Success

Nesting success was greater in 1985, largely because of less predation (Table 6). Most predation occurred during the egg stage, rather than during the nestling phase, but the differences were not significant (Table 7).

Earlier clutches were more successful than later ones, although nesting success late in the season is difficult to evaluate because of the small number of nests (Table 8). Hatching success was greatest in clutches of four in both the percentage of nests with all nestlings hatching and in the percentage of nestlings hatching in all active nests (Table 9). The mean number of young hatched per active nest was highest in clutches of five and increased significantly with clutch size (one-way ANOVA: F=62.9, d.f.=3,93, p<.001, Table 9). Fledging success was lowest in broods of five

Table 6. Nesting success of active Least Flycatcher nests found before the last egg was laid, Delta Marsh, Manitoba. Data for 1984 and 1985 combined.

	1984	1985	Totals
No. of active nests	78	84	162
No. of successful nests	17	42	59
Percent active nests successful	21.8	50.0	36.4
No. nests depredated	51	33	84
Percent active nests depredated	65.4	39.3	51.9
No. nests blown out by wind	7	3	10
No. nests where nest-tree fell over	0	2	2
No. nests where all nestlings died	0	1	1
No. nests where adult killed on nest	1[a]	0	1
No. nests where eggs abandoned for no apparent reason	1	1	2
No. nests where eggs abandoned after a period of prolonged incubation	1[b]	2	3
Percent active nests failed, excluding predation	12.8	10.7	11.7

[a] Presumptive female, with a severe abdominal laceration, found dead on an intact clutch of four eggs.

[b] Clutch of four eggs was buried in this nest after an incubation period of 28 d.

Table 7. Frequency of depredation of Least Flycatcher nests in relation to the stage of the nesting cycle. Data for 1984 and 1985 combined.

Nesting stage	No. nests depredated		Duration of nesting stage (d)	Daily mortality rate [a]
	Total	Percent		
Laying	15	9.3	4	2.33[b]
Incubation	42	25.9	14	1.85
Nestling	27	16.7	15	1.11
Total	84	51.9	33	1.57

[a] Daily mortality rate = percent nests depredated ÷ duration of nesting stage. Thus, a daily mortality rate of 1.57 means that of the original 162 active nests, 1.57% were lost each day as a result of predation.

[b] $x^2=4.14$, d.f.=2, p>.05.

Table 8. Success of Least Flycatcher clutches in relation to date they were initiated. Sample sizes given in parentheses.

Year	Success of nests initiated (%)				
	Before 9 June	10-19 June	20-29 June	30 June-9 July	After 10 July
1984	28.9(11/38)	15.4(4/26)	10.0(1/10)	25.0(1/4)	---
1985	39.6(19/48)	68.2(15/22)	57.1(4/7)	75.0(3/4)	33.3(1/3)
Both years	34.9(30/86)	39.6(19/48)	29.4(5/17)	50.0(4/8)	33.3(1/3)
1981[a]	61.3(19/31)	60.0(12/20)	20.0(1/5)	20.0(1/5)	25.0(1/4)

[a] Data from Sealy and Biermann (1983).

Table 9. Hatching success in the Least Flycatcher. Sample sizes given in parentheses. Data for 1984 and 1985 combined.

	Clutch size[1]			
	2	3	4	5
No. nests active through hatching	7	26	56	8
Percent nests with all nestlings hatching	71.4(5)	76.9(20)	80.4(45)	50.0(4)
Percent nestlings hatched in all active nests	85.7(12/14)	91.0(71/78)	95.1(213/224)	85.0(34/40)
Mean no. nestlings hatched per active nest ($\pm$S.E.)	1.71 ± 0.18	2.73 ± 0.10	3.80 ± 0.05	4.25 ± 0.31

[1] Includes clutches experiencing partial clutch loss prior to hatching.

(Table 10). The mean brood size at fledging in unmanipulated nests was highest in broods of five and increased with brood size (Table 10), but this increase was not significant (one-way ANOVA: $F=1.27$, d.f.$=2,64$, $p>.29$). If enlarged broods are included, then broods of five produced significantly more fledglings than four-egg clutches (one-tailed t-test: $t=2.49$, d.f.$=61$, $p<.05$).

Post-fledging survival, represented by frequency of recapture, did not vary significantly with brood size at fledging (Table 11) or hatching order (Table 12).

Egg Size

Eggs in clutches of three, four, and five (Table 13) varied significantly in breadth (two-way ANOVA: $F=36.3$, d.f.$=2,204$, $p<.0001$), length ($F=24.1$, $p<.0001$), and volume ($F=44.3$, $p<.0001$). Egg size decreased significantly with increasing clutch size in all pair-wise comparisons (Tukey's least significant difference T-test for multiple comparisons: $p<.05$ for all comparisons).

Egg size increased significantly with laying sequence in four-egg clutches (two-way ANOVA for breadth: $F=25.7$, d.f.$=3,114$, $p<.0001$; length: $F=7.1$, $p<.0003$; volume: $F=24.0$, $p<.0001$, Table 14). Egg volume differed significantly in each pair-wise comparison (T-test: $p<.05$ for all comparisons). Despite this, laying sequence accounted for

Table 10. Fledging success in unmanipulated[1] Least Flycatcher nests in relation to initial clutch size at laying. Data for 1984 and 1985 combined.

	Clutch size at laying		
	3	4	5
No. active nests	21	108	12
No. active nests fledging	10	53	4
Percent active nests fledging	52.6	49.1	33.3
Mean brood size at fledging ($\pm$S.E.)	2.80$\pm$0.13	3.21$\pm$0.13	3.50$\pm$ 0.29[a]

[1] Twelve broods from 1985 that were experimentally increased or decreased are excluded from this analysis.

[a] Mean+S.E. brood size at fledging including enlarged broods of five: 4.00$\pm$0.26 (N=10).

Table 11. Post-fledging survival in Least Flycatchers in relation to brood size. Only birds recaptured 12-35 days after fledging are included in the analysis. Data from 1981-1985, and all hatching orders combined.

	Brood size at fledging		
	1-3	4	5
Number of nestlings banded	167	195	27
Number of recaptures	32	49	8
Percent recaptured[1]	19.2	25.1	29.6

[1] $x^2 = 1.98$, d.f.$=2$, $p > .05$.

Table 12. Post-fledging survival in Least Flycatchers in relation to hatching order. Only birds recaptured 12-35 days after fledging are included in the analysis. Data from 1984-1985, all brood sizes combined.

	Hatching order				
	1	2	3	4	5
Number of nestlings banded[1]	52	46	33	23	5
Number of recaptures	10	16	7	6	2
Percent recaptured[2]	19.2	34.8	21.2	26.1	40.0

[1] The number of nestlings of known brood size was greater than that of known hatching order.

[2] x^2=2.66, d.f.=3, p>.05, where hatching orders 4 and 5 are combined in the analysis to reduce the number of cells with expected frequencies less than 5.

Table 13. Mean egg size in different sized clutches of Least Flycatcher. Data from both years are combined. Figures are means$\pm$S.E. Sample sizes given in parentheses.[1]

	Clutch size		
	3(30)	4(192)	5(50)
Length (mm)	16.85$\pm$0.09	16.73$\pm$0.04	16.36$\pm$0.08
Breadth (mm)	13.17$\pm$0.06	13.07$\pm$0.03	12.76$\pm$0.08
Volume (cm^3)	1.50$\pm$0.02	1.46$\pm$0.13	1.36$\pm$0.02

[1] Derived from 10, 48, and 10 clutches of 3, 4, and 5 eggs, respectively.

Table 14. Mean egg size with laying sequence in 4-egg clutches of Least Flycatcher. Data from both years are combined. Figures are means±S.E. Sample size equals 39 for all laying sequences.

	Sequence in laying			
	1	2	3	4
Length (mm)	16.59±0.09	16.70±0.09	16.89±0.10	16.88±0.09
Breadth (mm)	12.97±0.07	13.03±0.07	13.16±0.07	13.29±0.08
Volume (cm^3)	1.42±0.02	1.45±0.02	1.50±0.02	1.52±0.02

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only 9.3% of the variation in egg volume. Over 76.1% of the variation was attributable to inter-nest differences. Mean volume per clutch ranged from 1.27 to 1.78 cm. The three egg dimensions varied significantly among nests (two-way ANOVA for breadth: F=21.2, d.f.=38,114, p<.0001; length: F=9.0, p<.0001; volume: F=15.6, p<.0001). The remaining 14.6% variation was due to factors other than laying sequence or nest differences.

The mean increase in volume from first- to last-laid eggs was only 6.5%. However, not all clutches followed this pattern (Table 15). Although most eggs ranked from smallest to largest with laying sequence, a few clutches exhibited the opposite pattern.

To examine seasonal changes in egg size, the mean egg volume per clutch in four-egg clutches was plotted against the relative laying date, where day 1 was equivalent to the date the first clutch was initiated that year. Since laying commenced earlier in 1985, the dates each clutch was initiated do not correspond exactly (see Table 4). There was no linear change in egg volume through the season in 1984 (r=.05), 1985 (r=.26), or in both years combined (r=.10, Figure 5). When all four-egg clutches measured throughout each breeding season were combined (Table 16), egg breadth and volume, but not length, were significantly greater in 1985 than in 1984 (two-way ANOVA for breadth: F=13.6, d.f.=1,117, p<.0003; volume: F=12.2, p<.0007; length:

Table 15. Egg volume rank (largest [1] to smallest [4]) in relation to laying sequence (1, 2, 3, 4).

Egg volume rank	Laying sequence			
	1	2	3	4
1	4	3	6	26
2	5	3	24	7
3	7	23	5	4
4	23	10	4	2

