The Auk 116(3):825–830, 1999

Intraclutch Egg-Size Variation in the Eurasian Kestrel: Advantages and Disadvantages of Hatching from Large Eggs

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Egg size in birds may be positively correlated with hatching success (Järvinen and Väisänen 1983, Magrath 1992a), hatchling mass (Magrath 1992a, Nilsson and Svensson 1993), and nestling growth and survival (Schifferli 1973, Moss et al. 1981, Williams 1990). Hence, egg size could influence offspring fitness (Williams 1994). Egg size varies among and within clutches, the former accounting for most of the variation (Ojanen et al. 1979, Järvinen and Väisänen 1983, Wiggins 1990). However, variation in egg size within clutches may have greater fitness consequences than that among clutches because young that hatch from smaller eggs compete with larger siblings and have a higher risk of starvation (Nilsson and Svensson 1993).

Generally, egg size varies with laying order following patterns that are typical for a species or population; e.g. increasing (Howe 1976, Mead and Morton 1985), decreasing (Parsons 1972, Nisbet and Cohen 1975), or increasing up to the middle egg and decreasing thereafter (Arnold 1991, Williams et al. 1993). These patterns may change relative to food supply (Simmons 1994), year (Jover et al. 1993), or clutch size (Viñuela 1997) and may result from physiological or nutritional constraints on the female and/or be adaptive strategies to improve breeding success.

Several constraints could cause intraclutch variation in egg size. For example, egg size may increase with laying sequence because females are "gearing up" physiologically for starting egg production (Parsons 1976). Last-laid eggs may be smaller because prolactin blood levels, which increase with the onset of incubation, could reduce the size of developing follicles (Leblanc 1987). Egg size also could decline with laying sequence because energy reserves for egg formation are depleted throughout laying (Rydén 1978, Pierotti and Bellrose 1986). Finally, fluctuating environmental conditions at the time of egg laying associated with low temperatures (Ojanen et al. 1981, Järvinen and Ylimaunu 1986, Magrath 1992b) or with changes in food availability (Järvinen and Väisänen 1983) may cause variation in egg size independent of laying order.

At least three hypotheses have been proposed to explain the function of intraclutch variation in egg size. First, variation in egg size relative to laying order may have evolved to influence the degree of sibling competition. Howe (1976) suggested that an increase in egg size with laying sequence is an adaptation to counteract the effect of asynchronous hatching, whereas a decline in egg size with laying sequence would accentuate the effect of hatching asynchrony and facilitate brood reduction (Slagsvold et al. 1984). However, this hypothesis does not consider the costs of producing and incubating large eggs. Second, if the incubation period is longer for larger eggs, then egg-size variation could lead to differences in incubation periods that either facilitate or hinder brood reduction. In this case, a smaller last egg may reduce the degree of hatching asynchrony (Parsons 1972). Finally, egg-size variation may be adaptive because females allocate nutrients differentially based on the probability that an egg in a given position in the laying order will produce an offspring (Ankney 1980, Leblanc 1987, Williams et al. 1993, Viñuela 1997).

I performed a feeding experiment to test whether food supply determines the pattern of intraclutch egg-size variation in Eurasian Kestrels (*Falco tinnunculus*). Moreover, I analyzed costs and benefits of large eggs in relation to laying position in order to test the two supposed adaptive functions related with increasing/decreasing hatching span.

Methods.—This study was conducted on a population of kestrels in the province of Cuenca, central Spain (40°08'N, 02°18'W). The study area is an agricultural plain cultivated mainly with cereals and sunflowers. Kestrels breed in natural rock cavities and to a lesser extent in old corvid nests in trees. Pair formation and selection of nest sites begin in February. Females are fed by their mates during courtship, laying, and incubation, the main prey types being rodents, lizards, and birds. Egg laying begins in the middle of April, and clutches range from three to six eggs and yield, on average, about three fledglings (Aparicio 1998).

Breeding pairs were found several weeks before the onset of laying. Half of the pairs found in 1990 were randomly selected to be fed with supplementary food. Feedings started at least 17 days before egg laying, i.e. kestrels were fed at least twice as long as the nine days that they normally require to develop the first egg (Meijer et al. 1989). Each pair was

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supplemented every two days with 120 to 150 g of whole chickens, which represents the energy demand of a pair for 1.5 days. I confirmed that chicks were eaten by kestrels because yellow-colored pellets were found around all nests. Feeding ceased when the pair had completed egg laying (Aparicio 1994).

