

HATCHING ASYNCHRONY, EGG SIZE, GROWTH, AND FLEDGING IN TREE SWALLOWS¹

RETO ZACH

Atomic Energy of Canada Limited, Whiteshell Nuclear Research Establishment,
Pinawa, Manitoba R0E 1L0, Canada

ABSTRACT.—Marked asynchronous hatching was observed in Tree Swallows (*Iridoprocne bicolor*), apparently because incubation started before the full clutch was laid. Asynchronous hatching resulted in pronounced size differences of nestlings. Immediately after hatching, the first-hatched nestling was, on average, 94% heavier than the last-hatched. Clearly, a weight hierarchy was established, with small late-hatched young at a disadvantage. Egg weight increased with laying order, and last-laid eggs tended to hatch last. Thus, egg-size differences did not enhance the weight hierarchy due to hatching asynchrony. Early hatchlings had longer nestling times than late hatchlings. The former also had a higher observed asymptotic weight and longer primaries at fledging than the latter. Late-hatched young were less likely to fledge than early hatchlings. The number of young fledged increased with hatching asynchrony but so did brood size. Tree Swallows appear to use brood reduction to maximize reproductive output, but alternative hypotheses cannot be ruled out. Received 21 September 1981, accepted 8 March 1982.

THERE has been considerable interest in the reproductive strategies of passerines, in particular the maximization of reproductive output by parents through control of the mortality pattern of their young, as proposed by the brood-reduction hypothesis (e.g. Ricklefs 1965, Lack 1968, Howe 1976, O'Connor 1977, Bryant 1978, Hahn 1981). A central theme of this hypothesis is that the probability of survival of young may not be constant within broods, depending on the exact allocation of reproductive effort by parents to individual eggs or nestlings, the state of incubation in relation to egg laying, and environmental conditions such as the size and predictability of the food supply. Several rival hypotheses have been proposed, as discussed by Hussell (1972) and Clark and Wilson (1981).

We have previously reported on the growth and survival of nestling Tree Swallows (*Iridoprocne bicolor*) (Zach and Mayoh 1982) and will now explore the relationships between egg size, hatching, weight increase, primary-feather growth, and fledging. Here, we present data that suggest that Tree Swallows may use brood reduction, that is, partial loss of the brood under adverse feeding conditions, to maximize reproductive output, although other hypotheses cannot be rejected completely.

METHODS

Our studies were carried out in 1980 and 1981 at the Whiteshell Nuclear Research Establishment near Pinawa, Manitoba, Canada. Methods are essentially the same as those reported by Zach and Mayoh (1982). In 1980 we studied hatching, growth, fledging, and breeding success of 35 broods but did not measure egg weights. Therefore, in 1981 we individually weighed 234 eggs (5.70 ± 0.12 eggs, $n = 41$ clutches) to study size variation. On the day of laying, each egg was numbered and then weighed to ± 0.1 g in a small plastic bag with a Pesola spring scale. In both years, nests were inspected near mid-morning. Around hatching, some nests were visited more than once daily. Weight and primary-growth model-parameter values were taken from Zach and Mayoh (1982), who showed that weight and primary-feather growth of nestling Tree Swallows can be best described by the logistic and the Gompertz models, respectively. All means are quoted with their standard errors. Statistical tests and procedures were taken from Sokal and Rohlf (1969).

RESULTS

Tree Swallows have marked asynchronous hatching (Table 1). Of 35 broods, young from only 8.6% hatched all on the same day. Asynchronous hatching is probably due to Tree Swallows starting to incubate before laying the full clutch or to intermittent incubation while laying (Bryant 1978, Dring 1980, Clark and Wilson 1981).

Asynchronous hatching resulted in pro-

¹ Issued as AECL-7353.

TABLE 1. Mean (\pm SE) percentage of Tree Swallows hatching and fledging on days 1-4.

Day of hatching or fledging ^a	Hatching (n = 35)	Fledging (n = 29)
1	56.8 \pm 4.3	50.2 \pm 5.1
2	33.2 \pm 3.4	41.6 \pm 4.8
3	9.4 \pm 2.2	7.6 \pm 2.7
4 ^b	0.6 \pm 0.6	0.6 \pm 0.6

^a Hatching day 1 is the day on which the first egg hatched in each clutch; fledging day 1 is the day on which the first young fledged in each brood.

