

## WHAT LIMITS MOURNING DOVES TO A CLUTCH OF TWO EGGS?<sup>1</sup>

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*Abstract.* To examine factors that possibly limit clutch size in Mourning Doves (*Zenaida macroura*), we exchanged eggs of equal age among nests to create clutches of one and three eggs. We compared the breeding success of parents rearing these clutches to that of parents rearing natural, two-egg clutches. Adults were fully capable of incubating three-egg clutches and brooding three nestlings. Nestlings in enlarged broods grew more slowly than those in control (two-young) broods during the crop-milk stage and generally had less full crops throughout the nestling period. Enlarged broods took 1.3 days longer to fledge. After reaching the growth asymptote, nestlings in enlarged broods had normal carpometacarpus lengths but weighed 26% less than those in control broods. Parents of enlarged broods fledged an estimated 30% more offspring than those of control broods. However, low postfledging survival may negate the advantage to parents rearing three offspring per nest.

*Key words:* Clutch size; Mourning Dove; crop milk; growth rates; brooding.

### INTRODUCTION

Since Lack's (1947, 1948) classic treatise on the significance of clutch size in birds, the topic has received considerable theoretical (e.g., Cody 1966, Charnov and Krebs 1974, Foster 1974, Brockelman 1975) and empirical (e.g., Ricklefs 1968, Safriel 1975, Crossner 1977, Haymes and Morris 1977, Greenlaw 1978) attention. Most has focused on explaining variation in clutch size. For example, Lack (1947) contended that clutch size in nidicolous birds varies in tandem with local food supply. This idea has been supported by some studies (Plumb 1965, Lloyd 1977) and rejected in others (Vermeer 1963, Harris 1970). Various other hypotheses (e.g., Cody 1966, Ricklefs 1970, Charnov and Krebs 1974) have been proposed to explain clutch-size variation.

At least one group of birds, granivorous pigeons and doves (family Columbidae: subfamily Columbinae), is enigmatic; these species virtually always lay two eggs (Goodwin 1983), so most clutch-size hypotheses are irrelevant to them. This lack of clutch-size variation has not constrained the adaptive radiation of columbids; representatives occupy habitats from jungles to deserts, and live on every continent (except Antarctica) and most major islands in the world (Goodwin 1983).

By manipulating clutches, we tested several possible limitations on the clutch size of Mourning

Doves (*Zenaida macroura*). This species ranges across North America and breeds in habitats as diverse as deserts and forests, yet it almost always lays a clutch of two eggs (Weeks 1980). Specifically, we addressed four hypotheses: first, clutch size may be limited by the inability of parents to incubate three eggs and/or brood three nestlings. This seems reasonable because columbids do not have the vascularized brood patch typical of other birds (Jones 1971, Maridon and Holcomb 1971), and they build small, poorly insulated nests (Ricklefs 1974). Second, clutch size may be limited because adults cannot produce an adequate supply of crop milk for three young. Nestlings are fed crop milk for the first 5 to 6 days of life (Taylor 1941, Laub 1956). Third, clutch size could be limited because parents cannot gather enough seeds for nestlings after the crop-milk period. An inadequate food supply during either phase of nestling growth would be indicated by starvation or underweight nestlings/fledglings. Finally, clutch size in columbids may be a compromise between the risk of predation and the maximum number of young that can be reared (*sensu* Lack 1948). Nestlings in large broods may grow more slowly and stay in the nest longer, thus increasing the likelihood of the nest being discovered by a predator.

### METHODS

Field work began in early May and continued through August in 1984 and 1985 at Big Creek

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State Park in Polk County, central Iowa. The park contains several kilometers of coniferous tree windbreaks that are used by nesting doves. Between the windbreaks (a space of about 60 m), land use is rotated between corn, alfalfa, oats, or nonuse.

We searched the windbreaks at least once every 2 weeks. When a nest was discovered, we recorded light intensity (as a percentage of ambient light intensity), the amount of cover around the nest, distance from the nest to the top of the tree, and nest width. Westmoreland and Best (1985) found that these features are related to nesting outcome; details of how they were measured can be found therein. Each clutch was aged by candling (Hanson and Kossack 1963). We created experimental clutch sizes of one and three eggs by randomly exchanging eggs of equal age (i.e., laid on the same day) between nests; some nests (controls) were not manipulated. The egg exchanges were done as soon after nests were discovered as possible. Some nests were found after hatch, however, and data collected from these were used in the control treatment. To minimize losses to predation, nests were visited infrequently or not at all during incubation.

