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VARIATION IN SIZE AND SHAPE OF LEAST FLYCATCHER EGGS

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Abstract.—We measured Least Flycatcher (*Empidonax minimus*) eggs during 1984 and 1985 at Delta Marsh, Manitoba, to investigate which factors were correlated with egg size and shape. Egg volume increased with laying sequence, was smaller in clutches of five than in clutches of three or four, and was greater in 1985 when food was more abundant. Egg volume was not correlated with laying date but it increased when ambient temperatures were low 4-6 d before egg-laying. In contrast to volume, egg shape was similar between years, clutch sizes, and laying sequences. Hatchability was not affected by egg size or laying sequence. Because large eggs produced large hatchlings, increased egg size with laying could enhance the survival of later-hatched offspring, although in flycatchers this advantage was small. Small eggs in clutches of five may not be an adaptation to increase incubation efficiency, but may reflect the inability of females to produce large clutches without compromising investment per egg.

VARIACIONES EN EL TAMAÑO Y FORMA DE HUEVOS DE *EMPIDONAX MINIMUS*

Sinopsis.—Durante el 1984 y 1985 se midieron huevos de *Empidonax minimus* para determinar que factores estaban relacionados con el tamaño y forma de estos. El estudio se llevó a cabo en Delta Marsh, Manitoba. Se encontró un incremento en el volumen de los huevos relacionadó a la secuencia de postura. Este incremento fue menor en camadas de cinco huevos que en de tres o cuatro y mayor durante el 1985 cuando hubo una mayor abundancia de alimento. El volumen de los huevos no pudo ser relacionadó con la fecha de puesta, pero aumentó cuando las temperaturas del medio ambiente fueron bajas de 4-6 d previo a la puesta. En contraste con el volumen, la forma de los huevos fue similar entre años, tamaño de las camadas y secuencia de puestas. El eclosionamiento no fue afectado por el tamaño del huevo o secuencia de puesta. Debido a que de un huevo grande surge un polluelo grande, un incremento en el tamaño del huevo con las puestas, podría ayudar en la sobrevivencia de polluelos eclosiondos tarde en la época reproductiva, aunque en los papamoscas esta ventaja fue muy pequeña. Huevos pequeños en camadas de cinco, no parece ser una adaptación a incrementar la eficiencia de incubación. No obstante, podría reflejar la incapacidad de hembras en producir camadas grandes sin comprometer una gran inversion energética por huevo.

One way birds can adjust the magnitude and pattern of their reproductive effort in relation to variations in environmental quality or their own physiological condition is by changing egg size. Some patterns of egg-size variation (e.g., with laying sequence; Slagsvold et al. 1984) are hypothesized to be adaptive because egg size is often correlated positively with nutrient reserves in the egg (e.g., Bancroft 1985, Bryant 1978), hatchability (e.g., Rofstad and Sandvik 1985, Slagsvold et al. 1984), and nestling survival (e.g., Nisbet 1978, Parsons 1970, Schifferli 1973). Alternatively, variation in egg size and composition may reflect proximate

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conditions such as food available to a laying female (Nisbet 1973) or parental condition (Murphy 1986).

Understanding how egg size contributes to reproductive success requires a knowledge of which factors are correlated with changes in egg size and, therefore, might act as selective agents for particular patterns of variation. In this paper, we examine variation in the size and shape of Least Flycatcher (*Empidonax minimus*) eggs in relation to laying sequence, clutch size, ambient temperature, and food availability. We then determine how these patterns correspond to variation in hatchability and hatchling size.

