

# AN EXPERIMENTAL STUDY OF BROOD REDUCTION AND HATCHING ASYNCHRONY IN YELLOW WARBLERS<sup>1</sup>

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**Abstract.** The purpose of this study was to examine Lack's (1947, 1954) brood-reduction hypothesis concerning hatching asynchrony, and its importance in explaining the evolution of hatching asynchrony in Yellow Warblers (*Dendroica petechia*). The study was conducted during the summers of 1988-1990 on a population of Yellow Warblers breeding in the dune-ridge forest at Delta Marsh, Manitoba, Canada (58°11'N, 98°19'W).

I examined the brood-reduction hypothesis experimentally by inducing a sample of females to delay incubation until clutch completion. This was achieved by removing eggs as they were laid, and placing them in a cooler at 20°C until clutch completion. As a result, eggs in each manipulated clutch hatched synchronously (hatch spread between first- and last-hatched nestling  $\leq 24$  hr). Subsequently, I compared the fledging mass and survival rate of nestlings in asynchronously (unmanipulated broods, hatch spread  $> 24$  hr) and synchronously (manipulated) hatching broods. Consistent with the hypothesis, nestling mortality was concentrated in last-hatched nestlings in asynchronous broods and random with respect to hatch order in synchronous broods. Also in agreement with the hypothesis, fledging mass and survival rates of first-hatched chicks were generally higher in asynchronous broods. However, contrary to the hypothesis, fledging mass and survival rates were similar for last-hatched chicks in asynchronous and synchronous broods. Also consistent with the hypothesis, fledging success (no. fledged/clutch) in broods of five tended to be higher in asynchronously hatched broods, regardless of food availability. Finally, fledging rate (no. fledged/no. hatched) was significantly greater in asynchronous broods (four and five nestlings combined) when compared to synchronous broods, especially when food was limiting.

**Key words:** *Dendroica petechia*; *Yellow Warbler*; *hatching asynchrony*; *brood reduction*.

## INTRODUCTION

In many species of birds, incubation begins prior to clutch completion (see review by Clark and Wilson 1981). Consequently, first-laid eggs receive a developmental head start, and eggs within a clutch typically hatch asynchronously, i.e., early-laid egg(s) hatch at least 24 hr before their sibling(s). Subsequently, a competitive size hierarchy is established among siblings, such that within a brood, first-hatched chicks usually dominate, and last-hatched chicks are generally at the bottom of the hierarchy (see review by Magrath 1990). As a result, last-hatched chicks may grow more slowly and may even starve (e.g., Ricklefs 1965, Howe 1976, Bancroft 1985, Lessells and Avery 1989).

Lack (1947, 1954) hypothesized that hatching asynchrony is a mechanism by which parents

facilitate brood reduction, especially during periods of food stress. According to Lack's brood-reduction hypothesis, when food is scarce the size hierarchy allows parents to channel food to the older and presumably fitter chicks. The size hierarchy created by hatching asynchrony thus allows parents to adjust brood size and brood quality to prevailing food conditions, and thereby maximize lifetime reproductive success (O'Connor 1978, Temme and Charnov 1987). Conversely, if food is plentiful, all chicks survive. If hatching is synchronous, and if food is limiting, all nestlings in a brood may suffer reduced growth rates, and therefore lower survival probabilities, or starve (Ricklefs 1965, Perrins 1966).

The brood-reduction hypothesis is supported mainly by studies that observed that last-hatched nestlings have lower growth rates (e.g., Parsons 1975, Howe 1976, Bryant 1978, Drummond et al. 1986), or lower survival rates (e.g., Nisbet and Cohen 1975, Cash and Evans 1986, Smith 1988, Stouffer and Power 1990) than their elder sibs. However, experimental tests of the brood-reduction hypothesis have been equivocal. For example, most studies in which hatching synchrony

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(hatch spread usually  $\leq 24$  hr) has been experimentally induced have not supported the prediction that broods hatching asynchronously should produce more young than broods hatching synchronously (see reviews by Magrath 1990, Amundsen and Slagsvold 1991a). This is true of experiments involving species with long nestling periods (e.g., boobies, Anderson 1989; cormorants, Shaw 1985; egrets, Fujioka 1985; and gulls, Hébert and Barclay 1986; but see Hahn 1981), as well as species with relatively short nestling periods (e.g., passerines, Slagsvold 1982, 1986a; Bengtsson and Ryden 1983; Skagen 1987; Amundsen and Slagsvold 1991b; Harper et al. 1992; but see Magrath 1989).