In 1984, we found that nestlings in enlarged broods often fell or were pushed from nests. Because we wanted to test the food limitation hypothesis for the entire nestling period, we installed camouflaged, wire-mesh cones under each nest that successfully hatched in 1985. We removed the nest while wiring the cone to branches and then placed the nest and nestlings securely in the center of the cone. Cones were about 25 cm in diameter, considerably increasing the surface area of nests.

After hatching, nestlings were individually marked on the abdomen with ink spots and were visited at 2- to 3-day intervals until they were 10 days old. Most visits were between 10:00 and 14:00. At each visit, nestlings were weighed to the nearest 0.5 g, gular temperatures were measured with a digital thermometer, and carpo-metacarpus length (CL) was recorded. CL was measured from the bend of the wing to the distal tip of soft tissue; we did not include the length of feathers in this measure. We also palpated crops to determine fullness (0 = empty to 4 = full). Nestlings more than 10 days old tend to fledge when approached closely, so direct handling of young birds ended then. To determine the length of the nesting cycle, we checked the

nest with binoculars each day until the young fledged.

Growth curves were fitted to logistic, exponential, and negative exponential equations with the nonlinear analysis program of SAS (Helwig and Council 1979). Growth-rate constants and inflection points were compared by using *z*-tests. Nestling ages, weights, temperatures, CLs, and crop fullnesses were averaged when more than one nestling was present in a nest because each brood was an experimental unit. When partial failure (i.e., death of some, but not all nestlings) occurred in a brood, we used only the data collected before the loss. Nest success was calculated by the Mayfield (1975) method and evaluated by using two-tailed tests with a significance level of  $P < 0.1$  because the test is susceptible to Type II error (Hensler and Nichols 1981). Two-tailed tests with a significance level of  $P < 0.05$  were used for all other analyses.

## RESULTS

Of the 292 nests that we found, 27 were abandoned and 14 were eliminated for various reasons (research-related nest failure, eggs collected for other purposes, etc.), leaving 251 nests for analyses. ANOVAs for each nest-site feature showed no significant differences among treatments (distance from nest to top of tree— $2.2 \pm 0.1$  m [mean  $\pm$  SE, treatments pooled]; relative light intensity— $16.9 \pm 0.8\%$ ; index of nest cover— $2.2 \pm 0.1$ ; nest width— $119 \pm 1.2$  mm), so it is unlikely that nest placement influenced the treatment differences reported here.

### ABILITY TO INCUBATE EGGS

All fertile eggs not eaten by predators hatched successfully, regardless of clutch size. The length of incubation did not differ among treatments (Table 1), but egg exchanges usually were not made until midway through the incubation period.

### ABILITY TO BROOD AND FEED NESTLINGS

*Growth rates.* Both body weight and CL were indices of nestling growth, and the two variables were strongly correlated ( $r = 0.95$ ,  $n = 510$ ). Nestling weight had greater coefficients of variation than CL, probably because of variation in the fullness of nestling crops. Therefore, we used CL in growth analyses.

Growth rates were inversely related to brood size (Fig. 1, Table 2); enlarged broods grew sig-

TABLE 1. Lengths of egg laying, incubation, and nesting periods for each treatment (mean  $\pm$  SE). Values with the same letter within a column are not significantly different (Duncan's multiple range test,  $P < 0.05$ ).