STUDY AREA AND METHODS

We measured egg size in Least Flycatchers nesting in the forested dune-ridge that separates Lake Manitoba from Delta Marsh, Manitoba, during 1984 and 1985 (see MacKenzie 1982 for description of study site). We located nests by searching suitable breeding habitat throughout spring and summer. Nests were flagged with numbered tape and visited regularly to monitor their progress. Flycatchers laid two to five eggs per clutch in our study area, but clutches of four were the most frequent (78.6% of 192 clutches; Briskie and Sealy, 1989a). After laying was complete, we measured all eggs in a sample of 68 clutches containing three to five eggs. Clutches with known partial losses were excluded. Daily visits permitted us to determine laying sequence in 39 clutches of four eggs. Maximum egg length (L) and greatest breadth (B) were measured to the nearest 0.05 mm using sliding calipers. Volume (V) was calculated using the formula given by Hoyt (1979):

$$V = 0.51LB^2$$

Twenty-eight freshly laid eggs (less than 12 h old) were also weighed to 0.1 g in the field using a triple-beam balance housed in a wind proof box.

Our study area experiences several large emergences of midges annually (Chironomidae; see photo in Briskie and Sealy 1989a), which provide abundant prey over most of the breeding season. To determine the relationship between egg size and food availability we compared mean egg size per clutch with mean arthropod abundance during the laying period as measured by counts of arthropods in sweep-net samples. Each sweep-net sample consisted of 40 non-overlapping sweeps through the vegetation with a 37-cm diameter net from heights of 0.5 to 4.0 m. All sweeps were made in a 1-ha area in the middle of the study site. Three samples were taken every five days over both breeding seasons. One sample each was taken in the morning (approximately 0700–0800 h CDT), afternoon (1300–1400 h), and evening (1800–1900 h) periods. Arthropod abundance was estimated by averaging the number of arthropods in the three samples from the sampling day just prior to clutch initiation at each nest. We used daily means since most of the variation between samples was explained by date of sampling (85.4%; nested ANOVA) rather than time of day (14.6%). Daily estimates were normalized by log transformation for the purposes of linear regression.

Our method of estimating arthropod abundances may be inadequate for several reasons. First, sweep samples do not always provide an unbiased sample of the entire arthropod fauna present in an area. Nevertheless, we felt it was the best method available for sampling arthropods in areas that birds foraged. Second, by restricting our sampling to a single central area, we may not have always estimated the arthropods available to individual females within their territories; however, we feel this problem is minimized by the fact that all nests studied were within 750 m of the central sampling site and that the habitat was continuous and vegetatively similar in all areas. Lastly, by sampling only every five days, laying and arthropod estimates may have been off by as much as four days. For all these reasons we view our correlation results as preliminary.

Mean temperature during each female's egg-laying period was obtained from an Environment Canada meteorological station located on the study area. Since eggs require approximately 24 h to form (Sturkie 1976), we used mean temperature on the day before the laying of each egg to calculate mean temperature over the laying period of each clutch. To determine if longer periods of high or low temperatures also affected egg size, we correlated egg volume with mean temperature for periods ranging from two to 10 d before laying. Mean temperature over earlier periods prior to laying might be important if, for example, there is a time lag between a female's ability to produce large eggs and bouts of good or poor weather.

We compared the shape of flycatcher eggs with an elongation index (E):

$$E = L/B$$

A mean E was determined for each clutch when comparisons were made between different clutch sizes since eggs within a clutch were not independent samples.

The relationship between egg size and hatchling size was determined by comparing egg volume with flattened wing lengths of newly hatched young from those eggs. Flattened wing lengths were measured with sliding calipers to 0.05 mm. The down on all hatchlings was still wet, indicating they had hatched within the previous hour (pers. obs.).

Standard error of the mean (SE) was calculated for all results.

RESULTS

Egg size.—The mean volume of 272 eggs was 1.45 ± 0.01 ml (range 1.08–1.90 ml) and fresh-egg mass averaged 1.50 ± 0.03 g ($n = 28$, range 1.2–1.9). Egg volume was highly correlated with fresh-egg mass ($r = 0.65$, df = 27, $P = 0.0003$).

Rahn et al. (1975) provided an allometric regression that predicts egg mass (M) in birds based on their body mass (W):

$$M = 0.34W^{0.677}$$

For Least Flycatchers, observed egg mass (1.5 g) was less than that predicted (1.68 g) by body mass. During the peak laying period in early June, adult mass averaged 10.6 ± 0.9 g (sexes combined; Biermann and Sealy 1985), thus, a clutch of four eggs represented about 57% of adult body mass. For clutches of three and five, clutch mass comprised about 44 and 66% of adult body mass, respectively.