The above results alone cannot be used to disqualify the brood-reduction hypothesis, since few studies (Skagen 1988, Magrath 1989) have quantified or experimentally manipulated food availability in addition to manipulating hatching spreads (Magrath 1990). In this paper I present results from an experimental field study of hatching asynchrony in Yellow Warblers (*Dendroica petechia*), during which time a period of relatively low food availability occurred fortuitously.

The purpose of this study then was to examine the importance of the brood-reduction hypothesis in explaining the evolution of hatching asynchrony in the Yellow Warbler. I examined the following predictions based on the brood-reduction hypothesis: (1) in asynchronous broods nestling mortality will be concentrated in the last-hatched nestling(s), whereas in synchronous broods nestling mortality will be random among positions in the hatching sequence. The critical predictions of the brood-reduction hypothesis are that, if food is limiting: (2) the fledging mass and survival rate of first-hatched nestlings in asynchronous broods will be greater than that of first-hatched nestlings in synchronous broods, (3) fledging mass and survival rates of last-hatched nestlings in asynchronous broods will be less than that of last-hatched nestlings in synchronous broods, and (4) reproductive success will be higher for parents with asynchronous broods compared to synchronous broods.

Predictions 1–3 are based on the assumption that in the absence of hatching asynchrony, a stable competitive hierarchy is not established, such that all nestlings are of similar competitive ability. Prediction 4 assumes that in the absence of a competitive hierarchy, all nestlings are fed equally, albeit inadequately (see Ricklefs 1965).

## METHODS

The study was conducted, during mid-May to mid-July from 1988–1990, on a population of Yellow Warblers breeding in the forested dune-ridge at Delta Marsh, Manitoba, Canada (58°11'N, 98°19'W; see MacKenzie 1982 for a description). The Yellow Warbler is a small (about 10 g), essentially monogamous, insectivorous passerine (Biermann and Sealy 1985, Reid and Sealy 1986), with an average clutch size of 4.5 eggs. Eggs are laid on consecutive days, and incubation averages 11–12 days, and generally shows a seasonal decline (Goossen 1978).

The study area was searched daily for nests from mid-May to late June. Nests were numbered and flagged, and visited daily through egg laying, and every other day after clutch completion until the anticipated date of hatching. Also, during laying, eggs were marked on the blunt end according to their position in the laying sequence. During hatching, nests were visited four times daily (05:00, 10:00, 15:00, and 19:00 CST) until the last young hatched. At hatching, nestlings were individually color-marked with felt markers according to their position in the hatching sequence. In some instances ( $n = 8$ , 1988–1990 combined) the last egg disappeared at hatching or did not hatch. As a result, hatch spreads in these nests were estimated based on the fact that the last egg would have hatched 24 hr after the penultimate egg hatched. Data on hatching times were used to estimate the hatch spread between first- and last-hatched nestlings (FLAST).

Nest visits, either to record hatching, or to weigh nestlings generally took less than 5 min/nest. Females typically returned to the nest immediately after I left (pers. observ.), and hence it is unlikely that the nest visits had an important effect on hatching spreads. When hatching was complete nests were visited daily until they were empty.

The brood-reduction hypothesis was tested experimentally in 1989 and 1990 by inducing some females to hatch their young synchronously, i.e., within 24 hr. This was done by removing eggs as they were laid and placing them in a container at approximately 20°C until the day after clutch completion (four-egg clutches) or the day of clutch completion (five-egg clutches). This induced the female to delay incubation until the last egg was laid. Eggs that were removed from the nest dur-

ing egg-laying were replaced with Yellow Warbler eggs collected as part of other experiments (Sealy 1992).

