and Evolution Biology (G. G. E. Scudder and J. L. Reveal, eds.), Hunt Institute for Botanical Documentation, Pittsburgh, pp. 133–138.

Zahavi, A., 1987, The theory of signal selection and some of its implications, in: *Proceedings of the International Symposium on Biology and Evolution* (V. P. Delfino, ed.), Adriatica Editrica, Bari, Italy, pp. 305–327.

Zahavi, A., 1991, On the definition of sexual selection, Fisher's model, and the evolution of waste and of signals in general, *Anim. Behav.* 42:501–503.

Zuk, M., 1991, Parasites and bright birds: new data and a new prediction, in: *Bird-Parasite Interactions: Ecology, Evolution, and Behavior* (J. E. Loye and M. Zuk, eds.), Oxford University Press, Oxford, pp. 317–327.

Zuk, M., Thornhill, R., Ligon, J. D., Johnson, K., Austad, S., Ligon, S. H., Thornhill, N. W., and Costin, C., 1990, The role of male ornaments and courtship behavior in female mate choice of Red Jungle Fowl, *Amer. Nat.* 136:459–473.

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CHAPTER 6

HATCHING ASYNCHRONY AND THE ONSET OF INCUBATION IN BIRDS, REVISITED

When Is the Critical Period?

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1. INTRODUCTION

In most animals, offspring from a reproductive bout usually hatch, emerge, or are born within a relatively short time of each other compared to the time required for their development. Thus, hatching or birthing in most animals is synchronous. This is especially likely to be true for animals with internal fertilization and development, where the birth of all offspring occurs simultaneously (e.g., some fishes, snakes, and most mammals). Synchronous reproduction also occurs in animals with external fertilization or development when all zygotes are subject to the same environmental conditions (e.g., many insects, anurans, and fishes). Thus, in most animals the behavior of parents has little effect on the time between the emergence of their first and last young.

In contrast, birds can influence birthing (i.e., hatching) intervals

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through parental care. Avian parents can influence the onset of development of eggs, and the resultant synchrony of birth, by determining when to begin incubation. This is possible because avian eggs develop externally and development generally does not begin until a parent warms the eggs by initiating incubation (White and Kinney, 1974; Drent, 1975; O'Connor, 1984). Birds can lay only one egg daily, so if incubation is initiated before the last egg is laid (hereafter "early incubation"), eggs may hatch over a period of a few days to several weeks (Lack, 1968; O'Connor, 1984; Beissinger and Waltman, 1991). In contrast, if incubation is delayed until all eggs of a clutch have been laid, development and hatching will be synchronous. Eggs of a variety of birds hatch asynchronously (e.g., raptors, herons, parrots, and many passerines), and asynchronous hatching occurs in avian families nearly as often as synchronous hatching (Clark and Wilson, 1981; Slagsvold, 1986b; Ricklefs, 1993).

1.1. The Paradox of Hatching Asynchrony

Early incubation in altricial birds results in nestlings of different sizes (Lack, 1947; Bryant, 1978; Stokland and Amundsen, 1988). Often this size hierarchy contributes directly to the death of the later-hatched young (O'Connor, 1978; Mock *et al.*, 1990). This illustrates the *Paradox of Hatching Asynchrony*: avian parents are unique in having some control over birthing intervals, but many opt for a strategy that seems to be a maladaptive waste of parental effort and resources.

Historically, asynchronous hatching was viewed as a mechanism to promote adaptive brood reduction (Lack, 1954; Ricklefs, 1965). Recent debate has questioned whether asynchronous hatching in birds confers survival advantages for parents or selected offspring after hatching, or is a result of physiological constraints, resource limitations or behavioral factors that affect the onset of incubation. In many ways, the *Paradox of Hatching Asynchrony* reflects current concerns about our understanding of the evolution of parental care patterns: it is not always clear to what extent differences in parental care among species reflect variation in the benefits to offspring and costs to parents (Ridley, 1978; Tallamy, 1984; Clutton-Brock, 1991), or to what extent parental care is constrained by environmental limitations, endogenous factors, and phylogenetic history (Emlen and Oring, 1977; Silver *et al.*, 1985; Brooks and McLennan, 1991). Studies of the onset of incubation provide good tests of the role of adaptation, constraint, and phylogeny in the evolution of parental care patterns.

The *Paradox of Hatching Asynchrony* was recognized by early

ornithologists because they were concerned with the adaptive significance of the early onset of incubation. For example, Dunlop (1910) first suggested that early incubation served to protect eggs. The mortality of smallest chicks was viewed as enigmatic, or in the case of siblicidal brood reduction in raptors, as an example of the ferocious nature of the species (Bent, 1961). David Lack (1947) presented a resolution to the paradox by suggesting an adaptive function for the mortality that results from asynchronous hatching. He proposed that when a species' food supply was unpredictable at the time of egg laying, parents should lay an optimistic clutch. If resources are scarce, asynchronous hatching enables parents to reduce the size of their brood to fit available food resources (the *Brood Reduction Hypothesis*).

Lack's hypothesis was quickly accepted, in part because it was an elegant and intuitive idea, and became the dominant paradigm of the field. An extensive theoretical basis was developed for this hypothesis, based on the trade-off between offspring quality and quantity (e.g., O'Connor, 1978; Lloyd, 1987; Godfray and Harper, 1990; Haig, D., 1990), and the trade-off in reproductive success between good and bad years (Pijanowski, 1992). Because Lack's hypothesis has dominated the field, hatching asynchrony has generally become equated with adaptive brood reduction, even when the conditions or assumptions of the hypothesis (such as unpredictability of food supply) are not appropriate. Despite the fact that the onset of incubation generally determines hatching patterns, scientific focus has remained fixed on the adaptive significance of hatching patterns (Bortolotti and Wiebe, 1993).

The *Brood Reduction Hypothesis* was not experimentally tested until the 1970's (Howe, 1976, 1978; Werschkul, 1979). Recently, a number of experiments have tested Lack's hypothesis in a variety of taxa, but have produced results that have rarely supported the predictions (Magrath, 1990; Amundsen and Slagsvold, 1991b). Perhaps because of the lack of verification of the *Brood Reduction Hypothesis*, a plethora of alternative hypotheses have been proposed (Magrath, 1990). However, these have lacked a cohesive conceptual organization, and have received scant experimental or theoretical attention. Few studies have examined environmental conditions or parental behaviors during egg-laying to assess possible benefits of early incubation that might offset the inherent costs of asynchrony. With few exceptions (e.g., Clark and Wilson, 1981; Hébert and Sealy, 1992; Veiga, 1992), most research has remained focused on adaptive hatching patterns.

The lack of unambiguous support for any single hypothesis has resulted in relatively little progress toward understanding the causes of hatching patterns in birds. Work on this subject has probably generated more hypotheses than it has understanding, prompting one anonymous reviewer of our recent National Science Foundation proposal to dismiss the subject of hatching asynchrony as "a stagnant backwater of population biology." We, however, feel this situation is common among complex but interesting biological phenomena. The failure of any one hypothesis to fully explain the wide variety of hatching patterns is characteristic of processes with multiple causal factors (Hilborn and Stearns, 1982). Significant understanding can be achieved by broadening our focus to examine all factors that may affect hatching patterns, especially those that influence the onset of incubation directly, and by going beyond the testing of single factors to consider multiple causes.

1.2. Goals of this Review

In this review, we examine the causes and consequences of the onset of incubation and resulting hatching patterns. Although Magrath (1990) recently reviewed the hatching asynchrony literature, the many disparate hypotheses that characterize this field were not synthesized into a cohesive framework. We develop a conceptual framework for understanding the effects and interactions of different factors affecting the onset of incubation and hatching asynchrony. In addition, since Magrath's review, several new hypotheses of potentially broad relevance have been proposed, and numerous experimental studies have been conducted.

Whereas most previous work has focused almost exclusively on hatching patterns, we will emphasize factors affecting the onset of incubation. First, we discuss the bases and patterns of the onset of incubation, as well as other factors that may influence hatching patterns. We critically review 17 hypotheses for hatching asynchrony that have been proposed in the literature, and concentrate on the assumptions, requirements, and critical predictions of each. Finally, we propose a stochastic modeling approach to evaluate empirical data as a method to assess multiple hypotheses.

2. THE ONSET OF INCUBATION AS THE PRINCIPAL PROXIMATE CAUSE OF HATCHING PATTERNS

The initiation of incubation and pattern of attentiveness of incubating birds controls the temporal pattern of hatching within a clutch. Therefore, to better understand hatching asynchrony, it is necessary to examine the proximate factors that affect incubation behavior. At the physiological level, the different phases of reproduction are regulated by various hormones. Patterns of attentiveness represent a compromise between a range of exogenous factors: the tolerance of embryos to survive when neglected by their parents, the energy needs and balance of parents, and the avoidance of predation (Vleck, 1981; Magrath, 1988; Weathers and Sullivan, 1989).

2.1. The Timing of Periods in the Nesting Cycle

Avian embryos generally do not begin to develop until parents supply heat by incubating (Drent, 1975). If parents defer incubation until all the eggs of a clutch are laid, embryos will develop simultaneously, and hatching and fledging will be relatively synchronous (Fig. 1a). When parents begin incubation on the first egg, development begins immediately, and eggs will hatch asynchronously (Fig. 1c). Beginning incubation on an intermediate egg will produce an intermediate hatching pattern (Fig. 1b). Differential rates of embryonic development and parental incubation efficiency can also affect the timing of hatching (Clark and Wilson, 1981; Bortolotti and Wiebe, 1993). Variable growth rates of nestlings can cause patterns of fledging to differ from hatching patterns, either by decreasing the degree of asynchrony (M. L. Morton, personal communication) or by amplifying the degree of asynchrony (e.g., Bryant, 1978; Emlen *et al.*, 1991; Viñuela and Bustamente, 1993).

The lengths of some periods in the nesting cycle vary with incubation and hatching patterns. The period from the start of egg-laying until the onset of incubation is longest when hatching is synchronous (Fig. 1), and nonexistent with completely asynchronous hatching. During this period eggs are most vulnerable to environmental conditions and predators. The period from the onset of incubation to the first hatch is nearly constant. Therefore, the time that a nest contains only eggs is maximized with synchronous hatching, and minimized with asynchrony. The time from first hatching to first fledging is nearly constant. The fledging period, from the fledging of the first young to the fledging of the last young, is longest with completely asynchronous hatching, and least with synchronous hatching (Fig. 1). Thus, the time that a nest contains nestlings is maximized with asynchrony, and minimized with synchrony. Synchronous hatching allows for rapid transitions from incubation to brooding and from tending nestlings to tending fledglings.

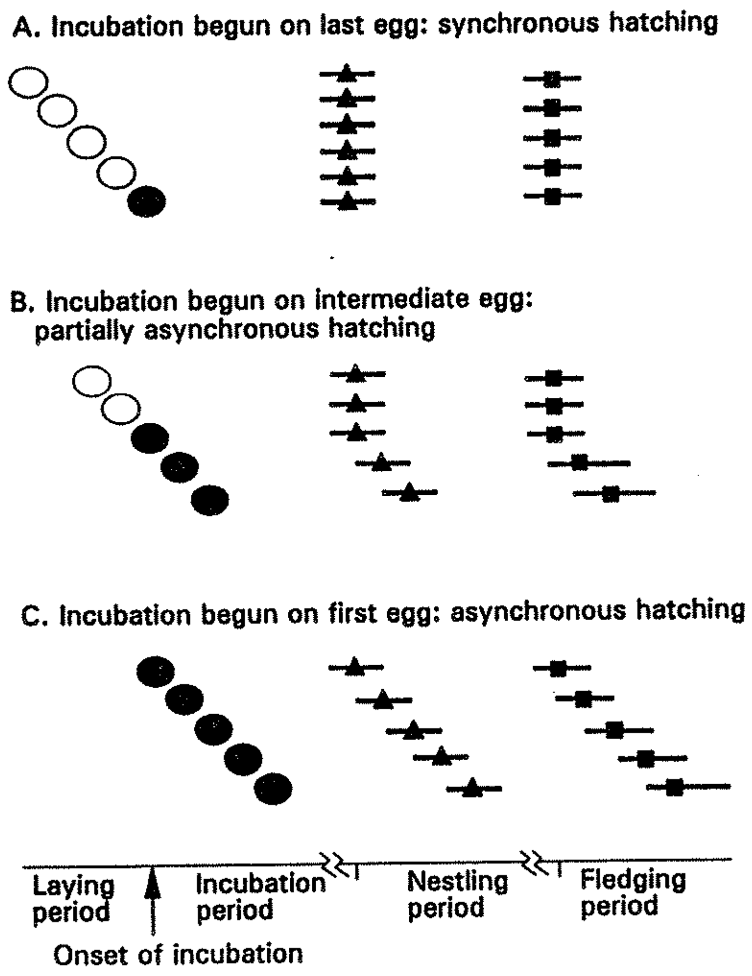

FIGURE 1. A graphic representation of the relationship between the onset of incubation, and hatching and fledging patterns. Ovals represent the laying of eggs, filled ovals indicate the onset of incubation. Triangles represent hatching, and squares represent fledging. Bars represent potential variation in hatching and fledging times due to differences in embryonic development or nestling growth. Initiating incubation on the last egg results in synchronous hatching (A), on an intermediate egg results in partially asynchronous hatching (B), and on the first egg produces completely asynchronous hatching (C).

2.2. Physiological Bases for the Onset of Incubation

The onset of incubation is controlled at the proximate level by hormones. Several hormones have been identified that control different aspects of egg-laying and incubation behaviors, based primarily on studies of domestic fowl and pigeons. Changes in photoperiod, rainfall, or other environmental cues trigger the release of FSH from the adenohypophysis, which stimulates the growth of ovarian follicles (Balthazart, 1983). An increase in plasma-luteinizing hormone causes the release of the ovum from its follicle. Ovulation occurs from 15 minutes to several hours after the laying of the preceding egg (Rol'nik, 1970; Sturkie and Mueller, 1976). The amount of time an egg spends within the oviduct, and therefore the laying interval, varies among taxa from 24 hours in chickens and most passerines to several days in larger nonpasserines (Rol'nik, 1970; Sturkie and Mueller, 1976).

The onset of incubation is associated with a decrease in levels of plasma-luteinizing hormone and steroidal hormones, frequently with a corresponding increase in levels of prolactin (Epple and Stetson, 1980; Hall and Goldsmith, 1983). However, the exact function of prolactin in incubation is unclear and controversial (Goldsmith and Williams, 1980; Goldsmith, 1983; Ball, 1991). Prolactin appears to initiate broodiness, and hence incubation in birds that delay incubation until their last or penultimate egg (Drent, 1975; Mead and Morton, 1985). Levels of prolactin increase through laying and peak during incubation in most species (Goldsmith and Williams, 1980; Balthazart, 1983; Goldsmith, 1983). However, prolactin levels of males also peak during the incubation period in species where males do not incubate (Goldsmith, 1983).

Other evidence suggests that prolactin may maintain incubation behavior, but does not trigger it (Drent, 1975; Goldsmith, 1983). In Ringed Doves (*Streptopelia risoria*), progesterone appears to induce incubation. Experimentally injecting doves with progesterone produced incubatory behavior (van Tienhoven, 1983). Tactile stimuli produced by the contact of the brood patch with eggs may induce both the onset of incubation and an increase in prolactin levels (Parsons, 1976; Goldsmith, 1983; Hall and Goldsmith, 1983). In general, ovulation and egg-laying are governed by various hormones, while prolactin is associated with incubation. However, the exact role of prolactin in incubation is not yet clear, and may vary among taxa.

2.3. External Factors Affecting the Onset of Incubation

Once laying has begun, eggs are exposed to various conditions that may affect their subsequent survival and hatchability. A parent's decision of when to begin to incubate involves a trade-off between ensuring its own survival, maximizing embryo survival, and maximizing expected survivorship of offspring after hatching.

Before embryological development begins, eggs can remain viable for a period of time without incubation, and can tolerate exposure to very low temperatures (Hussell, 1972; Drent, 1973; Webb, 1987). Embryos do not begin to develop until eggs reach a temperature of about 27–28°C, and this threshold is called "physiological zero" (Webb, 1987). Once development begins, eggs must remain within a narrow range of temperatures for development to be normal (Romanoff and Romanoff, 1972; Deeming and Ferguson, 1992). Prolonged exposure to temperatures above physiological zero, but below normal incubation temperatures, causes abnormal growth and mortality in embryos (Romanoff and Romanoff, 1972; White and Kinney, 1974). The embryological tolerance to chilling varies greatly among different taxa. Some species can neglect their eggs for long periods without effect (Drent, 1975; Roby and Ricklefs, 1984; Gaston and Powell, 1989; Ewert, 1992). Temperatures above 41–45°C are fatal to embryos regardless of the stage of development (Drent, 1973; White and Kinney, 1974; Webb, 1987). Therefore, birds in extremely hot climates must show constant attentiveness to their eggs, and exhibit mechanisms to keep eggs cooler than ambient temperatures, such as wetting the egg or using the brood patch to dissipate heat (Yom-Tov *et al.*, 1978; Grant, 1982; Walsberg and Voss-Roberts, 1983; Jehl and Mahoney, 1987). Similarly, high-altitude species probably must incubate when eggs are exposed to strong, direct solar radiation (Morton and Pereyra, 1985).

Although eggs can remain viable for an extended period without incubation if temperatures do not exceed physiological zero, this prolongs exposure to potential predators and brood parasites. Once incubation begins, the sitting adult may also be more vulnerable to predation, especially if its ability to escape is limited, as in cavity nesters (Drent, 1970; Nilsson, 1986; Martin, 1992).

The onset of incubation may also be constrained by the mating system of the species, and by which sex incubates. Nest attentiveness is usually greater and begins earlier when both sexes incubate than when only one sex incubates, or when the nonincubating sex provides the incubator with all of its food requirements (Skutch, 1957; Lyon and Montgomerie, 1985; Lifjeld and Slagsvold, 1986; Nilsson and Smith, 1988; Williams, 1991; Nilsson, 1993a). If females incubate alone and must forage for themselves, they may be constrained by the high nutrient requirements of egg production to delay incubation until after the clutch is nearly complete (Drent, 1975; Magrath, 1988; Slagsvold and Lifjeld, 1989a). When laying females of some species were given supplemental food, they began incubating earlier than control females (Moreno, 1989a; Nilsson, 1993b; but see Wiebe and Bortolotti, 1994a). In species where males incubate, males may delay initiating incubation until a full clutch has been laid to guard their mates to prevent cuckoldry (Power *et al.*, 1981).

2.4. Patterns of the Onset of Incubation

Unfortunately, patterns of incubation have received scant attention, and what data exist are primarily circumstantial or qualitative. Few studies have published data on the actual timing of the onset of incubation, especially with respect to egg-laying (e.g., Haftorn, 1981; Zerba and Morton, 1983; Morton and Pereyra, 1985; Kennamer *et al.*, 1990; Meijer, 1990). Parent birds may be particularly sensitive to disturbance and prone to desert their nests during egg-laying (Lessells and Avery, 1989; Götmark, 1992). This often makes direct observation of the onset of incubation difficult. Sometimes incubation is inferred when a parent is seen leaving the nest area. However, attendance at the nest does not necessarily indicate incubation (Ligon, 1968; Haftorn, 1981).

As a result of these difficulties, incubation patterns are frequently inferred from hatching patterns, and it is assumed that eggs hatch in the order they are laid (e.g., Drent, 1975; Clark and Wilson, 1981; Slagsvold and Lifjeld, 1989a). This assumption has been documented in relatively few species (e.g., Cargill and Cooke, 1981; Beissinger and Waltman, 1991; Bowman, 1992). However, the hatching sequence of eggs may bear little relation to their laying order, because incubating birds may not be able to cover all eggs within a clutch (Bortolotti and Wiebe, 1993), or because last eggs may require less time to hatch than earlier-laid eggs (Viñuela, 1991). Thus, inferences about incubation patterns made from hatching patterns may not be valid. In addition, parents may not have as complete control over the spread of hatching of their young as has been assumed (Bortolotti and Wiebe, 1993). This is a potentially critical point, because hypotheses that posit an adaptive role to hatching patterns are based on parental control of those patterns (Magrath, 1990; Ricklefs, 1993).

Parents may initiate incubation in a variety of ways. Some species begin with full incubation (e.g., Wilson *et al.*, 1986; Ward, 1990; Beissinger and Waltman, 1991). Many bird species do not begin incubating fully, but instead gradually increase the amount of daylight hours spent incubating until complete incubation is achieved (e.g., Drent, 1970; Bengtsson and Rydén, 1981; Briskie and Sealy, 1989; Lessells and

Avery, 1989). In such cases the hatch spread is shorter than the laying spread. In other taxa, incomplete clutches are not incubated during the day but are brooded at night. In these species, full incubation begins after all eggs are laid and the resulting clutch hatches somewhat asynchronously (e.g., Gibb, 1950; Kavanau, 1987; Hébert and Sealy, 1992).

For both types of partial incubation, inferences made about the onset of incubation based on hatching patterns may differ from inferences made from occasional nest observations, because different incubation regimes can produce similar hatching patterns (Fig. 2). A clutch that hatches with an intermediate degree of asynchrony may be produced by beginning full incubation after laying half the clutch, or by beginning gradual nocturnal or diurnal incubation on the first egg.

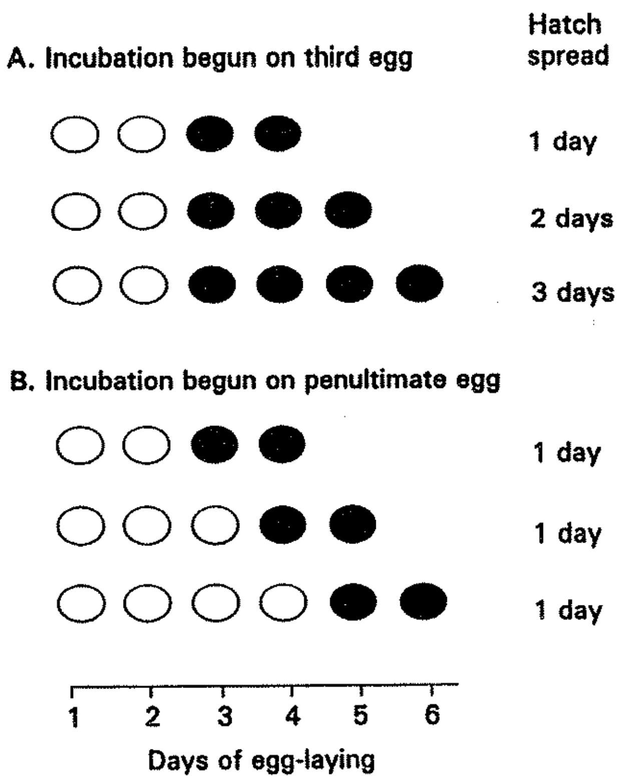

FIGURE 2. A graphic representation of the effects on hatch spread of different patterns of incubation for three clutch sizes. Filled ovals represent eggs incubated immediately after laying, and hollow ovals represent eggs laid before the onset of incubation. (A) When the onset of incubation is constant relative to the beginning of laying, regardless of clutch size, hatch spread varies with clutch size. (B) When the onset of incubation is constant relative to the end of laying, hatch spread is constant.

The hatch spread of some bird species can vary with clutch size (e.g., Smith, 1988; Briskie and Sealy, 1989; Stouffer and Power, 1990; Hébert and Sealy, 1992). In species that begin incubation with a specific egg, the onset of incubation may be considered invariant with respect to laying order (Fig. 2a). Species that begin incubation on the first egg hatch their eggs completely asynchronously, and hatch spread is dependent on clutch size. For example, clutch size in the Green-rumped Parrotlet (*Forpus passerinus*) ranges from 4 to 10 eggs, and initiating incubation on the first egg produces hatch spreads from 6 to 15 days (Beissinger and Waltman, 1991). Species that have only partially asynchronous hatching can also exhibit an invariable onset of incubation. Incubation in the Dark-eyed Junco (*Junco hymenalis*) is usually begun on the third egg, but clutch size ranges from three to five eggs (Smith, 1988).

In other taxa, incubation may begin on a particular egg relative to the end of laying (e.g., the last or penultimate egg). If clutch size in these species varies, then the initiation of incubation will be variable with respect to laying order (Fig. 2b). The resulting hatch spread will be constant, and independent of clutch size (e.g., Zerba and Morton, 1983; Hébert and Sealy, 1992). This pattern is thought to characterize many passerine species, in which incubation is frequently begun on the penultimate egg (Clark and Wilson, 1981).

The lack of variation in a trait may be the result of strong selection, or may indicate ecological or phylogenetic constraints on the trait (Stearns, 1980). The lack of variation in the onset of incubation in some avian taxa may indicate selection for a particular pattern of incubation (Fig. 2a). Conversely, an invariable hatch spread, independent of clutch size, may indicate that the hatching patterns themselves are adaptive.

2.5. Other Proximate Factors Affecting Hatching Patterns

Nestling size hierarchies can be affected by intraclutch variation in egg size as well as by hatching asynchrony. Production of relatively small last eggs may be a mechanism to handicap last-hatched chicks to facilitate their elimination through brood reduction, either alone or in conjunction with asynchronous hatching. Penguins of the genus *Eudyptes* normally raise only a single chick from the larger second egg in two-egg clutches. These species exhibit the greatest degree of egg-size difference of any bird and the size disparity is sufficient to counter any effects of slight asynchrony in hatching (Lamey, 1990). Because chicks hatched from small eggs frequently have a lower probability of survival than their sibs (e.g., Parsons, 1975; Amundsen and Stokland, 1990), and because within-clutch variation in egg size can be greater in years of poor food availability (Pietiäinen *et al.*, 1986), it has been suggested that the combination of hatching asynchrony and small last eggs constitutes a "brood reduction strategy" (Slagsvold *et al.*, 1984).

