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EFFECT OF SELECTION FOR SUCCESSFUL REPRODUCTION ON HATCHING SYNCHRONY AND ASYNCHRONY

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ABSTRACT.—Hypotheses regarding the evolution of asynchronous hatching in birds are evaluated with respect to the Murray-Nolan clutch-size equation, which distinguishes between the number of broods successfully reared per female during a breeding season ($\Sigma_1^n P_i$) and within-brood survivorship (which affects $\Sigma_\alpha^\omega \lambda_x$). Asynchronous hatching is best interpreted as an adaptation that reduces the probability of whole-brood loss to predation, inclement weather, or other cause of whole-brood mortality (i.e. it increases a female's probability of rearing at least one young to nest-leaving from a clutch, s_n, and increases $\Sigma_1^n P_i$). This hypothesis constitutes a different form of the hypotheses of Tyrväinen, Hussell, and Clark and Wilson. The equations of Clark and Wilson and of Hussell erred in assuming a stepped function of the probability of daily survivorship (d_s) during the nesting cycle. Instead, I assume a smooth curve and argue that if $d_s < 1$ and if $s_n = \Pi\ d_s$, then asynchronous hatching results in increasing s_n and $\Sigma_1^n P_i$ of the clutch-size equation. Alternative hypotheses explaining the evolution of asynchronous hatching seem better interpreted as explanations for increasing within-brood success, increasing the number of young to nest-leaving (k_n) of successful broods, and increasing $\Sigma_\alpha^\omega \lambda_x$ of the clutch-size equation, or as unselected consequences of selection for reducing whole-brood loss. *Received 26 July 1993, accepted 11 January 1994.*

BIRDS LAY no more than one egg per day, and incubation may begin at any time during the laying sequence. If incubation begins before the last egg is laid, hatching may be asynchronous. Several hypotheses have been proposed to explain the evolution of asynchronous hatching. They include the notions that asynchronous hatching may: (1) result in rapid brood reduction when feeding conditions are poor (Lack 1947, 1954, Ricklefs 1965, Pijanowski 1992); (2) reduce the probability of whole brood loss (Tyrväinen 1969, Hussell 1972, Clark and Wilson 1981); (3) reduce the peak feeding load on adults (Hussell 1972, 1985a); (4) result from laying "insurance" eggs after incubation has begun (Dorward 1962, Nisbet and Cohen 1975, Stinson 1979); (5) shorten the time during which a clutch is vulnerable to brood parasitism (Wiley and Wiley 1980, Lombardo et al. 1989); (6) reduce sibling rivalry (Hahn 1981); (7) reduce the time that adults are exposed to predation (Magrath 1988); (8) result in greater paternal contribution to the brood (Slagsvold and Lifjeld 1989); or (9) reduce the loss of early laid eggs to inviability (Veiga 1992). Mead and Morton (1985), however, suggested that asynchronous hatching is not adaptive at all but an incidental consequence of the hormonal mechanism controlling the transition from egg laying to incubation.

From my clutch-size theory (Murray 1979, 1991a), I infer that asynchronous hatching increases the probability of successful reproduction of parents by reducing the probability of whole-brood loss. Thus, the clutch-size theory lends support to the "nest-failure" hypothesis of Tyrväinen (1969), Hussell (1972), and Clark and Wilson (1981), although my argument is different from theirs. Empirical data gleaned from the literature, however, indicate that hatching is more synchronous than expected from the theory (Clark and Wilson 1981, Slagsvold 1986, Magrath 1990). Furthermore, studies on the Boat-tailed Grackle (*Quiscalus major*; Bancroft 1985), Least Flycatcher (*Empidonax minimus*; Briskie and Sealy 1989), and Yellow Warbler (*Dendroica petechia*; Hébert and Sealy 1993), specifically undertaken to test the hypothesis, confirm that hatching is more synchronous than expected from the formulations of Clark and Wilson (1981) and Hussell (1985a, b). Thus, the nest-failure hypothesis seems to have little empirical support.

In this paper I examine the nest-failure hypothesis and some other hypotheses on asynchronous hatching in light of my clutch-size theory.

THE HUSSELL EQUATION

Tyrväinen (1969), Hussell (1972), and Clark and Wilson (1981) proposed that asynchronous hatching evolved as a means of reducing the probability of parents losing an entire brood before any young leave the nest. Clark and Wilson (1981) also proposed an equation for calculating the number of young leaving the nest (W_m), given the daily probabilities of surviving during the nesting period, with which one could evaluate the effect on the production of young of starting incubation with different eggs in the laying sequence. Incubation should begin such that W_m is maximized.