In unmanipulated broods, eggs generally hatched in the sequence they were laid. In manipulated broods (synchronous hatching), penultimate and last-laid eggs commonly hatched before the first-laid eggs. In addition, the first-laid egg in manipulated broods sometimes hatched last. For the purpose of analyses dealing with fledging mass, begging frequency and survival rate, the data were grouped by hatch order such that the first two and three nestlings to hatch in broods of four and five nestlings, respectively, were classified as FIRST nestlings, since they typically hatched within 24 hr of each other. The penultimate (PEN) and last-hatched (LAST) nestlings were treated separately. Nestlings that hatched after 15:00 hr were significantly lighter at six days of age compared to nestlings hatching before 15:00 hr ( $t = 2.77$ ,  $df = 86$ ,  $P = 0.009$ ). Therefore, the hatch date (day = 0) of nestlings found hatched after 15:00 hr (in 1989 and 1990) was assigned to the next day for the purposes of calculating survival and mass.

In both asynchronous (unmanipulated, FLAST > 24 hr) and synchronous (manipulated, FLAST ≤ 24 hr) broods, nestlings were weighed daily, to the nearest 0.05 g using an Ohaus portable electronic scale, until the oldest nestling was seven days old. However, some nestlings fledged on day 6, and therefore comparisons involving FIRST and PEN nestlings use mass at day 6. As last-hatched nestlings in asynchronous broods were one to two days younger than their older sibs, comparisons between asynchronous and synchronous broods involving LAST nestlings were done using mass at day 5. Nestling mass was compared between asynchronous and synchronous broods in which all eggs hatched and at least one nestling survived to day 6 post-hatch.

To determine if the size hierarchy affected feeding of nestlings, I recorded the identity of nestlings that begged when I visited nests in 1990. Begging could be stimulated by a tap on the rim of the nest. The number of visits during which FIRST, PEN and LAST nestlings begged was then compared within brood types and between brood types.

Survival rates (no. fledged/no. hatched) for FIRST, PEN and LAST nestlings were calculated for nests in which all eggs hatched. The effects of hatch spread on survival rate were compared

between nestlings in asynchronously and synchronously hatched broods. Finally, to determine the relative effects of asynchronous and synchronous hatching, fledging success (no. fledged/clutch) and fledging rate (no. fledged/no. hatched) were determined for those nests in which all eggs hatched, and total nest-failure did not occur in a single day.

To investigate possible relationships between hatching asynchrony, brood reduction and food availability between years, I collected insect samples every 3–4 days in 1989 and 1990. Insect samples were collected using a sweep net with a diameter of 37 cm. Each sample consisted of five sweeps, in a 180° arc, at about 3 m (in overstory), and five sweeps at approximately 1 m, through the vegetation. Sampling usually occurred between 11:00–14:00 hr. Samples were frozen and processed after the field season. Samples were sorted into midges, geometrid larvae, and other (all other insects). It has previously been shown that Yellow Warblers principally feed their young midges and geometrid larvae (Biermann and Sealy 1982). However, as with Biermann and Sealy's (1982) study, geometrid larvae were under-represented in the insect samples, and therefore only the midge data are presented. Also, for the purposes of analysis the high and low sweeps are combined, and only the data from 5 June to 8 July are presented. This period encompasses the egg laying and nestling period in both years.

#### STATISTICAL ANALYSES

Analyses (except *G*-tests and Fisher's Exact Probability Test) were done using SAS for personal computers (SAS 1985). Furthermore, all comparisons between asynchronous and synchronous groups involving FIRST and LAST nestlings, unless otherwise mentioned, are one-tailed since they are based on a priori predictions (Zar 1974). Consequently, *P*-values for between group comparisons are based on one-tailed distributions, and the null hypothesis is rejected when  $P \leq 0.05$ .

Comparison of hatch spreads among years by clutch size was done using analysis of variance (ANOVA), and the SNK test for multiple comparisons to identify differences. As there were no differences between brood-sizes, mass and survival rates were combined across brood-size. Between group comparisons of fledging mass were done using analysis of covariance (ANCOVA, brood size as covariate). Survival rates among

TABLE 1. Relative abundance of midges at Delta Marsh in 1989 and 1990, for four sampling periods ( $n$  = no. of sweeps during sampling period).

Sampling period	1989		1990	
		$n$		$n$
I	2	30	113	30
II	12	30	324	30
III	0	30	80	10
IV	13	30	509	20
Total	27	120	1,026	90

Note: Sampling period I = 5-11 June; II = 14-20 June; III = 23-29 June; IV = 2-8 July.

FIRST, PEN and LAST nestlings, and brood types were examined using  $G$ -tests. If >25% of cells had expected frequencies less than 5, I used Fisher's Exact Probability Test (FEPT, hereafter). Fledging success was compared between groups using non-parametric analysis of variance (NPAR1WAY, SAS 1985).

