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EFFECTS OF PARENTAL AGE ON HATCHING ASYNCHRONY, EGG SIZE AND THIRD-CHICK DISADVANTAGE IN WESTERN GULLS

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ABSTRACT.—We examined the relationships among parental age, hatching asynchrony, egg size, and the "third-chick disadvantage" of Western Gulls (*Larus occidentalis*) on Southeast Farallon Island, California, during the 1984-1990 breeding seasons. Third chicks showed lower survival than first or second chicks for all parental age classes combined. Fledging success of first- and second-hatched chicks was related to parental age in a parabolic fashion, whereas fledging success of the third chick increased sigmoidally with increasing age; the probability of fledging of first-, second-, and third-hatched chicks converged for birds greater than 15 years old, negating the third-chick disadvantage for the oldest parents. Egg volume increased with increasing age for females 4 to 13 years old, and levelled off or declined slightly thereafter. For older females, the size disadvantage of third-laid eggs was relatively less than for younger females. Egg volume did not affect fledging success when parental age and year were considered in a multiple logistic (binomial) regression analysis. Hatching asynchrony decreased slightly with increasing parental age. Fledging success of third-hatched chicks decreased significantly with increasing hatching asynchrony. The greater hatching synchrony in broods of older parents may increase the competitive ability of third chicks. The third-chick disadvantage, often viewed as an adaptive response to variable food supplies, may be a nonadaptive effect of resource availability governed, in part, by the foraging efficiency and/or reproductive effort of the parents. *Received 22 March 1991, accepted 10 January 1992.*

ASYNCHRONOUS hatching in birds has received considerable attention from evolutionary ecologists because of its apparent cost. Often the last-hatched offspring shows significantly higher mortality than its elder siblings. Lack (1954, 1968) proposed that hatching asynchrony may be adaptive if, by creating an age and size hierarchy, parents can reduce their brood size through selective starvation to match available food resources. Less time and energy would be wasted on the last-hatched chick if it starved relatively soon after hatching and did not compete with elder siblings for parental care (Hahn 1981, Bryant and Tatner 1990). Asynchronous hatching also may function to lessen the peak brood energy demands (Bryant and Gardiner 1979), reduce parental investment (Gibbons 1987), or be a nonadaptive effect of varying food resources (Mead and Morton 1985). Alternatively, the last-hatched chick may be viewed as insurance against hatching failure or early mortality of the first or second eggs or chicks (Stinson 1979, Graves et al. 1984) or, if it survives, a bonus which maximizes fitness when conditions are favorable (Graves et al. 1984).

In large *Larus* gulls, the typical clutch size is three eggs (Winkler and Walters 1983, Reid 1987). The third-laid eggs are usually smaller and hatch after the first two eggs (Parsons 1975, Coulter 1977, Mills 1979, Hahn 1981, Slagsvold et al. 1984; but see Pierotti and Bellrose 1986), and chicks from smaller eggs are lighter at hatching and grow less rapidly than larger siblings (Coulter 1977, Davis 1975, Parsons 1975; but see Pierotti and Bellrose 1986). Intrabrood age and size asymmetry of the chicks attributable to variation in egg size and asynchronous hatching, and the resulting nestling mortality have been termed the "third-chick disadvantage" (TCD).

Pierotti and Bellrose (1986) investigated the TCD in a small, coastal population of Western Gulls (*L. occidentalis*) in California, and found it was nonexistent. They hypothesized that when females are not energy limited (i.e. when food availability is high and the need for territorial defense is low), the TCD should be reduced or absent altogether. Furthermore, they suggested that variation in egg size was a facultative, nonadaptive response to varying food availability (see also Mills 1979, Schreiber et al. 1979). In this paper, we also examine the TCD in Western Gulls, but our study was conducted on the large, dense, pelagic-feeding colony inhabiting

Southeast Farallon Island, California. Previous work on Western Gulls of this island has shown that reproductive success increases with increasing age and previous breeding experience: older birds lay larger clutches, initiate breeding earlier each season, and hatch and fledge a greater proportion of their eggs and chicks (Pyle et al. 1991, Sydeman et al. 1991b). We believe that age-specific variation in reproductive success is due, in part, to increases in foraging efficiency with age, which could, in turn, influence body condition. In this paper, we examine the relationship among parental age, annual food availability, and the TCD (including egg size and hatching asynchrony) to further investigate the possible nonadaptive nature of asynchronous hatching and the TCD in this species. We hypothesize that, if foraging efficiency or body condition (energetic reserves) improves with increasing age or breeding experience, the TCD and its components would also vary with parental age. We also correlate egg volume and the degree of hatching asynchrony with fledging success to investigate possible mechanisms that could explain age-specific variation in the TCD.