^b In subsequent tables and analyses, day 4 hatchlings were pooled with day 3 hatchlings.

nounced size differences in nestlings. As soon as hatching was completed, we ranked nestlings according to weight and then computed the maximum difference for each brood. On average, the largest young was $93.7 \pm 10.8\%$ heavier than the smallest. Broods hatching over 2 days were significantly more variable in weight than those hatching over 1 day, and those hatching over 3 days were significantly more variable than those hatching over 2 days (Table 2). The percentage weight difference between the largest and smallest nestlings also showed a significant increase in response to length of hatching period (Table 2). Clearly, a weight hierarchy is established by asynchronous hatching, with smaller young potentially disadvantaged during feeding (Lohrl 1968, Bryant 1978, Hahn 1981).

The relationship between hatching order and position in the initial weight hierarchy following completion of hatching can be investigated by determining the hatching day of the lightest and heaviest young in each brood. Based on 32 broods, 96.9% of the heaviest young hatched on the first day, and 96.9% of the lightest young hatched on the last day. These results support

the conclusion that differences in weight of nestling Tree Swallows are due to asynchronous hatching.

In many passerines, egg size varies systematically with laying order, which might cause weight differences among young (Howe 1976, O'Connor 1977, Ricklefs et al. 1978, Clark and Wilson 1981). A nested analysis of variance of our 1981 data did not indicate any significant differences in egg weights for clutches of various sizes (clutch size 4: 1.72 ± 0.06 g, $n = 12$; 5: 1.86 ± 0.03 g, $n = 50$; 6: 1.79 ± 0.01 g, $n = 144$; 7: 1.83 ± 0.04 g, $n = 28$). There were significant differences associated with laying order for most clutch sizes (Table 3). In general, egg weight increased with laying order. These results agree with those for House Martins (*Delichon urbica*) (Bryant 1975) and support the conclusion that weight hierarchies within Tree Swallow broods are due to asynchronous hatching and not egg size variation. In fact, egg-size variation with laying order would seem to decrease rather than enhance weight differences of nestling Tree Swallows.

In 8 of 14 broods, the first egg laid hatched on the first day, and in 11 cases the last egg laid hatched on the last day of hatching. From the number of eggs hatched on various days, the corresponding expected numbers under random conditions are 7.3 and 5.9 eggs. These expected values are based on the assumption that each egg of a given clutch has an equal chance of hatching on any of the days on which hatching actually occurred. There is no significant tendency for first-laid eggs to hatch first, but last laid eggs tend to hatch last ($P < 0.01$, Chi-square test). These results support our observation that Tree Swallows usually start incubation before laying the last egg.

Mean egg weights of different clutches ranged from a low of 1.55 ± 0.02 g ($n = 4$) to a high of 2.14 ± 0.02 g ($n = 5$). Considering all the

TABLE 2. Mean (\pm SE) coefficient of variation (CV) of weights of nestling Tree Swallows following hatching of the last egg and mean percentage weight difference between the lightest and heaviest young for clutches hatching over 1, 2, and 3 days.

	Length of hatching period (days)				
	1 (n = 3)	vs.	2 (n = 20)	vs.	3 (n = 12)
CV weight (%) ^a	5.1 \pm 1.6	$P < 0.01^b$	20.4 \pm 1.8	$P < 0.01$	29.4 \pm 1.8
Percentage weight difference	11.4 \pm 3.5	$P < 0.01$	86.4 \pm 15.1	$P < 0.025$	126.5 \pm 11.9

^a Coefficient of variation $CV = S_x \cdot 100\%/k$.

^b Probability levels refer to Wilcoxon's two-sample tests comparing clutches hatching over 1 and 2 days and over 2 and 3 days.

TABLE 3. Mean fresh egg weights (g) of successively laid eggs of Tree Swallow clutches ranging from 4 to 7 eggs and mean ($\bar{x} \pm SE$) weights for all clutches.