Mean egg volume varied significantly with clutch size (Fig. 1A, ANOVA: $F = 4.45$, df = 67, $P = 0.016$). Eggs in clutches of five were smaller than those in both clutches of four and three (Tukey's multiple range test: $P < 0.05$), but eggs in clutches of four and three did not differ from each other ($P > 0.05$). Because egg size was correlated with clutch size we conducted all subsequent analyses using four-egg clutches only. Our samples were too small to perform parallel analyses in either clutches of three or five.

Arthropod abundance was greater during the egg-laying period in 1985 ($\bar{x} = 2398 \pm 629$ arthropods/sample, $n = 13$) than in 1984 ($\bar{x} = 1424 \pm 561$, $n = 14$, Mann-Whitney U-test: $P = 0.04$). If egg size was partly a function of food availability, then eggs should have been larger in 1985: for four-egg clutches, mean egg volume in 1985 was greater than in 1984 (Fig. 1B, one-tailed t-test: $t = 1.93$, df = 47, $P < 0.05$). Since mean temperature was greater during the clutch initiation period in 1984 ($\bar{x} = 16.5 \pm 0.4$ C) than in 1985 ($\bar{x} = 12.9 \pm 0.7$ C; $t = 4.47$, $P < 0.005$), this difference was apparent even with cooler weather in the high food year. A regression analysis comparing mean egg volume per four-egg clutch to the mean arthropod abundance, revealed no significant trend ($r = 0.08$, df = 47, $P = 0.60$); however, this could also reflect errors in estimating the quantity of food available to a particular female rather than a lack of an effect.

Egg volume was not related to mean temperature one, two, three, or seven or more days prior to laying (r-values ranged from 0.04 to 0.23, df = 47, P-values from 0.08 to 0.53) but it was correlated negatively with mean temperature from four to six days prior to laying ($r = 0.30$ to 0.33, $P = 0.02$ to 0.04). Consequently, the large eggs produced in 1985 may have resulted from cooler temperatures in addition to the greater arthropod numbers that year.

Seasonal change in egg size was determined by comparing mean egg volume per clutch against laying date. Within four-egg clutches there was no significant relationship between egg volume and laying date in 1984 ($r = 0.05$, df = 24, $P = 0.79$), 1985 ($r = 0.27$, df = 22, $P = 0.22$) or in both years combined ($r = 0.17$, df = 47, $P = 0.25$). This suggests that the relationship between temperature and egg size we found above was not an artifact of seasonal changes in egg size.

Mean egg size varied with laying sequence within clutches of four (Fig. 2, ANOVA: $F = 5.16$, df = 155, $P = 0.002$), but only first-laid and last-laid eggs differed significantly from each other (Tukey's multiple range test: $P < 0.05$). Mean volume increased 6.5% from first- to last-laid eggs, although not all clutches followed this pattern. Egg-size rank corresponded

