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BREEDING PATTERNS OF EASTERN PHOEBES IN KANSAS: ADAPTIVE STRATEGIES OR PHYSIOLOGICAL CONSTRAINT?

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ABSTRACT.—Data were collected on annual (1980–1983) and seasonal (spring vs. summer) variation in reproduction by the double-brooded Eastern Phoebe (*Sayornis phoebe*) to test the proposal that phoebes modify reproductive patterns on a seasonal basis and switch from being brood survivalists in spring to brood reductionists in summer. Clutch size did not differ between spring and summer broods nor among years, but spring nests fledged one more nestling than summer nests. In 1981 breeding began earlier, eggs were larger, and nestlings grew faster than in all other years. Clutch size and egg mass within spring clutches increased seasonally. Egg mass was also larger in summer clutches. These observations suggest that food is usually limited during the initiation of spring clutches. However, because spring broods were more productive than summer broods, I predicted that phoebes should act as brood survivalists in spring, but become brood reductionists in summer. All predictions were supported. During the spring: (a) clutches hatched synchronously; (b) egg mass increased significantly with laying order; (c) hatch order had little impact on nestling growth and; (d) last-hatched young fledged as frequently as their siblings. However, during the summer: (a) clutches hatched asynchronously; (b) egg mass did not consistently vary with laying sequence; (c) hatch order had a significant negative impact on growth; and (d) last-hatched young fledged only about 50% of the time. Thus, phoebes seemed to adaptively shift reproductive patterns seasonally, switching from a brood-survivalist strategy in spring to a brood-reductionist strategy in summer. However, I suggest that proximate responses to food availability provide a more parsimonious explanation for the observed patterns. The increase in egg mass with laying sequence was most likely the result of progressive increases in food availability in spring. Higher food availability and reduced energy demands during summer probably also allowed females to lay uniformly large eggs and start incubation sooner. The latter resulted in greater hatching asynchrony in summer clutches. The poorer growth and higher mortality of last-hatched young in summer resulted from a severe size disadvantage that was the result of the greater asynchrony of summer broods. Thus, brood reduction in summer was probably an incidental and nonadaptive outcome of hatching asynchrony. Received 21 January 1993, accepted 31 May 1993.

FOOD HAS A DIRECT, proximate impact on avian reproductive processes (Davies and Lundberg 1985, Hussell and Quinney 1987, Martin 1987, Nilsson 1991) and variation in the availability of food may have greatly influenced the evolution of reproductive patterns of birds (Lack 1947, Howe 1976, 1978, O'Connor 1978, Martin 1987). For most birds, especially those that feed their young, future unpredictability of food is a major constraint, and females may often enter the breeding season without being able to predict optimal clutch size (i.e. size that produces maximum number of fledglings). Lack (1947) and Ricklefs (1965) argued that the combination of hatching asynchrony and brood reduction

(i.e. starvation of smallest nestling during periods of food shortage) was an evolved, adaptive phenomenon that allowed parents to contend with unpredictability in food supplies. Asynchronously hatched clutches made it possible for parents to (1) fledge all of their young during occasional periods of high food availability, yet also (2) reduce brood size to a level commensurate with their feeding capacity when food was in short supply. Experimental evidence exists to support Lack's model (e.g. Magrath 1989, Hebert 1993). However, several other variables have been suggested as important factors in the evolution of hatching asynchrony (for review, see Magrath 1990, Nilsson 1993), the most widely acknowledged being nest predation (Clark and Wilson 1981, Hussell 1985; see below). Although generally presented as alternatives, it is possible for two or more fac-

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tors to act in concert to favor the evolution of hatching asynchrony (Murphy and Fleischer 1986, D. J. T. Hussell pers. comm.).

Howe's (1976, 1978) observations and experiments on Common Grackles (*Quiscalus quisqualis*) added a new dimension to the basic brood-reduction model. He described an antagonistic pattern in which last-hatching, last-laid eggs were the largest in a clutch. He interpreted this as a strategy of providing extra resources to last-hatched young to offset the disadvantage imposed upon them by hatching asynchrony. The relatively larger size of the last-hatched young presumably allowed them to avoid starvation at a time (early spring) when food supplies were uncertain, but potentially able to improve greatly within a period of just a few days. However, Clark and Wilson (1981) interpreted Howe's results differently. A theoretical treatment and literature review led them to conclude that hatching asynchrony evolved primarily as a predator avoidance mechanism. They argued that the high nest-predation rates typical of small songbirds (Ricklefs 1969, Martin and Li 1992) favored an early onset of incubation to minimize the amount of time eggs and nestlings spent in the nest. The result was hatching asynchrony, which then gave rise to nonadaptive nestling starvation. Clark and Wilson (1981) viewed the large, last-laid eggs of Common Grackles, and other species (reviewed by Slagsvold et al. 1984), as a possible adaptation to minimize nestling starvation arising from hatching asynchrony.

The evaluation of intraclutch egg-size variation by Slagsvold et al. (1984) led to a proposed resolution. They suggested that most birds could be described as either brood reductionists or brood survivalists, and that the two strategies could be distinguished by the patterns of intraclutch egg-size variation. Specifically, the percent deviation of the final egg from the mean egg size of the clutch (i.e. %D) was proposed as a predictor of breeding strategy. Slagsvold et al. (1984) argued that the classical brood reductionist (sensu Lack 1947) exploits food supplies with low future predictability, but high temporal stability. Thus, if food supplies at hatching are low they will remain low, last-laid eggs should not receive extra provisioning (low %D) and young will starve quickly. Brood survivalists also exploit food supplies with low future predictability, but stability is lower than for brood reductionists. If food is scarce at hatch-

ing, it may become relatively abundant in the near future. Given these circumstances, selection should favor traits that reduce the frequency of early nestling starvation. Large final eggs (high %D) were argued to be the primary defense against unnecessary nestling starvation.

This contrast of birds as either brood reductionists or brood survivalists has led to a predicted set of traits that presumably either facilitates nestling starvation or minimizes the unnecessary loss of nestlings (Slagsvold et al. 1984, Jarvinen and Ylimaunu 1986, Ylimaunu and Jarvinen 1987). For example, brood reductionists are predicted to (1) hatch eggs highly asynchronously, (2) show no increase of egg mass with laying order (but possibly decline), and (3) exhibit an inverse relationship between hatch order and nestling growth. Moreover, (4) nestling starvation should be relatively common (but variable over time and space) and (5) last-hatched nestlings should suffer the brunt of mortality if food is limiting. Brood survivalists are predicted to exhibit (1) low levels of hatching asynchrony, (2) increases in egg mass as laying progresses, (3) no relationship between hatch sequence and growth, (4) relatively low levels of nestling starvation, and (5) no tendency for last-hatched young to experience most mortality.

In this paper I test the Slagsvold et al. (1984) hypothesis by comparing the reproductive patterns of spring and summer broods of Eastern Phoebes (*Sayornis phoebe*). The results will be presented in two sections. In part 1, I describe and analyze annual and seasonal variability in the reproductive biology of phoebes breeding in eastern Kansas. After summarizing the findings, I then make specific predictions and test the brood-survival/brood-reduction dichotomy in part 2. As I will show, the description of annual and seasonal variability is essential for an accurate interpretation of the tests presented in part 2.

NATURAL HISTORY AND METHODS

Natural history.—Eastern Phoebes are short-distance migrants that breed from northeastern British Columbia south through the prairie provinces to southern Ontario and Quebec, down through the United States to northeastern New Mexico east to central Georgia. They overwinter in the southern U.S. and northern Mexico (AOU 1983). Their early return to the breeding grounds, placement of adherent, mud

nests in protected niches (for review, see Hill and Gates 1988), and generalist feeding habits (Via 1979) allow phoebes to begin breeding well before all other tyrant flycatchers (except congeners; Murphy 1989). Phoebes are also usually double brooded (i.e. a second brood is attempted after a successful first brood). At any given locality phoebes are among the earliest breeding songbirds, and second clutches are generally laid during the main pulse of breeding by Neotropical migrants. Clutch size varies between three and six eggs, but five is most common (Middleton and Johnston 1956, Klass 1970, Weeks 1978, 1979, Faanes 1980, Conrad and Robertson 1992). Earlier work on a neighboring population showed that (1) phoebes are monogamous, (2) pairs defend all-purpose territories, and (3) the incubation and nestlings periods require 16 and 18 days, respectively (Klass 1970).

