

HATCHING ASYNCHRONY IN THE MOUNTAIN
WHITE-CROWNED SPARROW
(*ZONOTRICHIA LEUCOPHRYS ORIANTHA*):
A SELECTED OR INCIDENTAL TRAIT?

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ABSTRACT.—Female Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) begin diurnal attentiveness with the laying of the first egg but withhold nocturnal incubation until the penultimate egg is laid. To better understand this behavior, we measured hatching times, egg volumes, and patterns of nestling growth and mortality over a 4-yr period in *Z. l. oriantha* breeding at Tioga Pass, California. Additional data from 11 yr of study on nestling mortality and nest predation also were examined.

Hatching patterns matched the attentiveness patterns observed during the egg-laying period. Eggs tended to hatch in the order of laying, and the time period between hatching of the last two eggs was greater than between other successive eggs. The lag between the hatching of the last two eggs showed a slight increase over the course of the breeding season.

Although chicks from last-laid eggs came from generally larger eggs, they tended to be smaller than their siblings because of the hatching asynchrony. Smaller chicks died or disappeared with greater frequency than their larger siblings from nests when the effective food supply had been reduced experimentally. Such selective starvation or "brood reduction" may occur naturally in as many as 14% of all successful nests.

The phenomenon of brood reduction is discussed in relation to four current hypotheses, while also considering the implications of intraclutch variations in egg volume. Although hatching asynchrony may provide the advantages proposed in these hypotheses, there is reason to believe that it originally evolved for other reasons. We propose that hatching asynchrony is an epiphenomenon of the hormonal mechanism governing egg-laying and incubation. This hypothesis provides a testable alternative to existing "adaptive" hypotheses.

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BIRDS with altricial young commonly begin incubation before their clutches are complete. This behavior gives early-laid eggs a developmental head start and results in asynchronous hatching of the clutch. A number of hypotheses have been advanced to explain the phenomenon of hatching asynchrony. The "brood reduction" hypothesis suggests that hatching asynchrony facilitates selective starvation of late-hatched chicks when the food supply is insufficient to rear the entire brood (Lack 1954). The "insurance" hypothesis extends this idea, linking brood reduction with the laying of an extra egg to provide insurance against inviable eggs (Stinson 1979). The "demand reduction" hypothesis holds that asynchronous hatching increases reproductive potential by spreading out the feeding demands of the brood (Hussell 1972), and the "nest failure" hypothesis suggests that slight hatching asynchrony minimizes predation on nestlings (Clark and Wilson 1981).

Hypotheses for hatching asynchrony are complicated by intraclutch variation in egg size. Egg volume varies with laying order in a number of species, with the pattern ranging from a decrease in the size of successively laid eggs in clutches of some larids (Parsons 1972) to an increase in size in a number of passerines (Gibb 1950, Howe 1976, Zach 1982). Howe (1976) demonstrated that in the absence of hatching asynchrony, egg volume is positively correlated with a nestling's size and competitive ability. Thus, the tendency among passerines for the last egg to be larger and hatch later than the other eggs has been interpreted variously as an embellishment on the brood-reduction model (Howe 1976) or as a contradiction to it (Clark and Wilson 1981).

Female Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) begin full nighttime incubation with the laying of the penultimate egg. Eggs are also attended by females and reach developmental temperatures

TABLE 1. Hatching order of *Z. l. oriantha* eggs vs. order of laying (number of hatchings).

Hatching order	Laying order			
	1	2	3	4
1	23	5	2	2
2	5	19	6	0
3	3	5	23	2
4	0	1	3	37

for brief periods during the day, beginning with the laying of the first egg (Zerba and Morton 1983a, b). In this paper we examine the hatching pattern generated by this incubation schedule and seek to determine if this pattern affects reproductive success. Variation in egg volume also is described and related to patterns of hatching.

METHODS

The study was conducted in the Sierra Nevada at Tioga Pass, Mono County, California. The study area is comprised of contiguous subalpine meadows, ranging from 2,900 to 3,140 m in elevation. All are bordered by stands of pine (*Pinus*) and contain dense clumps of willows (*Salix*).

For 11 summers, beginning in 1968, nests of *Z. l. oriantha* breeding at Tioga Pass were located and hatching success, nest predation, fledging, and pre-fledging reductions in brood size were recorded. During the summers of 1980 through 1983, we located nests before eggs were laid and monitored them daily, marking the eggs as they appeared. After clutch completion, we measured the width and length of each egg with calipers and calculated egg volume using the equation of Hoyt (1979): $V = 0.509 LW^2$, where V is volume in cm^3 , L is maximum length in mm, and W is maximum width in mm. To control for sources of between-clutch variation, we standardized egg volumes by subtracting from each egg volume the mean volume for the clutch from which it was taken.