METHODS

Our study site is Southeast Farallon Island, located 35 km west of San Francisco, California (37°42'N, 123°00'W). The island is located in the center of the California eastern-boundary current system; food availability varies annually (Ainley and Boekelheide 1990, Sydeman et al. 1991b). We assessed annual food availability quantitatively by calculating the proportion of rockfish (*Sebastes* spp., mostly *Sebastes jordani*) in the diet of Common Murre (*Uria aalge*) chicks. Western Gull annual reproductive success is positively related to the proportion of rockfish in the murre diet (Ainley and Boekelheide 1990, Sydeman et al. 1991b).

As a result of a banding program initiated by D. G. Ainley in 1971 (see methods in Spear et al. 1987, Sydeman et al. 1991b), approximately 2,000 gulls on the island are of known age. The colony has been stable for at least the last 10 years and numbers approximately 12,500 pairs (Spear et al. 1987; Point Reyes Bird Observatory, unpubl. data). Nest density is high, with most nest bowls located 2 to 3 m from each other. Territorial interactions are numerous; habitat saturation may limit the breeding population (Pierotti 1981, Ainley and Boekelheide 1990). We studied the breeding biology of known-age birds from 1984 to 1990. We checked nests every second day in 1987 through 1990, and every third day in 1986. In 1984 and 1985, 75% of the nests were checked every three days, while the remaining quarter were monitored every day. We marked eggs with nontoxic black ink and chicks with yellow dye (picric acid). Our marking scheme allowed recognition of individual eggs and chicks relative to their laying and hatching sequence. After clutch completion, we left the nest undisturbed for 24 days. Thereafter, we returned to mark the egg teeth of pipping chicks, which enabled us to maintain the egg order when chicks from first or second eggs hatched on the same day. Sample sizes for third eggs and chicks are larger than first or second eggs and chicks, because often we found nests for the first time with two eggs, and because first and second eggs often hatch synchronously.

We analyzed data on laying and hatching asynchrony, egg volume, and fledging success in relation to parental age for parents that produced a three-egg clutch or brood in which laying and hatching sequence were known. Synchronous hatching was defined as hatching of the first and third egg within a two-day (48-h) period. Asynchrony was indexed as the difference, in days, between the date of laying/hatching of the first and third egg/chick. Due to our different monitoring schedule in 1984 to 1986, we calculated asynchrony only for the period 1987 to 1990. Egg volume was calculated by the formula:

$$\text{volume (cm}^3) = \text{length (mm)} \times \text{breadth (mm)}^2 \times 4.866 \times 10^{-2}$$

(Coulson 1963). Fledging success was defined as survival of a chick to six weeks of age (see Sydeman et al. 1991b).

Means ± 1 SE are presented as summary statistics. We analyzed the relationships between parental age, laying/hatching asynchrony, and egg volume using linear regression; for egg volume, we restricted analyses to females only. We analyzed the relationships between hatching asynchrony, egg volume, parental age and fledging success using logistic regression (LOGIT; Cox and Snell 1989). We selected logistic regression for analyses on breeding success because the outcome variable, fledging success, follows a binomial distribution (survived or did not survive). We report the likelihood-ratio statistic (LRS) in the text as a test of the significance of individual terms in logistic regression. We address the confounding effects of food availability and date of breeding (either clutch initiation date or hatching date) by including "year" and "date" as covariates in all analyses on fledging success. The significance of these factors was $P < 0.01$ (see Ainley and Boekelheide [1990] and Sydeman et al. [1991b] for more detailed analyses).

We tested for curvilinear trends in the data by modelling the quadratic and cubic relationships of parental age, and the quadratic of date and egg volume. We report parametric regression coefficients in the text for analyses on egg volume. If we found significant departure from linearity, the "linear" regression coefficients in the text represent the first term, b_1(as

TABLE 1. Food availability (%), laying asynchrony, hatching asynchrony, and egg volume in relation to laying order by year for Western Gulls on Southeast Farallon Island, 1984-1990. Mean ± SE given for laying and hatching asynchrony, and for egg volume. Food availability is percentage rockfish in diet of Common Murre chicks. Sample sizes in parentheses; NA not available.

