

**THE RELATIVE IMPORTANCE OF BROOD REDUCTION, PREDATION  
AND PARENTAL INVESTMENT IN THE EVOLUTION OF HATCHING  
ASYNCHRONY IN YELLOW WARBLERS (DENDROICA PETECHIA)**

**BY**

**PERCY NORMAN HÉBERT**

**A thesis presented to the University of Manitoba in partial  
fulfillment of the requirements for the degree of Doctor of  
Philosophy.**

**Winnipeg, Manitoba**

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the University of Manitoba in partial fulfillment of the requirements  
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## ABSTRACT

The purpose of this study was to examine four hypotheses concerning hatching asynchrony, and their relative importance in explaining the evolution of hatching asynchrony in the Yellow Warbler (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).

Firstly, I examined Lack's (1947, 1954) 'brood reduction' hypothesis that hatching asynchrony has evolved to facilitate brood reduction during periods of food stress. Consistent with the hypothesis, fledging mass and survival rates of first-hatched chicks were generally higher in asynchronous broods, and nestling mortality in asynchronous broods was concentrated in last-hatched nestlings. In synchronous broods, on the other hand, nestling mortality was random with respect to hatching order. The trend for fledging success to be higher in asynchronously hatched broods, especially when food was apparently limiting was also consistent with the hypothesis. However, contrary to the hypothesis, fledging mass and survival rates were similar for last-hatched chicks in asynchronous and synchronous broods. These results, for the most part, are consistent with the predictions based on Lack's (1947) hypothesis.

Daily survival probabilities (DSP) of nests, throughout the nesting cycle, were used to calculate expected productivity ratios to test Clark and Wilson's (1985) 'nest-failure' hypothesis, which proposes that hatching asynchrony is an adaptive response to variations in the probability of total nest failure due to predation during the nesting

cycle. The DSP of nests increased significantly from laying to fledging. As a result, expected productivity ratios were greatest when incubation began with the laying of the first egg. However, observed hatching spreads indicated that female Yellow Warblers delayed incubation at least until the laying of the ante-penultimate egg. This suggests that the probability of total nest failure due to predation has likely not played an important role in the evolution of hatching asynchrony in Yellow Warblers.

Slagsvold and Lifjeld (1989) proposed that hatching asynchrony, in bird species where only the female incubates, is a female strategy to extract a greater contribution of parental investment from the male. I examined this hypothesis by comparing feeding rates of males and females tending asynchronously and synchronously hatched broods. Feeding rates over the entire nestling period were generally similar for females tending asynchronous and synchronous broods of 4 or 5 nestlings. Male feeding rates over the entire nestling period were lower in asynchronous broods, and significantly so in broods of 5, compared to males tending synchronous broods. Thus, contrary to the sexual-conflict hypothesis, there appears to be no conflict between the sexes as to when incubation should begin.

I also tested the hypothesis (Mead and Morton 1985) that hatching asynchrony, in bird species where the female alone incubates, is caused by a hormonal surge associated with the ovulation of the last ovum, which is believed to stimulate females to initiate full incubation. Observations showed that, contrary to the hypothesis, full incubation was delayed until the last egg was laid or later, and

despite similar incubation attentiveness during egg laying, hatch spreads between 4- and 5-egg clutches differed significantly. The data also showed that incubation attentiveness is increased experimentally by adding eggs during early egg laying. These results suggest that initiation of full incubation is not rigidly controlled by hormonal changes associated with the laying of the penultimate egg.

Finally, I examined the hypothesis that the larger size of last-laid eggs is part of a brood survival strategy (Slagsvold et al. 1984). Despite a tendency for last-hatched nestlings in broods of 4 to have higher survival rates than their counterparts in broods of 5, there were no differences between clutch sizes in the mass of last-laid eggs relative to the mass of their clutch-mates. The mass of the last egg also was not correlated with hatch spreads, or date of clutch initiation. These results are contrary to the brood survival hypothesis.

**Cette page est dédiée à ma grand-mère, Valeda Hébert.**

**This thesis is dedicated to Norman and Margaret Hébert.**



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## GENERAL INTRODUCTION

"Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved by the term of Natural Selection..." (Darwin 1859: 115).

A large body of theoretical and empirical literature deals with the adaptive significance of phenotypic variation observed in life-history strategies (e.g. Williams 1966a; Lack 1954, 1968; MacArthur 1968; see also review by Stearns 1976). Life-history strategies are collections of compromises, and much research has been focused on the compromises that affect reproductive rates, especially offspring size and the number of offspring produced (Smith and Fretwell 1974, Brockelman 1975, McGinley et al. 1987). In birds, brood size is known to be affected by clutch size (Lack 1947, 1954), sex-ratio of the brood (Trivers and Willard 1973), hatching pattern (Lack 1954, Clark and Wilson 1981), and intra-clutch variation in egg size (Howe 1976, Lundberg and Vaisanen 1979, Hebert and Barclay 1988).

Clutch size most importantly affects reproductive rates in birds, and several hypotheses have been proposed in explanation of its evolution (Lack 1947, 1954; Wynne-Edwards 1962; Cody 1966, see

review by Klomp 1970). Lack (1947:319) hypothesized that "...in nidicolous species, the average clutch-size is ultimately determined by the average maximum number of young which the parents can successfully raise in the region and at the season in question...".

Consequently, the modal clutch size in a population should be the most productive, and young from these clutches should fledge at masses optimal for survival. Evidence exists that this is true (e.g. Red-winged Blackbirds, Agelaius phoeniceus, Cronmiller and Thompson 1980; Blue Tit, Parus caeruleus, Nur 1984a,b; see also review by Klomp 1970). There is also evidence that young from natural and experimentally enlarged broods that are larger than the modal clutch size exhibit lighter fledging mass, or produce fewer young (Lack et al. 1957, Bryant 1975, Ricklefs 1968, Murphy 1983, Moreno 1987).

Lack's (1947) hypothesis has been widely accepted, sometimes in spite of contradictory data (Ydenberg and Bertram 1989). For example, in some species, it has been observed that adults with experimentally enlarged broods are capable of rearing more offspring (e.g. Haymes and Morris 1977, Westmoreland and Best 1987, Briskie and Sealy 1989b, see also Daan et al. 1988). The most common clutch size, especially in nidicolous species, is often smaller than the most productive (Perrins and Moss 1975, Bryant 1975, Goossen and Sealy 1982, Wiklund 1985). These observations, and others, have led to adjustments of Lack's 'food-limitation' hypothesis. The most notable of the 'refinements' is that clutch size in addition to being affected by the number of offspring that adults can raise, may also be significantly and positively correlated with adult mortality, future reproductive success, and predation on eggs (Skutch 1949, Snow 1958, Williams 1966b, Charnov

and Krebs 1973, Nur 1984a, Slagsvold 1984, Roskaft 1985, Kulesza 1990). As natural selection favors individuals exhibiting phenotypes that maximize lifetime reproductive success (i.e. laying an optimal clutch size; Hussell 1972), then individuals that produce clutches smaller than the most productive will be favored when an increase in clutch size incurs a decrease in the survival probability of the parents and/or reduced future reproductive success (Williams 1966a, b; Charnov and Krebs 1973; Nur 1984b; Ydenberg and Bertram 1989).

That birds produce clutches of optimal size is evidenced by the fact that few studies have reported upward adjustments in clutch size when food has been most abundant (Kallander 1974, Sealy 1980, Slagsvold et al. 1984; but see Gibb 1950). Such a phenomenon is more evident in species with more variable clutch sizes, especially hole nesters (e.g. Great Tits P. major, Gibb 1950, Tawny Owls Strix aluco, Southern 1970; Tree Swallows Iridoprocne procne, Hussell and Quinney 1987; but see also MacArthur 1958, Bay-breasted Warblers Dendroica castanea). Also, it is generally agreed that food abundance increases through the laying period, whereas clutch size normally decreases (Bryant 1975, Perrins 1979, Briskie 1986). This seasonal decline in clutch size is believed to be associated with a decline in the reproductive value of eggs (Daan et al. 1988). In addition, food supplement experiments (Dijkstra et al. 1982, Ewald and Rohwer 1982, Graves et al. 1984, Dhindsa and Boag 1990, see also Davies and Lundberg 1985) have shown clutch size is not influenced positively by extra food (but see Newton and Marquiss 1981, Hogstedt 1981). This suggests that, at least proximally, food availability has little, if any, positive effect on clutch size (Slagsvold et al. 1984).

Food availability after clutch completion, especially during the nestling period, however, can have an important effect on the number of offspring that survive. Temporal variation in food availability as a result of inclement weather (Dunn 1975, Bryant 1978b, Stinson 1980, Hébert 1987, but see Stinson et al. 1987) or simply a reduction in the abundance of prey species (Smith et al. 1981, Bechard 1983) have been observed to affect brood size negatively through starvation of the young. Such 'brood-reduction', Lack (1947) hypothesized, is adaptive because it allows parents to adjust brood size to prevailing food conditions. Lack (1947) also proposed that brood reduction during periods of food stress was facilitated as a result of the competitive hierarchy within broods, created by hatching asynchrony. That is, hatching asynchrony produces a competitive size hierarchy amongst members of a brood, and if food resources become limiting then parents can eliminate, efficiently and quickly, the last-hatched nestling(s) by selectively feeding the older nestlings. In the absence of hatching asynchrony, and the resulting size hierarchy, food stress may presumably result in the entire brood starving or fledging at sub-optimal weights, since adults would try to feed all nestlings, albeit inadequately (Lack 1947, Ricklefs 1965). Consequently, not only does hatching asynchrony facilitate brood reduction, it also enhances the probability that older nestlings will survive, especially when food resources are limiting (Lack 1954, O'Connor 1978, Husby 1986, Magrath 1989a).

In addition to facilitating brood reduction, hatching asynchrony has been hypothesized to affect the division of parental effort (Slagsvold and Lifjeld 1989a), probability of predation on adults (Magrath 1989b)

and nest contents (Lack 1947; Hussell 1972, 1985; Clark and Wilson 1981, 1985), egg viability (Arnold et al. 1987), and sex-ratio within broods (Slagsvold 1990). Some of these hypotheses are complementary (e.g. Hussell 1972, Hahn 1981), while others are contradictory (e.g. Clark and Wilson 1981, Mead and Morton 1985; see Magrath 1990 for a review).

The primary objective of the present study was to examine four hypotheses that have been proposed to explain the evolution of hatching asynchrony and to evaluate their relative importance in the evolution of hatching asynchrony in Yellow Warblers (*D. petechia*), and birds in general. In Chapter 1, the 'brood-reduction' and 'nest-failure' hypotheses (Lack 1947, Clark and Wilson 1981, respectively) are examined. Clark and Wilson's (1981) hypothesis suggests that hatching asynchrony is a function of the ratio of the probability of total nest failure, due to predation, during the nestling and fledging periods and the egg laying and incubation. From their hypothesis they suggest that the brood reduction generally associated with hatching asynchrony is not adaptive, but rather is a cost associated with hatching asynchrony.

In Chapter 2, I examine the hypothesis that hatching asynchrony results from female-dominated conflict between adult males and females (Slagsvold and Lifjeld 1989a). The 'sexual-conflict' hypothesis suggests that, in addition to benefiting from increased quality and quantity of offspring produced, females also benefit from hatching asynchrony because it increases the males' contribution to the brood, and thereby decreases the females' potential contribution, especially early in the nestling period. To my knowledge, this is the first test of the hypothesis based on behavioral observations.

The above hypotheses have assigned an adaptive function to hatching asynchrony. Recently, Mead and Morton (1985) hypothesized that hatching asynchrony, in species like the Yellow Warbler where only females incubate, is the result of hormonal fluxes associated with egg-laying, and consequently advantages accrued from hatching asynchrony are merely 'epiphenomena'. This hypothesis was tested experimentally, and the results are presented in Chapter 3. These data also constitute the first experimental test of the 'hormonal' hypothesis.

In addition to clutch size, reproductive rates can also be affected by offspring fitness, which in birds has been shown to be related to egg size or mass (Nisbet 1978, Lundberg and Vaisanen 1979). As selection ultimately maximizes expected offspring fitness and not the number of offspring (Brockelman 1975), egg-size variation within and between clutches are of particular interest. Of significance to the 'brood reduction' strategy is the size of the last egg within a clutch. In species such as cormorants (Snow 1960, Stokland and Amundsen 1988), eagles (Meyburg 1974), gulls (Parsons 1972, Mills 1979, but see Pierotti and Bellrose 1986), terns (Nisbet 1978), and grackles (Howe 1976), egg size decreases with laying order. Such a decrease in egg size with laying order is seen as an embellishment to the role hatching asynchrony plays in facilitating brood reduction. That is, nestlings hatching from the last-laid egg are put at once at a competitive disadvantage because they hatch after the rest of their brood mates, as well as having hatched from smaller eggs (Parsons 1970, Clark and Wilson 1981, Slagsvold et al. 1984).

A major point of contention with Lack's 'brood reduction' hypothesis is that, in some species, especially open-cup nesting passerines, egg



size increases with laying order (Slagsvold 1982, Briskie and Sealy 1990, Wiggins 1990; see review by Slagsvold et al. 1984). Clark and Wilson (1981) argued that this was counter-adaptive to the role of hatching asynchrony in brood reduction since nestlings from larger eggs usually enjoy greater probabilities of survival (Schifferli 1973, Nisbet 1978, Slagsvold et al. 1984, Hébert and Barclay 1988). This dichotomy in correlations of egg mass with laying order has been hypothesized recently to be the result of two different co-adapted life-history strategies associated with hatching asynchrony. Slagsvold et al. (1984) proposed that a decrease in egg size with laying order (e.g. gulls) is an adaptation to facilitate brood reduction, and the opposite trend, an increase in egg size with laying order (e.g. Yellow Warblers), is an adaptation to enhance brood survival, while still enjoying some of the proposed benefits of hatching asynchrony (see above). A secondary objective of this study then was to examine the significance of egg-size variation in Yellow Warblers with respect to clutch size, laying order, hatching asynchrony and nestling survival (Chapter 4).

## STUDY SPECIES

The Yellow Warbler is a small insectivorous passerine that has a breeding distribution that spans continental America from the northern treeline south to Mexico, Ecuador, Colombia and the Caribbean (Bent 1953, Godfrey 1966). Eight subspecies have been described, of which two (*D. p. amnicola* and *D. p. aestiva*) have distributions overlapping central and southern Manitoba (Bent 1953, Godfrey 1966). The sexes are dimorphic in that males have bright yellow underparts with heavy brownish streaking on the breast, whereas females are pale yellow and have little or no streaking. The intensity of the yellow, and the brown streaking, on adult males varies geographically (Bent 1953, Godfrey 1966), as well as within populations (Studd and Robertson 1988). Males and females have similar mass (Biermann and Sealy 1985), but males have slightly longer wings (Godfrey 1966). Both sexes breed in their first year, and have an average life span of ca. 1.5 years (Sutherland 1987). Yellow Warblers are monogamous, but extra-pair copulations and polygyny occur infrequently (Sealy 1984, Della Sala 1985, Reid and Sealy 1986, Hobson and Sealy 1989a).

Females alone build the nest, though there have been some reports of males providing minimal assistance (Bent 1953). At Delta Marsh, Manitoba, nests are generally built between 1 and 2 meters from the ground, with a range of 0.5 to over 15 m (Goossen 1978; Briskie et al. 1990; Hebert, unpubl. data). Egg laying usually begins in the last week of May and peaks by the first to second week of June. Clutch initiation is negatively correlated with temperature and positively correlated with the amount of rainfall in May (Goossen and Sealy 1982). Clutch

initiation normally extends through the first week of July (Goossen 1978, S. G. Sealy, pers. comm.).

Clutch size in Yellow Warblers averages 4.5 eggs, and generally shows a seasonal decline (Goossen 1978). Male Yellow Warblers feed their mates during the egg-laying, incubation and nestling periods, and both sexes feed the young (Biermann and Sealy 1982, Sutherland 1987). Although males guard their mates during the egg-laying period (Hobson and Sealy 1989b), as well as guard the territory, defence of the nest is generally the female's domain (Hobson et al. 1988, Hobson and Sealy 1989b, Hobson and Sealy 1990). Nest defence usually involves a distraction display that consists of wing fluttering and injury feigning (Reid and Sealy 1986).

Incubation, by the female alone, averages 9 days from the laying of the last egg to the hatching of the first egg, and ca. 10-12 days from laying to hatching of the last egg (Bent 1953, Schrantz 1943, Goossen 1978). Incubation also decreases over the season (Goossen 1978). Hatching usually peaks in the second to third week of June, with fledging peaking in the last week of June to the first week of July (Goossen 1978). Fledging can occur as early as six days if disturbed, but usually occurs at 9 -12 days after hatching. As a result of hatching asynchrony, the young also fledge asynchronously with an average of 2.5 days between the first- and last-fledged nestlings in 4- and 5-nestling broods (Goossen 1978). The young are dependent on the parents for approximately another 10 - 14 days (Schrantz 1943, Goossen 1978). Juvenile Yellow Warblers begin leaving the study area during the last week of July through to mid-August (S. G. Sealy, pers. comm.).

From the above it can be seen that the Yellow Warbler is ideal for this study because it exhibits hatching asynchrony, and the sexes are dichromatic. This last characteristic is important since it allowed me to estimate the relative contributions made by male and female parents in the feeding of young.

## STUDY AREA

The study was conducted on a population of Yellow Warblers breeding in the forested dune-ridge at Delta Marsh, Manitoba, Canada (58° 11' N., 98° 19' W; see Sealy 1980). The dune-ridge forest, which separates Lake Manitoba from Delta Marsh, exhibits a gradient from north to south in soil patterns and vegetation (Mackenzie 1982). The study site for this project consisted of a 1.5 km stretch of the dune-ridge forest, with an average width of 80 m.

### Vegetation

The overstory vegetation in the southern half of the dune-ridge forest consists mainly of sandbar willow (Salix interior) and Manitoba maple (Acer negundo), as well as some eastern cottonwoods (Populus deltoides). Overstory vegetation on the northern half, closest to the lake, is characterized by peach-leaved willow (S. amygdaloides), green ash (Fraxinus pennsylvanica), as well as some sandbar willows and Manitoba maples (Mackenzie 1982).