Beginning on day 10 after clutch completion, we visited each nest and felt the eggs for signs of pipping. We repeated this once or twice on days 11 and 12 as necessary. Once it was determined that at least one egg in a clutch was pipped, we no longer handled the eggs, except for an occasional rolling to expose markings. From the time of pipping until all eggs had hatched, we visited nests at intervals of 1–6 h, depending upon the degree of pipping. Upon hatching, we clipped each chick's toenails in a unique pattern and kept notes on its relative dryness. This allowed us, with some experience, to estimate more accurately the time of hatching.

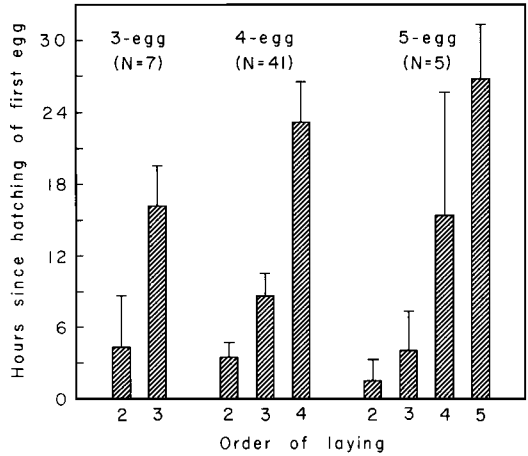


Fig. 1. Hatching times of *Z. l. oriantha* eggs relative to their order of laying in clutches of 3, 4, and 5 eggs. In some instances order of laying is inferred from order of hatching. Vertical lines represent two standard errors above the means.

To evaluate the effects of food shortage on nestling survival, we selected 6 nests and weighed the nestlings daily starting at hatching. When the chicks were between 3 and 5 days of age, we trapped the male parent and held him in captivity. Adult males are known to help feed nestlings but do not incubate or otherwise attend to their thermal requirements. We continued to weigh the chicks until all had either fledged or died. Nestlings from control nests where the male parent was not trapped also were weighed every 1–2 days.

To determine the effects of nestling size on the feeding behavior of the parent, we erected blinds by two nests. We individually marked the chicks on the wing, back, or neck with a felt pen. The pattern of marking was different in the two nests, such that the chick marked on the right wing was the largest in one nest and the smallest in the other. Each nest was observed for three consecutive days, one for a total of 15 h, the other for 11 h. The data gathered included the sex and position of the feeding parent, which chicks begged, their position relative to the parent, and which chicks received food offers.

RESULTS

Hatching times.—Eggs generally hatched in the order in which they were laid ($\chi^2 = 97.4$, $df = 6$, $P < 0.001$; Table 1), but the time between hatchings was not consistent throughout the clutch. In clutches of 3 and 4 eggs, the time between hatching of the last 2 eggs tended to be greater than the time between hatch-

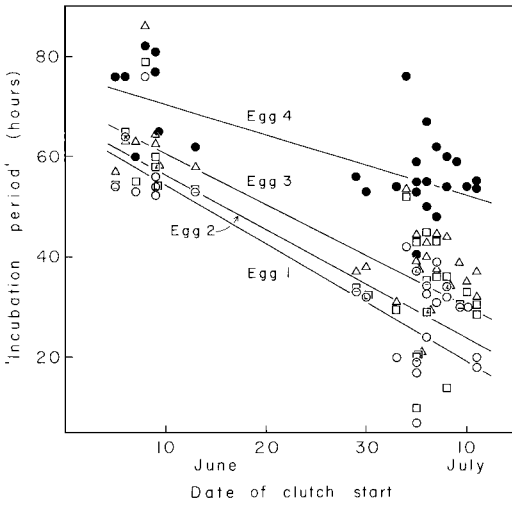


Fig. 2. Seasonal variation in the incubation period of *Z. l. orientha* eggs. Incubation period measured in hours between midnight of day 10 after clutch completion and hatching.

ing of other consecutive eggs (Fig. 1). This pattern was generally true for clutches of 5 eggs as well. Of the 5-egg clutches whose hatching we observed, there were 4 in which the fifth egg alone hatched asynchronously and 1 in which the fourth egg hatched asynchronously at about the same time as the fifth.

In an effort to explain some of the variation seen in the degree of hatching asynchrony, we examined the hatching times of 4-egg clutches relative to the date of clutch completion. Data for three seasons were used. A linear regression indicated that hatching asynchrony increased as the season progressed, accounting for 24% of the variation in the time period between the hatching of the third and fourth eggs ($r = 0.496, P < 0.005$).