Clutch size ^a	n	Egg sequence						
		1	2	3	4	5	6	7
4	3	1.80	1.77	1.67	1.67			
5**	10	1.82	1.82	1.81	1.92	1.93		
6***	24	1.77	1.75	1.78	1.79	1.83	1.83	
7*	4	1.78	1.72	1.80	1.88	1.83	2.00	1.80
\bar{x}	41	1.78	1.77	1.78	1.82	1.86	1.85	1.80
SE		0.03	0.03	0.03	0.03	0.02	0.03	0.09

^a * $P < 0.05$, ** $P < 0.025$, *** $P < 0.001$, two-way analysis of variance.

clutches, 57.7% of the variation in egg weight was due to differences among clutches ($P < 0.001$, nested analysis of variance). Most nestling weight and primary-feather 9 growth parameters, based on the logistic and Gompertz models, respectively, have a similar pattern of variation (Zach and Mayoh 1982). Therefore, we transformed growth parameter values ($x - \bar{x}$) to remove differences among broods before relating them to hatching order. Nestlings that failed to fledge were excluded from this analysis, because they had greatly depressed growth (Zach and Mayoh 1982).

To investigate growth of nestlings in relation to hatching day, we carried out a one-way analysis of variance followed by two a priori multiple comparisons for each of the parameters listed in Table 4. Observed primary length at fledging and nestling time differed signifi-

cantly overall ($P < 0.001$, in both cases), and the same was true for the observed weight asymptote ($P < 0.05$). These data indicate that nestling time decreased with day of hatching and that early hatchlings reached a higher observed asymptotic weight and had longer primaries at fledging than late hatchlings. Multiple comparisons for the weight asymptote, A_w , and the weight growth-rate constant, K_w , predicted by the logistic model are in agreement with these findings (Table 4). Surprisingly, the primary growth-rate constant, K_p , predicted by the Gompertz model suggests that late hatchlings have more rapid feather growth than early hatchlings (Table 4). Although this result seems to be contradictory, it must be remembered that the age at which primaries make their appearance is quite variable (Zach and Mayoh 1982). Further, at fledging, primary

TABLE 4. Mean transformed weight asymptote, A_w , weight growth rate constant, K_w , observed weight asymptote, observed weight at fledging, primary-feather 9 growth-rate constant K_p , observed primary 9 length at fledging, and nestling time for Tree Swallows hatched on days 1-3, and actual mean values ($\pm SE$) irrespective of hatching day.^a

	Day of hatching ^b						Actual values (n = 58)
	1 (n = 25)	vs.	2 (n = 24)	vs.	3 (n = 9)		
Weight asymptote A_w (g) ^c	0.282	$P < 0.001^d$	-0.236		-0.156	22.72 \pm 0.25	
Weight growth-rate constant K_w (d^{-1}) ^c	0.004		0.002	$P < 0.05$	-0.019	0.51 \pm 0.01	
Observed weight asymptote (g)	0.180		-0.027	$P < 0.025$	-0.614	22.44 \pm 0.19	
Observed weight at fledging (g)	-0.061		-0.017		0.222	19.75 \pm 0.19	
Primary growth-rate constant K_p (d^{-1}) ^c	-0.002		-0.003	$P < 0.05$	0.010	0.22 \pm 0.01	
Observed primary length at fledging (mm)	1.287	$P < 0.05$	-0.117	$P < 0.005$	-3.003	56.95 \pm 0.54	
Nestling time (days)	0.259	$P < 0.025$	-0.042	$P < 0.01$	-0.583	20.14 \pm 0.18	

^a Except for actual values, all the values shown are mean differences, $x - \bar{x}$, where \bar{x} is the mean value for each brood.

^b Day 1 is the day on which the first egg hatched in each brood.

^c A_w and K_w are based on the logistic growth model for nestling weight and K_p on the Gompertz growth model for primary 9 length, as calculated by Zach and Mayoh (1982).

^d Probability levels refer to a priori multiple comparisons using modified *t*-tests, contrasting day 1 with day 2 hatchlings and day 2 with day 3 hatchlings.

TABLE 5. Mean (\pm SE) clutch size; percentage of eggs hatched; number of young fledged; percentage of eggs resulting in fledged young for all clutches of Tree Swallows hatching over 1, 2, and 3 days; and percentage of eggs resulting in fledged young for 5- and 6-egg clutches.