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Figure 5. Relationship between day of clutch initia-
           tion and mean egg volume per clutch. Tri-
           angles are for 1984 nests, circles for 1985
           nests.
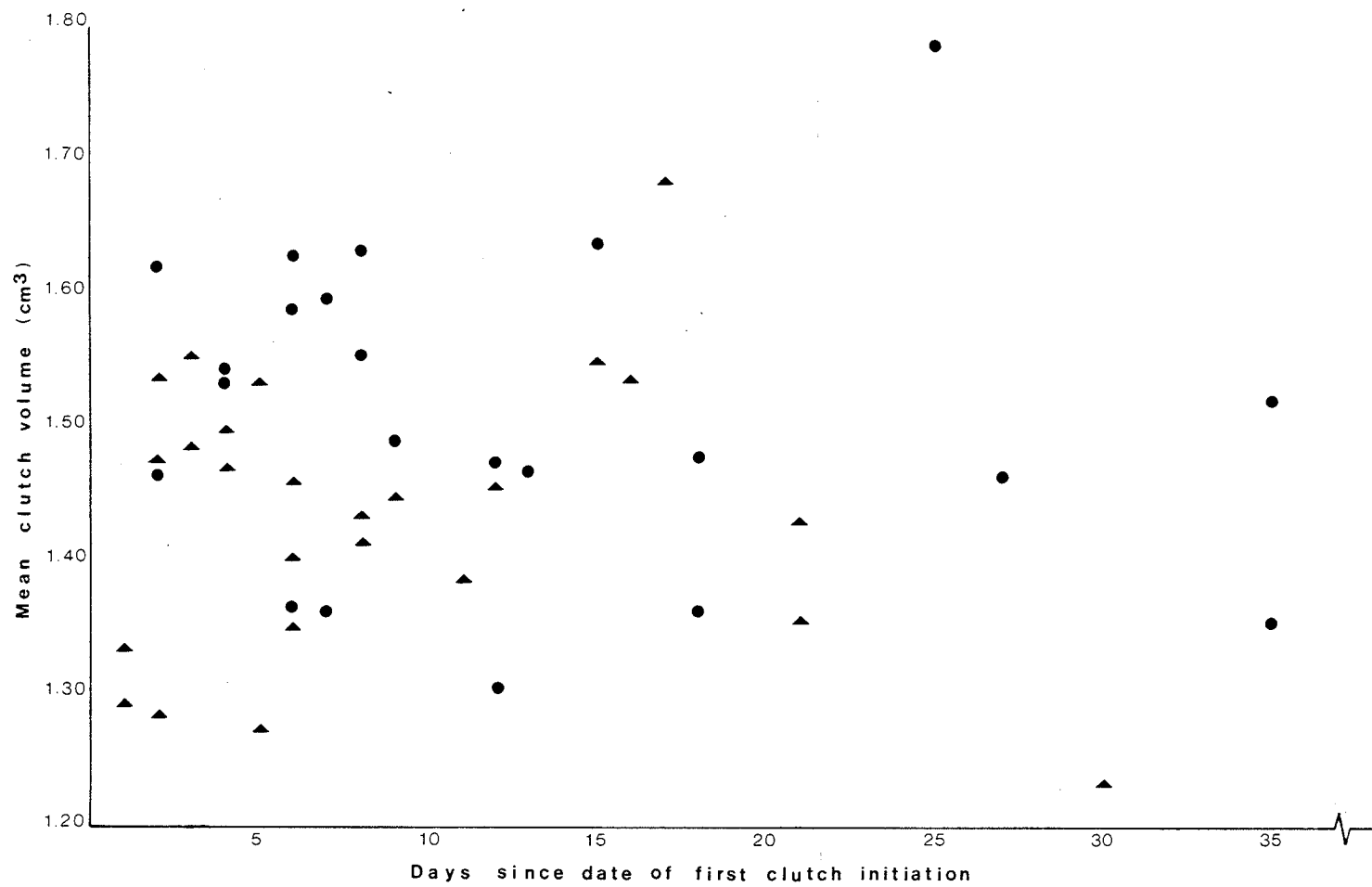
Table 16. Annual variation in mean egg size in 4-egg clutches of the Least Flycatcher. Figures are means±S.E. Sample sizes given in parentheses.

Egg size	Year	
	1984(80)	1985(76)
Breadth (mm)	13.05±0.05	13.18±0.05
Length (mm)	16.74±0.06	16.79±0.07
Volume (cm^3)	1.46±0.01	1.50±0.02

F=.9, p>.36; two-tailed t-test for both breadth and volume:
p<.05; length: p>.05).

Initiation of Incubation

Daytime incubation was initiated gradually and in-
creased as each successive egg was laid (Figure 6). Full-
time incubation began with the third egg, but clutches with
only one and two eggs recieved varying amounts of incuba-
tion. A similar pattern of increasing incubation was shown
by the increasing proportion of nests that contained warm
eggs when checked during laying (Table 17). Preliminary
data from night nest-checks suggest that the initiation of
nocturnal incubation parallels the development of diurnal
incubation behavior (Table 18).

Hatching Asynchrony

Hatching spread varied from less than 7 h to over 64 h
(both extremes in 4-egg clutches). Most clutches hatched
within a period of 24-36 h (Figure 7). Hatching spread in-
creased with clutch size (one-way ANOVA: F=8.1, d.f.=2,31,
p<.0015). Although it was not always known from which egg a
particular chick hatched, in those cases in which eggs and
chicks could be matched, the hatching sequence typically
followed the laying sequence. No hatching spread was great-
er than the laying interval, thus eggs hatch more synchro-
nously than they are laid.

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Figure 6.   Nest attentiveness in relation to laying
            sequence.   Day 1 is equivalent to the day
            of clutch initiation.   Day 5 is equivalent
            to the day after clutch completion (4 eggs).
            Horizontal line is mean, vertical bar is
            +S.D.   Number of half-hour observation
            periods is given above vertical bar.
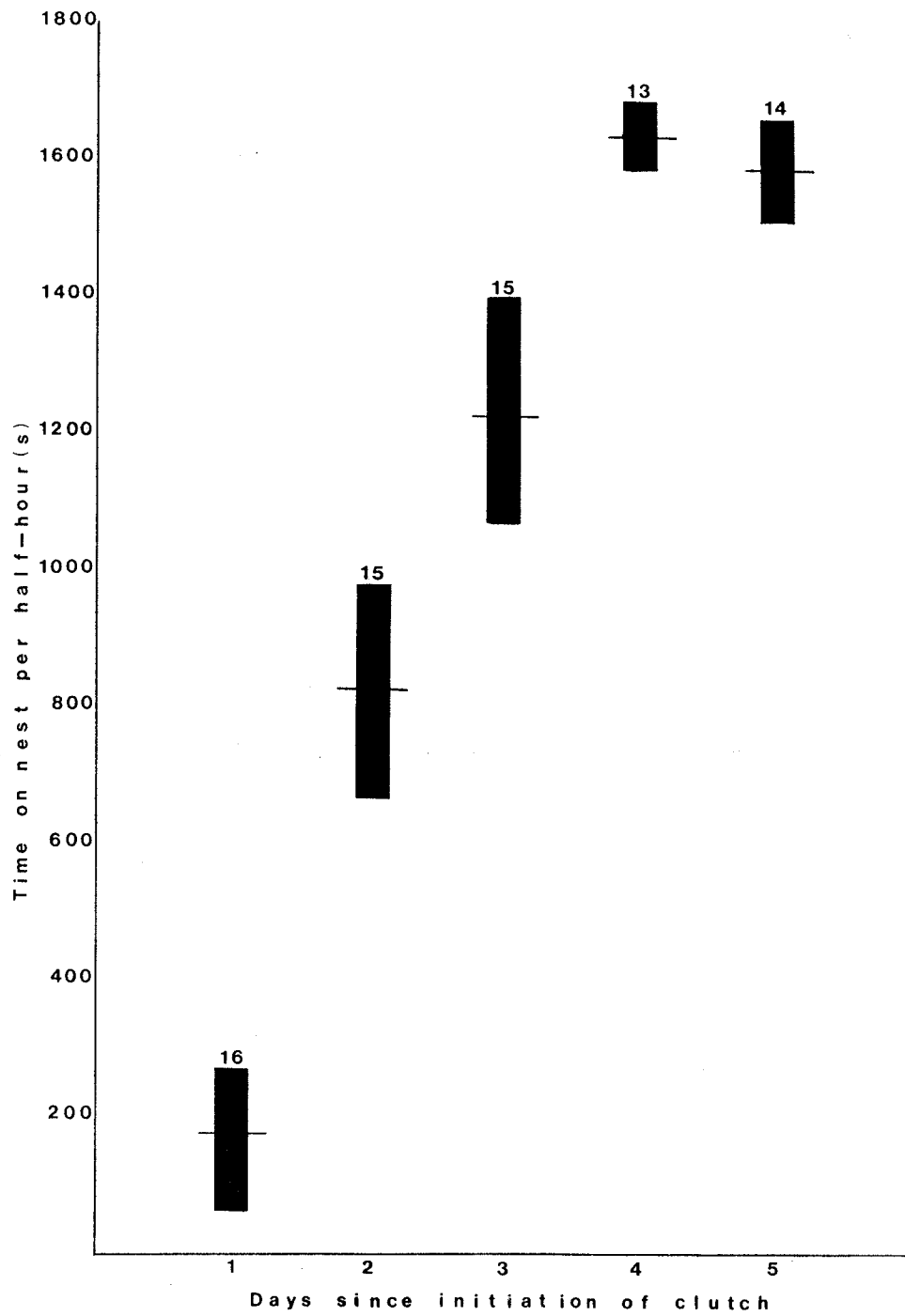
Table 17. Relative egg temperature in relation to stage of laying. Figures are percent frequency. Sample sizes given in parentheses.

Relative temperature	Day since initiation of clutch				
	1	2	3	4	5
Warm	21.3(10)	35.8(19)	85.7(42)	100.0(36)	100.0(24)
Cold	78.7(37)	64.2(34)	14.3(7)	0	0

Table 18. Preliminary results of night roosting/incubation checks at Least Fly-catcher nests, 1985. Sample sizes given in parentheses (with permission of R. Barclay).

Nesting stage	Proportion of females on nest during check
Pre-laying and nest building	0 (0/15)
Night before first egg laid	0 (0/3)
Night after first egg laid	0.33(3/9)
Night after second egg laid	0.40(6/15)
Night after third egg laid	0.29(2/7)
Night after fourth egg laid	0.83(5/6)

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Figure 7.   Frequency distribution of hatching spreads
in clutches of three (open bars), four
(light bars), and five (dark bars) eggs in
the Least Flycatcher. Mean hatching spread
$\pm$S.E. (N in parentheses); clutches of three:
26.4 ± 1.9 h (14); clutches of four: 36.4 ± 3.8
h (14); clutches of five: 45.8 ± 2.0 h (6).

Effect of Hatching Order on Growth

Mean mass in relation to hatching order in each brood size is presented in Table 19. The fitted nonlinear regression parameters appear in Table 20. The growth-rate constant (k) did not vary significantly with hatching order in any brood size (Tukey's least-significant difference T-test for multiple comparisons: broods of three; T=0.17, d.f.=3,12, p>.05; broods of four: T=0.25, d.f.=4,16, p>.05; broods of five: T=0.19, d.f.=5,20, p>.05). The time-scale constant (b) increased with hatching order in all brood sizes. However, this was largely an effect of intra-brood age differences. To illustrate the function of b upon the form of the fitted equation, the ages of the second oldest to youngest nestlings in each brood size were adjusted to their estimated real values. Approximate ages were determined by dividing the mean hatching spread by the brood size (n-1). In all cases the differences in the adjusted b' were less than in in unadjusted curves. As expected, neither k nor the residual variance were affected by the time scale adjustment.

Mean tarsus length followed the same pattern as body maass (Tables 21 and 22). No significant differences in k or b' were found with hatching order in any brood size (broods of three: T=0.09, d.f.=3,12, p>.05; broods of four: T=0.11, d.f.=4,16, p>.05; broods of five: T=0.09, d.f.=5,20, p>.05).

Table 19. Mean mass (g) of nestling Least Flycatchers in relation to brood size and hatching order. Figures are means±S.E. Sample sizes given in parentheses. Data for 1984 and 1985 combined.

Brood size	Hatching order	Days since first hatch				
		2	4	6	8	10
	1	2.49±0.13 (14)	4.73±0.12 (14)	7.20±0.20 (13)	9.19±0.14 (12)	10.19±0.19 (10)
3	2	2.17±0.12 (14)	4.19±0.17 (14)	6.67±0.27 (13)	8.59±0.32 (11)	9.90±0.27 (10)
	3	1.71±0.15 (14)	3.49±0.21 (14)	5.84±0.29 (13)	8.16±0.29 (12)	9.68±0.28 (9)
	1	2.41±0.10 (14)	4.42±0.09 (16)	7.22±0.18 (14)	9.15±0.15 (13)	10.29±0.16 (10)
	2	2.21±0.08 (14)	4.15±0.10 (16)	6.70±0.23 (14)	8.66±0.28 (14)	10.03±0.25 (10)
4	3	1.91±0.09 (14)	3.54±0.12 (16)	6.09±0.18 (14)	8.17±0.19 (14)	9.67±0.19 (10)
	4	1.66±0.09 (10)	2.78±0.18 (16)	5.24±0.29 (14)	7.35±0.28 (13)	9.25±0.21 (10)
	1	2.67±0.11 (9)	4.83±0.20 (9)	7.29±0.28 (9)	9.16±0.21 (9)	10.10±0.35 (8)
	2	2.47±0.11 (9)	4.59±0.21 (9)	7.10±0.27 (9)	8.96±0.18 (9)	9.82±0.27 (8)
5	3	2.06±0.13 (9)	4.00±0.21 (9)	6.37±0.29 (8)	8.55±0.15 (8)	9.74±0.14 (7)
	4	1.90±0.13 (9)	3.74±0.27 (9)	5.93±0.39 (9)	8.06±0.29 (9)	9.77±0.34 (7)
	5	1.44±0.07 (8)	2.67±0.20 (9)	5.13±0.34 (7)	7.36±0.22 (7)	9.05±0.53 (6)

Table 20.   Model parameters for growth curves of mass in relation to hatching order and brood size.   Figures are parameter estimates±S.E.

