DETERMINATION OF CLUTCH SIZE IN THE LEAST FLYCATCHER

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Abstract.—We examined three factors (predation rate, incubation ability, and feeding ability) that might limit clutch size in the Least Flycatcher (*Empidonax minimus*) in an area where large emergences of midges (Chironomidae) provided abundant food for adults and nestlings. Clutch size ranged from two to five eggs, but clutches of four were most frequent (78.6% of 192 clutches) during our study. Rate of nest predation was not correlated with either clutch or brood size which suggests that Least Flycatchers did not lay smaller clutches in order to minimize predation. Incubation efficiency declined as clutch size increased, but both natural and experimental clutches of five produced more hatchlings than clutches of four. Brood size was not limited by incubation ability of females. Least Flycatchers successfully raised broods larger than the modal clutch size; neither growth rates (as measured by mass and tarsus length) nor relative survival after fledging (as indicated by frequency of recapture in mist nets) varied with brood size. We suggest several alternative hypotheses to explain why larger clutches were not more common in this local area of food abundance. *Received 18 February 1988, accepted 14 December 1988.*

LACK (1954) proposed that clutch size in altricial birds is determined by the maximum number of young that parents can feed adequately. One testable prediction of this hypothesis is that modal clutch size also should be the most productive. Nonetheless, brood enlargement experiments designed to test the "food-limitation" hypothesis have been equivocal (see summary in Lessells 1986). In some species, broods with extra young fared worse than young in normal-sized clutches (e.g. Mourning Dove, *Zenaida macroura*, Westmoreland and Best 1987), while in others, enlarged broods produced more surviving young (e.g. Blue Tit, *Parus caeruleus*, Nur 1984a). Although enlarged broods sometimes were more productive, young from these nests often fledged at below average mass (e.g. European Starling, *Sturnus vulgaris*, Crossner 1977). Because postfledging survival is correlated positively with prefledging mass (Perrins 1965), an increase in the number of fledglings does not in itself disprove the food-limitation hypothesis. Only when brood-enlargement experiments produce more surviving offspring can this hypothesis be rejected (Lack 1954).

The ability to provide food for a growing brood is probably the most fundamental factor governing clutch size in altricial birds. However, several alternative hypotheses have been proposed to explain why some birds seem capable of raising enlarged broods (see review in Murphy and Haukioja 1986). By manipulating clutches and broods, we tested three factors that might constrain clutch size in Least Flycatchers (*Empidonax minimus*).

First, we recorded the risk of predation in relation to clutch size, because selection might favor reduced clutches if predation falls disproportionately upon large clutches (Skutch 1949). Large clutches could experience higher predation rates for various reasons (see review in Slagsvold 1982a). For example, laying larger clutches necessitates a longer nesting cycle and, as a result, increases the duration of exposure to predators. Larger broods also might attract more predators if they require larger and more conspicuous nests (Snow 1978) or if parents must increase the number of trips to and from the nest (Skutch 1949).

Second, we increased clutch size to determine if brood size was limited by the inability of females to incubate a larger number of eggs. Although most birds are able to hatch more chicks in experimentally enlarged clutches (e.g. American Coot, *Fulica americana*, Fredrickson 1969; Fieldfare, *Turdus pilaris*, Slagsvold 1982b), some apparently cannot (e.g. Long-tailed Skuas, *Stercorarius longicaudus*, Andersson 1976; various Charadrii, Hills 1980). In the latter species, the number of eggs laid by a female corresponds to the maximum she can successfully incubate or brood; the upper limit is below that which could be raised (Lack 1947, Cody 1966).

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Finally, we increased brood size to determine whether clutch size was limited by the brood-rearing ability of adult Least Flycatchers. Because feeding demands of fledglings may exceed those of nestlings (e.g. Morehouse and Brewer 1968), we used both growth rates of nestlings and their relative survival to independence as measures of brood-rearing success.