RESULTS

*Arthropod abundance.* In each sampling period, as well as overall, the relative abundance of midges was lower in 1989 compared to 1990 (Table 1).

*Hatching spreads.* In 1989 and 1990, mean FLAST hatch spreads for four-egg clutches were longer in asynchronous clutches compared to synchronous clutches (Table 2). Similarly, in five-egg clutches the FLAST hatch spread, in both 1989 and 1990, was longer in asynchronous clutches compared to synchronous clutches (Table 2).

*Nestling survivorship.* Overall, survival rates tended to differ among FIRST, PEN and LAST nestlings in asynchronous broods of four nestlings ( $G = 4.27$ ,  $df = 2$ ,  $P = 0.10$ ). This was due mainly to the higher survival rate of FIRST nestlings compared to LAST nestlings (FEPT,  $P = 0.037$ ). Survival rates, in asynchronous broods of five, were significantly different among FIRST,

PEN and LAST nestlings ( $G = 14.81$ ,  $df = 2$ ,  $P = 0.001$ ). Again, this was due to the fact that FIRST nestlings had a significantly higher survival rate than LAST nestlings ( $G = 11.26$ ,  $df = 1$ ,  $P < 0.001$ ). In synchronous broods, the survival rates of FIRST, PEN and LAST nestlings were similar in broods of four ( $G = 0.04$ ,  $df = 2$ ,  $P > 0.98$ ) and five nestlings ( $G = 0.60$ ,  $df = 2$ ,  $P > 0.90$ ). There were no differences in 1989 or 1990 between brood sizes in the survival rates of FIRST, PEN or LAST nestlings in either asynchronous (but see Hébert and Sealy, in press a) or synchronous broods. Therefore, in the following analyses data on survival rate were combined across brood size.

In 1989, as predicted, FIRST nestlings in asynchronous broods had significantly higher survival rates than FIRST nestlings in synchronous broods ( $G = 7.09$ ,  $df = 1$ ,  $P < 0.01$ ; Table 3). However, the survival rates of PEN and LAST nestlings were similar in asynchronous and synchronous broods (Table 3).

In 1990, there was a tendency for FIRST nestlings in asynchronous broods to have a higher survival rate than their counterparts in synchronous broods ( $G = 2.30$ ,  $df = 1$ ,  $P > 0.10$ ; Table 3). As in 1989, the survival rates, in 1990, of PEN and LAST nestlings in asynchronous broods were similar to those of PEN and LAST nestlings in synchronous broods (Table 3).

*Nestling mass.* At hatching, nestlings in asynchronous ( $1.32 \pm 0.02$  g,  $n = 112$ ) and synchronous broods ( $1.31 \pm 0.03$  g,  $n = 42$ ) were of similar mass (ANOVA,  $F = 0.05$ ,  $df = 153$ ,  $P > 0.50$ ).

Between groups in 1989, the mass of six-day old FIRST nestlings in asynchronous broods was significantly greater than that of FIRST nestlings in synchronous broods (Table 4). Likewise, six-day old PEN nestlings in asynchronous broods tended to be heavier than their counterparts in synchronous broods ( $P = 0.085$ ; Table 4). LAST

TABLE 2. Comparison of mean ( $\bar{x} \pm SE$ ) hatch spreads (hr) between first- and last-hatched eggs in asynchronous (ASYNCH) and synchronous (SYNCH) clutches initiated in 1989 and 1990.

Clutch size	Clutch type	Year			
		1989	$n$	1990	$n$
4	ASYNCH	27.6 $\pm$ 2.4	14	36.7 $\pm$ 2.2	19
	SYNCH	16.5 $\pm$ 2.4	2	9.9 $\pm$ 2.8	8
5	ASYNCH	33.7 $\pm$ 2.6	7	50.5 $\pm$ 2.0	21
	SYNCH	19.0 $\pm$ 5.0	4	7.6 $\pm$ 1.7	7

TABLE 3. Survival rates of FIRST, PEN and LAST Yellow Warbler nestlings in asynchronous (ASYNCH) and synchronous (SYNCH) broods in which all eggs hatched. For sample sizes see Table 6.