Nests were checked every two days from the middle of April until the first egg was laid. During the laying period, nests were visited daily to determine laying sequence. Eggs were marked with a waterproof felt tip pen and their length (L) and maximum breadth (B) were measured to the nearest 0.01 mm with vernier callipers. Egg volume (V) was estimated using the index of Tatum (1975):

$$V = \pi L B^2/6{,}000. \qquad (1)$$

Nests were checked daily 25 days after laying of the last egg to determine hatching time and to match hatchlings with the eggs from which they came. Duration of incubation was estimated for last eggs as the time between day of laying and day of hatching. The incubation period was regarded as "*n*" if hatching occurred before noon on the *n*th day and as "*n*½" if it was between midday and sunset on the *n*th day. Hatching asynchrony was estimated as the spread of hatching dates within a brood. An analysis of covariance (ANCOVA) showed that hatching asynchrony was dependent on clutch size ($F = 8.19$, df = 1 and 18, $P = 0.01$) and hatching success of the last egg ($F = 9.57$, df = 1 and 18, $P = 0.01$) but not on hatching success of the first egg ($F = 0.6$, df = 1 and 18, $P = 0.40$). Therefore, I confined my analyses involving hatching asynchrony to broods where the last egg hatched successfully and used standardized hatching asynchrony, i.e. the residuals from the linear regression of hatching span on clutch size. Hatchlings were individually marked, weighed to the nearest 0.1 g, and their tarsus and wing length were measured to the nearest 0.01 mm. Some young were weighed and measured again before 24 h after hatching to determine growth rate during the first day of postnatal development.

Results.—Egg volume of clutches produced by food-supplemented birds ($\bar{x} = 20.63 \pm$ SE of 0.54 mL, $n = 11$) was slightly (but not significantly) larger than that of control clutches (19.93 ± 0.61 mL, $n = 10$; Mann-Whitney U-test, $Z = 1.27$, $P = 0.26$). The mean coefficient of variation in egg volume within clutches of food-supplemented birds (2.90 ± 0.36) also was similar to that of control clutches (2.16 ± 0.32; $Z = 1.55$, $P = 0.13$). I performed a repeated-measures ANOVA to analyze the effects of supplemental feeding and laying order on egg size. Because clutch size varied between three and six eggs, laying orders were recoded as 1 (first egg), 2 (middle eggs), and 3 (last egg). Egg volume was not significantly affected by treatment ($F = 0.99$, df = 1 and 19, $P = 0.30$) or laying order ($F = 2.89$, df = 2 and 38, $P = 0.07$); however, the interaction between the two factors was significant ($F = 3.40$, df = 2 and 38, $P = 0.04$). The volume of first-laid eggs was significantly larger in supplemented than in control clutches (Scheffé test, $P = 0.0006$); however, neither middle nor last eggs differed significantly in volume between fed and unfed treatments ($P > 0.3$ in each case; Fig. 1). An analysis for five-egg clutches, which were the most frequent in both treatments (five control and eight experimental clutches), gave similar results (treatment, $F = 0.50$, df = 1 and 10, $P = 0.50$; laying order, $F = 1.2$, df = 4 and 40, $P = 0.30$; interaction, $F = 3.50$, df = 4 and 40, $P = 0.01$), and the only significant difference occurred between treatments for the first egg (Scheffé test, $P = 0.003$). Mean egg size decreased throughout the laying sequence ($r_s = -0.54$, $P < 0.001$) in clutches laid by food-supplemented birds. In contrast, the first egg was smallest, and egg size increased until the penultimate egg in clutches laid by control birds (Fig. 2).

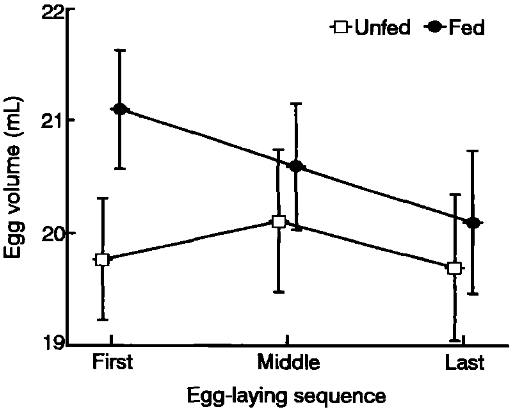

FIG. 1. Relationship between egg volume and laying sequence ($\bar{x} \pm$ SE) for food-supplemented ($n = 11$) and control ($n = 10$) pairs of Eurasian Kestrels. All clutches are included in this figure.