Year	Food availability	Asynchrony (days)		Egg volume (cm^3)		
		Laying	Hatching	First	Second	Third
1984	69	NA	NA	83.95 ± 0.837 (73)	82.17 ± 0.776 (73)	75.11 ± 0.658 (75)
1985	74	NA	NA	82.93 ± 0.637 (87)	81.76 ± 0.681 (81)	75.43 ± 0.688 (98)
1986	28	NA	NA	NA	NA	NA
1987	87	4.50 ± 0.054 (350)	1.93 ± 0.074 (260)	83.89 ± 0.660 (81)	82.71 ± 0.603 (81)	76.80 ± 0.705 (87)
1988	82	4.53 ± 0.049 (372)	1.99 ± 0.078 (260)	83.05 ± 0.529 (68)	82.22 ± 0.631 (68)	77.58 ± 0.862 (76)
1989	47	4.58 ± 0.047 (426)	1.83 ± 0.070 (623)	82.37 ± 0.382 (183)	82.71 ± 0.381 (183)	76.17 ± 0.402 (196)
1990	20	4.70 ± 0.050 (427)	2.12 ± 0.068 (240)	82.36 ± 0.500 (175)	81.60 ± 0.499 (174)	73.59 ± 0.414 (188)

opposed to b_2) in a quadratic model. In logistic regression, if we found significant curvilinear trends in the data, we used a logarithmic and inverse transformation of the independent variable to test whether the data would be better expressed as an ever-increasing (yet in diminishing steps; logarithmic) or asymptotic (inverse) function. We modelled these transformations to aid in determining the shape of these functions. Sydeman et al. (1991a) discussed the use of logistic regression in an ecological context, and presented information on the biological inference of logarithmic and inverse transformations. We based our determination of the "best" model on the significance of the coefficients, explanatory power of the model, and examination of the residuals.

RESULTS

Laying and hatching asynchrony.—Laying asynchrony varied significantly by year (Table 1; ANCOVA; $n = 1{,}575$, $F = 4.11$, $P = 0.007$) and date of breeding ($F = 13.83$, $P = 0.008$, $b_1 = -0.0173$), but had no relationship to parental age (Table 2; $F = 1.74$, $P = 0.184$, $b_1 = -0.0091$). Pairwise comparisons by year indicated that only 1990 and 1987 were different (Bonferroni t-tests, $n = 6$, $P < 0.008$). The shortest average laying durations occurred in 1987 and 1988, years in which rockfish availability in the Gulf of the Farallones was considerably higher than 1989 and 1990 (Table 1). The duration of egg laying per clutch became shorter later in each breeding season. We found no curvilinear trend in laying asynchrony with either timing of breeding or parental age ($P > 0.10$).

Hatching asynchrony did not vary significantly by year (Table 1; ANCOVA; $n = 978$, $F = 2.36$, $P = 0.069$), but decreased significantly, albeit slightly (partial $r^2 = 0.004$), as parental age increased (Table 2; $F = 4.15$, $P = 0.039$, $b_1 = -0.0215$) and increased with date during the breeding season ($F = 13.64$, $P < 0.001$, $b_1 = 0.0260$). We found no curvature in age or date effects ($P > 0.10$).

Egg volume.—Egg volume by laying order and age are shown in Figure 1. Volume of first-laid eggs did not vary significantly by year (Table 1; ANCOVA; $n = 666$, $F = 1.50$, $P = 0.190$), but was significantly related to date of breeding ($F = 5.82$, $P = 0.016$, $b_1 = 10.14$) and parental age (F [linear term] $= 14.8$, $P < 0.001$, $b_1 = 151.37$; F [quadratic term] $= 13.2$, $P < 0.001$, $b_2 = -6.58$). Regression coefficients indicated that first-egg volume peaked for females 11.5 years old, although the data show a peak at 8 years of age. These differing values result from correcting for date effects in the regression model. The fact that first-egg volume increased as the breeding season progressed was unexpected and will be considered in further detail elsewhere.