The seasonal increase in hatching asynchrony of the fourth egg might have been caused by either retarded development of the fourth egg or accelerated development of the first three eggs. We calculated the relative incubation period of each egg as the number of hours between midnight of the tenth day after clutch completion and the time of hatching. These values were then compared with the date of clutch completion (Fig. 2). Excluded from this analysis were those nests for which laying order was not known exactly or for which a day was skipped between the laying of the last

TABLE 2. Standardized volume (mm^3) for *Z. l. orientha* eggs of known laying order (see text for method of standardization; P values determined by ANOVA).

Year	Egg order				P	n
	1	2	3	4		
1980	-82	+11	+63	+12	NS	20
1981	+46	-32	-43	+43	<0.01	76
1982	-58	+7	+8	+47	<0.001	97
1983	-56	+13	+48	+26	<0.05	69

two eggs (1 nest). As measured, the incubation period of all eggs became shorter as the season progressed (ANOVA, $F = 179, P < 0.001$). The incubation period of the fourth egg, however, was shortened significantly less than that of the others (ANOVA, $F = 5.0, P < 0.03$), resulting in an overall increase in the degree of hatching asynchrony.

Egg volume.—The relationship between laying order and standardized egg volume was not the same over the four years in which it was measured in this study. On the average, the first egg was the smallest in 1980, 1982, and 1983 (Table 2). In these three years there was a tendency for egg volume to increase with order, although this trend was not significant in 1980, possibly because of the small sample size. In 1981 the first egg had the largest mean volume, the third egg the smallest, and the fourth egg the second to largest. Combining the data for all four years, there was a significant increase in egg volume with laying order (ANOVA, $F = 10.2, P < 0.005$). This increase was due primarily to the large size of the fourth egg; mean volume increased with laying order among the first three eggs, but not significantly ($P > 0.2$; Fig. 3).

Nestling survivorship.—Observations of feeding bouts indicated that when a parent approached a nest and all of the nestlings begged, the smallest chick received significantly fewer feeding offers ($\chi^2 = 8.38, df = 3, P < 0.05$; Table 3). No correlation was observed between the position of the nestling(s) offered food and the position or sex of the parent.

That the competitive ability of chicks is size-dependent is further indicated by the growth of chicks both in nests where the size of the brood was reduced naturally and in nests where the feeding rate was experimentally reduced by trapping the male parent. The growth curves

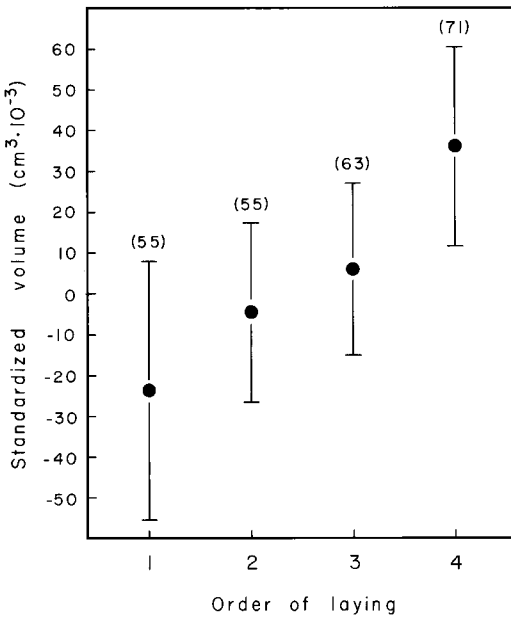


Fig. 3. Variation in egg volume with laying order in 4-egg clutches of *Z. l. oriantha*. Brackets indicate two standard errors above and below the mean. See text for method of standardization of egg volume.

of chicks in a nest that suffered no mortality are presented in Fig. 4A. The chicks displayed normal growth as determined by comparison with other nests. Note that while the last chick was somewhat smaller than the others as a result of hatching asynchronously, its growth rate remained quite similar to that of the largest chick. Figure 4B and C depict naturally occurring incidents of brood reduction. The growth rates of the older chicks in B seem relatively normal; only the fourth chick showed a sub-normal rate. In C, all four chicks grew at a reduced rate. After the death of the smallest chick, the largest chick showed a sudden weight gain, reaching a size that was approximately normal for a chick of its age. In both B and C the smallest chick died first.

The remaining three graphs (Fig. 4D-F) are from experimental nests where the male parent was trapped. The removal of the male did not result in the death of any chicks in the nest depicted in panel D, but the two youngest chicks were underweight on the last day of weighing. In the nests depicted in E and F, all chicks died. In both of these nests the smallest chick died soon after the male parent was

TABLE 3. Number of feedings offered to nestlings according to their order of hatching.

Nest number	Hatching order				P
	1	2	3	4	
LVC#26	32	39	31	16	<0.05
TPM#5	31	29	27	23	NS
Total	63	68	58	39	<0.05

trapped, while the other chicks continued to grow at least temporarily.