Female kestrels usually start incubation before the last egg is laid (Beukeboom et al. 1988), and nest attentiveness is very high during incubation (pers. obs.). Therefore, the time between the laying and hatching of the last egg may be an accurate measure of incubation length in this species. An ANCOVA with treatment (experimental vs. control) as the main effect and laying date and egg volume as covariates showed that neither treatment ($F = 0.23$, df = 1 and 11, $P = 0.6$) nor laying date ($F = 0.07$, df = 1 and 11, $P = 0.80$) influenced length of the incubation period. In contrast, egg volume had a significant effect on duration of incubation ($F = 13.8$, df = 1 and 11, $P = 0.003$). On average, the incubation period was prolonged by 0.21 ± SE of 0.05 days per mL of egg volume (Fig. 3).

To analyze the effect of egg size on hatchling size, I performed an ANCOVA with treatment as the main

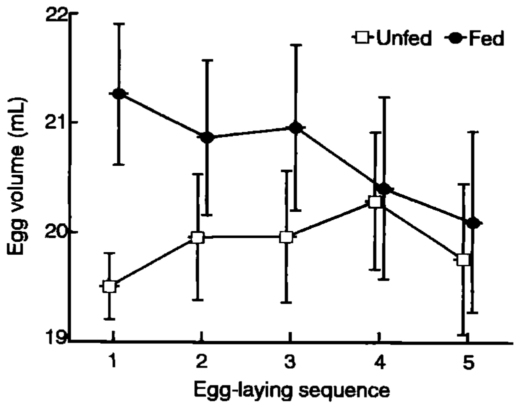

FIG. 2. Relationship between egg volume and laying sequence ($\bar{x}$ ± SE) for food-supplemented ($n = 8$) and control ($n = 5$) pairs of Eurasian Kestrels. Only five-egg clutches are included in this figure.

effect and relative egg volume (i.e. egg volume minus the mean volume of all eggs in the clutch) and absolute egg volume as covariates. Neither treatment nor relative egg volume had a significant effect on cube-transformed tarsus length at hatching (treatment, $F = 2.40$, df = 1 and 14, $P = 0.14$; relative egg volume, $F = 4.08$, $P = 0.06$) or hatchling mass (treatment, $F = 2.60$, df = 1 and 12, $P = 0.14$; relative egg volume, $F = 4.12$, $P = 0.07$). However, absolute egg size had a strong positive effect on both tarsus length ($F = 25.6$, df = 1 and 14, $P < 0.001$) and mass at hatching ($F = 129.8$, df = 1 and 12, $P < 0.0001$), as was expected. On average, body mass and tarsus length at hatching increased 0.72 ± 0.07 g ($r = 0.88$, $n = 15$, $P < 0.0001$) and 0.47 ± 0.10 mm ($r = 0.75$, $n = 18$, $P = 0.0003$) per mL of egg volume, respectively.

To determine whether the costs in incubation time are counteracted by the benefits of larger size at hatching, I examined the development of hatchlings. Chicks gained 4.54 ± SE of 0.32 g ($n = 31$) in mass and 1.54 ± 0.11 mm ($n = 31$) in tarsus length during the first 24 h after hatching. Tarsus growth rate was not affected by hatching order, treatment, absolute egg volume, or relative egg volume (ANCOVA, all Ps > 0.14). Relative egg volume had a negative effect on mass gain ($F = 6.40$, df = 1 and 24, $P = 0.02$), but mass gain was not affected by any other variable (all Ps > 0.19). Thus, chicks that hatched from relatively small eggs gained more mass during the first day than those that hatched from relatively large eggs. However, this result might be an artifact because large eggs may produce hatchlings with more reserves for early postnatal growth. Thus, when these chicks were weighted at hatching, their reserves used for growth were also included.

To test whether sequential trends in egg size influence hatching span, I measured egg size within each clutch as the volume of the last-laid egg minus that of the first-laid egg. This method seems reasonable because hatching span is defined as the difference in hatching time between the first-hatched chick (generally the first laid egg) and the last one. The size of the last egg relative to the first one was positively correlated with standardized hatching span in supplemented clutches ($r_s = 0.72$, $n = 10$, $P = 0.02$) but not in control clutches ($r_s = 0.00$, $n = 8$, $P = 1.0$). Including only clutches with hatching asynchrony lower than the mean, standardized hatching span was positively correlated with egg-size trend ($r_s = 0.73$, $n = 9$, $P = 0.025$; Fig. 4).