METHODS

Study area.—The Least Flycatcher is a small, insectivorous passerine that nests at high densities in the dune-ridge forest at Delta Marsh, Manitoba (see MacKenzie 1982). This area is characterized by large, periodic emergences of adult midges (Chironomidae; see Fig. 1) which form the major component of both adult (Pohajdak 1988) and nestling diets (Briskie 1985). Clutches are initiated in late May and early June and in most years coincide with the first large emergences of midges (unpubl. data). A detailed description of breeding chronology and migration in this population is given by Sealy and Biermann (1983).

Flycatchers built compact, open-cup nests in crotches or saddled on limbs of deciduous trees at heights ranging from 1.0 to 11.7 m ($\bar{x} \pm$ SE: 4.1 $\pm$ 0.2 m, $n =$ 100). Nests were located by searching suitable breeding habitat within a 3-km length of the dune-ridge forest. We monitored 348 active nests (i.e. containing at least one egg) from 1984 to 1986. In 1987, we used 19 additional nests in clutch-size manipulations.

Seasonal change in arthropod abundance was determined by taking three sweep-net samples once every 5 days from clutch initiation (late May) until the end of the breeding season (mid-August). Each sample consisted of 40 non-overlapping sweeps through the vegetation with a 37-cm diameter net at heights of 0.5 to 4.0 m. Counts from the three samples were averaged to estimate arthropod abundance on that day. All estimates were normalized by log transformation.

Nest success.—Upon discovery, each nest was flagged with numbered tape and visited every 1–3 days to monitor progress. As some nests were located after clutch initiation, we calculated nesting success using the Mayfield (1975) method. To test the nest-predation hypothesis, we compared differences in daily survival probabilities among clutch sizes (Hensler and Nichols 1981). Differences were deemed significant at a level of $P < 0.10$ because this test is prone to Type II error (Hensler and Nichols 1981). Separate survival estimates were calculated for egg laying, incubation, and nestling periods. The *incubation period* was defined as the time from laying of the final egg to hatching of the first nestling. The *nestling period* was the time from hatching of the first nestling to fledging of the last nestling. These are not standard definitions of nestling and incubation periods but
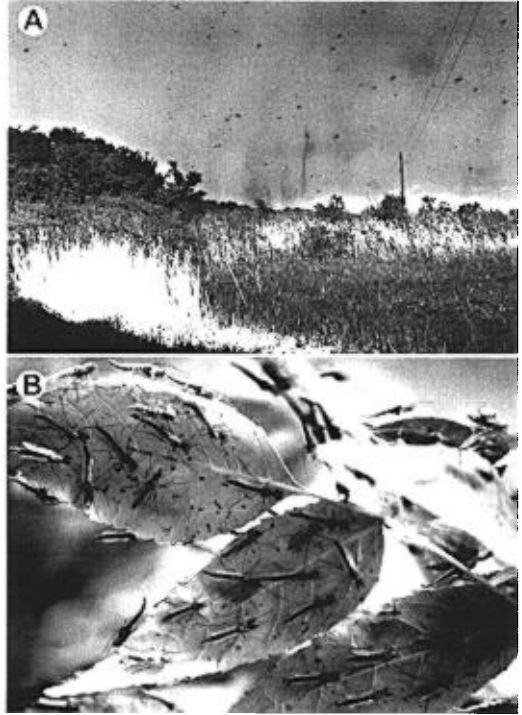
Fig. 1. (A) Adult chironomids swarming along the southern edge of the dune-ridge forest, Delta Marsh, Manitoba, June 1986. (B) Adult chironomids on foliage of dune-ridge forest.

represent instead the periods with or without nestlings, respectively. We felt this division was more appropriate because it reflects two periods of very different levels of parental activity.

Clutch size.—To avoid including clutches reduced by partial nest predation or egg loss, we recorded clutch size only in nests visited during laying or within the first 5 days after clutch completion. Although clutch size still might be underestimated by loss of one or more eggs during laying or early incubation, observations of egg losses in nests monitored closely during this period indicated this error was small. We visited 106 nests daily during laying and only 5 (4.7%) experienced partial clutch loss, compared to 26 (24.8%) clutches which were completely removed.

We excluded nests parasitized by Brown-headed Cowbirds (*Molothrus ater*) from the analysis because cowbirds sometimes remove host eggs (Friedmann 1963). Least Flycatchers accept cowbird eggs (Briskie and Sealy 1987a); thus, all other clutches probably were not altered through unobserved parasitism.