Study site and years.—Data were collected from 1980 through 1983 in Douglas County, Kansas. The region has an abundance of small streams that are crossed by concrete bridges. All phoebe nests studied were attached to either the walls or ceilings (when cross beams were available) of these bridges. The main study site encompassed the roads and bridges surrounding Clinton Lake. A second area was located 20 km NE of the first site near the Natural History Reservation of the University of Kansas. In both areas the primary habitats were grazed pastures, shrubby fields, and forest edge. I followed first clutches of the season (hereafter called spring broods) in all four years. Second and replacement clutches (summer broods) were studied in 1980 and 1981.

Weather.—Weather records from 1950 through 1983 were obtained from a weather station located in Lawrence, Kansas. I calculated mean temperature for each day of the breeding season by averaging the observed minimum and maximum temperatures. To summarize annual differences I computed running five-day average temperature for each year and compared these values for each season to the long-term average based on the past 25 years. Rainfall was compared by computing average values for April through July of each year and comparing these values to the long-term average (see Murphy 1986).

Field procedures.—I began to check bridges for past breeding sites and to determine the progress of nest construction and egg laying at all potential nest sites by late March. Most nests were checked from the ground. Higher nests were reached by ladder. Once nest construction appeared to be complete, I checked most nests daily in the afternoon to determine (a) dates of egg laying, (b) sizes of eggs as they were laid, (c) clutch size, (d) losses of eggs during egg laying, and (e) instances of cowbird (*Molothrus ater*) parasitism. A clutch was considered complete when no new eggs were added for one day following the laying of the fifth or sixth egg. I checked nests for two days following the laying of the last egg if four or fewer eggs were in the nest. Eggs were numbered at the

blunt end with a pencil in the order that they were laid. On the day of laying, I measured mass to the nearest 0.05 g using a 10-g Pesola spring scale and measured maximum length and breadth to the nearest 0.05 mm using dial calipers. Although phoebe eggs are white, I observed that last-laid eggs were virtually always covered at the blunt end by a small number of brown spots. In a few cases more than one egg was covered by spots, but in all such instances the last-laid egg had the greatest density of spots. Hence, in the minority of nests where I did not follow eggs through laying (but all of 1983), I was able to determine the last-laid egg by checking the spotting patterns.

I usually visited nests only once or twice between the end of egg laying and the day before the expected date of hatch, at which point I recorded nest failures or losses of individual eggs from clutches. I continued checking nests daily until the 14th day of the nestling period to record the (a) failure of eggs to hatch, (b) hatching order of nestlings, (c) losses of nestlings during the nestling period, (d) productivity (number of young fledged), and (e) growth of nestlings. The latter included mass, tarsometatarsus length (=tarsus) and ninth-primary length (=primary; for specific methods, see Murphy 1981). All measurements of nestling growth were taken between 1200 and 1800 CST and at approximately the same time every day. Nests were not checked after day 14 to avoid premature fledging of young. I assumed that all nestlings present at day 14 fledged.

My pattern of nest visitation (once per day) did not allow me to associate most hatchlings with particular eggs, or determine the exact length of time that elapsed between the hatching of the first and last eggs. Nonetheless, I am certain that I was able to identify the first- and last-hatched nestlings by differences in the appearance of down and skin color (Murphy 1981). Thus, in all analyses of growth and survival in relation to hatching order within a nest, I distinguish three categories of hatching: first (one nestling), middle (one to four nestlings) and last (one nestling).

Based on direct observation and comparisons of the sizes of the first- and last-hatched nestlings, nests were categorized as requiring the following number of hours for hatching of all nestlings: <24; 24–36; 37–48; >48. If all nestlings appeared between two consecutive nest visits I classified the nest as requiring less than 24 h to hatch. Nests that required four visits before all young hatched were classified as requiring more than 48 h to complete hatching. If three nest visits elapsed between the hatching of all eggs, I resorted to measurements of the sizes of the first- and last-hatched nestlings on the first day both were present in the nest to classify the nest as requiring either 24 to 36, or 37 to 48 h to hatch all young. The latter method relied on the fact that early nestling growth is linear (Murphy 1981). Nestling phoebes averaged 1.91 g and 2.77 g at the end of days 1 (=hatch) and

2, respectively (Murphy 1981). Assuming that growth occurs continuously, I assumed that at an age of 36 h a nestling phoebe averages 2.34 g. If the ratio of largest to smallest was less than 1.22 (2.34/1.91), I assumed that all nestlings hatched in 24 to 36 h. Values greater than 1.22 indicated a hatching spread of 37 to 48 h. Although my estimates of hatching asynchrony are only approximate, they are adequate for testing for seasonal differences in hatching patterns.

I calculated nest success as the percentage of nests to fledge at least one young. I attempted to classify the causes of failure for other nests into one of the following categories: predation, ectoparasitism, floods, detachment of nest from wall of bridge, or brood parasitism. Intact but empty nests were assumed to have been depredated. Nests found on the floor of the bridge containing feathers and/or egg-shell fragments were assumed to have been depredated. Loss of a nest to ectoparasitism by the northern fowl mite (*Ornithonyssus sylviarum*) was indicated by a gradual build up of the mite population and then the discovery of dead nestlings. Floods were assumed to have caused the failure of a nest when the entire nest disappeared immediately after a heavy rainstorm that left evidence of flooding at the bridge. Nests that slipped from the wall were found on the floor of the bridge. Losses to brood parasitism were mostly eliminated because I removed cowbirds eggs for another study. Nests that failed but for which I was uncertain of the cause were put into an "unknown" category. Most of these were probably depredated by black rat snakes (*Elaphe obsoleta*), which were common and on several occasions found either hanging from nests or climbing vertical, concrete walls to reach nests.

Statistical analyses.—I adjusted for annual variation in the onset of breeding (see below) in some analyses by subtracting the mean date of breeding from the date of the first egg in each clutch. This standardized mean laying date to day zero in all years, but retained the same absolute level of variation. Likewise, to examine variation in egg size with respect to laying order on a population level it was necessary to first control for differences in egg mass among females. Therefore, I subtracted the mean egg mass of each clutch from each egg in that clutch (see Howe 1976, 1978, Murphy 1983). I then used least-squares linear regression to test for relationships between adjusted egg mass and laying sequence. I also calculated percent deviation (%D) of the final egg laid from the mean egg size of the other eggs in the clutch ($100 \text{ [mass of final egg} - \text{mean egg mass] / mean egg mass}$; see Magrath 1992).

I tested for differences in nestling growth in relation to season, year and hatch order for 1980 and 1981 by comparing average size during the linear phase of growth using analysis of covariance (ANCOVA). The linear phase of growth for mass, tarsus length, and primary length correspond to days 3–10, 2–9, and 6–13 of the nestling period, respectively. I compared

the average heights of the growth curve among nestlings using age as the covariate. This and most other analyses were performed using SAS (SAS Institute 1985). I used the STATISTIX analytical software (Siegel 1992) to conduct multiple-regression analyses. The details of specific tests are given at the appropriate sections in the results. I used the 0.05 probability level to establish statistical significance.

RESULTS

PART I: ANNUAL AND SEASONAL VARIATION

Timing of breeding.—Spring clutches were begun in April in all four years, but initiation dates of first clutches differed significantly among years (Kruskal-Wallis test, $H = 55.1$, $P < 0.001$; Table 1). For example, the final clutch in the spring of 1981 was begun on the first day that eggs were laid in spring 1983 and, overall, there was an 18-day difference in mean breeding date in these two years (Table 1). The initiation of summer clutches in 1980 (6 June \pm SD of 9.50 days, $n = 10$) and 1981 (21 May \pm 7.62 days, $n = 15$) differed significantly (Wilcoxon two-sample test, $Z = 2.49$, $P = 0.013$), but in both years second clutches were begun six to seven weeks after spring clutches.