The frequency with which a portion of a brood failed to fledge was tabulated for the 11-yr study period. Of 263 nests known to have fledged young, 37 nests (14%) suffered the loss of one or more chicks (43 of 719 chicks died). Unfortunately, the identity of the dead chick or the cause of mortality was not known in some cases. It is, therefore, difficult to determine how much of this mortality was due to competition among nestlings for food and how much was the result of accidental injury or other factors not related to food supply. In any event, the data clearly indicate that in a large number of nests (86%) the entire brood fledged. In nests where limited mortality occurred and hatching order was known, there was a significant tendency for the chick that died to be the youngest of the brood ($\chi^2 = 12.6$, $P < 0.01$; Table 4).

Predation rates.—Data on the effects of predation on egg and nestling survivorship are available for 11 yr (Table 5). From 1981 through 1983, we avoided visiting nests with eggs, but visited nests with chicks frequently to collect data on nestling growth rates. The daily predation rate on nestlings jumped almost threefold in 1981–1983 over that for the previous 8 yr of study. Data from this 8-yr period indicated that predation on nestlings was in fact lower than that on eggs for the incubation period as a whole and for the 6 days just prior to hatching.

DISCUSSION

The pattern of hatching in *Z. l. oriantha* bears a strong and logical relationship to the incubation pattern of the female during egg-laying. Females begin daytime attentiveness with the laying of the first egg but withhold nighttime incubation until the penultimate egg has been

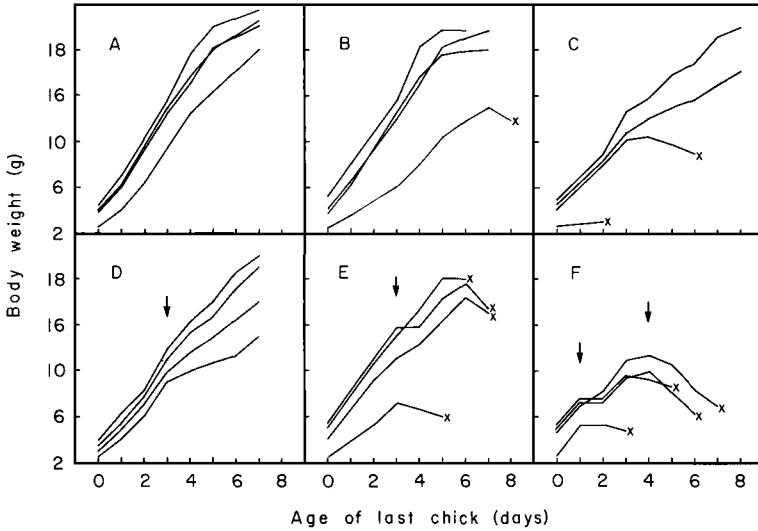


Fig. 4. Growth curves for nestlings in six *Z. l. oriantha* nests. Arrows in D, E, and F denote removal of male parent; second arrow in F indicates male's release. Death of a chick is marked with an X.

laid (Zerba and Morton 1983a). Eggs tend to hatch in the order of laying, with a short lag between all but the last two eggs. The last egg in each clutch hatches disproportionately later than the others, producing in each nest one chick that is noticeably smaller than its siblings.

Why selection should favor the production of a "runt" chick has been the subject of considerable speculation. In one of the more widely espoused hypotheses, Lack (1954) suggested that hatching asynchrony was an adaptation that allowed an orderly reduction in the size of the brood when food was inadequate to raise the entire brood. Lack assumed that females were often unable to predict at the time of egg-laying what the food supply would be when the eggs actually hatched. Asynchronous hatching would result in the formation of a competitive hierarchy among nestlings. Older and larger nestlings would be fed first, while younger ones would be fed only when and if the others were sated. By assuring the quality of the older nestlings, hatching asynchrony would allow females to maximize their reproductive fitness over a wider range of environmental conditions. This, the brood-reduction hypothesis, has been used to explain hatching asynchrony in raptors (Lack 1954, Ingram 1959), the Curve-billed Thrasher (*Toxostoma curvirostre*; Ricklefs 1965), the Great Tit (*Parus major*;

Gibb 1950), and the Common Grackle (*Quiscalus quiscula*; Howe 1976, 1978).

Because it concerns a trade-off between the quality and quantity of offspring, the brood-reduction hypothesis is difficult to test directly. Nonetheless, our data support its basic tenets. Hatching asynchrony does produce a hierarchy in the competitive abilities of siblings. Chicks hatched from the last egg are less competitive when begging for food and, under the conditions of our study, appear to die of starvation more frequently. This mechanism seems to be fairly effective in maintaining the size and presumably the quality of the older chicks since in several nests the youngest chick was eliminated without or prior to reduction in the growth rates of its siblings.