The understory vegetation in the southern half of the dune-ridge forest is characterized mostly by stinging nettle (Urtica dioica), with some raspberry (Rubus idaeus) as well as wild cucumber (Echinocystis lobata) and hops (Humulus lupulus). In the northern half of the ridge the main shrubs of the understory include stinging nettle and elderberry (Sambucus pubens; Mackenzie 1982, pers. obs.).

### **Food Resources**

Large emergences of insects are common in the study area during late spring through late summer. These emergences consist of mosquitoes (Culicidae) and chironomids (Chironomidae). Insect abundance on the study area has previously been described as, "...continuous and possibly unlimited..." (MacKenzie et al. 1982; see Busby and Sealy 1979, Biermann and Sealy 1982), although arthropod abundance usually peaks in late June - early July (Pohajdak 1988), coincidental with the peak in nestling and fledgling feeding periods of the insectivorous passerines breeding on the ridge and in the marsh (Pohajdak 1988). Despite the apparent abundance of insects at Delta Marsh, previous studies have found that insect availability is affected by the timing of emergences by midges (Pohajdak 1988) as well as normal seasonal declines (Guinan and Sealy 1987, Pohajdak 1988), weather (i.e. temperature, wind, rain: Pohajdak 1988) as well as daily, seasonal and yearly variations in the total insect biomass (Briskie 1986, Guinan and Sealy 1987, Pohajdak 1988 ).

When foraging for themselves, adult Yellow Warblers tend to feed mainly on Diptera, especially chironomids (Busby and Sealy 1979). Nestlings are also fed chironomids, of which the proportion in the diet changes with nestling age. Initially, young nestlings are fed mainly geometrid larvae, with chironomids gaining prominence as the nestlings get older (Biermann and Sealy 1982, Sutherland 1987).

## CHAPTER 1

# BROOD REDUCTION AND TOTAL NEST FAILURE: THE EVOLUTION OF HATCHING ASYNCHRONY IN YELLOW WARBLERS

## 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 hours before their sib(s). By contrast, hatching synchrony is uncommon and limited to a few orders, most notably the Anseriformes, Galliformes and the Charadriiformes (except suborder Lari; Slagsvold 1990). An important difference between the two hatching patterns is that species with asynchronous hatching generally have young that depend on their parents for food, whereas in species with synchronous hatching the young can feed themselves soon after hatching (Slagsvold 1990).

Lack (1947,1954) hypothesized that hatching asynchrony is a mechanism by which parents facilitate brood reduction, especially during periods of food stress, by creating a competitive size hierarchy among siblings. 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). According to Lack's (1947, 1954) 'brood reduction' hypothesis, when food is scarce the size hierarchy allows

parents to channel food to the older and presumably fitter chick(s). As a result, last-hatched chicks may grow more slowly and may even starve (Ricklefs 1965; Howe 1976, 1978; Bancroft 1985a; Mead and Morton 1985; Hébert and Barclay 1986; Lessells and Avery 1989). Thus, the size hierarchy created by asynchronous hatching allows parents to adjust brood size and fitness of the brood 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. In the absence of brood reduction, if food is limiting, nestlings may all suffer reduced growth rates, and therefore lower survival probabilities (Perrins 1966), or starve (Ricklefs 1965).

Evidence that supports the 'brood reduction' hypothesis has come mainly from studies of species that have long nestling periods, such as boobies (Kepler 1969, Anderson 1989), cormorants (Shaw 1985, but see Amundsen and Stokland 1988), pelicans (Cash and Evans 1986), gulls (Parsons 1975, Hahn 1981, Hébert and Barclay 1986), terns (Nisbet and Cohen 1975), eagles (Edwards and Collopy 1983, Meyburg 1974), owls (Ingram 1959), and egrets (Mock and Ploger 1987). However, evidence for passerines, which have relatively shorter nestling periods, is somewhat equivocal (e.g. Hussell 1972, Skagen 1987, Briskie and Sealy 1989a, Stouffer and Power 1991, see also reviews by Clark and Wilson 1981, Magrath 1990). Nestling mortality due to starvation is apparently infrequent in passerines (Ricklefs 1969, Slagsvold 1982, Skagen 1987, Briskie and Sealy 1989a, but see Howe 1976, Smith 1988), which makes the 'brood reduction' hypothesis appear inappropriate as an explanation of the evolution of hatching asynchrony in that group of



birds. In fact, Lack (1947: 325) posited that, in passerines, the advantage of hatching asynchrony (facilitation of brood reduction), "...is evidently outweighed by the need to raise the young as quickly as possible, owing to their vulnerability to predators" (see also Hussell 1972, Clark and Wilson 1981).

In passerines, especially open-cup nesters, predation is an important factor affecting reproductive success (Ricklefs 1969). The probability of total nest failure due to predation varies during the reproductive cycle such that some species may be more prone to predation during the egg-laying/incubation period, while others may be more prone to predation during the nestling/fledgling period (Clark and Wilson 1981, and references therein). From this, Clark and Wilson (1981) hypothesized that hatching asynchrony is a parental mechanism that minimizes the risk of total nest failure due to predation. In support of their hypothesis, Clark and Wilson (1981) presented their nest failure model to predict optimal degrees of hatching asynchrony with respect to temporal patterns in the probability of total nest failure.

According to the nest failure model, the degree of hatching asynchrony will be a function of the ratio between the probability of total nest failure during the nestling/fledgling period and the egg-laying/incubation period. That is, in those species where total nest failure due to predation is concentrated during the egg stage, selection will favor individuals that minimize the time their nests contain only eggs. Such species would hatch asynchronously. On the other hand, in species where the probability of total nest failure is greatest during the nestling/fledgling stage, selection will favor individuals that

minimize the length of time the nest contains nestlings, or in other words, maximize the amount of time the nest contains only eggs. Such species would hatch their eggs less asynchronously. Synchronous hatching, however, delays the first fledging, thereby increasing the risk of total nest failure early in the fledging period (Briskie and Sealy 1989a). Thus the optimal degree of hatching asynchrony is a result of the trade-off between the benefits of reduced predation afforded by increased hatching synchrony and the costs associated with delayed first-fledging (Clark and Wilson 1981, Briskie and Sealy 1989a).

The purpose of Chapter I then is to examine the importance of the 'brood reduction' and 'nest-failure' hypotheses in explaining the evolution of hatching asynchrony in Yellow Warblers, and passerines in general. I examined the following predictions based on the 'brood reduction' hypothesis: 1) the degree of hatching asynchrony will be correlated positively with clutch size, and date of clutch initiation, 2) in broods hatching asynchronously brood reduction will be concentrated in the last-hatched chick(s), whereas in broods that hatch synchronously, brood reduction will be random among positions in the hatching sequence. The critical predictions of the 'brood reduction' hypothesis are that, if food is limiting: 3) 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, 4) fledging mass and survival rate of last-hatched nestlings in asynchronous broods will be less than that of last-hatched nestlings in synchronous broods, and 5) reproductive success will be higher in asynchronous broods compared to synchronous broods.

With respect to clutch-size, prediction 1 assumes that regardless of parental age, or date of clutch initiation, smaller broods are easier to feed (Royama 1966, Nur 1984b, Drent and Daan 1980), and therefore less susceptible to variations in food availability. In terms of hatch spreads, prediction 1 is based on the fact that birds breeding early in the breeding season are older (Sutherland 1987), and therefore presumably more experienced. Also, the young of early breeders will hatch in close alignment with the peak availability of their food resources (Daan et al. 1988). It follows then that those pairs breeding later in the breeding season are younger birds (excluding renesters), and their young will be raised during the period when the food resources are declining and less predictable (Lack 1954, Nisbet and Cohen 1975, Daan et al. 1988). Predictions 2-4 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 5 assumes that in the absence of a competitive hierarchy, all nestlings are fed equally, albeit inadequately.

The 'nest-failure' hypothesis predicts that hatch spreads will be a function of the probability of total nest failure due to predation. As previously mentioned, Clark and Wilson (1981) based their model on daily survival probabilities during the egg-laying/incubation stage, and nestling/fledgling stage. Recently, Hussell (1985) showed that the only relevant survival probabilities that determine the optimal degree of hatching asynchrony are those prior to the initiation of incubation, and after the first nestling has fledged. Therefore the optimal degree of hatching asynchrony will be a function of the daily survival

probability of nests prior to incubation and after the first nestling has fledged.

Hence, the nest failure model (with Hussell's 1985 modifications) predicts that optimal asynchrony will occur when the ratio  $W_{m+k}/W_N$  is maximized (Clark and Wilson 1981, Hussell 1985). In this instance,  $W_{m+k}$  is the productivity of clutches exhibiting a certain degree of hatching asynchrony, and  $W_N$  is the productivity of synchronously hatching clutches. If the ratio is greater than one, then asynchronous hatching is more productive than synchronous hatching. If the ratio is less than one, then synchronous hatching will be more productive. The productivity ratio (as modified by Hussell 1985) is given by:

$$W_{m+k}$$

$$W_N$$

where  $m$  is the egg on which incubation begins, and varies from 1 to  $N$  (1 indicating complete asynchrony and  $N$  complete synchrony),  $N$  is clutch size,  $t$  is the laying interval (days between successive eggs),  $P_0$  is the daily probability of survival of nest contents from start of laying to start of incubation ( $m$ ),  $P_3$  is the daily probability of survival of the nest contents from first fledge to last fledge,  $q$  is the probability of survival of the last-hatched nestling (in successful nests), and  $k$  is the delay between the laying of the egg on which incubation begins ( $m$ ) and the start of incubation (expressed as a fraction of  $t$ ). From this model it can be predicted that observed

hatching spreads should maximize reproductive success given the patterns of total nest failure observed.

## METHODS

The study was conducted during mid-May to mid-July from 1988-1990. 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 (see Goossen 1978). For each nest found the date of clutch initiation and clutch size were recorded. Clutch initiation dates were scored from 1 May=1 such that 1 June=32. During hatching nests were visited four times daily (0600, 1100, 1600, and 2000 h CDT) until the last young hatched. At hatching, nestlings were individually color marked with felt markers according to their position in the hatching sequence.

Data on hatching times were used to estimate the hatch spread between first- and last-hatched nestlings (FLAST), ante-penultimate and last-hatched nestlings (APLAST), and the penultimate- and last-hatched nestlings (PLAST). 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 (casual obs.), 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 frequent visits allowed a fairly accurate determination of the hatching spread (hours) between eggs as well as the daily survival probability of nests, and their contents from egg laying through fledging. These data were used to examine the 'brood reduction' hypothesis in terms of the relationships, if any, between the

degree of hatching asynchrony, date of clutch initiation, and clutch size.

As date of clutch initiation and hatch spreads varied significantly between years, the relationships between hatching spreads and date of clutch initiation were examined by standardizing the data on clutch initiation date and hatching spread (Perrins and McCleery 1985). This was done by subtracting the yearly mean from each observation, and then dividing the result by the yearly standard deviation. Subsequent analyses were then performed on the resulting units of standard deviation.

The 'brood reduction' hypothesis was tested experimentally in 1989 and 1990 by inducing some females to hatch their young synchronously, i.e. within 24 h. This was done by removing eggs as they were laid and placing them in a cooler at approximately 20° C. until the clutch was complete. At clutch completion the eggs were returned to the nest. This had the effect of inducing the female to begin incubating after the last egg was laid. Eggs that were removed from the nest during egg-laying were replaced with Yellow Warbler eggs collected as part of other experiments (S. G. Sealy, unpubl. data)

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 first two and three nestlings to hatch in broods of 4 and 5 nestlings, respectively, were classified as FIRST nestlings, since they typically hatched within 24 hours of each other.

The penultimate (PEN) and last-hatched (LAST) nestlings were treated separately. Nestlings that hatched after 1600 h, were significantly lighter at 6 days of age compared to nestlings hatching before 1600 h ( $t=2.77$ ,  $df=86$ ,  $P=0.009$ ). Therefore, the hatch date (day=0) of nestlings found hatched after 1600 h (in 1989 and 1990) was assigned to the next day for the purposes of calculating survival and mass.

In both asynchronously (unmanipulated,  $FLAST > 24$  h) and synchronously (manipulated,  $FLAST \leq 24$  h) hatched broods, nestlings were weighed daily, to the nearest 0.05 g using an Ohaus portable electronic scale, until the oldest nestling was 7 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 1 to 2 days younger than their older sibs, comparisons between asynchronous and synchronous broods involving LAST nestlings were done using mass at 5 days of age. Data from nine unmanipulated broods of 4 nestlings that hatched synchronously ( $FLAST \leq 24$  h) are combined with those of experimental synchronously hatched broods. Nestling mass (g) was compared between asynchronous and synchronous (natural and experimental) 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. Begging could be stimulated by a gentle 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 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. Again, data from unmanipulated broods of 4 nestlings that hatched synchronously were grouped with the data from experimental synchronous broods. Finally, to determine the relative effects of asynchronous and synchronous hatching, fledging success (no. fledged/clutch) was determined for those nests in which all eggs hatched, and total nest-failure did not occur on a single day. This was done so as not to include losses due to predation alone.

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 5 sweeps, in a 180° arc, at ca. 3 m (in overstory), and 5 sweeps at approximately 1 m, through the vegetation. Sampling usually occurred between 1100-1400 h. Samples were frozen and later 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.

To test the 'nest-failure' hypothesis I used data collected during nest visits to calculate the daily survival probability (DSP) of nests

during the pre-incubation (P<sub>0</sub>), incubation (P<sub>1</sub>), nestling (P<sub>2</sub>), and fledging (P<sub>3</sub>) periods. DSP were calculated using the Mayfield (1975) method, and compared using the method described by Hensler and Nichols (1981). For the purposes of this analysis, the survival rate (q) of last-hatched nestlings (no. fledged/no. hatched) was calculated using all non-experimental broods where all young hatched, and at least one nestling survived to fledge. That is, in this instance, data from control broods of 4 nestlings that hatched synchronously were included in the determination of the survival rate of last-hatched nestlings.

Furthermore, in 1990, data were collected on nest visibility to determine if there was a relationship between the probability of predation (i.e. nest visibility) and hatching spreads. At each nest, I measured visibility at two randomly chosen cardinal points, on the day the first or second egg was laid. Visibility was estimated using a small ruler with ten 0.5-cm dots placed at 1-cm intervals. The ruler was centered on the rim of the nest, and the number of visible dots was counted from 1 m away. The more dots that were visible the more visible the nest was. For the purpose of analysis, the two measurements for each nest were averaged. These data were then compared between clutch sizes and date of clutch initiation.

## 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). Comparison of clutch initiation dates between years was done using single factor analysis of variance (ANOVA) and Student-Newman-Keuls (hereafter SNK) multiple comparisons test to determine where the differences lie. Relationships between standardized date of clutch initiation and standardized hatch spreads were examined using correlation analysis, and 2-factor analysis of variance with first order interactions (ANOVA2; with year as the second factor, see Results). Comparison of hatch spreads by clutch size within years was done using t-tests, and among years using the SNK test for multiple comparisons. Mass at fledging between groups involving broods of 5 nestlings was examined using analysis of covariance (ANCOVA) since mean mass on day 6 of FIRST nestlings in asynchronous broods of 5 was significantly different between years. Survival rates among FIRST, PEN and LAST nestlings, and brood types were examined using G-tests. If >25% of cells had expected frequencies less than 5 then I used Fisher's exact probability test (FEPT, hereafter). Fledging success was compared between groups using t-tests.

To test the 'nest-failure' hypothesis (Clark and Wilson 1981) daily survival probabilities of nests were compared using the method described by Hensler and Nichols (1981). I used a significance level of

$P < 0.10$  to reject the null hypothesis, since this test is prone to Type II error (Hensler and Nichols 1981).

Throughout the thesis, statistical comparisons between groups (asynchronous vs synchronous hatching) are one-tailed since they are based on a priori predictions. Consequently, P-values for between group comparisons are based on one-tailed distributions, and as such the null hypothesis is rejected when  $P \leq 0.05$ .

## RESULTS

### Brood Reduction Hypothesis

Mean ( $\bar{x} \pm$  SE days) clutch initiation dates were significantly different between years for 4- (ANOVA,  $P=0.0001$ ) and 5-egg (ANOVA,  $P<0.0001$ ) clutches (Table 1). Clutches of 4 were initiated significantly earlier in 1988 compared to 1989 (SNK,  $q=11.62$ ,  $P<0.001$ ) and 1990 (SNK,  $q=12.44$ ,  $P<0.001$ ), whereas clutch initiation dates of 4-egg clutches in 1989 were not significantly different from 1990 (Table 1). Initiation dates for 5-egg clutches were significantly earlier in 1988 compared to 1989 (SNK,  $q=39.96$ ,  $P<0.0001$ ) and 1990 (SNK,  $q=27.03$ ,  $P<0.0001$ ). Also, 5-egg clutches were initiated significantly earlier in 1989 than 1990 (SNK,  $q=6.88$ ,  $P<0.001$ ). Four-egg clutches were initiated later than 5-egg clutches in all years, except 1990 (Table 1).

**Hatching Spreads.** In control asynchronously hatched broods, mean ( $\bar{x} \pm$  SE hours) FLAST hatch spreads (h) for 4-egg clutches differed significantly between years (ANOVA,  $F=3.21$ ,  $P=0.049$ ). That is, FLAST hatch spreads in 1988 and 1990 were significantly longer than in 1989 (SNK, 1988 vs 1989,  $q=3.00$ ,  $P<0.05$ ; 1989 vs 1990,  $q=3.35$ ,  $P<0.05$ ; Table 2). APLAST hatch spreads in 4-egg clutches also differed significantly between years (ANOVA,  $F=3.29$ ,  $P=0.046$ ; SNK, 1988 vs 1989,  $q=3.17$ ,  $P<0.05$ ; 1989 vs 1990,  $q=3.36$ ,  $P<0.05$ ; Table 2). There was also a tendency for the PLAST hatch spread in 4-egg clutches to differ between years (ANOVA,  $F=2.26$ ,  $P=0.11$ ), due mainly to a significant difference in the mean PLAST hatch spread between 1989 and 1990 (SNK,  $q=2.93$ ,  $P<0.05$ ; Table 2).

TABLE 1. Mean ( $\bar{x} \pm SE$ ) clutch initiation dates in relation to clutch size for 1988, 1989, and 1990. Clutch initiation dates are scored as 1 May=1, such that 1 June=32, etc.