Except in *Eudyptes* penguins, it is difficult to differentiate the effect of egg size from the effects of hatching asynchrony. Attempts to partition the variance in nestling size between these two factors have found a negligible role for egg size variation (Pierotti and Bellrose, 1986; Meathrel and Ryder, 1987; Stokland and Amundsen, 1988; Magrath, 1992; Sydeman and Emslie, 1992; Jover *et al.*, 1993). Reduced size of last eggs may not be an adaptation, but may simply indicate a decline in essential nutrients required for egg production in females (Murphy, 1986; Meathrel and Ryder, 1987; Bolton, 1991). Alternatively, egg size reduction may be mediated through the interactions of hormones governing egg production and incubation behavior (Parsons, 1976).

In many passerines egg size actually increases with laying order (e.g., Howe, 1976; Zach, 1982; Haftorn, 1986). Because hatching from a larger egg may improve the competitive ability of last-hatched young, this pattern has been suggested as a "brood survival strategy" (Howe, 1976, 1978; Slagsvold *et al.*, 1984), since it may promote the survival of chicks under conditions of hatching asynchrony. As yet, there is little evidence to support or refute the idea of an adaptive role for increasing egg size within a clutch. Therefore, designating an adaptive function to egg size variation must be considered premature (Pierotti and Bellrose, 1986).

In some precocial species, embryos can exert some control over the timing of hatching. Laboratory studies of quail and geese have shown that acoustic signals between embryos within a brood increases the synchronization of hatching of the brood (Vince, 1964, 1968; Drent, 1973; Davies and Cooke, 1983). Synchronization is achieved primarily through accelerating the development and hatching of later-laid eggs (Vince, 1964; Davies and Cooke, 1983). In Northern Bobwhites (*Colinus virginianus*), embryonic communication also causes more advanced embryos to retard their hatching as well (Vince, 1968). Thus, hatching patterns in precocial species may not reflect incubation behaviors. Many precocial species begin incubation early (e.g., Cannon *et al.*, 1986; Arnold *et al.*, 1987; Kennamer *et al.*, 1990) perhaps in response to some of the same selection pressures as altricial species. However, precocial species have generally been ignored in studies of asynchrony (see Arnold *et al.*, 1987 for a notable exception).

Laboratory evidence suggests that embryonic communication is possible in asynchronously-hatching altricial birds. Glaucous-winged Gull (*Larus glaucescens*) eggs incubated in contact with each other had shorter hatching spreads than eggs that were separated. However, this effect was not evident under field conditions (Schwagmeyer *et al.*, 1991). Embryos of the American White Pelican (*Pelecanus erythrorhynchos*) vocalize to parents to elicit greater attentiveness during pipping (Evans, 1988, 1990a). The general applicability and importance of embryonic control of hatching times in altricial and semiprecocial species is not yet known.

3. HATCHING PATTERNS IN BIRDS

All birds hatch their eggs asynchronously to some extent, since complete synchrony is virtually impossible due in part to within-clutch variation in hatching time (Clark and Wilson, 1981). Hatch spreads vary greatly, ranging from a few hours in many precocial species to two weeks or more in some owls and parrots with large clutches (Wilson *et al.*, 1986; Beissinger and Waltman, 1991). Within a species, hatch spreads may vary from early to late in the nesting season, or among broods which hatch at about the same time (Slagsvold and Lifjeld, 1989a; Stouffer and Power, 1990; Harper *et al.*, 1992).

3.1. Quantification of Asynchrony

Asynchrony has generally been classified by hatch spreads. Hatch spreads of less than 24 hours have been considered synchronous, and all spreads greater than 24 hours have been considered asynchronous (cf. Ricklefs, 1993). Unfortunately, this simple dichotomy neglects much of the variation that exists in hatching patterns. Because of their focus on the onset of incubation, Clark and Wilson (1981) chose to classify asynchrony according to which egg a bird begins to incubate fully. For example, incubation on the last egg is designated as n, on the penultimate as $n - 1$, and on the first egg as 1. This system has the advantages of being able to describe the whole range of possible incubation patterns, and being applicable to precocial species in which hatch spreads are reduced. However, it ignores partial incubation, which can influence hatching patterns (see section 2.4.). In addition, classifications can be ambiguous: the first egg of a two-egg clutch may be designated as 1 or $n - 1$ (Ricklefs, 1993). Finally, the correlation between incubation and hatching patterns can be poor (Bortolotti and Wiebe, 1993).

3.2. Phylogenetic Patterns of Incubation and Hatching Asynchrony

Much of the variation in patterns of incubation and hatching occurs at the taxonomic levels of family and order, as with many life history traits (Stearns, 1980; Harvey and Pagel, 1991). In this section we review the patterns of variation in the onset of incubation and hatching asynchrony in relation to phylogeny. Although it is controversial, we follow the taxonomy of Sibley and colleagues (Sibley and Ahlquist, 1990; Sibley and Monroe, 1990). Those taxa with single-egg clutches or for which we could find no information are not included. Details of incubation and hatching patterns are based on data from regional handbooks, monographs, and original papers. In many cases generalizations were made from relatively few examples.

3.2.1. The Eoaves and Lower Neoaves

The Eoaves comprise the orders Struthioniformes and Tinamiformes (Fig. 3). The most basal parvclass of the neoaves, the Galloanserae, comprises the Craciformes, Galliformes, and Anseriformes. All of these groups have precocial young, and generally hatch their young synchronously (e.g., Palmer, 1962; Marion and Fleetwood, 1978; Boag and Schroeder, 1992; Zwickel, 1992). There are a few exceptional species that exhibit hatch spreads of slightly over 24 hours (e.g., Cargill and Cooke, 1981). Several species begin incubation early, but embryonic communication facilitates the synchronous hatching of eggs (Vince, 1964; Arnold *et al.*, 1987). The taxonomic affinities of the button-quail (Turniciformes) remain uncertain (Sibley and Monroe 1990), but incubation, hatching, and developmental patterns are similar to the orders discussed above (Cramp, 1980).

3.2.2. The Higher Neoaves

The orders Piciformes and Galbuliformes have altricial young, yet hatch their young relatively synchronously (Skutch, 1969, 1983; but see Stanback, 1991). The Bucerotiformes and Upupiformes exhibit complete asynchrony, while the Trogoniformes are somewhat asynchronous (Kemp, 1978; Skutch, 1983; Cramp, 1985). The Coraciiformes are mixed with regard to hatching patterns. Within the Coraciiformes, the Cerylidae, Coraciidae, Dacelonidae, Meropidae, Momotidae, and Todidae tend to have moderate to extreme asynchrony of hatching (Parry, 1973; Kepler, 1977; Orejuela, 1977; Cramp, 1985; Scott and Martin, 1986; Bryant and Tatner, 1990; Wrege and Emlen, 1991), while the Alcedinidae and Cerylidae appear to have relatively synchronous hatching patterns (Douthwaite, 1978; Boag, 1982; Skutch, 1983). However, the breeding biology of these families is poorly known, partly because they are predominantly tropical in distribution, and are all burrow or cavity-nesters.

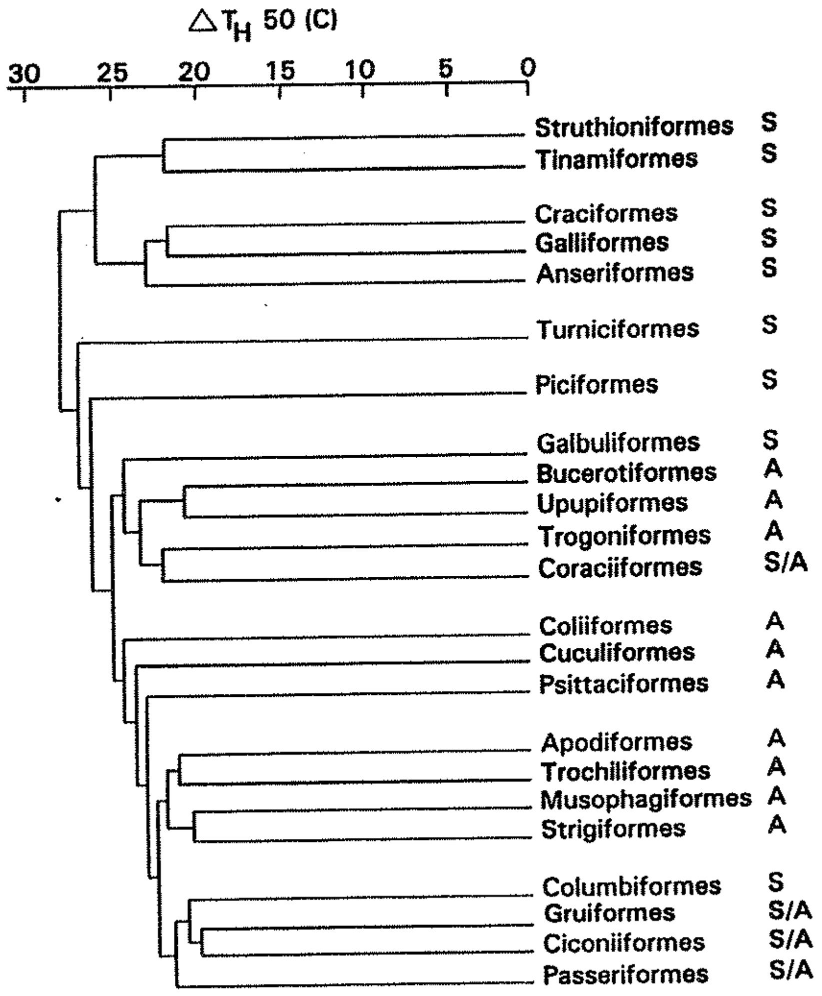

FIGURE 3. A phylogeny of orders in the Class Aves based on Sibley and Ahlquist (1990), indicating the predominant hatching pattern for each order. S = synchronous hatching (defined here as < 24 hrs), A = asynchronous hatching (≥ 24 hrs), S/A = both hatching patterns regularly occur within the order. Orders for which no information on hatching patterns could be found have been omitted.

Extreme asynchrony predominates in the Coliiformes, Cuculiformes, Psittaciformes, Apodiformes, and Trochiliformes (Rowan, 1967, 1983; Lack, 1973; Balph, 1975; Smith and Saunders, 1986; Strahl, 1988; Forshaw, 1989; Bryant and Tatner, 1990; Taplin and Beurteaux, 1992; Fig. 3). Birds in all of these groups usually begin incubation on the first or second egg. The hatch spreads of some psittacine species with large clutch sizes are among the most extreme recorded (Navarro and Bucher, 1990; Beissinger and Waltman, 1991). Extreme asynchrony results in offspring mortality in some psittacines (Beissinger and Stoleson, 1991), but not in others (Snyder et *al.*, 1987). All of the Trochilidae lay two eggs and begin incubation with the first (Skutch, 1964, 1969; Calder and Calder, 1992).

The Strigimorphae have somewhat more advanced development of hatchlings than the more basal Neoaves (semialtricial versus altricial; Ricklefs, 1983). The Strigidae and Tytonidae exhibit extreme asynchrony, and include another contender for the longest hatch spread recorded for any species: the Barn Owl (*Tyto alba*; Voous, 1975; Wilson et *al.*, 1986). All of the semiprecocial Caprimulgidae initiate incubation on the first of their two eggs (Skutch, 1972; Jackson, 1985; Csada and Brigham, 1992). The aberrant nocturnal, frugivorous Oilbird (*Steatornis caripensis*) also begins incubation on its first egg, and hatches its two to four eggs over a span of up to 12 days (Snow, 1961). Incubation and hatching patterns of the Musophagiformes are poorly known in the wild. Data from captive birds suggest incubation begins on the second egg, and hatch spread varies with clutch size (Rowan, 1983; Candy, 1984; Hewston, 1984).

The superorder Passerimorphae shows a wide variety of incubation and hatching patterns, both among and within orders (Fig. 3). The Columbiformes are limited to clutches or one of two eggs. Most species with two eggs appear to begin incubation gradually on the first egg, but generally hatch both eggs within a 24-hour period (Rowan, 1983; Skutch, 1983; Bowman, 1992; Mueller, 1992). The Gruiformes display a variety of incubation and hatching patterns (Fig. 4). The Eurypygidae, Gruidae, and at least some Otididae begin incubation with the first egg (Cramp, 1980; Thomas and Strahl, 1990; Tacha et *al.*, 1992). In contrast, the Heliornithidae may not begin to incubate until both eggs are laid (Alvarez del Toro, 1971). Hatching patterns within the Rallidae vary, with most species hatching large clutches over a 24- to 36-hour period, but some species are completely asynchronous (Cramp, 1980; Kaufmann, 1989; Horsfall, 1991; Meanley, 1992). Cranes (Gruidae) are highly asynchronous, show much sibling aggression, and siblicide is common (Tacha et *al.*, 1992).

The Ciconiiformes as delineated by Sibley and Ahlquist (1990) comprise numerous taxa that were previously grouped in several other orders, including the Gaviiformes, Podicipediformes, Pelecaniformes, Sphenisciformes, Charadriiformes, and Falconiformes, as well as the Ciconiiformes (Pettingill, 1985; Sibley and Monroe, 1990; Fig. 4). These differ markedly in morphology, ecology, and developmental mode (al-

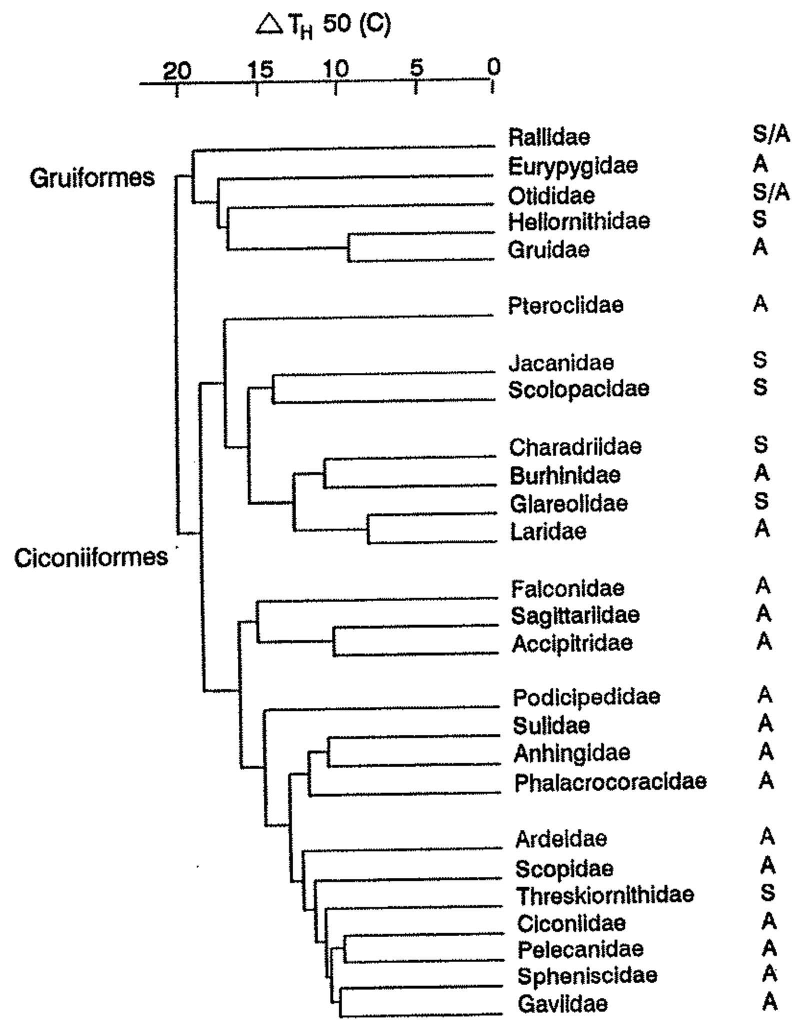

FIGURE 4. A detailed phylogeny based on Sibley and Ahlquist (19909) of families in the orders Gruiformes and Ciconiiformes, indicating the predominant hatching pattern for each family. Families with single-egg clutches or for which no information on hatching patterns could be found have been omitted. S, A, and S/A as in Fig. 3.

tricial to precocial-2), perhaps suggesting a dubious monophyly. Incubation and hatching patterns vary widely within this order as well, from complete synchrony to complete asynchrony (Fig. 4).

Within the Ciconiiformes (*sensu* Sibley and Monroe), most taxa with altricial or semialtricial development exhibit a high degree of hatching asynchrony (Fig. 4). Penguins (Spheniscidae) show a variety of patterns within the constraints of one or two egg clutches (Lamey, 1990). Most species hatch their eggs extremely asynchronously, and egg-size variation and brood reduction is common. However, Yellow-eyed Penguins (*Megadyptes antipodes*) hatch similar-sized eggs synchronously with little offspring mortality (van Heezik and Davis, 1990). The Ardeidae, Ciconiidae, and Scopidae tend to be completely asynchronous, and sibling aggression is frequent (Kahl, 1966; Anthony and Sherry, 1980; Thomas, 1984; Mock and Parker, 1986; Wilson *et al.*, 1987; Butler, 1992). In contrast, the Threskiornithidae tend to delay incubation until completion of the clutch and thus hatch synchronously (Palmer, 1962; Cramp, 1980). The Bald Ibis (*Geronticus eremita*) is an exception, being completely asynchronous, and the only ground-nesting species in this family for which information could be found (Cramp, 1980). The raptors (Accipitridae, Sagittariidae, and Falconidae) also begin incubation early and hatch very asynchronously (Brown and Amadon, 1968). Offspring mortality and sibling aggression is common, and siblicide is prevalent in the largest species (Brown and Amadon, 1968; Meyburg, 1978; Stinson, 1979; Edwards and Collopy, 1983). The altricial families characterized by having totipalmate feet (the Pelecanidae, Anhingidae, Phalacrocoracidae, and Sulidae) all begin incubation with their first or second egg. Hatching is extremely asynchronous, sibling aggression is common, and siblicide occurs in many species (Dorward, 1962; Olver, 1984; Shaw, 1985; Cash and Evans, 1986; Drummond, 1987; Stokland and Amundsen, 1988; Anderson, 1989).

Ciconiiform families with semiprecocial and precocial chicks are variable in hatching patterns (Fig. 4). The semiprecocial Laridae all begin at least partial incubation on the first egg, and the resulting asynchrony usually results in high mortality for last-hatched young (e.g., Nisbet and Cohen, 1975; Hahn, 1981; Hébert and Barclay, 1986; Bollinger *et al.*, 1990). Siblicidal aggression is common only in the skuas, subfamily Stercorariinae (Spellerberg, 1971; Williams, 1980), but has been reported in other species as well (e.g., Braun and Hunt, 1983). The Gaviidae and Podicipedidae, which have downy, mobile young that are not self-feeding at hatching (precocial-4; Ricklefs, 1983), begin incubation with the first egg, and so are completely asynchronous (Palmer, 1962; Ferguson and Sealy, 1983; Forbes and Ankney, 1987). Sibling aggression is common in some species, but siblicide is not known to occur.

The shorebirds (Charadriidae, Scolopacidae, Jacanidae, Glareolidae) generally do not begin incubation until the full clutch has been laid, and therefore hatch synchronously (Parmalee, 1970; Gibson, 1971; Jehl, 1973; Osborne and Bourne, 1977; Gratto-Trevor, 1992; Haig, S. M., 1992). There are exceptions, such as the Black-bellied Plover (*Pluvialis squaterola*) which partially incubates early eggs and has hatch spreads of over 24 hours (Hussell and Page, 1976). The predominantly tropical Thick-knees (Burhinidae) are also an exception to the general shorebird pattern. They begin incubation with the first egg, and chicks hatch over several days (Freese, 1975; Cramp, 1983). In these species the young, though mobile, are brooded in the nest until all eggs have hatched. Sandgrouse (Pteroclididae) are also completely asynchronous, but early-hatched young leave the nest with one parent while the other continues to incubate (Cramp, 1983).

There is much variation in incubation and hatching patterns among the Passeriformes (Fig. 3). The patterns in this group have been examined in some depth by Clark and Wilson (1981), Slagsvold (1986b), and Ricklefs (1993). Therefore we present only some broad generalizations. Passerines tend to begin full incubation on the penultimate or last egg, but frequently increase their attentiveness gradually prior to full incubation. Thus, most species are partially asynchronous with hatch spreads of 24 to 48 hours (Clark and Wilson, 1981). Few passerine species are known to hatch their eggs completely asynchronously. Among these are a tropical blackbird (*Agelaius icterocephalus*; Wiley and Wiley, 1980), a weaver (*Ploceus taeniopterus*; Jackson, 1993), tropical tityras (*Tityra*; Skutch, 1969), and the Australian butcherbirds (*Cracticus*; Courtney and Marchant, 1971).

3.2.3. Overview of Phylogenetic Patterns

Synchronous hatching appears to be the primitive condition in birds, and is widespread in the lower, most precocial orders (Fig. 3). A major transition in character state from synchronous to asynchronous hatching occurred in the Parvclass Coraciae (Galbuliformes through Coraciiformes in Fig. 3). In the Coraciiformes, Columbiformes, and some Gruiformes, Ciconiiformes, and Passeriformes, synchrony is secondarily derived and not necessarily associated with precocial development. Asynchronous hatching predominates in most higher orders, and is most often associated with altricial or semialtricial development.

However, very different hatching patterns can be found in closely related families, such as the Glareolidae and Laridae, or even within a family, as in the Rallidae (Fig. 4). In these taxa, asynchrony is more likely to be a true adaptation rather than a result of phylogenetic constraints.

3.3. Other Correlates of Asynchrony

Birds vary in the degree of nestling development at hatching, based on presence or absence of down, degree of mobility, and dependence on parents (Nice, 1962; Ricklefs, 1983). Hatching asynchrony is generally considered a phenomenon confined to altricial species, while precocial species hatch synchronously. Although most common in altricial and semialtricial species, hatching asynchrony occurs across a broad range of developmental modes. Semiprecocial chicks are mobile to a limited extent, but remain in the nest and are dependent on parental feeding. Complete asynchrony is the norm in several semiprecocial families including the Laridae (excluding the Alcidinae), Caprimulgidae, and Eurypygidae. Chicks that are categorized as precocial-four are downy and mobile at birth, but rely on parental feeding for a brief period after hatching (Ricklefs, 1983). In this category the Gaviidae, Podicipedidae, Burhinidae, Gruidae, and (some) Otididae are completely asynchronous, while the Rallidae range from completely asynchronous to synchronous hatching. Hatching asynchrony occurs in some families where chicks are self-feeding at hatching (Precocial-3,2,1) (Ricklefs, 1983), such as the Pteroclidae, which begin incubation on the first egg. Clearly asynchrony in these taxa cannot be explained by hypotheses based on limits to parental ability to feed young (e.g., *Brood Reduction, Peak Load Reduction, Hurry-up, Dietary Diversity,* and *Sibling Rivalry*).

Several researchers have identified correlates of hatching asynchrony other than developmental mode. Clark and Wilson (1981) found that hole-nesting species tended to hatch their eggs more asynchronously than species with open nests. They suggested that higher predation rates of open nests favor minimizing the length of the nestling period through the synchronization of hatching (see section 4.5.2.). They used the same argument of differential rates of nest predation to explain the predominance of asynchrony in tree-nesting species versus those that nest in bushes or on the ground, and in temperate species versus tropical species. Their analyses were reexamined by Slagsvold (1986b). He found asynchrony to be correlated with hole-nesting only in tropical areas when the effects of geographic distribution and clutch size were controlled. He found no other significant relation between asynchrony and geographic range.

Hatching patterns can vary independently of clutch size in species with partial asynchrony. Frequently the degree of hatching asynchrony increases during the course of the breeding season. For example, early clutches of the Common Moorhen (*Gallinula chloropus*) hatch completely synchronously, while late nests and second broods may require three or more days to hatch (Cramp, 1977). The usual explanation is that greater asynchrony reflects seasonal declines in food resources, and hence a greater utility of adaptive brood reduction (e.g., Bryant, 1978; Newton and Marquiss, 1984; Hussell and Quinney, 1987; Skagen, 1987; Perrins and McCleery, 1989). However, other hypotheses offer alternative interpretations of this phenomenon, and will be discussed in the following sections.

3.4. Summary of Hatching Patterns

Incubation patterns are poorly known, and difficult to quantify. Therefore, most studies have focused on hatching patterns. Hatching patterns range from complete synchrony to complete asynchrony, and vary greatly among and sometimes within taxa. Synchronous hatching is generally associated with precocial development, and is the primitive condition in birds. Asynchrony is associated with altricial development. Many species exhibit an increase in the degree of hatching asynchrony during the course of the nesting season. The onset of incubation may be affected by a number of factors, including the physiology of eggs and embryos, and the ecology of species. Other factors may influence hatching patterns directly. This multitude of factors has resulted in many hypotheses being proposed for the evolution of hatching asynchrony in birds.

4. HYPOTHESES FOR THE EVOLUTION OF HATCHING ASYNCHRONY

The plethora of hypotheses for the evolution of asynchronous hatching have been reviewed to varying extent by Slagsvold (1986b), Skagen (1988), Lessells and Avery (1989), and Magrath (1990). However, to date, these hypotheses have lacked a conceptual framework to relate hatching patterns with various selection pressures that potentially affect incubation behavior.

4.1. A Conceptual Framework

We categorize hypotheses for the evolution of hatching asynchrony into four groups (Table I), based on the factors that could potentially produce hatching asynchrony. Two hypotheses suggest that asynchrony is an epiphenomenon of constraints on incubation. According to these hypotheses, neither the onset of incubation nor the resulting hatching pattern necessarily have an adaptive function. Four hypotheses view asynchronous hatching as a consequence of factors selecting for the early onset of incubation, regardless of its effect on nestling survival. Most of these hypotheses ascribe some sort of protective function to early incubation. The subsequent asynchrony in hatching is a nonadaptive consequence which sometimes entails a cost in the form of mortality of later-hatched young. The majority of hypotheses (eight) consider the nestling size-hierarchy produced by asynchronous hatching to be adaptive for nestling survival or to decrease the costs of reproduction for parents. Finally there are three hypotheses that posit that selection acts on the timing of different phases of the nesting cycle through adult and offspring mortality and costs of reproduction.