Volume of second-laid eggs also did not vary significantly by year (ANCOVA; $n = 659$, $F = 1.08$, $P = 0.371$), but was significantly related to date of breeding ($F = 12.31$, $P < 0.001$, $b_1 = 14.38$) and parental age (F [linear term] $= 15.9$,

TABLE 2. Relationship between laying and hatching asynchrony ($\bar{x}$ ± SE) and age of parent. Sample sizes in parentheses.

Age	Laying asynchrony	Hatching asynchrony
3	5.00 ± 0.575 (4)	— (1)
4	4.62 ± 0.250 (42)	2.46 ± 0.229 (26)
5	4.75 ± 0.102 (126)	1.93 ± 0.131 (67)
6	4.51 ± 0.061 (215)	2.15 ± 0.092 (144)
7	4.60 ± 0.084 (154)	2.02 ± 0.108 (106)
8	4.53 ± 0.073 (172)	2.15 ± 0.106 (131)
9	4.67 ± 0.088 (128)	1.81 ± 0.128 (85)
10	4.51 ± 0.085 (114)	1.81 ± 0.137 (75)
11	4.65 ± 0.126 (76)	1.81 ± 0.136 (52)
12	4.36 ± 0.089 (76)	1.90 ± 0.136 (52)
13	4.61 ± 0.073 (172)	1.91 ± 0.103 (111)
14	4.54 ± 0.087 (105)	1.59 ± 0.202 (69)
15	4.53 ± 0.089 (80)	2.04 ± 0.180 (49)
16	4.60 ± 0.127 (56)	2.00 ± 0.321 (28)
17	4.33 ± 0.146 (30)	1.60 ± 0.265 (10)
18	5.05 ± 0.280 (19)	1.85 ± 0.355 (13)
19	4.67 ± 0.420 (6)	2.50 ± 0.478 (4)

$P < 0.001$, $b_1 = 155.26$; F [quadratic term] = 11.7, $P < 0.001$, $b_2 = -6.11$). The curvilinear relationship between age and second-egg volume peaked at 12.7 years, and the data indicated a peak at 12.

Volume of last-laid eggs varied significantly by year (ANCOVA; $n = 697$, $F = 7.75$, $P < 0.001$) and was significantly related to timing of breeding ($F = 19.10$, $P < 0.001$, $b_1 = 18.61$) and parental age (F [linear term] = 10.7, $P = 0.001$, $b_1 = 130.77$; F [quadratic term] = 6.35, $P = 0.012$, $b_2 = -4.66$). The regression between female age and third-egg volume indicated a peak at 14.1 years, whereas the data showed a peak at 12 years. Thus, because peak volumes occur at progressively greater female age, regression models and the data indicate that the size of the third egg relative to that of the first two eggs increases with age. A more direct test of this idea can be made by subtracting the volume of third eggs from that of the average volume of first and second eggs combined. The difference in egg size between combined first- and second-laid eggs and the third egg decreased, although not significantly, with increasing female age (ANCOVA with year; $n = 646$, $F = 3.28$, $P = 0.07$, $b_1 = -11.63$). However, difference in size between first and third eggs decreased significantly with increasing female age ($n = 648$, $F = 5.65$, $P = 0.018$, $b_1 = -17.79$). We conclude that the third eggs of older parents are relatively larger than the third eggs of younger birds, although this pattern requires further investigation.

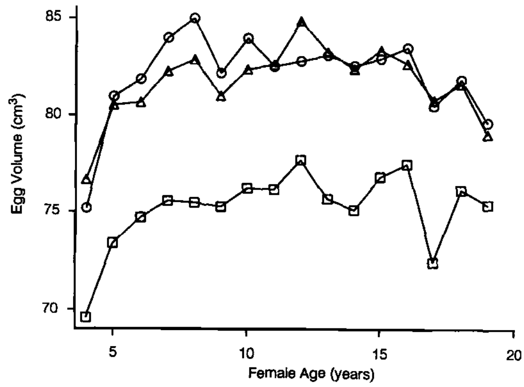

Fig. 1. Patterns of variation in egg volume of first-, second-, and third-laid eggs (○, △, □, respectively) with female age. Points represent mean values for each age class. Error bars omitted for clarity.