Brood size	Hatching order	Model parameters				Residual variance
		m	k	b	b'	
3	1		0.66±0.018	50.6±4.8	50.6±4.8	0.0062
	2	2.90	0.62±0.021	58.3±6.9	41.6±4.5	0.0101
	3		0.64±0.015	95.4±8.9	47.2±3.6	0.0053
4	1		0.73±0.024	101.0±12.7	101.0±12.7	0.0086
	2		0.68±0.025	100.5±14.1	71.1±9.1	0.0116
	3	3.18	0.67±0.025	134.1±20.4	67.9±8.7	0.0128
	4		0.65±0.030	198.1±40.1	73.1±11.5	0.0205
5	1		0.62±0.009	38.4±1.7	39.4±1.7	0.0016
	2		0.61±0.017	41.4±3.9	31.0±2.6	0.0069
	3	2.84	0.61±0.012	58.6±4.1	32.5±1.9	0.0036
	4		0.60±0.024	65.8±9.8	27.9±3.2	0.0157
	5		0.61±0.027	114.2±20.7	35.8±4.7	0.0192

Table 21. Mean tarsus length (mm) of nestling Least Flycatchers in relation to brood size and hatching order. Figures are means±S.E. Sample sizes as in Table 19. Data for 1984 and 1985 combined.

Brood size	Hatching order	Days since first hatch				
		2	4	6	8	10
	1	6.22+0.15	8.69+0.14	11.02+0.17	13.07+0.13	14.71+0.16
3	2	5.82+0.16	8.16+0.21	10.54+0.19	12.53+0.31	14.06+0.28
	3	5.33+0.17	7.21+0.22	9.67+0.24	11.87+0.21	13.60+0.29
	1	6.16+0.14	8.44+0.13	10.96+0.18	12.90+0.21	14.46+0.21
	2	5.96+0.15	7.93+0.15	10.51+0.16	12.37+0.29	14.01+0.23
4	3	5.51+0.16	7.41+0.16	9.99+0.15	12.06+0.26	13.57+0.15
	4	5.27+0.12	6.52+0.21	8.98+0.22	10.99+0.27	13.06+0.23
	1	6.52+0.21	9.07+0.20	11.28+0.28	13.34+0.17	14.64+0.28
	2	6.23+0.15	8.56+0.23	10.99+0.27	13.10+0.17	14.42+0.21
5	3	5.91+0.25	8.18+0.23	10.46+0.25	12.66+0.16	14.00+0.31
	4	5.71+0.21	7.86+0.33	10.10+0.34	12.17+0.30	13.74+0.40
	5	5.52+0.14	6.87+0.20	9.33+0.41	11.67+0.32	13.25+0.35

Table 22. Model parameters for growth curves of tarsus length in relation to hatching order and brood size. Figures are parameter estimates±S.E.

| Brood size | Hatching order | Model parameters | | | | Residual variance |
		m	k	b	b'	
3	1		0.44+0.011	20.4+1.2	20.4+1.2	0.0089
	2	3.40	0.42+0.012	22.3+1.5	17.7+1.1	0.0118
	3		0.42+0.006	29.8+1.2	18.8+0.6	0.0039
4	1		0.41+0.006	13.5+0.4	13.5+0.4	0.0029
	2		0.38+0.009	14.1+0.8	11.6+0.6	0.0090
	3	3.04	0.38+0.010	16.7+1.0	11.3+0.6	0.0119
	4		0.36+0.017	19.8+2.2	11.4+1.0	0.0363
5	1		0.40+0.008	9.8+0.4	9.8+0.4	0.0051
	2		0.40+0.002	11.0+0.1	9.1+0.1	0.0005
	3	2.90	0.38+0.006	11.8+0.4	8.2+0.2	0.0035
	4		0.36+0.003	12.3+0.2	7.3+0.1	0.0008
	5		0.36+0.017	14.8+1.6	7.5+0.6	0.0383

Log mean flattened wing length was fitted by linear regression and homogeneity of slopes tested by one-way ANOVA (Sokal and Rohlf 1969) (broods of three: $F=0.021$, d.f.=2,9, $p>.05$; broods of four: $F=0.25$, d.f.=3,12, $p>.05$; broods of five: $F=0.13$, d.f.=4,15, $p>.05$, Table 23). The slopes of the equation did not differ significantly with hatching order in any of the three brood sizes.

Growth, as represented by $\underline{k}$ in the nonlinear regression and by slope in the linear regression, did not vary with hatching order except with respect to time ($\underline{b}$ parameter in nonlinear regression). In biological terms, the youngest nestling in a brood weighed less and was smaller simply because it was younger and not as a consequence of any disadvantages caused by the order in which it hatched.

Effect of Brood Size on Growth

As a result of greater hatching spread, larger broods contain last-hatched nestlings that were younger than those in smaller broods. This depresses mean brood mass spuriously. To reduce this bias, growth in the three brood sizes was compared using only the three oldest nestlings in each brood (Table 24).

Neither $\underline{k}$ nor $\underline{b}$ varied significantly with brood size for both mass and tarsus length (mass: $T=0.12$, d.f.=3,12, $p>.05$; tarsus: $T=0.04$, $p>.05$, Table 25). No significant

Table 23. Mean flattened wing length (mm) of nestling Least Flycatchers in relation to brood size and hatching order. Figures are means±S.E. Sample sizes as in Table 19. Data for 1984 and 1985 combined.

Brood size	Hatching order	Days since first hatch				
		2	4	6	8	10
	1	7.52+0.19	10.82+0.26	17.56+0.42	25.05+0.36	33.23+0.38
3	2	6.96+0.19	10.14+0.28	15.89+0.56	23.15+0.72	30.36+1.09
	3	6.40+0.19	9.01+0.35	13.79+0.74	20.56+0.82	28.10+1.18
	1	7.51+0.19	10.65+0.24	16.90+0.50	24.38+0.62	31.81+0.70
	2	7.12+0.14	9.92+0.18	15.87+0.45	23.24+0.86	30.38+0.89
4	3	6.79+0.16	9.30+0.19	14.61+0.48	21.35+0.88	28.27+0.78
	4	6.51+0.16	8.11+0.29	12.24+0.61	18.54+0.99	25.42+1.12
	1	8.02+0.25	11.39+0.34	18.36+0.77	25.76+0.68	33.27+0.82
	2	7.67+0.21	11.12+0.29	17.64+0.74	24.73+0.73	32.15+0.89
5	3	7.18+0.28	10.10+0.23	15.49+0.46	22.65+0.54	30.27+0.61
	4	6.99+0.21	9.76+0.37	14.61+0.74	21.69+0.87	27.36+2.06
	5	6.60+0.16	8.49+0.25	12.34+0.63	19.47+0.85	26.20+1.10

Table 24. Growth in the three oldest nestlings in relation to brood size. Figures are means±S.E.

Brood size		Days since first hatch				
		2	4	6	8	10
3	N	42	42	39	35	29
	Mass (g)	2.12±0.09	4.14±0.13	6.57±0.17	8.65±0.16	9.93±0.14
	Tarsus (mm)	5.79±0.11	8.02±0.14	10.41±0.14	12.49±0.15	14.14±0.16
	Flattened wing (mm)	6.96±0.13	9.99±0.21	15.75±0.41	22.91±0.49	30.65±0.65
4	N	42	48	42	41	30
	Mass	2.18±0.06	4.04±0.08	6.67±0.13	8.65±0.14	10.00±0.12
	Tarsus	5.87±0.10	7.93±0.10	10.48±0.11	12.43±0.16	14.01±0.13
	Flattened wing	7.14±0.10	9.96±0.14	15.80±0.31	22.95±0.49	30.15±0.52
5	N	27	27	26	26	23
	Mass	2.40±0.08	4.47±0.13	6.94±0.17	8.90±0.11	9.90±0.15
	Tarsus	6.22±0.13	8.60±0.14	10.93±0.16	13.05±0.11	14.37±0.16
	Flattened wing	7.62±0.16	10.87±0.19	17.23±0.45	24.45±0.45	31.97±0.51

Table 25. Model parameters for growth curves in mass and tarsus length in relation to brood size for the three oldest nestlings in each brood. Figures are parameter estimates±S.E.

	Brood size	Model parameters			Residual variance
		m	k	b	
Mass (g)	3	2.61	0.59±0.014	37.6±2.8	0.0047
	4	2.61	0.60±0.017	38.7±3.7	0.0076
	5		0.58±0.004	30.2±0.7	0.0004
Tarsus (mm)	3		0.39±0.003	14.2±0.3	0.0012
	4	2.99	0.38±0.007	13.7±0.5	0.0048
	5		0.40±0.004	12.1±0.3	0.0015

variation in slope with brood size was found by linear regression of log flattened wing length (broods of three: logY= 0.082X+0.683; broods of four: logY=0.081X+0.694; broods of five: logY=0.080X+0.730; one-way ANOVA: F=0.11, d.f.=2,9, p>.05). Thus, increasing brood size did not affect the growth of nestling Least Flycatchers in any of the three measurements recorded.

Effect of Ectoparasites on Growth

Growth of young in nests heavily infested by blood-feeding ectoparasitic mites (Acarina: Macronyssidae) were compared with unaffected broods. All brood sizes and hatching orders were combined in the analysis since sample sizes of parasitized broods were small (Table 26).

Mites were concentrated on the nape, in and around the ears and anus, under the wings, between the thighs and abdomen, and between the pin feathers. As the feathers unsheathed, mites were found over the entire surface of the bird. All nestlings in infected nests bore mites. Mites remained in the lining of nests after fledging. Adults frequently picked mites off the young but because they were so small and abundant, it is unlikely an infestation could be stopped in the later stages.

Growth in mass and tarsus length, but not flattened wing length was significantly reduced as a result of ecto-

Table 26. Growth in Least Flycatcher nestlings infested with ectoparasitic mites (Acarina: Macronyssidae). Data from all brood sizes and hatching orders combined. Figures are means±S.E.

| | | Days since first hatch | | | | |
		2	4	6	8	10
Nonparasitized	N	138	151	137	131	105
	Mass (g)	2.11+0.04	3.91+0.07	6.42+0.09	8.46+0.09	9.82+0.08
	Tarsus (mm)	5.84+0.06	7.86+0.08	10.31+0.09	12.39+0.09	13.97+0.09
	Flattened wing (mm)	7.09+0.07	9.83+0.11	15.44+0.23	22.53+0.29	29.82+0.37
Parasitized	N	15	15	15	11	9
	Mass	1.55+0.12	2.75+0.26	4.07+0.40	5.77+0.65	8.07+0.47
	Tarsus	5.37+0.14	6.74+0.28	8.09+0.38	10.09+0.53	12.41+0.50
	Flattened wing	6.21+0.17	8.00+0.39	10.44+0.85	15.31+1.73	23.56+1.87

parasitism (one-tailed t-test for mass: $t=14.6$, d.f.$=8$, p$<.05$; tarsus: $t=14.8$, p$<.05$; one-way ANOVA for homogeneity of slopes of flattened wing length: $F=1.91$, d.f.$=1,6$, p$>.05$, Table 27). Two of four heavily-infested nests experienced brood reduction. In a brood of 4 nestlings the fourth- and third-hatched chicks died at 8 and 10 days, respectively. In a brood of 3 young the third-hatched nestling died at 10 days. All nestlings in a heavily infested brood of five fledged, although the nestling period extended to 19 days--four days longer than average.