Hatching success and incubation ability.—Under the incubation-ability hypothesis, the modal clutch size of four eggs (see later) should produce the greatest number of hatchlings. To examine this possibility, we

recorded hatching success in natural clutches of three, four and five eggs. In 1987, we tested the ability of Least Flycatchers to incubate five eggs by adding one or two eggs to 19 nests during laying or early incubation. Hatching success was defined as number of young that hatched relative to number of eggs present just before hatching began.

Growth and survival in relation to brood size.—We measured growth and survival of nestlings to determine if modal brood size was most productive. Upon hatching, all nestlings in a random sample of each brood size were marked individually with nontoxic felt ink. The day the first nestling hatched was defined as Day 0. Beginning at Day 2, all nestlings were measured every 48 h ($\pm$1 h) to 10 days post-hatching (mean nestling period: 14.9 $\pm$ 0.2 days, n = 36). Hatching was asynchronous, and the day nestlings were measured corresponds only to the age of the first-hatched young. Because length of hatching spread increased with clutch size (Briskie and Sealy 1989), larger broods contained younger last-hatched nestlings than smaller broods. Taking an average of all young in a brood would have spuriously depressed mean nestling size in larger clutches, so we compared growth rates between broods by using the mean of only the three oldest nestlings within each brood. Hatching sequence did not affect growth rates within a brood size (Briskie and Sealy 1989), so we felt justified in restricting our analysis in this manner.

We used mass and tarsus length to estimate growth rate. Nestling mass was recorded to the nearest 0.1 g with a triple beam balance from 24 to 30 June 1984, and with an Ohaus digital scale for the remainder of 1984 and all of 1985. Young were not weighed in 1986 or 1987. Nestlings were induced to defecate by handling before being weighed. Tarsus length was measured to the nearest 0.1 mm with sliding calipers. Each nestling was banded with a numbered aluminum band and a year-specific color band. There were no differences in growth rates between 1984 and 1985, so data were combined in further analyses.

In 1985, seven broods of five nestlings were created by transferring a single nestling within 4 h after it hatched. Young were added to broods of four such that normal hatching asynchrony was maintained as closely as possible. Transferred nestlings came from a variety of hatching sequences but all were placed into foster nests as "last-hatched" nestlings. All were accepted by their foster parents.

To compare the growth of nestlings in relation to brood size we fitted growth curves to the logistic equation,

$$M(t) = A \cdot (1 + \exp[-K (t - I)])^{-1}$$

where $M(t)$ is size at time t, A is the asymptote, K is the growth-rate constant, and I is age at the inflection point. In a logistic curve the inflection point (i.e. point of maximum growth rate) occurs at $\frac{1}{2}$ asymptotic size. Growth-rate constants and age at inflection points

were compared among brood sizes with Tukey's multiple range test (Sokal and Rohlf 1969). We found no differences between the few natural broods of five and those we created, so they were combined in further analyses. A few nests in 1985 were heavily infested with ectoparasitic mites (*Ornithonyssus sylviarum*). As the mites obviously affected growth and survival, we excluded these broods from our analysis (see Briskie and Sealy 1989 for discussion of these nests).

Asymptotic mass was obtained by recapturing fledglings from nests studied earlier. There were no differences in fledgling mass among brood sizes (ANOVA: F = 0.18; df = 2, 38; P = 0.84), so all data were combined to calculate a single asymptote (10.45 $\pm$ 0.11 g, n = 41). Asymptotic tarsal lengths were measured on 25 adult Least Flycatcher study skins collected at Delta Marsh and housed in the University of Manitoba Zoology Museum collection. We assumed asymptotic tarsal length was the same for both sexes and for all brood sizes.