Clutch/ brood size	Egg laying* (n)	Length of period (days)	
		Incubation (n)	Nesting period (n)
1	0	13.9 $\pm$ 0.09 A (48)	11.8 $\pm$ 0.33 A (31)
2	1.5	13.8 $\pm$ 0.11 A (53)	12.6 $\pm$ 0.47 A (25)
3	3.0	14.0 $\pm$ 0.08 A (42)	13.9 $\pm$ 0.15 B (15)

\* Hanson and Kossack (1963) estimate a laying interval of 1.5 days for Mourning Doves.

nificantly slower and had growth curves with significantly later inflection points. To determine whether this slow growth occurred primarily during the crop-milk or granivorous phase of nestling growth, we analyzed the two phases independently, excluding a brief period when nestlings are fed an equal proportion of milk and seeds (between days 5 and 6). From days 0 to 5, nestling Mourning Doves are primarily fed crop milk; we used the exponential equation to fit this portion of the curve. After reaching 6 days of age, nestlings are granivorous (Taylor 1941, Laub 1956); we used a negative exponential function for this portion of the curve. Because different equations are used, growth-rate constants are not comparable between the growth phases, but treatments within a growth phase can be compared.

Enlarged broods had smaller growth-rate constants than control broods during both phases of growth (Table 2). This difference was significant during the crop-milk phase but not during the granivorous phase.

*Brood temperatures.* Because Mourning Dove nestlings less than 6 days old have not fully developed the ability to thermoregulate (Breitenbach and Baskett 1967), hypothermia could account for the slow growth of enlarged broods. To examine the ability of parents to brood three offspring, we regressed nestling temperature on age during this period for each treatment. The resulting relationships were weak but significant (slopes  $> 0$ ,  $P < 0.05$ ) or nearly so ( $P < 0.1$ ) for all three treatments; mean brood temperature increased as nestlings aged (Fig. 2). An analysis of covariance revealed no treatment  $\times$  age interaction; comparisons of least-squared means showed no significant difference in brood tem-

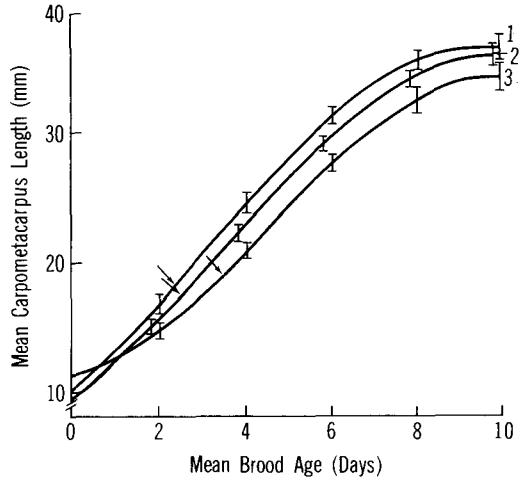


FIGURE 1. Growth of nestling Mourning Doves in broods of one, two, or three nestlings. Vertical bars represent 95% confidence intervals for mean values. Arrows indicate the inflection points.

peratures between control and enlarged broods. Therefore, it seems that Mourning Doves are fully capable of brooding three young, even though adults do not have vascularized incubation patches.

*Crop fullness.* Crop fullness was inversely related to nestling age in all three treatments (Fig. 3), indicating that crops grew at a faster rate than parents could fill them. There was a significant interaction among slopes; the decrease in fullness occurred at a slower rate for lone nestlings than for nestlings in other treatments. A comparison of least-squared means revealed that enlarged broods had significantly less in their crops than other broods.

Starvation or sibling competition resulted in partial nest failures in 17 (37%) three-young nests, but in only four (5%) two-young nests. In 1984, before we reinforced nests with metal cones, nestlings were sometimes found dead or moribund beneath nests. Because they often had food in their crops, we surmised that they died of exposure rather than starvation. Nestlings may have been pushed from nests during feeding bouts because siblings flap their wings vigorously when begging. In 1985, nestlings usually died without falling from the reinforced nests; they seemed to have been crushed by siblings or to have starved.

*Growth of successful, enlarged broods.* For any factor to effectively curtail the evolution of larger clutch size in columbids, it must affect all breed-

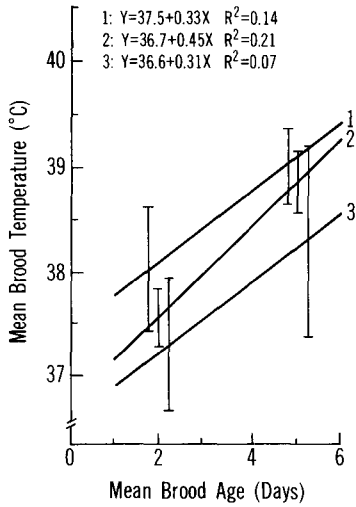


FIGURE 2. Relationship between nestling age and gular temperatures for broods of different size. Vertical bars represent 95% confidence intervals for mean values.