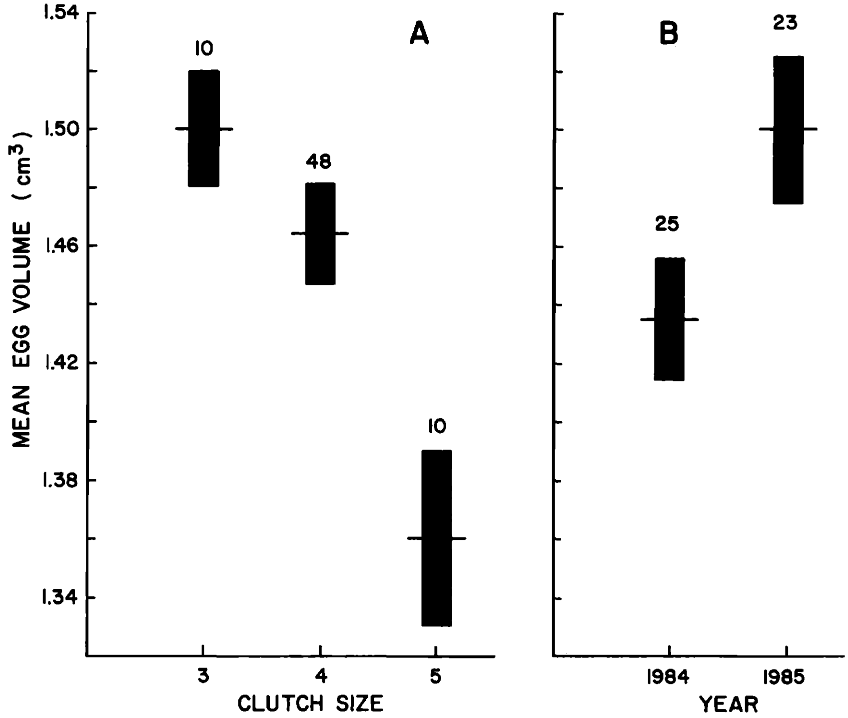

FIGURE 1. Mean volume of Least Flycatcher eggs at Delta Marsh, Manitoba in relation to (A) clutch size and (B) year. Figures are means ± SE. Numbers above bars indicate number of clutches measured.

to laying sequence in most clutches, but a few clutches exhibited the reverse pattern (Table 1).

Generally, eggs were laid at daily intervals, although some females skipped a day between eggs (25.6%, $n = 39$). In clutches of four, skipping was most frequent between third- and fourth-laid eggs (80%, $n = 10$). One female each skipped between the first- and second-laid eggs and between the second- and third-laid eggs, respectively. The greater frequency of skipping later in laying suggests that this was a real delay in laying rather than the loss of a single egg through predation which presumably would occur more randomly over the laying cycle. If skipping was related to inadequate resources for egg production, then third-laid eggs that preceded a skip ($\bar{x} = 1.45 \pm 0.03$ ml, $n = 8$) should be smaller than those that were not followed by a skip in laying ($\bar{x} = 1.51 \pm 0.02$, $n = 29$); however, this difference was not significant ($t = 1.30$, $P = 0.20$). Last-laid eggs in nests where laying was continuous ($\bar{x} = 1.54 \pm 0.03$ ml, $n = 29$) also did not differ from eggs in nests where females skipped a day ($\bar{x} = 1.49 \pm 0.04$ ml, $n = 8$; $t = 0.90$, $P = 0.37$).

Egg shape.—Elongation indices of Least Flycatcher eggs did not vary significantly with either laying sequence (Table 2; ANOVA: $F = 0.38$,

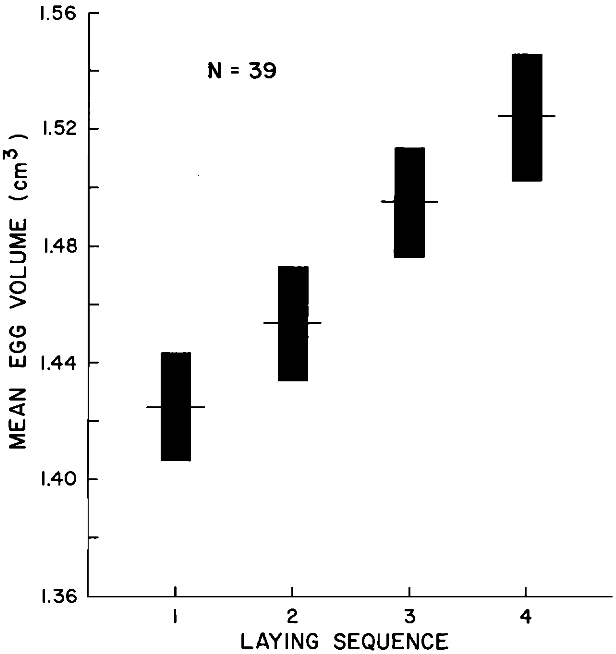

FIGURE 2. Mean volume of Least Flycatcher eggs at Delta Marsh, Manitoba in relation to laying sequence. Figures are means ± SE. N is number of clutches measured.

df = 3, 152, $P = 0.76$), clutch size (Table 3; $F = 0.07$, df = 2, 65, $P = 0.93$) or between 1984 ($\bar{x} = 1.283 \pm 0.012$, $n = 23$) and 1985 ($\bar{x} = 1.276 \pm 0.009$, $n = 23$; $t = 0.51$, $P = 0.61$). This indicates that egg shape did not change concordantly with egg size despite the increase in egg volume in smaller clutches and last-laid eggs.