The various hypotheses are based on the effects of different factors that are predominantly intrinsic to the organism (e.g., behavior or physiology) or predominantly extrinsic (e.g., environmental variation, predators, or nest site availability). For each hypothesis, there is a critical period in the nesting cycle which constrains reproductive success, and this period differs among the categories of hypotheses. The critical period for nonadaptive hypotheses and hypotheses based on adaptive hatching patterns is egg-laying, while the nestling period is critical for hypotheses invoking adaptive hatching patterns. Hypotheses based on both have two critical periods: egg-laying, and either brooding or fledging. It is the relative timing of these critical periods which is essential.

Critical periods in the nesting cycle should be considered when evaluating experimental tests of hatching asynchrony in birds. For example, manipulating the hatching pattern does not alter the pattern of incubation, and therefore can not address hypotheses for which egg-laying is the critical period. Thus, ambiguous or negative results of such manipulations suggest that hypotheses based on incubation patterns may be of greater importance than those based on hatching patterns for the species in question.

In the following sections we review the hypotheses proposed for the evolution of hatching asynchrony, and relate them to critical periods of the nesting cycle. For each hypothesis, we describe its theoretical

TABLE I
Hypotheses for the Evolution of Hatching Asynchrony.[a]

Evolutionary significance of asynchrony	Hatching asynchrony results from	Intrinsic or extrinsic	Constraint or selective force	Hypothesis	Critical period in the nesting cycle	Number of experimental tests
Nonadaptive	Constraint	Intrinsic	Physiology	Hormone	laying	1
				Energy constraints	laying	2
Adaptive	Adaptive incubation patterns	Extrinsic	Environment	Egg viability	laying	2
				Limited breeding opportunity	laying	0
			Predation	Egg protection	laying	0
			Social system	Brood parasitism	laying	0
	Adaptive hatching patterns	Intrinsic	Parental efficiency	Peak load reduction	nestling	3
				Dietary diversity	nestling	0
				Larder	nestling	0
				Sibling rivalry	nestling	4
			Sexual dimorphism	Sex ratio manipulation	nestling	0
		Extrinsic	Environment	Brood reduction	nestling	32
				Hurry-up	nestling	0
			Stochastic events	Insurance	nestling	2
	Incubation and hatching	Intrinsic	Mating system	Sexual conflict	laying/brooding	3
		Extrinsic	Predation	Nest failure	laying/fledging	4[b]
				Adult predation	laying/brooding	0

[a] For each hypothesis, the adaptive significance of asynchrony, the nature of the selective force and whether that force is predominately intrinsic or extrinsic to the organism, and the critical period in the nesting cycle are indicated. The number of experimental tests of each hypothesis is noted; references for these are annotated with "(T1)" in the References section.

[b] Not experimentally tested but vital rates measured and compared to results from a model.

basis and applicability, identify its important assumptions and predictions, review any correlational or experimental support or refutation, and suggest how it should be tested experimentally.

4.2. Factors Affecting the Onset of Incubation: Nonadaptive Constraints

Perhaps the simplest hypotheses consider hatching asynchrony to be the mechanistic result of physiological or environmental constraints on the initiation of incubation, so that neither asynchrony nor the resulting nestling size hierarchy are themselves necessarily adaptive.

4.2.1. Energy Constraints Hypothesis

Hatching patterns may reflect environmental constraints on egg-laying (the *Energy Constraints Hypothesis*). When females experience poor feeding conditions during laying, they may need to forage for a greater part of the day, allowing less time for incubation, and causing eggs to hatch more synchronously than normal (Greig-Smith, 1985; Slagsvold, 1986a; Enemar and Arheimer, 1989; Moreno, 1989a). If food availability increases through the course of a breeding season, females can spend less time foraging and more time incubating during laying, thereby hatching their eggs more asynchronously (Gibb, 1950; Nisbet and Cohen, 1975; Mead and Morton, 1985; Slagsvold, 1986b; Slagsvold and Lifjeld, 1989a; Slagsvold and Amundsen, 1992). For similar reasons, Pied Flycatcher (*Ficedula hypoleuca*) clutches hatched more asynchronously in high-quality habitats than in low-quality habitats (Slagsvold, 1986a). This hypothesis is not applicable to species in which males provide all the food requirements of incubating females. It implies that early incubation and asynchronous hatching are the preferred or default patterns, since synchrony is induced by environmental stress.

The *Energy Constraints Hypothesis* predicts that females provided with supplemental food prior to and during laying should hatch their eggs more asynchronously than controls (Wiebe and Bortolotti, 1994a). Marsh Tits (*Parus palustris*) provided with supplemental food did hatch their eggs more asynchronously than controls (Nilsson, 1993b). However, female American Kestrels (*Falco sparverius*) receiving food hatched their eggs more synchronously than control females, contrary to the predictions (Wiebe and Bortolotti, 1994a).

4.2.2. Hormone Hypothesis

Hatching asynchrony may result if the same hormone or hormones that cause the termination of ovulation also stimulate the initiation of incubation (the *Hormone Hypothesis;* Mead and Morton, 1985). In most birds, eggs are laid one day after ovulation (Woodard and Mather, 1964; Gilbert, 1971). If one hormonal mechanism controls both functions simultaneously, females should begin incubation on the penultimate egg. Initiating incubation on the penultimate egg may be the most common pattern in passerine birds (Clark and Wilson, 1981). However, many species begin incubation gradually, or on the first or second egg, and much intraspecific variation in the onset of incubation occurs (Lessells and Avery, 1989; Magrath, 1990; Hébert and Sealy, 1992; Ricklefs, 1993).

The hormonal mechanisms regulating avian reproduction are imperfectly known (Balthazart, 1983; Ball, 1991). In many species prolactin is associated with incubation but plasma-luteinizing hormone appears to control egg-laying (e.g., Myers *et al.*, 1989). It is unclear whether prolactin induces incubation or is itself a result of incubation behavior (Goldsmith and Williams, 1980; Balthazart, 1983). The roles of various hormones in controlling parental behaviors must be clarified for this hypothesis to be tenable.

When applicable, this hypothesis makes several testable predictions. Full incubation attentiveness should begin with the penultimate egg, regardless of clutch size. Hatch spreads produced by these patterns of incubation should not vary with clutch size, nor with the experimental addition of extra eggs during egg laying (Mead and Morton, 1985). This hypothesis has been tested only in the Yellow Warbler (*Dendroica petechia*). Hatch spreads in the warbler varied with clutch size, and experimentally adding eggs during early egg-laying advanced the onset of incubation and increased hatch spreads, contrary to predictions (Hébert and Sealy, 1992).

4.3. Factors Producing Adaptive Incubation Patterns

The focus on adaptive hatching patterns has drawn attention away from the behavior that actually causes hatching asynchrony—the onset of incubation—and the mechanisms that control it. The following four hypotheses are based on the potential benefits of early incubation, and consider the resulting hatching asynchrony and nestling size hierarchy as incidental. Possible functions of early incubation include maintaining the viability of eggs, and protecting the clutch from predators and conspecifics that might depredate or parasitize it, or usurp the nest site.

4.3.1. Egg Viability Hypothesis

Initiating incubation before the clutch is completed could serve to maintain the viability of first-laid eggs (the *Egg Viability Hypothesis;* Arnold *et al.*, 1987). Avian embryos do not begin to develop appreciably until egg temperatures reach about 34°C, and no development occurs below physiological zero (Drent, 1973; O'Connor, 1984; Webb, 1987). Once embryonic development begins, embryos are much more sensitive to exposure to temperatures above or below incubation temperature. Prolonged exposure to temperatures above physiological zero, yet below normal incubation levels (36–38°C), results in abnormal development and embryo mortality (Romanoff and Romanoff, 1972; White and Kinney, 1974; Webb, 1987). Survivorship of embryos depends upon the temperature, and the duration and frequency of exposure (Rol'nik, 1970; Drent, 1975; O'Connor, 1984), and varies among taxa (Roby and Ricklefs, 1984; Webb, 1987; Gaston and Powell, 1989; Astheimer, 1991). In all avian species studied, high temperatures have a much greater effect on embryo survival than lower temperatures (Yom-Tov *et al.*, 1978; Bennett and Dawson, 1979; Carey, 1980; Grant, 1982; Walsberg and Voss-Roberts, 1983; Webb, 1987).

Clutch size in waterfowl may be constrained by the decreasing viability of unincubated eggs (Arnold et *al.*, 1987). Waterfowl chicks are precocial and incubation is usually initiated before the termination of egg-laying. Yet eggs normally hatch synchronously. Arnold *et al.* (1987) demonstrated that egg hatchability declined during the laying period if eggs were unincubated. They suggested that early incubation may prevent a reduction in egg viability, but would constrain the number of eggs that could hatch synchronously (see also Cannon *et al.*, 1986; Kennamer *et al.*, 1990; Arnold, 1993).

Veiga (1992) extended this idea to asynchronously hatching altricial species. He demonstrated that House Sparrow (*Passer domesticus*) eggs that were left unincubated for three or more days had lower hatching success than those unincubated for shorter periods, and the degree of hatching asynchrony increased when ambient temperatures regularly exceeded physiological zero later in the season. Veiga concluded that hatching asynchrony may be a nonadaptive result of a behavioral mechanism to maintain the viability of first-hatched eggs.

The Egg *Viability Hypothesis* applies only to species whose laying period is long enough to affect egg viability, and whose laying takes place when ambient temperatures rise above physiological zero or below freezing for extended periods. Under these conditions, the hypothesis predicts that the hatchability of unincubated eggs should decrease with increasing length of exposure to ambient temperatures, and that development of embryos should occur in the absence of incubation. This can be tested experimentally by removing eggs immediately after laying, exposing them to ambient temperatures for specific time periods, and then allowing them to be incubated to complete development. Hatchability of experimental eggs should be compared to that of appropriate controls. Results from our preliminary experimental tests of this hypothesis with the Green-rumped Parrotlet indicated a significant drop in hatchability may occur after just one day of exposure, and a rapid decline with longer exposure times.

Three general predictions can be derived from this hypothesis. With an increasing average ambient temperature, such as with a latitudinal or seasonal gradient, species that hatch their eggs synchronously should show either a decrease in average clutch size, or a decrease in the average hatchability of eggs. Alternatively, there may be an increase in the prevalence and degree of hatching asynchrony as latitude decreases or the breeding season progresses. A latitudinal decline in clutch size has been well documented and is the subject of considerable debate (Klomp, 1970; Murray, 1985; Skutch, 1985; Godfray *et al.*, 1991). Koenig (1982) found a highly significant decline in hatchability with decreasing latitude from a sample consisting of 42 different avian families. Numerous studies have reported a seasonal decline in average clutch size (e.g., Gibb, 1950; Klomp, 1970; Hussell, 1972; Bryant, 1978; Slagsvold, 1982; Ferguson and Sealy, 1983). Although usually attributed to seasonal declines in food resources, declines in clutch size can be independent of food supply in some species (De Steven, 1980; Stutchbury and Robertson, 1988; Arnold, 1993).

Data on the relative occurrence of asynchronous hatching in the tropics versus the temperate zone are ambiguous or lacking. Clark and Wilson (1981) reported a tendency for greater synchrony in the tropics, based on a survey of 87 species. However, their sample of tropical species included a disproportionate number of passerines, and their analysis did not account for smaller clutches typical of tropical passerines (Slagsvold, 1986b).

Two caveats must be made concerning the Egg *Viability Hypothesis*. First, asynchronous hatching may lead to reduced hatchability of final eggs due to parental neglect (Slagsvold, 1985; Evans, 1990b, Nilsson, 1993b). Parents may spend less time incubating terminal eggs to provide care to first-hatched young. Reduced attentiveness has been shown to reduce hatchability (Evans, 1990c; Beissinger and Waltman, 1991). Experimentally increasing the hatch spreads of several temperate passerines produced a significant decline in the hatchability of final eggs compared to control nests (Slagsvold, 1985).

Second, a decline in the viability of unincubated eggs may be a consequence of early incubation rather than a cause. If a species has evolved complete asynchrony for some reason other than the maintenance of egg viability, eggs may no longer be subject to selection to remain viable when not incubated. Experiments that demonstrate a decline in hatchability when eggs are not incubated do not necessarily prove that egg viability was the ultimate selective force causing asynchrony. Comparative and experimental analyses will be needed to discriminate between cause and effect.

4.3.2. Egg Protection Hypothesis

Early incubation may be an adaptation to protect eggs from dangers other than unfavorable environmental conditions (Swanberg, 1950; Oring, 1982). Dunlop (1910) first proposed that parent birds could reduce the risk of predation on eggs by beginning incubation on the first egg (the *Egg Protection Hypothesis*). Incubation may be a more efficient defense against predation of eggs than other active behaviors (Thompson and Raveling, 1987). Parental brooding for the purpose of protecting eggs has been noted in some fish (Salfert and Moodie, 1984) and invertebrates (Milne and Calow, 1990). For egg protection to be a significant function of early incubation, a species must be subject to a substantial rate of egg loss prior to the start of incubation due to predation or to destruction by conspecifics. The latter case represents a form of reproductive interference. The net benefits obtained by protecting early eggs must be greater than the potential costs of nestling mortality resulting from asynchrony.

Colonial species do not defend all-purpose territories. They might be expected to begin incubation early to reduce losses of first-laid eggs due to intraspecific interference, and to hatch their eggs more asynchronously than territorial species. Egg protection has been proposed as the function of early incubation in colonial Common Terns (*Sterna hirundo*; Bollinger *et al.*, 1990) and Herring Gulls (*Larus argentatus*; Parsons, 1976). Embryonic synchronization of hatching (Vince, 1964, 1968) may enable precocial species to protect eggs through early incubation with little hatching asynchrony (Cannon *et al.*, 1986). Cavity-nesting species are frequently thought to experience lower rates of predation than open-nesting species, and so might be expected to hatch their eggs more synchronously. However, conclusions about rates of predation on cavity nests are based on studies of birds using nest boxes, and may not reflect rates of predation on natural cavity nests (Møller, 1989; Robertson and Rendell, 1990; Kuitunen and Aleknonis, 1992). Open nests and natural cavity nests may be subject to equal rates of predation (Nilsson, 1986). Therefore, cavity nesters may not necessarily hatch their eggs more synchronously than open nesting species.

Testing the *Egg Protection Hypothesis* experimentally is problematic because it is difficult to manipulate parents to lay eggs but not incubate them. One approach is to correlate the constancy of incubation during the laying period with the rate of egg loss. For example, incubation constancy was lower for Common Tern nests that were depredated than for those that were not in nests with two or more eggs (Bollinger *et al.*, 1990). However, such correlations may not take into account the ability of parents to defend nests by means other than incubation.

4.3.3. Limited Breeding Opportunities Hypothesis

Species that use nest sites that are limited in number may be forced to protect the site. For species that do not defend an all-purpose territory, this might be best accomplished by occupying the nest itself. In this way one bird would be free to forage, for itself and its mate, while the other bird defended the nest site by initiating incubation (the *Limited Breeding Opportunities Hypothesis*; Beissinger and Waltman, 1991). In the Green-rumped Parrotlet there are high rates of interactions between pairs at nest sites and a significant proportion of the population consists of nonbreeders (Beissinger and Bucher, 1992; Waltman and Beissinger, 1992). This pattern appears to be common in psittacines, which typically hatch their young very asynchronously (Saunders, 1986; Snyder *et al.*, 1987; Beissinger and Bucher, 1992). Female Elf Owls (*Micrathene whitneyi*) occupy their nest cavities for several weeks prior to laying, presumably to avoid losing them to other species, and also hatch their eggs very asynchronously (Ligon, 1968).

Because nest sites tend to be limited for secondary cavity-nesters in general (Alerstam and Högstedt, 1981; Nilsson, 1986; Brawn and Balda, 1988; Land *et al.*, 1989; Sedgwick and Knopf, 1990; Caine and Marion, 1991; Martin, 1993), this hypothesis predicts that asynchronous hatching should be more common in secondary cavity nesters than in primary cavity nesters or in open nesting species. This trend has been demonstrated, although with small sample sizes (Slagsvold, 1986b). The prevalence or degree of asynchrony should be correlated with the proportion of nonbreeders in the population, or with the abundance of nest-site competitors.

Because birds can sit on their nests without incubating (Swanberg, 1950; Vinuela, 1991), this hypothesis may be insufficient by itself to explain hatching asynchrony. However, nest site defense may function in conjunction with other factors, such as protecting eggs, minimizing the time females are in the nest, or by accelerating the hatching and fledging of first-laid eggs (Beissinger and Waltman, 1991).

4.3.4. Brood Parasitism Hypothesis

Early incubation may help to protect a clutch from brood parasitism (the *Brood Parasitism Hypothesis*) as well as predation. By initiating incubation early, females may reduce the opportunity for intraspecific (Kendra *et al.*, 1988; Lombardo *et al.*, 1989; Romagnano *et al.*, 1990) or interspecific parasitism (Wiley and Wiley, 1980). Interestingly, Jackson (1993) suggested that extreme asynchrony can promote intraspecific brood parasitism. Northern Masked Weavers (*Ploceus taeniopterus*) hatch their broods completely asynchronously, and third or fourth-hatched chicks rarely survive. Females may derive greater reproductive success from third or fourth eggs by laying them in another bird's nest than by laying in their own nest, if they hatch as the first or second chick (Jackson, 1993).

The early initiation of incubation could be advantageous if a clutch is parasitized, because the resulting brood will be larger than the original clutch and asynchronous hatching may facilitate the adjustment of the brood size through brood reduction (see section 4.4.1.; Wiley and Wiley, 1980; Magrath, 1990). In joint-nesting species (Brown, 1987), there may be a similar competition between laying females at a nest. Females may initiate incubation as soon as possible after the laying of their first egg to increase the probability that their own young will hatch first and thereby be competitively superior (Ricklefs, 1993). This may explain why Acorn Woodpeckers (*Melanerpes formicivorus*) and Pied Kingfishers (*Ceryle rudis*) exhibit significant asynchrony when relatively synchronous hatching is the norm in the Picidae and Alcedinidae (Stanback, 1991; Ricklefs, 1993).

This hypothesis can be tested experimentally by simulating nests in the process of laying without incubating parents, either by using artificial nests or by temporary removal of parents. The hypothesis predicts that nests without incubating birds should receive parasitic eggs with a greater frequency than normally incubated nests. Comparisons of different populations or species should show that the degree of asynchrony is correlated with the prevalence of brood parasitism.

4.4. Factors Selecting for Adaptive Hatching Patterns

The following hypotheses posit that asynchronous hatching patterns are adaptive in their own right, and that early incubation functions to produce those patterns. The first three hypotheses use nestling size-hierarchies to prioritize young within a brood, so that low priority young are eliminated through sibling competition or parental neglect. In the remaining hypotheses, asynchronous hatching serves to increase parental efficiency.

4.4.1. Brood Reduction Hypothesis

David Lack (1947, 1954) proposed that for bird species in which the food supply varies unpredictably, the optimal clutch size should reflect the average maximum number of young that can be raised under favorable conditions. In the event of food scarcity, the youngest nestlings are either actively neglected or are outcompeted by their larger sibs, and starve to death (Lack, 1954; Ricklefs, 1965). Brood size is adjusted to the parental ability to supply food by the elimination of the nestling(s) in which parents have invested the least or that will require the most future investment (Hébert and Barclay, 1986). If hatching was synchronous, all nestlings would be equally competitive, and all would suffer undernourishment or starvation (Lack, 1954). This hypothesis is best known as the *Brood Reduction Hypothesis*, but recently was called the *Resource Tracking Hypothesis* to differentiate it from the following two hypotheses for which asynchrony also functions to allow an adaptive reduction in brood size (Forbes, 1991; Ploger, 1992). Although the latter term describes the concept of the hypothesis more accurately, for the sake of clarity we will use the more familiar term.

Hatching asynchrony is not necessarily a prerequisite for a size hierarchy to develop among nestlings (Nelson, 1964; Bengtsson and Rydén, 1983; Groves, 1984; Amundsen and Slagsvold, 1991a). Also, brood reduction can occur in synchronously-hatched nests (Clark and Wilson, 1981; Bancroft, 1985). Therefore, the hypothesis has been modified to state that hatching asynchrony facilitates efficient brood reduction (Lack, 1966; Husby, 1986; Mock and Parker, 1986; Magrath, 1989). Plants also may adjust parental investment to track available resources by terminating flowering, ovary development, or fruit set. This process is most efficient when flowering is staggered, i.e., asynchronous (Lloyd, 1980; Haig, D., 1992).

Brood reduction in asynchronously-hatched nests can, but does not always, improve the condition or growth rate of surviving offspring (Gibb, 1950; Ricklefs, 1965; Stouffer and Power, 1991). For example, surviving nestlings in broods of common Starlings (*Sturnus vulgaris*) did not show an increase in growth rate or condition following the mortality of their youngest sibs (Stouffer and Power, 1991).

Numerous models have been constructed to provide a theoretical framework for the concept of adaptive brood reduction. O'Connor (1978) used Hamilton's (1964) concept of inclusive fitness to predict that there should be greater conflict between parents and young over when brood reduction should occur when parents have a relatively high investment in each chick (small broods). This should occur because surviving offspring benefit more from brood reduction than do parents. This parent-offspring conflict (Trivers, 1974) can result in the larger offspring initiating brood reduction through sibling aggression (Mock, 1984a; Mock and Parker, 1986; Drummond and García-Chavelas, 1989). Siblicidal behavior that seems to be contingent on inadequate food supplies is termed facultative siblicide (Mock, 1984a). For example, siblicidal brood reduction is much more frequent in Black-legged Kittiwakes (*Rissa tridactyla*) when food is scarce and nestling growth rates are low (Braun and Hunt, 1983). Drummond and García-Chavelas (1989) demonstrated that sibling aggression in the Blue-footed Booby (*Sula nebouxii*) was inversely proportional to food intake and weight increase. However, sibling aggression may not necessarily be correlated with food supply (Mock, 1984b, 1985b, 1987; Sullivan, 1988).

There is a growing body of evidence that some nestling mortality resulting from asynchrony is unrelated to food supply. In most species the feeding capacity of the parents is not exceeded in very young broods, the time when most chick mortality occurs (Bengtsson and Rydén, 1981; Graves *et al.*, 1984; Amundsen and Stokland, 1988). Steidl and Griffin (1991) used very high growth rates as evidence of abundant food in a colony of Ospreys (*Pandion haliaetus*), yet noted widespread brood reduction. The probability of chick mortality was found to be related with the degree of hatching asynchrony but not food abundance for numerous species with variable degrees of hatching asynchrony (e.g., Bryant, 1978; Strehl, 1978; Stouffer and Power, 1990; Seddon and van Heezik, 1991a,b; Stanback, 1991). In unmanipulated Common Starling nests, clutches that hatched synchronously had lower levels of nestling mortality than similarly-sized asynchronously-

hatched nests (Stouffer and Power, 1990), indicating a clear cost of asynchrony. Penultimately hatched and last-hatched chicks in large broods of Green-rumped Parrotlets had very low fledging success (Beissinger and Waltman, 1991). Manual feeding with a commercial parrot nestling formula increased the probability of survival of last chicks but did not affect the survival of penultimate chicks (Stoleson and Beissinger, in prep.).

Other models have shown that parents derive the most benefit from brood reduction when it occurs while their investment in the youngest chick is small, during the early part of the nestling period (Lloyd, 1987; Forbes and Ydenberg, 1992). Pijanowski (1992) created a model that included a cost to asynchronous hatching in good food years. Asynchrony to facilitate brood reduction is still favored over synchronous hatching when good food years are infrequent, when the cost of asynchrony in good years is small, when the survival of chicks in synchronous broods in bad food years is uniformly low, or when bad food years are not severe (Pijanowski, 1992).

Several predictions can be derived from the *Brood Reduction Hypothesis*. The quantity of food available at the time of laying and the onset of incubation should be unrelated to the quantity of food available after hatching. Demonstrating variability in the food supply is insufficient to support this prediction. Also, the frequency and extent of partial brood losses should be directly related to food scarcity. This is the only hypothesis for which there is a well-established experimental methodology. Synchronously-hatching broods are created by swapping eggs or newly hatched chicks between nests. The hypothesis predicts that when food is scarce, asynchronous broods should produce more fledglings, fledglings of higher quality, or both, than synchronously-hatched broods. Asynchronous broods need not show greater reproductive success than synchronous broods when food is abundant (Pijanowski, 1992). However, if comparisons are based on broods manipulated to create a degree of synchrony not normally encountered in the species under study, parent birds may invest an "imprudent" degree of effort into the brood, ultimately with a negative effect on lifetime reproductive success (D. W. Mock, personal communication). Therefore parental effort should be monitored. Contrary to much published work, this hypothesis does *not* predict that last-hatched young in asynchronous broods are the most likely to die. Such mortality is the phenomenon the hypothesis was formulated to explain, and therefore is a premise of the hypothesis. Proving a premise false does not disprove a hypothesis, but rather indicates that the hypothesis is not relevant to the situation (Copi, 1972).

4.4.2. Insurance Hypothesis

In some bird species, the last egg appears to serve strictly as a replacement for earlier eggs or chicks that fail (the *Insurance Egg Hypothesis*; Stinson, 1979; Cash and Evans, 1986). For example, Hooded Grebe (*Podiceps gallardoi*) parents abandon the second of two eggs if the first hatches, but continue incubating the second egg if the first one fails (Neuchterlein and Johnson, 1981). Herring Gulls (*Larus argentatus*) may also abandon their third egg after successfully hatching their first two eggs (Graves *et al.*, 1984).