Hussell (1985a, b) modified the Clark and Wilson equation by breaking the nesting period into four parts, it becoming (here I substitute Ψ for the original Ps in order to distinguish them from the Ps of equation 2, below)

$$W_m = \Psi_0^{(m-1)t_1}\Psi_1^{t_2}\Psi_2^{t_3}\left(m + \sum_{i=1}^{N-m} \Psi_3^{it_1}\right), \quad (1)$$

where Ψ_0 is the daily probability of survival of the nest contents from start of laying to start of incubation, Ψ_1 is the daily probability of survival of the nest contents from start of incubation to first hatch, Ψ_2 is the daily probability of survival of the nest contents from first hatch to first fledge, Ψ_3 is the daily probability of survival of the nest contents from first fledge to last fledge, N is the clutch size, m is the egg with which incubation starts, t_1 is the laying interval (in days) between eggs, t_2 is the incubation period (in days) for an individual egg, and t_3 is the nestling period (in days) for an individual chick.

The unstated assumption of the mathematical equations of Clark and Wilson (1981) and Hussell (1985a) is that the different periods of the nesting cycle are characterized by different daily probabilities of survival, which are constant during each period, resulting in a stepped function of the daily probability of survival of the nest contents (Fig. 1). In the Yellow Warbler, for example, $\Psi_0 = 0.9469$, $\Psi_1 = 0.9870$, $\Psi_2 = 0.9765$, and $\Psi_3 = 0.9924$ (Hébert and Sealy 1993). Thus, if a female Yellow Warbler lays a four-egg clutch and begins incubation on completion of the clutch (day 3), the daily probability of survival changes from 0.9469 to 0.9870 on day 3. According to equation 1, if incubation begins with the penultimate egg, the change occurs on day 2; if with the antepenultimate egg, on day 1; and if with the first egg, on day 0.

This unstated but inherent assumption is probably in error and may be responsible for the discrepancies between theory and fact. The assumption that survivorship is flat throughout each of the four stages seems contrary to fact, judging from daily survivorship curves of eggs and nestlings (Willis 1961, Young 1963, Horn 1968, Holcomb 1972, Caccamise 1976, Woolfenden and Fitzpatrick 1984). Ornithologists typically do not report daily rates of whole-brood loss; for an exception, see Petrinovich and Patterson (1983), who showed an uneven relationship only during the nestling phase.

The method of calculating Ψ_0, Ψ_1, Ψ_2, and Ψ_3 from field data contributes to the error. In practice, with few exceptions, investigators calculate the proportion of nests that survive during one of the four periods and convert that proportion to a mean daily probability of surviving during that period (Hussell 1985a, Briskie and Sealy 1989, Hébert and Sealy 1993). The mean d_s is then presumed to be the actual d_s for each day, when d_s may vary daily during the egg-laying, incubation, brooding, and the departure periods. The usual method of calculating the daily probabilities compounds the theoretical error described in the previous paragraph.

Suppose instead that d_s varies as a smooth curve (Fig. 2) or even as a straight line, which increases, decreases, or remains constant through the nesting period. On day 2, for example, d_s is the same regardless of whether a parent has begun incubating or not. If d_s is measured in the normal manner described above, however, d_s could be different for each stage of the nesting cycle. From the data used to plot Figure 2, I have calculated the mean values of d_s for the different parts of the nesting period (i.e. Ψ_0, Ψ_1, Ψ_2, and Ψ_3), assuming that incubation begins on day 0, 1, 2, or 3. The result is the stepped functions shown in Figure 1. This method of calculation gives a misleading picture of the survivorship of nest contents when incubation begins on different days (Fig. 3).

Although its mathematical formulation is in error, leading to discrepancies between theoretical expectations and fact, the nest-failure hypothesis is not necessarily wrong. In the following sections, I propose a different formulation.