ing pairs. If some Mourning Dove pairs could rear enlarged broods as successfully as the average two-young brood, selection would favor an increase in clutch size if it occurred in such pairs. To examine this, we compared CL growth of the 15 enlarged broods that did not suffer partial failure (pairs "good" at raising enlarged broods) with that of control broods. The treatments did not differ significantly in inflection points nor in growth-rate constants (Table 2). Using data from the last nest visit for each treatment, we compared the growth indices of 9- to 11-day-old broods; at this age, nestlings have generally reached the growth asymptote (Fig. 1). Nestlings in enlarged broods had CLs comparable to those in control broods but weighed only 74% of control-brood weight. Thus, successful enlarged broods probably were not as well prepared for postfledging survival as control broods.

#### CLUTCH SIZE AND THE RISK OF PREDATION

Nestling periods differed significantly among treatments, with enlarged broods taking about 1.3 days longer to fledge than control broods (Table 1). Daily survival probabilities (based on failures of entire clutches) did not differ significantly among treatments (Table 3), but the disparity between control and manipulated clutches approached significance ( $P = 0.14$ ). After we manipulated clutches, both sexes continued to ex-

TABLE 2. Growth parameters and sizes of 9- to 11-day-old broods for each treatment. Values with the same letter within a column are not significantly different (z-test).

Brood size	Growth-rate constants (K) for each period <sup>a</sup>		Entire period <sup>d</sup>		Mean brood size at 9 to 11 days old	
	Crop milk <sup>b</sup>	Granivorous <sup>c</sup>			CL (mm)	Weight (g) <sup>e</sup>
1	0.187 ± 0.01 <sup>c</sup> AB	0.319 ± 0.040 A	0.427 ± 0.027 A		39.1 ± 0.6 A	64 ± 1.01 <sup>c</sup> A
2	0.199 ± 0.009 A	0.283 ± 0.042 AB	0.405 ± 0.022 A		35.6 ± 0.6 A	62 ± 1.01 A
3	0.169 ± 0.008 B	0.194 ± 0.039 B	0.249 ± 0.021 B		—	—
Successful broods of three	0.187 ± 0.012 AB	0.243 ± 0.056 AB	0.359 ± 0.035 AB		34.2 ± 0.2 A	46 ± 2.06 B

<sup>a</sup> These parameters based on equations derived for CL growth (see text).

<sup>b</sup> Curve fitted to the exponential equation ( $Y = b_0 e^{kx}$ ), where  $b_0$  is the Y-intercept, K is the growth rate constant, and e is the base of the natural logarithm.

<sup>c</sup> Curve fitted to the negative exponential equation ( $Y = a(1 - e^{-kx})$ ), where a is the asymptote and the other parameters are as above.

<sup>d</sup> Curve fitted to the logistic equation ( $Y = a/[1 + e^{-k(x-x_0)}]$ ), where 1 is the inflection point and the other parameters are as listed above.

<sup>e</sup> Asymptotic standard error (Galant 1975).

<sup>f</sup> Effects of crop fullness on weight removed by using crop fullness as a covariate.

<sup>g</sup> Standard error.

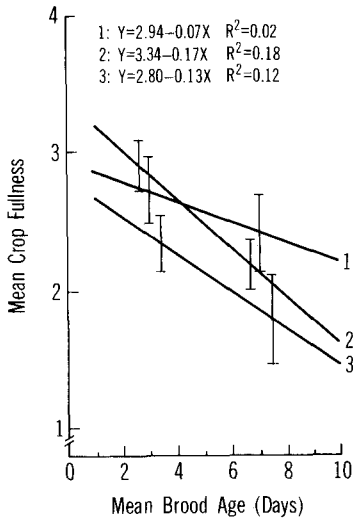


FIGURE 3. Relationship between nestling age and the fullness of nestling crops for broods of different size. Vertical bars represent 95% confidence intervals for mean values.

change nest duties at the normal time intervals (Harris et al. 1963, Blockstein 1982), so activity near the nest did not seem to differ among treatments. In addition, researcher disturbance can have a strong effect on estimates of daily survival probabilities (Westmoreland and Best 1985); therefore, we calculated reproductive success assuming that treatments did not differ in daily survival probabilities. Mayfield (1975) estimates of nesting success were calculated by using the daily survival probabilities of 0.966 for egg laying and incubation and 0.947 for the nestling

period. These survival probabilities were reported by Westmoreland and Best (1985) for unvisited Mourning Dove nests.