The *Insurance Hypothesis* pertains primarily to the evolution of clutch size in birds. Specifically, it is an explanation for why birds lay more eggs than they can normally fledge. Applied to asynchronous hatching, this hypothesis suggests that hatching asynchrony functions to facilitate the elimination of last-hatched chicks if and when they become redundant (Forbes, 1990). The *Insurance Egg Hypothesis* can be considered a food-independent analog of the *Brood Reduction Hypothesis*—asynchronous hatching is viewed as an adaptation to variability in egg hatchability or the mortality of first-hatched nestlings due to causes other than starvation (e.g., accident, predation, or congenital defect; Stinson, 1979; Anderson, 1990; Forbes, 1990). The benefits derived from insurance eggs are through reduced variance in reproductive success (Forbes, 1991). The *Insurance Hypothesis* suggests that parents initiate the onset of incubation to maximize benefits for the "base" clutch. Asynchronous hatching of insurance eggs would be a consequence of such behavior, and would not necessarily have an adaptive significance.

In species with regular brood reduction, an extra egg can have insurance value as well as extra reproductive value, depending on the fate of older chicks. Mock and Parker (1986) defined two different types of reproductive value for last-hatched nestlings in heron broods: extra reproductive value, when a chick survives in addition to older chicks, and insurance reproductive value, when a chick serves as a replacement for an older chick that died. For example, in Little Blue Herons (*Egretta caerulea*), last-hatched young normally die unless an older sibling dies first, in which case youngest chicks have a high probability of fledging (Werschkul, 1979). The dominant component of the total reproductive value of last-laid and penultimately laid Green-rumped Parrotlet eggs in small and medium sized clutches was insurance reproductive value (Beissinger and Waltman, 1991).

This hypothesis is most relevant for species with obligate brood reduction, where last-laid eggs are thought to serve strictly as insurance. In such species under normal conditions last-hatched chicks never survive due to sibling aggression. Such mortality appears to be independent of food supply. Anderson (1990) noted that the Masked Booby (*Sula dactylatra*) lays two eggs, but because of siblicide almost never fledges more than one young. Its eggs have a low probability of hatching, perhaps a consequence of its ground-nesting habits, where its eggs are vulnerable to ground predators and high surface heat. In contrast, the sympatric Red-footed Booby (*Sula sula*) builds tree nests and exhibits high hatchability, but lays a single egg.

The *Insurance Hypothesis* predicts that in the absence of synchrony, the elimination of excess chicks should occur less often, or at a greater age, than with asynchrony. In Masked Boobies, the probability and timing of siblicidal brood reduction was highly correlated with the degree of asynchrony (Anderson, 1989). However, some experiments with obligately siblicidal species found that one chick was eliminated even in experimentally synchronized broods (Dorward, 1962; Meyburg, 1978; Gargett, 1982), suggesting asynchrony may not be necessary for brood reduction to occur.

Testing the *Insurance Hypothesis* as a cause of hatching asynchrony is a different, and more difficult issue, than demonstrating that parents derive benefits from laying insurance eggs. Normally asynchronous clutches should produce more fledglings, on average, than either synchronized clutches of equal size, or asynchronous clutches that have had their last egg removed. The hypothesis requires that the survival of the smallest chicks be correlated with the mortality of earlier eggs or chicks, and that the mortality of the smallest chicks is independent of food supply.

4.4.3. Sex Ratio Manipulation Hypothesis

Selection may favor equal parental investment in offspring of each sex (Fisher, 1930). In sexually dimorphic species, the larger sex should have greater food demands than the smaller sex, and therefore be more expensive in terms of parental investment per chick (Slagsvold *et al.*, 1986; Teather and Weatherhead, 1988; Breitwisch, 1989, but see Stamps *et al.*, 1987). Parents should invest more in the smaller sex or manipulate sex ratios to maintain equal levels of investment (Trivers and Willard, 1973; Bednarz and Hayden, 1991). Alternatively, parents may facultatively manipulate the sex ratio of their offspring to capitalize on current ecological or social conditions (Myers, 1978; Gowaty, 1991). Because unequal sex ratios at hatching are uncommon in birds (Clutton-Brock, 1986; but see Gowaty and Lennartz, 1985; Ligon and Ligon, 1990; Gowaty, 1991), hatching asynchrony may provide a means for parents to manipulate the sex ratio of broods by selectively starving later-hatched young of the more expensive sex (the *Sex Ratio Manipulation Hypothesis*; Slagsvold, 1990).

Sex-biased mortality has been shown in some sexually dimorphic species when food is scarce (Howe, 1976; Cronmiller and Thompson, 1981; Roskaft and Slagsvold, 1985; Bortolotti, 1986; Teather and Weatherhead, 1989; Bednarz and Hayden, 1991; Slagsvold *et al.*, 1992). But such results appear to be a nonadaptive consequence of sex-specific susceptibility to starvation, rather than manipulation on the part of parents (Weatherhead and Teather, 1991). Slagsvold *et al.* (1986) noted that parent Rooks (*Corvus frugilegus*) did not preferentially feed offspring of one sex over the other, yet the larger male offspring fledged at a much lower rate. Harris' Hawks (*Parabuteo unicinctus*) fledge more young when the oldest nestling is the smaller sex (male) than when the first nestling is female, and the sex of first-hatched young is usually skewed towards males (Bednarz and Hayden, 1991). Furthermore, in the Blue-footed Booby, extreme size dimorphism does not seem to affect nestling dominance hierarchies based on hatching order, and there is no sex-biased mortality (Drummond *et al.*, 1991).

The strongest evidence of parental manipulation of nestling sex-ratios comes from two studies of captive birds. Color-banded Zebra Finches (*Poephila guttata*) with favored band colors preferentially fed offspring of their own sex, resulting in sex-biased mortality (Burley, 1986). Both male and female Budgerigars brought food to female-biased broods at a higher rate than other broods. However, females were not fed preferentially within broods, and males and and females fledged at similar ages and weights (Stamps *et al.*, 1987). Manipulation of offspring sex-ratio has been documented in rodents. When food was severely restricted, lactating wood rats (*Neotoma floridana*) actively discriminated against male young, resulting in female-biased litters (McClure, 1981).

This hypothesis is relevant only to species with a relatively large degree of sexual size dimorphism. It predicts that offspring of the larger sex suffer higher mortality during the period of prenatal care (Slagsvold, 1990). Therefore, the sex ratio of fledglings should be biased towards the smaller sex (Slagsvold *et al.*, 1992). In experimentally synchronized broods, parents should over-invest in the larger sex, and should result in a fledgling sex ratio that is skewed towards the larger sex, compared to asynchronous broods.

4.4.4. Peak Load Reduction Hypothesis

Asynchronous hatching may serve to maximize parental efficiency without promoting offspring mortality. Ingram (1959) suggested that the extreme nestling size hierarchy produced by asynchronous hatching in large broods of Short-eared Owls (*Asio flammeus*) might serve to spread out the total food demand of the brood. Hussell (1972) argued that such a mechanism may exist in species with sharp peaks in food demands of individual nestlings (the *Peak Load Reduction Hypothesis*). For example, House Martins appear to have a sharp peak in nestling energy demands, and the total brood demand is reduced by 7% to 8% through asynchronous hatching (Bryant and Gardiner, 1979).

Models by Mock and Schwagmeyer (1990) suggest that any energy savings due to asynchrony would be minimal, except in species with very large brood sizes (up to 10 chicks) and extreme hatching asynchrony (10–14 days). In addition, the food demands of nestlings must show a peak for any benefits to accrue. The hypothesis predicts that the peak energy expenditure of parents tending asynchronous broods would be less than the peak energy expenditure of parents tending synchronous broods of equal size. Although feeding rates may be used as an estimate of energy expenditure (Bryant and Tatner, 1991), it is preferable to measure energy expenditure directly using the doubly-labeled water method (Lifson and McClintock, 1966; Speakman and Racey, 1988; but see cautions in McNab, 1989).

4.4.5. Dietary Diversity Hypothesis

In some species asynchronous hatching may not stagger the peak energy demands, but instead staggers the demand for a special food resource needed only during a portion of the nestling period (the *Dietary Diversity Hypothesis*; Magrath, 1990). For example, hatchling Yellow Warblers were fed minute geometrid larvae almost exclusively, while older chicks received a wider variety of food. Asynchronous hatching may reduce the number of nestlings requiring the specific food items at any one time (Hébert, 1993a).

This hypothesis requires that nestlings are dependent on a specific food source at some age, and that the food itself is limited in quantity, or that parents are limited in their ability to procure the food. It predicts that parents at synchronous broods should be unable to raise their entire brood, and that nestling mortality should be due to starvation at a particular period in the nestling period. The *Dietary Diversity Hypothesis* can be tested by supplementing the supply of the special food resource at a subset of synchronized broods, and comparing fledging success to control asynchronous nests.

4.4.6. Hurry-Up Hypothesis

By beginning incubation during laying, first-hatched nestlings will hatch and fledge earlier than they would otherwise. This should increase the probability of nesting success for species which experience a dwindling food supply as the breeding season progresses (the *Hurry-up Hypothesis*), and would ensure that at least some young fledge (Hussell, 1972; Slagsvold, 1986a). The *Hurry-up Hypothesis* has been suggested to explain why many species hatch their eggs more asynchronously as the breeding season progresses (Hussell, 1972; Skagen, 1987).

This hypothesis requires a rapid decline in food availability with time. Few studies have documented such a decline, and most of these used parental provisioning rates as an index of food availability (e.g., Nisbet and Cohen, 1975; Skagen, 1987). Other measures, such as a decline in clutch size or fledging success, are also used, but may confound the effects of parental quality, territory quality, or thermoregulatory abilities of nestlings with food availability (van Balen and Cavé, 1970; Bryant, 1978; Newton and Marquiss, 1984; Skagen, 1987; Stutchbury and Robertson, 1988). Ideally, the degree of hatching asynchrony should be correlated with a direct measure of food availability. Bryant (1978) documented a seasonal decline in the food supply of House Martins (*Delichon urbica*), but found no correlation with hatch spread.

This hypothesis is probably irrelevant for species that lay multiple clutches during a breeding season without any variation in the degree of asynchrony. For example, Green-rumped Parrotlets are completely asynchronous and can raise up to three broods per season (Beissinger and Waltman, 1991; Waltman and Beissinger, 1992).

4.4.7. Sibling Rivalry Hypothesis

Asynchronous hatching may serve to impose a stable dominance hierarchy on a brood. This would avoid wasteful scramble competition (Hahn, 1981) and make more efficient use of parental resources regardless of the food supply (the *Sibling Rivalry Hypothesis*). Hahn found that natural, asynchronous broods of the Laughing Gull (*Larus atricilla*) had a higher fledging success than artificially synchronized broods. She suggested a reduction in sibling competition may have contributed to this result, although no measures of sibling rivalry were reported.

This hypothesis assumes that a stable dominance hierarchy among nestlings is facilitated by hatching asynchrony. However, stable dominance orders can be established in synchronously-hatched broods (Bancroft, 1984; Groves, 1984; Magrath, 1990), whereas the dominance hierarchies imposed by asynchronous hatching are not necessarily stable (Greig-Smith, 1985).

The hypothesis predicts that asynchrony reduces the level of sibling competition. The only direct support for this hypothesis comes from studies of Cattle Egrets (*Bubulcus ibis*), where experimentally synchronized broods fought more often than asynchronous broods (Mock and Ploger, 1987). Also, parent American Kestrels provisioned synchronized broods at higher rates than asynchronous broods, suggesting that asynchrony may reduce energy expenditures of nestlings (Wiebe and Bortolotti, 1994b). However, direct measures of energy expenditure of nestling bee-eaters (*Merops viridis*) determined that daily energy costs were lower in broods with same-sized chicks than in broods with a pronounced size hierarchy (Bryant and Tatner, 1990). This suggests that a greater degree of synchrony may be more energetically efficient.

Most sibling rivalry is nonaggressive, and is manifested through begging or maneuvering for preferred positions within the nest (Rydén and Bengtsson, 1980; Lamey and Mock, 1991; Redondo and Castro, 1992; McRae *et al.*, 1993). Often, the average begging level of a brood appears to determine the rates of parental feeding (Bengtsson and Rydén, 1983; Hussell, 1991; Smith and Montgomerie, 1991; Redondo and Castro, 1992). Parents generally tend to feed the largest or closest nestling (Rydén and Bengtsson, 1980; Bengtsson and Rydén, 1981, 1983; Nuechterlein, 1981; Smith and Montgomerie, 1991; but see Stamps *et al.*, 1985). Therefore, the smallest nestlings in asynchronous broods normally are often not fed, and expend more time and energy than their nestmates in begging and maneuvering, i.e., sibling rivalry (Bengtsson and Rydén, 1983; Redondo and Castro, 1992).

For the *Sibling Rivalry Hypothesis* to be viable, the costs inherent to maintain high levels of begging in smaller nestlings must be offset by benefits to older nestlings, probably through reduced begging costs. The hypothesis predicts that the total energy expenditure of synchronously-hatched broods will be greater than that of asynchronously-hatched broods because of the extra energy expended on scramble competition. Begging rates can be used as an index of energy expenditure in species without overt aggression, or energy expenditure can be measured directly using the doubly-labeled water method (Lifson and McClintock, 1966; Speakman and Racey, 1988).

Ricklefs (1993) proposed that complete asynchrony may eliminate the evolutionary consequences of sibling competition. If hatching completely asynchronously does in fact predetermine the dominance hierarchy among nestlings, then there should be no selection for accelerated embryo growth and earlier hatching. Prolonged incubation periods may result. There may be fitness advantages to prolonged incubation periods that are as yet unidentified. Ricklefs proposed a possible link between slow embryonic growth, longevity, and delayed senescence, mediated through extended maturation of the immune system (Ricklefs, 1992, 1993). Thus, complete asynchrony may be favored when fitness advantages can be gained through prolonged embryonic development and consequent effects on other life-history characters.

4.4.8. Larder Hypothesis

Later-laid eggs may represent a food larder for the oldest chicks (the *Larder Hypothesis;* also called the *Ice-box Hypothesis,* Alexander, 1974). By investing energy in extra eggs during the laying stage, parents may reduce their energetic demands later in the nestling stage because older chicks could eat their younger sibs (Murton and Westwood, 1977). However, laying, incubating, and feeding the last young would involve a significant waste of energy (Magrath, 1990). In addition, the amount of food energy contained in the extra nestlings is likely to be insignificant compared to both the total amount of food required by older nestlings through the entire nestling cycle, and to the amount of energy invested by parents in maintaining the extra nestlings until needed (Magrath, 1990). Although obligate siblicide is widespread in raptors (Stinson, 1979), skuas (Spellerberg, 1971), and pelicans (Drummond, 1987) cannibalism by nestlings is rare (Anderson, 1990; Magrath, 1990; Ploger, 1992; Stanback and Koenig, 1992; but see Bortolotti *et al.*, 1991; Viñuela, 1991). It is noteworthy that both a chrysomelid beetle (*Labidomera clivicollis*) and a land snail (*Arianta arbustorum*) lay large clutches that hatch asynchronously in which the first-hatched larvae cannibalize their younger sibs (Eickwort, 1973; Baur and Baur, 1986). In these species, there is no parental care beyond egg-laying, so laying extra eggs to act as a larder may be the only mechanism for females to increase investment in their first-hatched offspring.

This hypothesis is unlikely to be relevant for birds. It should be considered only for species that show regular cannibalization of youngest chicks by their older sibs. The hypothesis predicts that older chicks will eat younger ones, at least during periods of food shortage. The amount of food that parents can supply is likely to have a limit that is below the peak demand in the nestling period. Therefore the hypothesis predicts that parents should be unable to successfully raise broods if the extra nestlings are removed before being consumed.

4.5. Factors Influencing the Timing of the Entire Nesting Cycle

The onset of incubation determines the lengths of the laying and fledging periods in the nesting cycle (Fig. 1). Parents may manipulate the lengths of these periods to maximize benefits by reducing the probability of total nest failure or their own depredation. Alternatively, females may manipulate the length of these periods to minimize their own share of parental care at the expense of their mates.

4.5.1. Sexual Conflict Hypothesis

Slagsvold and Lifjeld (1989b) proposed a unique interpretation of asynchronous hatching as a result of parental behavior based on sexual conflict (the *Sexual Conflict Hypothesis*). Because a parent may attempt to minimize its share of parental care at the expense of its mate (Trivers, 1972), a conflict could result over the degree of parental investment made by either sex. Initiating incubation before the end of egg-laying may be a tactic that permits females to increase the parental effort of their mates. Early incubation would increase the time that females are on eggs, and asynchronous hatching would lengthen the time that females brood young nestlings. Thus, the total time that males must provision the female would be greater in asynchronously hatching broods than if eggs hatched synchronously. In addition, the early presence of nestlings may reduce a male's opportunity to attract a second female (Slagsvold and Lifjeld, 1989b).

The *Sexual Conflict Hypothesis* assumes that incubation is less energy demanding than alternative activities. Experimental evidence generally supports this supposition (Walsberg and King, 1978; Ricklefs and Hussell, 1984; Westerterp and Bryant, 1984), except for species at high latitudes that experience low ambient temperatures during incubation (Biebach, 1981; Moreno and Carlson, 1989). This hypothesis applies only to species with uniparental incubation where males provide food for incubating and brooding females (Slagsvold and Lifjeld, 1989b). However, incubation feeding by males may enhance the reproductive success of both sexes, and may indicate sexual cooperation rather than conflict (Lyon and Montgomerie, 1985; Lifjeld and Slagsvold, 1986; Alatalo *et al.*, 1988). Males of some raptors provide most of the food for females before and during laying (Poole, 1985;

Beissinger, 1987; Bortolotti and Wiebe, 1993). Yet incubation may not be initiated with the first egg, again suggesting cooperation between the sexes rather than female manipulation. Cooperation between the sexes is especially likely in species with long-term monogamous pair bonds, in which reproductive success is frequently correlated with the length of association of pairs (Mader, 1982; Mock, 1985a; Alatalo *et al.*, 1988; Bradley *et al.*, 1990; Emslie *et al.*, 1992).

The *Sexual Conflict Hypothesis* makes several testable predictions. Females may continue brooding beyond the point that the brood is capable of effective thermoregulation. Effective thermoregulatory ability can be determined for broods of different ages using the methodology of Dunn (1975) and Ricklefs (1987). Also, females at asynchronous broods should expend less energy than females at synchronous broods, and males at asynchronous broods should be manipulated into expending more energy than males at synchronous broods. Energy expenditures can be estimated using feeding rates as an index (Hébert, 1993b), or measured directly using the doubly-labeled water method (Lifson and McClintock, 1966; Speakman and Racey, 1988). Mass loss in females may be used as an index of parental effort (Bryant, 1988; Slagsvold and Lifjeld, 1989b), unless mass loss is part of an adaptive parental strategy (Norberg, 1981; Ricklefs and Hussell, 1984; Gaston and Jones, 1989; Moreno, 1989b).

Two tests of this hypothesis have been published. Females at asynchronous broods appeared to expend less energy than females at synchronous broods in both Pied Flycatchers and Yellow Warblers (Slagsvold and Lifjeld, 1989b; Hébert, 1993b). However, the patterns of effort by males of both species did not support the predictions. Thus, neither test fully supported the premise that there is conflict between the sexes. Recently, Slagsvold *et al.* (1994) showed that in Blue Tits (*Parus caeruleus*), female parents of broods with a reduced degree of asynchrony had a higher subsequent survival rate than those with more asynchronous broods. The opposite result was found for males. Because females appear to benefit from synchronous hatching, these results contradict the original hypothesis. However, they demonstrate that sexual conflict over the timing of hatching can exist, even if the reasons for the conflict are unclear.

4.5.2. Nest Failure Hypothesis

Relative to synchronous hatching, asynchronous hatching reduces the amount of time that a nest contains only eggs, and reduces the amount of time before the first chick fledges, but increases the total time a nest contains nestlings. Hussell (1972) suggested that asynchronous hatching is an adaptation to minimize total nest loss due to predation. The *Nest Failure Hypothesis* was formulated as a model to predict the optimal degree of asynchrony based on the probability of total nest failure during different phases of the nesting cycle (Clark and Wilson, 1981, 1985). In this model it is not the absolute rate of nest failure that is important, but rather the nest failure ratio: the ratio of the daily probability of nest failure during the nestling period to the daily probability of failure during the egg period (NFR, Clark and Wilson, 1981). Because the time from the onset of incubation to the first hatch and from the first hatch to the first fledge does not depend on when incubation is begun (Fig. 1), the relevant model parameters are the probability of nest loss during laying and during fledging (Hussell, 1985). A greater probability of nest failure during fledging favors increased synchrony, while an equal or greater probability of failure before incubation is begun favors increased asynchrony. The model predicts that even in the absence of brood reduction, most species should begin incubation before the last egg is laid.

This hypothesis cannot be tested experimentally, but nest failure rates can be measured for the different periods of the nesting cycle. The observed degree of asynchrony in Snow Buntings (*Plectrophenax nivalis*) was consistent with that predicted by the model (Hussell, 1985). Bancroft (1985) modified the hypothesis to include partial brood losses; his model predicted greater levels of asynchrony than he observed in Boat-tailed Grackles (*Quiscalus major*). Least Flycatchers (*Empidonax minimus*) and Yellow Warblers also hatched their eggs more synchronously than predicted by the model (Briskie and Sealy, 1989; Hébert and Sealy, 1993). It is unclear in these tests if the differences between the predictions of the model and observed hatching patterns are because the estimates of model parameters are wrong, or because the hypothesis has been falsified (Magrath, 1990). Recent work by Murray (in press) questions the validity of some of the assumptions of this model.

4.5.3. Adult Predation Hypothesis

The risk of predation on incubating or brooding adults may affect the optimal time to initiate incubation (Hussell, 1972; Weathers and Sullivan, 1989). Magrath (1988) included the effects of predation on adults in the Nest Failure model (Clark and Wilson, 1981, 1985; Hussell, 1985) to show that the rate of nest-content loss, the risk to incubating adults, and the probability of adults breeding again can interact to affect the timing of the onset of incubation (the *Adult Predation Hypothesis*). As in the *Nest Failure Hypothesis*, the relative rates of survival during different phases of the nesting cycle determine the optimal hatching pattern (Magrath, 1988). The two crucial values are the rate of survival of females during laying before and after incubation starts. A lower probability of survival while incubating should cause birds to delay the onset of incubation to minimize the time spent incubating, and would cause birds to hatch their eggs more synchronously than otherwise expected.

Like the *Nest Failure Hypothesis*, this hypothesis cannot be tested experimentally. The rates of nest failure and survival of females must be calculated and used in the model. To date, this hypothesis has not been tested, perhaps because it is difficult to determine survival rates of females.

4.6. Summary of Hypotheses

The categorization of hypotheses in Table I illustrates that a single species may be subject to multiple, potentially conflicting, selection pressures in different periods of the nesting cycle that affect patterns of incubation and hatching. The actual patterns observed in any species represent a compromise between the relevant intrinsic and extrinsic selective influences on both incubation and hatching patterns. The great variety of hatching patterns that exists in birds results from differences in the costs and benefits derived from these factors among taxa with different life history.strategies.

Not all of the hypotheses should be considered of equal importance. Some will only apply to a subset of species with particular natural history traits. More importantly, however, different factors represented by various hypotheses affect reproductive success in a hierarchical manner. For example, for factors affecting nestling survival to be relevant, eggs must survive until hatching. Patterns of incubation that promote the survival of eggs may not necessarily produce hatching patterns that maximize fledging success. Therefore, factors that promote egg survival may constrain the influence of those that affect nestling survival.

The various hypotheses reviewed above differ in how amenable they are to experimental testing, to being compared, and to being incorporated into a model. The *Nest Failure* and *Adult Predation* hypotheses are not testable by experimental manipulation. However, they are the only hypotheses that yield quantitative predictions. The *Egg Protection, Limited Breeding Opportunites, Hurry-up,* and *Larder* hypotheses are difficult to test. Some hypotheses, such as the *Egg Viability Hypothesis*, can be tested singly, such that other factors are excluded. For many others, the proposed methodology cannot isolate single factors. For example, the differences in fledging success between synchronized and asynchronous broods may be due to any or all of the hypotheses based on adaptive hatching patterns (section 4.4.). Furthermore, the effects of different factors are measured using different currencies. Most can be assessed in terms of how they may affect the expected number of fledglings per brood, but the *Limited Breeding Opportunities* hypothesis deals with breeding versus not breeding, the *Sexual Conflict* hypothesis is based on benefits to just females in breeding pairs, and the *Adult Predation* hypothesis is based on parental survival. It may be difficult to compare or model the costs and benefits of factors if their effects are not expressed in the same units.

5. FINDINGS FROM EXPERIMENTAL TESTS

5.1. Experimental Designs

Although asynchronous hatching is a common phenomenon among altricial birds, there have been relatively few experimental tests of the hypotheses compared to the number of observational studies (Clark and Wilson, 1981). Magrath (1990) and Amundsen and Slagsvold (1991b) summarized results of 29 manipulative experiments designed to test hypotheses for the evolution of hatching asynchrony. Several more studies have been published or presented since these reviews (Beissinger and Stoleson, 1991; Seddon and van Heezik, 1991b; Stanback, 1991; Bowman, 1992; Harper *et al.*, 1992; Hébert and Sealy, 1992, 1993; Ploger, 1992; Bortolotti and Wiebe, 1993; Hébert, 1993a,b; Slagsvold *et al.*, 1994; Wiebe and Bortolotti, 1994a,b).