Year	4-eggs	n	5-eggs	n	t	P
1988	32.69 $\pm$ 0.80 <sup>a</sup>	43	30.04 $\pm$ 0.27 <sup>d</sup>	49	3.12	0.002
1989	40.71 $\pm$ 0.68 <sup>b</sup>	39	38.96 $\pm$ 0.33 <sup>e</sup>	28	2.29	0.03
1990	41.28 $\pm$ 0.38 <sup>b</sup>	43	41.23 $\pm$ 0.37 <sup>f</sup>	47	0.08	0.93

NOTE: Means within a clutch with the same superscript are not significantly different (SNK,  $P > 0.05$ ).

TABLE 2. Comparison of mean ( $\bar{x} \pm SE$ ) hatch spreads (h) between eggs for clutches initiated in 1988, 1989, and 1990. FLAST is the hatch spread between the first- and last-hatched nestlings, APLAST is the hatch spread between the ante-penultimate and last-hatched nestling, and PLAST is the hatch spread between the penultimate- and last-hatched nestling.

Year	Hatch Spread	Clutch Size				t	P
		4-egg	n	5-egg	n		
1988	FLAST	35.8 $\pm$ 3.0	18	57.9 $\pm$ 1.8	8	6.18	0.0001
	APLAST	32.3 $\pm$ 3.0	17	40.2 $\pm$ 1.6	10	2.29	0.015
	PLAST	20.7 $\pm$ 1.8	18	25.5 $\pm$ 1.1	10	2.25	0.015
1989	FLAST	27.6 $\pm$ 2.4	14	33.7 $\pm$ 2.6	7	1.55	0.07
	APLAST	23.8 $\pm$ 1.9	11	28.2 $\pm$ 2.7	6	1.31	0.10
	PLAST	17.6 $\pm$ 1.3	14	18.5 $\pm$ 1.5	8	0.44	0.33
1990	FLAST	36.7 $\pm$ 2.2	19	50.5 $\pm$ 2.0	21	4.63	0.0001
	APLAST	32.6 $\pm$ 2.0	19	39.8 $\pm$ 1.3	18	3.08	0.02
	PLAST	21.7 $\pm$ 0.7	19	22.6 $\pm$ 0.6	21	0.96	0.17
Combined <sup>a</sup>							
	FLAST	-0.45 $\pm$ 0.1	51	0.64 $\pm$ 0.1	36	6.06	0.0001
	APLAST	-0.32 $\pm$ 0.1	47	0.45 $\pm$ 0.1	34	4.07	0.0001
	PLAST	-0.17 $\pm$ 0.1	51	0.22 $\pm$ 0.1	39	1.86	0.035

<sup>a</sup> Data are combined for 1988-1990, and hatch spreads are standardized as described by Perrins and McCleery (1985). See Methods for details.

In 5-egg clutches the FLAST hatch spread differed significantly between years (ANOVA,  $F=17.61$ ,  $P=0.0001$ ), due mainly to significantly longer FLAST hatch spreads in 1988 and 1990 compared to 1989 (SNK, 1988 vs 1989,  $q=7.84$ ,  $P<0.05$ ; 1989 vs 1990,  $q=6.72$ ,  $P<0.05$  Table 2). Likewise, the APLAST hatch spread differed significantly between years (ANOVA,  $F=7.24$ ,  $P=0.002$ ), due to significantly shorter APLAST hatch spreads in 1989 than in 1988 ( $q=5.91$ ,  $P<0.05$ ) and 1990 ( $q=6.27$ ,  $P<0.05$ ; Table 2). PLAST hatch spreads also differed significantly between years (ANOVA,  $F=10.3$ ,  $P=0.0002$ ), again because PLAST hatch spreads in 1989 were significantly shorter than in 1988 ( $q=6.42$ ,  $P<0.05$ ) and 1990 ( $q=4.27$ ,  $P<0.05$ ; Table 2). These differences are apparently due to differences among the three years in ambient temperatures during egg-laying. That is, the shorter hatch spreads observed in 1989 may be due to the cooler temperatures observed in that year (see Appendix 1, also see Moreno 1989).

Within years, the hatch spread between the first- and last-hatched nestling (FLAST) and between the ante-penultimate and last-hatched nestling (APLAST) was significantly shorter in 4-egg clutches than 5-egg clutches in 1988 and 1990, but not 1989 (Table 2). The hatch spread between the penultimately hatched and last-hatched nestling (PLAST) was shorter in 4-egg clutches than 5-egg clutches in 1988, but not in 1989 and 1990 (Table 2). When the data are standardized across years, the FLAST, APLAST, and PLAST hatch spreads are significantly shorter in 4-egg clutches (Table 2).

In all three years, FLAST, APLAST, and PLAST hatch spreads were generally positively correlated with date of clutch initiation in 4-egg clutches. When the data were combined for the three years, the



standardized FLAST, APLAST hatch spreads were significantly and positively correlated with standardized date of clutch initiation (Table 3). A similar but non-significant trend ( $P=0.06$ ) was also observed for the standardized PLAST hatch spread. Again, since these correlations were based on an a priori prediction, P-values are based on the one-tailed distribution.

The FLAST, APLAST and PLAST hatch spreads in 5-egg clutches were generally positively correlated with date of clutch initiation (except for FLAST in 1988). However, only the correlation for the APLAST hatch spread with date of clutch initiation for 1989 was significant (Table 3). For the three years combined, the standardized FLAST, APLAST and PLAST hatch spreads were positively but not significantly correlated with date of clutch initiation (Table 3).

**Nestling Mass.** In control (asynchronous) broods with 4 nestlings, mean ( $\bar{x} \pm SE$ ) nestling mass (g) of 6-day-old FIRST and PEN nestlings, and 5-day-old LAST nestlings was similar in 1989 and 1990 (Table 4). In control broods of 5 nestlings, the mass of FIRST nestlings on day 6 was significantly different between years (ANOVA,  $F=9.60$ ,  $P=0.003$ ), whereas the mass of PEN and LAST nestlings did not differ between 1989 and 1990 (Table 4).

In synchronous broods with 4 nestlings, there were no differences between years in the mean mass of 6-day-old FIRST and PEN nestlings, and 5-day-old LAST nestlings (Table 4). For synchronous broods with 5 nestlings there was a non-significant tendency for the mean mass of FIRST nestlings to be greater in 1990 compared to 1989 (ANOVA,  $F=4.05$ ,  $P=0.06$ ).

TABLE 3. Correlation coefficients and levels of significance (1-tailed) of hatching spreads (FLAST, APLAST, and PLAST) with date of clutch initiation for 4- and 5-egg clutches initiated in 1988, 1989, and 1990. Sample sizes are in parentheses.

Clutch Size	Year	Hatch Spread		
		FLAST	APLAST	PLAST
4	1988	0.3572	0.3689	0.1445
		0.07	0.07	0.28
		(18)	(17)	(18)
	1989	0.5451	0.1036	0.3856
		0.02	0.38	0.08
		(14)	(11)	(14)
	1990	0.3371	0.3103	0.4100
		0.08	0.10	0.04
		(19)	(19)	(19)
Combined		0.3991	0.2814	0.3066
		0.002	0.03	0.06
		(51)	(47)	(51)
5	1988	-0.0905	0.3694	0.0155
		0.42	0.15	0.48
		(8)	(10)	(10)
	1989	0.3731	0.8794	0.5722
		0.23	0.03	0.09
		(7)	(6)	(8)
	1990	0.2769	0.1188	0.0125
		0.11	0.32	0.48
		(21)	(18)	(21)
Combined <sup>a</sup>		0.2215	0.2744	0.1556
		0.10	0.06	0.18
		(36)	(34)	(39)

<sup>a</sup> Data are combined for the three years. Date of clutch initiation, and hatch spread are standardized as described by Perrins and McLeery (1985). See Methods for details.

TABLE 4. Mean ( $\bar{x} \pm SE$ ) mass (g) of 6-day-old Yellow Warbler FIRST and PEN nestlings, and 5-day-old LAST nestlings in broods of 4 and 5 nestlings.

Brood size	Year	Nestling	Age	Brood Type		n	t	P	
				Asynchronous	Synchronous				
4	1989	FIRST	6	8.78 $\pm$ 0.35	10	8.79 $\pm$ 0.34	9	0.02	0.50
		PEN	6	8.80 $\pm$ 0.82	6	8.38 $\pm$ 0.45	5	0.75	0.28
		LAST	5	7.64 $\pm$ 0.54	4	8.32 $\pm$ 0.40	6	1.00	0.17
	1990	FIRST	6	8.86 $\pm$ 0.11	18	8.37 $\pm$ 0.11	19	3.20	0.0015
		PEN	6	8.70 $\pm$ 0.11	9	8.01 $\pm$ 0.43	8	1.64	0.06
		LAST	5	7.96 $\pm$ 0.26	8	7.79 $\pm$ 0.20	10	0.52	0.30
5	1989	FIRST	6	9.28 $\pm$ 0.23	17	8.31 $\pm$ 0.27	6	2.72	0.01
		PEN	6	8.66 $\pm$ 0.62	6	8.17 $\pm$ 0.62	2	0.55	0.31
		LAST	5	8.82 $\pm$ 0.31	3	7.90 $\pm$ 0.90	2	0.96	0.25
	1990	FIRST	6	8.62 $\pm$ 0.10	43	8.84 $\pm$ 0.12	16	1.36	0.09
		PEN	6	8.48 $\pm$ 0.14	13	8.62 $\pm$ 0.30	4	0.42	0.35
		LAST	5	7.53 $\pm$ 0.38	11	7.63 $\pm$ 0.31	5	0.19	0.42

There were no differences between years in the mass at fledging of PEN and LAST nestlings (Table 4).

Between groups, in 1989, the mass of FIRST, PEN and LAST nestlings were similar in asynchronous and synchronous broods of 4 (Table 4). In 1990, the mass of 6-day-old FIRST nestlings in asynchronous broods of 4 was significantly greater than that of FIRST nestlings in synchronous broods. There were no differences in the fledging mass of PEN and LAST nestlings in asynchronous and synchronous broods in 1990, although there was a non-significant tendency ( $P=0.06$ ) for PEN nestlings in asynchronous broods to be heavier than PEN nestlings from synchronous broods (Table 4).

When the data for 1989 and 1990 were combined, the mass at fledging of FIRST nestlings ( $8.83 \pm 0.14$  g) in asynchronous broods of 4 nestlings was significantly greater than that of FIRST nestlings ( $8.51 \pm 0.13$  g) in synchronous broods of 4 ( $t=1.70$ ,  $P=0.045$ ). The mass of LAST nestlings was similar between asynchronous and synchronous broods of 4.

For broods of 5 nestlings, in 1989, the mass of 6-day-old FIRST nestlings in asynchronous broods was significantly greater than that of their counterparts in synchronous broods (Table 4). The mass of 6-day-old PEN and 5-day-old LAST nestlings in asynchronous broods of 5 was similar to that of PEN and LAST nestlings in synchronous broods. In 1990, there was a trend for the mass of 6-day-old FIRST nestlings in asynchronous broods to be lower than that of FIRST nestlings in synchronous broods ( $t=1.36$ ,  $P=0.09$ ; Table 4). As in 1989, the fledging mass, in 1990, of PEN and LAST nestlings in asynchronous broods of 5

was similar to that of PEN and LAST nestlings in synchronous broods of 5 (Table 4).

When the data were combined across years, the mean fledging mass of FIRST nestlings ( $8.81 \pm 0.10$  g) in asynchronous broods of 5 nestlings was significantly greater compared to FIRST nestlings ( $8.69 \pm 0.12$  g) in synchronous broods (ANCOVA,  $F=9.30$ ,  $P=0.0015$ ). The comparison of mass of FIRST nestlings also yielded a significant interaction between year and brood type ( $P=0.003$ ), although the effect of year was not significant ( $P=0.73$ ). Therefore, although the mass difference of FIRST nestlings between the two groups was significant, this result must nevertheless be viewed cautiously. Also, when the data were combined for the two years, there were no differences between asynchronous and synchronous broods in the mass of 5-day-old LAST nestlings.

Lack's (1954) hypothesis predicts that brood reduction enhances the fitness of the surviving brood members. To examine this prediction I compared the mass of 6-day-old FIRST nestlings in asynchronous broods that had suffered brood reduction to the mass of 6-day-old FIRST nestlings in synchronous broods that had not suffered brood reduction. As predicted, FIRST nestlings in reduced asynchronous broods were significantly heavier than FIRST nestlings in whole synchronous broods ( $t=1.89$ ,  $df=57$ ,  $P=0.035$ ).

To determine if the observed differences in mass between nestlings in asynchronous and synchronous broods were due to initial differences in mass, I compared the average egg mass between the two groups. There were no significant differences in average egg mass between the two groups (Table 5).

TABLE 5. Comparison of mean ( $\bar{x} \pm SE$ ) egg mass (g) between Yellow Warbler 4- and 5-egg clutches that hatched asynchronously and synchronously. Data are combined for 1989 and 1990.

Clutch size	Clutch Type				t	P
	Asynchronous	n	Synchronous	n		
4	1.48 $\pm$ 0.02	42	1.42 $\pm$ 0.04	14	1.55	0.13
5	1.51 $\pm$ 0.02	30	1.59 $\pm$ 0.03	7	1.66	0.10

**Nestling Begging.** For control broods of 4 and 5 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 ( $X^2=34.89$ ,  $df=2$ ,  $P<0.0001$ , Table 6). That is, FIRST ( $X^2=33.45$ ,  $df=1$ ,  $P=0.0001$ ) and PEN ( $X^2=8.34$ ,  $df=1$ ,  $P<0.005$ ) nestlings begged during significantly fewer visits than LAST nestlings (Table 6). In synchronous broods, begging was random with respect to hatching order ( $X^2=2.20$ ,  $df=2$ ,  $P>0.25$ ; Table 6). Between groups, FIRST nestlings in asynchronous broods begged significantly less often than their counterparts in synchronous broods (Table 6). PEN and LAST nestlings in asynchronous broods were observed begging as often as their counterparts in synchronous broods (Table 6).

**Nestling Survivorship.** Overall, survival rates tended to differ among FIRST, PEN and LAST nestlings in asynchronous broods of 4 nestlings ( $G=4.13$ ,  $df=2$ ,  $P=0.10$ ). This was due mainly to the higher survival rates of FIRST nestlings compared to LAST nestlings (FEPT,  $P=0.038$ ). Survival rates, in asynchronous broods of 5, were significantly different among FIRST, PEN and LAST nestlings ( $G=13.56$ ,  $df=2$ ,  $P=0.001$ ). Again this was due to the fact that FIRST nestlings had a significantly higher survival rate than LAST nestlings (FEPT,  $P=0.0003$ ).

In synchronous broods, the survival rate of FIRST, PEN and LAST nestlings were similar in broods of 4 ( $G=0.04$ ,  $df=2$ ,  $P>0.98$ ) and 5 nestlings ( $G=0.60$ ,  $df=2$ ,  $P>0.90$ ).

There were no differences between brood sizes in the survival rates of FIRST, PEN or LAST nestlings in either asynchronous or synchronous

TABLE 6. Begging frequencies (no. of times begged/no. of nest visits) of Yellow Warbler FIRST, PEN, and LAST nestlings in asynchronous and synchronous broods. Data were combined for broods of 4 and 5 nestlings.

Nestling	Brood Type		$\chi^2$	P		
	Asynchronous	(%)			Synchronous	(%)
FIRST	42/265	(16)	65/200	(32)	16.91	<0.001
PEN	25/99	(25)	29/84	(34)	1.46	>0.10
LAST	43/93	(46)	35/84	(42)	0.21	>0.50



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 ( $G=4.28$ ,  $df=1$ ,  $P=0.03$ ; Table 7). However, the survival rates of PEN and LAST were similar in asynchronous and synchronous broods (Table 7).

In 1990, there was a tendency for FIRST nestlings in asynchronous broods to have a higher survival rate than their counterparts in synchronous broods. This difference, however, was not significant ( $G=1.98$ ,  $df=1$ ,  $P=0.18$ ; Table 7). 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 7).

When the data were combined across years, FIRST nestlings in asynchronous broods had a higher survival rate compared to FIRST nestlings in synchronous broods ( $G=9.81$ ,  $df=1$ ,  $P=0.003$ ; Table 7). The survival rates of PEN and LAST nestlings were similar between the two brood types (Table 7).

**Fledging Success.** In 1989, there was a tendency for fledging success to be higher in asynchronous broods of 4 nestlings compared to synchronous broods of 4 nestlings ( $P=0.07$ ; Table 8). Fledging success was similar in 1990 between asynchronous and synchronous broods of 4. In broods of 5 nestlings, fledging success was higher in asynchronous broods compared to synchronous broods in both 1989 and 1990, but only significantly so in 1990. The lack of a significant difference in 1989 was probably due to small sample sizes (Table 8).

TABLE 7. Survival rates of FIRST, PEN and LAST Yellow Warbler nestlings in asynchronous (ASYNCH) and synchronous (SYNCH) broods.

Year	Nestling	Brood Type			
		ASYNCH		SYNCH	
		Number Hatched	Percent Fledged	Number Hatched	Percent Fledged
1989	FIRST	41	92.7	25	68.0*
	PEN	16	93.7	11	81.8
	LAST	16	56.2	11	72.7
1990	FIRST	80	93.7	43	83.7
	PEN	31	83.9	18	72.2
	LAST	31	74.2	18	83.3
Combined	FIRST	121	93.4	68	77.9**
	PEN	47	87.2	29	75.9
	LAST	47	68.1	29	79.3

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

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

TABLE 8. Mean fledging success (no. fledged/clutch) for asynchronous and synchronous Yellow Warbler broods of 4 and 5 nestlings.

Year	Brood size	Brood type				t	P
		Asynchronous	n	Synchronous	n		
1989	4	3.86 ± 0.14	7	3.00 ± 0.50	8	1.54	0.07
	5	4.11 ± 0.54	9	3.33 ± 1.67	3	0.44	0.35
1990	4	3.53 ± 0.18	13	3.54 ± 0.25	11	0.02	0.98
	5	4.31 ± 0.24	19	3.14 ± 0.80	7	1.90	0.03
Total	4	3.65 ± 0.26	20	3.31 ± 0.25	19	1.18	0.12
	5	4.25 ± 0.23	28	3.20 ± 0.70	10	1.85	0.03

When the data were combined for both years, asynchronous and synchronous broods of 4 had similar fledging success. In broods of 5, fledging success was significantly higher in asynchronous broods (Table 8).