The role of hatching asynchrony in facilitating brood reduction can be discounted if there is no evidence that brood reduction occurs in nature. At Tioga Pass, one and sometimes two

TABLE 4. Frequency of nestling mortality by relative size.

	Nestling mortality by size	
	Smallest chick	Larger chicks
Observed	16	8
Expected	7.1	16.9

TABLE 5. Mortality of *Z. l. oriantha* eggs and nestlings. The total number of nests containing eggs, the total number containing nestlings, and the percent predation per day on nests with eggs and with nestlings is given in two groups on the basis of year. Predation on eggs also is broken down into the first and second halves of the incubation period for a subset of the data (total $n = 471$).

	No. of nests with eggs	No. of nests with chicks	Predation (%/day)			
			Eggs			Nestlings
			Total	First half of incubation	Second half of incubation	
1968-1970, 1973, 1976, 1978-1980	326	258	1.49	1.50	1.25	1.21
1981, 1982, 1983	164	128	1.56	1.38	1.06	3.13
Total	490	386	1.52	1.46	1.20	1.84

chicks disappeared from 14% of otherwise successful *Z. l. oriantha* nests. Because of the nature of the data from which it was taken, this figure may include the loss of nestlings other than the smallest due to factors other than starvation. Nonetheless, there is reason to believe that much of this 14% loss was due to starvation of the youngest chick. Detailed data from the last three years of our study indicate that chicks died or disappeared from six nonexperimental nests in which the other chicks fledged. In one nest this was apparently due to storm damage, while in the other five it was due to the reduced growth and eventual death of the youngest chick. In one instance the second to youngest also appears to have starved (Fig. 4C).

It is difficult to know how great a selective force this frequency of brood reduction may represent. The brood-reduction hypothesis is based on the assumption that variations in environmental conditions occur within and among breeding seasons. Certainly these requisites are met at Tioga Pass (Morton 1978). It follows that the need for brood reduction will vary. In many years there may be no need, while in others the ability to reduce brood size may be a major determinant of reproductive success. Over the course of our study, the annual frequency of brood reduction varied from 2% to 30%. In the end, the potential advantage of asynchronous hatching can be determined only in rare, "bottleneck" years when the frequency of brood reduction is particularly high.

Neither the insurance nor the demand-reduction hypothesis is supported by our data. The first proposes that females combine hatching asynchrony with routine laying of an extra egg as a form of insurance against inviable eggs (Stinson 1979; for a possible example see Par-

sons 1975). If all the eggs hatch, the last chick can be eliminated through starvation. The functional distinction between the insurance and brood-reduction hypotheses lies in the frequency of starvation of the last chick. Under the insurance hypothesis, the last chick is expected to fledge only if one of its siblings dies or fails to hatch. At Tioga Pass hatchability is greater than 90% (Zerba and Morton 1983b), so there is scant incentive for investment in an additional egg. More importantly, 86% of broods that fledged did so without the death of any chicks, indicating that most females are not producing more offspring than they can hope to fledge.

The demand-reduction hypothesis suggests that by spreading the ages of their offspring, parents reduce the total amount of food needed by the brood at any given time. This scheme envisions that during growth each chick has a period of peak food demand, after which its requirements decline. This may be applicable in species such as Tree Swallows (*Tachycineta bicolor*) in which there is a prefledging reduction in weight and possibly food requirements (Zach 1982). It does not seem applicable to our population, however, since there is no obvious weight regression in *Z. l. oriantha* nestlings (Morton and Carey 1971). Furthermore, if asynchronous hatching of the last chick were to reduce the feeding demands on the parents, asynchronous hatching of the second and third chicks should result in even greater savings. By itself, this hypothesis is inadequate to explain why only the last-laid egg hatches with distinct asynchrony.

A final hypothesis, the nest-failure hypothesis (Clark and Wilson 1981), holds that chicks are more likely to attract predators than are

eggs. If so, selection should favor synchronous hatching as a means of minimizing the amount of time that the nest will contain nestlings. On the other hand, complete hatching synchrony, produced by beginning incubation only after clutch completion, generally will not be favored because it lengthens the total time between the laying and fledging of the first few eggs. This would increase the vulnerability of the first-laid eggs to predation. Clark and Wilson (1981) suggested that under most circumstances the ideal balance between the advantages and disadvantages of hatching asynchrony is produced when incubation begins with the penultimate egg.