Nearly all experimental studies have focused on adaptive hatching patterns (Table I). These typically employed an experimental design that synchronized broods by moving either eggs or nestlings among nests (35 studies). Success at experimentally synchronous nests was compared to nests with a natural degree of hatching asynchrony. Six studies included results from nests manipulated to have an exaggerated degree of hatching asynchrony. Most experimental studies have explicitly or implicitly tested the *Brood Reduction Hypothesis* (Table I), although many did not state any hypotheses to be tested *a priori*. Many studies have simply described the outcome of synchronization of hatching without testing any specific predictions.

5.2. Summary of Results

All of the hypotheses based on adaptive hatching patterns (Table I) predict equal or greater fledging success for nests with a natural degree of hatching asynchrony than experimentally synchronized nests.

Fledging success of experimentally synchronous nests was frequently equal to or greater than that of asynchronous broods (Table II). Only one study reported consistently greater success in asynchronous broods (Hahn, 1981). In another, asynchronous broods fledged more young in one of two years (Hébert, 1993a). However, the *Brood Reduction Hypothesis* predicts greater success from asynchrony only when food is limited (Magrath, 1989; Pijanowski, 1992). Two studies manipulated food availability. Synchronous broods of Eurasian Blackbirds showed lower fledging success when food was limited (Magrath, 1989), but there was no similar trend in captive Zebra Finches (*Poephila guttata*; Skagen, 1988). Three studies monitored natural food supplies. Fledging success of synchronous broods of White-crowned Pigeons (*Columba leucocephala*) and House Wrens (*Troglodytes aedon*) did not differ from that of asynchronous broods during periods of food shortage (Bowman, 1992; Harper et al., 1992). Synchronized pigeon broods fledged more young than asynchronous broods when food was abundant (Bowman, 1992).

Hypotheses based on food limitations or parental efficiency (Table I) predict that synchronously-hatched nests should experience lower growth rates and lower fledging masses of nestlings, increased parental effort, and assume a greater age of mortality for those chicks that die compared to nestlings in asynchronous broods. None of the 14 experimental studies that measured growth rates found significant differences between average growth rates of young from synchronous and asynchronous broods of equal size (Table II). Of 26 studies that reported prefledging masses of nestlings, most (69%) found no significant differences between masses of nestlings from synchronous and asynchronous broods. One found that only male nestlings from synchronous broods were significantly lighter (Howe, 1976). Only five studies reported postfledging survival, and four found no differences based on synchrony (Hébert and Barclay, 1986; Beissinger and Stoleson, 1991; Harper *et al.*, 1992; Slagsvold *et al.*, 1994); the fourth found that young fledged from asynchronous broods had a higher survival rate than young fledged from synchronous broods in a food-poor year, and the opposite in a food-abundant year (Magrath, 1989). Only six studies have measured parental effort, using either feeding rates (Fujioka, 1985; Héberg and Barclay, 1986; Mock and Ploger, 1987; Beissinger and Stoleson, 1991; Bowman, 1992) or using female mass loss (Amundsen and Slagsvold, 1991a). Two of these studies found higher feeding rates for parents of synchronous broods of Cattle Egrets (Fujioka, 1985; Mock and Ploger, 1987), but the others found no differences (Table II). Only one study measured the effects of experimental synchrony on the subsequent survival of adults and found no differences when sexes were pooled, but significant differences between the sexes (Slagsvold *et al.*, 1994). In 60% of the 15 studies that included information on the timing of offspring mortality, chicks died in synchronous nests at a later age than did chicks in asynchronous nests; the remainder reported no significant differences. Overall only three experimental tests unambiguously support predictions of the *Brood Reduction Hypothesis* (Hahn, 1981; Magrath, 1989; Hébert, 1993a), although the methodology and analyses used in Hahn's study make her results difficult to interpret (Table II).

We conclude that most of these experiments provide little evidence that early incubation and asynchronous hatching confer advantages for offspring survival after hatching. Asynchronous and synchronous broods generally produced equal numbers of fledglings, of similar quality, with similar degrees of parental care. However, the absence of supporting evidence does not constitute rejection of the *Brood Reduction Hypothesis*, especially since the hypothesis may have been misapplied to species that do not experience unpredictable food supplies.

Few hypotheses other than *Brood Reduction* have been tested experimentally (Table I). The nest failure model produced predictions congruent with observed hatching patterns in only one of four studies

TABLE II

Summary of the Results of 35 Experimental Tests of Hatching Asynchrony that Compared Asynchronous with Synchronized Broods. Numbers indicate the number of studies in each category. S = Synchronous, A = Asynchronous. References for experimental tests are annotated with "(T2)" in the Literature Cited. Modified after Magrath (1990) and Amundsen and Slagsvold (1991b).

	Relative outcome of experiment			
Measure	S = A[a]	S > A	S < A	Not reported
Number of young fledging	15.5[b]	17.5[b]	2	0
Post-fledging survival	4	0.5[b]	0.5[b]	30
Age of nestling mortality	6	9	0	20
Fledging weight	18	2	6	9
Growth rate	11	3	0	21
Parental effort	4	2	0	29
Parental survival	1[c]	0	0	34

[a] Includes small differences that were not statistically significant.
[b] Opposite effects in good and bad years are counted as 0.5 for each.
[c] Overall survival equal, but sexes differed by treatment (see text).

(Bancroft, 1985; Hussell, 1985; Briskie and Sealy, 1989; Hébert and Sealy, 1993). Various studies have supported predictions of the *Insurance Egg Hypothesis* (Anderson, 1990; Bollinger *et al.*, 1990), the *Egg Viability Hypothesis* (Viñuela, 1991; Veiga, 1992; Stoleson and Beissinger, in prep.); and the *Sibling Rivalry Hypothesis* (Wiebe and Bortolotti, 1994b). Predictions were not supported in tests of the *Sibling Rivalry Hypothesis* (Bollinger *et al.*, 1990), the *Sexual Conflict Hypothesis* (Slagsvold and Lifjeld, 1989b; Hébert and Sealy, 1993; Slagsvold *et al.*, 1994), or the *Peak Load Reduction Hypothesis* (Beissinger and Stoleson, 1991; Wiebe and Bortolotti, 1994b). Unfortunately, there are few predictions exclusive to a single hypothesis (Magrath, 1990), and in most studies alternative hypotheses could not be eliminated.

5.3. Problems with Experimental Tests of Hypotheses for Hatching Asynchrony

Of the 39 experimental tests of hatching asynchrony, 34 have been confined primarily to colonial water birds with small clutch sizes (12 studies), and passerines with slight degrees of hatching asynchrony (23 studies). Little experimental work has been done on groups in which asynchrony is the norm, such as raptors, grebes, gruiformes, coraciiformes, or psittacines (one study each of a bee-eater, a raptor, a parrot, a pigeon, and a swift). In addition, almost all studies have been conducted with temperate zone species. Tropical species are thought to have lower energetic requirements (Weathers, 1979; Bryant and Hails, 1983), slower growth (Ricklefs, 1976), lower prevalence of blood parasites (Ricklefs, 1992), and higher nest failure rates (Ricklefs, 1969), and consequently are probably subject to different selective pressures than temperate species.

Only 14 studies manipulated asynchronous broods to control for the possible effects of experimental manipulation. Negative effects of brood manipulations, such as decreased attentiveness, lower egg hatchability, and lower feeding rates, have been demonstrated (Bryant and Tatner, 1990; Götmark, 1992). Therefore caution should be used when interpreting results from studies that compared unmanipulated asynchronous broods to manipulated synchronous broods. Most studies have not quantified important measures, such as nestling growth rates, postfledging survival, and parental effort, that are crucial to assess the effects of asynchronous hatching on parental investment and reproductive success.

Finally, sample sizes in most experimental studies have been small, and therefore have lacked sufficient statistical power to detect any but gross differences between treatments. This problem is not confined to hatching asynchrony (Peterman, 1990; Graves, 1991; Taylor and Gerrodette, 1993). Asynchrony studies have typically employed sample sizes of 25 or less for synchronized broods (median sample size = 21). Testing for differences in the means of two treatments with equal variances with a student's *t*-test (two-tailed) using $\alpha = 0.05$ would have a statistical power of 0.11 assuming a "small" but real effect of treatment. A small effect as defined by Cohen (1988) signifies an approximate 15% nonoverlap of the distributions of synchronous and asynchronous scores. In other words, sample sizes of 25 would give an 11% probability of detecting a real difference between treatments. Therefore, failure to detect a difference between treatments would be ambiguous. Statistical power would increase slightly to 0.41 for a "medium" effect (approximately 33% nonoverlap of distributions; Cohen, 1988). Cohen (1988) proposed a statistical power of 0.80 as a convention for determining adequate sample sizes; this equates to a 20% probability of accepting a false null hypothesis (Type II error). In the example above, the sample sizes necessary to obtain a power of 0.80 are 310 for a small effect and 50 for a medium effect. Few experimental tests of hatching asynchrony have had sample sizes over 50 for both treatments (Slagsvold, 1982, 1986a; Bowman, 1992; Harper *et al.*, 1992).

6. SYNTHESIS: INTEGRATING MULTIPLE HYPOTHESES THROUGH MODELING

6.1. Prior Efforts to Integrate Multiple Hypotheses

Numerous authors have suggested that the broad array of hatching patterns exhibited by birds may be the result of trade-offs between multiple factors affecting the onset of incubation and hatching patterns. Clark and Wilson (1981, 1985) suggested that observed hatch spreads may represent a trade-off between nest predation and brood reduction. Mock and Parker (1986) postulated both brood reduction and insurance functions of smallest nestlings. Others have recognized the probability that multiple factors interact to produce observed hatching patterns (e.g., Bollinger *et al.*, 1990; Viñuela, 1991; Bowman, 1992; Veiga and Viñuela, 1993).

Few researchers have attempted to integrate the effects of multiple factors on hatching patterns. In a different context, Arnold *et al.* (1987) combined the effects of egg viability and risk of nest loss to determine constraints on clutch size in waterfowl. The risk of predation of adults was combined with the nest failure model by Magrath (1988). Stouffer

(1989) created a stochastic model based on empirical data to evaluate the effects of nest failure, brood parasitism, egg removal, and brood reduction on reproductive success in Starlings.

Recently, Konarzewski (1993) created a mathematical model that includes the influence of hatching asynchrony, hatching failure, nestling failure, brood reduction, and environmental variation on clutch size. This model is a useful heuristic tool to understand the joint effects and relative strengths of different factors on reproductive success. However, its general applicability is limited for several reasons. The model is based on incubation beginning after a base clutch is laid, and examining the effects of laying additional eggs that hatch progressively more asynchronously. This pattern may apply to some species, such as the Dark-eyed Junco (Smith, 1988), but may be inappropriate for others in which asynchrony is not a function of clutch size, or for those that begin incubation on the first egg. Egg hatchability was considered only in terms of how it may affect the insurance value of extra eggs. The model does not consider the fact that viability of eggs may be a function of the onset of incubation. Some of the required parameters of the model are difficult to measure empirically, such as the additional effort expended by parents prior to the death of extra chicks. Konarzewski included environmental variability in the model as the proportion of "good" years. He defined good food years as those years in which an extra nestling survives even when all of its older sibs hatch. Thus, the model ignores mortality of last-hatched nestlings due only to size differences, though empirical evidence suggests this is a widespread cost of hatching asynchrony (Stanback, 1991). Furthermore, Konarzewski suggested that his model shows environmental variation has a significant effect on the fitness benefits of extra, asynchronously-hatched eggs. This conclusion is hardly surprising since environmental variation was defined in terms of its effects on fitness. Thus, his model is of limited value in evaluating the relative effects of factors influencing the onset of incubation among different species, and is mostly irrelevant for the interpretation of results of experimental tests of hypotheses for hatching asynchrony.

6.2. Modeling Trade-offs in the Onset of Incubation

A clear methodology is needed to integrate the explicit trade-offs between factors affecting the onset of incubation. We advocate the use of stochastic models based on empirical data, such as that used by Stouffer (1989), to quantitatively assess the effects of multiple factors on fledging success. Because reproduction is a hierarchical process, transition probabilities of survivorship for each egg from one reproductive stage to the next (e.g., preincubation, incubation, brooding, postbrooding, and fledging) can be determined in relation to the effects on survivorship of the onset of incubation. Perhaps the most readily quantifiable factors that affect survivorship are: (1) the duration of exposure to eggs before incubation begins and its effects on nest predation and egg hatchability; (2) hatching spread and its effect on brood reduction; and (3) the time between the fledging of first and last chicks and the likelihood of nest predation (Fig. 5). Delaying incubation may cause a decline in the viability of first-laid eggs. But initiating incubation early results in an increased likelihood of brood reduction of last-hatched chicks (Fig. 6). Different aspects of nest failure are affected as incubation is delayed. Delaying incubation increases the time until fledging of the first young and so increases the chances of total brood failure. However, initiating incubation early causes nests to contain chicks for a longer period of time (Fig. 6). In many species nestlings may be more likely to be depredated than eggs, so this may increase the risk of nest failure.

The trade-offs that a parent makes when initiating incubation can be stochastically simulated by using transition probabilities to estimate the survivorship of individual eggs in a clutch and expected reproductive success under different scenarios for the onset of incubation. Survival probabilities from egg viability, brood reduction, and nest failure can be parameterized for each egg based on empirical data (Fig. 5).

In our model (Figure 7), each egg is given a probability of surviving from laying to hatching (P_h). This probability is the product of the probability of an egg remaining viable (P_v), derived from the relation between duration of exposure (*i*) and egg viability, and the probability of nest failure during the laying period (P_n). Each hatchling is given a

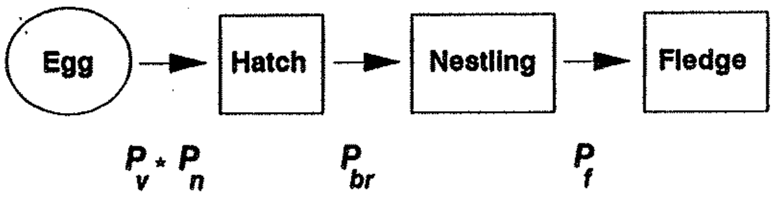

FIGURE 5. Transition probabilities used to construct a simple model of hatching asynchrony. P_v = the probability of an egg remaining viable before the onset of incubation. P_n = the probability of the nest surviving the period before the onset of incubation. P_{br} = the probability of a nestling surviving the period of brood reduction. P_f = the probability of a nestling surviving the period from the fledging of the first nestling until it fledges itself.

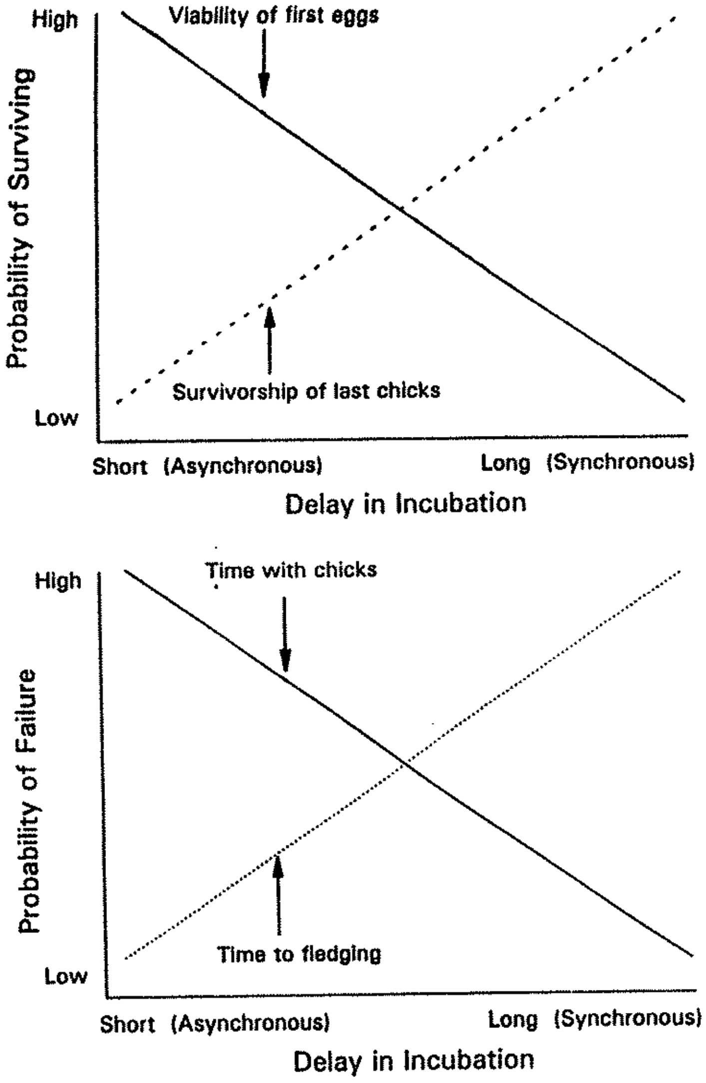

FIGURE 6. A graphical representation of the trade-offs from the onset of incubation on offspring survival. As synchrony increases, delaying incubation may cause a decline in the viability of first-laid eggs, but may improve the likelihood of survival for last-hatched chicks. Delaying incubation increases the time until fledging of the first young, thus increasing the chances for total brood failure. However, delaying incubation also decreases the amount of time the nest contains chicks, which may decrease the probability of nest failure.

probability of surviving from hatching through the period of brood reduction (P_{br}). This probability is a function of the age difference between the current nestling and the first-hatched nestling (a). However, other conditions may influence it as well. The probability of surviving the brood reduction stage may also depend on the number of surviving older siblings, the total brood size, the sex of the individual nestling, or the food supply. The transitional probability P_{br} must be determined for individual species based on empirical data. The likelihood of total nest failure from the onset of incubation until the first fledging is ignored in the model, because those stages of the nesting cycle are constant in duration and unaffected by changes in the onset of incubation (Fig. 1). Those nestlings that survive the brood reduction period are given a probability of surviving the period of fledging (P_f, or P_4 of Clark and Wilson, 1981). This probability is a function of the interval between the fledging of the first young and the current young (f), and may be considered an index of predation pressure exerted on nestlings as a result of asynchrony.

In the stochastic simulation, the survival of each egg or chick is determined by drawing a random number from a binomial distribution with parameters based on the transitional probabilities for that particular stage of the nesting cycle. The number of young surviving to fledging from the brood is then tallied for each iteration (Fig. 7). The mean number of chicks that fledge can then be compared between different incubation regimes.

Transition probabilities can be either absolute measures of survival during the nesting stages, or relative measures. Relative measures indicate the effect of individual factors on survivorship. For example, Veiga (1992) reported hatching success for experimental and unmanipulated control eggs in his viability experiments. The reported hatching success of experimental eggs is an absolute measure of P_v, and includes hatching failures for causes other than loss of viability due to exposure to ambient temperatures. The difference in hatching success between experimental eggs and their controls is a relative measure, and represents that fraction of hatchability that is due to the viability effect. The use of relative rather than absolute measures involves a loss of quantitative accuracy for predictions of fledging success, but provides a better assessment of the relative importance of individual factors. Also when using relative measures, the use of appropriate experimental controls becomes critical.

It may be possible to incorporate other hypotheses into this modeling framework if their effects on offspring survival can be quantified. For example, Stouffer (1989) included the effects of brood parasitism

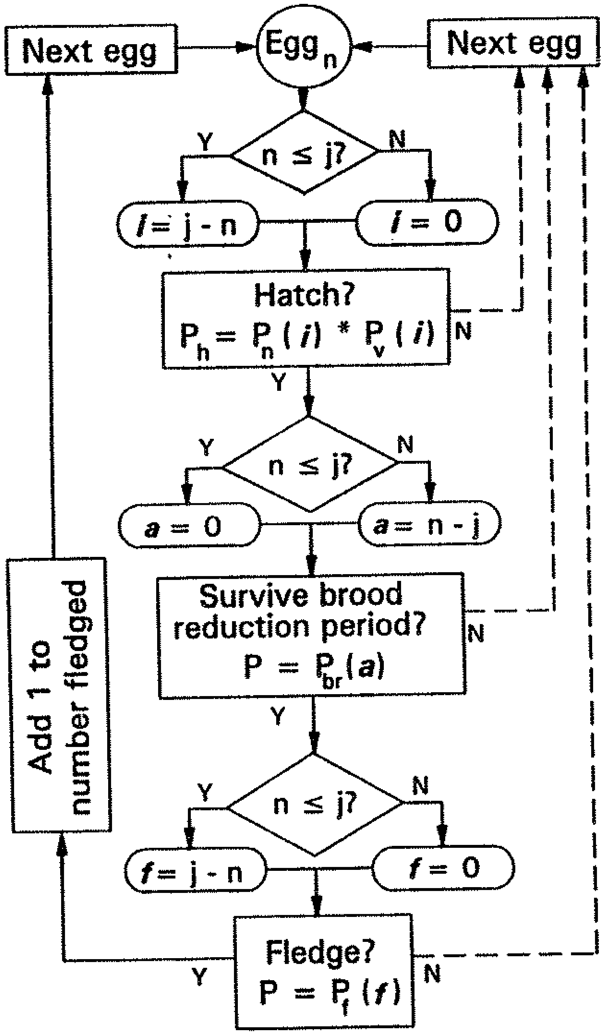

FIGURE 7. Flow chart of the stochastic model of the effects of egg viability, brood reduction, and total nest failure on breeding success in the House Sparrow. Each iteration determined the fate of all eggs in a clutch of five, based on initiating incubation on egg j. For each egg n, the interval *i* between the laying of the first egg and the nth egg was calculated as a function of j. The egg was assigned a probability $P_n(i)$ of escaping total nest failure during interval i, and a probability $P_v(i)$ of remaining viable as a function of the duration of *i*. These two probabilities were compared to two random numbers from binomial distributions. If both $P_n(i)$ and $P_v(i)$ were greater than their respective random numbers, then egg *n* hatched (Y). Otherwise, the egg did not hatch (N) and the model considered the next egg. If egg n hatched, the spread *a* between the hatch of egg *n* and the first egg was calculated. The nestling was assigned a probability $P_{br}(a)$ of surviving the brood reduction period as a function of *a*. If $P_{br}(a)$ was greater than a random number from a binomial distribution, then nestlings survived (Y). Otherwise, the nestling died (N), and the model considered the next egg. For surviving nestlings, the interval *f* between the fledging of the first chick and chick *n* was calculated as a function of j. Chicks were assigned a probability $P_f(f)$ of escaping total nest failure during the fledging period as a function of *f*. If $P_f(f)$ was greater than a random number from a binomial distribution, then the nestling fledged (Y). Otherwise, the nestling died before fledging, and the model considered the next egg (N). The number of eggs that survive to fledge was tallied for each clutch.

on reproductive success. It may also be possible to incorporate environmental variation in the model if it can be defined in a noncircular manner. If successful, such a modeling procedure would allow the evaluation of the relative importance of various hypotheses for hatching asynchrony, and identify the critical period in the nesting cycle for the species in question. The model may also provide a framework for designing studies of and making predictions for other species.

6.3. Modeling Asynchrony: An Example Using the House Sparrow

We present an example that incorporates empirical data from the literature into the model to illustrate its parameterization and use. Unfortunately, adequate data do not exist for any single species. We chose the House Sparrow because it is the only altricial species for which the effects of incubation patterns on egg viability have been published (Veiga, 1992). These include separate values for the effects of exposure for nests initiated early and late in the season (Table III). We calculated the relative effect of exposure on hatchability as the difference in hatchability between control and experimental eggs. Nest failure rates are taken from Table I of Clark and Wilson's review (1981) for a different population of sparrows. There are no data on the daily probability of nest failure prior to the onset of incubation or after the first fledging, so we used failure rates for incubation and rates from first hatch to first fledge, respectively (P_2 and P_3 of Clark and Wilson). The length of these stages are from Lowther and Cink (1992). Survival probabilities for the brood reduction stage were estimated from Veiga (1990) and Veiga and Viñuela (1993). These values for P_{br} are likely to be overestimates because the original data present the probability of survival as a function of hatch order rather than as a function of *a*, the hatch spread, and cover the entire nesting period rather than a well-defined brood reduction period. Our model used only the modal clutch size of five eggs.

TABLE III
Parameter Values Used in Stochastic Simulations of Breeding in the House Sparrow[a]

Interval i, a, or f	P_v Early	P_v Late	P_v Average	P_{br}	P_n	P_f
0	0.988	0.951	0.965	1.000	1.000	1.000
1	0.986	0.960	0.972	0.950	0.983	0.984
2	0.930	0.955	0.940	0.930	0.967	0.967
3	0.874	0.785	0.834	0.870	0.950	0.951
4	0.829	0.723	0.774	0.550	0.934	0.936

[a] P_v = the probability of an egg being viable; P_{br} = the probability of a nestling surviving the brood reduction period; P_n = the probability of nest failure prior to the onset of incubation, P_f = the probability of nest failure after the first fledge; i = the interval in days between the laying of an egg and the onset of incubation; a = the interval in days between the hatching of the first nestling and the hatching of the nth nestling; f = the interval in days between the fledging of the first nestling and the *n*th nestling.

Separate simulations of the model were performed beginning with incubation on each of the five eggs, and for both early and late season nests. All simulations were run for 1000 iterations. Results of the simulations were in the form of integer values of the expected number of young fledged. These values were compared among simulations differing in the onset of incubation using Chi-square tests (Manly, 1991).

Results of all simulations showed that the maximum number of fledglings was produced by initiating incubation on the third egg (Fig. 8). Using early season values for egg viability, initiating incubation on the second, third, or fourth eggs did not produce significantly different fledging success (pairwise comparisons, all $\chi^2 < 5.36$, df = 2, $P > 0.137$). Fledging success produced by beginning incubation on the first or fifth egg differed from each other and from yields for other incubation patterns (pairwise comparisons, all $\chi^2 > 28.0$, df = 2, $P < 0.001$). For late season viability values, fledging success differed significantly among all incubation strategies (all pairwise comparisons, $\chi^2 > 9.5$, df = 2, $P < 0.01$). Early and late season viability values produced similar fledging success when incubation was begun on the first, second, or third eggs (pairwise comparisons, all $\chi^2 < 1.78$, df = 3, $P > 0.60$; Fig. 8). However, late season nests produced fewer fledglings than early season nests when incubation was begun on the fourth or fifth egg ($\chi^2 > 13.0$, df = 3, $P < 0.01$ for both). This was a result of the greater decrease in viability as air temperature increased later in the nesting season (Veiga, 1992).