THE CLUTCH-SIZE EQUATION

Murray and Nolan (1989) proposed an equation for calculating the mean clutch size of a

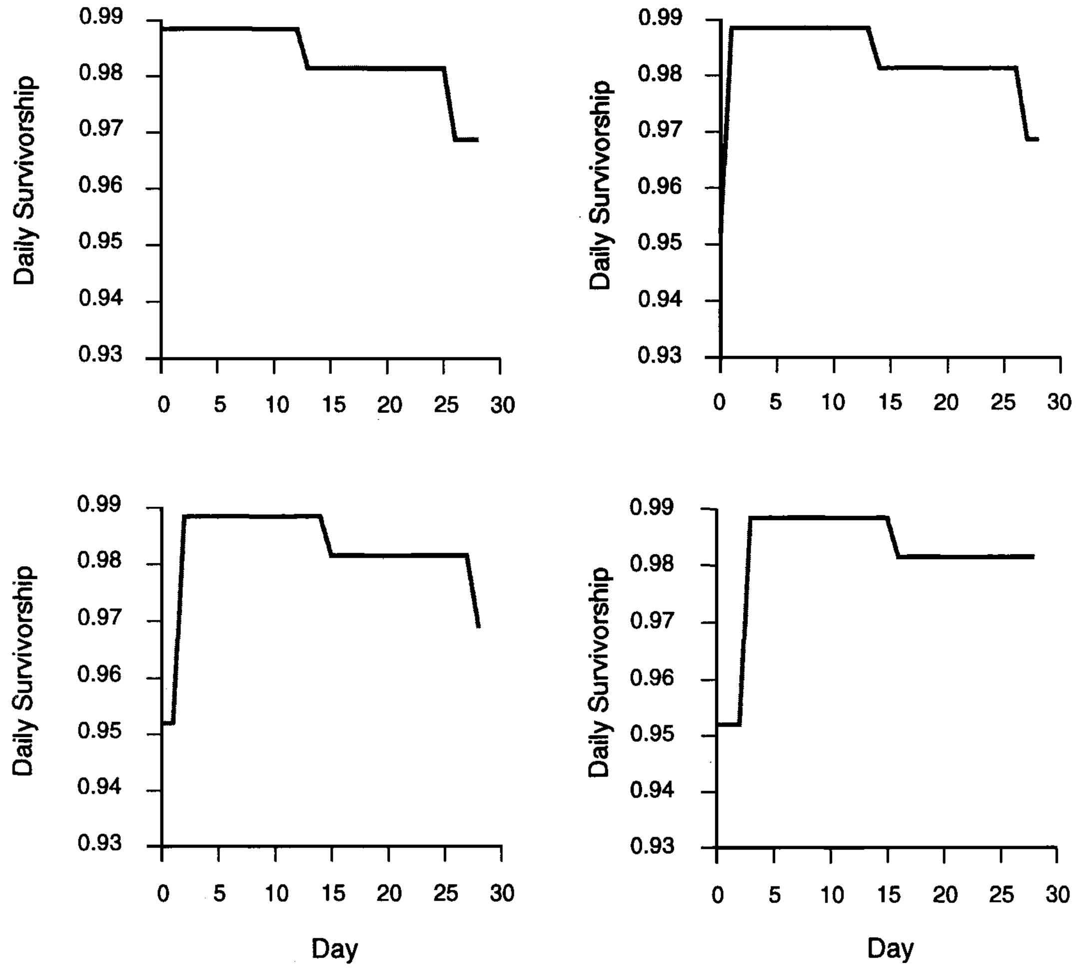

Fig. 1. Daily survivorship of nest contents, calculated with Hussell equation from mean survivorship from start of laying to start of incubation (Ψ_0), from start of incubation to first hatching (Ψ_1), from first hatching to first fledging (Ψ_2), and from first fledging to last fledging (Ψ_3). Data were those used to construct curve in Figure 2. Incubation begins on first (upper left), second (upper right), third (lower left), or fourth day (lower right).

population of females with a particular genotype,

$$CS = \frac{a + 1}{\sum_{\alpha}^{\omega} \lambda_x \sum_{1}^{n} P_i}, \qquad (2)$$

where a is the primary sex ratio (assumed to be 1 in birds), λ_x is the probability of surviving from birth (in birds, from the laying of the egg) to age x of those individuals from successful clutches or litters, α is the average age of first breeding, ω is the age of last breeding, and $\Sigma_1^n P_i$ is the number of broods reared per female in a breeding season.

In this equation, $\Sigma_1^n P_i$ measures success of females in rearing broods and reflects the effect of whole-brood loss, whereas $\Sigma_\alpha^\omega \lambda_x$ measures survivorship of individuals from eggs laid in successful clutches and, thus, reflects the effect of within-brood loss because survivorship through nest-leaving in successful nests affects all subsequent values of λ_x. In discussing hatching asynchrony, it is important to keep distinct the effects of whole-brood loss and within-brood loss.