The nest-failure hypothesis is particularly difficult to evaluate. Our frequent visits to nests during the last three years of this study appear to have increased greatly the predation rate on nestlings. Taking the first eight years as the more natural sample, the data for *Z. l. oriantha* indicate that predation is lower on nestlings than on eggs. At first glance this would appear to contradict the basic premise of the nest-failure hypothesis. It may be, however, that nestlings are still more likely to attract predators, but they simply happen to be in nests that are more difficult to find (as indicated by their having survived to the nestling stage). Others (e.g. Willis 1973) have reported such a crypticity effect, and the fact that predation on eggs drops over the course of incubation (Table 5) further supports this idea. Thus, a reversal in the expected predation rates may not invalidate the nest-failure hypothesis; it does nonetheless preclude testing the hypothesis by comparing the observed onset of incubation with that predicted on the basis of the observed predation rates. Instead, we test the nest-failure hypothesis by determining, first, if it adequately explains the incubation patterns for clutches of all sizes, and second, under what circumstances it is favored as an explanation for hatching asynchrony in our population.

The nest-failure hypothesis predicts that beginning incubation with the penultimate egg is the optimal strategy for the widest range of predation rates. The specific range of rates covered, however, depends upon clutch size. At Tioga Pass, clutch size varies from three to five eggs. Using the same conditions as Clark and Wilson (1981), we calculated the degree of overlap in predation rates for which beginning incubation with the penultimate egg would re-

main the optimal strategy for all three clutch sizes. We found that a variation in the rate of predation on nestlings of more than 3% would favor beginning incubation either with the last egg in clutches of three or the third egg in clutches of five. It seems to us unlikely that predation rates should stay within such a narrow range.

As proposed by Clark and Wilson, the nest-failure hypothesis is an opposing strategy to that of brood reduction. Brood reduction is still expected to occur, but it is viewed as an incidental cost of a strategy aimed at reducing predation. Richter (1982) has already argued that the cost of brood reduction is too great for this to be true in most circumstances. Using his methods, we calculated the maximum frequency of brood reduction allowed, given the observed rate of predation on *Z. l. oriantha* nests. We found that if brood reduction is to be an incidental cost, it must occur in fewer than 5% of all successful nests. While this value is somewhat lower than the mean value of 14% that we recorded, there are years when the frequency of brood reduction falls below this level. As noted by Richter (1982), it is perhaps better to view the nest-failure and brood-reduction hypotheses as complementary mechanisms that work under different ecological conditions. In this regard, it is quite possible that hatching asynchrony originally evolved as a response to predation, and only later, in species such as *Z. l. oriantha* that have colonized unpredictable habitats, has its role in facilitating brood reduction become more important. It is also possible, as we shall argue shortly, that hatching asynchrony evolved for still another reason and that its advantages in terms of both brood reduction and nest predation are derived secondarily. Finally, it is important to note that very little is known about the heritability of hatching patterns. Both the brood-reduction and nest-failure hypotheses assume that hatching asynchrony can be selected for. Until it is shown that variations in hatching patterns are passed along to offspring, neither of these hypotheses will have been adequately tested.

Intraseasonal variation in hatching asynchrony.—Time-related variation in hatching asynchrony was observed in our population and has been reported also for *P. major* by Gibb (1950). This provides the opportunity to test various hypotheses by correlating changes in the relevant factors (e.g. predation, starvation)

with the naturally occurring variation in hatching asynchrony. Unfortunately, our efforts to do so have failed. There is an increased likelihood of precipitation at Tioga Pass late in the breeding season, and this may affect parents' ability to feed nestlings. Nonetheless, our data do not indicate a significant change in the frequency of brood reduction. Vegetation also changes over the breeding season, providing greater cover for nests, but this is not reflected in a consistent decrease in the rate of predation. It is possible, of course, that temporal changes in hatching asynchrony are merely the result of changes in the development of the female's brood patch and are themselves devoid of adaptive significance.

Variation in egg volume.—This study adds *Z. l. oriantha* to the list of passerines in which egg volume increases with laying order (e.g. Gibb 1950, Kendeigh et al. 1956, Pinkowski 1975, Howe 1976, Ryden 1978, Zach 1982). In our study the pattern was not the same in all four years. In 1981 the pattern was reversed for the first three eggs, while the fourth egg remained relatively large. Interestingly, this was also a year of average snow fall at Tioga Pass (97% of the norm; State of California Bull. 129, Snow Survey Measurements). In contrast, snowpack depths were unusually great in 1980 (158% of the norm), 1982 (176%), and 1983 (225%). Absolute egg volume does vary with snow cover (unpubl. data), but it is not clear why patterns of intraclutch variation in volume should be affected. Regardless of the pattern among the first three eggs, the last egg in clutches of four remained relatively large in all four years, being on the whole distinctly larger than any of the others and begging a correlation with hatching asynchrony.