Year	Nestling	ASYNCH		SYNCH	
		Number hatched	Percent fledged	Number hatched	Percent fledged
1989	FIRST	41	92.7	16	62.5**
	PEN	16	93.7	6	66.7
	LAST	16	56.2	6	66.7
	Total	73	84.9	28	64.3*
1990	FIRST	83	89.1	37	78.4
	PEN	32	84.4	15	73.3
	LAST	32	71.9	15	73.3
	Total	147	84.3	67	76.1

\*  $P < 0.05$ , \*\*  $P < 0.01$ .

Note: FIRST = first-hatched nestling, PEN = penultimately hatched nestling, and LAST = last-hatched nestling.

nestlings in asynchronous and synchronous broods in 1989 were similar in mass at five days of age (Table 4). In 1990, the mass of six-day-old FIRST nestlings in asynchronous broods was greater than that of FIRST nestlings in synchronous broods, but this difference was not significant ( $P = 0.12$ ; Table 4). Again, there was also a non-significant tendency for PEN nestlings in asynchronous broods to be heavier than PEN nestlings in synchronous broods (Table 4). Contrary to what was predicted, in 1990 five-day-old LAST nestlings in asynchronous and synchronous broods were similar in mass (Table 4).

Lack's (1954) hypothesis also predicts that brood reduction enhances the fitness of the surviving brood members. To examine this prediction, I compared the mass of six-day-old FIRST nestlings in asynchronous broods of four and five nestlings that had suffered brood reduction to the mass of six-day-old FIRST nestlings in synchronous broods that had not suffered brood reduction. In 1989, as predicted, FIRST nestlings in reduced asynchronous broods ( $9.03 \pm 0.3$  g,  $n = 12$ ) were heavier than FIRST nestlings in whole synchronous broods ( $8.19 \pm 0.2$  g,  $n = 10$ ; ANOVA,  $F = 6.34$ ,  $P = 0.01$ ). In 1990, six-day-old

FIRST nestlings in asynchronous broods that had suffered brood reduction were not heavier ( $8.67 \pm 0.2$  g,  $n = 13$ ) than FIRST nestlings in whole synchronous broods ( $8.43 \pm 0.2$  g,  $n = 21$ ; ANOVA,  $F = 0.80$ ,  $P > 0.19$ ).

*Nestling begging.* In 1990, for control broods of four and five nestlings combined, the number of nest visits during which FIRST, PEN and LAST nestlings begged was not random with respect to position in the hatching sequence ( $\chi^2 = 49.06$ ,  $df = 2$ ,  $P < 0.0001$ , Table 5). That is, FIRST ( $\chi^2 = 35.13$ ,  $df = 1$ ,  $P = 0.0001$ ) and PEN ( $\chi^2 = 8.38$ ,  $df = 1$ ,  $P < 0.005$ ) nestlings begged during significantly fewer visits than LAST nestlings (Table 5). In synchronous broods, begging was random with respect to hatching order ( $\chi^2 = 1.46$ ,  $df = 2$ ,  $P > 0.25$ ; Table 5). Between groups, FIRST nestlings in asynchronous broods begged significantly less often than their counterparts of similar age in synchronous broods (Table 5). PEN and LAST nestlings in asynchronous broods were observed begging as often as their counterparts in synchronous broods (Table 5).

*Fledging success.* In 1989, fledging success was similar for asynchronous and synchronous broods

TABLE 4. Mean ( $\pm$ SE) mass (g) of Yellow Warbler FIRST, PEN, and LAST nestlings in asynchronous (ASYNCH) and synchronous (SYNCH) broods. Data are combined for broods of four and five.

Year	Nestling	Age	Brood type				F	P
			ASYNCH	n	SYNCH	n		
1989	FIRST	6	$9.09 \pm 0.19$	27	$8.22 \pm 0.17$	10	6.28	0.01
	PEN	6	$8.71 \pm 0.34$	12	$7.79 \pm 0.33$	4	2.07	0.09
	LAST	5	$8.53 \pm 0.35$	7	$7.99 \pm 0.45$	4	0.91	0.19
1990	FIRST	6	$8.73 \pm 0.07$	63	$8.54 \pm 0.15$	28	1.39	0.12
	PEN	6	$8.64 \pm 0.10$	21	$8.40 \pm 0.24$	10	1.12	0.15
	LAST	5	$7.87 \pm 0.21$	19	$7.82 \pm 0.18$	11	0.06	0.80

TABLE 5. Begging frequencies (no. of times begged/no. of nest visits) of Yellow Warbler FIRST, PEN, and LAST nestlings in asynchronous (ASYNCH) and synchronous (SYNCH) broods. Data are from 1990, and were combined for broods of four and five nestlings.