Fledging success, hatching order, and egg size.—Fledging success decreased with hatching order (LRS = 85.0, $P < 0.001$); first and second chicks were more likely to survive to fledge than third chicks. Survival of the first-hatched chick to fledging was related to parental age using a quadratic model (LOGIT [year and date of laying included in all models]; $n = 1{,}219$, LRS = 6.91, df = 2, $P = 0.032$). The cubic of age, and the log and inverse transformations of age were not significantly related to first-chick survival (cubic, LRS = 0.05; log, LRS = 0.10; inverse, LRS = 0.58; all df = 1, all $P > 0.50$). Survival of the second chick also was best related to the quadratic of age ($n = 1{,}168$, LRS = 13.85, df = 2, $P < 0.001$). The cubic of age, and the log and inverse transformations of age were not related to second-chick survival (cubic, LRS = 1.34; log, LRS = 1.00; inverse, LRS = 1.79; all $P > 0.15$). The pattern of survival of the third chick with parental age was more complex. We found significant relationships with the quadratic ($n = 1{,}531$, LRS = 8.74, df = 2, $P = 0.013$) and cubic of age (LRS = 5.52, df = 1, $P = 0.003$), as well as the log (LRS = 3.79, df = 1, $P = 0.052$) and inverse (LRS = 6.70, df = 1, $P = 0.010$) transformations. Because the cubic of age explained the greatest amount of variation (total LRS = 14.26, df = 3, $P < 0.001$) in third-chick fledging success, we selected this as the "best" regression model.

The predicted fledging success of first-, sec-

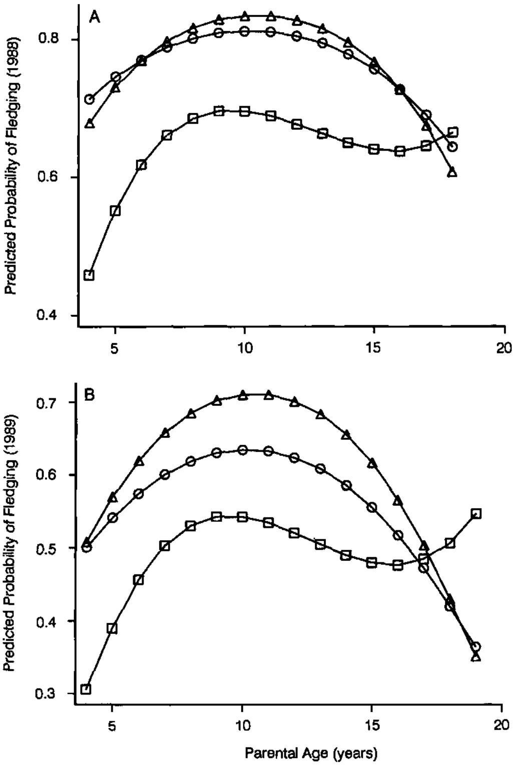

Fig. 2. Predicted probability of fledging (regression curves) for first-, second-, and third-hatched chicks (O, △, □, respectively) with parental age in (A) 1988 and (B) 1989. Curves generated by fitting age, age^2, and age^3 in logistic (binomial) regression analysis. Parabolic relationships for first- and second-hatched chicks are maintained although age^3 is included in the model.

ond-, and third-hatched chicks in relation to parental age in 1988 and 1989 is depicted in Figure 2. Regression lines and predicted points are based on polynomial logistic regression including age, age^2 and age^3 in each analysis for each chick (hatching sequence). The projected probabilities of fledging for first and second chicks follow a parabolic trajectory in both years, whereas the likelihood of survival for the third chick is sigmoidal. Thus, for the oldest parents there is little difference with hatching order in the probability of chick survival.

Egg volume had a slight, but nonsignificant, effect on first-hatched chicks ($n = 756$, LRS = 2.6, df = 1, $P = 0.062$), and no influence on second- ($n = 729$, LRS = 0.0, df = 1, $P > 0.50$) or third-chick ($n = 875$, LRS = 1.4, df = 1, $P > 0.50$) survival to fledging after the confounding effects of year and parental age were included in a multiple logistic regression. We found no departures from linearity between egg volume and fledging success.

TABLE 3. Relationship between hatching asynchrony and fledging success for first-, second- and third-hatched chicks. Sample sizes in parentheses.