An increase in egg volume with laying order is considered by some to be incompatible with the brood-reduction hypothesis. Clark and Wilson (1981) point out that if a female induces hatching asynchrony to decrease the size of the last chick relative to its siblings, she should not simultaneously increase its size at hatching by laying a larger egg. These authors contend, rather, that females increase their investment to compensate the last chick for hatching late. Although increasing the size of the last egg may reduce the size differential between siblings, it is unlikely to compensate for age-related neurological differences. Chicks increasingly orient their begging behavior toward the

parent as senses and coordination improve (Ryden and Bengtsson 1980), and late-hatched chicks still will be likely to starve when competition is severe. Thus, it becomes difficult to separate this explanation from one that views extra provisioning as an effort to prevent premature brood reduction (Howe 1976, O'Connor 1977). Both predict the potential elimination of the youngest chick. Still, the latter explanation seems somewhat contrived. Why should females increase investment in an offspring that under the brood-reduction hypothesis is more likely to die, when they might achieve the same end merely by reducing the degree of hatching asynchrony?

Building on the notion that increases in volume may reflect compensation, Slagsvold et al. (1984) examined intraclutch patterns in egg volume in a number of species with hatching asynchrony. They proposed that different patterns reflect different reproductive strategies. Birds utilizing a brood-reduction strategy tend to lay smaller last eggs to facilitate elimination of the last chick. Conversely, those with a "brood-survival strategy" lay larger last eggs in an effort to prevent brood reduction. They found, in general, that hole-nesting species tended to be brood reductionists, while open nesters tended to be brood survivalists.

This appealing hypothesis fits well with our observations on *Z. l. oriantha*. It may explain the relatively low rate of brood reduction we observed, as well as the variations in egg volume. In doing so, however, it further emphasizes the inability of existing hypotheses to explain hatching asynchrony. All of the hypotheses mentioned so far are based on the idea that hatching asynchrony has been selected for as part of some specific reproductive strategy. The hypothesis of Slagsvold et al. (1984) divorces hatching asynchrony from any particular reproductive strategy. It becomes egg volume, not hatching asynchrony *per se*, that determines whether or not a female is engaged in a brood-reduction strategy. Why did hatching asynchrony evolve? Relying on conventional hypotheses, Slagsvold et al. (1984) are forced to invoke two separate explanations. They suggest that in one ecological subset, the brood reductionists, hatching asynchrony evolved as proposed by the brood-reduction hypothesis, while in another subset, the brood survivalists, the existence of asynchrony is explained by the nest-failure hypothesis. An alternate and, we

feel, more plausible approach is to relinquish the notion that hatching asynchrony is the goal of some selective process. We propose a mechanism by which selection for an unrelated trait may result incidentally in asynchronous hatching. This single hypothesis predicts the existence of hatching asynchrony regardless of reproductive strategy. Furthermore, because this hypothesis views hatching asynchrony as a basic and relatively immutable trait, it implies that birds evolving a survivalist strategy will do so through the provisioning of offspring rather than the elimination of hatching asynchrony. Our idea does not negate the advantages of asynchronous hatching as proposed by others; rather, it suggests that these advantages are epiphenomena or "exaptations" (see Gould and Vrba 1982).

The hormonal hypothesis for hatching asynchrony.—In the course of reproduction, a bird must make a general transition from egg-laying to incubation. This transition involves two basic functions: the inhibition of ovulation and the initiation and maintenance of incubation. It is common in nature for complementary physiological effects to be regulated by the same hormonal mechanism. Insulin, for example, has a wide range of effects, all of which serve to lower blood sugar. We propose that evolution has shown the same frugality in avian reproduction; specifically, that the same hormonal mechanism is responsible for turning off ovulation and turning on incubation. While the mechanism responsible for this transition is not yet fully understood, much of the evidence points toward a dual role for prolactin.

Ovulation in birds is believed to involve positive feedback from progesterone on LH release (Sharp 1980, Kamiyoshi and Tanaka 1983). Release of LH from the anterior pituitary stimulates the mature follicle to release progesterone (Etches et al. 1982), which in turn further enhances LH release (Etches and Cunningham 1976). This mutual stimulation produces a sharp peak in plasma levels of both hormones. This peak, possibly through interaction with a similar peak in FSH levels, results in ovulation several hours later (Kamiyoshi and Tanaka 1972, 1983; Sharp 1980; Etches et al. 1982; Sharp et al. 1984; Cunningham et al. 1984). At the end of the egg-laying period, LH levels fall in a number of species (Campbell et al. 1978, Sharp et al. 1979, Dawson and Goldsmith 1982, Hall and Goldsmith 1983, Bluhm et al. 1983), in-

cluding *Z. leucophrys* (Wingfield and Farner 1978).