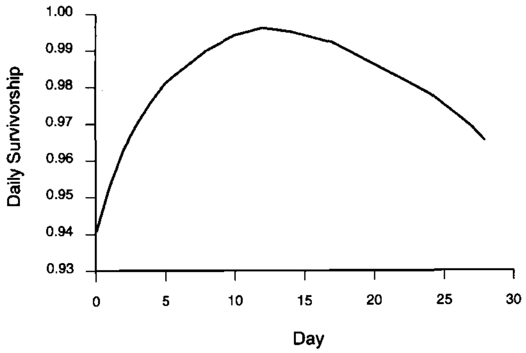

Fig. 2. Daily survivorship (d_s) of nest contents.

ASYNCHRONOUS HATCHING

The annual reproductive success of females of a genotype is the product of the mean number of broods successfully reared during the breeding season and the mean number of young reared from a successful brood. The mean number of broods reared per female is

$$\text{ARS(b)} = \sum_{1}^{n} P_i \tag{3}$$

$$= P_1 + P_2 \ldots + P_n \tag{4}$$

$$= c_1 s_1 + c_2 s_2 \ldots + c_n s_n, \tag{5}$$

where: P_1, P_2, and P_n are the probabilities of the females' successfully rearing at least one, two, and n broods during a breeding season; c_1, c_2, and c_n are the mean number of clutches laid in producing a first, second, and nth brood; and s_1, s_2, and s_n are the probabilities that first, second, and nth brood clutches produce at least one young to independence (Murray 1991a, b).

The mean number of young successfully reared during a breeding season is

$$\text{ARS(k)} = \sum_{1}^{n} c_i s_i k_i, \tag{6}$$

where k_i is the number of young reared per successful brood (Murray 1991b).

The genotype of females that rear more broods during a breeding season should be favored over those of females that rear fewer. Also, for a clutch of four eggs, for example, a genotype that rears on average three chicks from the clutch should be favored over a genotype that rears two, and either should be favored over a genotype that rears only one. Thus, traits that increase the probability of a female's rearing a brood from a clutch (s_n) and that maximize the number of young reared successfully from a clutch of a particular size (k_n) should be favored over those that do not. Increasing s_n increases $\Sigma_1^n P_i$, and increasing k_n increases $\Sigma_\alpha^\omega \lambda_x$ (because survivorship through nest-leaving affects all subsequent values of λ_x). The two aspects of reproductive success, reduction of whole-brood loss (increasing s_n) and the mean number of young in a successful brood (k_n), however, cannot be simultaneously maximized.

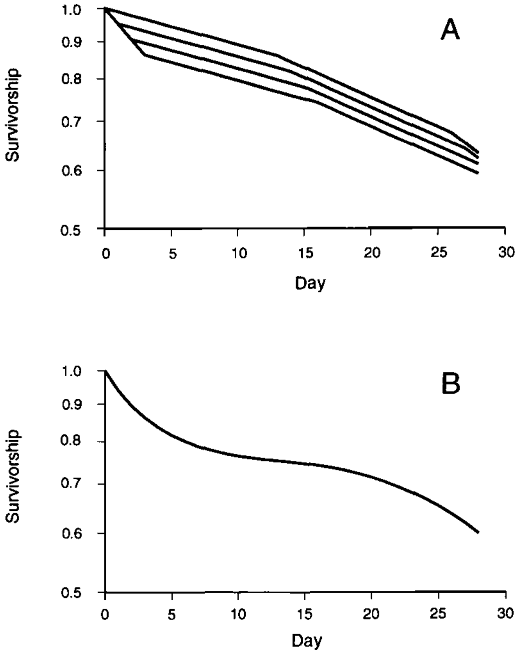

Fig. 3. Survivorship of nest contents plotted from data used to construct curves in Figures 1 and 2. (A) Calculated with Hussell equation. (B) Calculated with $s_n = \Pi\ d_s$.

Regardless of the shape of the d_s function (whether curvilinear or increasing, decreasing, or constant in time), the probability of rearing any portion of a brood (s_n) from a clutch is

$$s_n = \Pi\ d_s. \tag{7}$$

This probability can be increased by shortening the time that eggs and chicks are exposed to loss from predation, inclement weather, or other cause of mortality. The maximum s_n, then, is achieved by beginning incubation with the laying of the first egg. Incubation, however, does not often begin with the first egg because doing so lowers k_n. The feeding of already hatched chicks may interfere with incubation of unhatched eggs (Bancroft 1985, Slagsvold 1982, 1985, 1986, Nilsson 1993), and the time required to feed out-of-the-nest chicks may interfere with the adequate feeding of the chicks remaining in the nest. Either would result in lowering k_n.