We estimated relative survival of young after fledging by using recapture frequencies of banded nestlings known to have fledged. All fledglings were recaptured during routine mist-netting on the study site. Six to 10 nets were run for ca. 6–8 h each day. Nets were set across the entire length of the study area from mid-May through early September each year (except 1987) but netting was not conducted on windy or rainy days. Only fledglings recaptured after 12 days postfledging were included in the analysis as young were still fed by their parents to this age (pers. obs.). Some fledglings remained on the study area up to 40 days after fledging. We assumed all fledglings had an equal probability of being netted and that the proportion of young recaptured from each brood size was an indication of their relative survival. Only a few young return to breed on our study area and we could not determine if brood size affected survival to first breeding.

Analyses followed standard statistical texts (e.g. Sokal and Rohlf 1969). All tests were two-tailed. Standard error of the mean (SE) was calculated for all mean values.

RESULTS

Clutch size.—Least Flycatchers laid two to five eggs per clutch, but four-egg clutches were the most frequent (Table 1). Clutches of five were rare (6.8% of 192 clutches) and restricted to early nesting attempts. Most clutches initiated after the first 2 weeks of the breeding season were renests of nesting attempts that had failed earlier (as indicated by a small sample of marked birds), although at least two nests were known to be second broods (Briskie and Sealy 1987b).

TABLE 1. Least Flycatcher clutch size at Delta Marsh, Manitoba, from 1984 to 1986 combined. Breeding season is divided into five 10-day periods, beginning on day of first clutch initiation.

Days since clutch initiated[1]	Clutch size				Clutch size ($\bar{x} \pm$ SE)
	2	3	4	5	
1–10	0	4	81	11	4.07 ± 0.04
11–20	0	10	44	2	3.86 ± 0.06
21–30	0	5	13	0	3.72 ± 0.11
31–40	1	2	6	0	3.56 ± 0.24
After 40	0	6	7	0	3.54 ± 0.14
Total	1	27	151	13	3.92 ± 0.03

[1] Day 1 corresponds to 3 June 1984, 29 May 1985, and 28 May 1986.

A single clutch of two eggs was laid in 1984, but this nest was unusual because earlier the female had incubated a clutch of four nonviable eggs 10 days beyond the normal incubation period (see Briskie and Sealy 1988).

Clutch size did not vary among years (Kruskal-Wallis: $H = 0.90$, df $= 2$, $P = 0.64$). Clutch size decreased as the season progressed in 1984 (Spearman's rank correlation coefficient: $r = -0.41$, $P = 0.001$, $n = 66$) and 1985 ($r = -0.41$, $P < 0.001$, $n = 87$), but not in 1986 ($r = -0.26$, $P = 0.11$, $n = 39$). Smaller clutches in renests possibly accounted for most of the seasonal decline, although some first nests contained only three eggs. Seasonal decline in clutch size could also reflect a decline in food availability. Once clutch initiation began, arthropod abundance declined over the season in 1984 ($r = -0.85$, $P < 0.001$) and 1986 ($r = -0.70$, $P = 0.008$), but not in 1985 ($r = -0.29$, $P = 0.29$); thus, only in one year did the decrease in food availability coincide with a seasonal decline in clutch size.

Hatching success.—To test whether handling

TABLE 3. Survival of Least Flycatcher nests in relation to clutch size and stage of nesting cycle. Natural and experimental broods of five were combined in analyses. No differences in daily survival probabilities (DSP) were significant.

Nest period	Nests (n)	Failures (n)	DSP ± SE	Estimated success[1] (%)
Incubation				
3 eggs	47	14	0.964 ± 0.0094	64
4 eggs	176	55	0.966 ± 0.0045	67
5 eggs	15	3	0.977 ± 0.0126	76
Nestling				
3 nestlings	59	20	0.960 ± 0.0088	54
4 nestlings	76	16	0.977 ± 0.0055	71
5 nestlings	14	5	0.967 ± 0.0145	61
Combined				
3	74	34	0.962 ± 0.0064	30[2]
4	179	71	0.970 ± 0.0035	38
5	20	8	0.972 ± 0.0097	38

[1] Calculated using egg-laying, incubation, and nestling periods given in Results.
[2] Includes DSP ± SE for egg-laying period: 0.953 ± 0.0098 (188 nests, 22 failures).

of eggs reduced hatchability, we examined all unhatched eggs in experimental nests for embryonic development. Of 14 experimental nests that survived to hatching, 10 contained unhatched eggs. Embryonic development was apparent in unhatched eggs in 5 of these nests. Moreover, in 5 nests where eggs showed no embryonic development, 3 were laid by the host female. Only in 2 nests did the added eggs neither hatch nor exhibit embryonic development. Excluding these nests from analyses did not affect the outcome; thus, we do not feel our manipulations significantly affected hatchability.