Most of the heavily infested nests had been initiated later in the season. The four infested nests at which nestlings were measured were initiated on 5 June and 2, 11 and 13 July 1985, respectively. In addition, all infestations that involved less than five mites were recorded in clutches initiated in July. The known double-brood with nestlings was lightly infested.

Effect of Weather on Growth

Figure 8 shows the mean mass of the three oldest nestlings in all brood sizes as a function of date in 1985. A period of low mean nestling mass during 24-28 June corresponded to a period of extended cool, rainy weather. Two broods were reduced due to starvation and (or) cold exposure during this time. The fifth- and third-hatched nestlings in a natural brood of 5 died at 6 days of age while an entire

Table 27. Model parameters for growth curves in mass and tarsus length for parasitized and nonparasitized nestlings. Figures are parameter estimates±S.E.

| | | Model parameters | | | Residual variance |
		m	k	b	
Nonparasitized	Mass (g)	2.65	0.58±0.011	41.6±2.6	0.0032
	Tarsus (mm)	3.08	0.39±0.004	15.6±0.4	0.0016
Parasitized	Mass	2.65	0.45±0.026	54.6±10.3	0.0277
	Tarsus	3.08	0.31±0.023	17.8±2.7	0.0731

Figure 8.   Mean mass at eight days of three oldest
nestlings in broods of three (squares),
four (circles), and five (triangles) young
in relation to mean daily temperature in
1985. Open symbols indicate nests located
on the north half of the ridge, solid sym-
bols indicate nests on the south side.
Range given by vertical lines. The 't'
indicates a nest in which brood reduction
occurred. Broods parasitized by mites are
excluded in the analysis.
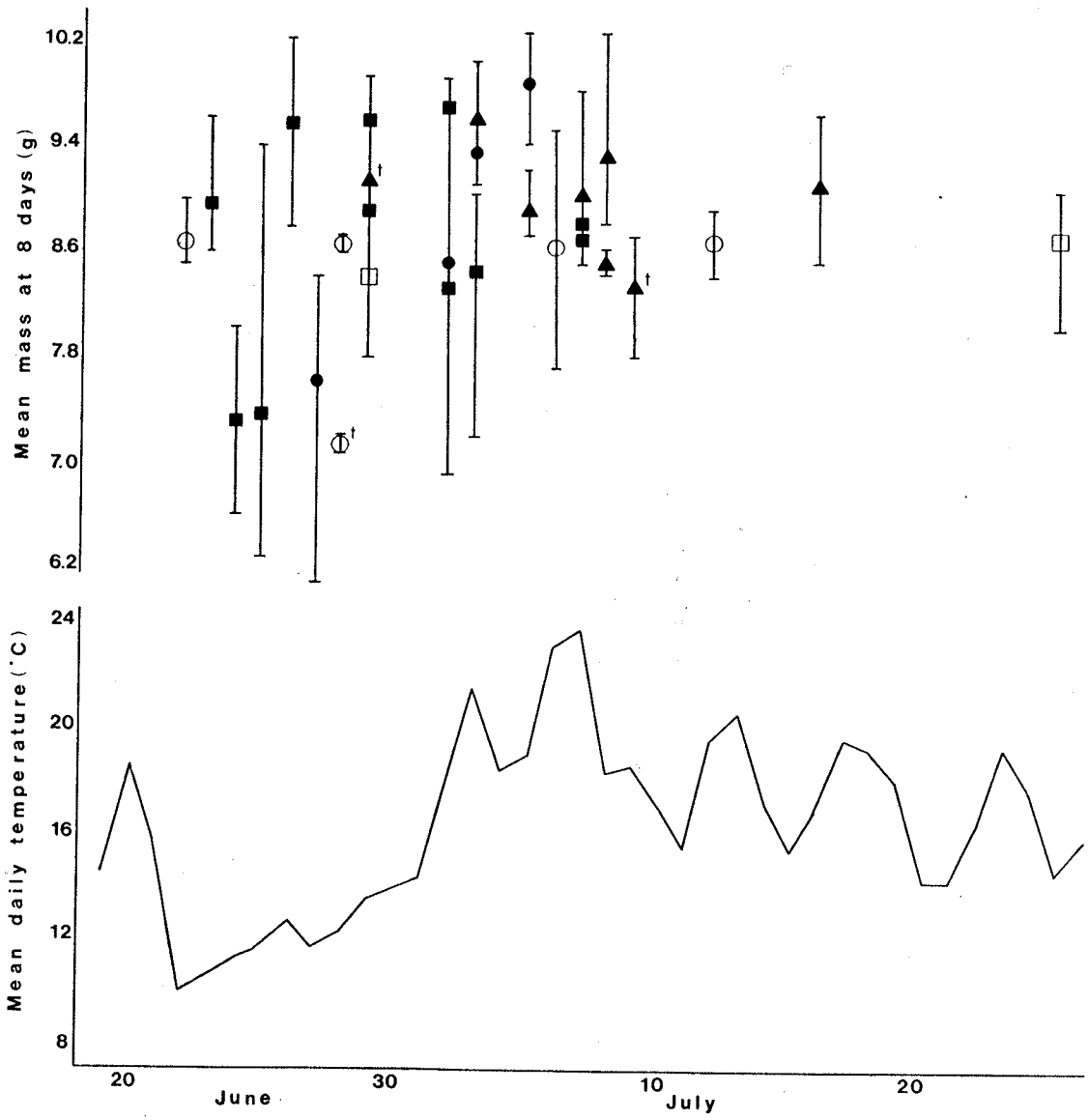
brood of 4 died over the span of 8 to 10 days. On the day of weighing prior to death all of these nestlings recorded somewhat lower mass. However, they were all within the normal range exhibited by other nestlings in successful broods.

Broods in the more exposed nests on the northern half of the dune-ridge forest weighed less (Figure 8), although sample sizes were small.

Arthropod Abundance

Chironomids and culicids were the predominant insect groups throughout both breeding seasons (Figure 9). Chironomids emerged earlier and were more abundant through the summer in 1985. Except for occasional emergences of ephemeropterans and trichopterans, the abundance of the other arthropod groups fluctuated around moderate densities.

DISCUSSION

Determination of Egg Size

Egg size varies with clutch size (Gibb 1950, Ojanen et al. 1978, Otto 1979, Jarvinen and Vaisanen 1983), laying sequence (Gibb 1950, Coulson et al. 1969, Vaisanen et al. 1972, Howe 1976, 1978, Ryden 1978, O'Connor 1979, Bancroft 1984, Rofstad and Sandvik 1985), age of the laying female (Richdale 1955, Coulson et al. 1969, Davis 1975, Furness 1983), size and condition of the female (Miller 1979, Otto

65

Figure 9.   Mean numbers of arthropods in each group
            collected from sweep net samples.   Solid
            lines are for 1984, broken lines for 1985.

7100 8500

Chironomidae and
Culicidae

3000

1000

Other Diptera

300

100

Mean number per sweep sample

Geometridae

10

Adult Lepidoptera
and Trichoptera

120

60

Ephemeroptera

3

Odonata

2

All other Insecta

200

100

Araneida

20   4   19   4   19   3
    June   July
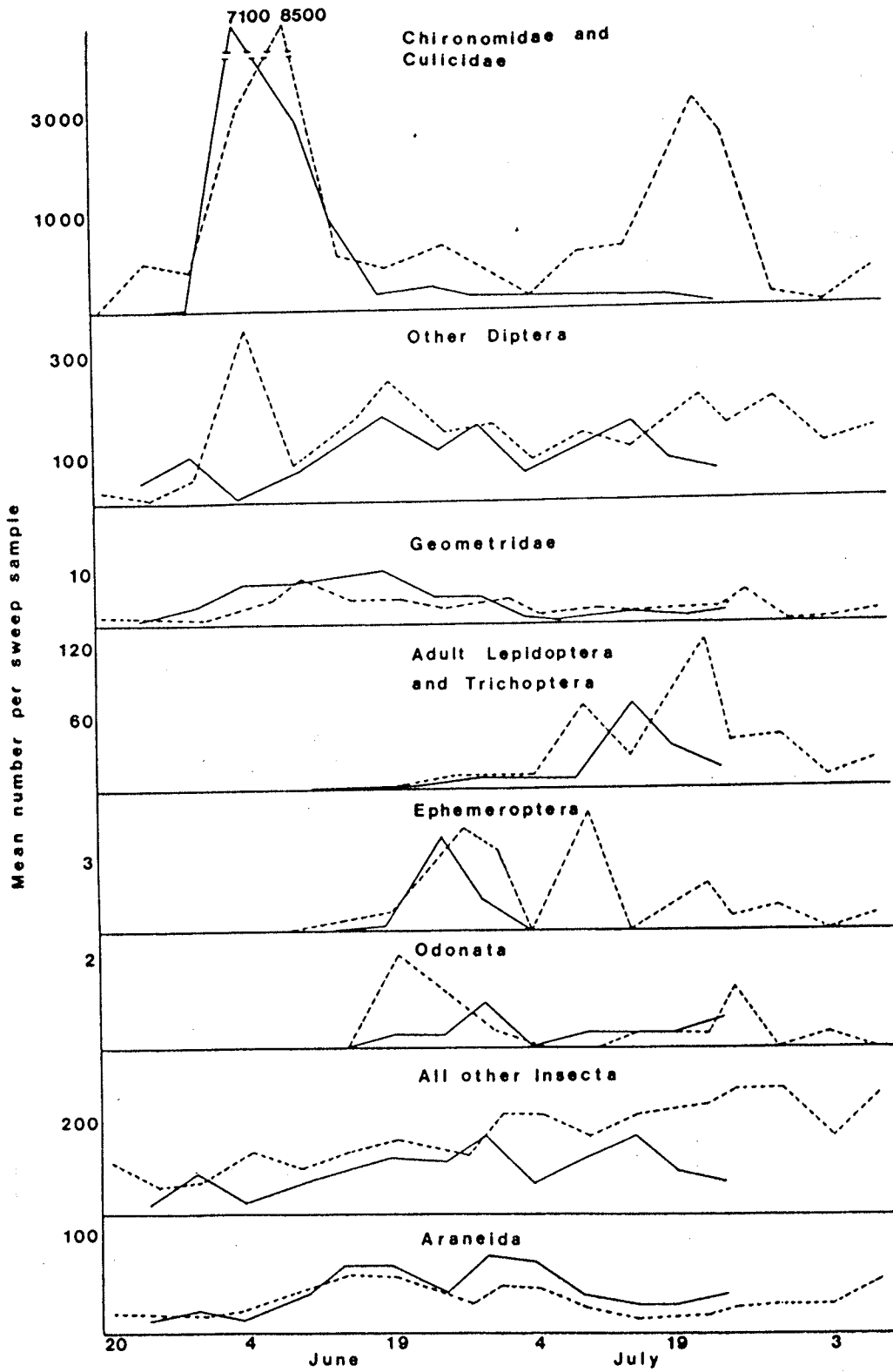
1979, Jarvinen and Vaisanen 1983), food availability before laying (Nisbet 1973, Otto 1979, O'Connor 1979, Hogstedt 1981), density (Otto 1979), season (Coulson et al. 1969, Davis 1975, Furness 1983, Bancroft 1984, Byrkjedal and Kalas 1985), temperature (Kendeigh 1941), and between years (Snow 1960, Anderson 1976). Large variation in egg size has been attributed to differences between individual females (Vaisanen et al. 1972, Howe 1976, 1978, Furness 1983, Bancroft 1984).