If early incubation reduces k_n, then postponing the start of incubation would result in increasing k_n but at the cost of a lower s_n. Selection for successful reproduction, then, involves a trade-off between successfully rearing any portion of a clutch (i.e. greater s_n, smaller k_n) and rearing a larger brood (i.e. smaller s_n, greater k_n). In the extreme case, selection for synchronous hatching occurs in those precocial species in which young and parents leave the nest shortly after hatching. The unhatched eggs have zero probability of surviving, and asynchronous hatching would be selected against. The trade-off between a higher probability of rearing a smaller brood and a lower probability of rearing a larger brood in altricial species could vary from species to species and may account for the observed variation in degree of asynchronous hatching.

Accordingly, asynchronous hatching is an adaptation that increases the probability of successfully rearing one or more young from a clutch (s_n). The degree of asynchronony, however, is a consequence of selection maximizing the survivorship of young in a successful brood (see below).

DISCUSSION

I have argued that starting incubation before completion of the clutch, resulting in asynchronous hatching, is an adaptation that reduces the probability of whole-brood loss to predation, inclement weather, or other cause of mortality. If the daily probability of surviving from one day to the next (d_s) is less than one, then asynchronous hatching seems inevitable. Asynchronous hatching, however, would be unexpected in precocial species (e.g. waterfowl, phasianids) in which parents and young leave the nest site shortly after hatching occurs.

Alternative hypotheses regarding the evolution of asynchronous hatching focus attention on within-brood loss (affecting $\Sigma_\alpha^\omega \lambda_x$) rather than on the probability of whole-brood loss (affecting $\Sigma_1^n P_i$). For example, Lack (1947, 1954) suggested that asynchronous hatching is a means of facilitating the reduction of a brood to manageable size should food become scarce during the brood-rearing period. Accordingly, brood reduction is an adaptation that maximizes k_n rather than s_n. Asynchronous hatching, however, does not necessarily lead to brood reduction, and brood reduction can be achieved by means other than asynchronous hatching (Clark and Wilson 1981). Although asynchronous hatching may facilitate brood reduction, it need not be the cause of brood reduction. Brood reduction seems to be a means of increasing k_n and $\Sigma_\alpha^\omega \lambda_x$ over what they would be if parents attempted to rear the entire brood in the face of food shortage.

Others have suggested that females lay eggs after beginning incubation as insurance against infertility or the failure of early-laid eggs or early-hatched nestlings (Dorward 1962, Nisbet and Cohen 1975, Stinson 1979, Veiga 1992). Infertility and other sorts of within-brood failure, however, affect k_n and $\Sigma_\alpha^\omega \lambda_x$, and thus the evolution of insurance eggs should be expected to evolve independently of whether eggs hatch asynchronously or not. If there is some probability of infertility of any of the eggs of a species with synchronous hatching, selection for successful reproduction should result in the evolution of larger clutches (eq. 2). Again, the probability of within-brood loss does not lead to the evolution of asynchronous hatching.

Some species with two-egg clutches never rear more than one young (e.g. Dorward 1962, Stinson 1979, Mock 1984, Anderson 1990). Indeed, in a few species the first-hatched chick actively kills or expels from the nest its younger sibling. In this case, it seems clear that the second egg can only provide insurance against the failure of the first-laid egg. This does not mean, however, that asynchronous hatching occurs because insurance eggs have been laid. A detailed examination of this case may be instructive.

Consider a genotype that is single-brooded and lays a single egg with little likelihood of laying replacement clutches following failures. The probability of rearing a young is s_n. In this special case, $k_n = s_n = \Sigma_1^n P_i$. Let us say these variables have a value of 0.65 (i.e. 65 of 100 breeding females successfully rear one young). If this value is inserted into the clutch-size equation (eq. 2), and if the predicted replacement clutch size is greater than one, then this genotype will become extinct. The population will also become extinct, unless there is an alternative genotype, "lay two eggs in a clutch." Thus, if this population exists, the females lay two eggs in a clutch because the alternative genotype, "one-egg clutch," cannot persist. Should the females with two-egg clutches begin incubation with their first or second egg? This is a different question from why they should lay two eggs rather than one. If they begin with the second egg, s_n should be less than 0.65 (fewer than 65 of 100 females will be successful; see eq. 7), although k_n could be greater than 0.65 (*only* if some females rear two young). If they begin incubating with the first egg, s_n will be 0.65 (whether or not the elder young kills its younger sibling), as before with a one-egg clutch, but $\Sigma_1^n P_i$ and k_n could be greater than 0.65 if losses of the first egg or early-stage young were recouped by success of the second egg (thus, more than 65 of 100 females rear one young). Accordingly, in species in which females lay two eggs but never rear more than one young at a time, asynchronous hatching is selected because it increases the probability of successful reproduction ($\Sigma_1^n P_i$) by reducing the probability of whole-brood loss rather than by promoting brood reduction, even though brood reduction is a consequence of laying two-egg clutches.