Nests with larger broods had longer nest cycles (1: 25.7 days, 2: 27.9 days, 3: 30.9 days; sum of rows from Table 1) and thus would also have lower probabilities of success (1: 0.32, 2: 0.30, 3: 0.26). Despite this, estimates of the number of young fledged per nesting attempt (1: 0.32, 2: 0.60, 3: 0.78) show that parents of enlarged broods could be expected to fledge 30% more young per nesting attempt than parents of control broods.

DISCUSSION

We can reject one of the hypothesized limitations to clutch size for columbids. Adults provided adequate heat for enlarged clutches/broods throughout the critical period of incubation and early nestling growth. Limited ability to feed three offspring, the risk of predation, and other constraints probably interact to limit the clutch size of Mourning Doves.

ABILITY TO FEED NESTLINGS

The crop-milk phase seems to be the period that imposes the strongest physiological limit to clutch size for Mourning Doves and other columbids. Haas (1980) found that Mourning Dove nestlings usually die when one parent is killed during the crop-milk period, but survive to fledge if the parent is killed later. Burley (1980) manipulated brood sizes of captive Rock Doves (*Columba livia*) and identified the crop-milk stage as the period of greatest parental demand.

TABLE 3. Nesting success estimates based on daily survival probabilities (DSP) for each treatment. No differences among treatments are significant (Hensler and Nichols [1981] test,  $P > 0.1$ ).

Nest stage	No. of nests	No. of failures	DSP ± SE	Estimated success (%) <sup>a</sup>
<b>Incubation</b>				
One egg	61	16	0.951 ± 0.012	50
Two eggs	89	33	0.931 ± 0.012	37
Three eggs	57	19	0.942 ± 0.013	43
<b>Nestling period</b>				
One nestling	60	21	0.960 ± 0.009	57
Two nestlings	74	31	0.954 ± 0.008	52
Three nestlings	49	17	0.969 ± 0.008	64
<b>Combined</b>				
Treatment 1	76	37	0.957 ± 0.007	28
Treatment 2	108	64	0.945 ± 0.007	20
Treatment 3	67	36	0.959 ± 0.007	31

<sup>a</sup> Based on incubation and nestling periods of 14 days each.

Limits to the rate of crop-milk production may explain the surprising constancy of clutch size in columbids. If the amount of crop milk produced is determined by resource abundance, one would expect the clutch size of Mourning Doves to vary as it does in other birds that rely on seeds when raising young. But if crop-milk production is limited by the maximal rate of some physiological process involved in its formation (e.g., mitosis, prolactin production, deposition of lipids in the nutritive epithelium, etc.), one would expect little variation in clutch size. Some evidence suggests that columbid parents require a relatively small increase in food intake when producing crop milk. For captive Ringed Turtle-Doves (*Streptopelia risoria*) producing crop milk, caloric intake increases by about 30% above non-breeding intake while fat indices remain constant (Brisbin 1969). Most birds seem to require 2.4 to 4 times more energy for metabolism when breeding than when resting (Utter and Lefebvre 1973, King 1974, Gaston 1985). The fact that crop-milk production is relatively inexpensive, but clutch sizes are nonetheless constant, supports our hypothesis that its production is rate-limited.

Although the difference in growth rates between enlarged and control broods was nonsignificant ( $P = 0.12$ ) during the granivorous phase, we cannot reject the hypothesis that food was a limiting factor during this period because of the potential for Type II error. Even if the difference had been significant, however, the slow growth of enlarged broods could be interpreted in two ways: (1) adults may have been unable to gather enough seeds to sustain normal growth in enlarged broods, or (2) growth of these broods lagged behind because of slow development during the crop-milk phase. Blockstein (1986) did an experiment similar to ours, but in some instances enlarged the brood size after the crop-milk period. For these broods, he found no evidence of food limitation on growth. In our study, the disparity in crop fullness between control and enlarged broods decreased as nestlings aged (Fig. 3). For these reasons, we doubt that clutch size in Mourning Doves is constrained during the granivorous phase.