Several lines of evidence suggest that prolactin may act in the termination of ovulation. It causes a decrease in ovarian size in fowl (Bates et al. 1935) and inhibits the response of the ovaries and oviducts to FSH and LH in White-throated Sparrows (*Z. albicollis*; Meier 1969), but not in *Z. leucophrys* (Stetson et al. 1973). The incongruity here may be due to species-specific variations in sensitivity to the hormone with time of day. Injection of prolactin prevents the preovulatory surge of estradiol and progesterone in turkeys (Camper and Burke 1977) and has been shown by Tanaka et al. (1971) to prevent ovulation when presented at the proper time. Finally, Lea et al. (1981) demonstrated that injection of prolactin antiserum increases LH levels in incubating hens, suggesting that prolactin may be responsible for the decrease in LH secretion that marks the end of laying.

In addition to its antigonadal effects, prolactin has long been associated with incubation behavior (Riddle et al. 1935, Cherms et al. 1962, Sharp 1980). Studies have shown that prolactin levels increase dramatically with the onset of incubation (Etches et al. 1979, Sharp et al. 1979, Lea et al. 1981, Dawson and Goldsmith 1982, Goldsmith 1982, Hall and Goldsmith 1983) and decrease with its termination (Burke et al. 1981, Goldsmith 1982, Bluhm et al. 1983). Whether prolactin alone is responsible for initiating incubation is not yet clear (Sharp 1980). There is strong evidence, for example, that progesterone stimulates the onset of incubation behavior in Ringed Turtle-Doves (*Streptopelia risoria*; Lehrman and Brody 1961, Lehrman 1965, Cheng and Silver 1975) and that prolactin serves only to maintain the behavior (Silver 1984).

If prolactin (or any other hormone) is responsible for both the inhibition of ovulation and the initiation of incubation, a number of consequences would be expected with regard to how eggs are produced and how they hatch, depending upon threshold characteristics and the rate of prolactin synthesis and release. For example, if there is variation in the level of prolactin that inhibits ovulation, then a slow increase in its titer over the course of several days is likely to promote variation in clutch size. Conversely, a rapid increase or surge in prolactin would lend itself to precise control of clutch size. Thus, one prediction of our hypothesis is that species exhibiting a rapid, de-

cisive onset of incubation behavior, triggered presumably by a surge of prolactin, also will show relatively little variation in clutch size. Species that show a gradual onset of incubation behavior will have a more variable clutch size. A possible example of the former is *Z. leucophrys* (see Zerba and Morton 1983a) and of the latter, *P. major* (see Gibb 1950, Haftorn 1981). Because of the great energetic costs involved, we assume that in most species selection will favor individuals with accurate control of their clutch size and hence a rapid increase in prolactin.

As presented, this arrangement is independent of the advantages of hatching asynchrony; it reflects the conservative nature of hormonal mechanisms and selection for control of clutch size. Nevertheless, because of the logistics of egg production, it would result in a specific pattern of hatching. In most birds eggs are ovulated on consecutive days. An individual egg may spend 21-27 h in the oviduct, but the usual period between ovulation and oviposition of the same egg is 24 h or slightly longer (Woodard and Mather 1964, Fraps 1965, Gilbert 1971). This model is based on galliform birds, principally chickens, but there is abundant evidence that the avian ovary functions with little interspecific variation (Lofts and Murton 1973). The relevant point is that about the time one egg is being laid, the next one is being ovulated. A sudden increase in prolactin to terminate ovulation would necessarily find the last egg of the clutch still in the oviduct. If that surge also is responsible for the onset of incubation, then females would be expected to greatly increase their incubation behavior during the 24-h period preceding the laying of the last egg.

Our hypothesis predicts that most birds will begin incubation with the laying of the penultimate egg, that this should occur regardless of clutch size, and that it is independent of the advantages of the hatching pattern so produced. On the basis of these predictions, one can explain the observations on *Z. l. oriantha* as well as the existence of hatching asynchrony in species with a variety of reproductive strategies. As mentioned earlier, such a hypothesis also helps to reconcile hatching asynchrony with intraclutch variations in egg volume. Tests of our hypothesis can be pursued along several lines. The prediction that most birds will begin incubation with the penultimate egg has al-

ready been confirmed for passerines (for literature reviews see Clark and Wilson 1981, Smith 1983). Any correlation between variation in clutch size and the rate of onset of incubation remains to be determined. Clearly, our hypothesis pertains only to species where the female parent incubates. Among species where only the male parent incubates, we foretell neither a tendency to begin incubation with a particular egg nor a correlation between variation in clutch size and the rate of onset of incubation. We should finish by noting that most of what is known about the hormonal regulation of ovulation and incubation has been determined using domestic fowl. Further work on these mechanisms in wild passerines should provide some insight into the validity of our arguments. If support is found, the pertinent question will switch from why so many birds begin incubation with the penultimate egg to why some do not.

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