

## LAYING ORDER AFFECTS INCUBATION DURATION IN THE BLACK KITE (*MILVUS MIGRANS*): COUNTERACTING HATCHING ASYNCHRONY?

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**ABSTRACT.**—I studied variation in the duration of the incubation period of Black Kites (*Milvus migrans*) with respect to laying order, egg size, clutch size, and timing of the start of incubation. I estimated the duration of the incubation period and the effect of the onset of incubation by experimentally advancing or delaying the start of incubation. Egg mass and clutch size had no clear effect on incubation duration. First-laid eggs in clutches where I delayed the start of incubation had the longest incubation periods. Hatching in these experimental clutches occurred in reverse order to that of laying. High environmental temperatures during the period that eggs were maintained unincubated prolonged the duration of incubation. Third-laid eggs in clutches where I advanced the start of incubation had the shortest incubation periods. This result was consistent with correlations found between total and partial hatching spreads of control clutches. Recent studies have provided evidence of shortened incubation periods of last-laid eggs in several groups of birds. Shortened incubation periods of last-laid eggs could be due to advanced hatching through vocal communication among embryos, which could counteract the negative influence of long hatching spreads on survival of last-hatched chicks. Aside from benefits to chicks of last-laid eggs, shortened incubation periods in the Black Kite also may serve parental interests, because there is evidence of a parent-offspring conflict over brood reduction. Final hatching spread (time between end of hatching of first and last eggs) mirrored initial hatching spread (time between start of hatching of first and last eggs) but was slightly longer. An additional (or alternative) function of vocalizations by unhatched chicks could be to enhance parental incubation of later-laid eggs after earlier-laid eggs have hatched.  
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HATCHING ASYNCHRONY affects mortality and growth of last-hatched chicks by establishing size hierarchies within broods (Newton 1979; Amundsen and Slagsvold 1991; Viñuela 1991, 1996). At least 17 hypotheses have been proposed to explain the origin and function of hatching asynchrony in birds (Stoleson and Beissinger 1995). In raptors, hatching asynchrony is thought to be an adaptation that promotes mortality of the youngest chicks when there is not enough food to raise the entire brood (Lack 1954, Meyburg 1974, Edwards and Collopy 1983). It is possible, however, that mortality of last-hatched chicks is a nonadaptive consequence of hatching asynchrony when the latter is favored for other reasons (Amundsen and Slagsvold 1991).

Hatching asynchrony usually is assumed to reflect the pattern of incubation during the laying period, although documentation is scarce (Veiga and Viñuela 1993, Ricklefs 1993, Stoleson and Beissinger 1995). In precocial species, highly synchronized hatching is attained through ad-

vanced hatching of late eggs and/or retarded hatching of early ones (i.e. by variable duration of incubation; Vince 1968). One study has reported embryonic control of hatching times in a semiprecocial species (Schwagmeyer et al. 1991), but no such evidence exists for semialtricial birds (despite its potential influence on hatching asynchrony; Stoleson and Beissinger 1995). Recent evidence suggests that other factors, such as female body size, affect hatching asynchrony in semialtricial species (Bortolotti and Wiebe 1993).

Incubation periods may vary considerably within species (Ricklefs and Smeraski 1983), but few studies have examined this variation or its effect on hatching asynchrony. Intraspecific variation in incubation periods usually is explained by differences in nest microclimate or parental attentiveness (Drent 1975). In addition, sibling competition can be a powerful selective force in promoting adaptive variation in the duration of incubation (Ricklefs 1993). Last-hatched chicks in asynchronous broods would

benefit by short incubation periods if this enhanced their survival, but no empirical studies support this hypothesis.

The Black Kite (*Milvus migrans*) is a medium-sized raptor that exhibits facultative siblicide and slow growth and high mortality of last-hatched chicks (Hiraldo et al. 1990, Veiga and Hiraldo 1990, Viñuela 1991). Incubation duration of Black Kite eggs is highly variable (25 to 38 days; Meyburg 1971). Possible reasons for this variation include differences in egg size, an effect of laying order on the duration of incubation, and/or variation in the start of incubation (Meyburg 1971). Additionally, behavioral data on Black Kites suggest that parent-offspring conflict exists over brood size (a trait apparently common in species exhibiting hatching asynchrony and brood reduction; Nilsson 1995). Last-hatched chicks may die from siblicide shortly after hatching independent of food abundance, but female parents (males usually do not feed chicks) selectively feed the smallest chicks and exhibit behaviors that reduce sibling aggression (Viñuela 1991).