Food limitation evidently sets an upper limit to clutch size for Mourning Doves, but it does not restrict them to a brood size of two nestlings. For nests that were not found by predators in this study, half of the adult pairs given an ad-

ditional nestling successfully fledged all three young. However, nestlings in enlarged broods sacrificed weight gain (perhaps fat deposition) for skeletal (CL) growth and fledged at lower weight than control nestlings. Murton et al. (1974) and Burley (1980) also reported low fledging weights for columbid nestlings in experimentally enlarged broods.

#### CLUTCH SIZE AND THE RISK OF PREDATION

One might expect that parents successful in fledging three young would realize a 50% enhancement of fitness than those rearing two young. The longer nesting cycle of enlarged broods reduced, but did not negate, this potential increase. The findings of Murton et al. (1974) and Burley (1980) also suggest an increase in fitness for columbid parents with enlarged broods. If it is advantageous for columbids to rear more young, why don't they? The reason probably is that other factors reduce fitness for parents of enlarged broods or otherwise constrain the evolution of larger clutches.

#### OTHER CONSTRAINTS

*Postfledging survival.* The advantage to rearing three-young broods could be reduced if underweight fledglings have low survival. For passerines, there seems to be a positive correlation between fledging weight and survival (Perrins 1963, 1965; Loman 1977). Fledgling Mourning Doves are gradually weaned from the parents during a 2-week, postfledging period (Hitchcock and Mirarchi 1984), when survival is surprisingly high (Grand et al. 1984). We used Grand et al.'s percentage mortality data to calculate a daily survival probability of 0.992 for normal fledglings during this period. If fledglings from enlarged broods in our study had daily survival probabilities of 0.974 or less, the potential increase in fitness for adults raising them would be negated. This difference in survival between fledglings from control vs. enlarged broods is well within that reported for Wood Pigeons (*Columba palumbus*). Murton et al. (1974) found that survival of fledglings from enlarged broods was 44% of that for control fledglings during a 1-month, postfledging period.

*Extended interval between nestings.* Underweight fledglings may require a longer period of postfledging parental care, resulting in a longer interval between successive nesting attempts. This

could lower the fitness of adults by reducing the number of nesting cycles possible in a season (Westmoreland et al. 1986). We followed one color-marked pair of adults through four nesting cycles and monitored renesting intervals after they raised broods of one, two, and three nestlings. The adults renested 4 days after the young fledged, regardless of the previous brood size. After a successful nesting, Mourning Doves usually begin a new clutch in 3 to 6 days (Harris et al. 1963, Caldwell 1964). These meager findings do not suggest a longer nesting interval for pairs raising enlarged broods, but such a relationship has been reported for House Sparrows (*Passer domesticus*; McGillivray 1983).

*Small nest size.* Survival of Mourning Dove nestlings may be curtailed by the small size of nests. We found that nestlings in enlarged broods often fell from nests not reinforced with cones. The size of Mourning Dove nests varies greatly, however, because they reuse nests built by other species (e.g., McClure 1950, Scanlon et al. 1981, Westmoreland and Best 1985). If selection favored an increase in clutch size, it seems likely that Mourning Doves could adapt to build larger nests or use other species' nests more frequently. Small nest size is probably a result, not a cause, of small clutches.

*Costs of oogenesis.* Finally, clutch size in columbids might be constrained by a factor that we could not measure—the cost of oogenesis. It seems unlikely that producing a clutch is energetically expensive to columbid females, however, because both the eggs and clutches are comparatively small. Rahn et al. (1975) found that columbids produce eggs that are on average less than half the size of those laid by other birds of equal weight. We (unpubl. data) examined the relationship between body weight and the total energy content (kcal/g  $\times$  egg weight  $\times$  clutch size) of clutches for 23 altricial, terrestrial bird species. Compared with Mourning Doves, non-columbids of comparable weight invest 2.5 times more energy in a clutch (15.9 vs. 40.3 kcal). In view of the large number of eggs that some birds have been induced to lay (reviewed in Klomp 1970), it seems unlikely that the cost of oogenesis imposes a limitation to clutch size for nidicolous species.