Hatchability and hatchling size.—Within clutches of four, egg size did not affect hatchability. The size of eggs which failed to hatch ($\bar{x} = 1.52 \pm 0.03$ ml, $n = 12$) did not differ significantly from that of eggs which hatched ($\bar{x} = 1.44 \pm 0.02$ ml, $n = 26$; $t = 1.93$, $P = 0.06$). The probability that an egg would fail to hatch was not related to laying sequence ($\chi^2 =$

TABLE 1. Egg volume rank in Least Flycatcher clutches of four in relation to laying sequence.

	Laying sequence			
Size rank	First	Second	Third	Fourth
Largest	4	3	6	26
Second	5	3	24	7
Third	7	23	5	4
Smallest	23	10	4	2

TABLE 2. Elongation indices of Least Flycatcher eggs in clutches of four in relation to laying sequence. Sample size is 39 complete clutches.

Laying sequence	x̄ ± SE	Range
First	1.281 ± 0.0092	1.17–1.41
Second	1.283 ± 0.0097	1.15–1.44
Third	1.285 ± 0.0097	1.15–1.41
Last	1.272 ± 0.0088	1.16–1.42

1.08, df = 3, $P > 0.05$). Hatchability decreased with increased clutch size (Briskie and Sealy 1989a), but this was not the result of decreased egg size. The proportion of eggs hatching in natural clutches of five did not differ from experimental five-egg clutches made up of eggs from clutches of four and three (Briskie and Sealy 1989a). This suggests that hatchability decreased as a result of less efficient incubation in larger clutches rather than decreased egg quality *per se*.

Flattened wing length of hatchlings was correlated positively with egg volume (Fig. 3); thus, large eggs gave rise to proportionately large hatchlings.

DISCUSSION

Variation in egg size has evolutionary significance only if it affects some measure of reproductive success. In Least Flycatchers, hatchability was not affected by egg size, but large eggs produced large young. Since large hatchlings survive better (e.g., Nisbet 1978, Schifferli 1973), differences in egg size may favor the survival of particular offspring over others. Increased egg size with laying sequence and after periods of cool weather and decreased egg size with greater clutch size are three possible patterns of egg size variation that may have survival consequences for offspring in flycatchers. Below, we discuss the possible adaptive value of these patterns of variation.

Temperature-related variation.—Least Flycatchers laid larger eggs four to six days following a period of cool weather but no effects were found for intervals greater or less than this. Large eggs possibly were laid to produce larger or better provisioned hatchlings that could then withstand a harsher environment. If this were the case then conditions prior to laying should reflect conditions expected at hatching. Since mean temperature four to six days before laying was not correlated with mean temperature at hatching (1984: $r = 0.14$, $P = 0.62$; 1985: $r = 0.37$, $P =$

TABLE 3. Elongation indices of Least Flycatcher egg in relation to clutch size.

Clutch size	n	x̄ ± SE	Range
3	10	1.281 ± 0.0124	1.23–1.33
4	48	1.280 ± 0.0073	1.16–1.39
5	10	1.286 ± 0.0159	1.21–1.36