The length of the incubation period is difficult to estimate accurately in the field because the start of incubation often differs for individual eggs depending on their laying order (Lack 1966) and because incubation constancy during the laying period may be intermittent (Newton 1979). By artificially controlling the start of incubation, I obtained accurate estimates of incubation duration in relation to laying order, egg mass, and incubation initiation in Black Kites. I provide the first documentation of reduced incubation periods of last-laid eggs in a semialtricial species and suggest that shortened incubation is a mechanism to counteract the negative effects of hatching asynchrony on the growth and survival of last-hatched chicks.

#### STUDY AREA AND METHODS

My study was conducted in Matas Gordas, Northern Doñana National Park, southwestern Spain (37°N 6°05'W). Matas Gordas contains open Mediterranean forest (dominated by cork oak [*Quercus suber*]), scrubland, and grassland near seasonally inundated marshland (see Viñuela and Veiga 1992, Viñuela 1993). I visited the study area almost daily throughout the breeding seasons (mid-March to late July) of 1987 to 1989. Before laying, nests were visited every two to eight days, depending on the stage of the nest during the previous visit. Advanced nests with well-developed linings (i.e. laying was imminent) were checked every

one to two days. Nests were visited daily during laying, and eggs were marked with felt pens and weighed ( $\pm 1$  g) using a Pesola spring balance. I considered laying to have ended when I found the third egg or after four days had elapsed since the previous egg was found. See Viñuela (1996) for additional details.

During 1988 and 1989, I experimentally altered hatching asynchrony of 52 randomly selected clutches. Only two- and three-egg clutches were included in this experiment. At these nests, I took the first two eggs on the days that they were found (day of laying for second eggs, and within one day of laying for first eggs). Kite eggs were replaced with domestic chicken eggs with artificial markings to mimic the pigmentation of kite eggs. Three days after the second egg was laid, I put the original eggs back in their respective nests, marking and weighing the third egg (if present) without removing it. I made a final visit on the next day to assess acceptance of new eggs and to determine if a third egg had been laid. In all three-egg clutches included in this sample, the third egg was laid three (19 cases) or four (1 case) days after the second egg. Clutches were assigned to one of two treatments: (1) synchronous clutches (eggs maintained at ambient temperature until they were returned to the nest); and (2) asynchronous clutches (eggs maintained throughout the removal period at 37–38°C, with water containers inside the incubators and below the eggs; Campbell and Flood 1977; Burnham 1978, 1983). Eggs in both experiment treatments were turned 180° twice daily. Hereafter, I refer to experimental nests as either "asynchronous" or "synchronous" nests, and to nests with unaltered hatching asynchrony as "control" nests. Aside from the experimental manipulations, all methods, including the number of nest visits, were the same at control and experimental nests.

Females Black Kites usually initiate incubation between the laying of the first and second eggs, but slightly later in three-egg clutches (Viñuela 1991, 1996). Eggs were mild or warm to the touch during all of the nest checks made on days that third eggs were laid (Viñuela 1991). Thus, females attained constant incubation sometime between the laying of their second and third eggs (Viñuela 1991). Consequently, my experiments provided accurate data on the duration of incubation, because I controlled the onset of incubation during laying and returned experimental eggs to the nests once constant incubation behavior of adults was reached.

I define incubation period as the number of complete days of incubation elapsed between the day that incubation started (i.e. when eggs in synchronous nests were returned to the nest and when eggs in asynchronous nests were put in the incubator) and the day that hatching started. Sounds could be heard inside the egg even before any sign of hatching in the eggshell could be detected (see Viñuela 1996). Consequently, the day in which incubation started and the

TABLE 1. ANCOVA examining effects of laying order, year, experimental treatment (eggs incubated from day of laying vs. eggs kept unincubated until end of laying period), and clutch size on duration of incubation period of eggs of Black Kites (hatching period excluded). The covariate (egg mass) and other interactions had no significant effects on incubation duration and were removed from the final model.