Clutch size and egg mass.—Phoebes showed no significant variation in clutch size among years (Table 1; ANOVA $F_{3,75} = 1.09$, ns), nor between spring (4.84 ± 0.645 eggs, $n = 44$) and summer (4.75 ± 0.645 eggs, $n = 28$) of 1980 and 1981 ($t = 0.58$, $df = 70$, ns). In all years and seasons modal clutch size was five (77.6%, $n = 107$). Clutch size was also not correlated with laying date in spring broods when all four years were combined ($r = 0.098$, $df = 76$), but positive relationships existed in 1980 ($r = 0.468$, $n = 19$, $P = 0.043$) and 1983 ($r = 0.423$, $n = 21$, $P = 0.071$; 1981, $r = -0.026$, $n = 25$, ns; 1982, $r = 0.154$, $n = 16$, ns). Because of the variation in average annual breeding date, I also evaluated clutch size in relation to adjusted breeding date. A significant relationship existed between clutch size and laying date in the four-year sample ($r = 0.273$, $df = 76$, $P < 0.02$). The size of summer clutches declined towards the end of the breeding season in 1980 ($r = -0.638$, $n = 10$, $P < 0.05$) but not in 1981 ($r = -0.055$, $n = 14$, ns). In the combined 1980 and 1981 samples, clutch size declined with actual date of laying ($r = -0.399$, $n = 24$, $P = 0.054$), but not with adjusted date ($r = -0.234$). Overall, the largest clutches

TABLE 1. Annual variation ($\bar{x} \pm SD$, with n in parentheses) in timing of breeding, clutch size and egg mass in spring clutches of Eastern Phoebes breeding in eastern Kansas.

Year	Breeding date	Clutch size	Egg mass (g)
1980	18 April \pm 6.25 days (21)	4.89 \pm 0.658 (19)	2.02 \pm 0.135 (18)
1981	9 April \pm 4.08 days (27)	4.80 \pm 0.645 (25)	2.14 \pm 0.128 (27)
1982	17 April \pm 5.00 days (18)	5.06 \pm 0.442 (16)	2.06 \pm 0.175 (18)
1983	27 April \pm 4.31 days (21)	4.68 \pm 0.582 (19)	2.11 \pm 0.125 (20)

tended to be laid near the middle of the breeding season, and a second-order-polynomial regression relating clutch size to adjusted breeding date for spring and summer clutches of 1980 and 1981 was significant ($r = 0.344$, $P = 0.02$).

Egg mass varied significantly among spring seasons (Table 1; $F_{3,79} = 3.25$, $P < 0.05$). Average egg mass was also lighter in spring (2.09 ± 0.141 g, $n = 45$) than in summer clutches (2.17 ± 0.148 g, $n = 28$ nests; $t = 2.28$, $df = 71$, $P = 0.032$). The annual difference was the result of the small and large eggs laid in 1980 and 1981, respectively (sums-of-squares simultaneous test procedure; Sokal and Rohlf 1981). In all years, average egg mass of spring clutches tended to increase seasonally (1980, $r = 0.479$, $P = 0.039$; 1981, $r = 0.111$, ns; 1982, $r = 0.412$, $P = 0.090$; 1983, $r = 0.333$, $P = 0.160$; sample sizes in Table 1). When the data for 1981 were excluded, egg mass varied significantly with laying date (Fig. 1). Thus, in most years the smallest eggs of spring clutches tended to be produced by the females that laid earliest. Egg mass did not vary with season in the summer of 1980 ($r = -0.344$, $n = 10$) or 1981 ($r = 0.336$, $n = 14$), or in the combined sample using adjusted breeding date ($r = 0.115$, $n = 24$).

Nest success.—Nest success data were available for three of four spring and two summer breeding seasons. The lowest nest success occurred in the spring of 1983 (Table 2). Success in the other four seasons never dropped below 48% (Table 2). Despite the low success in the spring of 1983, spring broods averaged 48.6% success, a value which did not differ from the average success of summer broods (57.1%; 2×2 G-test of independence, $G = 1.05$, $df = 1$, ns; Sokal and Rohlf 1981).

Although overall nest success was similar in the spring and summer, the causes of nest failure differed (Table 2). Cowbird parasitism (negative effects being assumed), floods, and predators were the main reasons nests failed in the spring. Only one summer nest was parasitized

by cowbirds (the nest was then depredated), and only one summer nest was lost to a flood (Table 2). Known predation accounted for the failure of over twice as many nests in the summer as compared to the spring. Ectoparasitic mites were never a problem for spring broods, but were present during both summer breeding seasons, and caused the death of all nestlings in two nests. In sum, factors causing the sudden and complete loss of nests (predation, floods, slipped nest, unknown factors) accounted for 37.9 and 33.3% of all spring and summer broods, respectively. The causes of nest failures differed between seasons ($X^2 = 10.50$, $df = 3$, $P < 0.025$) due to the difference in the forms of parasitism prevalent in the spring and summer breeding seasons.

An analysis of success based on the fates of individual nestlings suggested that nestlings were in fact more likely to fledge if hatched in the spring ($G = 7.88$, $df = 1$, $P = 0.005$; Table

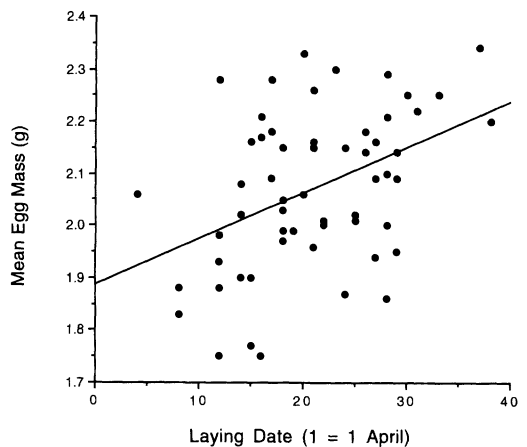


Fig. 1. Seasonal variation in mean mass of eggs within spring clutches of Eastern Phoebes in Eastern Kansas for 1980, 1982, and 1983. Date refers to calendar date on which first egg appeared in nest. Egg mass = $1.88 + 0.009(\text{Date})$, $r^2 = 0.182$, $n = 57$, $P < 0.001$.

TABLE 2. Nest success (percent of nests to fledge young) in Eastern Phoebes by season and year. Percentage of nests to fail due to mortality factors. Mean number of young to fledge from successful nests.

	Spring			Summer	
	1980	1981	1983	1980	1981
<i>n</i>	21	26	19	9	12
	Percent of nests to fledge young^a				
	47.6 (42.8)	61.5 (57.7)	36.8 (26.3)	66.7 (—)	50.0 (—)
Factors	Mortality (% of losses) due to				
Predation	4.8	11.5	15.8	22.2	25.0
Flood ^b	9.5	11.5	26.3	0.0	8.3
Mites	0.0	0.0	0.0	0.0	16.7
Cowbirds	19.0	11.5	5.3	0.0	0.0
Unknown	19.0	3.8	15.8	11.1	0.0
	No. fledglings/successful nest (±SD)				
	4.0 ± 1.25	4.1 ± 1.24	3.7 ± 1.60	3.2 ± 0.98	3.0 ± 1.00

^a Value in parentheses assumes that nests receiving cowbird eggs would have failed without my removal of the parasite egg.

^b Includes two nests that slipped from wall of bridge due to build up of moisture.

3). As for entire nests (Table 2), predation was more common in summer broods. Moreover, individual nestlings were almost five times more likely to disappear from a nest in summer. On average, successful spring nests fledged one more nestling than did successful summer nests (Table 2). Thus, spring nests that survived to hatching had high probabilities of fledging complete broods.