Nestling	Brood type				$\chi^2$	<i>P</i>
	ASYNCH	(%)	SYNCH	(%)		
FIRST	36/249	(14)	58/190	(30)	15.59	<0.001
PEN	23/95	(24)	22/81	(27)	0.75	>0.12
LAST	43/95	(45)	29/81	(36)	1.25	>0.13

of four nestlings (Table 6). Fledging success was also similar in 1990 between asynchronous and synchronous broods of four. In broods of five nestlings, there was a tendency ( $P = 0.11$ ) in 1989 for fledging success to be higher in asynchronous broods compared to synchronous broods. In 1990 fledging success was significantly higher in asynchronous broods of five compared to synchronous broods of five (Table 6). The lack of a significant difference in 1989 was probably due to small sample sizes (Table 6). In addition, when the data were combined across brood-sizes in 1989, the fledging rate (no. fledged/no. hatched), as predicted, was greater in asynchronous broods (84.9%,  $n = 73$ ) compared to synchronous broods (64.3%,  $n = 28$ ;  $G = 4.06$ ,  $df = 1$ ,  $P < 0.05$ ). In 1990 when food was relatively more abundant the fledging rate (no. fledged/no. hatched) of asynchronous broods (86.4%,  $n = 147$ ) was similar to that of synchronous broods (76.1%,  $n = 67$ ;  $G = 1.60$ ,  $df = 1$ ,  $P > 0.20$ ).

## DISCUSSION

The results of this study suggest that, as hypothesized by Lack (1947, 1954), hatching asynchrony facilitates brood reduction, particularly in larger broods. The data also agree with the notion that hatching asynchrony maximizes reproductive success when food is relatively scarce (e.g., 1989), as well as when food is relatively abundant (e.g., 1990), especially in larger broods.

Lack's (1947, 1954) hypothesis predicts that nestling mortality in asynchronous broods will fall disproportionately on LAST nestlings. In

agreement with this LAST nestlings in asynchronous Yellow Warbler broods had lower survival rates than older sibs, especially LAST nestlings in broods of five (see also Hébert and Sealy 1993). In synchronously hatched broods, FIRST, PEN, and LAST nestlings had similar survival rates. This supports the parallel prediction that nestling mortality in synchronously hatched broods would be random with respect to hatch order. The concentration of mortality in last-hatched nestlings has been observed in many studies, and is usually associated with food stress where older sibs are fed selectively (Braun and Hunt 1983, Greig-Smith 1985, Hébert and Barclay 1986, Mock and Parker 1986, Bryant and Tatner 1990, but see Stamps et al. 1985) or older sibs intimidate or kill their younger sibs as a result of proximate or anticipated food stress (Drummond et al. 1986, Ploger and Mock 1986, Anderson 1989, Parker et al. 1989, see also review by Mock 1984).

As predicted, in 1989 when food was relatively less abundant, the survival rate of FIRST nestlings in asynchronous broods was greater than that of their counterparts in synchronous broods (Table 5). However, in 1990 FIRST nestlings in asynchronous and synchronous broods had similar survival rates. Again, it is relevant that food was less abundant in 1989 compared to 1990. Thus the overall tendency for FIRST nestlings in asynchronous broods to enjoy higher survival rates than FIRST nestlings in synchronous broods, especially when food was limiting, suggests that hatching asynchrony may favor FIRST

TABLE 6. Mean fledging success (no. fledged/clutch) for asynchronous (ASYNCH) and synchronous (SYNCH) Yellow Warbler broods of four and five nestlings in which all eggs hatched.

Year	Brood size	Brood type				<i>F</i>	<i>P</i>
		ASYNCH	<i>n</i>	SYNCH	<i>n</i>		
1989	4	3.71 ± 0.18	7	4.00 ± 0.00	2	0.62	0.23
	5	4.11 ± 0.54	9	2.50 ± 1.44	4	1.72	0.11
1990	4	3.46 ± 0.31	13	3.25 ± 0.52	8	0.13	0.35
	5	4.31 ± 0.24	19	3.14 ± 0.80	7	3.60	0.04

nestlings by enhancing their competitive size advantage.