Variable	df	F	P
Laying order (1st, 2nd, or 3rd)	2	4.23	0.02
Year (1988 vs. 1989)	1	1.67	0.20
Treatment	1	8.06	0.006
Clutch size (2 vs. 3)	1	2.67	0.11
Year × treatment interaction	1	8.37	0.005
Residual	67		

day in which hatching started were excluded. Because eggs in the asynchronous treatment usually were put in incubators in the afternoon, and eggs in the synchronous treatment were returned to the nests at approximately the same time, no appreciable bias could affect my results with respect to the start of incubation. The same was true for the start of hatching, and unless the hour at which the chicks started to hatch could be biased with respect to laying order or treatment, this could not have affected my results. For comparative purposes, I measured incubation duration from 37 last-laid eggs in control clutches.

Meteorological data were obtained from the Instituto Nacional de Meteorología station located 2-5 km from the study nests. For clutches included in the synchronization experiment, I calculated the average maximum daily temperature during the period that eggs were maintained unincubated. I used maximum temperatures because minimum temperatures in Doñana during this time of year are relatively high and approximate the optimal temperatures needed to maintain the viability of unincubated eggs (about 10°C; Olsen and Haynes 1948, Campbell and Flood 1977). In contrast, maximum temperatures often exceed the "physiological zero" temperature (i.e. 24–27°C, below which no embryonic development occurs; Haftorn 1981, Webb 1987). Exposure of unincubated eggs to temperatures below that for optimal incubation (i.e. 35–38°C; Webb 1987) but above physiological zero, is more deleterious than exposure to temperatures below physiological zero (White and Kinney 1974, Haftorn 1988).

Nests were visited daily during hatching to record the condition of each egg or recently hatched chick (see Viñuela 1996). Hatching asynchrony (in hours) was estimated from these daily visits (see Viñuela 1996). Because I studied the duration of incubation with respect to the start of hatching, and duration of the hatching process varies among eggs (A. B. Clark pers. comm., J. Viñuela unpubl. data), it may be important to explore if timing of chick emergence mir-

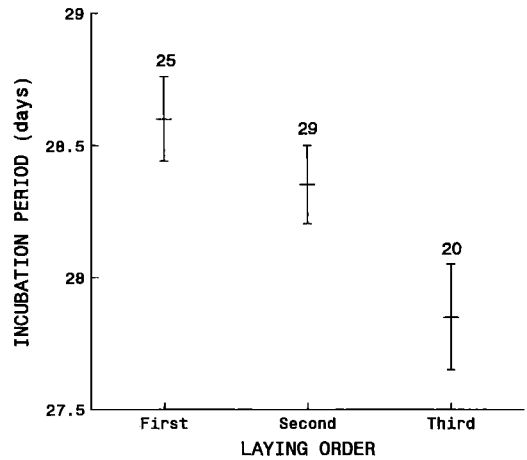


FIG. 1. Variation in incubation period ( $\bar{x} \pm SE$ ; excluding hatching period) among laying orders. Experimental synchronous and asynchronous clutches pooled. Sample sizes above bars.

rors the timing of start of hatching. With this purpose, I calculated the initial hatching spread (estimated time elapsed between the start of hatching of first and last eggs) and final hatching spread (time elapsed between the end of hatching of first and last eggs) for all nests in which the hatching process was recorded (experimental and control pooled; see Viñuela 1996).

I tested the effects of laying order, year, experimental treatment, and clutch size on incubation duration using ANCOVA, with egg mass as the covariate (Table 1). To avoid confounding interactions (there were no experimental clutches in 1987 or accurate estimates of incubation duration for first-laid eggs in control clutches), only experimental eggs were included. Non-significant interactions and covariates were removed from the final model to increase the power of the test.

## RESULTS

*Incubation duration.*—Incubation duration was determined for 74 eggs in experimental clutches ( $\bar{x} = 28.3 \pm SD$  of 0.88 days, range 27 to 31 days), and 37 last-laid eggs in control clutches ( $28.2 \pm 0.97$  days). The difference between experimental and control eggs was not significant ( $t = 0.79$ ,  $P = 0.43$ ).