Synopsis of annual and seasonal comparisons.—Phoebes begin to breed before major increases in arthropod abundance occur in Kansas (see Johnston 1967, Robins 1970, Murphy 1986). My data suggest that phoebe reproduction in the early spring is food limited, and that breeding is linked to prevailing weather conditions (as found by Klass 1970). It is not possible, with the data available, to distinguish between the effects of food itself and weather. The major

point is, however, that phoebes are stressed energetically during laying in the early spring. The clearest indication of the importance of weather was that clutches were begun very early in the warm, dry spring of 1981, whereas the cold, wet conditions of 1983 produced a very late breeding season (for weather summary see Murphy 1986:fig. 1).

The favorable conditions of 1981 also resulted in relatively large eggs (Table 1). Furthermore, it was the only year in which clutch size showed no tendency to increase seasonally. The significant seasonal increase in egg mass within the combined samples from 1980, 1982, and 1983 (and in some years individually), and the greater size of eggs during summer suggest that in most years Eastern Phoebes are food/energy limited in the early breeding season. An additional indication that food is limited to laying females is the observation by Weeks (1979) that larger clutches tend to be produced by females that reuse old nests, or construct statant instead of adherent nests. New and adherent nests require considerably more flights to transport mud during nest construction and the energy expended presumably acts as a drain on egg production (Weeks 1979).

On average, spring and summer nests had about a 50% chance of producing a fledgling. Predation was a persistent problem in both seasons, but other factors varied seasonally with losses to floods and brood parasitism being about equally important in the spring. In contrast, a comparison of productivity (i.e. number of

TABLE 3. Number of nestling Eastern Phoebes (percent in parentheses) lost to different sources or fledged in both the spring (*n* = 208) or summer (*n* = 73) periods. Cowbird eggs were removed from spring nests.

Fate	Spring	Summer
Died at hatching	2 (1.0)	0 (0.0)
Found on ground	7 (3.4)	2 (2.7)
Missing (starved?)	6 (2.9)	10 (13.7)
Depredated	29 (13.9)	16 (21.9)
Lost to mites	0 (0.0)	10 (13.7)
Floods/poor nest	19 (9.1)	0 (0.0)
Lost (unknown factor)	9 (4.3)	1 (1.4)
Fledged	136 (65.4)	34 (46.6)

young fledged per successful nest) in spring and summer indicates that more young fledged from spring nests (Table 2). Individual nestlings were nearly five times more likely to turn up missing, presumably starved, if hatched in a summer nest (Table 3). Although conditions at the start of the breeding season between 1980 and 1983 varied greatly, resulting in wide variation in a number of reproductive traits, the level of environmental variability was not unusual. My data do not differ in any substantial way from those collected nearly 20 years earlier by Klass (1970). The population studied by Klass occurred in an area close to my study area and had nearly identical (1) spans in clutch initiation dates (10–24 April vs. 9–27 April), (2) nest success (52.4 vs. 51.7%), (3) fledglings per successful nest (3.8 in both studies), and (4) causes of nest mortality. Klass found that only 4.2% of hatched young disappeared from nests before fledging (spring and summer nests combined). In my study, 3% and 14% of spring and summer nestlings, respectively, disappeared and many of these probably starved or possibly fell from the nest while begging for food. Kendeigh (1942 in Howe 1978) found that 19% of nestling phoebes starved in an Illinois population. The only difference between this and Klass' study was in the size of spring clutches (4.44 ± 0.854 eggs [$n = 105$] vs. 4.86 ± 0.593 eggs [$n = 79$]; $t = 3.73$, $P < 0.001$). I suspect that at least part of this difference was a result of a higher frequency of undetected loss of eggs to cowbirds during Klass' study.

PART II: SEASONAL SHIFT IN BREEDING STRATEGY

The preceding suggests that in most years food in the early spring may be limited when eggs for initial clutches are being formed. However, conditions seem to improve rapidly because prospects for nestling survival are high, presumably due to the growth of arthropod populations (Johnston 1967, Robins 1970, Murphy 1986). A different situation exists in summer. Food is abundant during the production of summer clutches, and possibly when young are being fed, but several factors indicate that breeding conditions deteriorate towards the latter half of the breeding season. First, drought-like conditions (Murphy 1986:fig. 1) often characterize eastern Kansas in midsummer; more young disappeared in summer than in spring

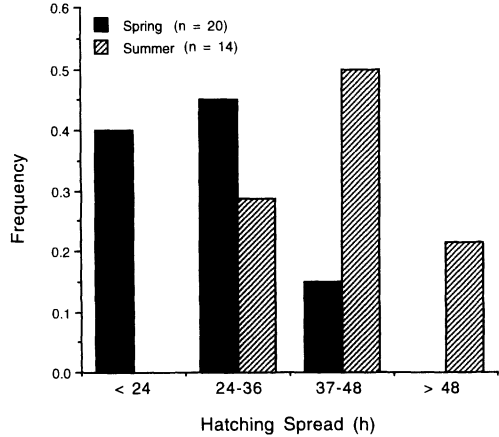


Fig. 2. Hatching spreads (approximate time elapsed between appearance of first- and last-hatched nestling in spring ($n = 20$) and summer ($n = 14$) clutches of Eastern Phoebes. Based on a X^2 contingency-table analysis of observed versus expected number of clutches hatching within each category ($X^2 = 14.21$, $df = 3$, $P = 0.001$).

(Table 3), most likely because they starved or fell from the nest. Thus, spring nestlings appear to be of relatively greater value (i.e. at hatching their prospects of survival and eventual recruitment are higher) than summer nestlings, and I suggest that breeding patterns should evolve to minimize the chances of losing a nestling from a spring brood. The lower probability of nestling survival in summer (due to various factors) should favor the evolution of traits that allow parents to fledge at least some young from each nest. Hence, I predicted that phoebes would follow a brood-survivalist strategy in spring, but become brood reductionists in the summer. Predictions (Slagsvold et al. 1984, Jarvinen and Ylimaunu 1986, Ylimaunu and Jarvinen 1987) are that: (1) broods will hatch more asynchronously in summer; (2) egg mass will increase with laying order in spring but not summer clutches; (3) nestling growth will vary with hatch order in summer but not spring broods; and (4) final eggs should be relatively unproductive in summer, but will be of average productivity in spring.

Prediction 1: Hatching patterns.—I restricted my analysis to clutches of five eggs from the spring and summer of 1980 and 1981. In both spring seasons all clutches hatched in less than 48 h and almost all hatched within 36 h (4 of 6, and 13 of 14, respectively) and, of these, eight hatched within 24 h. In neither summer season