Wiley and Wiley (1980) and Lombardo et al. (1989) suggested that asynchronous hatching may shorten the time during which a clutch is vulnerable to brood parasitism because incubation begins earlier. An adult sitting on the nest presumably deters brood parasites from laying their eggs. Considering the cost of successful brood parasitism, the reduction of both k_n (and $\Sigma_\alpha^\omega \lambda_x$) and s_n (and $\Sigma_1^n P_i$), this hypothesis seems highly attractive. Nevertheless, it is hardly a general explanation for the occurrence of asynchronous hatching. It could also be an unselected consequence of selection for reducing the probability of whole-brood loss. The possibility that asynchronous hatching reduces sibling rivalry (Hahn 1981) or reduces the peak feeding load on adults (Hussell 1972, 1985a), when either occurs, could also be unselected consequences of selection for reducing the probability of whole-brood loss.

Magrath (1988) proposed that asynchronous hatching may shorten the time that adults are exposed to predation. Like brood parasitism, predation on sitting adults reduces both k_n (and $\Sigma_\alpha^\omega \lambda_x$) and s_n (and $\Sigma_1^n P_i$) for their genotype. Also, like brood parasitism, predation on adults can hardly be a general explanation for the occurrence of asynchronous hatching. When survivorship of adults increases with shortening of the nesting period, it is an unselected consequence of beginning incubation before the clutch is complete.

The one common drawback of these alternative hypotheses is their lack of generality; whereas, if d_s is less than one, asynchronous hatching *always* improves the probability of rearing at least some portion of a brood. Nevertheless, each hypothesis may seem the best explanation for a particular species or situation. In contrast, the "reduction-of-total-nest-failure" hypothesis, which seems the best descriptive name for the hypothesis of Tyrväinen (1969), Hussell (1972), Clark and Wilson (1981), and me (as argued above), is applicable to all species and all situations.

The problem of asynchronous hatching highlights a philosophical issue—the difficulty of applying the ad hoc (i.e. nongeneral) and inductive approaches to scientific problems (Murray 1992). First, in explaining their observations, biologists often confound two separate evolutionary problems. With regard to asynchronous hatching, an adaptation that reduces the probability of whole-brood loss (increasing s_n) is confounded with adaptations that reduce the probability of within-brood loss (increasing k_n). With regard to mating systems, when biologists distinguish between promiscuity and polygyny, for example, they confound the problem of why males and females bond or do not bond with the problem of why males have the number of mates they do (Murray 1985). With regard to sexual size dimorphism, ornithologists often confound the evolution of the direction of such dimorphism with the evolution of the magnitude of the dimorphism (Jehl and Murray 1986, 1989). This confounding of issues is common in biology and interferes with the development of predictive theory.

Second, biologists tend to confound proximate factors with ultimate factors. With regard to asynchronous hatching, the ultimate factor is the probability of whole-brood loss. Proximate factors affecting whole-brood loss include predation on eggs or nestlings, predation on adults, inclement weather, starvation, and many other causes of mortality. However important these proximate factors are in particular populations, none can be construed to be a universal explanation for asynchronous hatching. Yet, biologists tend to pit one ad hoc hypothesis against another as *the* explanation of asynchronous hatching in birds.

Third, the ad hoc approach involves a subtle teleology. Despite frequent protestations that a correlation between two events does not necessarily mean that a cause-and-effect relationship exists between them, biologists readily interpret correlations as cause-and-effect relationships. For example, asynchronous hatching and brood reduction most obviously occur in raptors, and Lack (1947, 1954) hypothesized that asynchronous hatching evolved as an adaptation facilitating brood reduction. There is, however, no cause-and-effect relation between asynchronous hatching and brood reduction (Clark and Wilson 1981).

I urge ornithologists to measure and report d_s, s_n, c_n, and k_n.

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