ESTABLISHMENT OF MASS HIERARCHIES IN BROODS OF THE BLACK KITE[1]

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Abstract. The relative importance of hatching asynchrony, egg mass and chick growth were studied to establish mass hierarchies in broods of the Black Kite (*Milvus migrans*). Relative growth of first-hatched chicks was the best predictor of degree of chick mass hierarchy, while the effect of egg mass differences was negligible. A quadratic equation best explained the relationship between hatching asynchrony and growth of first-hatched chicks, probably due to the logistic growth curves in birds. Growth of the first-hatched chicks during the hatching period was not related to weather, breeder experience, brood size or year, but had a slight negative correlation with laying date and a positive correlation with amount of food in nests. Growth of chicks during such a short period in a stage of low energy demand may be little affected by environmental factors.

Key words: intra-brood size hierarchy; hatching asynchrony; egg mass; growth; Black Kite; Milvus migrans.

INTRODUCTION

Mass hierarchies after hatching are common in avian broods, especially in raptors (Lack 1968, Skutch 1976, Newton 1979). These hierarchies have an important influence on the mortality of last-hatched chicks, because their smaller size may prevent them from obtaining food when competing against larger siblings (Lack 1954). In Falconiformes and some other avian groups, the smaller size of last-hatched chicks is a disadvantage in cases of sibling fights (O'Connor 1978, Stinson 1979, Mock 1984). Mass hierarchies also may ensure an optimal growth of first-hatched chicks (T. Slagsvold, pers. comm.).

Size hierarchies may be established by hatching asynchrony or by differences in egg mass within a laying sequence (Slagsvold et al. 1984, Magrath 1992). Little is known on the relative importance of these factors in raptors (Newton 1979). Egg size could play a significant role in this group, since some eagles showing obligate fratricide had larger intraclutch size differences than species with facultative fratricide (Edwards and Collopy 1983). However, in other groups of birds, especially Passerines, there is growing evidence showing that egg size has little effect on the establishment of mass hierarchies (reviewed

in Magrath 1990, 1992). Hatching asynchrony may promote the establishment of mass hierarchies because first-hatched chicks receive a head-start on growth. Few studies have quantified the variability of growth during this critical period. Growth of first-hatched chicks during the hatching period could be affected by several factors (O'Connor 1984) that, consequently, may indirectly influence development of mass hierarchies. This may be especially important in a species with highly flexible growth, such as the Black Kite (Hiraldo et al. 1990).

In this study, I examine the relative importance of hatching asynchrony, growth of first-hatched chicks during hatching, and egg mass in establishment of size hierarchies in broods of a medium-sized raptor, the Black Kite (*Milvus migrans*). I also examine the possible influence of brood size, laying date, breeder experience, food, and weather during hatching on the development of size hierarchies.

METHODS

The study was conducted in Matas Gordas, northern Doñana National Park in southwest Spain (37°N 6°5'W). This is a flat area of Mediterranean forest of cork oaks (*Quercus suber*), scrublands, and grasslands, on the edge of a seasonally flooded marshland. See Viñuela and Veiga (1992) for a detailed description of the area.

The breeding area was visited almost daily from mid-March to the end of July in 1987–1989. Nests were found by checking all known nests

from previous years and by inspecting trees in new territories. Nests were visited every 2–8 days before laying, depending on the construction stage at the previous visit. Nests with a well-developed cup lining, where laying was expected, were checked every 1–2 days. Refer to Desai and Malhotra (1979) and Viñuela (1993) for descriptions of nest building in this species. Nests were visited daily during laying. Eggs were marked with felt pens, weighed to the nearest gram using a Pesola balance, and measured with a Vernier caliper. Laying was considered finished when I found the third egg or if 4 days had elapsed after the previous one was found. Clutch size was 1–3 eggs. Only broods with at least two hatched chicks were considered in this study. Fresh weight of 248 eggs in 58 two- and 50 three-egg clutches were recorded. Only eggs found on the day of laying or the day after laying were used, to avoid mass changes due to incubation (Rahn and Ar 1974, Olsen and Olsen 1987). Egg weights were regressed against egg volumes following Hoyt (1979) to determine the following linear equation:

$$y = 1.78 + 0.00053LB^2$$
$$R^2 = 0.96, \qquad n = 248$$

where y = fresh egg weight (g), L = egg length (mm) and B = maximum egg breadth (mm). This equation was used to estimate mass of eggs found two or more days after laying.

Nests were not visited again until 28–30 days after laying of the first egg. Nests were visited daily during hatching to record the condition of each egg (see below) or recently hatched chick. Chicks were weighed the day of hatching and marked in the underside of the wing with felt pens. On the day of hatching of last-laid eggs, all chicks in the brood were weighed. I avoided visiting the nests during rainy weather, early in the morning and at mid-day to minimize the exposure of eggs or chicks to extreme thermal conditions.

HATCHING ASYNCHRONY

Hatching asynchrony was quantified as the time in hours that elapsed between the estimated hatching time of the first and the last chick in a brood. For every recently hatched chick, I distinguished whether they were wet, partially dry or totally dry, and recorded the attitude of the chick. Chicks were either in embryonic position with closed eyes (attitude 1), laying down on the

nest, with open eyes, but still unable to raise the head (attitude 2) or able to raise the head and beg for food (attitude 3).