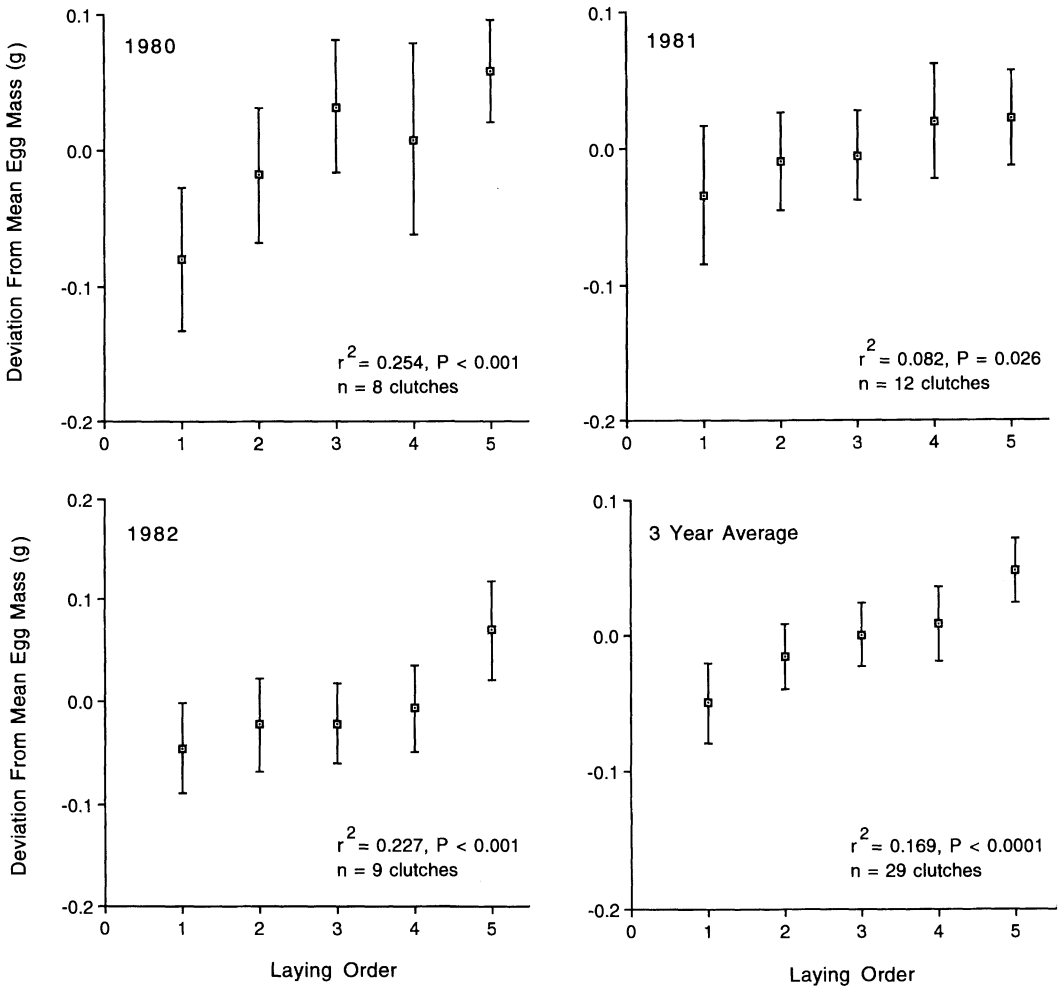


Fig. 3. Deviation from mean egg mass (egg mass – mean egg mass) with respect to laying order within five-egg spring clutches of Eastern Phoebes for 1980, 1981, 1982, and combined three-year sample.

did any clutch hatch within 24 h, but instead, 3 of 14 clutches required more than 48 h to hatch all young. Thus, summer broods on average took considerably longer to complete hatching (Fig. 2). Prediction I was supported.

Prediction II: Intraclutch egg size variation.—Data on intraclutch egg-size variation within clutches of five were available for three of four spring and both summer breeding periods. Egg mass increased as laying progressed within spring clutches of five eggs in all three years, individually and in the combined sample (Fig. 3). There was no tendency for egg mass to increase with laying sequence in summer 1980 ($r^2 = 0.002$, $n = 6$ clutches), but egg mass increased significantly as laying progressed in clutches of five in summer 1981 ($r^2 = 0.223$, $n = 6$, $P < 0.01$).

The composite sample from the two summer periods indicated a significant increase in mass with laying order ($r^2 = 0.076$, $n = 12$, $P = 0.034$). Thus, prediction II was rejected.

A possible alternative explanation for the increase of egg mass with laying order was that females were able to shunt more energy towards egg production as laying progressed because of gradual improvements in the thermal environment during the period of egg formation. To test this possibility I performed multiple-regression analyses on adjusted egg mass in clutches of five, using laying position and mean temperature over the four-day period preceding the laying of each egg as the predictor variables. The results confirmed that in 1980, and especially 1981, larger eggs tended to be

TABLE 4. Results (*t*-values) of multiple-regression analyses relating adjusted egg mass in Eastern Phoebes to position in laying sequence and mean air temperature over four-day period preceding laying of each egg. Coefficient of determination (R^2) given for two-variable model of order and temperature. Pearson-product moment correlation coefficient (*r*) presented for relationship between air temperature and laying order.

Year	Laying order	Temperature	R^2	<i>r</i>
Spring				
1980	3.66***	1.91	0.321***	0.029
1981	1.47	4.55***	0.327***	0.241
1983	3.68***	1.22	0.254**	-0.527***
All years	5.88***	3.72***	0.243***	-0.071
Summer				
1980	0.50	-0.44	0.010	0.837***
1981	1.80	1.27	0.267*	0.516***
All years	1.12	0.88	0.089	0.634***

***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; other ns, $P > 0.05$.

associated with warmer temperatures (Table 4; *t*-values calculated after controlling for the effect of the other variable in the model). Temperature also had a significant effect in the composite sample from the three years. However, after controlling for temperature, 1981 was the only spring period when laying order did not contribute significantly to variation in egg mass (Table 4). Laying order and air temperature were not correlated in any spring period except 1983 (Table 4), and in that year the correlation was negative. This is opposite of what would be expected if the relationship with laying order was an incidental outcome of gradually increasing temperatures. Thus, the relationship between egg mass and laying order in spring was independent of the effects of air temperature. The same cannot be said of summer clutches. In both years and in the combined sample, air temperature and laying order were correlated positively (Table 4), and when both variables were forced into the regression models neither made significant independent contributions to variation in intraclutch egg mass during any period. In 1981, despite over one-quarter of intraclutch variation in egg mass being accounted for (Table 4), I cannot isolate the contributions of laying order and air temperature because egg mass varied with both temperature during laying ($r^2 = 0.178$, $P = 0.02$) and order (see above). Given these results, the rejection of prediction II was premature.

Two corollaries of prediction II are that as clutch size increases, the trend for egg mass to increase with laying sequence should become stronger, and last-laid eggs should become increasingly larger (i.e. %D should increase) as

clutch size increases. I tested both predictions by combining data from all spring seasons. The predicted patterns were observed (Fig. 4). Egg mass did not vary significantly with laying sequence in clutches of four, but in clutches of five and six the pattern was significant, and %D varied directly with clutch size (Fig. 4). Thus, as clutch size increased the last-laid egg became increasingly larger compared to the other eggs in the clutch. Finally, the last egg was 3.1% larger than the other eggs in the clutch during spring, but only 1.8% larger in summer.

Prediction III: Nestling growth.—Changes in mass in larger broods (four to six young) are shown in relation to hatch order according to season and year in Figure 5. Seasonal differences are apparent. Spring broods gained mass faster and effects of hatch order were less pronounced than in summer broods (Fig. 5, Table 5). Hatch order had significant influences on changes in mass in three of four season-year comparisons (ANCOVA; Table 5), the exception being the spring of 1980. Even though last-hatched young grew more slowly than first- and middle-hatched young in the spring of 1981, the differences were small in comparison to the effects of hatch order in both summer breeding seasons (Fig. 5). During the summer in both years, first-hatched young grew faster than middle-hatched nestlings, which grew faster than last-hatched nestlings (Table 5). First-hatched young gained mass at about the same rate during this phase of growth during all four periods (average height of the growth curve never less than 10 g; Table 5). However, last-hatched young grew at substantially different rates between spring and summer breeding seasons, with the