**Arthropod abundance.** In each sampling period, as well as overall, the relative abundance of midges was lower in 1989 compared to 1990 (Table 9).

### **Nest-Failure Hypothesis**

**Survival Rates.** When the data were combined for 1988-1990, the survival rate ( $q$ ) of LAST nestlings, in unmanipulated broods, was higher in broods of 4 than broods of 5 ( $G=4.06$ ,  $df=1$ ,  $P<0.05$ ; Table 10). Daily survival probabilities (DSP) of nests generally increased through the breeding cycle (Table 11). The DSP of nests during egg laying ( $P_0$ ) was significantly less than during the incubation ( $P_1$ ), nestling ( $P_2$ ) and fledging ( $P_3$ ) periods (Table 11).  $P_1$  and  $P_2$  DSP were also significantly less than the  $P_3$  DSP (Table 11).

Productivity ratios ( $W_{m+k}/W_N$ ) were calculated for  $m$  from 1 to  $N$  for both 4- and 5-egg clutches (Table 12). The calculated productivity ratios indicate that, given the daily survival probabilities observed during this study, female Yellow Warblers would maximize productivity if they initiated incubation on the first egg (Table 12). Productivity ratios observed during this study were, however, less than that predicted by the nest-failure hypothesis (Table 13). Also, the observed hatch spreads indicate that female Yellow Warblers hatched their eggs significantly more synchronously than predicted by the 'nest-failure'

TABLE 9. Relative abundance of midges at Delta Marsh in 1989 and 1990, for 4 sampling periods. (n= no. of sweeps during sampling period).

Sampling period	1989	n	1990	n
I	2	30	113	30
II	12	30	324	30
III	0	30	80	10
IV	13	30	509	20
Total	27	120	1026	90

NOTE: Sampling period I=5-11 Jn; II=14-20 Jn; III=23-29 JN;  
IV=2-8 JY.

TABLE 10. Survival rates (q) for last-hatched Yellow Warbler nestlings from nests in which all eggs hatched and at least one nestling survived to fledge. Data were combined for 1988-1990.

Brood size	<u>Number of last-hatched young</u>		(q)
	Hatched	fledged	
4	39	32	0.821
5	33	19	0.576

(G=4.06, df=1, P<0.05)

TABLE 11. Daily survivorship probabilities (DSP) of Yellow Warbler nests prior to initiation of incubation (P<sub>0</sub>), during incubation (P<sub>1</sub>), the nestling period (P<sub>2</sub>), and from first fledge to last fledge (P<sub>3</sub>), for nests initiated in 1988, 1989 and 1990. Data were combined for 4- and 5-egg clutches. DSP followed by the same superscript are not significantly different ( $P < 0.1$ , Hensler and Nichols 1981).

Period	No. of Nests	No. of Exposure days	No. of Losses	DSP
P <sub>0</sub>	208	320	17	0.9469 ± 0.0125 <sup>A</sup>
P <sub>1</sub>	177	1852	24	0.9870 ± 0.0026 <sup>B</sup>
P <sub>2</sub>	113	639	15	0.9765 ± 0.0060 <sup>B</sup>
P <sub>3</sub>	92	266	3	0.9924 ± 0.0065 <sup>C</sup>

TABLE 12. Calculated productivity ratios  
 $(W_{m+k}/W_N)$  for Yellow Warbler 4- and 5-  
 egg clutches in relation to the egg on  
 which incubation is initiated (m).

m	Clutch size	
	4	5
1	1.16	1.22
2	1.11	1.17
3	1.05	1.11
4	—	1.05



TABLE 13. Expected and observed productivity ratios ( $\bar{W}_{m+k}/\bar{W}_N$ ) and hatch spreads (hours) for Yellow Warbler 4- and 5-egg clutches.

Clutch Size	Max. ( $\bar{W}_{m+k}/\bar{W}_N$ ) <sup>a</sup>	Observed ( $\bar{W}_{m+k}/\bar{W}_N$ )	Optimal Hatch Spread (h)	Observed Hatch Spread (h) <sup>b</sup>
4	1.16	1.08	72	33.8
5	1.22	1.11	96	48.9

<sup>a</sup>From Table 12.

<sup>b</sup>From Table 2. Average FLAST for the three years combined.

hypothesis (c/4:  $t=24.02$ ,  $df=50$ ,  $P<0.0001$ ; c/5:  $t=25.06$ ,  $df=35$ ,  $P<0.0001$ ; Table 13).

**Nest Visibility.** The mean ( $\bar{x} \pm SE$ ) visibility of 4-egg clutches ( $4.44 \pm 0.4$  dots,  $n=37$ ) was not significantly different from that of 5-egg clutches ( $4.28 \pm 0.3$ ,  $n=36$ ;  $t=0.29$ ,  $df=71$ ,  $P=0.77$ ). Nest visibility was negatively correlated with date of clutch initiation ( $r=-0.2551$ ,  $P=0.03$ ,  $n=73$ ). However, the APLAST hatch spread was not correlated with visibility in 4- ( $r=0.1759$ ,  $P=0.50$ ,  $n=17$ ) or 5-egg ( $r=0.1205$ ,  $P=0.62$ ,  $n=19$ ) clutches. Therefore, there was no relationship between visibility of the nest and hatch spreads.

## DISCUSSION

### Brood Reduction Hypothesis

The results of this study suggest that, as hypothesized by Lack (1947, 1954), hatching asynchrony may facilitate brood reduction, particularly in larger broods (i.e. broods of 5 nestlings, see Table 10). 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), again especially in larger broods. The results of this study, however, do not support the 'nest-failure' hypothesis (Clark and Wilson 1981).

In agreement with the first prediction, hatch spreads were significantly shorter in 4-egg clutches than 5-egg clutches, in both 1988 and 1990, and there was a similar but non-significant trend in 1989. The same trend was revealed when the data were combined over the three years (Table 2). Greater hatch spreads in larger clutches have also been observed in other studies of hatching asynchrony (e.g. Howe 1976, Bryant 1978a, Richter 1984, Hussell 1985, Slagsvold 1986a, Smith 1988, Briskie and Sealy 1989a, Slagsvold and Lifjeld 1989b; but see Lessells and Avery 1989). In terms of the 'brood reduction' hypothesis (Lack 1947), these results indicate that smaller broods are easier to raise and are less susceptible to fluctuations in the availability of food resources (see Mock and Parker 1986). The higher survival rate of last-hatched nestlings in broods of 4 (see Table 10) also suggests that they are less susceptible to variations in the food supply compared to broods of 5 nestlings (see also Howe 1978; see Chapter 2). Brood-size dependent starvation, especially of last-

hatched nestlings, has been observed in several other studies (e.g. Seel 1970, Parsons 1975, Greig-Smith 1985, Mock and Parker 1986, Smith 1988, Magrath 1989a; but see Richter 1984, Briskie and Sealy 1989a).

Although there was a trend for feeding rates to be lower in asynchronous broods of 4 compared to broods of 5 nestlings (see Chapter 2), this difference was not significant. Previous studies have observed that higher feeding rates for larger broods do not necessarily translate into higher feeding rates per nestling (Royama 1966, Nur 1984a, see also Klomp 1970 for a review). Therefore, in this study, nestlings in asynchronous broods of 4, especially LAST nestlings, likely received more food than their counterparts in broods of 5.

It is generally accepted that breeding seasons are timed to coincide with the peak in abundance of prey populations, and that the availability of prey becomes unpredictable late in the breeding season (Lack 1954, Nisbet and Cohen 1975, Perrins 1979). It follows then that if hatching asynchrony has evolved to facilitate brood reduction during periods of food stress, then it can be predicted that individuals that initiate clutches later in the breeding season will hatch their eggs more asynchronously than individuals breeding earlier. This prediction is partially supported by the results of this study, despite significant inter-year variation in date of clutch initiation and ambient temperature during the egg-laying period (Table 3) That is, in 4-egg clutches, especially when the data were combined for the three years, the FLAST, APLAST hatch spreads were all significantly and positively correlated with date of clutch initiation. Similar but non-significant trends were also observed in 5-egg clutches.

The lack of a correlation for hatch spread with date of clutch initiation in 5-egg clutches may be due to the limited range of clutch initiation dates they exhibited in 2 of the 3 years of this study. Clutches of 5 eggs are typically initiated during the early (late May) to mid part (mid-June) of the breeding season (Goossen and Sealy 1982). However, during 1989 and 1990 clutch initiation was delayed by approximately one week, thereby compressing the range of clutch initiation dates, and thus the range of hatching spreads of 5-egg clutches.

Seasonal increases in hatching spread have been observed in other species (e.g. Courtney 1979, Mead and Morton 1985, Slagsvold 1986a). Such seasonal increases in hatch spreads are apparently due, in part, to an increase in incubation attentiveness during egg laying (Haftorn 1981). In accordance with Lack's (1947) 'brood reduction' hypothesis, such increases in hatch spread are usually attributed to a seasonal decline in the predictability of food resources (Lack 1968, Nisbet and Cohen 1975, Mead and Morton 1985). At Delta Marsh, the diet of nestling Yellow Warblers consists mainly of adult chironomids and larval geometrids (Biermann and Sealy 1982). These insects, particularly chironomids, have previously been described as abundant (Busby and Sealy 1979, Guinan and Sealy 1987). Nevertheless, food shortages do occur on the ridge, especially during periods of adverse weather (Pohajdak 1988, pers. obs.) as well as a general decline in biomass over the nesting period (Guinan and Sealy 1987, Pohajdak 1988, Briskie and Sealy 1989b). Recently, however, Slagsvold (1986b) hypothesized that a seasonal increase in hatch spreads was the result of physiological or environmental constraints incurred by females at

the time of laying. That is, females that initiated clutches early in the breeding season may have less stored energy for egg formation, encounter lower ambient temperatures and limited food availability, and therefore must spend more time foraging, and less time incubating during laying. Females initiating clutches later in the breeding season generally enjoy higher ambient temperatures, higher food availability, and have had time to store energy for egg production. Thus they can spend more time incubating during laying (Slagsvold 1986b).

Supportive of this is the fact that the relative abundance of midges was lower in 1989 than in 1990. Coincidentally, hatch spreads were also shorter in 1989. However, although not significant, 4-egg clutches exhibited shorter hatch spreads compared to 5-egg clutches, even though the mean clutch initiation date for 4-egg clutches is generally later than that of 5-egg clutches. Also, Kremetz and Ankney (1986) estimated that female House Sparrows (Passer domesticus) are not constrained energetically during egg production (see also Parsons 1970, Arnold 1991). In addition, Jones (1989) showed that female Barn Swallows (Hirundo rustica) required less than 5 min. out of every hour to maintain their optimum mass during incubation. Thus, hatching asynchrony is probably not entirely the result of energetic constraints during laying (see also Bryant 1978b).

Furthermore, the results of this study (see Chapter 3) also show that asynchronous hatching does not require full incubation. That is, female Yellow Warblers spent less than 50% of their time incubating on the day they laid the penultimate egg, and ca. 75% of their time incubating on the day they laid the last egg, but despite this hatching was significantly asynchronous.

Lack's (1947) hypothesis also predicts that brood reduction in asynchronously hatched broods will fall disproportionately on LAST nestlings. In agreement with this Yellow Warbler LAST nestlings in asynchronous broods had lower survival rates than older sibs, especially LAST nestlings in broods of 5 (see Table 10). In synchronously hatched broods, FIRST, PEN, and LAST nestlings had similar survival rates. This supports the parallel prediction that brood reduction in synchronously hatched broods would be random with respect to hatch order. The disadvantage incurred by last-hatched nestlings can result from hatching asynchrony and/or differential investment by the parents (Richter 1984, Amundsen and Stokland 1988). However, last-laid eggs are generally heavier than their clutch-mates (see Chapter 4), and 5-day-old LAST nestlings have similar mass as 5-day-old FIRST nestlings (see Appendix 2). Therefore, any disadvantage incurred by LAST nestlings is apparently because they hatched last, and hence were at a competitive size disadvantage (see also Bryant 1978b, Zach 1982, Richter 1984, Stockland and Amundsen 1988, Briskie and Sealy 1989a).

The concentration of mortality in last-hatched nestlings has been observed in many studies (e.g. Ricklefs 1965, Nisbet and Cohen 1975, Howe 1976, Bryant 1978, Richter 1984, Hébert and Barclay 1986, Haydock and Ligon 1986, and others). Brood reduction in these studies is usually associated with food stress where older sibs are fed selectively (Braun and Hunt 1983, Stinson 1979, Horsfall 1984, Greig-Smith 1985, Hebert 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 (Stinson 1979, Drummond et al. 1986, Ploger and Mock 1986, Anderson 1989, Parker et al. 1989, see also review by Mock 1984).

The results of this study are, for the most part, consistent with the prediction that first-hatched nestlings in asynchronous broods would exhibit greater fledging mass than their counterparts in synchronous broods (Table 4). In 1989, only in asynchronous broods of 5 nestlings was the mass of FIRST nestlings significantly greater than that of FIRST nestlings in synchronous broods. It is relevant that food was less abundant in 1989. Also in agreement with the prediction is that, when the data for 1989 and 1990 were combined, 6-day-old FIRST nestlings in asynchronous broods of 4 and 5 were significantly heavier than their counterparts in synchronous broods. Skagen (1988) observed a similar trend for heavier nestlings in 'food-stressed' Zebra Finch (*Poephila guttata*) asynchronous broods. The greater mass of nestlings in asynchronous broods, especially FIRST nestlings may be the result of a more efficient utilization of resources, and/or effective competition for preferred feeding positions. Hahn (1981) hypothesized that the competitive size hierarchy that results from asynchronous hatching, 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 asynchronous hatching 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. In broods that hatch synchronously all nestlings are the same size and presumably of the same competitive ability. Therefore, older



nestlings, and presumably the younger nestlings as well may never be satiated and thus expend more energy begging for food.

Furthermore, because of the size hierarchy in broods that hatch asynchronously, larger nestling(s) 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 nestling(s) may be fed (but see Stamps et al. 1985, Gottlander 1987). In synchronous broods where the competitive hierarchy is less established preferred feeding locations cannot be monopolized, and consequently all nestlings are fed equally, and potentially inadequately. In agreement with this, nestlings in synchronous broods begged more often than their counterparts in asynchronous broods.

Despite a tendency for asynchronous broods to be fed less often than synchronous broods (see Chapter 2), they did not exhibit lower fledging masses. Greater fledging mass in asynchronous broods has been observed in few experimental studies of hatching asynchrony (e.g. Slagsvold 1986a). Rather, most studies where synchronous hatching has been induced experimentally have observed no differences in the average mass of asynchronous and synchronous broods (Slagsvold 1982, 1985; Bengtsson and Ryden 1983, Haydock and Ligon 1986; Skagen 1987; Moreno 1987; Amundsen and Stokland 1988). This may be the result of using average brood mass, combining brood sizes, and/or using brood size at hatching rather than original clutch size.

As predicted, in 1989 the survival rate of FIRST nestlings in asynchronous broods was greater than that of their counterparts in

synchronous broods (Table 7). 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. The overall tendency for FIRST nestlings in asynchronous broods to enjoy higher survival rates than first nestlings in synchronous broods suggests that hatching asynchrony favors FIRST nestlings by enhancing their competitive size advantage. That is, in synchronous broods, LAST nestlings are still last, but they hatch closer in time to FIRST nestlings, and thus the competitive hierarchy is diminished. Therefore, FIRST nestlings in synchronous broods have less of a competitive advantage, and hence must compete harder, whereas in asynchronous broods, FIRST nestlings have a distinct advantage.

The predictions that LAST nestlings in asynchronous broods would have a lower fledging mass and survival rate than LAST nestlings in synchronous broods were not supported by the results of this study. These predictions were 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.

If Lack's (1947) 'brood reduction' hypothesis is to be accepted, it must be shown that hatching asynchrony facilitates brood reduction as opposed to total brood loss due to starvation, and that the fitness of the remaining nestlings is enhanced. Consistent with the 'brood reduction' hypothesis I observed less total brood loss in asynchronous

broods compared to synchronous broods (2.1% vs 10.3%, respectively). This difference, however, was not significant (FEPT,  $P=0.13$ ). Also in support of the 'brood reduction' hypothesis, I observed that the mass of 6-day-old nestlings in asynchronous broods that had suffered brood reduction was significantly greater than that of their counterparts in synchronous broods that did not suffer brood reduction. Therefore, it appears that hatching asynchrony does enhance the fitness of surviving brood members.

If hatching asynchrony has evolved as hypothesized by Lack (1947) 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 4 nestlings was greater than that of synchronous broods, in 1989 (Table 8) when food was apparently less abundant. However this difference was not significant ( $P=0.07$ ). A similar trend was also observed for broods of 5 in 1989, but again this difference was not significant, probably due to small sample size (Table 8). This is in contrast to most studies where hatch spreads have been manipulated (but see Hahn 1981, Magrath 1989). In addition, in 1990, when food was more abundant, reproductive success was similar between asynchronous and synchronous broods of 4 nestlings, however, fledging success was higher in asynchronous broods of 5 nestlings compared to their synchronous counterparts. When the data for 1989 and 1990 were combined, fledging success was similar for asynchronous and synchronous broods of 4. However, fledging success was significantly greater in asynchronous broods of 5 compared to synchronous broods of 5 when the data were combined across years.

This emphasizes the advantages of hatching asynchrony in larger broods that are apparently more susceptible to variations in food availability (see Slagsvold 1986a, b).

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.).

In summary, hatching asynchrony creates a competitive size hierarchy among brood mates, and this hierarchy favors FIRST nestlings at the expense of LAST nestlings. The results also suggest that, as hypothesized by Lack (1947), hatching asynchrony facilitates brood reduction, and enhances the fitness of surviving nestlings.