Because only a few natural clutches of five

TABLE 2. Hatching success in the Least Flycatcher in relation to clutch size. Values from all years combined for unmanipulated clutches. Experimental clutches were from 1987 only.

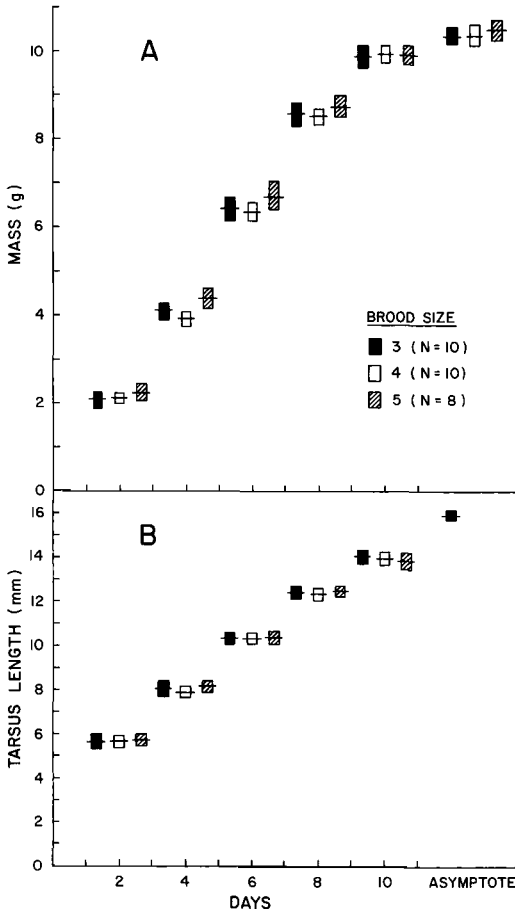|	Clutch size at hatching				
			5		
	3	4	Unmanipulated	Experimental	Combined
Number of nests	29	75	9	14	23
Clutches with complete hatch (%)	79.3	82.7	55.9	35.7	43.5
Eggs hatching (%)	92.0	95.0	86.7	82.9	84.3
Brood size at hatching ($\bar{x} \pm$ SE)	2.76 ± 0.09	3.80 ± 0.04	4.33 ± 0.31	4.14 ± 0.21	4.22 ± 0.16

Fig. 2. Growth of Least Flycatchers in broods of three, four and five nestlings for (A) mass and (B) tarsus length. Rectangles are $\bar{x} \pm$ SE. The asymptote for tarsus length represents a composite measure from 25 male and female adult flycatchers collected on the study area. Brood size was not known for these birds.

survived to hatching in a given year, we had to combine control nests from all years. Hatching success did not differ among years in either clutches of four (Kruskal-Wallis: $H = 0.92$, df =

2, $P = 0.63$) or three ($H = 4.9$, df = 2, $P = 0.10$). It is unlikely that combining data from clutches of five introduced any bias to our results. We recorded no differences in hatching success ($x^2 = 0.08$, $P > 0.70$) or brood size at hatching (Mann-Whitney: $U = 72.5$, $P > 0.05$) between unmanipulated and experimental clutches of five, and both were combined in further analyses (Table 2).

Number of hatchlings varied with clutch size (Table 2; Kruskal-Wallis: $H = 62.8$, df = 2, $P < 0.001$). Clutches of five produced more hatchlings than clutches of four (Mann-Whitney: $U = 1413$, $z = 2.90$, $P = 0.004$), which in turn produced more than clutches of three ($U = 602$, $z = 7.70$, $P < 0.001$). Although clutches of five produced the most hatchlings, both proportion of eggs hatching per clutch ($x^2 = 12.9$, df = 2, $P < 0.01$) and proportion of clutches hatching all eggs ($x^2 = 14.7$, df = 2, $P < 0.01$) decreased with increasing clutch size (Table 2).