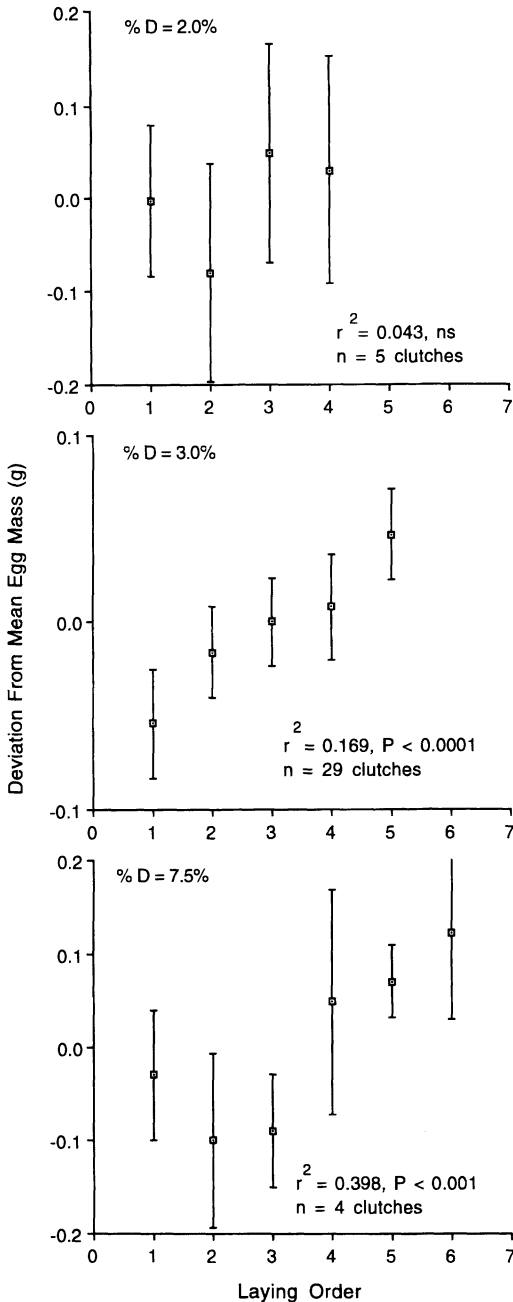


Fig. 4. Deviation in mean egg mass with respect to laying order for spring clutches of four, five, and six eggs of Eastern Phoebes. Also, percent deviation (%D) in mass of final egg in clutch from mean egg size for each clutch size. Data based on clutches from 1980, 1981, and 1982.

height of the growth curve ranging from only 8.5 g to over 10 g (Table 5). Thus, prediction III is supported.

Identical analyses of changes in tarsus length and primary length are also summarized in Table 5. Among summer broods, hatch order had the same general influences on changes in tarsus and primary lengths. Last-hatched young always grew the slowest. Among spring broods, hatch order had a less predictable influence on changes in tarsus and primary length. Primary growth did not differ with respect to hatch order in 1980, but middle-hatched young tended to exhibit the slowest tarsus growth during the same period (Table 5). However, tarsus growth was fastest in middle-hatched young during the spring of 1981, and primary growth varied inversely with hatch order.

Conceivably, small, last-hatched young may fledge at the same size as other nestlings if they grow for a longer period than nestlings that were hatched earlier. To test this possibility, I compared the sizes of young at day 13 (the last day for which measurements were available for most last-hatched young) with respect to hatch order, season, and year (three-way ANOVA). All three ANOVAs were highly significant (Table 6). Season had the most consistent influence in that summer nestlings were always smaller than spring nestlings for all three morphological traits (P for primary length = 0.059). Hatch order, however, was not a significant contributor to differences in mass or tarsus length at day 13 (Table 6). Within seasons, nestlings were heavier in 1981 than in 1980. Although tarsi were longer in spring than in summer, differences between years were not significant. Primary length was the only structure that was significantly affected by hatch order. The significant interaction terms in the analyses of tarsus and primary lengths (Table 6) complicate the interpretation of these results, but agree with my previous conclusion that hatch order had less consistent influences on the growth of these structures.

Prediction IV: Nestling mortality.—The growth analyses yielded conflicting results. Although the ANCOVAs supported the prediction that hatch order would differentially affect growth in the summer and spring, the three-way ANOVAs of size on day 13 indicated that only primary length was influenced significantly by hatch order. A possible explanation is that more

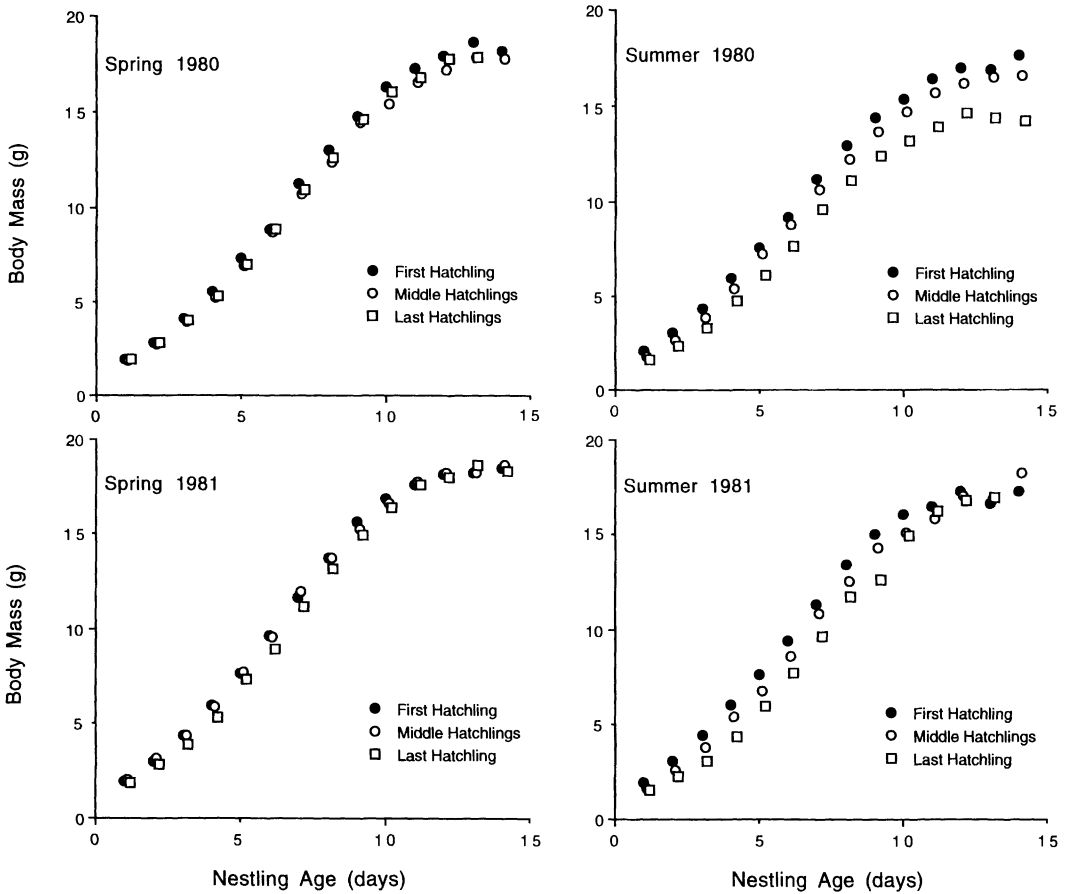


Fig. 5. Changes in body mass of nestling Eastern Phoebes during first 14 days after hatching for spring and summer broods of 1980 and 1981 which held four, five, or six young. Within each plot, data separated by hatch order. See Table 5 for statistical analysis of growth.

low-mass, last-hatched nestlings died before day 13 than did either first- or middle-hatched young. An alternative explanation is that by day 13, growth in mass and tarsus length are nearly complete, and last-hatched nestlings have caught up to their older siblings. Primaries are still growing rapidly, however, and provide evidence of depressed growth in younger nestlings.

To examine the former possibility, and test prediction IV, I checked for a relationship between hatch order and the probability of dying during the measurement period. For 37 nests with complete information on fledging success, 3 of 37 (8.1%) first-hatched, 10 of 99 (10.1%) middle-hatched, and 9 of 37 (24.3%) last-hatched nestlings died. The trend towards greater mortality in last-hatched nestlings was not signif-

icant (G-test for independence, $G = 5.13$, $df = 2$, $P = 0.081$). However, because mortality within nests was lower in the spring than the summer (8.4 vs. 19.0%, $X^2 = 4.435$, $df = 1$, $P = 0.037$), I reanalyzed spring and summer data separately. In spring, 1 of 24 (4.2%) first-hatched, 6 of 66 (9.1%) middle-hatched, and 3 of 24 (12.5%) last-hatched nestlings died ($X^2 = 0.106$, $df = 1$, ns; first- and middle-hatched nestlings combined to increase sample size and Yate's correction for continuity applied), but in summer 2 of 13 (15.4%) first-hatched, 4 of 33 (12.1%) middle-hatched, and 6 of 13 (46.2%) last-hatched nestlings died ($X^2 = 5.168$, $df = 1$, $P < 0.01$; same procedure as for spring broods). Thus, the higher mortality of small, last-hatched nestlings prior to measurement on day 13 suggests that the failure of mass and tarsus length to vary

TABLE 5. Results of analysis of nestling growth in Eastern Phoebes in relation to hatch order by season and year using ANCOVA (covariate was age). Values are average heights \pm SE of growth curve attained during linear phase of growth (see methods).