In agreement with this, FIRST nestlings in asynchronous broods, as predicted, were heavier at fledging compared to their counterparts in synchronous broods (Table 4). That is, in 1989 when food was relatively less abundant, the mass of FIRST nestlings in asynchronous broods was significantly greater than that of FIRST nestlings in synchronous broods. Several experimental studies of hatching asynchrony have observed similar trends (see review by Amundsen and Slagsvold 1991a). For example, Haydock and Ligon (1986) observed that the asymptotic mass of nestling Chihuahuan Ravens (*Corvus cryptoleucus*) in asynchronous broods of six was significantly greater than that of synchronous broods of six. The difference in asymptotic mass between the two groups increased from 9.5% in a relatively good food year (i.e., 1981) to 18.2% in 1982 when breeding conditions were poorer (Haydock and Ligon 1986). Also in agreement with the brood-reduction hypothesis, the mass of six-day-old nestlings in asynchronous broods that had suffered brood reduction, in 1989, was greater than that of their counterparts in synchronous broods that did not suffer brood reduction (see also Husby 1986). A similar trend was observed in 1990, but this difference was not significant. Taken together, the above results suggest that hatching asynchrony can enhance the quality of surviving brood members (Husby 1986, Haydock and Ligon 1986, see also review by Amundsen and Slagsvold 1991a).

The prediction that LAST nestlings in asynchronous broods would have a lower fledging mass and survival rate than LAST nestlings in synchronous broods was not supported by this study. This prediction was based on the assumption that LAST nestlings would not be at a competitive disadvantage in synchronous broods. However, it is possible that feeding in asynchronous broods was more efficient, and thus nestlings spent less time expending energy begging for food, as suggested by Hahn (1981). These results may also indicate that hatching asynchrony benefits FIRST nestlings more than LAST nestlings.

The tendency for nestlings in asynchronous broods, especially FIRST nestlings, to be heavier than nestlings in synchronous broods may be the result of a more efficient utilization of resources, and/or effective competition for preferred feeding positions. For example, during this study,

nestlings in asynchronous broods were generally fed less often than nestlings in synchronous broods (Hébert and Sealy, in press b), however FIRST nestlings in asynchronous broods tended to be heavier than their counterparts in synchronous broods. Hahn (1981) hypothesized that the competitive size hierarchy that results from hatching asynchrony may, in addition to facilitating brood reduction, reduce sibling aggression and therefore minimize the amount of energy wasted on aggression. Although nestling Yellow Warblers apparently do not exhibit aggressive behavior, they may benefit from hatching asynchrony as suggested by Hahn (1981), especially since nestlings in asynchronous broods, particularly FIRST nestlings, were observed begging significantly less often than nestlings in synchronous broods.

Furthermore, because of the size hierarchy in broods that hatch asynchronously, larger nestlings may occupy preferred feeding locations in the nest or may beg more conspicuously (Ryden and Bengtsson 1980, Reed 1981, Greig-Smith 1985). As a result, older nestlings may sequester most of the food until they are satiated at which time the smaller nestlings may be fed (but see Stamps et al. 1985, Gottlander 1987). In synchronous broods the size hierarchy is less established, hence preferred feeding locations cannot be monopolized and consequently all nestlings are fed equally and potentially inadequately. In agreement with this, FIRST nestlings in synchronous broods begged more often than their counterparts of similar age in asynchronous broods (see also Haydock and Ligon 1986).

If Lack's (1947, 1954) brood-reduction hypothesis is to be accepted, it must be shown that hatching asynchrony facilitates brood reduction as opposed to total brood loss. Consistent with the brood-reduction hypothesis I observed less total brood loss in asynchronous broods compared to synchronous broods (4.2% vs. 19.1%, respectively) and this difference approached significance (FEPT,  $P = 0.08$ ). The higher rate of total brood loss in synchronous broods is indicative of the lower survival rate of FIRST nestlings in synchronous broods.