	Length of hatchling period (days)		
	1 ($n = 3$)	2 ($n = 20$)	3 ($n = 12$)
Clutch size ^a	4.7 \pm 0.3	5.4 \pm 0.2	5.9 \pm 0.2
Percentage hatching	78.3 \pm 11.7	95.2 \pm 2.3	95.0 \pm 2.2
Number fledged ^a	2.0 \pm 1.0	3.9 \pm 0.4	4.5 \pm 0.5
Percentage fledged	45.0 \pm 22.9	72.6 \pm 7.9	78.6 \pm 8.7
Percentage fledged 5 eggs	30.0 \pm 30.0	60.0 \pm 24.5	86.7 \pm 13.3
Percentage fledged 6 eggs		69.7 \pm 8.9	81.5 \pm 10.6

^a * = $P < 0.05$, Kruskal-Wallis test.

growth is only 65% completed, and this makes it difficult to fit growth models (Zach and Mayoh 1982).

DISCUSSION

On the whole, our data suggest that early hatchlings grow better than late hatchlings. We can only speculate as to whether or not less-developed late hatchlings have poorer survival following fledging than the more-developed early hatchlings. Heavy Great Tit nestlings (*Parus major*) survive better than light ones following fledging (Perrins 1965). Garnett (1981) has shown that this is probably due to a dominance hierarchy based on size, with large fledglings at an advantage.

Tree Swallows have pronounced asynchronous fledging (Table 1). Of 29 nests, young from only 13.8% fledged on the same day. The similarity of the hatching and fledging percentages for days 1 to 4 (Table 1) suggests a link: the heaviest and lightest nestlings in the initial weight hierarchy of a given nest ought to fledge first and last, respectively. In 8 of 26 broods, the heaviest nestling fledged on the first day, and in 7 cases the lightest nestling fledged on the last day of fledging. From the number of young fledged on various days, the corresponding expected numbers under random conditions are 11.5 and 12.8. Thus, there is no significant tendency for the heaviest young to fledge first, but the lightest or last-hatched young tend to fledge earlier than expected ($P < 0.025$). It could be that sibling competition for food or space forced late hatchlings to fledge prematurely. Alternatively, early hatchlings may have remained longer in the nest boxes than actually required. Our observations sug-

gest that fledging in Tree Swallows is not rigidly linked to a fixed level or degree of development.

Ignoring broods that failed entirely, the probability of fledging for young hatched on days 1, 2, and 3 was 0.82 ± 0.06 , 0.75 ± 0.08 , and 0.69 ± 0.12 , respectively. Thus, there was a steady decline over successive hatching days, as predicted by the brood-reduction hypothesis (O'Connor 1977, Hahn 1981). There was no significant interaction between hatching day and fledging, however, indicating that this trend is not statistically significant.

A crucial part of the brood-reduction strategy is whether or not broods with asynchronous hatching are more productive than those without (Hahn 1981). In this study, hatching asynchrony and the consequent weight hierarchy in nestling Tree Swallows were not independent of clutch size, as large clutches hatched significantly more asynchronously (Table 5). Hatching success was not significantly related to hatching asynchrony, but the number fledged was, with the more asynchronous clutches yielding more young (Table 5). This was largely due to differences in clutch size, however, as the percentages of eggs resulting in fledged young did not vary significantly with hatching asynchrony (Table 5). Considering clutches with 5 and 6 eggs separately, percentages of eggs giving rise to fledged young increased with hatching asynchrony, but the trends were not statistically significant (Table 5). Too few data were available to analyze clutches with 4 and 7 eggs. Our results show that asynchronously hatching clutches were more productive, as predicted by the brood-reduction hypothesis, but this was due to differences in clutch size rather than asynchrony.

Brood reduction, as a main or back-up strategy, is most likely to evolve when the food supply undergoes random short-term fluctuations (O'Connor 1977). Many observers have noted the sensitivity of Tree Swallows to adverse weather conditions when aerial insects are scarce (Austin and Low 1932, Paynter 1954, Chapman 1955). Presumably, such fluctuations cannot be predicted at egg laying. Consequently, brood reduction is the most adaptive strategy (O'Connor 1977). Our Tree Swallow data indicate several important characteristics of this strategy, asynchronous hatching leading to a pronounced weight hierarchy within broods in particular. Thus, Tree Swallows and House Martins (Bryant 1978) seem to have similar reproductive strategies. In Tree Swallows, relatively high growth rates ($K_w = 0.51 \pm 0.01 d^{-1}$, $n = 136$; Zach and Mayoh 1982), compared to those of other swallow species ($K_w = 0.43 \pm 0.01 d^{-1}$, $n = 5$; Ricklefs 1968), may enhance sibling differences created by hatching asynchrony (O'Connor 1977).