Season	Hatch order			F
	First	Middle	Last	
Nestling mass				
Spring 1980	10.2 \pm 0.17 ^a	9.7 \pm 0.10 ^a	9.9 \pm 0.17 ^a	2.62
Summer 1980	10.0 \pm 0.11 ^a	9.5 \pm 0.07 ^b	8.5 \pm 0.12 ^c	46.30***
Spring 1981	10.6 \pm 0.09 ^a	10.6 \pm 0.05 ^a	10.1 \pm 0.09 ^b	14.91***
Summer 1981	10.3 \pm 0.19 ^a	9.6 \pm 0.11 ^b	8.6 \pm 0.18 ^c	20.10***
Tarsus length				
Spring 1980	10.6 \pm 0.10 ^a	10.3 \pm 0.06 ^b	10.5 \pm 0.10 ^{ab}	5.03**
Summer 1980	10.9 \pm 0.08 ^a	10.6 \pm 0.05 ^b	9.9 \pm 0.09 ^c	35.95***
Spring 1981	10.8 \pm 0.06 ^a	11.0 \pm 0.04 ^b	10.6 \pm 0.06 ^c	14.69***
Summer 1981	10.8 \pm 0.09 ^a	10.2 \pm 0.06 ^b	10.0 \pm 0.09 ^c	22.30***
Primary length				
Spring 1980	16.0 \pm 0.24 ^a	15.5 \pm 0.15 ^a	15.6 \pm 0.25 ^a	1.42
Summer 1980	17.3 \pm 0.13 ^a	16.2 \pm 0.08 ^b	15.1 \pm 0.15 ^c	59.30***
Spring 1981	17.5 \pm 0.15 ^a	17.0 \pm 0.09 ^b	16.2 \pm 0.15 ^c	18.70***
Summer 1981	16.1 \pm 0.38 ^a	14.4 \pm 0.22 ^b	14.3 \pm 0.38 ^b	8.19***

***, $P < 0.001$; **, $P < 0.01$; all others ns, $P > 0.05$.

^{a,b,c} Within-season differences in "size" among first-, middle- and last-hatched nestlings indicated by different superscripts.

with hatch order on day 13 (Table 6) was the result of the loss of slow growing, last-hatched nestlings. These findings are in agreement with prediction IV.

A final question concerned the relative importance of season, hatching pattern, and brood size as factors influencing the number of young dying in a nest. For this analysis I performed a multiple regression on the number of young fledged using brood size, degree of hatching asynchrony and season as independent variables. The degree of hatching asynchrony

emerged as the most important factor affecting the number of young dying ($r = 0.478$, $df = 40$, $P = 0.001$). A multiple-regression analysis in which all three variables were forced to enter ($R^2 = 0.243$, $F = 4.05$, $P = 0.01$) indicated that the degree of hatching asynchrony remained the most important correlate of within-nest mortality. After accounting for the effects of the other two variables, the F -values for season, brood size, and degree of hatching asynchrony were 0.40 ($P = 0.53$), 0.47 ($P = 0.50$), and 4.84 ($P = 0.03$), respectively. Thus, increased nestling mortality was associated with greater hatching asynchrony.

TABLE 6. Results (F -values) of three-way ANOVA of mass, tarsus length, and ninth-primary length on day 13 of nestling period in phoebes.

Source of variation	Mass	Tarsus length	Primary length
Hatch order ^a	0.61	1.81	4.13*
Season ^b	36.17***	11.25***	3.66
Year ^c	4.15*	3.10	1.10
Hatch \times season	1.87	2.59	0.68
Season \times year	0.00	0.75	20.71***
Hatch \times year	2.25	4.32*	0.69
Hatch \times season \times year	0.30	3.73*	1.65
Full model	4.41***	3.64***	3.61***
R^2	0.364	0.320	0.319

***, $P < 0.001$; *, $P < 0.05$; all others ns, $P > 0.05$.

^a First, middle, and last.

^b Spring and summer.

^c 1980 and 1981.

DISCUSSION

Eastern Phoebes exhibit little variation in clutch size despite wide variation in breeding conditions across their geographic range and among years within a single location (Middleton and Johnston 1956, Klass 1970, Weeks 1979, Faanes 1980, Conrad and Robertson 1992, this study). Clearly, phoebes do not adjust clutch size to prevailing conditions for breeding. Rather, they contend with the unpredictability of their environment through behavioral plasticity and a flexible mix of alternative tactics.

My test of the brood-survivalist/brood-reductionist contrast was based on an initial assumption that the spring breeding period was

the more favorable period for raising offspring. The argument for this is that food supplies improve steadily throughout the spring and early summer as first-brood young are raised to independence. Food in the general environment is more abundant during summer (Johnston 1967, Robins 1970, Murphy 1986), but very droughtlike conditions occur frequently in mid- to late summer in Kansas (see Murphy 1986). Given that phoebes prefer moister microenvironments and usually nest near streams (Hill and Gates 1988), Kansas summers may be a period of either food shortage and/or heat stress. Furthermore, in many species of birds recruitment is inversely related to fledging date (review in Murphy 1986, Drilling and Thompson 1988, Nilsson 1989, Krementz et al. 1989), and since spring fledglings have about two more months to grow and develop before migration, I would expect spring broods to yield more recruits.

My data support the belief that the summer period is the more difficult one for fledging young. During the summer the growth of nestlings was poorer, starvation was more frequent, and mite infestations often debilitated or killed nestlings. On average, one less nestling fledged from successful summer nests than spring nests, despite no difference in clutch size. These same effects might be produced, however, if parents provided less care to summer broods. Reduced parental care for summer broods would be favored if (1) summer broods produced few recruits, and (2) reproductive effort and parental survivorship were inversely related (D. J. T. Hussell pers. comm.). I have no data to test either condition, but Conrad and Robertson (1993) found no difference in per capita nestling feeding rates between spring and summer broods of phoebes in Ontario, suggesting that the intensity of parental care does not vary seasonally. The poorer prospects for the success of summer nestlings seems likely to be due to changes in the physical environment. Consequently, my expectation of a switch in reproductive behavior seems justified.

A cursory examination of the results of the four tests also leads to the conclusion that phoebes followed the predicted patterns. In the spring, most nests hatched in less than 36 h and many within 24 h. Last-laid eggs tended to be the largest in every year. In both spring periods, hatching order had little effect on either growth or survival. Finally, the relative size of the final

egg (%D) increased directly with clutch size in the spring. Conversely, hatching was more asynchronous in summer broods, egg mass did not vary consistently with laying order (air temperature contributed to intraclutch egg mass variation in 1981), and middle- and especially last-hatched nestlings grew poorly compared to the oldest nestling. However, note that first-hatched nestlings grew at about the same rate in all measurement periods. Finally, nearly 50% of last-hatched nestlings died in summer. I cannot reject any of the predictions.

However, before final conclusions are drawn, it is essential that alternative explanations are examined. As Howe (1978) noted in reference to his own work, "Adaptation is invoked only where alternative explanation fails, in keeping with the premise that observed attributes of organisms may be effects of unseen attributes or consequences of population structure rather than traits evolved by natural selection on individual phenotypes."