### **Nest Failure Hypothesis**

The risk of total failure of Yellow Warbler nests was highest during the egg-laying period, and decreased through the fledging period. The 'nest-failure' hypothesis (Clark and Wilson 1981) thus predicts that reproductive success will be optimized if females begin incubation with the laying of the first egg. However, the observed hatching spreads between first- and last-hatched Yellow Warbler nestlings were significantly less than that predicted by the 'nest-failure' hypothesis. Therefore, it appears that Clark and Wilson's (1981) 'nest-failure' model cannot adequately explain, at least in Yellow Warblers, the evolution of hatching asynchrony.

Two other studies investigating the relevance of the 'nest-failure' model regarding the evolution of hatching asynchrony, have also obtained contradictory evidence. Briskie and Sealy (1989a) observed that Least Flycatchers (Empidonax minimus) breeding at Delta Marsh hatch their clutches more synchronously than would be predicted by the 'nest-failure' model. That is, as in this study, Briskie and Sealy (1989a) found that the daily survival probability of flycatcher nests was lowest during egg laying, and increased significantly during fledging. Productivity in Least Flycatchers would have been maximized had the females begun incubation on the first egg (Briskie and Sealy 1989a). Similar results have also been obtained in the Boat-tailed Grackle (Quiscalus major; Bancroft 1985a).

Support for the 'nest-failure' hypothesis was obtained by Hussell (1985) in a study on Snow Buntings (Plectrophenax nivalis). In this species, the daily survival probability of nests and their contents was highest during egg laying, and decreased through to fledging (Hussell 1985). The observed hatching spreads for clutches ranging from 4-7 were not significantly different from those predicted by the 'nest-failure' model (Hussell 1985). Therefore, with the exception of Hussell's (1985) study, the above observations indicate that for those species in which the risk of nest-failure is highest during egg laying the 'nest-failure' hypothesis predicts a greater degree of hatching asynchrony than observed.

Greater degrees of hatching asynchrony may be selected against for a variety of reasons. For example, Slagsvold (1986a) observed that nestling mortality was greater in broods with experimentally increased hatching spreads compared to control broods. Another factor that may

prevent the evolution of greater hatch spreads is a decrease in the hatching success of last-laid eggs. Slagsvold (1986a) observed lower hatching success in broods with experimentally increased hatching spreads. Also, Arnold et al. (1987) observed that the hatchability of dabbling duck (*Anas* spp.) eggs decreased significantly with an increase in the length of the pre-incubation delay.

The hatch spread between first- and last-hatched Yellow Warbler nestlings increased through the breeding season. This trend would support the 'nest-failure' hypothesis (Clark and Wilson 1981) if the risk of total nest-failure decreased through the breeding season (Slagsvold 1986b). However, the visibility of Yellow Warbler nests was negatively correlated to date of clutch initiation, thus indicating that nests initiated later in the breeding season were less susceptible to predation. As hatch spreads were greater in 5-egg clutches, and 5-egg clutches were initiated significantly earlier than 4-egg clutches, we would then predict that 4-egg clutches were less visible than 5-egg clutches. However, contrary to the 'nest-failure' hypothesis, nest visibility did not differ significantly between clutch sizes.

An important underlying theme, which is highlighted by the results of this study, is that the degree, and relative benefits of hatching asynchrony, were different for 4- and 5-egg clutches. Hatching was more synchronous in 4-egg clutches, but the effects of hatching synchrony (reduced nestling survivorship, lower fledging mass) were not as severe as in 5-egg clutches. In light of this it is interesting to note, as previously mentioned, that some unmanipulated 4-egg clutches hatched synchronously, an observation never made for 5-egg clutches. This, together with the tendency for feeding rates to be greater in

broods of 5 nestlings strongly, is compatible with the hypothesis that hatching asynchrony evolved as an adaptation to facilitate brood reduction, especially when food is limiting.

In conclusion, the results of this study are generally consistent with Lack's (1947) 'brood reduction' hypothesis (Table 14). Hatching spreads and trends in nest visibility observed in this study do not support the 'nest-failure hypothesis (Clark and Wilson 1981). Female Yellow Warblers generally hatched their eggs more synchronously than predicted by the 'nest-failure' model. Increased hatching asynchrony may be selected against due to decreased hatchability or survival of the last-hatched nestling.

TABLE 14. Summary of results in relation to the predictions derived from the brood reduction hypothesis (Lack 1954).

Prediction	Result	Agrees With Hypothesis
1a. Hatching asynchrony increases with clutch size	Hatch spreads greater in 5-egg clutches	Yes
1b. Hatching asynchrony positively correlated to date of clutch	Only hatch spreads of 4-egg clutches increased with date of clutch initiation	Partial
2. Brood reduction in asynchronous broods concentrated in last hatched nestling, and random in synchronous broods.	Survival rates of last-hatched nestlings in asynchronous broods lower than brood mates, survival rates in synchronous broods not affected by hatch order.	Yes
3. If food is limiting mass and survival rate of first-hatched nestlings will be higher in asynchronous broods.	Mass and survival rate of first-hatched nestlings generally higher in asynchronous broods, especially larger broods	Yes
4. If food is limiting mass and survival rate of last-hatched nestlings will be lower in asynchronous broods	Mass and survival rate of last-hatched nestlings similar in asynchronous and synchronous broods.	No
5. If food is limiting reproductive success will be higher in asynchronous broods.	Reproductive success generally higher in asynchronous broods. Problem with sample size.	Partial



## CHAPTER 2

### HATCHING ASYNCHRONY AND PARENTAL INVESTMENT IN YELLOW WARBLERS: A TEST OF THE SEXUAL-CONFLICT HYPOTHESIS

#### INTRODUCTION

Slagsvold and Lifjeld (1989a) hypothesized that hatching asynchrony, especially in birds that exhibit asymmetries in parental duties, results from female-dominated conflict between adult males and females. Thus, in species where only the female incubates, hatching asynchrony allows females to extract a greater contribution of investment from males. Slagsvold and Lifjeld (1989a) suggested that in addition to increasing the quantity (Clark and Wilson 1981; Hussell 1972, 1985) or quality of the young raised (Lack 1954, Hussell 1972, Nisbet and Cohen 1975, Hahn 1981, Hébert and Barclay 1986, Husby 1986), females also benefit when their young hatch asynchronously because: 1) first-laid eggs hatch earlier, which extends the time males have available to feed nestlings, thereby reducing the females' overall contributions, and 2) it minimizes the amount of time males have to acquire additional females, thereby maximizing the potential male contribution to the brood.

The purpose of this part of the study was to test the relative importance of the 'sexual-conflict' hypothesis in the evolution of hatching asynchrony in Yellow Warblers. Since the Yellow Warbler is essentially monogamous (but see Reid and Sealy 1986, Hobson and Sealy

1989a) this study could not address the effects of hatching asynchrony on polygyny in male Yellow Warblers but only the effects of hatching asynchrony on male and female contributions to broods.

Incubation by females alone is characteristic of many avian species, especially hawks, owls and passerines (see references in Slagsvold and Lifjeld 1989a). In species whose young hatch asynchronously, females may brood the young almost constantly for several days, during which time the male provides most or all the food to the female and nestlings (Newton 1979, Biermann and Sealy 1982, Bedard and Meunier 1983, Knapton 1984, Grundel 1987, Lifjeld et al. 1987, Sutherland 1987). Accordingly, the 'sexual-conflict' hypothesis states that hatching asynchrony allows a, "...female to 'manipulate' the male to contribute a few extra days' worth of parental effort, thereby reducing her own share" (Slagsvold and Lifjeld 1989a: 240). From this I predicted that: 1) females tending asynchronously hatching broods will make fewer feeds to the brood than females tending synchronously hatched broods, since 2) males tending asynchronously hatched broods would contribute more feeds than those tending synchronously hatched broods, especially during the early nestling period.

## METHODS

To examine the effect, if any, of asynchronous hatching on nestling feeding by male and female Yellow Warblers, some clutches were induced to hatch synchronously (hatch spread between the first and last-hatched nestling  $\leq 24$  h) as described in Chapter 1.

Feeding rates (no. of feeds/0.5 h) of parents with asynchronously and synchronously hatched broods were quantified during daily 0.5-h observation periods beginning when the first-hatched nestling was one day old, and on each following day until the oldest nestling was 7 days old. During the observation periods the sex of the parent feeding the nestlings was recorded, and whether the male fed the nestlings indirectly by giving food to the female first, as well as the number of times the male fed the female at the nest. The feeding rate of males, therefore, included feeds made directly and indirectly to the nestlings, as well as those made to the female in which she ingested.

Feeding rates were compared between the sexes both within and between the two experimental groups (asynchronous and synchronous broods) over four time periods. First, the early nestling period comprised the first two days (day=1 and 2) after the first nestling hatched (day=0). This 2-day period was chosen because this was the longest time normally required for all eggs in asynchronous clutches to hatch (see Chapter 1; Goossen 1978). The second period (mid-nestling period) consisted of days 3-5 after the hatching of the first nestling, and is the period of rapid growth. The third period (late nestling period), comprised days 6 and 7 post-hatch of the first nestling, and approximated the spread in fledging dates between first- and last-

hatched nestlings in normally asynchronous broods (Goossen 1978, see also Chapter 1). Feeding rates over the entire nestling period (total nestling period) were also compared between the two groups.

Feeding rates of females tending control broods of 4 nestlings in 1989 were significantly different from 1990 (see Results). Therefore, all comparisons involving females tending control broods of 4 nestlings were done with analysis of covariance with year as the covariate using the GLM program in SAS (1985). Comparisons between groups (asynchronous vs synchronous hatching) are one-tailed since they are based on a priori predictions.

## RESULTS

Females tending asynchronously or synchronously hatched broods of 4 had significantly higher feeding rates in 1989 compared to 1990 (Table 15). There were no differences between years in the feeding rates of females tending asynchronously or synchronously hatched broods of 5 nestlings (Table 15). Mean ( $\bar{x} \pm SE$ ) feeding rates (feeds/0.5 hr) were similar between years for males tending either asynchronously or synchronously hatched broods of 4 or 5 nestlings (Table 16).

Regardless of brood-size, there were no differences in the feeding rates of males and females tending control broods during the early, mid-, and late-nestling periods (Table 17). Consequently, the mean feeding rate over the entire nestling period was also similar between the sexes (Table 17). Males tending synchronously hatched 4- and 5-nestling broods made significantly more feeds than females during the mid-nestling period, and over the entire nestling period (Table 18).

### Female Feeding Rates

Overall, there was a non-significant tendency for females tending asynchronously hatched broods of 4 nestlings to make fewer feeds than females tending broods of 5 nestlings ( $F=2.62$ ,  $P=0.11$ ). When the data were combined for the two years, there was a non-significant tendency for females tending synchronously hatched broods of 4 nestlings to make fewer feeds than females tending synchronous broods of 5 nestlings ( $F=3.56$ ,  $P=0.06$ ).

TABLE 15. Comparison of mean ( $\bar{x} \pm SE$ ) number of feeds/0.5 h by female Yellow Warblers tending control asynchronously (ASYNCH) and experimental and unmanipulated synchronously (SYNCH) hatched broods of 4 and 5 nestlings, in 1989 and 1990.

Brood size	Brood type	Year				t	P
		1989	n	1990	n		
4	ASYNCH	2.7 $\pm$ 0.5	17	0.9 $\pm$ 0.2	24	3.50	0.002
	SYNCH	2.8 $\pm$ 0.6	20	1.4 $\pm$ 0.2	37	2.43	0.02
5	ASYNCH	2.2 $\pm$ 0.6	12	2.7 $\pm$ 0.3	35	0.81	0.42
	SYNCH	2.2 $\pm$ 0.9	11	2.3 $\pm$ 0.4	29	0.17	0.86

TABLE 16. Mean ( $\bar{x} \pm SE$ ) number of feeds/0.5 h by male Yellow Warblers tending asynchronously (ASYNCH) and synchronously (SYNCH) hatched broods of 4 and 5 nestlings in 1989 and 1990.

Brood size	Brood type	Year				t	P
		1989	n	1990	n		
4	ASYNCH	3.2 $\pm$ 1.0	17	1.8 $\pm$ 0.3	24	1.28	0.21
	SYNCH	2.5 $\pm$ 0.5	20	2.9 $\pm$ 0.5	37	0.63	0.52
5	ASYNCH	2.1 $\pm$ 0.5	11	3.2 $\pm$ 0.5	29	1.32	0.19
	SYNCH	3.7 $\pm$ 1.0	12	4.2 $\pm$ 0.4	35	0.49	0.63

TABLE 17. Comparison of feeding rates of males and females tending control asynchronous broods of 4- and 5-nestlings during the early, mid- and late nestling periods. The data are combined for 1989 and 1990.

Brood size	Period	Sex				F1/t	P
		Female	n	Male	n		
4	Early	1.0 ± 0.3	12	1.5 ± 0.4	12	0.98	0.33
	Mid	1.3 ± 0.5	16	2.2 ± 0.7	16	1.35	0.25
	Late	2.6 ± 0.5	13	3.4 ± 1.1	13	0.45	0.51
	Overall	1.6 ± 0.3	41	2.4 ± 0.5	41	2.20	0.14
5	Early	1.6 ± 0.5	11	2.2 ± 0.4	11	0.82	0.26
	Mid	1.9 ± 0.5	20	3.0 ± 0.6	20	1.49	0.14
	Late	4.0 ± 1.3	9	3.4 ± 1.0	9	0.34	0.73
	Overall	2.3 ± 0.4	40	2.9 ± 0.4	40	1.04	0.30

1. Comparisons between males and females with broods of 4 were done using analysis of covariance. The F-statistic was calculated using the Type III SS. Comparisons involving broods of 5 nestlings were done with two-tailed t-tests. See results for details.



TABLE 18. Comparison of feeding rates of males and females tending experimental and unmanipulated synchronous broods of 4- and 5-nestlings during the early, mid- and late nestling periods. The data are combined for 1989 and 1990.

Brood Size	Period	Sex				F1/t	P
		Female	n	Male	n		
4	Early	1.2 ± 0.2	22	1.3 ± 0.2	22	0.07	0.79
	Mid	2.0 ± 0.3	21	3.3 ± 0.6	21	3.95	0.054
	Late	2.9 ± 0.8	14	4.4 ± 0.9	14	1.84	0.18
	Total	1.9 ± 0.2	57	2.8 ± 0.3	57	4.28	0.04
5	Early	2.1 ± 0.5	15	3.1 ± 0.7	15	1.24	0.22
	Mid	2.4 ± 0.4	21	4.6 ± 0.6	21	2.97	0.005
	Late	3.6 ± 0.7	11	4.4 ± 0.9	11	0.72	0.5
	Total	2.6 ± 0.3	47	4.1 ± 0.4	47	2.97	0.004

1. Comparisons between males and females tending broods of 4 were done using analysis of covariance. The F-statistic was calculated using the Type III SS. Comparisons involving broods of 5 nestlings were done using two-tailed t-tests. See results for details.

Between groups, there were no differences in the mean feeding rate of females tending asynchronously or synchronously hatched broods of 4 in the early or late nestling periods (Table 19). However, during the mid-nestling period, females tending asynchronous broods of 4 nestlings made significantly fewer feeds than their counterparts with synchronous broods (Table 19). Mean total feeding rates were similar for females tending asynchronous and synchronous broods of 4 (Table 19). In broods of 5, there were no differences in the feeding rate of females tending asynchronous and synchronous broods during the early, mid- or late nestling periods, as well as for the total nestling period (Table 19).

#### **Male Feeding Rates**

When the data were combined for 1989 and 1990 the mean overall feeding rate of males with asynchronous broods of 4 nestlings ( $2.39 \pm 0.5$  feeds/0.5h,  $n=41$ ) was similar to that of males tending 5 ( $2.87 \pm 0.4$  feeds/0.5h,  $n=40$ ;  $t=0.82$ ,  $P=0.41$ ). For the two years combined, males tending synchronous broods of 4 nestlings made significantly fewer feeds ( $2.8 \pm 0.3$ ,  $n=57$ ) than males with 5 nestlings ( $4.1 \pm 0.4$ ,  $n=47$ ;  $t=2.37$ ,  $P=0.02$ ).

Between groups, males tending asynchronous broods of 4 nestlings had a similar feeding rate as males with synchronously hatched broods of 4 in the early, mid- and late-nestling periods (Table 20). The mean feeding rate over the entire nestling period was also similar for males tending asynchronous and synchronously hatched broods of 4 nestlings (Table 20).

TABLE 19. Comparison of mean ( $\bar{x} \pm SE$ ) number of feeds/0.5 hr by females tending control asynchronously (ASYNCH) and experimental and unmanipulated synchronously hatched broods (SYNCH). Data are combined for 1989 and 1990.

Brood size	Nestling period	Brood Type				F <sup>1</sup> /t	P
		ASYNCH	n	SYNCH	n		
4	Early	1.0 ± 0.3	12	1.2 ± 0.2	22	0.37	0.28
	Mid	1.3 ± 0.5	16	2.0 ± 0.3	21	3.04	0.04
	Late	2.6 ± 0.5	13	2.9 ± 0.8	14	2.40	0.06
	Overall	1.6 ± 0.3	41	1.9 ± 0.2	57	1.24	0.14
5	Early	1.6 ± 0.5	11	2.1 ± 0.5	15	0.56	0.29
	Mid	1.9 ± 0.5	20	2.4 ± 0.4	21	0.78	0.22
	Late	4.0 ± 1.3	9	3.6 ± 0.7	11	0.26	0.40
	Overall	2.3 ± 0.4	40	2.6 ± 0.3	47	0.54	0.30
Combined							
	Early	1.3 ± 0.3	23	1.6 ± 0.3	37	0.57	0.23
	Mid	1.6 ± 0.3	36	2.2 ± 0.2	42	1.85	0.08
	Late	3.2 ± 0.6	22	3.2 ± 0.5	25	0.60	0.22
	Overall	1.9 ± 0.2	81	2.2 ± 0.2	104	0.80	0.19

1. Comparisons involving control and experimental 4-nestling broods are based on analyses of covariance. The F-statistic was calculated using Type III sums of squares (SAS 1985). Comparisons of 5-nestling broods were made using t-tests. Values of P for both the F- and t-statistic are for the one-tailed distribution.

TABLE 20. Comparison of mean ( $\bar{x} \pm SE$ ) number of feeds/0.5 hr by males tending control asynchronously (ASYNCH) and experimental and unmanipulated synchronously (SYNCH) hatched broods. Data are combined for 1989 and 1990.