In the present study, the sizes of Least Flycatcher eggs varied significantly with clutch size, laying sequence, nest and year, but not over the season. In examining egg size variation it is important to separate proximate, environmental causes from ultimate, evolutionary adaptations. Food available to the egg-producing female is considered to have an important influence on egg size (Snow 1960, Nisbet 1973, Anderson 1973). Females laying under conditions of abundant food resources lay larger eggs than do food-stressed females (Nisbet 1973, Bryant 1978, Otto 1979, O'-Connor 1979). Hogstedt (1981) found that Black-billed Magpies (Pica pica) with experimentally increased food supplies in spring, not only laid earlier and enjoyed greater breeding success, but also laid larger eggs.

On the study area, Biermann and Sealy (1985) found unsexed Least Flycatchers lost body mass during the first four weeks after they arrived in spring, but then gained slightly

during incubation. They maintained this mass at a fairly constant level during the nestling period and until they migrated. As the production of an egg consumes a large part of the daily energy budget during laying (King 1973, Ricklefs 1974), this loss of mass in Least Flycatchers suggests food stress prior to and during laying. The yearly variation in egg size found in this study may be a response to the differences in food availability between the two years. In 1985, chironomids emerged in large numbers prior to clutch initiation and remained at high levels throughout the season (Figure 9). In 1984, large numbers of chironomids did not emerge until after laying had commenced, and after an initial high peak in early summer, they declined to moderate levels. As chironomids form the major component of the diet of adults (G. C. Biermann, pers. comm.), the lower availability of chironomids in 1984 during egg formation may have influenced the size of the developing eggs. A regression analysis comparing mean egg volume per clutch to the mean chironomid abundance on the nearest arthropod sampling day prior to clutch initiation, revealed no significant trend (r=.06). However, this may have reflected the crudeness of estimating food available to particular females, prior to laying, rather than a lack of correlation.

The high heritability of egg size (Kendeigh 1975, Ojanen et al. 1979, Furness 1983) implies that egg size should evolve rapidly in response to differential selection pres-

sures (Ojanen et al. 1979).   Selection should favor large eggs since they give rise to large chicks (Parsons 1970, Schifferli 1973, Bryant 1978, O'Connor 1979, Furness 1983, Bancroft 1984) which have a greater probability of surviving to fledging (Schifferli 1973, Howe 1976, Nisbet 1978, O'Connor 1979, Moss et al. 1981; but see Davis 1975).   In addition, larger eggs can be of a higher quality, containing more nutrient reserves (Bryant 1978, Bancroft 1984) and exhibiting greater hatchability (O'Connor 1979, Jarvinen and Vaisanen 1983, Rofstad and Sandvik 1985).

Intra-clutch variation in the size of birds' eggs has been suggested to have an ultimate, adaptive value when used in combination with asynchronous hatching (Slagsvold et al. 1984).   Since smaller eggs are less successful than larger ones, a decrease in egg size with laying order can be viewed as an adaptation to the "brood-reduction" strategy in that small final eggs will predispose the resulting chick to an early death should food be scarce at hatching (O'Connor 1979, Howe 1978).   The parental strategy is to produce an extra egg to insure against infertility or the remote probability of food supply becoming superabundant (Howe 1978). Alternatively, an increase in egg size with laying has been suggested to favor a "brood-survival" strategy (Slagsvold et al. 1984).   Large, last chicks moderate the effects of hatching asynchrony in such a way that the survival of the last-hatched young is prolonged in the advent that food

might improve unpredictably (Howe 1976, Ryden 1978). A female following this pattern of parental investment "hedges her bets" so as to maximize inclusive fitness. Increasing the size with successive eggs laid and asynchronous hatching are viewed as antagonistic forms of parental investment within the brood (Howe 1976). Large, last-laid eggs in Least Flycatcher support the view that this species follows the "brood-survival" strategy.

Egg size can increase or decrease with clutch size. Jarvinen and Vaisanen (1983) found egg size of Great Tits (Parus major) in Finland was correlated negatively with clutch size in the south but changed to a positive correlation in the north. The latter occurred when small clutches, with small-sized eggs, were laid during periods of unfavorable weather. During periods of favorable weather large clutches of large-sized eggs were laid (Jarvinen and Vaisanen 1983). The opposite pattern has not been explained satisfactorily (Rofstad and Sandvik 1985). Ojanen et al. (1978) found Great Tits laid smaller, rounder eggs in larger clutch sizes, and suggested that this was a mechanism to save calcium when laying, and also to reduce the overall volume of the clutch so that eggs could be more effectively incubated. Moss et al. (1981) suggested that the average female has finite resources for egg production and can channel these resources into producing either a large clutch of small eggs, or a small clutch containing large eggs.. In

Least Flycatchers, eggs in clutches of five were considerably smaller than eggs in either clutches of four or three. If the relationship between clutch size and egg size is viewed as a balance between two opposing selective forces then individual Least Flycatchers have two strategies. The first is to produce four (or three) large eggs, each with a high probability of hatching and survival. The second alternative is to lay five small eggs which produce small, weak nestlings, but which under favorable conditions can all fledge.

Determination of Clutch Size

Least Flycatchers that laid five eggs produced the most young. These young weighed as much and were the same size as young in smaller broods. As well, fledglings from the larger brood sizes did not experience greater post-fledging mortality. This suggests that five-egg clutches are the most productive in the dune-ridge forest. However, in both years four-egg clutches were the most frequent. Contrary to the "food-limitation" hypothesis, Least Flycatchers did not raise the maximum number of young they could feed during a single nesting attempt. If the ability to feed an enlarged brood adequately does not limit clutch size, then why do Least Flycatchers not lay five eggs more frequently?

A female's condition when laying begins can affect clutch size proximately (Klomp 1970, Newton and Marquiss 1981). Perhaps clutches of five are uncommon simply because most females cannot acquire the resources to lay that many eggs. However, the evidence suggests the contrary. Clutches were not larger in 1985 as might be expected. Moreover, clutch sizes off the study area, where presumably food is less abundant, were the same as those in the dune-ridge forest.

Selection should favor reduced clutch size if adult survival is lowered by larger broods (Williams 1966, Charnov and Krebs 1974). Adults tending larger broods lose body mass, a point that has been used as evidence of increased stress and decreased probability of survival (Hussell 1972, Askenmo 1982, but see Freed 1981). Biermann and Sealy (1985) found adult Least Flycatchers gained weight during incubation and maintained it through the nestling stage, but did not examine the effects of brood size. However, adults tending large broods should have sufficient time to recover from increased stress, especially when it is considered that some flycatchers on the study area are able to double-brood. In addition, a short-lived passerine like the Least Flycatcher should be expected to maximize its breeding effort at every attempt since the probability of it returning to breed again is so low (Stearns 1976).

In three out of nine broods of five, one or more nestlings fell out of the nest. Probably none of these nestlings survived, for they were still flightless and apparently not attended by the adults. In contrast, only one one nestling fell out of 50 other nests. In all cases the nestlings fell out a few days before fledging when the young began moving actively in the nest. In one nest the two oldest nestlings fell out, at a second nest the fourth oldest nestling fell out, while the hatch order of the nestling at the third nest was undetermined. Slagsvold (1982) found similar results with Fieldfares (Turdus pilaris). When he enlarged nests artificially, more young fledged. The influence of nest size on clutch size has been noted in some hole-nesting birds (Karlsson and Nilsson 1977, Balen 1984, Gustafsson and Nilsson 1985). For an open-nesting passerine, selection could easily favor the production of larger nests. However, if larger nests diminish the efficiency of incubation or are more conspicuous to predators, then the advantages might be outweighed by the overall reduced success (Slagsvold 1982, Wesolowski 1985).

Clutches of five might be less productive if peak demand occurs after fledging and the adults are unable to meet this demand adequately. Smith (1978) demonstrated that young demand more of their parents after they fledge than when they were in the nest. Alternatively, if the demands of an enlarged brood of fledglings can be met, but adult

survival decreases, then a similar decrease in clutch size might be expected. However, contrary to expectations, Smith (1981) found that females raising the largest broods survived better than those raising smaller broods. Least Flycatchers tend their fledglings for approximately 10-12 days after they fledge. Fledglings are not completely dependent and a proportion of their demands may be met by their own foraging (pers. obs.). Comparable rates of post-fledging survival in all brood sizes suggests feeding demands are not exceeded after fledging.

Finally, it must be remembered that the population of Least Flycatchers and the superabundance of food in the dune-ridge forest is local. Dispersal both to and from the study area is probably quite high (S. G. Sealy, unpubl. data). Without some degree of isolation, selection for a larger clutch may simply be swamped by the influx of birds from adjacent areas, where, as a result of the lower food availability, clutches of four may be the most productive.

In summary, Least Flycatchers at Delta Marsh apparently do not rear the maximum number of young they are capable of feeding. It seems unlikely food plays a proximate role in determining clutch size. Survival of the adults may favor smaller clutches but its significance for a short-lived passerine is not clear. Nest size may place an upper limit on clutch size. Lastly, the conditions necessary for enlarged clutch sizes to evolve must be considered when local areas are subjected to varying amounts of dispersal.

Incubation and Hatching Asynchrony

The amount of incubation a clutch receives during laying determines to a large extent the hatching spread. As incubation costs, not only in terms of heat production but also in lost foraging time (Walsberg and King 1978, Mertens 1980, Haftorn and Reinertsen 1985), the energy balance of a particular female may restrict when incubation can begin (Hussell 1972). This is especially true during laying when the costs of producing eggs have already strained the female physiologically (Jones and Ward 1976, Murphy 1978, Drent and Daan 1980). Decreased mass prior to laying and smaller eggs in larger clutches, suggest that female Least Flycatchers are stressed during laying. The variation in hatching spread observed in this study may reflect the different physical conditions of individuals.

Incubation before clutches are complete probably is the most important determinant of asynchrony, but other factors may be involved. As larger eggs must be incubated longer (Parsons 1972, 1975), large last-laid eggs can increase the spread of hatching. Increasing egg size with successive eggs, as in Least Flycatchers and many other passerines, may ensure at least some hatching asynchrony. A female that cannot incubate before its clutch is complete can still induce some asynchrony by laying different-sized eggs.

Hatching Order and Growth

Death of the youngest member of a brood has been related to decreases in the availability of food (Lack and Lack 1951, Owen 1960, Ricklefs 1965, Hussell 1972, Nisbet and Cohen 1975, Parsons 1975), as well as weather-induced restrictions in the ability of the parents to gather food (Lack and Lack 1951, Jehl and Hussell 1966, Hussell 1972, Dyrcz 1974, Zach and Mayoh 1982, Murphy 1983, 1985). Generally, reduced growth in late-hatching young precedes brood reduction, which may or may not happen (Langham 1972, LeCroy and LeCroy 1974, Henderson 1975, Parsons 1975, Howe 1976, Hahn 1981, Murphy 1983). However, brood reduction has been reported in the absence of any large effects on the growth and survival of the remaining nestlings (Richter 1984).

Least Flycatcher nestlings grew at the same rate regardless of their order of hatching. At any point in time, a well-defined weight hierarchy existed within a brood, but this was because of the time span between hatching and not due to differential provisioning of parental care (see also Holcomb and Twiest 1971, Richter 1984).

Although nestlings were seemingly well-fed in all broods and all hatching orders, brood reduction nevertheless occurred during prolonged, cool weather. The youngest nestling(s) were lost in all cases. No discernable effects were seen on the surviving young, and in fact, the dead

young weighed only slightly less than they did when weighed previously.   Death was rapid and may have resulted in part from exposure.   In any case, the brood was reduced to a size the adults could manage when conditions turned unpredictably poor.