Hatching asynchrony.—The expectation of adaptive, seasonal shifts in hatching pattern perforce assumes that females have control over incubation behavior. Evidence suggests that the initiation of incubation is associated with an increase in the secretion of prolactin (reviewed by Mead and Morton 1985) that occurs when the last ovum of the clutch is released. Indeed, Mead and Morton (1985) suggested that hatching asynchrony was an epiphenomenon resulting from the prolactin surge, causing females to begin full incubation with the laying of the penultimate egg. The latter hypothesis assumes that females have little control over the start of incubation. However, data from a number of studies have shown that hatching patterns vary with clutch size (Smith 1988, Stouffer and Power 1990, Hebert and Sealy 1992, Magrath 1992, Slagsvold and Amundsen 1992) and season (Mead and Morton 1985, Murphy and Fleischer 1986, Arnold 1991, Slagsvold and Amundsen, this study). Hebert and Sealy (1992) also demonstrated that the initiation of incubation by Yellow Warblers (*Dendroica petechia*) was independent of the ovulation of the last ovum and the hormonal changes (see also Magrath 1992). Thus, there is considerable evidence that incubation behavior is flexible and potentially an important element in the individual female's response to the environment.

All evidence suggests that female phoebes must have begun incubation sooner in the sum-

mer than in the spring (Fig. 2). Given that conditions for rearing offspring deteriorated during summer, the resulting pattern of greater asynchrony in summer broods conformed nicely to Lack's (1947) original view that hatching asynchrony allows parents to starve one or more young when food is in short supply. Unfortunately, I lack the necessary data to test the main alternative model for the evolution of hatching asynchrony, the nest-failure hypothesis (Clark and Wilson 1981, Hussell 1985). The latter hypothesis predicts greater asynchrony when egg mortality during laying is high compared to the mortality of young at the late nestling stage. Given that I ended my nest visits at day 14, four days before normal fledging, I do not have the information on the frequency of nest predation just prior to fledging that is needed to test the nest-failure hypothesis.

There are, however, at least two nonadaptive explanations for the observed pattern that should be considered. The first is that greater asynchrony in second clutches may be an epiphenomenon resulting from higher air temperatures during summer and the incidental warming of eggs in the nest (Murphy 1983, Hebert and Sealy 1992). I view this as unlikely in phoebes because their nests are located in cool microenvironments that are unlikely to result in much, if any, warming of eggs (for House Sparrows, [*Passer domesticus*], see Veiga and Vinuela 1993). However, thermal factors may operate in another manner. Differences in the start of incubation between seasons may be an incidental outcome of low food availability and high maintenance costs (because air temperature is much lower) in the spring. Data presented earlier suggested that the start of breeding and possibly clutch size were limited by food availability in early April. If food is in fact limiting, females may not be able to initiate incubation earlier in the spring because they have to either spend more time foraging to meet daily energy needs, or they may have to replace depleted body reserves after clutch formation. Similar arguments have been made to account for variation in hatching asynchrony in Pied Flycatchers (*Ficedula hypoleuca*; Slagsvold and Lifjeld 1989), European Blackbirds (*Turdus merula*; Magrath 1992) and Great Tits (*Parus major*; Slagsvold and Amundsen 1992). Furthermore, food provisioned Marsh Tits (*P. palustris*) began incubation sooner and hatched their clutches more asynchronously than unfed controls (Nilsson 1993).

Intraclutch egg-size variation.—One possible alternative to the view that large, last-laid eggs in the spring serve to offset disadvantages imposed upon last-hatched nestlings has already been excluded. Differences in energy availability due to variation in air temperature over the four-day period of egg formation did not explain the trend for egg mass to increase with laying sequence. The spring of 1981 was the only period when air temperature was positively related to egg mass within clutches, and this was the warmest year and also the year when egg mass was independent of laying order. In both 1980 and 1983, when egg mass and laying order were significantly associated, temperature had at best (1980) a secondary influence on egg mass. Hence, energetic stresses imposed on females by the thermal environment were not the cause of intraclutch egg-size variation. However, I cannot exclude temperature as a possible factor contributing to the significant increase in egg mass with laying sequence in the summer of 1981 (Table 4). It is clear that laying order had a stronger and more consistent influence on egg mass within spring clutches.

Food supplies no doubt have a more direct impact on egg production than temperature. As evidenced by the early breeding and lack of any suggestion of a seasonal increase in either clutch size ($r = -0.026$) or egg mass ($r = 0.111$), food was probably abundant from the start of laying in 1981, and this is the only spring season in which egg mass did not increase with laying sequence. The most parsimonious explanation for the increase in egg mass with laying order in the springs of 1980 and 1983 is that, unlike 1981, food supplies were lower and gradually increased over the laying period. The lower %D values and weaker tendency for egg mass to vary with laying sequence in summer is probably also related to higher food availability. Although my implication of food supplies is based on circumstantial evidence, and in need of direct testing, the conclusion seems justified given the uniformity of the data. Finally, I find it difficult to imagine that a 2 to 4% larger last-laid egg will to any degree offset disadvantages imposed by a 24-h difference in the time of hatching (both conditions are typical of spring broods). Stokland and Amundsen (1988) and Magrath (1992) both showed that hatching interval explained virtually all the variation in nestling size on the first day that all young were present in the nest. Thus, unless last-laid eggs are much larger than all others, even moderate

levels of hatching asynchrony will swamp the effects of differential investment in eggs. Hence, the results of my study suggest that intraclutch egg-size variation is not adaptive.

Position-dependent nestling growth and survival.—I examined the results of the last two predictions together because evidence shows that they are linked. First, the prediction that last-hatched young in spring would grow and survive as well as their earlier hatching siblings was verified, as was the prediction that hatch order would have a significant negative impact on both growth and survival of the youngest nestlings in summer. In short, mortality during the summer claimed mainly the smallest and youngest nestlings. In addition, first-hatched young grew equally well in all morphological traits in all seasons and years (Table 5). Both observations support a basic premise of the brood reduction-model, namely that hatching asynchrony and brood reduction allow parents to produce at least some high quality young under all circumstances (Lack 1947, Ricklefs 1965, Howe 1976, 1978).

However, was the poorer performance of later hatched nestlings in summer inevitable, or was it the unavoidable outcome of greater hatching asynchrony? My attempt to account for intrabrood mortality using brood size, season of hatch, and degree of hatching asynchrony points to hatching asynchrony as the principal cause of intrabrood mortality. Asynchronously hatched broods, whether found in the summer or spring, were most likely to lose offspring. Although last-hatched young were more than twice as likely to die before fledging in the summer, after controlling for the degree of asynchrony I found that season had no relationship to nestling mortality. The alternative explanation is that individual females fine-tuned their incubation behavior to produce a pattern of hatching that matched food supplies in their immediate environment. I find this very unlikely. Rather, it seems more plausible to assume that the imposition of a severe size disadvantage at hatching led to a high probability of death (see also Slagsvold 1982, Amundsen and Stokland 1988, Stouffer and Power 1990). Thus, hatching asynchrony and brood reduction did not appear to be part of an adaptive strategy to scale brood size down to a level that matched food availability.

Overall, patterns of hatching asynchrony, intraclutch egg-size variation and nestling growth and survival in spring and summer clutches of

Eastern Phoebes conformed remarkably well with predictions derived from the brood-survival/brood-reduction hypothesis (Slagsvold et al. 1984). However, I believe that the apparent match between empirical data and theoretical predictions was coincidental and came about because the proximate responses to variation in food availability were identical to the predicted adaptations. Proximate physiological constraints on egg production and female behavior appear to play the more important role in establishing the observed patterns. Although final conclusions must await empirical testing using food-supplementation experiments (e.g. Horsfall 1984, Arnold 1991, Nilsson 1993), at present there is no evidence that hatching patterns, intraclutch egg-size variation, or position-dependent growth and survival in Eastern Phoebes has an evolved, adaptive basis. My results and conclusions highlight the pitfalls that can occur if data are collected and interpreted without careful attention to natural-history and population-level responses to environmental variation.

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