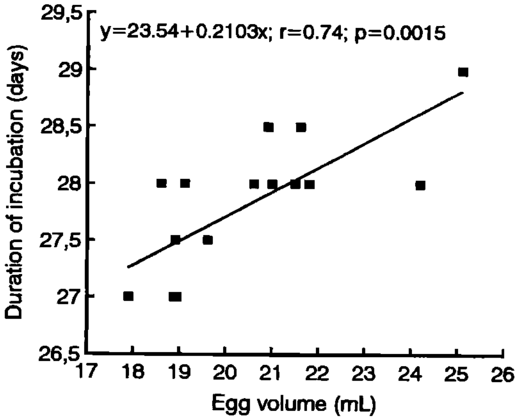

FIG. 3. Relationship between absolute egg volume and duration of incubation for the last-laid eggs of Eurasian Kestrels.

Discussion.—Although mean egg size of experimentally fed kestrels was not significantly different

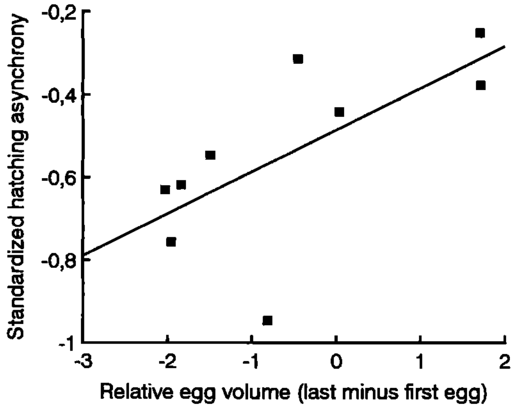

FIG. 4. Relationship between standardized hatching span and volume of last-laid egg relative to that of first-laid egg in Eurasian Kestrels. Only clutches with hatching asynchrony lower than the mean were included in the analysis.

from that of unfed controls, supplementary food altered egg-size hierarchies within clutches, suggesting that energy constraints determine patterns of intraclutch variation in egg size. If fluctuating environmental conditions at the time of egg laying increase egg-size variation, egg size should vary more within control clutches than within food-supplemented clutches. In the Eurasian Kestrel, the coefficient of variation in egg volume within clutches did not change when supplementary food was provided. In the American Kestrel (*Falco sparverius*), supplementary food caused an increase in egg size but did not change the coefficient of variation of egg size within clutches (Wiebe and Bortolotti 1996). In contrast, intraclutch egg-size variation was reduced in American Coots (*Fulica americana*) and Blue Tits (*Parus caeruleus*) that were given supplemental food (Arnold 1991, Nilsson and Svensson 1993). When feeding conditions are unstable, egg size may be more variable because of energy constraints, at least in small birds. The pattern of egg-size variation was irregular in some clutches of Eurasian Kestrels, which is difficult to explain except by fluctuating energy constraints. However, this did not appear to be the principal cause of intraclutch egg-size variation in the birds I studied.

A second hypothesis on proximate causes postulates that females are constrained to start egg laying because internal organs must be geared up to produce eggs. Thus, at least in clutches laid by females in poor condition, egg size would increase with laying sequence (Parsons 1976). My results agree with this hypothesis. In control clutches, egg size increased from the first to the penultimate egg. Moreover, supplementary food had a significant effect only on the size of first eggs, which were larger in experimental clutches than in control ones. However, this hypothesis does not explain why egg size decreased with laying order in clutches of food-supplemented birds.

One explanation for this is that endogenous reserves were depleted throughout egg formation, although it is hard to think that depletion of reserves was more severe for food-supplemented females than for controls. Eurasian Kestrels could produce eggs using body reserves and daily food intake, as do American Kestrels (Wiebe and Bortolotti 1996); however, the relative importance of either source of resources could depend on territory and/or male quality. A female might be able to store enough reserves, even before the onset of egg production, if she is provided with extra food experimentally (Meijer et al. 1988) or if her territory is of such high quality that her mate delivers many prey items during courtship. These reserves should be depleted throughout egg production so that the size of final eggs may depend almost exclusively on daily energy intake. In contrast, in control (or poor-quality) pairs, males could delay courtship feeding until shortly before egg formation, which would result in females having lower body reserves. Hence, the size of the eggs produced by these females would depend primarily on daily energy intake, and the depletion of reserves would affect intraclutch egg-size variation to a lesser extent in these females than in food-supplemented or high-quality females. Moreover, if the initiation of egg formation entails a cost, egg size of poor-quality females should increase with laying sequence, whereas high-quality females should be able to pay that cost with endogenous reserves and produce larger first eggs. However, final eggs could be of similar size in control and supplemented pairs because the daily energy intake during egg formation normally is so high that experimental feeding would not have a significant effect on final egg size.