Egg size did not influence incubation duration ( $F = 1.2$ ,  $df = 1$  and 71,  $P = 0.27$ ) and was removed from the final model. Clutch size and year also had no significant effects on incubation duration (Table 1). Incubation duration was influenced by laying order (Table 1), with third-laid eggs having the shortest incubation periods

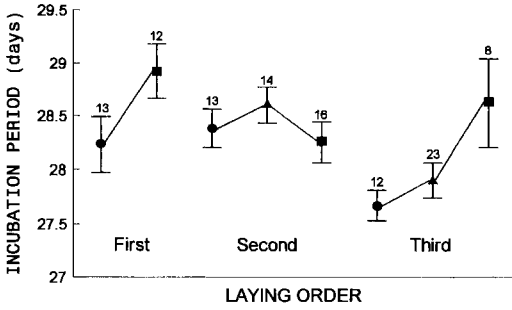


FIG. 2. Variation in incubation period ( $\bar{x} \pm SE$ ; excluding hatching period) among laying orders and treatments. Circles = asynchronous nests; squares = synchronous nests; triangles = second (two-egg clutches) and third (three-egg clutches) eggs of control clutches. Sample sizes above bars.

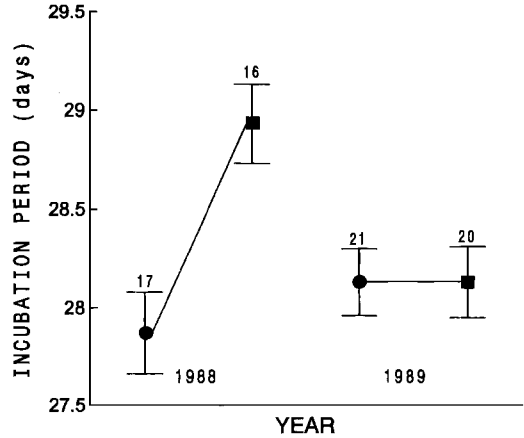


FIG. 3. Variation in incubation period ( $\bar{x} \pm SE$ ; excluding hatching period) among years and treatments. Symbols as in Figure 2. Sample sizes above bars.

(Fig. 1). Treatment also had a significant effect on the length of the incubation period (Table 1); eggs in synchronous clutches had longer incubation periods ( $28.5 \pm 0.9$  days,  $n = 36$ ) than eggs in asynchronous clutches ( $28.0 \pm 0.8$  days,  $n = 38$ ).

Third-laid eggs of asynchronous clutches had shorter incubation periods than third-laid eggs of synchronous clutches ( $t = 2.51$ ,  $P = 0.02$ ), whereas third eggs of control clutches had intermediate values of incubation duration (Fig. 2). First-laid eggs had longer incubation periods in synchronous clutches than in asynchronous clutches, but the difference was not significant ( $t = 1.88$ ,  $P = 0.07$ ; Fig. 2). Third-laid eggs were not manipulated, so delay or advance of the onset of incubation in experimental clutches did not affect third-laid eggs. In 12 out of 13 synchronous nests in which more than one egg hatched, the first-hatched eggs were laid in second or third order. These results suggest that a delay in the start of incubation may induce a protracted incubation period of first-laid eggs, whereas starting incubation with the first egg may induce a shortening of the incubation for third-laid eggs.

The interaction between treatment and year was significant (Table 1). Incubation periods of synchronous eggs from 1988 were longer than those of asynchronous eggs ( $F = 6.4$ ,  $df = 1$  and  $29$ ,  $P = 0.01$ ). This difference was due to a protracted incubation period of synchronous eggs during 1988, but no similar variation for asynchronous eggs was found (Fig. 3). The maximum temperatures to which synchronous

clutches were exposed during the laying period were higher during 1988 than during 1989 ( $21.1 \pm 2.6^\circ\text{C}$  vs.  $18.9 \pm 1.7^\circ\text{C}$ ,  $n = 7$  and  $11$ , respectively;  $t = 2.1$ ,  $P = 0.049$ ).