The   results presented here are consistent with the "brood-reduction" hypothesis.   In periods of abundant food, late-hatching young were not disadvantaged and grew at identical rates to their older siblings.   When the food available to a foraging flycatcher was reduced by poor weather, the size hierarchy in the brood facilitated the rapid readjustment of the brood to a size the parents could provide for, and without a noticeable detriment to the remaining siblings.   The question remains: does hatching asynchrony facilitate brood reduction or is it merely a consequence of some other proximate or ultimate factor?

In the "egg-insurance" hypothesis, hatching asynchrony is a mechanism to insure size and age inequality among the nestlings so that brood reduction will occur quickly, should an entire clutch hatch.   Brood reduction occurs regardless of food supply, the last-hatched chick insuring against the loss or infertility of an earlier-laid egg. High hatchability of the Least Flycatcher (90%), and the fact that adults can raise an entire clutch, suggest that this explanation does not apply.

In the "peak-load reduction" hypothesis, hatching asynchrony spreads out the peak demands of the individual nestlings, thus lowering the overall demands of the brood (Hussell 1972). However, considering the short hatching intervals passerines exhibit, the spread of nestling demands is likely to be inconsequential.

Clark and Wilson (1981) formalized the effects of predation in their "nest-failure" hypothesis. They viewed synchronous hatching as an adaptation to minimize the predation of nestlings by extending the time only eggs are in the nest. Their model assumed nestlings are more prone to predation than nests containing eggs. However, as the differential rate of predation between the two stages must be so high for complete synchrony to occur, most birds compromise and begin incubation with the penultimate egg. This hypothesis is difficult to relate to field data. Many birds suffer greater or equal rates of predation on eggs (Mead and Morton 1985, this study). This model also assumes incubation begins abruptly and a female could begin to incubate any time if it was advantageous, irrespective of physiological limitations. Incubation usually is initiated gradually (Morton and Pereyra 1985, this study). The "nest-failure" hypothesis seems plausible intuitively but its importance is difficult to evaluate.

In the "sibling-rivalry reduction" hypothesis, asynchrony is used to establish and maintain a dominance hier-

archy within a brood (Hahn 1981, Nuechterlein 1981). Wasteful aggression and competition are minimized, leading to efficient division of parental resources. The creation of the dominance hierarchy is through nestling-nestling interaction but the outcome is determined by the hatching sequence. Aggressive attacks between nestling Least Flycatchers were not witnessed during any nest watch (see Chapter II); therefore, this hypothesis can be dismissed.

Recently, Mead and Morton (1985) proposed that hatching asynchrony is an "epiphenomenon" resulting from the hormonal control of ovulation and incubation. Although what terminates ovulation and initiates incubation are not understood completely, it is thought prolactin is involved in regulating both events. Rapid increases in prolactin inhibits ovulation but simultaneously induces incubation behavior. As the increase in prolactin to terminate ovulation will necessarily occur with an egg in the oviduct, a bird begins incubation on the penultimate egg. If prolactin is released gradually, and if the mechanism for incubation behavior has a lower threshold than that of the termination of ovulation, then incubation may begin earlier. Hatching asynchrony is viewed as a consequence of a conservative endocrine system and not an adaptive feature. However, the manufacture and release of hormones is ultimately under genetic control. Thus, selection should still operate between varying degrees of asynchrony.

Timing of Breeding

Early nests were more successful, both in terms of the proportion of nests fledging, and the number of young fledging per nest, than those nests initiated later. They coincided with a period of increasing arthropod abundance while nests late in the season experienced a deteriorating food supply. Also, late nests possibly faced a greater risk of ectoparasitism by blood-feeding mites.

That early breeding is advantageous has been found in other species, and prompted Perrins (1965, 1970) to suggest birds are selected to breed as early as possible and that nesting even earlier is prevented by the individual's inability to obtain sufficient food to produce eggs. The advancement of laying by experimentally providing food supports this hypothesis (Kallander 1974, Bromssen and Jansson 1980, Newton and Marquiss 1981, Hogstedt 1981). However, in these studies laying was advanced by only a few days. The earlier laying by Least Flycatchers in 1985 followed a warm spring and early emergence of midges, suggesting the timing of nesting is determined by a combination of both environmental and endogenous factors. The timing of breeding in Yellow Warblers on the study area varies similarly (Goossen 1978).

In 1985 some successful early broods were followed by second nesting attempts. Known double-broods were initiated

in mid- to late July, a period of large midge emergences. Such late season emergences were absent in 1984 and it is tempting to speculate that the abundance of food in 1985 induced double-brooding at a time when most adults typically are leaving the study area for the wintering grounds (Sealy and Biermann 1983).

CHAPTER II

PARENTAL FEEDING OF NESTLING

LEAST FLYCATCHERS

INTRODUCTION

Feeding altricial young is probably the most demanding form of parental care adults must provide (Ricklefs 1974). Increasing nestling age and greater requirements in larger broods can lead to a compromise in parental care between more, low quality nestlings or fewer, high quality ones. Often the number of feeding trips increases with brood size, although not proportionally. Thus, individuals in large broods receive fewer feedings (Moreau 1947, Gibb 1950, Lack and Lack 1951, Royama 1966, Seel 1969, Walsberg 1978). Feeding rate by itself probably does not accurately reflect the energy supplied to the young (Royama 1966, Morehouse and Brewer 1968). Parental feeding can change by varying the food load, prey size, or prey type as well as the frequency of feeding trips. One or more of these variables have been addressed recently (Best 1977, Walsh 1978, Biermann and Sealy 1982, Johnson and Best 1982, Bedard and Meunier 1983, Meunier and Bedard 1984, Knapton 1984).

In Chapter I Least Flycatchers were found not to be raising the maximum number of young they are able to feed. Nestlings in broods of five grew and survived as well as nestlings from smaller broods. In this Chapter, the feeding and brooding of nestlings in relation to brood size and age are examined to determine if feeding strategies change as the demands of larger broods increase.

MATERIALS AND METHODS

Feeding Observations

Feeding rates were determined by observing Least Flycatcher nests with a 25-power spotting scope. Two-hour observation sessions were conducted in the morning (0630-0930 h), afternoon (1300-1600 h) and evening (1830-2100 h). Broods of 3, 4, and 5 nestlings were observed at ages of 2, 5, 8 and 11 days (Table 1). This observation method resulted in small sample sizes in each category. Because many nests were watched repeatedly, observation periods were not independent. In most cases, observation periods were divided proportionately over the day to minimize time effects. For practical reasons nests observed were lower (mean height $\pm$S.D.: 2.89+1.39m, N=22) than the mean nest height (mean height $\pm$S.D.: 4.08+2.29m, N=100; one- tailed t-test: t=2.34, d.f.=120, p<.05). Observations were not made during inclement weather since it is known to affect brooding and feeding behavior (Kendeigh 1952, Best 1977, Heagy and Best 1983).

Table 1. Number of hours of observation at Least Flycatcher nests in relation to age and brood size. Number of nests are given in parentheses. Data for 1984 and 1985 combined.

Age (days)	Brood size		
	3	4	5
2	8(3)	8(2)	8(3)
5	6(2)	8(4)	8(4)
8	10(4)	6(1)	8(3)
11	4(2)	8(3)	8(2)
Total	28(9)	30(8)	32(5)

At least one adult at each nest was banded (and usually also color-banded) and (or) painted for individual recognition (Table 2). Marked birds were females that were painted on the tail or head while they incubated. Birds were sexed by their behavior; only females incubate and brood (pers. obs.). Some females were sexed by the presence of a brood patch and a short flattened wing length, characteristic of females of this species (56.5-64.5 mm, Godfrey 1966).

For each feeding observation I recorded the sex of adult, time, number of prey items, and type of prey. The number of prey was estimated by counting the arthropods or parts of arthropods visible in the bill before they were fed to the nestlings. Larger food loads were subject to greater errors in estimation. When possible, the prey was identified to order or family. The identification of prey was biased towards larger items. However, 71.9% of the prey items delivered were identified, and all observations were made by the author.

Arthropod Sampling

Arthropod abundance was monitored in the territories of birds where feeding observations were made. After each observation bout, 40 sweeps were taken in and around the vicinity of the nest (see Chapter I, Arthropod Sampling). I sampled from the ground in areas where I had seen adults foraging earlier. Arthropod abundance, particularly Chiron-

Table 2. Number of nests at which feeding observations were made where male and female Least Flycatchers were individually marked or banded. Data from both years combined.

Males	Females		
	Banded	Painted	Unbanded/ unmarked
Banded	3	2	5
Unbanded	4	8	0

omidae, often is patchy and ephemeral on the ridge (Guinan 1985). Sampling immediately after each observation bout presumably reduced this variability. Samples were treated in the manner described earlier (Chapter I, page 22). The numbers and kinds of arthropods in each sample were then compared to the prey items fed to nestlings.

RESULTS

Feeding Rates and Prey Loads

The feeding rate by adult male and female Least Fly-catchers varied significantly with age but not brood size (Tables 3 and 4). The size of the load per feeding trip varied significantly with both brood size and nestling age (Tables 5 and 6). Males and females provided food approximately equally to the young (Table 7), except at two days of age in broods of five where the males provided more items. Young in larger broods did not seem to receive fewer items than young in small broods.

Food Items Available and Used

The number and kinds of arthropods male Least Fly-catchers fed to different-sized broods, and young of different ages are presented in Table 8. Observations were divided into broods of "young-nestlings" (YY: 2 and 5 days) and "old-nestlings" (OY: 8 and 11 days). Arthropod groups V to VII (see Table 8) were combined in the chi-square analysis

Table 3. Mean$\pm$S.E. feeding rates (trips per two h) by male Least Flycatchers in relation to brood size and age of nestlings. Number of two-h observation periods is given in parentheses.

Age (days)[2]	Brood size[1]		
	3	4	5
2	2.5+0.9 (4)	8.8+1.0 (4)	9.5+3.0 (4)
5	14.3+7.1 (3)	10.8+3.7 (4)	11.0+0.9 (4)
8	19.2+4.2 (5)	20.3+0.9 (3)	33.8+6.3 (4)
11	1.0 (2)	16.5+4.1 (4)	26.5+6.6 (4)

[1] Kruskal-Wallis test for brood size: x^2=4.43, d.f.=2, p>.05.
[2] Kruskal-Wallis test for age: x^2=18.2, d.f.=3, p<.05.

Table 4. Mean$\pm$S.E. feeding rates (trips per two h) by female Least Flycatchers in relation to brood size and age of nestlings. Number of two-h observation periods is given in parentheses. Sample size as in Table 3.

Age (days)[2]	Brood size[1]		
	3	4	5
2	7.3$\pm$4.1	16.0$\pm$5.1	1.5$\pm$1.0
5	20.0$\pm$1.7	19.8$\pm$3.4	15.5$\pm$5.0
8	30.8$\pm$7.2	25.0$\pm$1.0	22.8$\pm$2.8
11	23.0$\pm$7.0	31.5$\pm$4.9	19.5$\pm$3.9

[1] Kruskal-Wallis test for brood size: x^2=3.60, d.f.=2, p>.05.
[2] Kruskal-Wallis test for age: x^2=17.8, d.f.=3, p<.05.

Table 5. Mean number ($\pm$S.E., N in parentheses) of items brought per feeding trip by male Least Flycatchers in relation to brood size and age. Only feeding trips in which items could be counted are included.