Brood size	Nestling period	Brood Type				t	P
		ASYNCH	n	SYNCH	n		
4	Early	1.5 $\pm$ 0.4	12	1.3 $\pm$ 0.2	22	0.41	0.34
	Mid	2.2 $\pm$ 0.7	16	3.3 $\pm$ 0.6	21	1.13	0.13
	Late	3.4 $\pm$ 1.1	13	4.4 $\pm$ 0.9	14	0.75	0.23
	Overall	2.4 $\pm$ 0.5	41	2.8 $\pm$ 0.3	57	0.73	0.23
5	Early	2.2 $\pm$ 0.4	11	3.1 $\pm$ 0.7	15	1.22	0.12
	Mid	3.0 $\pm$ 0.6	20	4.6 $\pm$ 0.6	21	1.88	0.03
	Late	3.4 $\pm$ 1.0	9	4.4 $\pm$ 0.9	11	0.75	0.23
	Overall	2.9 $\pm$ 0.4	40	4.1 $\pm$ 0.4	47	2.16	0.01
Combined	Early	1.8 $\pm$ 0.3	23	2.0 $\pm$ 0.3	37	0.51	0.64
	Mid	2.7 $\pm$ 0.4	36	3.9 $\pm$ 0.4	42	2.04	0.02
	Late	3.4 $\pm$ 0.7	22	4.4 $\pm$ 0.6	25	1.08	0.14
	Overall	2.6 $\pm$ 0.3	81	3.4 $\pm$ 0.3	104	1.87	0.03

NOTE: Values of P are for the one-tailed distribution.

During the early and late nestling periods, males tending asynchronously hatched 5-nestling broods had similar feeding rates as males tending synchronously hatched 5-nestling broods. However, during the mid-nestling period, males tending asynchronously hatched broods of 5 made significantly fewer feeds than males tending synchronously hatched broods (Table 20). Also, males tending control 5-nestling broods had a significantly lower feeding rate over the entire nestling period compared with males tending experimental broods of 5 (Table 20).

## DISCUSSION

The results of this study are not consistent with Slagsvold and Lifjelds' (1989a) 'sexual-conflict' hypothesis. Feeding rates of both sexes during the early nestling period were similar within and between the asynchronous and synchronous groups. This indicates that, at least initially, the benefits of either hatching strategy are similar in terms of food provided by parents. Within the control group (asynchronous), although there was a tendency for males to make more feeding trips, males and females had similar feeding rates in each time period (Table 17). Thus female Yellow Warblers may not benefit from increased male investment in the brood as a result of hatching asynchrony in the manner predicted by the 'sexual-conflict' hypothesis (Slagsvold and Lifjeld 1989a).

### Female Feeding Rate

Female Yellow Warblers tending asynchronous broods, especially those with 5-nestlings, generally made fewer feeding trips than females tending synchronous broods, but this difference was not significant. This suggests that females may be neutral with respect to hatch spreads, at least in terms of feeding rates. This is contrary to the 'sexual-conflict' hypothesis (Slagsvold and Lifjeld 1989a), which suggests that females should favor hatching asynchrony since it minimizes energetic demands, at least during the nestling period. Nevertheless, females may be selected to favor hatching asynchrony as a result of benefits associated with energetic efficiency, as suggested

by Hahn (1981), or a reduction in the peak-load demand of the brood (Hussell 1972).

### **Male Feeding Rate**

Slagsvold and Lifjelds' (1989a) 'sexual-conflict' hypothesis predicts that asynchronously hatched broods will receive more male feeds, especially during the early nestling period, compared with females tending synchronously hatched broods. However, I observed that regardless of clutch-size, the number of feeds made by male Yellow Warblers tending asynchronous broods, during the early and late-nestling periods, did not differ from the number of feeds made by males tending synchronous broods. Furthermore, contrary to the 'sexual-conflict' hypothesis, there was a significant difference in male feeding rates during the mid-nestling period for males tending broods of 5-nestlings. That is, males tending asynchronous 5-nestling broods made significantly fewer feeds than their counterparts tending synchronous broods. Also, the overall feeding rate of males tending asynchronous broods of 5 was significantly lower than that of males tending synchronous 5-nestling broods. Similar but non-significant trends were also observed for males tending 4-nestling broods. In addition, there was a tendency ( $P < 0.10$ ) for the proportion of feeds made by males tending asynchronous broods to be less than that of males tending synchronous broods. It appears then that males tending asynchronously hatching broods provided less food than males tending synchronously hatched broods, especially males tending broods of 5 nestlings.

The amount of care afforded by males may be a function of several factors that may act independently or in concert. For example, Westneat (1988) observed that male Indigo Buntings (Passerina cyanea) breeding for the first time do not feed their young. In addition, male attentiveness tended to be positively correlated with brood size and certainty of paternity of the brood (Westneat 1988). Likewise, in the polygynous Yellow-headed Blackbird (Xanthocephalus xanthocephalus) males generally did not feed nestlings younger than 4 days (Willson 1966). Also, Beletsky and Orians (1990) observed that only 10% of breeding male Red-winged Blackbirds (Agelaius phoeniceus) fed their nestlings, despite its significant positive effect on reproductive success. Again, both of these species exhibit hatching asynchrony (Strehl 1978, Richter 1984), but apparently males do not contribute more to the feeding of the brood, especially during the early nestling period.

Other investigators have noted differences in effort by parents tending asynchronous and synchronous broods. For example, Fujioka (1985) and Mock and Ploger (1987) observed that parents tending synchronously hatched Cattle Egret (Bubulcus ibis) broods made significantly more feeds than those tending control or experimental asynchronous broods. Although not significant, a similar trend was observed in Herring Gulls by Hébert and Barclay (1986). Admittedly, both of these species exhibit biparental incubation; nevertheless, the observations do indicate that synchronous hatching requires a greater parental expenditure than asynchronous hatching. Also, Skagen (1988) found no effects of hatching spread on adult female or male Zebra Finch (Poephila guttata) mass at the end of the nestling period, whether or



not food was limited. Her results may be confounded by the fact that they were obtained in the laboratory under constant environmental conditions, but nevertheless are intriguing and are contrary to the 'sexual-conflict' hypothesis.

It may be argued that feeding rates are not an accurate measure of energy expenditure. However, Nur (1984a) observed a significant negative correlation between feeding rates and female mass. That is, the mass of females tending nests with high feeding rates was lower than that of females tending nests with lower feeding rates. Such a trend has been observed in other studies as well (e.g. Hussell 1972, Bryant and Westerterp 1983, Williams 1988). Therefore, although I did not record adult mass in this study, it can be inferred that males tending synchronous broods, in this study, did expend a greater amount of energy in feeding the young in light of their higher feeding rates. Since adult mass is positively correlated with survival and future reproductive success (Nur 1984b, 1987, and references therein), it appears that hatching asynchrony would be selected for in that it minimizes parental effort, and therefore increases the probability of survival. This is especially important since there is evidence that in altricial species, parents work at a level of daily energy expenditure that is close to their physiological maximum energy intake (Kirkwood 1983, but see Ydenberg and Bertram 1989). Therefore, any increase in parental effort (e.g. feeding rate) can have a significant negative impact on the individual fitness of the parents, as well as their inclusive fitness (*sensu* Hamilton 1964).

It appears from the results of this study, that conflict between the sexes, if it occurs at all, is limited to larger clutch sizes, since only

male Yellow Warblers tending synchronous broods of 5 nestlings had a significantly higher feeding rate than their counterparts tending control broods. Interestingly, hatching synchrony was observed in some control 4-nestling broods but not in 5-nestling broods. It is difficult to envisage why natural selection would not also favor females laying 4-egg clutches that extract greater contributions from their mates.

A basic assumption of Slagsvold and Lifjelds' (1989a) hypothesis is that hatching asynchrony increases the amount of time males have available to contribute to broods. The average nestling period of asynchronously hatching Yellow Warbler broods of 4 and 5 was longer than that of similar-sized synchronously hatching broods (see Appendix 3). Caution must be used in interpreting these data since they are ca. 1.5 days less than those observed by Goossen (1978). This is probably due to the frequent nest visits made during this study, which likely caused premature fledging. Nevertheless, these data agree with Slagsvold and Lifjeld's (1985) hypothesis, in that the time available to males to feed young is longer in asynchronous than synchronous broods. Nevertheless, the feeding rate of males tending synchronous broods was generally higher than that of males tending asynchronous broods. It appears that although males tending synchronous broods had less time available to contribute to the brood, they compensated for this by increasing their feeding rate. Likewise, there was also a non-significant tendency for females with synchronously hatched broods to have higher feeding rates than females tending asynchronous broods, thereby compensating for the reduced length of the nestling period. Overall then the total reproductive effort may be less for adults

tending asynchronous broods, suggesting that there is no conflict between the sexes with regard to which hatching strategy to employ.

In conclusion, Slagsvold and Lifjelds' (1989a) 'sexual-conflict' hypothesis, which seeks to explain the evolution of hatching asynchrony in those species exhibiting monoparental incubation and "apparently" asymmetric levels of parental investment is not supported by the results of this study. The use of data from studies on the Yellow Warbler (this study) and other monogamous species may be an inappropriate test of the 'sexual-conflict' hypothesis, which may better explain hatching asynchrony in polygynous species. However, as stated by Slagsvold and Lifjeld (1989a), their results on the Pied Flycatcher, a polygynous species, suggest that there may not be conflict between the sexes, such that females always favor hatching asynchrony, and males either favor hatching asynchrony or are neutral. The results of this study suggest that female Yellow Warblers are neutral with respect to hatch spreads, whereas males favor hatching asynchrony.

## CHAPTER 3

### THE ONSET OF INCUBATION IN YELLOW WARBLERS: A TEST OF THE HORMONAL HYPOTHESIS

#### INTRODUCTION

In most bird species, successful incubation requires the development of one or more brood patches on the abdominal surface of the incubating bird. Brood patches are often free of feathers, oedematous and with highly vascularized skin to enhance heat transfer (Pettingill 1985). Brood-patch development involves both defeathering and vascularization (Drent 1975), which are regulated by prolactin in concert with estrogen (e.g. Bailey 1952, Hinde et al. 1963, Selander and Kuich 1963, Lloyd 1965, Jones et al. 1970). There is evidence that vascularization is completed prior to egg laying (Bailey 1952, see also references in Drent 1975), and defeathering is completed at least by early incubation (Haftorn 1981, see review in Drent 1975). Therefore, incubation behavior, which is stimulated and/or maintained by tactile stimulation arising when the brood patch is in contact with the eggs (Hall and Goldsmith 1983), can be, and is effective, even during laying (Haftorn 1981).

Although prolactin may not initiate incubation behavior, there is evidence that it maintains incubation (Drent 1975). The secretion of prolactin is apparently stimulated by the act of incubation or associated stimuli (Eisner 1969, Hall and Goldsmith 1983). Prolactin levels gradually increase through laying and peak during the first half

of the incubation period (Silverin and Goldsmith 1983, Breitenbach et al. 1965).

Recently, Mead and Morton (1985) proposed that hatching asynchrony evolved as a result of selection on an unrelated trait(s), namely the hormonal control of the termination of ovulation and the onset of incubation, and the potential role that prolactin plays in each. That is, in concert with the ovulation of the last ovum there is a surge in the level of prolactin in the blood. This terminates ovulation, and stimulates the initiation of full incubation, which subsequently gives rise to hatching asynchrony (Mead and Morton 1985). Consequently, any advantages derived from hatching asynchrony (e.g., Lack 1954, Hussell 1972, Clark and Wilson 1981, Hahn 1981, Slagsvold and Lifjeld 1989a), are merely 'epiphenomena' (Mead and Morton 1985; equals "effects" sensu Williams 1966a).

From their hypothesis, Mead and Morton (1985) predicted that: 1) regardless of clutch-size, incubation attentiveness will peak when the penultimate egg is laid. If the 'hormonal' hypothesis is true, I predict that: 2) incubation attentiveness during egg laying will be similar at 4- and 5-egg clutches, especially on the days the penultimate and last eggs are laid, 3) hatching spreads will be similar whether clutches contain 4 or 5 eggs, and 4) incubation attentiveness will not be affected by experimentally adding eggs during laying. The purpose of this part of the study was to determine the onset of incubation behavior during laying in the Yellow Warbler, and test the predictions derived from the mechanistic aspect of the 'hormonal' hypothesis (Mead and Morton 1985).

The Yellow Warbler is an ideal species for this study because its young hatch asynchronously, it lays clutches of either 4 or 5 eggs (Goossen and Sealy 1982), and is a determinate layer (Sealy, in press). This last characteristic is important to Mead and Morton's (1985) hypothesis since they argued that hormonal influences should be more accurately reflected in determinate layers that show a characteristic sharp surge in the level of prolactin in the blood and in the onset of incubation behavior as opposed to indeterminate layers that are characterized by a gradual onset in incubation behavior and more variable clutch sizes.

## METHODS

The study was conducted during the summers of 1988-1990. I searched daily for nests, which when found were numbered and flagged, and visited through clutch completion. Each egg was marked on the blunt end to indicate its position in the laying sequence. Beginning with the day the second egg was laid a sample of control and experimental nests (described below) was observed for 0.5 h each day until clutch completion. Observations were made either between 0600 - 0900 h or 1845 - 2115 h CDT, during which the number of eggs in the nest was recorded as well as the amount of time females incubated (to the nearest second).

To test experimentally prediction (4) above, I added 2 eggs to one group of nests on the eve before the second egg was to be laid, or on the morning shortly after it was laid. One of the additional eggs was removed on the eve of, or the morning, that the fourth egg was laid. The second extra egg was removed the following day. No observations were made on experimental nests containing six eggs.

The data on incubation attentiveness were grouped for observations made on the days eggs were laid: the ante-penultimate egg (APEN), i.e., second egg in a 4-egg clutch, third egg in a 5-egg clutch; the penultimate egg (PEN); and last egg (LAST). Finally, to determine whether observed incubation patterns were reflected in subsequent hatching patterns, I recorded hatching spreads in control 4- and 5-egg clutches between the first- and last-hatched nestlings (FLAST), the ante-penultimate, and last-hatched nestlings (APLAST), and the penultimate and last-hatched nestlings (PLAST). Hatching spreads were determined by visiting each nest at 0600, 1100, 1600, and 2000

h during the hatching period. For the purposes of analyses I used data only from those nests where all eggs hatched.

Incubation attentiveness on the day the APEN, PEN and LAST eggs were laid, both within and between experimental groups, was analyzed using the General Linear Models (ANOVA with unequal sample sizes) program in SAS (1985), as well as the Student Newman Keuls (SNK) test for multiple comparisons (Zar 1974). The null hypothesis was rejected when  $P \leq 0.05$ . Because mean ( $\bar{x} \pm SE$ ) hatching spreads (h) differed significantly among years (see results), I minimized inter-year differences between hatching spreads by standardizing them using Perrins and McCleery's (1985) method. The yearly mean was subtracted from each observation, and the result was divided by the yearly standard deviation. The resulting standardized hatching spreads were compared using two-tailed t-tests. All comparisons based on a priori predictions are one-tailed. Consequently, P-values for these comparisons are based on 1-tailed distributions, and as such the null hypothesis is rejected when  $P \leq 0.05$ .



## RESULTS

Incubation attentiveness did not differ between years for females with 4- (GLM,  $F=0.86$ ,  $P=0.49$ ) or 5-egg (GLM,  $F=0.16$ ,  $P=0.95$ ) clutches. Also, when the data were combined over the three years, females tending 4- and 5-egg clutches exhibited similar patterns of incubation attentiveness during laying (GLM,  $F=0.65$ ,  $P=0.52$ ; Table 21). Therefore, I combined the data on incubation attentiveness for both clutch sizes.

Mean ( $\bar{x} \pm SE$ ) incubation attentiveness (sec) was significantly affected by the position of the egg in the laying sequence (GLM,  $F=15.14$ ,  $P=0.0001$ ; Table 22). Incubation attentiveness increased significantly through laying (Table 22). Females were more attentive on the day they laid the PEN egg compared with the APEN egg (SNK,  $q=4.74$ ,  $P<0.005$ ), and more attentive on the day they laid the LAST egg compared to the day they laid the APEN egg (SNK,  $q=7.70$ ,  $P<0.001$ ) and the PEN egg (SNK,  $q=2.94$ ,  $P<0.05$ ; Table 22).

Between groups, control females were significantly less attentive on the day the APEN and LAST eggs were laid compared to experimental females (Table 22). There was also a non-significant tendency for control females to incubate less on the day the PEN egg was laid than did experimental females, a difference that approached significance (Table 22).

In control nests the mean FLAST and APLAST hatching spreads in 4- and 5-egg nests differed significantly in 2 of the 3 years of the study (Table 23). The shorter hatch spreads in both clutch sizes in 1989 were probably due to below-average temperatures that persisted during the laying period (see Appendix 1). For the three years combined, the standardized FLAST and APLAST hatch spreads

TABLE 21. Comparison of mean ( $\bar{x} \pm SE$ ) incubation attentiveness (sec./0.5 h) of female Yellow Warblers tending 4- and 5-egg clutches. Data are combined for 1988-1990.

Egg	Clutch Size				t	P
	4-egg	n	5-egg	n		
APEN	296.43 $\pm$ 106.32	16	518.70 $\pm$ 191.10	10	1.10	0.32
PEN	971.25 $\pm$ 161.25	20	813.00 $\pm$ 187.65	9	0.58	0.56
LAST	1249.10 $\pm$ 128.33	20	1227.36 $\pm$ 185.24	11	0.09	0.92

NOTE: APEN, day ante-penultimate egg was laid; PEN, day penultimate egg was laid; and LAST, day last egg was laid.

TABLE 22. Comparison of mean ( $\bar{x} \pm SE$ ) incubation attentiveness (sec./0.5 h) between females tending control and experimental clutches. Data are combined for 1988-1990.

Egg	Clutch Size				t	P
	Control	n	Experimental	n		
APEN	381.92 $\pm$ 98.48 <sup>a</sup>	26	832.30 $\pm$ 133.66	23	2.75	0.008
PEN	922.13 $\pm$ 124.43 <sup>b</sup>	29	1226.62 $\pm$ 111.99	24	1.78	0.08
LAST	1241.38 $\pm$ 103.88 <sup>c</sup>	31	1555.00 $\pm$ 64.38	27	2.47	0.01

NOTE: Control means followed by the same superscript are not significantly different.  
Definition of APEN, PEN, and LAST as in Table 1.