Finally, if hatching asynchrony has evolved as hypothesized by Lack (1947, 1954) we would also expect fledging success to be higher in asynchronous broods compared to synchronous broods, especially when food is limiting. In agreement with the hypothesis, fledging success of asynchronous Yellow Warbler broods of five

nestlings tended ( $P = 0.11$ ) to be greater than that of synchronous broods, in 1989 when food was apparently less abundant (Table 6). Furthermore, when the data were combined across brood-sizes, the fledging rate (no. fledged/no. hatched) was greater for asynchronous broods compared to synchronous broods in 1989 ( $P < 0.05$ ). In 1990, however, when food was more abundant, reproductive success was similar between asynchronous and synchronous broods of four nestlings, whereas in broods of five nestlings, fledging success was higher in asynchronous broods compared to synchronous broods. These results emphasize the advantage of hatching asynchrony in larger broods that are apparently more susceptible to variations in food availability (see Slagsvold 1986a, 1986b).

Caution must be used in interpreting the results above though, since the real measure of reproductive success is the number of young that survive to breed. Obtaining such data in a neotropical migrant, however, poses significant logistical problems, especially since there is some differential philopatry between the sexes (S. G. Sealy, pers. comm.).

#### OTHER HYPOTHESES

Several other hypotheses have been proposed in explanation of hatching asynchrony in birds. Clark and Wilson (1981) hypothesized that hatching asynchrony was a parental strategy to minimize the risk of total nest failure due to predation during the egg-laying/incubation period (see also Hussell 1985). The daily survival probability of Yellow Warbler nests was significantly lower during the laying period compared to the early fledging period (Hébert and Sealy 1993). From this, the nest-failure model (Hussell 1985) predicted that female Yellow Warblers would initiate incubation with the laying of the first egg, thus producing hatch spreads of 96 or more hours. However, as with other studies examining the nest-failure hypothesis (Bancroft 1985, Briskie and Sealy 1989, but see Hussell 1985) hatch spreads in Yellow Warblers, observed during this study, were significantly shorter than that predicted by the nest-failure hypothesis (Hébert and Sealy 1993). Another hypothesis, the sexual-conflict hypothesis (Slagsvold and Lifjeld 1989), suggests that hatching asynchrony is a female strategy to extract from males a greater contribution to the brood. However, the feeding rates of male Yellow Warblers tending asynchronously hatched broods were

generally lower compared to males tending synchronously hatched broods (Hébert and Sealy, in press b).

Mead and Morton (1985) hypothesized that hatching asynchrony, in species where only the female incubates (e.g., Yellow Warblers), is the result of hormonal surges associated with the laying of the penultimate egg. However, an egg-addition experiment designed to test the mechanistic aspect of the hormonal hypothesis showed that incubation attentiveness in female Yellow Warblers is not rigidly controlled by hormonal activities during laying (Hébert and Sealy 1992).

The 'hurry-up' hypothesis (Slagsvold 1986a), originally proposed by Hussell (1972), suggests that hatching asynchrony is adaptive because it advances the fledging date of first-hatched nestlings, thus potentially avoiding sharp declines in food availability late in the breeding season. In agreement with this, hatch spreads in Yellow Warblers generally increased through the breeding season (Hébert 1991). The hurry-up hypothesis, however, is not mutually exclusive of the brood-reduction hypothesis. In either case, parents maximize the number of fit offspring produced in respect to food availability and time available.

Some researchers have questioned the brood-reduction hypothesis because brood reduction occurs even when food is apparently abundant, especially during the early nestling period (Skaugen 1988, Clark and Wilson 1981). Likewise, during this study, when relative insect abundance was significantly higher, i.e., 1990, brood reduction did occur. However, prey availability is not constant. Changes in wind direction, precipitation, visibility, and temperature may affect prey availability and parental foraging patterns (Stinson 1980, Hébert 1987, Pohajdak 1988). In addition, it is possible that differences in parental quality or territory quality will also be affected differently by diurnal and seasonal fluctuations in the availability of food resources. Thus, even though food may be abundant, it is not necessarily available.

In conclusion, my results are generally consistent with Lack's (1947) brood-reduction hypothesis. Hatching asynchrony created a competitive size hierarchy among brood mates, and this hierarchy favored FIRST nestlings at the expense of LAST nestlings. The results also suggest that, as hypothesized by Lack (1947), hatching asynchrony facilitates brood reduction, and may enhance the quality of surviving nestlings.



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