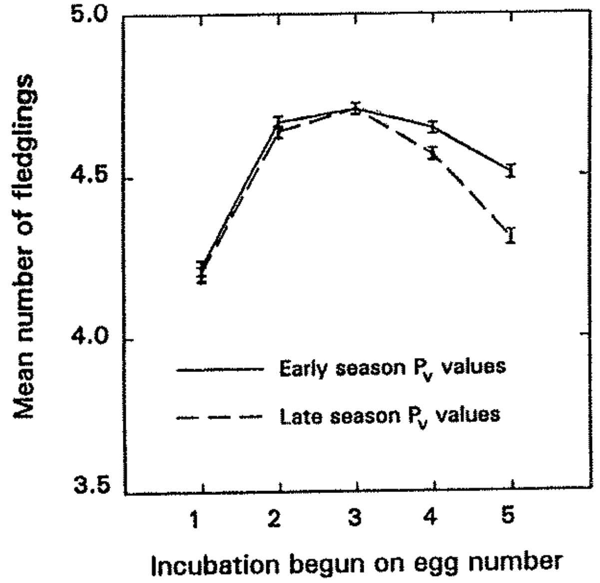

FIGURE 8. The mean number of fledglings per nest as a function of the egg on which incubation was begun, from a stochastic simulation of breeding in the House Sparrow. Simulations were run using viability probabilities (P_v) for early season and late season nests separately. All points represent the mean values of 1000 iterations, and bars represent standard errors of the means.

The relative importance of different factors in the simulation on reproductive success can be assessed by conducting a sensitivity analysis. The sensitivity of a parameter is measured as the proportional change in the expected yield of fledglings that results from changing the value of that parameter. We decreased each parameter by 10% for beginning on the first, third, and fifth egg (Table IV). For these simulations, we used an average of the early and late season viability values.

The impact of changing individual transition probabilities varied with the incubation strategy. Those parameters based on the period of egg laying before the onset of incubation, such as P_n and P_v values, had little effect on fledging success when incubation started on the first egg, and became progressively more important as the preincubation period lengthened. In contrast, P_{br} values became progressively less critical as incubation started later. In the House Sparrow, it appears that changes in nest failure rates (P_n and P_f) have little effect on overall success, perhaps because the original rates were very low, reflecting the species' preference for nesting in cavities.

TABLE IV
Sensitivity of the Expected Yield of Fledglings under Three Incubation Strategies to a 10% Decrease in Each Model Parameter[a]

Parameter	Incubation begun on: Egg 1	Egg 3	Egg 5
P_n	0.0	>0.1	0.3
P_f	>0.1	>0.1	0.0
P_v			
E_1	10.3	6.1	2.3
E_2	0.0	2.1	2.3
E_3	0.0	2.1	1.9
E_4	0.0	0.0	1.7
E_5	0.0	0.0	1.1
P_{br}			
N_1	2.7	6.6	10.0
N_2	2.1	1.9	0.0
N_3	2.4	1.9	0.0
N_4	2.1	0.0	0.0
N_5	1.5	0.0	0.0

[a] Expressed as percentage change from the initial value for that strategy.

The effects of viability and brood reduction were of similar magnitude in this model (Table IV). This relatively even trade-off is the reason that the intermediate incubation strategy, beginning on the third egg, has the greatest reproductive success. With this strategy, the costs of delaying incubation, expressed as a decline in the viability of first-laid eggs, counterbalanced the costs of initiating incubation early, expressed as a reduced survivorship of later-hatched chicks (Fig. 6). The balanced nature of this trade-off in the House Sparrow has some empirical support. Compared to relatively synchronous broods, relatively asynchronous broods experienced greater hatching success and lower survivorship of later-hatched nestlings, but overall fledging success did not differ between the two groups (Veiga and Viñuela, 1993).

In the model, the probability of nestling N_i surviving the brood reduction period (P_{br}) was strictly a function of the difference in age between N_i and N_1. In other words, the death of a nestling within the brood was assumed to have no effect on the survival of its nestmates. This simplistic approach was used because no data on conditional survival probabilities were available for the House Sparrow. However, nestling survival may be affected by brood size as well as age differences within a brood (e.g., Ricklefs, 1965; Werschkul, 1979; Stouffer, 1989). In particular, if an older nestling dies, the smallest nestling may have a greatly increased chance of survival (but see Stanback, 1991). This "insurance" effect was added to the House Sparrow model by incorporating a facultative adjustment to the size rank of nestlings based on the fate of their older sibs. For example, in a completely asynchronous brood, if N_2 dies, then N_3, N_4, and N_5 are given the transition probabilities for N_2, N_3, and N_4, respectively. Simulations were run of this modified age and brood size dependent model using an average of early and late season viability values.

Results from the age and brood size dependent model showed two major changes from the age dependent model (Fig. 9). The mean number of fledglings produced was greater in the age and brood size dependent model, which included the insurance effect, than in the age de-

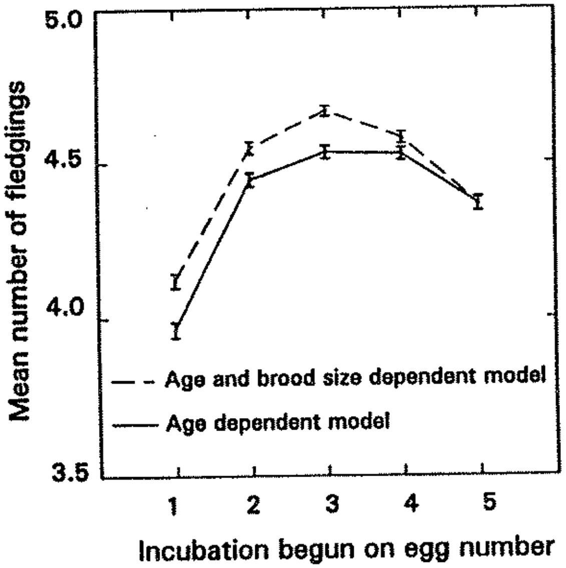

FIGURE 9. The mean number of fledglings per nest as a function of the egg on which incubation is begun, from a stochastic simulation of breeding in the House Sparrow using two different models of offspring survival during the brood reduction period. In the basic model, P_{br} was age-dependent. The second model was modified to include a facultative adjustment in the probability of surviving brood reduction based on the fate of older siblings, so that P_{br} was dependent on both age and brood size. See text for details of the models. Simulations used an average of early- and late-season viability values. All points represent the mean values of 1000 iterations, and bars represent standard errors of the means.

pendent model, for all incubation strategies except for starting on egg 5, when all nestlings had the same size rank. Because the probability of survival for younger nestlings increased if an older sib died, the inherent costs of brood reduction were reduced. When an average of early and late viability values were used, the age dependent model suggested similar fledging success when incubation was begun on egg 3 or 4 ($\chi^2 = 99.7$, $P = 0.53$; Fig. 9). Because the inherent costs of early incubation are mitigated in the age and brood size dependent model, beginning incubation on the third egg became a better strategy than beginning on the fourth egg ($\chi^2 = 202$, df $= 3$, $P < 0.001$). In general, when an insurance effect of clutch size can be demonstrated, early incubation becomes relatively more advantageous.

This approach of modeling multiple factors may provide a clear and consistent methodology for exploring the impact and interactions of different factors that potentially affect the onset of incubation and subsequent hatching patterns. It may help to identify the trade-offs that parents face in trying to maximize their reproductive success. To do so, however, will require that different factors or hypotheses (i.e., Section 4) can be measured in relation to their effects on egg or nestling survival. Not all hypotheses, however, are easily related or measured in those terms.

7. CONCLUSIONS

Asynchronous hatching of bird eggs has intrigued and puzzled ornithologists for decades, because of the *Paradox of Hatching Asynchrony:* parents primarily control the onset of development for eggs, yet appear to choose a pattern of hatching that frequently results in offspring mortality. The *Paradox of Hatching Asynchrony* has been the subject of considerable research, and 17 hypotheses have been proposed to account for this phenomenon (Table I). The *Brood Reduction Hypothesis* appeared to provide a solution. Most studies have tested this hypothesis or others that also seek an adaptive function for asynchronous hatching and the resulting nestling size hierarchy, i.e., those hypotheses for which the nestling period is the critical period of the nesting cycle (Table I). Such tests have provided little evidence that early incubation leading to asynchronous hatching confers advantages for offspring survival after hatching or reduces parental investments (Table II). These studies have ignored the physiological, environmental, and social constraints that directly affect the onset of incubation, and the possible adaptive significance of early incubation.

We feel it is important for studies of hatching asynchrony to refocus attention from the search for adaptive hatching patterns during the nestling period to the events surrounding the onset of incubation during egg-laying. Hatching patterns are primarily determined by the timing of the onset of incubation (Figs. 1 and 2). But the onset of incubation may reflect phylogenetic or physiological constraints. Asynchronous hatching appears to be a derived condition, and there is little variation in hatching patterns in many orders and families (Figs. 3 and 4). It is not clear if these similarities among species are due to similar selection regimes or because the traits are phylogenetically fixed. Hormonal controls of egg-laying and incubation behavior may circumscribe when incubation can begin. Likewise, fluctuations in the food available to laying females may also facultatively influence the initiation of incubation. These factors may constrain the range of possible incubation patterns and the resulting asynchrony of hatching patterns.

The onset of incubation involves a decision that results in trade-offs among promoting a parent's own survival, promoting survival of the embryos, and the costs and benefits inherent to a particular hatching pattern that affect nestling survival. There are a variety of benefits that birds may derive from the early onset of incubation, such as protecting eggs from adverse effects of the environment, predators, brood parasites, and reproductive interference. In many instances, it appears that asynchronous hatching may itself be the cost of initiating incubation early. This cost is manifested through increased offspring mortality due to age differences among offspring, from starvation, accidents, or passive competition among nestlings.

If birds derive benefits from early incubation itself, then the resulting nestling size hierarchy and the mortality of the smallest nestlings may simply be epiphenomena. One might then expect mechanisms to evolve to offset the competitive disadvantages experienced by smallest nestlings. Indeed, some species do exhibit such behaviors. In a number of species, one or both parents preferentially fed younger nestlings (Ferguson and Sealy, 1983; Stamps *et al.*, 1985; Gottlander, 1987; Sasvári, 1990). Maguari Stork (*Ciconia maguari*) parents fed their broods a variety of different-sized food items simultaneously; larger young tended to eat the largest items, allowing smaller young to feed on the smaller items (Thomas, 1984). No brood reduction occurs in this species despite an extreme disparity in nestling sizes. Finally, parents may even be more aggressive towards larger, more competitive chicks to allow smaller chicks more access to food (Leonard *et al.*, 1988). These observations are consistent with the premise that hatching asynchrony may be in part a consequence, and not the cause, of early incubation.

It has become increasingly obvious that no one hypothesis is sufficient to explain hatching patterns in all species. It is also likely that single species may be subject to multiple factors that influence the onset of incubation and the resulting hatching patterns. Variation in the onset of incubation among species is likely to be a function of the costs and benefits derived from these factors, and from their interactions. Thus, effects of the onset of incubation on survival of *both* eggs during the laying period (as a result of parental neglect) and chicks during the nestling period (as a result of size differences) must be considered, as shown in the House Sparrow examples (Figs. 8 and 9). Multiple factors should be tested, one at a time in a coordinated manner, to determine their effects on reproductive success as a function of different incubation strategies. Results should be integrated in models (e.g., Fig. 7) to evaluate the relative importance of each factor and the combinations that lead to greatest reproductive success. The effects on fitness of different factors affecting the onset of incubation may become evident only when considered jointly in this manner. If the interactions of different factors are simple enough, they can be evaluated analytically (e.g., Arnold *et al.*, 1987). More likely, interactions of different factors will be probablistic in nature, necessitating the use of stochastic models such as the one we presented.

Finally, important experimental results are most likely to be produced from studies of taxa where asynchrony is not merely a result of phylogenetic or physiological constraints. For example, it is not clear whether a small degree of asynchrony (24–48 hr), as is typical of passerines, represents an adaptation or is an incidental effect of the mechanics of egg-laying. Greater hatch spreads are more likely to indicate true adaptations. The majority of hatching asynchrony studies have been done with carnivorous or insectivorous species in temperate areas. Rapid advances are likely to occur by studying species with fundamentally different selective regimes. In taxonomic groups that exhibit variation in hatch spreads (e.g., the Rallidae), the variation in asynchrony among species may illustrate different factors affecting the onset of incubation in those species. Such taxa are especially amenable to comparative analyses. By rigorously assessing multiple factors in appropriate species and using modern comparative approaches, studies of hatching asynchrony will progress out of the "stagnant backwater of population biology" and into the mainstream.

8. SUMMARY

1. Birds are unique among animals in being able to influence the birthing intervals of their young through the timing of the onset incubation. However, many species hatch their young asynchronously, frequently resulting in reduced survivorship for later-hatched young. This is the *Paradox of Hatching Asynchrony.*

2. The *Brood Reduction Hypothesis* provided a resolution to the paradox by suggesting an adaptive function to the offspring mortality that results from asynchrony. Experimental tests have provided little support, and 16 alternative hypotheses have been proposed, but few have been tested. Most experimental tests have not measured important parameters such as parental effort and postfledging survival. Many have lacked adequate controls or sufficient statistical power.

3. We divide the hypotheses for hatching asynchrony into four categories based on the effects of intrinsic or extrinsic factors during a critical period of the nesting cycle which constrains reproductive success. Hatching asynchrony could be simply the consequence of the early onset of incubation during egg-laying, either as a result of physiological constraints on incubation or because parents derive fitness benefits from the protective function of early incubation. During the nestling period, hatching asynchrony could be adaptive if it allowed parents to eliminate one or more nestlings selectively, or increased parental efficiency. Alternatively, parents could manipulate the duration of the different periods of the nesting cycle to maximize benefits.

4. Because the onset of incubation generally determines hatching patterns, we encourage refocusing attention from the search for adaptive hatching patterns during the nestling period to the events surrounding the onset of incubation during egg-laying. Many factors can affect when incubation is begun, including physiology, and interactions with the environment, predators, competitors, and mates.

5. Patterns of the onset of incubation are difficult to determine and to quantify, in part because many birds begin incubating gradually, or at night. In some species, the onset of incubation varies with clutch size, but not in others.

6. The onset of incubation is the principle proximate control of hatching patterns, but other factors, such as egg size, embryonic vocalizations, and time of year may also affect hatching patterns.

7. Synchronous hatching is the primitive condition in birds, and is widespread in the lower, primarily precocial taxa. Most altricial species hatch their eggs asynchronously, although some exhibit synchrony as a secondarily derived trait. Hatching patterns show wide variation within some orders and families.

8. Patterns of the onset of incubation and hatching in a species may reflect the influence of multiple factors. The relative importance of those factors may depend on the trade-offs associated with the poten-

tial benefits of early incubation to the survival of eggs and the potential costs to the survivor of later-hatching young associated with nestling size hierarchies.

9. The relative effects of multiple factors can be examined by integrating the results of empirical tests of single factors through modeling.

10. We demonstrated the use of a stochastic model by using empirical data from the House Sparrow. Results revealed the trade-offs inherent in the onset of incubation from differences in egg viability and nestling survivorship. An intermediate onset of incubation produced the greatest fledging success.

11. Other factors may be integrated into such models if they can be measured in terms of their effects on fledging success. Different factors, represented by different hypotheses, vary in how readily they may be modeled.

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REFERENCES

Alatalo, R., Gottlander, K., and Lundberg, A., 1988, Conflict or cooperation between parents in feeding nestlings in the Pied Flycatcher *Ficedula hypoleuca*, *Ornis Scand.* 19:31–34.

Alerstam, T., and Högstedt, G., 1981, Evolution of hole-nesting in birds, *Ornis Scand.* 12:188–193.

Alexander, R. D., 1974, The evolution of social behavior, *Annu. Rev. Ecol. Syst.* 5:325–384.

Alvarez del Toro, M., 1971, On the biology of the American Finfoot in southern Mexico, *Living Bird* 10:79–88.

Amundsen, T., and Slagsvold, T., 1991a, Asynchronous hatching in the Pied Flycatcher: an experiment, *Ecology* 72:797–804. (T1 & T2)

Amundsen, T., and Slagsvold, T., 1991b, Hatching asynchrony: facilitating adaptive or maladaptive brood reduction?, *Acta XX Cong. Inter. Ornith.* 3:1707–1719. (T1 & T2)

Amundsen, T., and Stokland, J. N., 1988, Adaptive significance of asynchronous hatching in the shag: a test of the brood reduction hypothesis, *J. Anim. Ecol.* 57:329–344. (T1 & T2)

Amundsen, T., and Stokland, J. N., 1990, Egg size and parental quality influence nestling growth in the Shag, *Auk* 107:410–413.

Anderson, D. J., 1989, The role of hatching asynchrony in siblicidal brood reduction of two booby species, *Behav. Ecol. Sociobiol.* 25:363–368. (T1 & T2)

Anderson, D. J., 1990, Evolution of obligate siblicide in boobies. 1. A test of the insurance-egg hypothesis, *Am. Nat.* 135:334–350. (T1)

Anthony, A. J., and Sherry, B. Y., 1980, Openbill Storks breeding in the southwestern lowveld of Zimbabwe Rhodesia, *Ostrich* 58:1–6.

Arnold, T. W., 1993, Factors affecting egg viability and incubation time in prairie dabbling ducks, *Can. J. Zool.* 71:1146–1152.

Arnold, T. W., Rohwer, F. C., and Armstrong, T., 1987, Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks, *Am. Nat.* 130:643–653.

Astheimer, L. B., 1991, Embryo metabolism and egg neglect in Cassin's Auklets, *Condor* 93:486–495.

van Balen, J. H., and Cavé, A. J., 1970, Survival and weight loss of nestling Great Tits, *Parus major*, in relation to brood size and air temperature, *Neth. J. Zool.* 20:464–474.

Ball, G. F., 1991, Endocrine mechanisms and the evolution of avian parental care, *Acta XX Cong. Inter. Ornith.*: 984–991.

Balph, C. P., 1975, Life style of *Coccyzus pumilus*, a tropical cuckoo, *Condor* 77:60–72.

Balthazart, J., 1983, Hormonal correlates of behavior, in: *Avian Biology*, Vol. 7, (D. S. Farner, J. R. King, and K. C. Parkes, eds.), Academic Press, New York, pp. 221–365.

Bancroft, G. T., 1984, Growth and sexual dimorphism of the Boat-tailed Grackle, *Condor* 86:423–432.

Bancroft, G. T., 1985, The influence of total nest failure and partial losses on the evolution of asynchronous hatching, *Am. Nat.* 126:495–504. (T1)

Baur, B., and Baur, A., 1986, Proximate factors influencing egg cannibalism in the land snail *Arianata arbustorum* (Pulmonata, Helicidae), *Oecologia* 70:283–287.

Bednarz, J. C., and Hayden, T. J., 1991, Skewed brood sex-ratio and sex-biased hatching sequence in Harris' Hawks, *Am. Nat.* 137:116–132.

Beissinger, S. R., 1987, Anisogamy overcome: female strategies in Snail Kites, *Am. Nat.* 129:486–500.

Beissinger, S. R., and Bucher, E. H., 1992, Sustainable harvesting of parrots for conservation, in: *New World Parrots in Crisis: Solutions from Conservation Biology*, (S. R. Beissinger and N. F. R. Snyder, eds.), Smithsonian Institution Press, Washington, D.C., pp. 73–115.

Beissinger, S. R., and Stoleson, S. H., 1991, Nestling mortality patterns in relation to brood size and hatching asynchrony in Green-rumped Parrotlets, *Acta XX Cong. Inter. Ornith.*:1727–1733. (T1 & T2)

Beissinger, S. R., and Waltman, J. R., 1991, Extraordinary clutch size and hatching asynchrony of a neotropical parrot, *Auk* 108:863–871.

Bengtsson, H., and Rydén, O., 1981, Development of parent-young interaction in asynchronously hatched broods of altricial young, *Z. Tierpsychol.* 56:255–272.

Bengtsson, H., and Rydén, O., 1983, Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the Great Tit *Parus major*, *Behav. Ecol. Sociobiol.* 12:243–251.

Bennett, A. F., and Dawson, W. R., 1979, Physiological responses of embryonic Heermann's Gulls to temperature, *Physiol. Zool.* **52**:413–421.

Bent, A. C., 1961, *Life Histories of North American Birds of Prey*, Dover Publications, New York.

Biebach, H., 1981, Energetic costs of incubation on different clutch sizes in Starlings (*Sturnus vulgaris*), *Ardea* **69**:141–142.

Boag, D., 1982, *The Kingfisher*, Blanford Press, Dorset, UK.

Boag, D. A., and Schroeder, M. A., 1992, Spruce Grouse, in: *The Birds of North America*, No. 5, (A. Poole, P. Stettenheim, and F. Gills, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Bollinger, P. B., Bollinger, E. K., and Malecki, R. A., 1990, Tests of three hypotheses of hatching asynchrony in the Common Tern, *Auk* **107**:696–706. (T1 & T2)

Bolton, M., 1991, Determinants of chick survival in the Lesser Black-backed Gull: relative contributions of egg size and nestling quality, *J. Anim. Ecol.* **60**:949–960.

Bortolotti, G. R., 1986, Influence of sibling competition on nestling sex ratios of sexually dimorphic birds, *Am. Nat.* **127**:495–507.

Bortolotti, G. R., and Wiebe, K. L., 1993, Incubation behaviour and hatching patterns in the American Kestrel *Falco sparverius*, *Ornis Scand.* **24**:41–47.

Bortolotti, G. R., Wiebe, K. L., and Iko, W. M., 1991, Cannibalism of nestling American Kestrels by their parents and siblings, *Can. J. Zool.* **69**:1447–1453.

Bowman, R., 1992, Asynchronous hatching and brood reduction in the White-crowned Pigeon (*Columba leucocephala*), Ph.D. Dissertation, University of South Florida, Tampa. (T1 & T2)

Bradley, J. S., Wooller, R. D., Skira, I. J., and Serventy, D. L., 1990, The influence of mate retention and divorce upon reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*, *J. Anim. Ecol.* **59**:487–496.

Braun, B. M., and Hunt, G. L., Jr., 1983, Brood reduction in Black-legged Kittiwakes, *Auk* **100**:469–476.

Brawn, J. D., and Balda, R. P., 1988, Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities?, *Condor* **90**:61–71.

Breitwisch, R., 1989, Mortality patterns, sex ratios, and parental investment in monogamous birds, in: *Current Ornithology*, Vol. 6, (D. M. Power, ed.), Plenum Press, New York, pp. 1–50.

Briskie, J. V., and Sealy, S. G., 1989, Nest-failure and the evolution of hatching asynchrony in the Least Flycatcher, *J. Anim. Ecol.* **58**:653–665. (T1)

Brooks, D. R., and McLennan, D. A., 1991, *Phylogeny, Ecology, and Behavior*, University of Chicago Press, Chicago.

Brown, J. L., 1987, *Helping and Communal Breeding in Birds*, Princeton University Press, Princeton.

Brown, L., and Amadon, D., 1968, *Eagles, Hawks, and Falcons of the World*, McGraw Hill, New York.

Bryant, D. M., 1978, Establishment of weight hierarchies in the broods of House Martins *Delichon urbica*, *Ibis* **120**:16–26.

Bryant, D. M., 1988, Energy expenditure and body mass changes as measures of reproductive costs in birds, *Funct. Ecol.* **2**:23–34.

Bryant, D. M., and Gardiner, A., 1979, Energetics of growth in House Martins (*Delichon urbica*), *J. Zool., London.* **189**:275–304.

Bryant, D. M., and Hails, C. J., 1983, Energetics and growth patterns of three tropical bird species, *Auk* **100**:425–439.

Bryant, D. M., and Tatner, P., 1990, Hatching asynchrony, sibling competition and siblicide in nestling birds: studies of swiftlets and bee-eaters, *Anim. Behav.* **39**:657–671. (T1 & T2)

Bryant, D. M., and Tatner, P., 1991, Intraspecific variation in avian energy expenditure: correlates and constraints, *Ibis* **133**:236–245.

Burley, N., 1986, Sex-ratio manipulation in color-banded populations of Zebra Finches, *Evolution* **40**:1191–1206.

Butler, R. W., 1992, Great Blue Heron, in: *The Birds of North America*, No. 25, (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Caine, L. A., and Marion, W. R., 1991, Artificial addition of snags and nestboxes to slash pine plantations, *J. Field. Ornithol.* **62**:97–106.

Calder, W. A., and Calder, L. L., 1992, Broad-tailed Hummingbird, in: *The Birds of North America*, No. 16, (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Candy, M., 1984, Habits and breeding biology of the Great Blue Turaco, *J. East Afr. Nat. Hist. Soc. Natl. Mus.* **37**:1–19 (No. 180).

Cannon, M. E., Carpenter, R. E., and Ackerman, R. A., 1986, Synchronous hatching and oxygen consumption of Darwin's Rhea eggs (*Pterocnemia pennata*), *Physiol. Zool.* **59**:95–108.

Carey, C., 1980, The ecology of avian incubation, *BioScience* **30**:819–824.

Cargill, S. M., and Cooke, F., 1981, Correlation of laying and hatching sequences in clutches of the Lesser Snow Goose *Anser caerulescens caerulescens*), *Can. J. Zool.* **59**:1201–1204.