Some authors have suggested that a decrease in egg size with laying order enhances the effect of asynchronous hatching, whereas the opposite trend would reduce the disparity in hatchling sizes caused by asynchrony (Howe 1976, Slagsvold et al. 1984). On the contrary, Parsons (1972) suggested that smaller eggs have shorter incubation periods such that a decrease in egg size with laying order reduces hatching asynchrony. Up until now, only four studies have found a significant relationship between egg size and length of the incubation period (Parsons 1972, Martin and Arnold 1991, Bollinger 1994, Kattan 1995). In Eurasian Kestrels, the duration of incubation and body size at hatching were significantly positively related with egg size. Mass and tarsus length at hatching increased on average 0.72 g and 0.47 mm, respectively, per mL of egg volume. However, the duration of incubation was 0.21 days longer per mL of egg volume. During the first 24 h, chicks gained on average 4.54 g in mass, and their tarsus grew 1.54 mm. Thus, if two eggs in a clutch differ in size by VmL, and they are incubated at the same time, the smaller egg would hatch $0.21V$ days earlier that the larger one; when the large egg hatches, the differences in mass and tarsus length should be $-0.23V$ g ($0.72V - 0.21 \times 4.54V$) and $0.15V$ mm ($0.47V - 0.21 \times 1.54V$), respectively. Therefore, the smaller size of chicks hatched from small eggs would be compensated by postnatal growth that occurred during time provided by the shorter incubation period. In agreement with this notion, Birkhead and Nettleship (1982) found that growth rates of eggs were slower than those of chicks, and they suggested that to lay small eggs could be advantageous for Thick-billed Murres (*Uria lomvia*) if larger eggs took longer to produce or to incubate. In agreement with Parsons (1972), a decline in egg size with laying order may serve to reduce hatching asynchrony. It may be difficult for parents to synchronize hatching because embryonic development could begin if ambient temperatures exceed the so-called physiological zero, which ranges from 24 to 26°C (Webb 1987). In my study area, maximum temperatures frequently surpassed 25°C during the laying period; thus, first eggs could start development even without incubation. Kestrels could synchronize hatching by producing clutches whose eggs decrease in size with laying order and by postponing the onset of incubation until the clutch is complete. In agreement with this, standardized hatching span was positively correlated with the trend in egg size in broods with low hatching asynchrony.

In conclusion, the pattern of intraclutch egg-size variation in Eurasian Kestrels appears to be proximately determined by feeding conditions before and during egg formation. A high cost of initiating egg formation may cause poor-quality females to produce smaller initial eggs. On the other hand, high-quality females apparently accumulate energy reserves before initiating egg production. These reserves are used to initiate egg laying and are depleted such that egg size declines with laying sequence. The different patterns of intraclutch egg-size variation could serve to increase and reduce, respectively, hatching asynchrony. Studies have found that hatching asynchrony is advantageous when food availability is low, whereas synchronous hatching is more productive when food availability is high (Magrath 1989, Wiebe and Bortolotti 1994). Therefore, proximate constraints on variation in egg formation cause different patterns of intraclutch variation in egg size, which may be adaptive because they affect hatching asynchrony in an optimal way according to food availability.

Acknowledgments.—I thank T. Arnold, J. Viñuela, and an anonymous reviewer for valuable comments on the manuscript. This study was supported by a grant from the Ministerio de Educación y Cultura (PB87-0389) and by a postdoctoral contract (PB94-0070-C02-01).

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Received 26 January 1998, accepted 14 December 1998.
Associate Editor: K. L. Bildstein

The Auk 116(3):830–835, 1999

Mass, Reproductive Biology, and Nonrandom Pairing in Cooper's Hawks

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Several aspects of the ecology of many bird species are correlated with body mass of individuals, including fecundity (Ankney and MacInnes 1978, Aldrich and Raveling 1983), parasite load (Hurtez-Bousses et al. 1997), wintering distribution (Nolan and Ketterson 1983), molt (Cobley and Prince 1998), and predation risk (Lima 1986). In breeding birds of prey, body mass has been used to examine some of these themes and also to investigate the relationship of an individual's mass to the quality of its breeding territory (Newton et al. 1983, Korpimäki 1990) and to mate choice (Bowman 1987, Marti 1990, Bortolotti and Iko 1992). These studies underscore the importance of body mass in demographic and behavioral patterns in birds (Sauer and Slade 1987, Harvey and Bradbury 1991).

The Cooper's Hawk (*Accipiter cooperii*) is a medi-

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