Contrary to our expectations and those of others (e.g., Lack 1948) that have considered the paradox of constant clutch size and the success of columbids, physiological factors alone do not

restrict Mourning Doves to a clutch of only two eggs. Rather, physiological and ecological factors (limited crop-milk production, an extended nesting period, and low postfledging survival) associated with larger broods seem to interact to limit the species to a clutch of two eggs.

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#### LITERATURE CITED

- BLOCKSTEIN, D. E. 1982. Nesting behavior of Mourning Doves (*Zenaida macroura*) in Minnesota. M.Sc.thesis, Univ. Minnesota, Minneapolis.
- BLOCKSTEIN, D. E. 1986. Reproductive behavior and parental investment of Mourning Doves (*Zenaida macroura*). Ph.D.diss., Univ. of Minnesota, Minneapolis.
- BREITENBACH, R. P., AND T. S. BASKETT. 1967. Ontogeny of thermoregulation in the Mourning Dove. *Physiol. Zool.* 40:207–217.
- BRISBIN, I. L., JR. 1969. Bioenergetics of the breeding cycle of the Ring Dove. *Auk* 86:54–74.
- BROCKELMAN, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. *Am. Nat.* 109:677–699.
- BURLEY, N. 1980. Clutch overlap and clutch size: alternative and complementary reproductive tactics. *Am. Nat.* 115:223–246.
- CALDWELL, L. D. 1964. Dove production and nest site selection in southern Michigan. *J. Wildl. Manage.* 28:732–738.
- CHARNOV, E. L., AND J. R. KREBS. 1974. On clutch-size and fitness. *Ibid* 116:217–219.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20:174–184.
- CROSSNER, K. A. 1977. Natural selection and clutch size in the European Starling. *Ecology* 58:885–892.
- FOSTER, M. S. 1974. A model to explain molt-breeding overlap and clutch size in some tropical birds. *Evolution* 28:182–190.
- GALANT, A. R. 1975. Nonlinear regression. *Am. Stat.* 29:73–81.
- GASTON, A. J. 1985. Energy invested in reproduction by Thick-billed Murres (*Uria lomvia*). *Auk* 102:447–458.
- GOODWIN, D. 1983. Pigeons and doves of the world. 3rd ed. Cornell Univ. Press, Ithaca, NY.
- GRAND, J. B., R. R. HITCHCOCK, AND R. E. MIRARCHI. 1984. Mortality of nestling and fledgling Mourn-