Asynchrony	Hatching order		
	First	Second	Third
0	0.64 (156)	0.72 (151)	0.58 (176)
2	0.63 (654)	0.65 (650)	0.49 (783)
4	0.63 (120)	0.71 (120)	0.43 (133)
6	0.88 (9)	0.78 (9)	0.44 (9)

Fledging success decreased significantly with increasing hatching asynchrony for third chicks (Table 3; $n = 1{,}101$, LRS = 5.62, $P = 0.018$). However, there was no relationship between hatching asynchrony and fledging success for first ($n = 939$, LRS = 0.27) or second chicks ($n = 930$, LRS = 0.18; both $P > 0.50$).

DISCUSSION

In most birds, reproductive success improves with parental age (reviewed by Saether 1990); this pattern also has been documented for the Southeast Farallon Island population of Western Gulls (Sydeman et al. 1991b, Pyle et al. 1991). In this paper, we found that the TCD was absent for broods of older parents, providing additional evidence that reproductive success increases with parental age in our population. Our result suggests that the TCD for gulls on Southeast Farallon Island may be a facultative response to energy reserves of the parents. Furthermore, size of third eggs also was smaller than first and second eggs in each year, but the magnitude of these differences depended on environmental conditions probably related to food availability. Differences in egg volume were most pronounced in the year of poorest rockfish availability (1990). This result is consistent with the suggestion of Pierotti and Bellrose (1986) and others (i.e. Mead and Morton 1985) that egg size is a facultative response to varying food availability rather than a part of an adaptive strategy of brood reduction.

To explain age-related differences in chick survival with hatching sequence, we investigated egg volume and hatching asynchrony. Older females produced relatively larger third eggs than did younger birds, and hatching asynchrony decreased with increasing parental age. Although egg size and chick weight at hatching are positively correlated for Western Gulls on Southeast Farallon Island (Coulter 1973, 1977), we found little evidence that egg volume influenced fledging success after statistically controlling for year, laying date, and parental age. In a study of Kittiwakes (*Rissa tridactyla*), Thomas (1983) concluded that the effect of egg volume on fledging success was independent from parental age, but for Herring Gulls (*Larus argentatus*) Davis (1975) judged that the effect of egg volume on breeding success was due to covariation with parental age. Davis suggested that older, more experienced parents compensate for small eggs/chicks by providing additional food and protection in the early stages of the nestling period when egg size is most important to chick survival. In a recent experimental study on Magellanic Penguins (*Spheniscus magellanicus*), Reid and Boersma (1991) also concluded that egg volume did not have an effect independent from parental factors, such as age and date of breeding, on fledging success, but they acknowledged that egg volume may influence early chick survival more so than fledging success. Thus, results indicate that relative age is more important than relative body size in determining the outcome of competitive sibling interactions.

The degree of hatching asynchrony was less pronounced at the nests of older parents. Third chicks of older parents were closer to their siblings age (and size; see above) than the third chicks of younger parents. Additionally, we found that the fledging success of third chicks decreased significantly with increasing asynchrony. Third chicks from nests of older parents are likely more competitive with their siblings than third chicks of younger parents. In a related study, Parsons (1975) experimentally altered hatching sequence and found third eggs that hatched first showed higher survival than third eggs that hatched last.

Improved breeding success with parental age may be ascribed to increasing age-specific reproductive effort (Pugesek 1981, Pugesek and Diem 1990) or enhanced proficiency in breeding associated with prior reproductive experience and foraging efficiency (Nur 1984, Reid 1988, Pyle et al. 1991). In addition to our earlier work showing increasing clutch size and earlier nesting, we have demonstrated that egg volume increases and hatching asynchrony decreases with increasing parental age. These variables act to improve the chances of survival to fledging for the last-hatched chick and serve to enhance the reproductive success of older birds. The TCD in gulls has often been interpreted as an adaptive strategy to reproduction in a varying environment (Lack 1968, Hahn 1981, Graves et al. 1984). Our results suggest instead that the TCD is a nonadaptive effect of parental condition and environmental factors. Gibbons (1987) indicated that asynchronous hatching may be adaptive if, by the early mortality of chicks, parental investment is reduced. This hypothesis is compatible with our results, because younger birds may have greater parental investment costs and, hence, could gain more through reductions in parental care than older parents. However, data on survivorship and future fecundity in relation to hatching asynchrony and chick survival are needed to evaluate this hypothesis. In conclusion, we suggest that age-specific foraging efficiency or reproductive effort may play important roles in determining the magnitude of asynchronous hatching, egg size, and the TCD. Other apparently adaptive attributes of birds also may be artifacts of patterns in life history traits.

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