Cash, K. J., and Evans, R. M., 1986, Brood reduction in the American White Pelican (*Pelecanus erythrorhynchos*), *Behav. Ecol. Sociobiol.* **18**:413–418.

Clark, A. B., and Wilson, D. S., 1981, Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure, *Q. Rev. Biol.* **56**:253–277.

Clark, A. B., and Wilson, D. S., 1985, The onset of incubation in birds, *Am. Nat.* **125**:603–611.

Clutton-Brock, T. H., 1986, Sex ratio variation in birds, *Ibis* **128**:317–329.

Clutton-Brock, T. H., 1991, *The Evolution of Parental Care*, Princeton University Press, Princeton.

Cohen, J., 1988, *Statistical Power Analysis for the Behavioral Sciences*, 2nd ed., Lawrence Erlbaum Associates, Hillsdale, New Jersey.

Copi, I. M., 1972, *Introduction to Logic*, 4th ed., Macmillan, New York.

Courtney, J., and Marchant, S., 1971, Breeding details of some common birds in south-eastern Australia, *Emu.* **71**:121–133.

Cramp, S., 1977, *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. I. Ostrich to Ducks*, Oxford University Press, Oxford.

Cramp, S., 1980, *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. II. Hawks to Bustards*, Oxford University Press, Oxford.

Cramp, S., 1983, *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. III. Waders to Gulls*, Oxford University Press, Oxford.

Cramp, S., 1985, *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. IV. Terns to Woodpeckers*, Oxford University Press, Oxford.

Cronmiller, J. R., and Thompson, C. F., 1981, Sex-ratio adjustment in malnourished Red-winged Blackbird broods, *J. Field Ornithol.* **52**:65–67.

Csada, R. D., and Brigham, R. M., 1992, Common Poorwill, in: *The Birds of North America*, No. 32. (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Davies, J. C., and Cooke, F., 1983, Intraclutch hatch synchronization in the Lesser Snow Goose, *Can. J. Zool.* **61**:1398–1401.

Deeming, D. C., and Ferguson, M. W. J., 1992, Physiological effects of incubation temperature on embryonic development in reptiles and birds, in: *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles*, (D. C. Deeming and M. W. J. Ferguson, eds.), Cambridge University Press, Cambridge, pp. 147–173.

De Steven, D., 1980, Clutch size, breeding success, and parental survival in the Tree Swallow (*Iridoprocne bicolor*), *Evolution* **34**:278–291.

Dorward, D. F., 1962, Comparative biology of the White Booby and the Brown Booby *Sula* spp. at Ascension, *Ibis* **103b**:174–220.

Douthwaite, R. J., 1978, Breeding biology of the Pied Kingfisher *Ceryle rudis* on Lake Victoria, *J. East Afr. Nat. Hist. Soc. Natl. Mus.* **31** (No. 166).

Drent, R. H., 1970, Functional aspects of incubation in the Herring Gull, *Behav.* (Suppl.) **17**:1–125.

Drent, R. H., 1973, The natural history of incubation, in: *Breeding Biology of Birds*, (D. S. Farner, ed.), National Academy of Science, Washington D.C., pp. 262–322.

Drent, R. H., 1975, Incubation, in: *Avian Biology*, Vol. 5, (D. S. Farner and J. R. King, eds.), Academic Press, New York, pp. 333–420.

Drummond, H., 1987, A review of parent-offspring conflict and brood reduction in the Pelecaniformes, *Col. Waterbirds* **10**:1–15.

Drummond, H., and García Chavelas, C., 1989, Food shortage influences sibling aggression in the Blue-footed Booby, *Anim. Behav.* **37**:806–819.

Drummond, H., Osorna, J. L., Torres, R., García Chavelas, C., and Merchant Larios, H., 1991, Sexual size dimorphism and sibling competition: implications for avian sex ratios, *Am. Nat.* **138**:623–641.

Dunlop, E., 1910, On incubation, *British Birds* **4**:137–145.

Dunn, E. H., 1975, The timing of endothermy in the development of altricial birds, *Condor* **77**:288–293.

Edwards, T. C., and Collopy, M. W., 1983, Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide, *Auk* **100**:630–635.

Eickwort, K. R., 1973, Cannibalism and kin selection in *Labidomera clivicollis* (Coleoptera: Chrysomelidae), *Am. Nat.* **101**:452–453.

Emlen, S. T., and Oring, L. W., 1977, Ecology, sexual selection, and the evolution of mating systems, *Science* **197**:215–223.

Emlen, S. T., Wrege, P. H., Demong, N. J., and Hegner, R. E., 1991, Flexible growth rates in nestling White-fronted Bee-eaters: a possible adaptation to short-term food shortage, *Condor* **93**:591–597.

Emslie, S. D., Sydeman, W. J., and Pyle, P., 1992, The importance of mate retention and experience on breeding success in Cassin's Auklet (*Ptychoramphus aleuticus*), *Behav. Ecol.* **3**:189–195.

Enemar, A., and Arheimer, O., 1989, Developmental asynchrony and onset of incubation among passerine birds in a mountain birch forest of Swedish Lapland, *Ornis Fenn.* **66**:32–40.

Epple, A., and Stetson, M. H., 1980, *Avian Endocrinology*, Academic Press, New York.

Evans, R. M., 1988, Embryonic vocalizations as care-soliciting signals, with particular reference to the American White Pelican, *Proc. Int. Orn. Cong.* **19**:1467–1475.

Evans, R. M., 1990a, Vocal regulation of temperature by avian embryos: a laboratory study with pipped eggs of the American White Pelican, *Anim. Behav.* **40**:969–979.

Evans, R. M., 1990b, Terminal egg neglect in the American White Pelican, *Wilson Bull.* **102**:684–692.

Evans, R. M., 1990c, Effects of low incubation temperatures during the pipped egg stage on hatchability and hatching times in domestic chickens and Ring-billed Gulls, *Can. J. Zool.* **68**:836–840.

Ewert, M. A., 1992, Cold torpor, diapause, delayed hatching and aestivation in reptiles and birds, in: *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles*, (D. C. Deeming and M. W. J. Ferguson, eds.), Cambridge University Press, Cambridge, pp. 173–191.

Ferguson, R. S., and Sealy, S. G., 1983, Breeding ecology of the Horned Grebe, *Podiceps auritus*, in southwest Manitoba, *Can. Field. Nat.* **97**:401–408.

Fisher, R. A., 1930, *The Genetical Theory of Natural Selection*, Oxford Press, London.

Forbes, L. S., 1990, Insurance offspring and the evolution of avian clutch size, *J. Theor. Biol.* **147**:345–359.

Forbes, L. S., 1991, Insurance offspring and brood reduction in a variable environment: the costs and benefits of pessimism, *Oikos* **62**:325–332.

Forbes, L. S., and Ydenberg, R. D., 1992, Sibling rivalry in a variable environment, *Theor. Pop. Biol.* **41**:135–160.

Forbes, M. L. R., and Ankney, C. D., 1987, Hatching asynchrony and food allocation within broods of Pied-billed Grebes, *Podilymbus podiceps*, *Can. J. Zool.* **65**:2872–2877.

Forshaw, J. M., 1989, *Parrots of the World*, Landsdowne Editions, Willoughby, Australia.

Freese, C. H., 1975, Notes on nesting in the Double-striped Thick-knee (*Burhinus bistriatus*) in Costa Rica, *Condor* **77**:353–354.

Fujioka, M., 1985, Food delivery and sibling competition in experimentally even-aged broods of the Cattle Egret, *Behav. Ecol. Sociobiol.* **17**:67–74. (T1 & T2)

Gargett, V., 1982, Synchronous hatching and the Cain and Abel struggle in the Black Eagle, *Ostrich* **53**:147–150. (T1 & T2)

Gaston, A. J., and Jones, I. L., 1989, The relative importance of stress and programmed anorexia in determining mass loss by incubating Ancient Murrelets, *Auk* **106**:653–658.

Gaston, A. J., and Powell, D. W., 1989, Natural incubation, egg neglect, and hatchability in the Ancient Murrelet, *Auk* **106**:433–438.

Gibb, J., 1950, The breeding biology of the Great and Blue Titmice, *Ibis* **92**:507–539.

Gibbons, D. W., 1987, Hatching asynchrony reduces parental investment in the Jackdaw, *J. Anim. Ecol.* **56**:403–414. (T1 & T2)

Gibson, F., 1971, The breeding biology of the American Avocet (*Recurvirostra americana*) in central Oregon, *Condor* **73**:444–454.

Gilbert, A. B., 1971, Transport of the egg through the oviduct and oviposition, in: *Physiology and Biochemistry of the Domestic Fowl*, Vol. 3, (D. J. Bell and B. M. Freeman, eds.), Academic Press, New York, pp. 1345–1352.

Godfray, H. C. J., and Harper, A. B., 1990, The evolution of brood reduction by siblicide in birds, *J. Theor. Biol.* **145**:163–175.

Godfary, H. C. J., Partridge, L., and Harvey, P. H., 1991, Clutch size, *Annu. Rev. Ecol. Syst.* **22**:409–429.

Götmark, F., 1992, The effects of investigator disturbance on nesting birds, in *Current Ornithology*, Vol. 9, (D. M. Power, ed.), Plenum Press, New York, pp. 63–104.

Goldsmith, A. R., 1983, Prolactin in avian reproductive cycles, in: *Hormones and Behavior in Higher Vertebrates*, (J. Balthazart, E. Pröve, and R. Gilles, eds.), Springer-Verlag, Berlin, pp. 375–387.

Goldsmith, A. R., and Williams, D. M., 1980, Incubation in Mallards (*Anas platyrhynchos*): changes in plasma levels of prolactin and luteinizing hormone, *J. Endocrinol.* **86**:371–379.

Gottlander, K., 1987, Parental feeding behavior and sibling competition in the Pied Flycatcher *Ficedula hypoleuca*, *Ornis Scand.* **18**:269–276.

Gowaty, P. A., 1991, Facultative manipulation of sex ratios in birds: rare or rarely observed?, in *Current Ornithology*, Vol. 8, (D. M. Power, ed.), Plenum Press, New York, pp. 141–171.

Gowaty, P. A., and Lennartz, M. R., 1985, Sex ratios of nestling and fledgling Red-cockaded Woodpeckers (*Picoides borealis*) favor males, *Am. Nat.* **126**:347–353.

Grant, G. S., 1982, Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment, *Ornith. Monogr.* 30.

Gratto-Trevor, C. L., 1992, Semipalmated Sandpiper, in: *The Birds of North America*, No. 6, (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Graves, J., 1991, Comments on the sample sizes used to test the effect of experimental brood enlargement on adult survival, *Auk* **108**:967–969.

Graves, J., Whiten, A., and Henzi, P., 1984, Why does the Herring Gull lay three eggs?, *Anim. Behav.* **32**:798–805.

Greig-Smith, P., 1985, Weight differences, brood reduction, and sibling competiton among nestling Stonechats *Saxicola torquata* (Aves: Turdidae), *J. Zool.*, London. **205**:453–465.

Groves, S., 1984, Chick growth, sibling rivalry, and chick production in American Black Oystercatchers, *Auk* **101**:525–531.

Haftorn, S., 1981, Incubation during the egg-laying period in relation to clutch-size and other aspects of reproduction in the Great Tit *Parus major*, *Ornis Scand.* **12**:169–185.

Haftorn, S., 1986, Clutch size, intraclutch egg size variation, and breeding strategy in the Goldcrest *Regulus regulus*, *J. Ornithol.* **127**:291–301.

Hahn, D. C., 1981, Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry, *Anim. Behav.* **29**:421–427. (T1 & T2)

Haig, D., 1990, Brood reduction and optimal parental investment when offspring differ in quality, *Am. Nat.* **136**:550–566.

Haig, D., 1992, Brood reduction in gymnosperms, in: *Cannibalism: Ecology and Evolution Among Diverse Taxa*, (M. A. Elgar and B. J. Crespi, eds.), Oxford University Press, Oxford, pp. 63–84.

Haig, S. M., 1992, Piping Plover, in: *The Birds of North America*, No. 2, (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Hall, M. R., and Goldsmith, A. R., 1983, Factors affecting prolactin secretion during breeding and incubation in the domestic duck (*Anas platyrhynchus*), *Gen. Comp. Endocr.* **49**:270–276.

Hamilton, W. D., 1964, The genetical evolution of social behaviour, *J. Theor. Biol.* **7**:1–52.

Harper, R. G., Juliano, S. A., and Thompson, C. F., 1992, Hatching asynchrony in the House Wren, *Troglodytes aedon*: a test of the brood-reduction hypothesis, *Behav. Ecol.* **3**:76–83. (T1 & T2)

Harvey, P. H., and Pagel, M. D., 1991, *The Comparative Method in Evolutionary Biology*, Oxford University Press, New York.

Haydock, J., and Ligon, J. D., 1986, Brood reduction in the Chihuahuan Raven: an experimental study, *Ecology* **67**:1194–1205. (T1 & T2)

Hébert, P. N., 1993a, An experimental study of brood reduction and hatching asynchrony in Yellow Warblers, *Condor* **95**:362–371. (T1 & T2)

Hébert, P. N., 1993b, Hatching asynchrony in the Yellow Warbler: a test of the sexual conflict hypothesis, *Am. Nat.* **142**:881–892. (T1)

Hébert, P. N., and Barclay, R. M. R., 1986, Asynchronous and synchronous hatching: effect on early growth and survivorship of Herring Gull, *Larus argentatus*, chicks, *Can. J. Zool.* **64**:2357–2362. (T1 & T2)

Hébert, P. N., and Sealy, S. G., 1992, Onset of incubation in Yellow Warblers: a test of the hormonal hypothesis, *Auk* **109**:249–255. (T1)

Hébert, P. N., and Sealy, S. G., 1993, Hatching asynchrony in Yellow Warblers: a test of the nest-failure hypothesis, *Ornis Scand.* **24**:10–14. (T1)

Hewston, N., 1984, Breeding of the White-cheeked Touraco, *Tauraco leucotis leucotis*, *Avicul. Mag.* **90**:209–215.

Hilborn, R., and Stearns, S. C., 1982, On inference in ecology and evolutionary biology: the problem of multiple causes, *Acta Biotheor.* **31**:145–164.

Horsfall, J. A., 1991, Brood reduction and brood division in Coots, *Anim. Behav.* **32**:216–225.

Howe, H. F., 1976, Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle, *Ecology* **57**:1195–1207. (T1 & T2)

Howe, H. F., 1978, Initial investment, clutch size, and brood reduction in the Common Grackle *Quiscalus quiscula*, *Ecology* **59**:1109–1122.

Husby, M., 1986, On the adaptive value of brood reduction in birds: experiments with the magpie *Pica pica*, *J. Anim. Ecol.* **55**:75–83.

Hussell, D. J. T., 1972, Factors affecting clutch size in Arctic passerines, *Ecol. Monogr.* **42**:317–364.

Hussell, D. J. T., 1985, On the adaptive basis for hatching asynchrony: brood reduction, nest failure and asynchronous hatching in Snow Buntings, *Ornis Scand.* **16**:205–212. (T1)

Hussell, D. J. T., 1991, Regulation of food provisioning in broods of altricial birds, *Acta XX Cong. Inter. Ornith.*:946–960.

Hussell, D. J. T., and Page, G. W., 1976, Observations on the breeding biology of Black-bellied Plovers on Devon Island, Northwest Territories, Canada, *Wilson Bull.* **88**:632–653.

Hussell, D. J. T., and Quinney, T. E., 1987, Food abundance and clutch size of Tree Swallows *Tachycineta bicolor*, *Ibis* **129**:243–258.

Ingram, C., 1959, Cannibalism in the breeding biology of certain birds of prey, *Auk* **76**:218–226.

Jackson, H. D., 1985, Aspects of the breeding biology of the Fierynecked Nightjar, *Ostrich* **56**:263–276.

Jackson, W. M., 1993, Causes of conspecific nest parasitism in the northern masked weaver, *Behav. Ecol. Sociobiol.* **32**:119–126. (T1 & T2)

Jehl, J. R., Jr., 1973, Breeding biology and systematic relationships of the Stilt Sandpiper, *Wilson Bull.* **85**:115–147.

Jehl, J. R., Jr., and Mahoney, S. A., 1987, The roles of thermal environment and predation in habitat choice in the California Gull, *Condor* **89**:850–862.

Jover, L., Ruiz, X., and González-Martín, M., 1993, Significance of intraclutch egg size variation in the Purple Heron, *Ornis Scand.* **24**:127–134.

Kahl, M. P., 1966, A contribution to the ecology and reproductive biology of the Marabou Stork (*Leptoptilus crumeniferos*) in East Africa, *J. Zool.*, London. **148**:289–311.

Kaufmann, G. W., 1989, Breeding ecology of the Sora, *Porzana carolina*, and the Virginia Rail, *Rallus limicola*, *Can. Field Nat.* **103**:270–282.

Kavanau, J. L., 1987, *Lovebirds, Cockatiels, Budgerigars: Behavior and Evolution*, Science Software Systems, Inc., Los Angeles.

Kemp, A. C., 1978, A review of the hornbills: biology and radiation, *Living Bird* **17**:105–136.

Kendra, P. E., Roth, R. R., and Tallamy, D. W., 1988, Conspecific brood parasitism in the House Sparrow, *Wilson Bull.* **100**:80–90.

Kennamer, R. A., Harvey, W. F., IV, and Hepp, G. R., 1990, Embryonic development and nest attentiveness of Wood Ducks during egg laying, *Condor* **92**:587–592.

Kepler, A. K., 1977, Publications of the Nuttall Ornithological Club, No. 18, *Comparative Study of Todies (Todidae), With Emphasis on the Puerto Rican Tody, Todus mexicanus*, Nuttall Ornithological Club, Cambridge, Mass.

Klomp, H., 1970, The determination of clutch size in birds: a review, *Ardea* **58**:1–124.

Koenig, W. D., 1982, Ecological and social factors affecting hatchability of eggs, *Auk* **99**:526–536.

Konarzewski, M., 1993, The evolution of clutch size and hatching asynchrony in altricial birds: the effect of environmental variability, egg failure and predation, *Oikos* **67**:97–106.

Kuitunen, M., and Aleknonis, A., 1992, Nest predation and breeding success in Common Treecreepers nesting in boxes and natural cavities, *Ornis Fenn.* **69**:7–12.

Lack, D., 1947, The significance of clutch size, *Ibis* **89**:302–352.

Lack, D., 1954, *The Natural Regulation of Animal Numbers*, Oxford University Press, London.

Lack, D., 1966, *Population Studies of Birds*, Clarendon Press, Oxford.

Lack, D., 1968, *Ecological Adaptations for Breeding in Birds*, Methuen and Co., London.

Lack, D., 1973, *Swifts in a tower*, Chapman and Hall, London.

Lamey, T. C., 1990, Hatch asynchrony and brood reduction in penguins, in: *Penguin Biology*, (L. S. Davis and J. T. Darby, eds.), Academic Press, San Diego, pp. 399–416.

Lamey, T. C., and Mock, D. W., 1991, Nonaggressive brood reduction in birds, *Acta XX Cong. Inter. Ornith.*:1741–1751.

Land, D., Marion, W. R., and O'Meara, T. E., 1989, Snag availability and cavity nesting birds in slash pine plantations, *J. Wild. Man.* **53**:1165–1171.

Leonard, M. L., Horn, A. G., and Eden, S. F., 1988, Parent-offspring aggression in moorhens, *Behav. Ecol. Sociobiol.* **23**:265–270.

Lessells, C. M., and Avery, M. I., 1989, Hatching asynchrony in European Bee-eaters *Merops apiaster*, *J. Anim. Ecol.* **58**:815–835.

Lifjeld, J. T., and Slagsvold, T., 1986, The function of courtship feeding during incubation in the Pied Flycatcher *Ficedula hypoleuca*, *Anim. Behav.* **34**:1441–1453.

Lifson, N., and McClintock, R., 1966, Theory of use of the turnover rates of body water for measuring energy and material balance, *J. Theor. Biol.* **12**:46–74.

Ligon, J. D., 1968, Miscellaneous Publications of the Museum of Zoology, No. 136, *The Biology of the Elf Owl, Micrathene whitneyi*, The University of Michigan, Ann Arbor.

Ligon, J. D., and Ligon, S. H., 1990, Female-biased sex-ratios at hatching in the Green Woodhoopoe, *Auk* **107**:765–771.

Lloyd, D. G., 1980, Sexual strategies in plants. I. An hypothesis of sexual adjustment of maternal investment during one reproductive session, *New Phytol.* **86**:69–79.

Lloyd, D. G., 1987, Selection of offspring size at independence and other size-versus-number strategies, *Am. Nat.* **129**:800–817.

Lombardo, M. P., Power, H. W., Stouffer, P. C., Romagnano, L. C., and Hoffenberg, A. S., 1989, Egg removal and intraspecific brood parasitism in the European Starling (*Sturnus vulgaris*), *Behav. Ecol. Sociobiol.* **24**:214:223.

Lowther, P. E., and Cink, C. L., 1992, House Sparrow, in: *The Birds of North America*, No. 12, (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Lyon, B. E., and Montgomerie, R. D., 1985, Incubation feeding in Snow Buntings: female manipulation or indirect male parental care?, *Behav. Ecol. Sociobiol.* **17**:279–284.

Mader, W. J., 1982, Ecology and breeding habits of the Savanna Hawk in the llanos of Venezuela, *Condor* **84**:261–271.

Magrath, R. D., 1988, Hatching asynchrony in altricial birds: nest failure and adult survival, *Am. Nat.* **131**:893–900.

Magrath, R. D., 1989, Hatching asynchrony and reproductive success in the Blackbird, *Nature* **339**:536–538. (T1 & T2)

Magrath, R. D., 1990, Hatching asynchrony in altricial birds, *Biol. Rev.* **65**:587–622.

Magrath, R. D., 1992, Roles of egg mass and incubation pattern in establishment of hatching hierarchies in the Blackbird (*Turdus merulus*), *Auk* **109**:474–487.

Manly, B. F. J., 1991, *Randomization and Monte Carlo Methods in Biology*, Chapman and Hall, London.

Marion, W. R., and Fleetwood, R. J., 1978, Nesting ecology of the Plain Chachalaca in south Texas, *Wilson Bull.* **90**:386–395.

Martin, T. E., 1992, Interaction of nest predation and food limitations in reproductive strategies, *Current Ornithology*, Vol. 9, (D. M. Power, ed.), Plenum Press, New York, pp. 163–197.

Martin, T. E., 1993, Evolutionary determinants of clutch size in cavity-nesting birds: nest predation or limited breeding opportunities?, *Am. Nat.* **142**:937–946.

McClure, P. A., 1981, Sex-biased litter reduction in food-restricted wood rats (*Neotoma floridana*), *Science* **211**:1058–1060.

McNab, B. K., 1989, Laboratory and field studies of the energy expenditure of endotherms: a comparison, *TREE* **4**:111–112.

McRae, S. B., Weatherhead, P. J., and Montgomerie, R., 1993, American Robin nestlings compete by jockeying for position, *Behav. Ecol. Sociobiol.* **33**:101–106.

Mead, P. S., and Morton, M. L., 1985, Hatching asynchrony in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*): a selected or incidental trait?, *Auk* **102**:781–792.

Meanley, B., 1992, King Rail, in: *The Birds of North America*, No. 3, (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Meathrel, C. E., and Ryder, J. P., 1987, Intraclutch variation in the size, mass and composition of Ring-billed Gull eggs, *Condor* **89**:364–368.

Meijer, T., 1990, Incubation development and clutch size in the Starling, *Ornis Scand.* **21**:163–168.

Meyburg, B. U., 1978, Sibling aggression and cross-fostering eagles, in: Endangered Birds: *Symposium on Management Techniques for Preserving Endangered Birds, University of Wisconsin-Madison 1977*, (S. A. Temple, ed.), University of Wisconsin Press, Madison, pp. 195–200.

Milne, I. S., and Calow, P., 1990, Costs and benefits of brooding in Glossiphoniid leeches with special reference to hypoxia as a selection pressure, *J. Anim. Ecol.* **59**:41–56.

Mock, D. W., 1984a, Infanticide, siblicide, and avian nestling mortality, in: *Infanticide: Comparative and Evolutionary Perspectives*, (G. Hausfater and S. B. Hrdy, eds.), Aldine, New York, pp. 3–30.

Mock, D. W., 1984b, Siblicidal aggression and resource monopolization in birds, *Science* **225**:731–733.

Mock, D. W., 1985a, An introduction to the neglected mating system, *Ornith. Monogr.* **37**:1–10.

Mock, D. W., 1985b, Siblicidal brood reduction: The prey-size hypothesis, *Am. Nat.* **125**:327–343.

Mock, D. W., 1987, Siblicide, parent-offspring conflict, and unequal parental investment by egrets and herons, *Behav. Ecol. Sociobiol.* **20:**247–256.

Mock, D. W., and Parker, G. A., 1986, Advantages and disadvantages of egret and heron brood reduction, *Evolution* **40:**459–470.

Mock, D. W., and Ploger, B. J., 1987, Parental manipulations of optimal hatch asynchrony in cattle egrets: an experimental study, *Anim. Behav.* **35:**150–160. (T1 & T2)

Mock, D. W., and Schwagmeyer, P. L., 1990, The peak load reduction hypothesis for avian hatching asynchrony, *Evol. Ecol.* **4:**249–260.

Mock, D. W., Drummond, H., and Stinson, C. H., 1990, Avian siblicide, *Am. Sci.* **78:**438–449.

Møller, A. P., 1989, Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds?, *Oikos* **56:**421–423.

Moreno, J., 1989a, Energetic constraints on uniparental incubation in the Wheatear *Oenanthe oenanthe* (L.), *Ardea* **77:**107–115.

Moreno, J., 1989b, Strategies of mass change in breeding birds, *Biol. J. Linn. Soc.* **37:**297–310.