TABLE 23. Comparison of mean ( $\bar{x} \pm SE$ ) hatch spreads (h) for control 4- and 5-egg clutches.

Year	Hatch spread	Clutch Size				t	P
		4-egg	n	5-egg	n		
1988	FLAST <sup>a</sup>	35.7 $\pm$ 3.1	18	56.0 $\pm$ 2.0	5	5.49	0.0001
	APLAST	32.3 $\pm$ 3.0	17	39.7 $\pm$ 1.8	7	2.06	0.05
	PLAST	20.7 $\pm$ 1.8	18	26.1 $\pm$ 1.5	7	1.74	0.09
1989	FLAST	28.7 $\pm$ 2.4	13	33.7 $\pm$ 2.6	7	1.33	0.19
	APLAST	24.8 $\pm$ 2.2	10	28.2 $\pm$ 2.7	6	1.06	0.30
	PLAST	18.1 $\pm$ 1.3	13	18.5 $\pm$ 1.5	8	0.16	0.86
1990	FLAST	35.5 $\pm$ 2.0	18	50.4 $\pm$ 2.0	18	5.22	0.0001
	APLAST	32.0 $\pm$ 2.0	18	39.1 $\pm$ 1.2	15	3.02	0.005
	PLAST	21.5 $\pm$ 0.7	18	22.6 $\pm$ 0.7	18	1.06	0.29
COMBINED STANDARDIZED <sup>b</sup>							
	FLAST	-0.41 $\pm$ 0.1	49	0.67 $\pm$ 0.1	30	5.57	0.0001
	APLAST	-0.28 $\pm$ 0.1	45	0.45 $\pm$ 0.1	28	3.31	0.001
	PLAST	-0.14 $\pm$ 0.1	49	0.22 $\pm$ 0.1	33	1.69	0.09

<sup>a</sup> FLAST, hatch spread between first and last-hatched nestling; APLAST, hatch spread between ante-penultimate and last-hatched nestling; PLAST, hatch spread between penultimate and last-hatched nestling.

<sup>b</sup> See methods for explanation.

were shorter in 4- compared to 5-egg clutches (Table 23). Likewise, the PLAST hatch spread tended to be shorter in 4-egg as opposed to 5-egg clutches, but this difference was not significant ( $P=0.09$ ; Table 23).

As females tending control clutches were significantly less attentive during egg-laying than females tending nests to which eggs were added experimentally, the a priori prediction was made that hatch spreads in control nests would also be shorter than in experimental nests. The mean FLAST, PLAST and APLAST standardized hatch spreads, however, were similar in both groups when compared using a one-tailed t-test (Table 24). Nevertheless, as predicted, hatch spreads were shorter in control nests, with the exception of the APLAST hatch spread in 4-egg clutches (Table 24).

TABLE 24. Comparison of mean ( $\bar{x} \pm SE$ ) standardized<sup>1</sup> hatch spreads between control clutches and those to which eggs were added during laying. Data for 1988 and 1989 are combined.

Clutch size	Hatch spread	Clutch Type				t	P
		Control	n	Experimental	n		
4	FLAST	-0.02 ± 0.2	31	0.13 ± 0.3	5	0.32	0.37
	APLAST	0.005 ± 0.2	27	-0.04 ± 0.5	3	0.07	0.47
	PLAST	-0.03 ± 0.2	31	0.28 ± 0.5	4	0.59	0.28
5	FLAST	-0.87 ± 1.3	12	1.75 ± 1.4	6	1.25	0.11
	APLAST	-0.12 ± 0.2	13	0.33 ± 0.6	5	0.87	0.20
	PLAST	-0.10 ± 0.3	15	0.26 ± 0.3	6	0.75	0.27

<sup>1</sup>See Methods for details.

## DISCUSSION

The first prediction of the 'hormonal' hypothesis (Mead and Morton 1985) that full incubation behavior begins with the laying of the penultimate egg is not supported by the results of this study. Incubation attentiveness of female Yellow Warblers increased steadily through laying. Contrary to the 'hormonal' hypothesis, full incubation did not begin with the laying of the penultimate egg in either 4- or 5-egg clutches, but rather with the last egg. Females with 4- and 5-egg clutches spent only 54% and 45% of their time, respectively, incubating the penultimate egg, and this increased to 67% and 68%, respectively, for the last egg. This agrees with the evidence that the blood level of the hormone that influences incubation behavior increases steadily during the egg-laying/ incubation period (Silverin and Goldsmith 1983, see also review by Drent 1975). Full daytime incubation is also delayed until the laying of the last egg by Common Grackle females producing 3- or 4-egg clutches, but females producing 5- or 6-egg clutches initiate incubation prior to clutch completion (Howe 1978; see also Haftorn 1981, Zerba and Morton 1983, Briskie and Sealy 1989a).

In agreement with the 'hormonal' hypothesis, Yellow Warbler females producing 4- and 5-egg clutches exhibited similar patterns of incubation attentiveness, especially on the days they laid the PEN and LAST eggs. That is, from Mead and Morton's (1985) hypothesis, I predicted that incubation attentiveness would be similar between females producing clutches of different sizes since the hormonal influences associated with the ovulation of the last egg should be similar regardless of clutch size. However, if incubation attentiveness, during egg laying, is similar for females producing

clutches of different sizes, then a corollary prediction would be that hatching spreads would also be similar. This prediction is not supported by the data, since I observed significant differences between clutch sizes in two of three measures of standardized hatch spreads (FLAST and APLAST). The significant difference in the FLAST hatch spread in 4- and 5-egg clutches could, at least partially, be explained by the fact that there is one more egg in a 5-egg clutch, and that some incubation occurs before the penultimate egg is laid. There should not, however, be any differences in the APLAST and PLAST hatch spreads. Nevertheless, the APLAST hatch spreads recorded in the present study differed significantly between 4- and 5-egg clutches. The difference in the PLAST hatch spread approached significance ( $P=0.09$ ). These results are in contrast to the attentiveness patterns observed during laying. However, although not significant, I observed females that produced 5-egg clutches were more attentive on the day the ante-penultimate egg was laid compared to females that produced 4-egg clutches, which suggests that hatching spreads may be affected by variations in attentiveness patterns during early egg laying.

Other studies of hatching asynchrony in passerines have also reported significant differences in hatch spreads among clutch sizes (e.g. Smith 1988, Briskie and Sealy 1989a, Stouffer and Power 1990). Smith (1988) found that asynchronous hatching was greater in 5-egg Dark-eyed Junco (*Junco hyemalis*) clutches compared to 4-egg clutches. Stouffer and Power (1990) observed a similar trend in 4- and 5-egg Common Starling (*Sturnus vulgaris*) clutches. However, as with the Yellow Warbler data presented here, Meijer (1990) observed similar levels of incubation attentiveness for female Common Starlings with



different clutch sizes on the days they laid the ante-penultimate, penultimate and last eggs. Significant differences in hatch spreads between clutch sizes have been observed in other species (e.g., Least Flycatchers, Briskie and Sealy 1989a; House Martins, Delichon urbica, Bryant 1978a; Common Grackles Howe 1978). Again, the results of the present study, and evidence from other studies do not support the prediction that hatching spreads would be similar in different clutch sizes.

Significant differences in hatching spreads between clutch-sizes suggest that, contrary to the 'hormonal' hypothesis, advantages accrued through hatching asynchrony may be adaptive rather than merely being 'epiphenomena'. For example, greater hatch spreads in larger clutches (e.g., Howe 1976, Slagsvold 1986a, Briskie and Sealy 1989a, this study) suggest that food stress is greater, and therefore brood reduction will be more favorable (Lack 1954, O' Connor 1978), or the potential for sibling rivalry is greater in larger clutches (Hahn 1981). Also, several studies involving the experimental manipulation of hatching spreads have observed some advantages to asynchronous hatching (Hahn 1981; Slagsvold 1982, 1986a; Slagsvold and Lifjeld 1989a; Hébert and Barclay 1986; Husby 1986; Gibbons 1987; Skagen 1987, 1988; this study, see Chapter 1) although some of the results may be equivocal (Slagsvold 1986b, Amundsen and Stockland 1988).

A key element in Mead and Morton's (1985) argument is that Mountain White-crowned Sparrows delay nighttime incubation until the penultimate egg has been laid, and this delay is reflected in the hatching spreads. However, the proportion of Yellow Warbler females sitting in nests at night does not change from the night after the ante-

penultimate egg is laid through clutch completion, regardless of whether the female eventually produces 4 or 5 eggs (see Appendix 4). Again this suggests that in Yellow Warblers incubation behavior is not regulated exclusively by hormonal fluxes associated with the laying of the penultimate egg since females begin nighttime roosting well before they lay the penultimate egg. R. M. R. Barclay (unpub. data, in Briskie 1986) observed that although a certain proportion of female Least Flycatchers roosted overnight in their nests prior to laying the last egg (varying from 29 to 40% for the first 3 eggs laid), most females delayed nighttime attentiveness until the last egg was laid (83%, n=6). Also, of six female Dusky Flycatchers (*E. oberholseri*) observed by Morton and Pereyra (1985), three initiated nighttime sitting on the day the ante-penultimate egg was laid, and three began on the day the penultimate egg was laid. In fact, in most species observed, females exhibit some nighttime and/or daytime attentiveness from the day the first egg is laid (e.g.: Weeden 1966; Haftorn 1979, 1981; Zerba and Morton 1983; Morton and Pereyra 1985; Briskie and Sealy 1989a), including Yellow Warblers (S. G. Sealy, unpubl. data). This, in conjunction with hatching spreads that vary among clutch sizes, suggests that hatch spreads are not controlled only by hormonal surges coincidental to the laying of the penultimate egg, but rather by subtle changes in incubation attentiveness before the penultimate egg is laid, due perhaps to stimuli from the eggs.

If initiation of incubation behavior is rigidly controlled only by endogenously regulated hormonal fluxes, principally prolactin surges associated with ovulation of the last ova, then it would be predicted that adding eggs to a clutch prior to the laying of the penultimate egg

would not affect incubation attentiveness. The results of this study show that females can be induced to begin incubating prior to laying the penultimate egg. That is, females with control clutches were significantly less attentive than females with clutches to which eggs were added early during laying. Similar results were obtained by Beukeboom et al. (1988) in the European Kestrel (Falco tinnunculus) by adding eggs on the day prior to clutch initiation. Both female kestrels, for which Beukeboom et al. (1988) have data, exhibited higher levels of incubation attentiveness compared to control females.

From the above, I also predicted that hatching spreads would be shorter in control nests compared to nests in which eggs were added during egg laying. This prediction, however, was not supported by the results of this study. Nevertheless, the trends are in the right direction. It follows then that given the amount of variation observed in female attentiveness patterns and hatching spreads, rigid hormonal control of incubation behavior does not appear likely. The results of this study and others show that, although laying and incubation are under hormonal control, this control is not precise. If some of the variation in incubation attentiveness is genetic, then it is also possible that natural selection can affect incubation attentiveness (Magrath 1990).

Finally, if hatching patterns were controlled rigidly by hormonal activities associated with the ovulation of the last egg, we would expect little variation in hatching spreads between clutches, clutch-sizes, seasons and years. However, there is evidence that shows that hatch spreads vary between and among clutches of different sizes (e.g, Mead and Morton 1985, Briskie and Sealy 1989a, this

study), seasonally (e.g., Mead and Morton 1985, Slagsvold 1986), and annually (this study). This suggests that hormonal influences on incubation behavior do not preclude variation in hatch spreads. Some of this variation in hatch spreads is likely to be genetic, and therefore influenced by natural selection (Magrath 1990). Hence, contrary to the 'hormonal' hypothesis, advantages accrued through hatching asynchrony may be adaptive (e.g., Lack 1954, Hahn 1981, Slagsvold and Lifjeld 1989).

However, the experimental results of this study (see also Slater 1967, Beukeboom et al. 1988) also concur with previous studies showing that tactile stimuli (Hall and Goldsmith 1983) and/or temperature stimuli (White and Kinney 1974) from the eggs via the brood patch play a role in controlling incubation attentiveness during laying. Furthermore, the effect of these stimuli can also be moderated by other stimuli such as hunger, or stimuli from the environment (White and Kinney 1974, see also Slater 1967). Thus, any hypothesis regarding the causal mechanisms producing hatching asynchrony should include the effects of other stimuli, as well as hormonal influences.

In conclusion, the causal mechanisms for hatching asynchrony proposed by the 'hormonal' hypothesis, cannot adequately explain the evolution of hatching asynchrony in species where only females incubate. Incubation attentiveness patterns of laying Yellow Warblers suggest that full incubation does not begin when the penultimate egg is laid, as predicted by the 'hormonal' hypothesis. Also, hatch spreads observed in this and other studies do not reflect observed patterns of incubation during laying, or an abrupt onset

with the penultimate egg. That is, hatching asynchrony apparently does not require full incubation attentiveness during laying. Hatching spreads in Yellow Warblers and other species surveyed, in contrast to that predicted by the 'hormonal' hypothesis, differed significantly between clutch sizes, and these differences may be related to small differences in incubation attentiveness during laying. In addition, eggs added experimentally during laying increased incubation attentiveness. Clearly, incubation behavior, although under hormonal control, is not rigid and is not associated exclusively with hormonal fluxes associated specifically with the ovulation of the last ova. At a minimum, stimuli from eggs are also necessary, and can produce variation in incubation onset and therefore subsequent hatching spreads. Finally, the results of this part of the study, however, do not preclude the notion that hatching asynchrony is an epiphenomenon arising from selection acting on other traits.

## CHAPTER 4

### EGG SIZE IN YELLOW WARBLERS: APPORTIONMENT OF PARENTAL INVESTMENT

#### INTRODUCTION

In birds, egg mass usually varies considerably among females within a population (e.g. Ricklefs et al. 1978, Grant 1982, Coleman and Whittall 1990, Wiggins 1990). Such interclutch variation in egg mass is associated with differences in female age and/or breeding experience (e.g. Davis 1975, Wiggins 1990), the nutritional state of the female or the availability of food resources (Bryant 1978b, O' Connor 1979, Briskie 1986, Pierotti and Bellrose 1986), clutch size (Jarvinen and Vaisanen 1983, Briskie and Sealy 1990), male courtship feeding (Nisbet 1973) and season (Soler 1988).

There is substantial evidence indicating that female birds can vary egg mass within a clutch (see Slagsvold et al. 1984, Arnold 1991 for reviews). This intraclutch variation in egg mass generally takes one of two forms. In species such as some penguins (Williams 1981), cormorants (Shaw 1985, but see Stokland and Amundsen 1988), egrets (Custer and Frederick 1990), gulls (Mills 1979, Hahn 1981, Hébert and Barclay 1988, but see Pierotti and Bellrose 1986), terns (Nisbet 1978), eagles, (Edwards and Collopy 1983), corvids (Soler 1988, Verbeek 1990) and icterids (Bancroft 1984, 1985b), egg mass generally decreases with laying order. Such a trend is generally viewed as an embellishment on the brood reduction strategy (*sensu* Lack 1954; see O'

Connor 1978, Hahn 1981, Braun and Hunt 1983, Slagsvold et al. 1984, and references therein; but see Clark and Wilson 1981, Stokland and Amundsen 1988). That is, the facility with which brood reduction can occur is enhanced by the smaller size of the last laid egg (Slagsvold et al. 1984).

In small open-cup nesting passerines, such as the Yellow Warbler, egg mass normally increases with laying order (Briskie and Sealy 1990, Wiggins 1990, Coleman and Whittal 1990; see also Slagsvold et al. 1984 for a review). This phenomenon has been viewed as bet-hedging by the female (Howe 1976). That is, nestlings from larger eggs usually survive better, at least during the first few days after hatching (Bancroft 1984, and references therein), as well as grow faster (Schifferli 1973). Thus, producing larger last eggs may enhance the probability of fledging the last-hatched nestling if conditions are favorable, without adversely affecting the efficacy of brood reduction should resources be limiting. A larger last egg has also been argued to be antagonistic to the brood reduction strategy (Clark and Wilson 1981), since larger eggs generally produce larger nestlings, therefore reducing the facility with which brood reduction can occur.

The purpose of this part of the study was to document and examine the mass of Yellow Warbler eggs in 4- and 5-egg clutches with respect to clutch size, clutch mass, laying order, and survivorship of last-hatched nestlings. The data also allowed me to examine the brood survival hypothesis (Slagsvold et al. 1984).

## METHODS

Fresh egg mass was recorded, within 6 hours of laying, to the nearest 0.05 g using a portable electronic balance. Data were collected in 1989-1990, between 0600 and 0900 h. Only data from complete 4- and 5-egg clutches were used.

All statistical analyses were done using SAS (1985). Within clutch variation was analyzed using analysis of variance and multiple comparisons tests. Analysis of variance was also used to examine relationships between clutch size, egg mass, laying order and hatching spreads. Correlation analysis was used to determine relationships between clutch size, egg mass, date of clutch initiation and hatch spreads.