Age (days)[2]	Brood size[1]		
	3	4	5
2	1.3$\pm$0.3 (4)	1.2$\pm$0.1 (24)	1.0$\pm$0.1 (18)
5	1.5$\pm$0.1 (31)	1.3$\pm$0.1 (28)	2.0$\pm$0.3 (25)
8	1.9$\pm$0.2 (79)	2.4$\pm$0.2 (55)	1.9$\pm$0.1 (95)
11	1.5$\pm$0.5 (2)	2.7$\pm$0.3 (44)	3.0$\pm$0.2 (86)

[1] Kruskal-Wallis test for brood size: x^2=7.83, d.f.=2, p<.05.
[2] Kruskal-Wallis test for age: x^2=64.7, d.f.=3, p<.05.

Table 6. Mean number ($\pm$S.E., N in parentheses) of items brought per feeding trip by female Least Flycatchers in relation to brood size and age. Only feeding trips in which items could be counted are included.

Age (days)[2]	Brood size[1]		
	3	4	5
2	1.1±0.1 (19)	1.1±0.1 (41)	1.0±0.1 (16)
5	1.3±0.1 (51)	1.4±0.1 (48)	2.0±0.2 (50)
8	1.5±0.1 (121)	2.0±0.2 (47)	1.7±0.1 (62)
11	2.1±0.2 (29)	1.9±0.1 (84)	3.6±0.3 (69)

[1] Kruskal-Wallis test for brood size: $x^2=40.5$, d.f.=2, p<.05.
[2] Kruskal-Wallis test for age: $x^2=71.2$, d.f.=3, p<.05.

Table 7. Food items brought to nestling Least Flycatchers by adult males and females in relation to brood size and age. Figures are means±S.E.

Brood size	Age	Items per two h		t	d.f.	p[1]	Total food items per nestling
		Males	Females				
3	2	2.8±0.9	7.8±4.5	1.080	6	NS	3.5
	5	19.0±9.5	25.7±4.2	0.648	4	NS	14.9
	8	33.8±7.0	43.4±6.9	0.981	8	NS	25.7
	11	1.5±0.5	39.5±12.5	3.040	2	NS	13.7
4	2	9.8±1.3	17.3±6.0	1.220	6	NS	6.8
	5	12.5±4.2	24.8±5.9	1.700	6	NS	9.3
	8	46.0±3.0	41.7±3.0	1.082	4	NS	21.9
	11	35.3±10.1	51.8±13.8	0.968	6	NS	21.8
5	2	9.5±3.0	1.5±1.0	2.530	6	p<.05	2.2
	5	17.5±3.6	28.0±11.5	0.869	6	NS	9.1
	8	55.8±13.4	34.8±3.2	1.520	6	NS	18.1
	11	69.8±13.3	64.8±23.0	0.188	6	NS	26.9

[1] Two-tailed t-test.

Table 8. Numbers of arthropods in each group fed by male Least Flycatchers to nest-lings in three brood sizes at two age classes. Percentages of all observed prey items are given in parentheses. YY are "young-nestlings" (2 and 5 days) and OY are "old-nestlings" (8 and 11 days).

Arthropod group	Brood size and age					
	3YY	4YY	5YY	3OY	4OY	5OY
I. Chironomids and Culicids	28 (56)	24 (38)	56 (81)	129 (83)	214 (86)	411 (93)
II. Other Diptera	11 (22)	4 (6)	3 (4)	10 (6)	17 (9)	12 (3)
III. Geometrid larvae	5 (10)	20 (32)	8 (12)	4 (3)	5 (2)	4 (1)
IV. Adult Lepidoptera and Trichoptera	3 (6)	1 (2)	1 (1)	4 (3)	1 (0)	3 (1)
V. Ephemeroptera	0 (0)	9 (14)	0 (0)	0 (0)	5 (2)	1 (0)
VI. Odonata	0 (0)	0 (0)	0 (0)	4 (3)	5 (2)	6 (1)
VII. All Other Insecta	0 (0)	1 (2)	1 (0)	2 (1)	3 (1)	0 (0)
VIII. Araneida	3 (6)	4 (6)	0 (0)	2 (1)	0 (0)	3 (1)
Feeding trips with unident-ified prey	18	26	39	17	29	62
Total number of feeding trips observed	53	78	82	98	127	241

to decrease the number of cells with expected frequencies of less than five (Mendenhall 1979).

Males fed young and old nestlings in each brood size significantly different proportions of each arthropod group (YY: x^2 =53.4, d.f.=10, p<.05; OY: x^2=27.1, p<.05). Broods of four YY were fed more geometrid larvae and ephemeropterans, but fewer chironomids and culicids, than broods of three and five. Males brought OY in broods of five more chironomids and culicids, and fewer geometrid larvae and other dipterans than OY in broods of three and four. Males also brought significantly different proportions of items in each group of young compared to old-nestlings (broods of three: x^2=24.1, d.f.=5, p<.05; broods of four: x^2=95.2, p<.05; broods of five: x^2=30.7, p<.05). In all brood sizes, chironomids and culicids were brought more frequently to OY and geometrid larvae more frequently to YY.

At both ages, females brought significantly different proportions of arthropods to each brood size (YY: x^2=31.0, d.f=10, p<.05; OY: x^2=30.8, p<.05)(Table 9). Young-nestlings in broods of five were brought more chironomids and culicids; broods of four received more geometrid larvae, broods of three more other dipterans. Again, significant differences were found between arthropods fed to young, versus old-nestlings in each brood size (broods of three: x^2 =34.8, d.f.=5, p<.05; broods of four: x^2=37.6, p<.05; broods of five: x^2=13.1, p<.05). Young-nestlings in broods

Table 9. Numbers of arthropods in each group fed by female Least Flycatchers to nestlings in three brood sizes at two age classes. Percentages of all observed prey items are given in parentheses. Arthropod groups and nestling age as in Table 8.

Arthropod group	Brood size and age					
	3YY	4YY	5YY	30Y	40Y	50Y
I. Chironomids and Culicids	57 (65)	73 (65)	87 (87)	217 (89)	205 (81)	328 (95)
II. Other Diptera	9 (10)	5 (4)	3 (3)	14 (6)	28 (11)	10 (3)
III. Geometrid larvae	8 (9)	22 (19)	1 (1)	5 (2)	8 (3)	8 (2)
IV. Adult Lepidoptera and Trichoptera	2 (2)	3 (3)	3 (3)	5 (2)	2 (1)	4 (1)
V. Ephemeroptera	0 (0)	4 (4)	0 (0)	0 (0)	1 (0)	0 (0)
VI. Odonata	0 (0)	0 (0)	1 (1)	0 (0)	3 (1)	1 (0)
VII. All Other Insecta	6 (7)	3 (3)	3 (3)	1 (0)	4 (2)	1 (0)
VIII. Araneida	6 (7)	3 (3)	2 (2)	3 (1)	2 (1)	1 (0)
Feeding trips with unidentified prey	20	55	18	52	74	45
Total number of feeding trips observed	89	143	68	200	184	169

of three and four were brought more geometrid larvae and
fewer chironomids and culicids than OY; YY in broods of five
were fed proportionately fewer chironomids and culicids than
OY.

No significant inter-sexual differences in proportions
of food items brought to old-nestlings were found (broods of
three: x^2=6.99, d.f.=5, NS; broods of four: x^2=7.94, NS;
broods of five: x^2=5.36, NS). Males fed YY in broods of
four and five more geometrid larvae than they did broods of
three. No inter-sexual differences were significant in
broods of three young-nestlings (broods of three: x^2=8.11,
d.f.=5, NS; broods of four: x^2=13.5, p<.05; broods of five:
x^2=12.2, p<.05).

Estimates of prey availability from sweep-net samples
were compared to prey fed to the nestlings, by the Wilcoxon
matched-pairs signed-ranks test (Siegel 1956)(Figures 1 and
2). Adults selectively fed nestlings more chironomids and
culicids (T=11.5, p<.05) and more geometrid larvae (T=0,
p<.05) than expected. Other dipterans (T=0, p<.05) and all
other insects (T=0, p<.05) were selected in proportions less
than those represented in sweep net samples. Araneida
(T=19, p>.05) and adult lepidopterans and trichopterans
(T=32, p>.05) were taken in proportion to their abundance in
sweep net samples.

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Figure 1.   Proportion of arthropods in each group
             (I-VIII) in sweep net samples, and the
             proportion of arthropods in each group
             observed being fed to "young" (two and
             five days) Least Flycatchers in broods
             of three, four, and five, by adult males
             and females combined. Absolute numbers
             are given on the sides. Arthropod groups
             as in Table 8.

Available   Used

I	1512	85
II	643	20
III	6	13
IV	59	3	5
V	1	0
VI	6	0
VII	429	6
VIII	130	9

3658   97
1112   9
27   42
136   4   4
10   13
10   0
1273   4
258   7

16965   143
1214   6
59   9
217   5   4
25   0
11   1
921   4
503   2

80 60 40 20 0 20 40 60 80

Proportion in sample %   Proportion in diet %
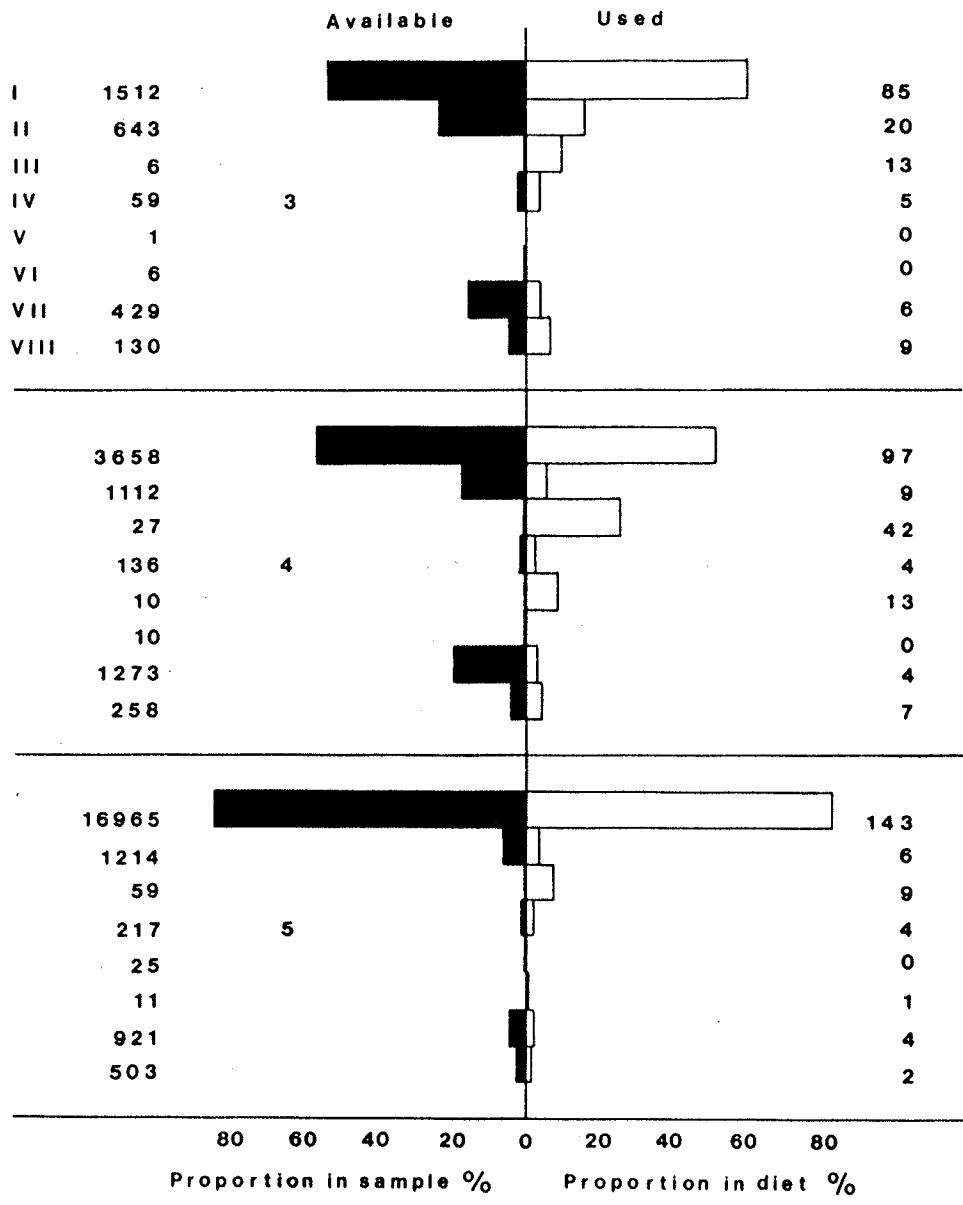
Figure 2.   Proportion of arthropods in each group
            (I-VIII) in sweep net samples, and the
            proportion of arthropods in each group
            observed being fed to "old" (8 and 11 days)
            Least Flycatchers in broods of 3, 4, and
            5, by adult males and females combined.
            Absolute numbers are given on the sides.
            Arthropod groups as in Table 8.