Nesting success.—Clutch size did not affect either length of incubation (clutches of three: 12.1 ± 0.2 days, $n = 16$; clutches of four: 11.9 ± 0.1, $n = 53$; clutches of five: 11.8 ± 0.2, $n = 6$; Tukey's multiple range test: $P < 0.05$ for all comparisons) or nestling periods (three: 15.2 ± 0.2, $n = 10$; four: 14.8 ± 0.3, $n = 20$; five: 14.8 ± 0.5, $n = 6$; $P < 0.05$ for all comparisons). Clutches of five required longer to lay (4.5 ± 0.3, $n = 4$) than either clutches of four (3.3 ± 0.1, $n = 56$) or three (2.6 ± 0.2, $n = 18$; $P < 0.05$ for all comparisons). Consequently, larger clutches were exposed to potential predators for a greater period.

Daily survival probabilities did not differ among different-sized clutches during either incubation or nestling periods or when both periods were combined (Table 3). When laying period was included, overall estimated nesting success was identical for clutches of four and five, and only slightly less for clutches of three (Table 3).

TABLE 4. Fledgling production in control and experimental Least Flycatcher nests at Delta Marsh, Manitoba. Data from 1985 only.

	Clutch size at laying			Experimental broods of 5
	3	4	5	
Nests (*n*)	9	33	4	7
Brood size at fledging ($\bar{x} \pm$ SE)	2.78 ± 0.15	3.27 ± 0.14	3.50 ± 0.29	4.71 ± 0.20
Range of brood size at fledging	2–3	1–4	3–4	4–5
Fledglings/nest attempt[1] ($\bar{x}$)	0.83	1.24	1.33	—

[1] Mean brood size at fledging × estimated probability of success from Table 3.

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TABLE 5. Growth-rate constants (K) and inflection point estimates (I) for mass and tarsus length of Least Flycatcher nestlings in relation to brood size. Within a column, values with the same letter are not significantly different (Tukey's multiple range test).

Brood size	Growth-rate constant $(K \pm SE)$		Day of inflection point $(I \pm SE)$	
	Mass	Tarsus	Mass	Tarsus
3	0.504 ± 0.019 A	0.316 ± 0.009 A	4.93 ± 0.19 A	3.93 ± 0.15 AB
4	0.505 ± 0.018 A	0.314 ± 0.011 A	4.97 ± 0.09 A	3.96 ± 0.09 A
5	0.499 ± 0.022 A	0.327 ± 0.011 A	4.58 ± 0.16 A	3.47 ± 0.18 B

Fledging success.—Brood enlargement experiments were done only in 1985, and data from this year were analyzed separately. Mean brood size at fledging varied with clutch size (Table 4; Kruskal-Wallis: $H = 17.1$, df $= 2$, $P < 0.001$). Experimental clutches of five produced more offspring than clutches of four (Mann-Whitney: $U = 204$, $z = 3.47$, $P = 0.0005$), which in turn produced more offspring than clutches of three $(U = 132$, $z = 2.05$, $P = 0.04)$. Experimentally enlarged broods of five also produced more offspring than natural clutches of five $(U = 119, z = 2.75, P < 0.01)$, but this was the result of lower initial brood sizes at hatching in unmanipulated clutches (see Table 2; all experimental broods began with five hatchlings).

Effect of brood size on growth and survival.— Growth rates (K) did not vary with brood size for either mass or tarsus length (Fig. 2, Table 5). The time to the inflection point (I) in mass was not affected by brood size; however, broods of five reached the inflection point for growth in tarsus length sooner than broods of four (Table 5). This result is opposite to that expected if increased brood size negatively affects growth.

Recapture frequency of young after fledging did not vary significantly with brood size (broods of three: 25.6%, $n = 86$; broods of four: 30.5%, $n = 95$; broods of five: 29.6%, $n = 27$; $\chi^2 = 1.98$, df $= 2$, $P > 0.05$). We believe that relative survival after fledging was similar in all brood sizes.