## RESULTS

Mean ( $\bar{x} \pm \text{SE}$ ) egg mass (g) was similar among years for 4-egg clutches (ANOVA,  $F=1.9$ ,  $P=0.15$ ; Fig. 1), but not for 5-egg clutches (ANOVA,  $F=14.19$ ,  $P=0.0002$ ; Fig. 1). Eggs in 5-egg clutches were lighter in 1989 than 1990 ( $F=14.2$ ,  $P=0.0002$ ; Fig. 1). Between clutch sizes, average egg mass was significantly lighter in 4-egg clutches compared to 5-egg clutches (ANCOVA,  $F=15.95$ ,  $P=0.0001$ , year is a covariate). Egg mass was significantly affected by laying order in 4-egg ( $F=5.94$ ,  $P=0.0006$ ) and 5-egg clutches ( $F=4.72$ ,  $P=0.001$ ) laid in 1990, but not 1989 ( $F=1.12$ ,  $P=0.36$ ; Fig. 1). Egg mass was also strongly correlated with the total mass of the other eggs in the clutch in both 4- and 5-egg clutches (Table 25). To determine if females producing 4- and 5-egg clutches laid last-eggs of relatively similar mass, I subtracted the mass of the last egg from the average mass of the clutch for each 4- and 5-egg clutch, and compared their mean differences. The mean difference in mass between last-laid eggs and the average mass of their clutch-mates in 4-egg clutches ( $0.07 \pm 0.01$  g,  $n=56$ ) was not significantly different from that of last-laid eggs in 5-egg clutches ( $0.07 \pm 0.02$  g,  $n=37$ ;  $t=0.11$ ,  $P=0.91$ ). There was nevertheless a non-significant tendency for the mass of last-laid eggs in 4-egg clutches ( $1.52 \pm 0.02$ , g) to be less than that of last-laid eggs in 5-egg clutches ( $1.52 \pm 0.02$  g;  $t=1.84$ ,  $df=91$ ,  $P=0.07$ ). To examine further the relationship between the mass of the last-laid egg and the average clutch mass I performed correlations on the data for 1990. I only used data for 1990 since the sample size was larger, and because there were differences between years in mean date of clutch initiation and hatching spreads. There were no significant correlations of the

**FIGURE 1. Mean ( $\bar{x} \pm SE$ ) mass (g) of Yellow Warbler eggs in 4- and 5-egg clutches. The first-laid egg is designated A, the second-laid egg B, etc.**

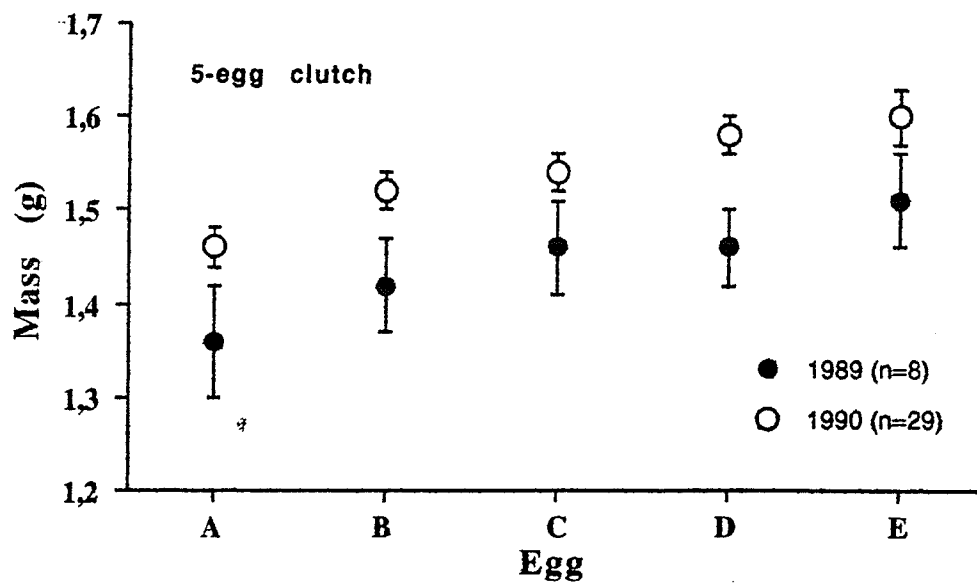
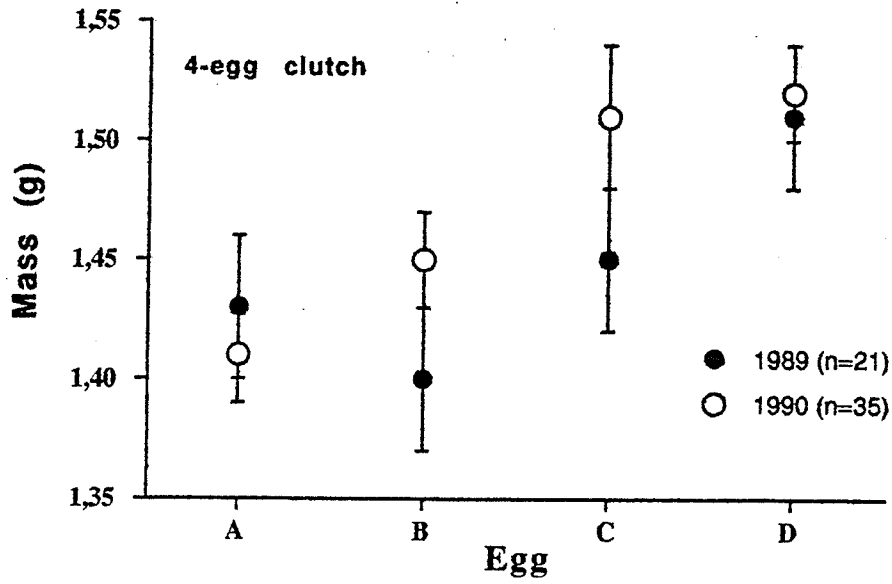


TABLE 25. Correlations of Yellow Warbler egg mass (g) in 4- and 5-egg clutches in relation to laying order. The mass of each egg in the laying sequence was compared to the average mass of the other eggs in the clutch. Data were combined for 1989 and 1990. All correlations are significant at  $P < 0.0001$ .

Clutch size	n	Egg				
		A	B	C	D	E
4	56	0.7590	0.8606	0.9122	0.8509	-
5	37	0.7105	0.8816	0.8373	0.8490	0.8784

difference in mass of the last-laid egg and average clutch mass with date of clutch initiation (c/4,  $r=0.2474$ ,  $P=0.15$ ,  $n=35$ ; c/5,  $r=0.1771$ ,  $P=0.35$ ,  $n=29$ ), length of incubation of the first-laid egg (c/4,  $r=-0.2631$ ,  $P=0.37$ ,  $n=17$ ; c/5,  $r=-0.1758$ ,  $P=0.51$ ,  $n=16$ ) and the hatch spread between the antepenultimate and last-laid eggs (c/4,  $r=0.0452$ ,  $P=0.89$ ,  $n=12$ ; c/5,  $r=0.3410$ ,  $P=0.27$ ,  $n=12$ ) in 4- and 5-egg clutches, respectively.

## DISCUSSION

As with other studies on passerines (e.g. Schrantz 1943, Howe 1976, Slagsvold 1982, but see Soler 1988), I observed a significant positive correlation of egg mass with laying order in both 4- and 5-egg Yellow Warbler clutches. It has been argued that an increase in egg mass with laying order is the result of selection on hatching patterns and nestling survival (Slagsvold et al. 1984). That is, in those species where hatching asynchrony has evolved as an adaptation to minimize total nest-failure due to predation, females are selected to minimize the adverse effects of hatching asynchrony by laying a relatively larger last egg, thereby maximizing the probability of survival of the last-hatched nestling (Clark and Wilson 1981, Slagsvold et al. 1984).

The brood survival hypothesis (Slagsvold et al. 1984) predicts that the mass of the last-laid egg relative to the mass of other eggs in the clutch should be positively correlated with the probability of survival of the last-hatched nestling. During this study I observed that last-hatched nestlings in broods of 4 had a higher probability of survival than last-hatched nestlings in broods of 5. Therefore, the relative mass of last-eggs should be different in the 2 clutch sizes. The results of this study do not support this prediction since the relative mass of last-laid eggs was similar in 4- and 5-egg clutches ( $P=0.91$ ). Also, we would expect the relative mass of the last egg to be correlated with hatching asynchrony, such that the greater the degree of hatching asynchrony, the greater the relative mass of the last-laid eggs so as to offset any disadvantages associated with hatching last. Again this prediction was not supported by the results of this study since the

relative mass of last-laid eggs was not correlated with hatching spreads, despite the fact that last-laid eggs in 5-egg clutches were heavier than their counterparts in 4-egg clutches. Similar evidence contrary to the brood survival hypothesis has been observed in other studies (Slagsvold and Lifjeld 1989b, Arnold 1991).

In passerines, especially in species like Yellow Warblers (Goossen and Sealy 1982) that nest in open cups, predation is an important factor affecting reproductive success (Ricklefs 1969). As with food supply during the nestling period, laying females cannot predict the occurrence of predation. As females are selected to begin incubation prior to clutch completion (Lack 1947, Hahn 1981, see also Chapter 1), then at any given moment during the nesting cycle, the egg or nestling that would require the least investment to fledge is the first-laid/first-hatched. Consequently, if predation should occur, females would incur a smaller cost if the egg that is taken is the egg that would require the most investment to produce a fledgling. Therefore, selection should favor females that "sacrifice" or predispose the last egg to being taken by a predator, should predation occur. I propose that one such mechanism may be the size of the egg. That is, by laying larger last eggs, females are putting them in discordance with their clutch-mates, and thus predisposing or sacrificing the last-laid egg to the unpredictable event of predation. Verbeek (1990) proposed a similar hypothesis for intra-clutch variation in egg color in Northwestern Crows (Corvus caurinus). His hypothesis suggests that female Northwestern Crows lay last eggs of different color so as to put them in discordance with the other eggs in the clutch, and therefore predispose them to being taken by a predator should predation occur.

In conclusion, egg mass in Yellow Warblers increases with laying order in both 4- and 5-egg clutches. Although eggs in 4-egg clutches are generally lighter than those in 5-egg clutches, last-laid eggs in both clutch sizes are of similar mass relative to the average mass of their clutch mates. The mass of last laid eggs also did not vary with the degree of hatching asynchrony.



## GENERAL DISCUSSION

In general the results of this study are consistent with, and provide some support for Lack's (1947) 'brood reduction' hypothesis, and refute the 'nest-failure' (Clark and Wilson 1981), 'sexual-conflict' (Slagsvold and Lifjeld 1989a) hypotheses. The mechanistic aspect of the 'hormonal' hypothesis (Mead and Morton 1985) is also not supported by the results of this study. Some of the results of this study are, nevertheless, apparently consistent with other hypotheses proposed to explain the evolution of hatching asynchrony.

The 'hurry-up' hypothesis (Slagsvold 1986a), originally proposed by Lack (1947), and by Hussell (1972), suggests that hatching asynchrony is adaptive because: 1) it minimizes the amount of time nests are susceptible to predation, and 2) it advances the fledging date of the first-hatched nestlings, thus potentially avoiding sharp declines in food availability late in the breeding season. These strategies are 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. In Yellow Warblers, early incubation results in first-laid eggs hatching only 1-2 days earlier. Thus the time saved by initiating incubation one egg earlier could also be achieved, possibly more efficiently, by laying one less egg (Pettifor et al. 1988).

The data on Yellow Warbler feeding rates presented in Chapter 2, as previously mentioned, are also apparently consistent with the 'peak-load reduction' hypothesis (Hussell 1972). Hussell's (1972) hypothesis suggests that hatching asynchrony is a parental mechanism to minimize the peak food demands of the brood by spreading them out. In

agreement with this, the observed feeding rates of male and female Yellow Warblers tending asynchronous broods were lower than those tending synchronous broods. Presumably, the greater feeding rates in synchronous broods reflect a greater demand for food by the nestlings. For parents to benefit from hatching asynchrony, Hussell (1972) suggested there must be a sharp peak in demand, and this peak must be for a period of time shorter than the hatching spread between the first- and last-hatched nestlings (Magrath 1990). However, the feeding rates in synchronous broods, as in asynchronous broods, increased consistently through the nestling period, and there was no peak (see Chapter 2). As such, the 'peak-load reduction' hypothesis appears inadequate to explain the results of this study. In addition, some studies have calculated that observed hatching spreads reduce the peak in food demand by only 1-8% (Bryant and Gardner 1979, Lessels and Avery 1989), and for open-cup nesters such as Yellow Warblers there may be no savings at all (Magrath 1990).

Another possibility, as suggested by Hahn (1981), is that hatching asynchrony creates a stable competitive size hierarchy that minimizes conflict between siblings and consequently reduces energy expended on strife. In a synchronous brood, the competitive size hierarchy may not be stable and consequently nestlings spend more energy competing for resources. The higher feeding rates by the parents tending synchronously hatched broods in this and other studies (e.g. Fujioka 1985, Mock and Ploger 1987) may reflect a greater energy demand by the nestlings due to an increase in sibling competition (but see Bryant and Tatner 1990). Again, also in agreement with this, is the fact that although feeding rates were higher in synchronous Yellow Warbler

broods, the mass of nestlings at fledging was not greater than that of nestlings in broods that hatched asynchronously (see Chapter 1).

Recently, Slagsvold (1990) proposed that hatching asynchrony is a parental strategy to manipulate offspring sex-ratios, especially in those species that are sexually dimorphic (e.g. raptors). That is, hatching asynchrony and resulting brood reduction allow parents to adjust unpredictable brood sex ratios to unpredictable food requirements. However, previous studies on dimorphic species have reported fledgling sex ratios close to unity (Clutton-Brock 1986, see also Magrath 1990, but see Barber 1991). The importance of this hypothesis has yet to be assessed, and appears inappropriate in explaining the evolution of hatching asynchrony in a monomorphic species such as the Yellow Warbler.

Some researchers have dismissed the 'brood reduction' hypothesis because brood reduction occurs even when food is apparently abundant (Skagen 1988, Clark and Wilson 1981). During this study, insect abundance was significantly lower in 1989 compared to 1990. Nevertheless, brood reduction did occur in 1990, especially in broods of five nestlings. Prey availability is not a constant since changes in wind direction, precipitation, visibility, and temperature may affect prey availability and parental foraging patterns (Stinson 1980, Hébert 1987, Pohajdak 1988). Thus even though food may be abundant, it is not necessarily available, and as a result parents must spend more time foraging.

Brood reduction during periods of relatively high food availability may still retain an adaptive function. Another possible explanation, which is not mutually exclusive from the 'brood reduction' hypothesis,

is that hatching asynchrony predisposes or "sacrifices" the last-hatched nestling to being taken by a predator, should predation occur. That is, as a result of the competitive size hierarchy, last-hatched nestlings must beg more often to receive food, either as a result of their smaller size or because they cannot effectively compete for the optimal feeding position in the nest (see Ryden and Bengtsson 1980). Therefore, a predator contacting the rim of the nest will initially stimulate a begging response from the hungry nestlings. In broods that have hatched asynchronously, this is usually the last-hatched nestling (see Chapter 1), and consequently this nestling may be more obvious to the predator, and thus more likely to be taken by it.

In synchronously hatched broods, the relative advantage of first-hatched nestlings is diminished, and therefore they spend more time begging compared to first-hatched nestlings in asynchronously hatched broods. In agreement with this is the fact that first-hatched nestlings in synchronous broods were observed begging more often than their counterparts in asynchronously hatched broods. Consequently, the probability of any one nestling in a synchronous brood being satiated is lower than in an asynchronous brood. Therefore the probability of begging during a predation event is random with respect to hatch order in a synchronously hatched brood. That brood reduction in synchronous broods was random with respect to hatch order is in agreement with the "sacrifice" hypothesis.

Finally, the mass of last-laid Yellow Warbler eggs was not related to hatch spreads, or clutch size. These results disagree with the brood survival hypothesis proposed by Slagsvold et al. (1984) in explanation of the larger size of last-laid eggs in many passerine species.

In summary, the results of this study provide some support for the 'brood reduction' hypothesis. The 'nest-failure' and 'sexual-conflict' hypotheses receive no support from the results of this study. The mechanistic or causal aspect of the 'hormonal' hypothesis which suggests that hatching asynchrony is the result of hormonal fluctuations during egg laying is also not supported by the results of this study. The results of this study suggest that in addition to hormone fluctuations, incubation attentiveness during egg laying is also affected by other stimuli such as the number of eggs in the nest and ambient temperature. Other hypotheses such as the 'sibling rivalry' and 'hurry-up' hypotheses are also supported by the results of this study. These hypotheses are not exclusive of the 'brood reduction' hypothesis, and therefore the results of this study as well as other studies suggest that hatching asynchrony may be adaptive for several reasons. The difficulty in discerning the relative importance of these complementary hypotheses is in discriminating between cause and effect (Magrath 1990), and this will be the challenge for future research.

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**APPENDIX 1:** Summary of average maximum daily temperatures ( $^{\circ}\text{C}$ )<sup>1</sup> from the day the first egg was laid to the day the last first-laid egg hatched and mean ( $\bar{x} \pm \text{SE}$ ) FLAST<sup>2</sup> hatch spread for Yellow Warbler 4- and 5-egg clutches initiated in 1988-1990.

Clutch					
size	Year	Temperature	n	FLAST	n
4	1988	28.4	35	$35.8 \pm 3.0$	18
	1989	21.6	26	$27.6 \pm 1.4$	14
	1990	23.5	25	$36.7 \pm 2.2$	19
5	1988	28.8	20	$57.9 \pm 1.8$	8
	1989	21.4	20	$33.7 \pm 2.6$	7
	1990	24.4	25	$50.5 \pm 2.0$	21

1. Maximum daily temperatures were averaged for the period including the day the first egg was laid through to the day the last laid first egg hatched.
2. FLAST is the hatch spread (h) between the first and last-hatched nestling in a brood.

**APPENDIX 2:** Summary of the mean ( $\bar{x} \pm SE$ ) mass (g) at 5 days of age of FIRST and LAST Yellow Warbler nestlings in asynchronously hatched broods of 4 and 5. Data were combined for 1989 and 1990. Sample sizes are in parentheses.

Clutch size	Nestling		t	P
	FIRST	LAST		
4	7.75 $\pm$ 0.17 (18)	7.90 $\pm$ 0.30 (9)	0.44	0.67
5	8.19 $\pm$ 0.11 (30)	7.78 $\pm$ 0.34 (10)	1.49	0.14

**APPENDIX 3:** Average length of nestling period (d) in Yellow Warbler broods of 4 and 5 nestlings in 1989 and 1990. Data were combined for the 2 years. Sample sizes are in parentheses.

Clutch size	Brood Type	
	Asynchronous	Synchronous
4	8.73 (11)	8.58 (12)
5	8.91 (11)	8.00 (5)

**APPENDIX 4: Number of female Yellow Warblers sitting in their nests at night during egg laying in 1985 and 1986. Data are from Sealy, Neudorf and Hobson, MS.**

Clutch size	No. of eggs in nest				
	1	2	3	4	5
4 no. of nests	15	16	15	15	-
no. nests occupied	12	16	14	15	-
% nests occupied	80	100	93	100	-
5 no. of nests	14	12	11	14	14
no. nests occupied	9	10	9	11	13
% nests occupied	64	83	82	79	93