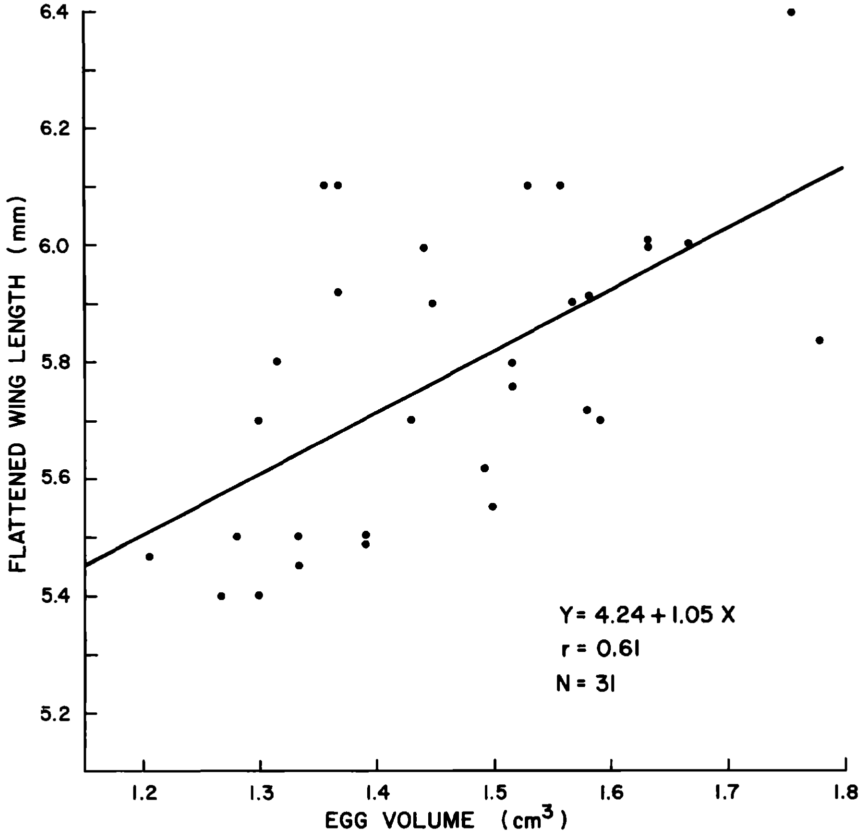

FIGURE 3. Relationship between volume of Least Flycatcher eggs and flattened wing length of chicks from these eggs.

0.17), it is unlikely temperature just before laying can be used to predict future conditions. Instead, large eggs may simply be a proximate consequence of increased foraging success by females as their arthropod prey become increasingly lethargic with cooler temperatures or if females increase foraging after a period of cool temperatures to compensate for any deterioration in body condition. In either case, an increase in resources allocated to egg production may be a part of a generalized increase to all tissues in response to greater overall food availability.

Intra-clutch variation.—Increasing egg size with laying sequence is a pattern commonly found among passerines (see Slagsvold et al. 1984), but it does not appear characteristic of tyrannid flycatchers. Egg size did not vary with laying sequence in either Acadian Flycatchers (*E. virescens*, Walkinshaw 1966a) or Willow Flycatchers (*E. traillii*, Holcomb 1972). Murphy (1983) found egg size increased during laying in Eastern Kingbirds (*Tyrannus tyrannus*) nesting in New York but not in Kansas. Data on intra-clutch variation in egg size for Least Flycatchers from other areas are not available; however, Murphy's (1983) observations on Eastern Kingbirds suggest that intra-clutch variation may depend on local conditions.

Increasing egg size with laying sequence is considered adaptive because large, final eggs produce large, last-hatched chicks, which may compensate for size disparities between siblings created by asynchronous hatching (Howe 1976). Slagsvold et al. (1984) termed this a "brood-survival" strategy because survival of last-hatched young is prolonged in case food availability improves unpredictably. On the other hand, a decrease in egg size with laying can also be viewed as an adaptive strategy in that small final eggs predispose resulting chicks to early death should food be scarce at hatching (Howe 1976, Slagsvold et al. 1984). Here, last-laid eggs are insurance against the infertility of earlier-laid eggs or the remote probability that food becomes abundant. Since these benefits arise irregularly, the cost of final eggs is minimized by their small size.