DISCUSSION

Experimentally enlarged broods of five produced the most young, which grew and survived as well as young in smaller broods. This suggests that broods of five were the most productive in the dune-ridge forest. However, in all years of our study, four-egg clutches were the most frequent. Contrary to the food-limi-

tation hypothesis, Least Flycatchers did not raise the maximum number of young they could feed during a single nesting attempt. The ability to feed an enlarged brood adequately does not limit clutch size and cannot explain why Least Flycatchers do not lay five eggs more frequently.

Our observations indicated that clutch size was not limited by the ability of females to incubate a larger number of eggs. Least Flycatchers successfully incubated clutches larger than the modal size, and although hatching efficiency declined with both larger natural and experimental clutches, the greatest number of hatchlings was produced from clutches of five. In this respect, Least Flycatchers appear similar to Wood Ducks (*Aix sponsa*, Leopold 1951), American Coots (Fredrickson 1969), Partridges (*Perdix perdix*, Lack 1947), Mourning Doves (Westmoreland and Best 1987), and Fieldfares (Slagsvold 1982b). In these species, the number of hatchlings continues to increase with clutch size beyond the modal size.

Winkler and Walters (1983) suggested recently that the incubation-ability hypothesis applies only to those taxa with truncated clutch-size distributions. For example, many Charadriiformes, which typically lay four eggs, experienced poor hatching success when clutches were increased by one (Hills 1980). Adding a fifth egg resulted in uneven heating of the entire clutch so that any individual egg might be put into a cold position long enough to kill the embryo. Presumably, reducing egg size could increase the ability of birds to cover them, but it might be disadvantageous in those species where larger eggs are required to produce large and precocial young (Andersson 1978). Least Flycatchers lay smaller eggs in clutches of five than they do in either clutches of three or four (Briskie 1985), but hatching success did not vary between natural and experimental five-egg clutches (which were made up of eggs from

three- and four-egg clutches), and this did not seem to be an adaptation to increase incubation efficiency.

The frequency of parental feeding deliveries increased with brood size in Least Flycatchers (Briskie 1985). Consequently, larger broods potentially were in greater jeopardy from predators that respond to parental activities when locating nests (Skutch 1949). Nevertheless, we found little evidence that predation pressure placed an upper limit on clutch size. Although nest predation was the greatest source of breeding failure on our study area, the rate of predation was similar for all clutch sizes.

Limits to clutch size in the Least Flycatcher.— None of the three factors we tested appeared to limit Least Flycatchers to a modal clutch size of four eggs. There are several additional factors which may limit clutch size below the number of young that can be raised.

First, clutches smaller than the most productive might be favored if parents that tend larger clutches experience greater mortality than those with smaller broods (Williams 1966, Charnov and Krebs 1974). The compromise between increased fecundity and decreased adult longevity has been recorded in a few field studies (Askenmo 1979, Nur 1984b), although most have reported little or no discernible relationship (Perrins 1965, Bryant 1979, De Steven 1980, Alerstam and Högstedt 1984), or even a positive relationship between survival and fecundity (Högstedt 1981a, Smith 1981). We did not examine adult survival in Least Flycatchers, so we do not know if larger broods sufficiently decrease adult survival to favor reduced effort at a current breeding attempt. Typically, flycatchers are short-lived birds. The oldest recapture in 6 years of banding was a single 4-yr-old male (S. G. Sealy unpubl. data). Given a short life expectancy, any particular individual will have a low probability of repeated breeding. This suggests that reproductive effort should be near the maximum at a given nesting attempt (Stearns 1976, De Steven 1980).

A second possibility is that optimal clutch size in one year may not necessarily be so the following season (Lack 1966). As a result, the most frequent clutch size is optimal, not for the current breeding attempt, but for previous environmental conditions. Because we performed brood enlargement experiments in 1985 only, we cannot be certain that smaller clutches were not optimal in previous years. However, we feel

this possibility was small. Midges have emerged in large numbers during every breeding season since 1974, when work first began in the dune-ridge forest (S. G. Sealy pers. obs.). Arthropod abundance monitored by sweep-net samples over several years also suggests that 1985 was not exceptionally above normal (Busby and Sealy 1979, Biermann 1980, Guinan and Sealy 1987) and, therefore, that Least Flycatchers could probably raise enlarged broods in most years.