Moreno, J., and Carlson, A., 1989, Clutch size and the costs of incubation in the Pied Flycatcher *Ficedula hypoleuca*, *Ornis Scand.* **20:**123–128.

Morton, M. L., and Pereyra, M. E., 1985, The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*), *Auk* **102:**25–37.

Mueller, A. J., 1992, Inca Dove, in: *The Birds of North America*, No. 28, (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Murphy, M. T., 1986, Body size and condition, timing of breeding, and aspects of egg production in Eastern Kingbirds, *Auk* **103:**465–476.

Murray, B. G., 1985, Evolution of clutch size in tropical species of birds, *Ornith. Monogr.* **36:**505–519.

Murray, B. G., In press, Effect of selection for successful reproduction on hatching synchrony and asynchrony, *Auk.*

Murton, R. K., and Westwood, N. J., 1977, *Avian Breeding Cycles*, Clarendon Press, Oxford.

Myers, J. H., 1978, Sex ratio adjustment under food stress: maximization of quality or numbers of offspring, *Am. Nat.* **112:**381–388.

Myers, S. A., Millam, J. R., and El Halawani, M. E., 1989, Plasma LH and prolactin levels during the reproductive cycle of the Cockatiel (*Nymphicus hollandicus*), *Gen. Comp. Endocr.* **73:**85–91.

Navarro, J. L., and Bucher, E. H., 1990, Growth of Monk Parakeets, *Wilson Bull.* **102:**520–524.

Nelson, J. B., 1964, Factors influencing clutch-size and chick growth in the North Atlantic Gannet *Sula bassana*, *Ibis* **106:**63–77.

Newton, I., and Marquiss, M., 1984, Seasonal trend in the breeding performance of sparrowhawks, *J. Anim. Ecol.* **53:**809–829.

Nice, M. M., 1962, Development of behavior in precocial birds, *Trans. Linn. Soc. N.Y.* **8:**1–211.

Nilsson, J.-Å., 1993a, Bisexual incubation facilitates hatching asynchrony, *Am. Nat.* **142:**712–717.

Nilsson, J.-Å., 1993b, Energetic constraints on hatching asynchrony, *Am. Nat.* **141:**158–166. (T1)

Nilsson, J.-Å., and Smith, H. G., 1988, Incubation feeding as a male tactic for early hatching, *Anim. Behav.* **36:**641–647.

Nilsson, S., 1986, Evolution of hole-nesting in birds: on balancing selection pressures, *Auk* **103:**432–435.

Nisbet, I. C. T., and Cohen, M. E., 1975, Asynchronous hatching in Common and Roseate Terns, *Sterna hirundo* and *Sterna dougallii*, *Ibis* **117:**374–379.

Norberg, R. Å., 1981, Temporary weight decrease in breeding birds may result in more fledged young, *Am. Nat.* **118:**838–850.

Neuchterlein, G. L., 1981, Asynchronous hatching and sibling competition in Western Grebes, *Can. J. Zool.* **59:**994–998.

Neuchterlein, G. L., and Johnson, A., 1981, The downy young of the Hooded Grebe, *Living Bird* **19:**69–71.

O'Connor, R. J., 1978, Brood reduction in birds: selection for fratricide, infanticide and suicide?, *Anim. Behav.* **26:**79–96.

O'Connor, R. J., 1984, *The Growth and Development of Birds*, John Wiley and Sons, New York.

Olver, M. D., 1984, Breeding biology of the Reed Cormorant, *Ostrich* **55:**133–140.

Orejuela, J. E., 1977, Comparative biology of Turquoise-browed and Blue-crowned Motmots in the Yucatán Peninsula, México, *Living Bird* **16:**193–208.

Oring, L., 1982, Avian mating systems, in: *Avian Biology*, Vol. 6, (D. S. Farner, J. R. King, and K. C. Parkes, eds.), Academic Press, New York, pp. 1–92.

Osborne, D. R., and Bourne, G. R., 1977, Breeding behavior and food habits of the Wattled Jacana, *Condor* **79:**98–105.

Palmer, R. S., 1962, *Handbook of North American Birds*, Vol. 1, Yale University Press, New Haven.

Parmalee, D. F., 1970, Breeding behavior of the Sanderling in the Canadian high arctic, *Living Bird* **9:**97–146.

Parry, V., 1973, The auxiliary social system and its effects on territory and breeding in Kookaburras, *Emu.* **73:**81–100.

Parsons, J., 1975, Asynchronous hatching and chick mortality in the Herring Gull *Larus argentatus*, *Ibis* **117:**517–520.

Parsons, J., 1976, Factors determining the number and size of eggs laid by the Herring Gull, *Condor* **78:**481–492.

Perrins, C. M., and McCleery, R. H., 1989, Laying dates and clutch size in the Great Tit, *Wilson Bull.* **101:**236–253.

Peterman, R. M., 1990, Statistical power analysis can improve fisheries research and management, *Can. J. Fish. Aquat. Sci.* **47:**2–15.

Pettingill, O. S., Jr., 1985, *Ornithology in Laboratory and Field*, 5th ed., Academic Press, Orlando.

Pierotti, R., and Bellrose, C. A., 1986, Proximate and ultimate causation of egg size and the "third-chick disadvantage" in the Western Gull, *Auk* **103:**401–407.

Pietiäinen, H., Saurola, P., and Väisänen, R. A., 1986, Parental investment in clutch size and egg size in the Ural Owl *Strix uralensis*, *Ornis Scand.* **17:**309–325.

Pijanowski, B. C., 1992, A review of Lack's brood reduction hypothesis, *Am. Nat.* **139:**1270–1292.

Ploger, B. J., 1992, Proximate and ultimate causes of brood reduction in Brown Pelicans (*Pelecanus occidentalis*), Ph.D. Dissertation, University of Florida, Gainsville. (T1)

Poole, A., 1985, Courtship feeding and Osprey reproduction, *Auk* **102:**479–492.

Power, H. W., Litovich, E., and Lombardo, M. P., 1981, Male Starlings delay incubation to avoid being cuckolded, *Auk* **98:**386–389.

Redondo, T., and Castro, F., 1992, Signalling of nutritional need by Magpie nestlings, *Ethology* **92:**193–204.

Ricklefs, R. E., 1965, Brood reduction in the Curve-billed Thrasher, *Condor* **67**:505–510.

Ricklefs, R. E., 1969, An analysis of nesting mortality in birds, *Smithsonian Cont. Zool.* **9**:1–48.

Ricklefs, R. E., 1976, Growth rates of birds in the humid new world tropics, *Ibis* **118**:179–207.

Ricklefs, R. E., 1983, Avian postnatal development, in: *Avian Biology*, Vol. 7, (D. S. Farner, J. R. King, and K. C. Parkes, eds), Academic Press, New York, pp. 1–83.

Ricklefs, R. E., 1987, Characterizing the development of homeothermy by rate of body cooling, *Funct. Ecol.* **1**:151–157.

Ricklefs, R. E., 1992, Embryonic development period and the prevalence of avian blood parasites, *Proc. Natl. Acad. Sci. USA* **89**:4722–4725.

Ricklefs, R. E., 1993, Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds, in: *Current Ornithology*, Vol. 11, (D. M. Power, ed.), Plenum Press, New York, pp. 199–276.

Ricklefs, R. E., and Hussell, D. J. T., 1984, Changes in adult mass associated with the nesting cycle in the European Starling, *Ornis Scand.* **15**:155–161.

Ridley, M., 1978, Paternal care, *Anim. Behav.* **26**:904–932.

Robertson, R. J., and Rendell, W. B., 1990, A comparison of the breeding ecology of a secondary cavity nesting bird, the Tree Swallow (*Tachycineta bicolor*), in nest boxes and natural cavities, *Can. J. Zool.* **68**:1046–1052.

Roby, D. D., and Ricklefs, R. E., 1984, Observations on the cooling tolerance of embryos of the Diving Petrel *Pelecanoides georgicus*, *Auk* **101**:160–161.

Rol'nik, V. V., 1970, *Bird Embryology*, Israeli Program for Scientific Translations, Jerusalem.

Romagnano, L., Hoffenberg, A. S., and Power, H. W., 1990, Intraspecific brood parasitism in the European Starling, *Wilson Bull.* **102**:279–291.

Romanoff, A. L., and Romanoff, A. J., 1972, *Pathogenesis of the Avian Embryo*, J. Wiley and Sons, New York.

Roskaft, E., and Slagsvold, T., 1985, Differential mortality of male and female offspring in experimentally manipulated broods of the Rook, *J. Anim. Ecol.* **54**:261–266.

Rowan, M. K., 1967, A study of the Colies of southern Africa, *Ostrich* **38**:63–115.

Rowan, M. K., 1983, *The Doves, Parrots, Louries, and Cuckoos of Southern Africa*, Croom Helm, Beckenham, Kent, UK.

Rydén, O., and Bengtsson, H., 1980, Differential begging and locomotory behaviour by early and late hatched nestlings affecting the distribution of food in asynchronously hatched broods of altricial young, *Z. Tierpsychol.* **53**:209–224.

Salfert, I. G., and Moodie, G. E. E., 1984, Filial egg-cannibalism in the brook stickleback, *Culaea inconstans* (Kirtland), *Behav.* **93**:82–100.

Sasvári, L., 1990, Feeding response of mated and widowed bird parents to fledglings: an experimental study, *Ornis Scand.* **21**:287–292.

Saunders, D. A., 1986, Breeding season, nesting success, and nestling growth in Carnaby's Cockatoo, *Calyptorhynchus funereus latirostris*, over sixteen years at Coomalla Creek, and a method for assessing the viability of populations in other areas, *Aust. Wildl. Res.* **13**:261–273.

Schwagmeyer, P. L., Mock, D. W., Lamey, T. C., Lamey, C. S., and Beecher, M. D., 1991, Effects of sibling contact on hatch timing in an asynchronously hatching bird, *Anim. Behav.* **41**:887–894.

Scott, P. E., and Martin, R. F., 1986, Clutch size and fledging success in the Turquoise-browed Motmot, *Auk* **103**:8–13.

Seddon, P. J., and van Heezik, Y. M., 1991a, Effects of hatching order, sibling asymmetries, and nest site on survival analysis of Jackass Penguin chicks, *Auk* **108**:548–555.

Seddon, P. J., and van Heezik, Y. M., 1991b, Hatching asynchrony and brood reduction in the Jackass Penguin: an experimental study, *Anim. Behav.* **42**:347–356. (T1 & T2)

Sedgwick, J. A., and Knopf, F. L., 1990, Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains, *J. Wild. Man.* **54**:112–124.

Shaw, P., 1985, Brood reduction in the Blue-eyed Shag *Phalacrocorax atriceps*, *Ibis* **127**:476–494. (T1 & T2)

Sibley, C. G., and Ahlquist, J. E., 1990, *Phylogeny and Classification of Birds: a Study in Molecular Evolution*, Yale University Press, New Haven.

Sibley, C. G., and Monroe, B. L., Jr., 1990, *Distribution and Taxonomy of Birds of the World*, Yale University Press, New Haven.

Silver, R., Andrews, H., and Ball, G. F., 1985, Parental care in an ecological perspective: a quantitative analysis of avian subfamilies, *Amer. Zool.* **25**:823–840.

Skagen, S. K., 1987, Hatching asynchrony in American Goldfinches: an experimental study, *Ecology* **68**:1747–1759. (T1 & T2)

Skagen, S. K., 1988, Asynchronous hatching and food limitation: a test of Lack's Hypothesis, *Auk* **105**:78–88. (T1 & T2)

Skutch, A. F., 1957, The incubation patterns of birds, *Ibis* **99**:69–93.

Skutch, A. F., 1964, Life history of the Scaly-breasted Hummingbird, *Condor* **66**:186–198.

Skutch, A. F., 1969, Pacific Coast Avifauna, No. 35, *Life Histories of Central American Birds*, Vol. 2, Cooper Ornithological Society, Berkeley.

Skutch, A. F., 1972, Publications of the Nuttall Ornithological Club, No. 10, *Studies of Tropial American Birds*, Nuttall Ornithological Club, Cambridge, Mass.

Skutch, A. F., 1983, *Birds of Tropical America*, University of Texas Press, Austin.

Skutch, A. F., 1985, Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed, *Ornith. Monogr.* **36**:575–594.

Slagsvold, T., 1982, Clutch size, nest size, and hatching asynchrony in birds: experiments with the Fieldfare (*Turdus pilaris*), *Ecology* **63**:1389–1399. (T1 & T2)

Slagsvold, T., 1985, Asynchronous hatching in passerine birds: influence of hatching failure and brood reduction, *Ornis Scand.* **16**:81–87.

Slagsvold, T., 1986a, Asynchronous versus synchronous hatching in birds: experiments with the Pied Flycatcher, *J. Anim. Ecol.* **55**:1155–1134. (T1 & T2)

Slagsvold, T., 1986b, Hatching asynchrony: interspecific comparisons of altricial birds, *Am. Nat.* **128**:120–125.

Slagsvold, T., 1990, Fisher's sex ratio theory may explain hatching patterns in birds, *Evolution* **44**:1009–1017.

Slagsvold, T., and Amundsen, T., 1992, Do Great Tits adjust hatching spread, egg size and offspring sex ratio to changes in clutch size?, *J. Anim. Ecol.* **61**:249–258.

Slagsvold, T., and Lifjeld, J. T., 1989a, Constraints on hatching asynchrony and egg size in Pied Flycatchers, *J. Anim. Ecol.* **58**:837–845.

Slagsvold, T., and Lifjeld, J. T., 1989b, Hatching asynchrony in birds: the hypothesis of sexual conflict over parental investment, *Am. Nat.* **134**:239–253. (T1)

Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, O., and Husby, M., 1984, On the adaptive value of intraclutch egg-size variation in birds, *Auk* **101**:685–697.

Slagsvold, T., Roskaft, E., and Engen, S., 1986, Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds, *Ornis Scand.* **17**:117–125.

Slagsvold, T., Husby, M., and Sandvik, J., 1992, Growth and sex ratio of nestlings in two species of crow: how important is hatching asynchrony?, *Oecologia* **90**:43–49.

Slagsvold, T., Amundsen, T., and Dale, S., 1994, Selection by sexual conflict for evenly spaced offspring in blue tits, *Nature* **370**:136–138. (T1 & T2)

Smith, G. T., and Saunders, D. A., 1986, Clutch size and productivity in three sympatric species of Cockatoo (Psittaciformes) in the southwest of Australia, *Aust. Wildl. Res.* 13:275–285.

Smith, H. G., and Montgomerie, R., 1991, Nestling American Robins compete with siblings by begging, *Behav. Ecol. Sociobiol.* 29:307–312.

Smith, K. G., 1988, Clutch-size dependent asynchronous hatching and brood reduction in *Junco hyemalis*, *Auk* 105:200–203.

Snow, D. W., 1961, The natural history of the Oilbird, *Steatornis caripensis*, in Trinidad, W.I. Part 1. General behavior and breeding habits, *Zool.* 46:27–48.

Snyder, N. F. R., Wiley, J. W., and Kepler, C. B., 1987, *The Parrots of Luquillo: Natural History and Conservation of the Puerto Rican Parrot*, Western Foundation of Vertebrate Zoology, Los Angeles.

Speakman, J. R., and Racey, P. A., 1988, The doubly-labelled water technique for measurement of energy expenditure in free-living animals, *Sci. Prog., Oxf.* 72:227–237.

Spellerberg, I. F., 1971, Breeding behavior of the McCormick Skua, *Ardea* 59:189–230.

Stamps, J., Clark, A., Arrowood, P., and Kus, B., 1985, Parent-offspring conflict in Budgerigars, *Behav.* 94:1–40.

Stamps, J., Clark, A., Kus, B., and Arrowood, P., 1987, The effects of parent and offspring gender on food allocation in Budgerigars, *Behav.* 101:177–199.

Stanback, M. T., 1991, Causes and consequences of nestling size variation in the cooperatively breeding Acorn Woodpecker *Melanerpes formicivorus*, Ph.D. Dissertation, University of California, Berkeley.

Stanback, M. T., and Koenig, W. D., 1992, Cannibalism in birds, in: *Cannibalism: Ecology and Evolution Among Diverse Taxa*, (M. A. Elgar and B. J. Crespi, eds.), Oxford University Press, Oxford, pp. 276–298.

Stearns, S. C., 1980, A new view of life-history evolution, *Oikos* 35:266–281.

Steidl, R. J., and Griffin, C. R., 1991, Growth and brood reduction of mid-Atlantic coast Ospreys, *Auk* 108:363–370.

Stinson, C. H., 1979, On the selective advantage of fratricide in raptors, *Evolution* 33:1219–1225.

Stokland, J. N., and Amundsen, T., 1988, Initial size hierarchy in broods of the Shag: relative significance of egg size and hatching asynchrony, *Auk* 105:308–315.

Stouffer, P. C., 1989, Hatching asynchrony in the European Starling, Ph.D. Dissertation, University of Pennsylvania, Philadelphia.

Stouffer, P. C., and Power, H. W., 1990, Density effects on asynchronous hatching and brood reduction in European Starlings, *Auk* 107:359–366.

Stouffer, P. C., and Power, H. W., 1991, An experimental test of the brood-reduction hypothesis in European Starlings, *Auk* 108:519–531. (T1 & T2)

Strahl, S. D., 1988, The social organization and behavior of the Hoatzin *Opisthocomus hoazin* in central Venezuela, *Ibis* 130:483–502.

Strehl, C., 1978, Asynchrony of hatching in Red-winged Blackbirds and survival of late and early hatching birds, *Wilson Bull.* 90:653–655.

Sturkie, P. D., and Mueller, W. J., 1976, Reproduction in the female and egg production, in: *Avian Physiology*, 3rd ed., (P. D. Sturkie, ed.), Springer-Verlag, New York, pp. 302–330.

Stutchbury, B. J., and Robertson, R. J., 1988, Within-season and age-related patterns of reproductive performance in female Tree Swallows (*Tachycineta bicolor*), *Can. J. Zool.* 66:827–834.

Sullivan, J. P., 1988, Effects of provisioning rates and number fledged on nestling aggression in Great Blue Herons, *Col. Waterbirds* 11:220–226.

Swanberg, P. O., 1950, On the concept of "incubation period," *Vår Fågalvärd* 9:63–77.

Sydeman, W. J., and Emslie, S. D., 1992, Effects of parental age on hatching asynchrony, egg size, and third-chick disadvantage in Western Gulls, *Auk* 109:242–248.

Tacha, T. C., Nesbitt, S. A., and Vohs, P. A., 1992, Sandhill Crane, in: *The Birds of North America*, No. 31, (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

Tallamy, D. W., 1984, Insect parental care, *BioScience* 34:20–24.

Taplin, A., and Beurteaux, Y., 1992, Aspects of the breeding biology of the Pheasant Coucal, *Emu.* 92:141–146.

Taylor, B. L., and Gerrodette, T., 1993, The uses of statistical power in conservation biology: the Vaquita and the Northern Spotted Owl, *Conserv. Bio.* 7:489–500.

Teather, K. L., and Weatherhead, P. J., 1988, Sex-specific energy requirements of Great-tailed Grackle (*Quiscalus mexicanus*) nestlings, *J. Anim. Ecol.* 57:659–668.

Teather, K. L., and Weatherhead, P. J., 1989, Sex-specific mortality in nestling Great-tailed Grackles, *Ecology* 70:1485–1493.

Thomas, B. T., 1984, Maguari Stork nesting: juvenile growth and behavior, *Auk* 101:812–823.

Thomas, B. T., and Strahl, S. D., 1990, Nesting behavior of Sunbitterns (*Eurypyga helias*) in Venezuela, *Condor* 92:576–581.

Thompson, S. C., and Raveling, D. G., 1987, Incubation behavior of Emperor Geese compared with other geese: interactions of predation, body size, and energetics, *Auk* 104:707–716.

Trivers, R. L., 1972, Parental investment and sexual selection, in: *Sexual Selection and the Descent of Man*, (B. Campbell, ed.), Aldine, Chicago, pp. 136–179.

Trivers, R. L., 1974, Parent-offspring conflict, *Amer. Zool.* 14:249–265.

Trivers, R. L., and Willard, D. E., 1973, Natural selection of parental ability to vary the sex ratio of offspring, *Science* 179:90–92.

van Heezik, Y. M., and Davis, L., 1990, Effects of food variability on growth rates, fledgling sizes and reproductive success in the Yellow-eyed Penguin *Megadyptes antipodes*, *Ibis* 132:354–365.

van Tienhoven, A., 1983, *Reproductive Physiology of Vertebrates*, Cornell University Press, Ithaca.

Veiga, J. P., 1990, A comparative study of reproductive adaptations in House and Tree Sparrows, *Auk* 107:45–59.

Veiga, J. P., 1992, Hatching asynchrony in the House Sparrow: a test of the egg-viability hypothesis, *Am. Nat.* 139:669–675. (T1)

Veiga, J. P., and Viñuela, J., 1993, Hatching asynchrony and hatching success in the House Sparrow: evidence for the egg viability hypothesis, *Ornis Scand.* 24:237–242.

Vince, M. A., 1964, Social facilitation of hatching in the Bobwhite Quail, *Anim. Behav.* 12:531–534.

Vince, M. A., 1968, Retardation as a factor in the synchronization of hatching, *Anim. Behav.* 16:332–335.

Viñuela, J., 1991, Ecología reproductiva del Milano Negro *Milvus migrans* en el Parque Nacional Doñana, PhD. Dissertation, Universidad Complutense de Madrid, Spain.

Viñuela, J., and Bustamante, J., 1993, Effect of growth and hatching asynchrony on the fledging age of Black and Red Kites, *Auk* 109:748–757.

Vleck, C. M., 1981, Energetic costs of incubation in the Zebra Finch, *Condor* 83:229–237.

Voous, K. H., 1975, *Owls of the Northern Hemisphere*, William Collins Sons & Co., Ltd., London.

Walsberg, G. E., and King, J. R., 1978, The energetic consequences of incubation for two passerine species, *Auk* 95:644–655.

Walsberg, G. E., and Voss-Roberts, K. A., 1983, Incubation in desert-nesting doves: mechanisms for egg-cooling, *Physiol. Zool.* **56**:88–93.

Waltman, J. R., and Beissinger, S. R., 1992, Breeding behavior of the Green-rumped Parrotlet, *Wilson Bull.* **104**:65–84.

Ward, D., 1990, Incubation temperatures and behavior of Crowned, Black-winged, and Lesser Black-winged Plovers, *Auk* **107**:10–17.

Weatherhead, P. J., and Teather, K. L., 1991, Are skewed fledgling sex ratios in sexually dimorphic birds adaptive?, *Am. Nat.* **138**:1159–1172.

Weathers, W. W., 1979, Climatic adaptation in avian standard metabolic rate, *Oecologia* **42**:81–89.

Weathers, W. W., and Sullivan, K. A., 1989, Nest attentiveness and egg temperature in the Yellow-eyed Junco, *Condor* **91**:628–633.

Webb, D. R., 1987, Thermal tolerance of avian embryos: a review, *Condor* **89**:874–898.

Werschkul, D. F., 1979, Nestling mortality and the adaptive significance of early locomotion in the Little Blue Heron, *Auk* **96**:116–130. (T1 & T2)

Westerterp, K. R., and Bryant, D. M., 1984, Energetics of free existence in swallows and martins (Hirundinidae) during breeding: a comparative study using doubly-labelled water, *Oecologia* **62**:376–381.

White, F. N., and Kinney, J. L., 1974, Avian incubation, *Science* **186**:107–115.

Wiebe, K. L., and Bortolotti, G. R., 1994, Food supply and hatching spans of birds: energy constraints or facultative manipulation?, *Ecology* **75**:813–823.

Wiebe, K. L., and Bortolotti, G. R., 1994b, Energetic efficiency of reproduction: the benefits of asynchronous hatching for American Kestrels, *J. Anim. Ecol.* **63**:551–560. (T1 & T2)

Wiley, R. H., and Wiley, M. S., 1980, Spacing and timing in the nesting ecology of a tropical blackbird: comparison of populations in different environments, *Ecol. Monogr.* **50**:153–178.

Williams, J. A., 1980, Aspects of the breeding biology of the Subantarctic Skua, *Ostrich* **58**:160–167.

Williams, J. B., 1991, On the importance of energy considerations to small birds with gynelateral intermittent incubation, *Acta XX Congr. Inter. Ornith.*:1964–1975.

Wilson, R. T., Wilson, M. P., and Durkin, J. W., 1986, Breeding biology of the Barn Owl *Tyto alba* in central Mali, *Ibis* **128**:81–90.

Wilson, R. T., Wilson, M. P., and Durkin, J. W., 1987, Aspects of the reproductive ecology of the Hamerkop *Scopus umbretta* in central Mali, *Ibis* **129**:382–388.

Woodard, A. E., and Mather, F. B., 1964, The timing of ovulation, movement of the ovum through the oviduct, pigmentation and shell deposition in Japanese Quail (*Coturnix coturnix japonica*), *Poultry Sci.* **43**:1427–1432.

Wrege, P. H., and Emlen, S. T., 1991, Breeding seasonality and reproductive success of White-fronted Bee-eaters in Kenya, *Auk* **108**:673–687.

Yom-Tov, Y., Ar, A., and Mendelssohn, H., 1978, Incubation behavior of the Dead Sea Sparrow, *Condor* **80**:340–343.

Zach, R., 1982, Hatching asynchrony, egg size, growth, and fledging in Tree Swallows, *Auk* **99**:695–700.

Zerba, E., and Morton, M. L., 1983, The rhythm of incubation from egg laying to hatching in Mountain White-crowned Sparrows, *Ornis Scand.* **14**:188–197.

Zwickel, F. C., 1992, Blue Grouse, in: *The Birds of North America*, No. 15, (A. Poole, P. Stettenheim, and F. Gill, eds.), The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.

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