- ing Doves in east-central Alabama. *J. Ala. Acad. Sci.* 55:131.
- GREENLAW, J. S. 1978. The relation of breeding schedule and clutch size to food supply in the Rufous-sided Towhee. *Condor* 80:24-33.
- HAAS, G. H. 1980. Success of single-parent Mourning Dove nests. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies* 34:426-429.
- HANSON, H. C., AND C. W. KOSSACK. 1963. The Mourning Dove in Illinois. *Ill. Dep. Conserv. Tech. Bull.* 2.
- HARRIS, M. P. 1970. Breeding ecology of the Swallow-tailed Gull, *Creagrus furcatus*. *Auk* 87:215-243.
- HARRIS, S. W., I. A. MORSE, AND W. H. LONGLEY. 1963. Nesting and production of the Mourning Dove in Minnesota. *Am. Midl. Nat.* 69:150-172.
- HAYMES, G. T., AND R. D. MORRIS. 1977. Brood size manipulations in Herring Gulls. *Can. J. Zool.* 55:1762-1766.
- HELWIG, J. T., AND K. A. COUNCIL. 1979. SAS user's guide. SAS Institute, Raleigh, NC.
- HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bull.* 93:42-53.
- HITCHCOCK, R. R., AND R. E. MIRARCHI. 1984. Duration of dependence of wild fledgling Mourning Doves upon parental care. *J. Wildl. Manage.* 48:99-108.
- JONES, R. E. 1971. The incubation patch of birds. *Biol. Rev.* 46:315-339.
- KING, J. R. 1974. Seasonal allocation of time and energy resources in birds. *Publ. Nuttall Ornithol. Club* 15:4-85.
- KLOMP, H. 1970. The determination of clutch-size in birds: a review. *Ardea* 58:1-124.
- LACK, D. 1947. The significance of clutch size. I, II. *Ibis* 89:302-352.
- LACK, D. 1948. The significance of clutch-size. Part III. Some interspecific comparisons. *Ibis* 90:25-45.
- LAUB, W. K. 1956. The relation of parental care and the condition of the glandular crop to the successful rearing of young Mourning Doves, *Zenaidura macroura* (L.). M.Sc.thesis, Ohio State Univ., Columbus.
- LLOYD, C. S. 1977. The ability of the Razorbill *Alca torda* to raise an additional chick to fledging. *Ornis Scand.* 8:155-159.
- LOMAN, J. 1977. Factors affecting clutch and brood size in the Crow, *Corvus cornix*. *Oikos* 29:294-301.
- MARIDON, B., AND L. C. HOLCOMB. 1971. No evidence for incubation patch changes in Mourning Doves throughout reproduction. *Condor* 33:374-375.
- MAYFIELD, H. F. 1975. Suggestions for calculating nesting success. *Wilson Bull.* 87:456-466.
- MCCLURE, H. E. 1950. An eleven-year summary of Mourning Dove observations in the west. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 15:335-346.
- McGILLIVRAY, W. B. 1983. Intra-seasonal reproductive costs for the House Sparrow (*Passer domesticus*). *Auk* 100:25-32.
- MURTON, R. K., N. J. WESTWOOD, AND A. J. ISAACSON. 1974. Factors affecting egg-weight, body-weight and moult of the Woodpigeon *Columba palumbus*. *Ibis* 116:52-73.
- PERRINS, C. M. 1963. Survival of the Great Tit, *Parus major*. *Proc. XIII Int. Ornithol. Congr.* (1962): 717-728.
- PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major* L. *J. Anim. Ecol.* 34:601-647.
- PLUMB, W. J. 1965. Observations on the breeding biology of the Razorbill. *Br. Birds* 58:449-456.
- RAHN, H., C. V. PAGANELLI, AND A. AR. 1975. Relation of avian egg weight to body weight. *Auk* 92:750-765.
- RICKLEFS, R. E. 1968. On the limitation of brood size in passerine birds by the ability of adults to nourish their young. *Proc. Natl. Acad. Sci. U.S.A.* 61:847-851.
- RICKLEFS, R. E. 1970. Clutch size in birds: outcome of opposing predator and prey limitations. *Science* 168:599-600.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. *Publ. Nuttall Ornithol. Club* 15:152-292.
- SAFRIEL, U. N. 1975. On the significance of clutch size in nidifugous birds. *Ecology* 56:703-708.
- SCANLON, P. F., J. E. CLARKE, C. J. FLICK, AND W. H. TAYLOR. 1981. Aspects of Mourning Dove nesting in Virginia. *Va. J. Sci.* 32:97.
- TAYLOR, M. H. 1941. Breeding and nesting activities of the Eastern Mourning Dove in North Carolina. M.Sc.thesis, North Carolina State Univ., Raleigh.
- UTTER, J. M., AND E. A. LEFEBVRE. 1973. Daily energy expenditure of Purple Martins (*Progne subis*) during the breeding season: estimates using  $D_2O^{18}$  and time budget methods. *Ecology* 54:597-604.
- VERMEER, K. 1963. The breeding ecology of the Glaucous-winged Gull (*Larus glaucescens*) on Mandarte Island, B.C. *Occas. Pap., B.C. Prov. Mus. Nat. Hist. Anthropol.* 13:1-104.
- WEEKS, H. P., JR. 1980. Unusual egg deposition in Mourning Doves. *Wilson Bull.* 92:258-260.
- WESTMORELAND, D., AND L. B. BEST. 1985. Effects of researcher disturbance on Mourning Dove nesting success. *Auk* 102:774-780.
- WESTMORELAND, D., L. B. BEST, AND D. E. BLOCKSTEIN. 1986. Multiple brooding as a reproductive strategy: time-conserving traits in Mourning Doves. *Auk* 103:196-203.