Because egg laying requires a substantial energy expenditure (Walsberg 1983), food available to laying females also might limit the number of eggs produced (von Haartman 1971). This hypothesis was applied initially to precocial species (e.g. Ryder 1970), but female condition is known to affect clutch size proximately in some altricial birds (Jones and Ward 1976, Pinowska 1979). For example, birds provisioned with extra food nested earlier, perhaps indicating that breeding was prevented until food availability reached a level when laying became possible (Perrins 1970, Källander 1974, Yom-Tov 1974, Smith et al. 1980). Our observation of a decrease in egg size with clutch size suggests flycatchers may have difficulty producing larger clutches without compromising investment per egg. Nonetheless, only one food-addition experiment on a passerine has documented a significant increase in clutch size (Magpie, *Pica pica*, Högstedt 1981b).

If food availability limited clutch size in Least Flycatchers, one might expect clutches to be larger at Delta Marsh because of the abundance of food created by the large emergences of midges. This did not appear to be the case. We calculated clutch size off the study area from nest-cards filed in the Prairie Nest Records Scheme (PNRS) deposited at the Manitoba Museum of Man and Nature, Winnipeg. Clutch size from nests reported to the PNRS ($\bar{x} = 3.89$, range 3–5, $n = 35$) was not significantly different from that on the study area (see Table 1, Mann-Whitney: $U = 2899$, $z = 0.83$, $P = 0.41$). The area covered by this system included the southern portions of the Canadian Prairie Provinces between approximately 49° and 54° N and 96° and 115° W. Most nests from the PNRS files were located in and around golf courses, suburban yards, city parks, or cottage lots. Although we do not know the availability of arthropods in these areas, the unusual abundance of insect prey at Delta Marsh (Fig. 1) suggests they would be lower. Clutch size in our population in Man-

itoba also did not differ from Least Flycatchers studied by Walkinshaw (1966) in Michigan ($\bar{x}$ = 3.95, range 3–5, n = 46; Mann-Whitney: U = 119, z = 0.56, P = 0.58).

Clearly, both comparisons are only indirect tests of the egg-production hypothesis. It is possible that the food levels necessary for egg production were not limiting in any of the populations under consideration. Ideally, a food-addition experiment would be necessary to test this hypothesis, but this could prove impossible with strictly insectivorous passerines. Alternatively, Hussell and Quinney (1987) correlated changes in clutch size with food availability in the Tree Swallow (*Tachycineta bicolor*) by using several populations and time periods differing in relative prey abundance.

For some species, the upper limit in clutch size may be constrained by nest size (Slagsvold 1982b). Slagsvold found Fieldfares raised more offspring when their original nests were substituted with larger artificial nests. Although open-nesting birds presumably could evolve larger nests, such nests might diminish efficiency of incubation or be more conspicuous to predators (Slagsvold 1982b). As a result, young in clutches larger than the nest can contain will suffer disproportionately higher mortality from trampling or falls. In the Least Flycatcher, we observed losses in three of nine broods of five that could be attributed to overcrowding. In all cases, a few days from fledging, we found young alive on the ground under the nest. These young were the oldest or second-oldest in the two nests in which nestlings were identified. At this stage, nestlings were still flightless, so their chances of survival were probably quite low. In comparison, only 1 nest out of 50 other broods of 3 or 4 experienced a similar loss. Despite this loss, broods of five still gave rise to more surviving offspring than smaller broods (Table 4). Presumably larger clutches should still be favored even with a greater potential of falling.

A final possibility may be the restricted nature of the study site. Although clutches of five were more productive in the dune-ridge forest, this may not be true elsewhere. Dispersal to and from the area is probably quite high. We recaptured <8% of all banded nestlings (n = 240, 1982–1986) in subsequent years through routine mist-netting. Without some degree of isolation, larger clutch sizes simply may not have been able to evolve in this restricted area of abundant food.

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