Least Flycatcher clutches hatch asynchronously, but the young very seldom die from starvation in our population because of the high availability of arthropods over the summer (Briskie and Sealy 1989b). Nevertheless, considering the small differences in egg size we recorded within Least Flycatcher clutches, it is difficult to envision how large, final eggs could offset any disadvantages imposed by hatching asynchrony as proposed by the brood-survival hypothesis. The mean increase from first- to last-laid eggs was only 6.5%. For a newly-hatched flycatcher this amounts to less than a 0.1-g advantage. As nestlings matured this relative advantage decreased rapidly. For example, the earliest instance of brood reduction we recorded in flycatchers occurred at six days of age, when last-hatched nestlings normally weigh between 4.5 and 5.5 g (Briskie and Sealy 1989b). If preserved, the initial size difference now amounts to only 1.2 to 1.5%. This is based on maximum egg-size variation within a clutch; differences between individual nestlings were substantially less (see Fig. 2). It seems unlikely that such small differences could promote the survival of later-hatched nestlings except over the briefest periods of food shortage.

Recently, Järvinen and Ylimaunu (1986) also cautioned against assuming intra-clutch variation in egg size always has an adaptive function. They found that Pied Flycatchers (*Ficedula hypoleuca*) laid large final eggs during periods of warm weather, but below 4 C eggs decreased in size with laying sequence. They attributed this change to decreased adult mass under the harsher conditions. We did not find a similar relationship in Least Flycatchers; however, the lowest mean temperature during our study was only 8.3 C (correlation between mean temperature and relative size of final egg: $r = 0.17$, $df = 38$, $P = 0.29$; see Järvinen and Ylimaunu 1986 for method of calculating relative egg size).

Clutch size variation.—The relationship between clutch size and egg size follows no general pattern in passerines. Egg size increases with clutch size in some species (e.g., Great Tit [*Parus major*] and European Starling [*Sturnus vulgaris*] Ojanen et al. 1978), decreases in others (e.g., Boat-tailed Grackle [*Quiscalus major*] Bancroft 1984; Least Flycatcher, this study) or can be uncorrelated altogether (e.g., Eastern Kingbird, Murphy 1983; Hooded Crow [*Corvus corone*] Rofstad and Sandvik 1985). Even within a species the pattern can vary. In the Pied Flycatcher, egg size and clutch size were correlated negatively in southern Finland, but this changed to a positive correlation in the north (Järvinen and Väisänen 1983).

An inverse relationship between egg and clutch size could represent either (1) energetic constraints on egg production or (2) an adaptation to increase incubation efficiency. Under the adaptive hypothesis, small eggs are advantageous in large clutches because they reduce overall clutch volume and insure that all eggs contact the brood patch. Since hatching success in flycatchers did not differ between natural clutches of five and those we created from clutches of four or three (Briskie and Sealy 1989a), small eggs probably are not an adaptation to increase incubation efficiency in larger clutches. Nevertheless, we obtained only indirect evidence that food availability limited egg size in flycatchers: eggs were smaller in 1984 when arthropods were less abundant. Even this evidence is not convincing since temperatures differed between the two years. Eggs from Delta Marsh were slightly larger than those reported by Walkinshaw (1966b) for Least Flycatchers in Michigan (mass = 1.35 g, n = 30; volume = 1.39 ml, n = 55; no SE reported for either mean) and although the amount of prey available to the Michigan birds is not known, the large emergences of midges at Delta suggest that food is almost certainly more abundant in our study area. Correlations between food availability and egg size have been found in other altricial birds (e.g., Järvinen and Väisänen 1984), but the most direct evidence for energetic limits on egg size come from food supplementation experiments (e.g., Ewald and Rohwer 1982, Högstedt 1981). One consequence of an energetic constraint on egg size is that females may be unable to lay larger clutches without compromising investment per egg. In Least Flycatchers, this situation appears most likely when switching from a clutch of four to five eggs.

Together, our observations suggest variation in egg size may be the result of both energetic limits on production and selection to favor the survival of late-hatching offspring. In Least Flycatchers, the advantage of a large last-laid egg appears small and is probably effective only over very short periods of food stress. The relative importance of food availability on egg production cannot be assessed directly with our data; however, the decrease in egg size in clutches of five provides evidence that such a constraint may be more critical for birds laying larger clutches.

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