Available   Used

I   6531   346
II   707   24
III   33   9
IV   165   3   9
V   14   0
VI   6   4
VII   1408   3
VIII   381   5

1046   419
1161   45
14   13
110   4   3
1   6
11   8
865   7
218   2

18011   739
716   22
35   12
470   5   7
2   1
13   7
879   1
176   4

          80   60   40   20   0   20   40   60   80

     Proportion in sample %   Proportion in diet %
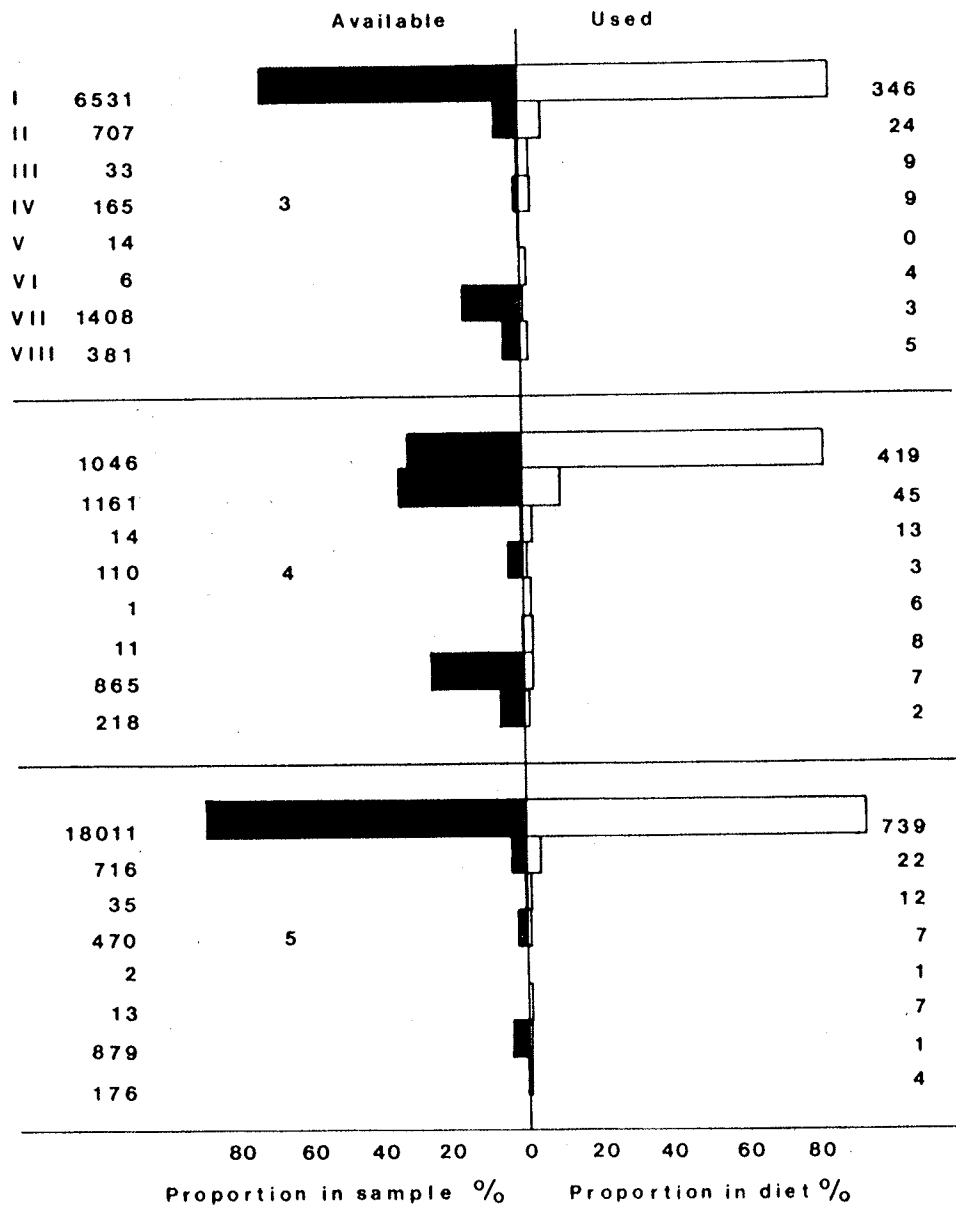
Brooding Time

Only female Least Flycatchers brooded nestlings. The mean time spent brooding per two-hour observation session decreased significantly as the nestlings grew older but did not vary significantly with brood size (Table 10).

DISCUSSION

Parental Care in Relation to Brood Size

Adult male and female Least Flycatchers responded to larger broods by varying both the frequency of feeding trips and the number of prey items they brought each trip. The nestlings' diet was similar in all brood sizes except that broods of five were brought geometrid larvae less frequently than were broods of three or four. There was no indication that nestlings in larger broods recieved fewer food items than those in smaller broods.

The fewer geometrid larvae brought to nestlings in broods of five may indicate a change in the pattern of provisioning. Geometrid larvae were selected for young-nestlings. The reduced delivery rate suggests that parents had difficulty locating adequate numbers of geometrid larvae, thus they substituted greater quantities of the more abundant chironomids. However, it seems unlikely that parental feeding abilities are exceeded when their nestlings are so young, even for large broods.

Table 10. Mean$\pm$S.E. brooding time (s) per two h by female Least Flycatchers in relation to brood size and age. Sample sizes as in Table 3.

Age (days)[2]	Brood size[1]		
	3	4	5
2	4710$\pm$444	5448$\pm$564	5424$\pm$414
5	3024$\pm$2046	3834$\pm$1296	4458$\pm$480
8	852$\pm$360	858$\pm$828	1482$\pm$1290
11	0	348$\pm$348	1308$\pm$762

[1] Kruskal-Wallis test for brood size: x^2=0.65, d.f.=2, p>.05.
[2] Kruskal-Wallis test for age: x^2=25.9, d.f.=3, p<.05.

Division of Parental Care

Male and female Least Flycatchers provisioned the young nearly equally. There were few inter-sexual differences in the type of prey delivered. Males brought more geometrid larvae to broods of three and four than did females.

At 6 of the 22 nests observed the male made less than 4 feeding trips per 2 hours. The variable participation by males among nests has been reported previously (Heagy and Best 1983, Knapton 1984, McGillivray 1984). This variation in Least Flycatchers at Delta Marsh may be due to the occurrence of polygyny. In 1985, a marked male was observed feeding two broods concurrently. One nest was visited frequently, while the other was tended irregularly. The division of labor found in Least Flycatchers closely parallels that observed in other essentially monogamous passerines (Knapton 1984, Biermann and Sealy 1982, Heagy and Best 1983, Bedard and Meunier 1983, Johnson and Best 1982).

Nestling Diet

Generally, Least Flycatchers selected the items they brought to their nestlings. Young-nestlings were fed a greater percentage of geometrid larvae than that present in sweep net samples, while old-nestlings were fed chiefly chironomids and culicids. Both chironomids and geometrid larvae were preferentially selected from the available arthro-

pods.   The   other prey groups were   taken in equal   or less
than expected proportions to that   collected in   sweep sam-
ples.

Yellow Warblers on the dune-ridge study area similarly
fed geometrid larvae to broods of young nestlings (Biermann
and Sealy 1982).   Adult chironomids and culicids,   on the
other hand,   predominated in the diet of older nestlings.
Changes in the diet as nestlings grow older have been found
in other species (e.g., Bedard and Meunier 1984, Knapton
1984).

Geometrid larvae are soft-bodied and selected presum-
ably for their easy digestability.   Chironomids have soft
abdomens and because they are lethargic (Busby 1978) are
easy prey for a foliage gleaning bird. Other groups such as
hemipterans, coleopterans and other dipterans generally have
harder exoskeletons. The predominance of chironomids in the
nestling diet reflects partly their suitability and avail-
ability, and partly the biases in the observation methods.
Myers et al (1980) addressed the problems most studies face
in relating field samples with diet samples.   For example,
geometrid larvae are under-represented in sweep-net samples
taken low in the canopy (Busby and. Sealy 1979).   Although
adult Least Flycatchers select the prey items they bring to
their nestlings, they probably remain opportunistic and re-
spond to local or temporary increases in the abundance of
other palatable items.

In summary, Least Flycatchers divide parental care between the sexes and adjust the feeding of nestlings according to the changing demands of age and brood size.   Prey items are preferentially selected, perhaps for easy digestability and (or) nutritional content.

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APPENDIX I. Development of plumage in nestling Least Flycatchers.

Age (days)	Plumage and other characteristics
0	downy neossoptiles on all feather tracts, skin orange-yellow, viscera visible through abdominal wall, eyes closed.
2	feather tracts turn gray, feather follicles visible as bumps under the skin, eyes closed.
4	pin feathers emerge from skin on ventral tract and beginning to emerge on crural, femoral, humeral and interscapular tracts, skin gray but viscera and muscles still visible, eyes closed.
6	pin feathers emerging on all feather tracts, feathers beginning to emerge from sheaths on humeral, ventral, crural, femoral and interscapular tracts, eyes beginning to open.
8	all feather tracts unsheathing, secondaries and most primaries unsheathing, emerging remiges buffy color, eyes opening.
10	two buffy, white wing bars evident, rectrices unsheathing, eyes wide open, beginning to crawl away when handled.

APPENDIX II. Summary of Least Flycatcher nest-site characteristics, Delta Marsh, Manitoba.

Nest tree	Percent frequency (N)	Mean dbh[1] (cm) [$\bar{x}$+S.D. (N)]	Mean nest height (m)	Mean nest-tree height (m)	Relative nest height[2]
Manitoba maple (Acer negundo)	43.6 (98)	13.6+10.1 (34)	4.8+2.6	9.3+4.6	0.54+0.19
Green ash (Fraxinus pennsylvanica)	29.3 (66)	13.9+6.3 (27)	5.5+1.7	10.4+3.1	0.54+0.13
Sandbar willow (Salix interior)	22.7 (51)	5.4+1.4 (36)	2.2+0.6	4.6+0.6	0.48+0.12
Peach-leaved willow (S. amygdaloides)	3.6 (8)	11.3+4.4 (3)	5.1+1.4	8.5+0.5	0.61+0.19
Eastern cottonwood (Populus deltoides)	0.4 (1)	-	-	-	-
Choke cherry (Prunus virginiana)	0.4 (1)	-	-	-	-
Total	100.0 (225)	10.7+7.9 (100)	4.1+2.3	7.9+4.1	0.52+0.15

[1] Diameter breast height

[2] Nest height ÷ nest-tree height