Although Tree Swallows have the prerequisites for brood reduction, we did not observe it in full operation. This is probably due to the generally favourable weather and feeding conditions during the 1980 season (Zach and Mayoh 1982). The question remaining is how our results relate to some of the alternative hypotheses.

Because early hatchlings had the longest nestling times (Table 4), it is unlikely that Tree Swallows start to incubate eggs before laying the full clutch in order to speed up the time of fledging for early hatchlings (Hussell 1972). It is entirely possible, however, that by spreading out hatching times parents may also spread out the peak food demands by individual nestlings (Hussell 1972). This could be particularly true for Tree Swallows, which have pronounced weight recession (Zach and Mayoh 1982). On the basis of a simple general model, Clark and Wilson (1981) recently predicted that, even in the absence of brood reduction, most bird species should commence incubation before laying the last egg in order to maximize reproductive output. Unfortunately, their nest-failure hypothesis is difficult to test, because it does not exclude brood reduction entirely. The nest-failure hypothesis predicts that egg size should increase with successive eggs laid, as was observed in our study (Table 3). Provided

egg quality remains constant, this trend is not in agreement with the brood-reduction hypothesis.

We agree with Clark and Wilson (1981) that much more data are required to increase our understanding of the reproductive strategies of birds. At the same time, the various hypotheses must be studied and contrasted to identify unique and testable predictions.

ACKNOWLEDGMENTS

I wish to thank K. R. Mayoh, D. Bjornson, and L. Gillert for able assistance, and all those who contributed to the study or helped to improve the manuscript.

LITERATURE CITED

- AUSTIN, O. L., JR., & S. H. LOW. 1932. Notes on the breeding of the Tree Swallow. *Bird-Banding* 3: 39-44.
- BRYANT, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. *Ibis* 117: 180-216.
- . 1978. Establishment of weight hierarchies in the broods of House Martins *Delichon urbica*. *Ibis* 120: 16-26.
- CHAPMAN, L. B. 1955. Studies of a Tree Swallow colony. *Bird-Banding* 26: 45-70.
- CLARK, A. B., & D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. *Quart. Rev. Biol.* 56: 253-277.
- DRING, P. 1980. Early incubation and asynchronous hatching in the Tree Swallow. *Bird-Banding* 52: 25.
- GARNETT, M. C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major*. *Ibis* 123: 31-41.
- HAHN, D. C. 1981. Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry. *Anim. Behav.* 29: 421-427.
- HOWE, H. F. 1976. Egg-size, hatching asynchrony, sex, and brood reduction in the Common Grackle. *Ecology* 57: 1195-1207.
- HUSSELL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. *Ecol. Monogr.* 42: 317-364.
- LACK, D. 1968. Ecological adaptations for breeding in birds. London, Chapman and Hall.
- LOHRL, H. 1968. Das Nesth kchen als biologisches Problem. *J. Ornithol.* 109: 383-395.
- O'CONNOR, R. J. 1977. Growth strategies in nestling passerines. *Living Bird* 16: 209-238.
- PAYNTER, R. A., JR. 1954. Interrelations between clutch size, brood size, pre fledging survival and weight in Kent Island Tree Swallows. *Bird-Banding* 25: 35-58.

- PERRINS, C. M. 1965. Population fluctuation and clutch size in the Great Tit *Parus major*. *J. Anim. Ecol.* 34: 601-647.
- RICKLEFS, R. E. 1965. Brood reduction in the Curve-billed Thrasher. *Condor* 67: 505-510.
- . 1968. Patterns of growth in birds. *Ibis* 110: 419-451.
- , D. C. HAHN, & W. A. MONTEVECCHI. 1978. The relationship between egg size and chick size in the Laughing Gull and Japanese Quail. *Auk* 95: 135-144.
- SOKAL, R. R., & F. J. ROHLF. 1969. *Biometry*. San Francisco, W. H. Freeman and Company.
- ZACH, R., & K. R. MAYOH. 1982. Weight and feather growth of nestling Tree Swallows. *Can. J. Zool.* 60: 1080-1090.