*Hatching asynchrony.*—The initial hatching spread was smaller than the final hatching spread ( $59.4 \pm 33.8$  h vs.  $65.3 \pm 32.8$  h; paired  $t$ -test,  $t = 3.98$ ,  $P < 0.001$ ), although they were strongly positively correlated ( $r = 0.93$ ,  $P < 0.001$ ). For 21 three-egg control clutches, I recorded total initial hatching spread ( $81.6 \pm 19.2$  h, range 22 to 103 h), initial hatching spread between first and second eggs ( $16.8 \pm 14.1$  h, range  $-8$  to 52 h; negative values for three nests in which the second egg began hatching before the first), and initial hatching spread between second and third eggs ( $62.6 \pm 20.6$ , range 0 to 93.5 h). Initial hatching spread between first and second eggs was more variable than that between second and third eggs (coefficient of variation 84% vs. 32.8%;  $F = 6.5$ ,  $df = 20$  and  $20$ ,  $P < 0.001$ ). Total initial hatching spread was positively correlated with hatching spread between first and second eggs ( $r_s = 0.7$ ,  $P = 0.001$ ), but not with that between second and third eggs ( $r_s = 0.23$ ,  $P = 0.3$ ). Hatching spread between first and second eggs was negatively correlated with hatching spread between second and third eggs ( $r_s = -0.44$ ,  $P = 0.05$ ). These results confirm those provided by experimental clutches; i.e. when hatching spread between first and second eggs increases, that between second and third eggs decreases. The lack of correlation be-

tween total hatching spread and hatching spread between second and third eggs also may be explained by the confounding effect of a reduction in hatching asynchrony between second and third eggs when hatching asynchrony between first and second egg increases.

#### DISCUSSION

Much of the previously described variation in incubation duration of Black Kite eggs may be erroneous, because some authors have assumed that incubation starts with the first egg (e.g. Meyburg 1971). However, Black Kites in my study area delayed the start of incubation until one to three days after the first egg was laid (Viñuela 1991). Moreover, incubation periods ranged from 27 to 31 days (29 to 33 days including two days of hatching period; Viñuela 1996), which is well below the published maximum period of 38 days (Meyburg 1971). I did not find any clear effect of egg mass on duration of incubation. A clear positive correlation exists between egg mass and incubation duration among bird species (Rahn and Ar 1974), but the available information within species is contradictory (Parsons 1972, Runde and Barret 1981, Nol and Blokpoel 1983, Ricklefs and Smeraski 1983, Martin and Arnold 1991, Kattan 1995).

Length of the incubation period was affected by the amount of incubation during the laying period and by laying order. I observed a trend toward protracted incubation of early eggs in synchronous clutches and a shortening of incubation duration of third eggs, especially in asynchronous clutches (Fig. 2). Exposure of eggs to temperatures below that for optimal incubation may reduce viability (Arnold et al. 1987, Viñuela 1991, Veiga 1992, Veiga and Viñuela 1993) or induce sub-lethal effects on embryonic development, such as a protracted incubation period (Webb 1987). Exposure of eggs to temperatures below optimal incubation temperature, but near physiological zero, seems to be especially detrimental (White and Kinney 1974, Webb 1987, Haftorn 1988). In agreement with this idea, the incubation period of synchronous Black Kite eggs was longer during 1988 than during 1989, and the maximum temperatures to which the eggs were exposed during the laying period were higher in 1988 but still were lower than the optimum temperature. Similar results were reported by Campbell and Flood (1977), who found protracted incubation periods for eggs of

Peregrine Falcons (*Falco peregrinus*) unincubated for six days after laying, and by Lessells and Avery (1989), who found a negative correlation between hatching asynchrony and length of the incubation period of the first egg in the European Bee-eater (*Merops apiaster*).

The shortest incubation periods occurred in third eggs in asynchronous clutches. Because these eggs were not removed from nests, their incubation duration was not affected by experimental treatments. Thus, advanced hatching of third eggs must be a consequence of the start of hatching of previous eggs, a result also supported by the negative correlation between partial hatching spreads of three-egg clutches in control nests. This result could be explained by vocal communication among siblings during hatching, as has been observed in precocial birds (Vince 1966). The sounds emitted by precocial chicks before and during hatching facilitate synchrony by advancing hatching of last-laid eggs and slowing hatching of first-hatched chicks (Vince 1966, Vince and Cheng 1970). Unhatched chicks of Black Kites called loudly and frequently before any external signs of shell-breaking could be detected (Viñuela 1996). This behavior is rare in nonprecocial species (Oppenheim 1972, O'Connor 1984) but has been reported in raptors (Gargett 1990), parrots (A. B. Clark pers. comm.), and pelicans (Evans 1988, 1989). Additional research is required before concluding that embryonic control of hatching times occurs in Black Kites. Evidence for this mechanism has been found in precocial species (Vince 1968, Vince and Cheng 1970) and in one laboratory study of a semiprecocial species (Schwagmeyer et al. 1991).

Shortened incubation periods of last-laid eggs in Black Kites could reduce hatching asynchrony and its possible negative effects on survival of last-hatched chicks, which often die from siblicide or starvation (Veiga and Hiraldo 1990, Viñuela 1991). Thus, accelerated hatching of last-laid eggs could serve the selfish interest of chicks. However, given the evidence for parent-offspring conflict over brood size in this species (Viñuela 1991), the accelerated hatching of last-laid eggs also could benefit the parents. Specifically, if first-hatched chicks tend to kill their smaller siblings even when food is abundant (i.e. cainism; Simmons 1988), then the shortened incubation period of last-laid eggs would be favored (because it increases total reproductive success), and females (the only sex that incu-

bates, broods, and feeds the chicks in this species) would collaborate in the process by keeping incubation as constant as possible.

Indirect evidence suggests that among non-precocial species, shortened incubation periods of last-laid eggs are not confined to Black Kites. For example, although hatching asynchrony does not vary with brood size in European Bee-eaters, incubation during laying begins earlier in larger clutches (Lessells and Avery 1989). In American Kestrels (*Falco sparverius*), hatching intervals of last-laid eggs are shorter than expected, and eggs frequently hatch in reverse order to that of laying (Bortolotti and Wiebe 1993). Among boobies, incubation apparently starts with the first egg, but hatching intervals are shorter than laying intervals (e.g. Drummond et al. 1986, Anderson 1989). These results suggest that shortened incubation periods of last-laid eggs are more prevalent in nonprecocial species than previously realized.

A nagging question remains: Why should so complex a mechanism have developed to counteract hatching asynchrony, which could have been reduced simply by delaying the start of incubation? A delay in the start of incubation of first eggs in three-egg clutches may induce a loss of viability of the embryos (Viñuela 1991, Veiga 1992), so the early onset of incubation may be necessary to preserve egg viability. Moreover, if hatching asynchrony arises for reasons other than promoting sibling hierarchies or differential mortality of chicks, then counteracting mechanisms may appear, such as shortened incubation periods of last-laid eggs (Howe 1978, Clark and Wilson 1981, Arnold et al. 1987).

The duration of the final hatching spread mirrored that of the initial hatching spread but was slightly longer. This may have resulted from reduced constancy of incubation after first-laid eggs had hatched, because females have to devote time to feeding the first hatchlings (Evans 1990). Thus, an additional (or alternative) function of embryonic vocalizations could be to enhance incubation of last-laid eggs, again in the same context of cooperation between females and their last-hatched chicks (Evans 1988, 1989; Brua et al. 1996).

My results indicate that length of the incubation period may be affected by the conditions to which the eggs are exposed during early stages of development. Adverse conditions during this delicate stage of development may prolong incubation (Webb 1987). This phenomenon could

explain, at least partly, the long incubation periods exhibited by bird species in which egg neglect is common (Boersma 1982). My results also give support to the idea that sibling competition is an important selective force acting on the duration of incubation (Ricklefs 1993). However, Ricklefs (1993) postulated that variation in the length of the incubation period cannot reverse the competitive hierarchy established by hatching asynchrony, given the relatively low intraspecific variance of this trait. Although the relatively short incubation period of last-laid eggs cannot completely compensate for the large difference in size among siblings that is imposed by hatching asynchrony (Viñuela 1996), it nonetheless could contribute to reduce this discrepancy.

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