I estimated the elapsed time from hatching based on the observations of three chicks raised in an incubator and kept at 37–38°C during and after hatching: (1) 3 hours—when the chick was wet and with attitude 1; (2) 5 hours—wet and attitude 2 or partially dry and attitude 1; (3) 7 hours—partially dry and attitude 2; or (4) 9 hours—partially dry and attitude 3 or dry and attitude 2.

When I found chicks that had hatched >9 hours earlier, I estimated the time of hatching following the method of Stokland and Amundsen (1988). This method is based on the existence of different stages of hatching that can be identified in the field (see O'Connor 1984 and references therein, Stokland and Amundsen 1988). I distinguished seven stages: (1) hatching start—identified by sounds inside the egg, but without external clues of hatching. The sounds are audible by holding the egg near the ear. The sounds are a mix of chick calls, breathing ("clicking," see O'Connor 1984), and pecking of the egg shell; (2) first shell breaking—slight cracking of the shell; (3) raised shell—shell raised at crack with respect to rest of the shell; (4) hole in shell—the longest stage of hatching (O'Connor 1984), divided into two stages, based on width of hole, (A) <10 mm or (B) >10 mm; (5) shell opening—chick expands the hole in shell by turning inside the egg, pecking and cutting a long fissure around the small axis. Included in this stage were all observations in which the hole in the shell was longer than one-fourth of circumference of the egg (this is the shortest and least frequently observed stage of the hatching process, Table 1); and (6) recently hatched chick—varied from almost completely open shell (<1 cm of shell not broken) to two shell halves and embryonic membranes in the nest and the chick wet, with eyes closed and in embryonic position.

EXPERIMENTAL MANIPULATION OF HATCHING ASYNCHRONY

Hatching asynchrony of 52 randomly selected clutches was experimentally altered during 1988 and 1989. Kite eggs were replaced with domestic chicken eggs artificially marked to mimic the natural pigmentation of Kite eggs. From these nests I took the two first-laid eggs on the days they were found. Three days after the second egg was

TABLE 1. Occurrence of seven stages of hatching during 1988 and 1989 for Black Kites. See methods for definition of each stage. The estimated duration of each stage was calculated from the relative frequency of observation of each stage (percentages of the total number of observations for every stage in brackets), assuming that overall duration of the hatching process was 48 h. Correction factors used to estimate the timing of hatching for each egg, calculated as half the duration of the stage summed to the duration of all the subsequent stages.

| | Hatching stages | | | | | | |
	1	2	3	4A	4B	5	6
1988 (%)	25	26	44	39	8	9	18
	(14.8)	(15.4)	(26)	(23.1)	(4.7)	(5.3)	(10.6)
1989 (%)	22	18	28	28	6	5	12
	(18.5)	(15.1)	(25.5)	(25.5)	(5)	(4.2)	(10.1)
Total (%)	47	44	72	67	14	14	30
	(16.3)	(15.3)	(25)	(23.3)	(4.9)	(4.9)	(10.9)
Estimated duration	7.8	7.3	12.0	11.2	2.3	2.3	5.0
Correction factors	44.1	36.5	26.8	15.2	8.5	6.2	2.5

laid they were returned to the nest. The third egg was marked when found, but not removed. Experimental clutches were assigned to one of two treatments: (1) Synchronous clutches had eggs maintained unincubated at ambient temperature until the day returned to the nest, and (2) asynchronous clutches had eggs maintained in incubators at 37–38°C, with water containers below the eggs (Campbell and Flood 1977; Burnham 1978, 1983). Eggs of both treatments were turned 180° twice daily. Hereafter I refer to experimental nests as asynchronous and synchronous nests, and to the nests with unaltered hatching asynchrony as control nests.

OTHER VARIABLES

For each nest check during the hatching period, prey remains on the nests were recorded following Viñuela and Veiga (1992). Black Kites usually do not remove prey remains from the nest, often storing large amounts of food when prey availability is high (Viñuela 1991). All remains without meat were removed and those that could still be eaten marked to avoid repeating counts in subsequent visits. Estimated biomass found during the hatching period was divided by the number of days of that period to estimate "daily biomass."

I define laying date as the estimated day of laying of the first egg in a clutch. I assumed that laying interval between the first and second egg was three days, which was the typical laying interval between second and third eggs (Viñuela 1991). Observed laying interval between first and second eggs was 1–3 days. Laying date "1" was

the earliest laying date recorded during the three study years (23 March).

For every clutch the egg mass hierarchy was calculated as the difference in mass between the first and last hatched eggs, expressed as a percentage of the average mass of the clutch. A negative value occurred when the last-hatched egg was heavier than the first-hatched one. For each brood I calculated the difference of mass between the first- and last-hatched chicks on the day of hatching of the last chick as a percentage of the average mass of all the chicks in the brood that day (chick mass hierarchy), and the percentage of mass increase of first-hatched chicks during the hatching period (growth of first chicks). In some cases data could not be recorded on egg mass hierarchy, chick mass hierarchy, growth of first-hatched chicks, or hatching asynchrony, resulting in differences in sample size between some analyses.

To explore the possible influence of weather during the hatching period, I calculated the average mean daily temperature and rainfall for every brood during the hatching period.

During the study period, the population of Black Kites in the study area steadily increased, due to the settlement of new inexperienced pairs (see Viñuela 1993 for details). I distinguished between pairs in their first or second breeding year in a nesting territory (inexperienced birds), and those with three or more years of settlement in the area (experienced birds), as I did not know the real age of the individuals.

Statistical analyses were performed on STATGRAPHICS and SPSS. Quadratic equations were
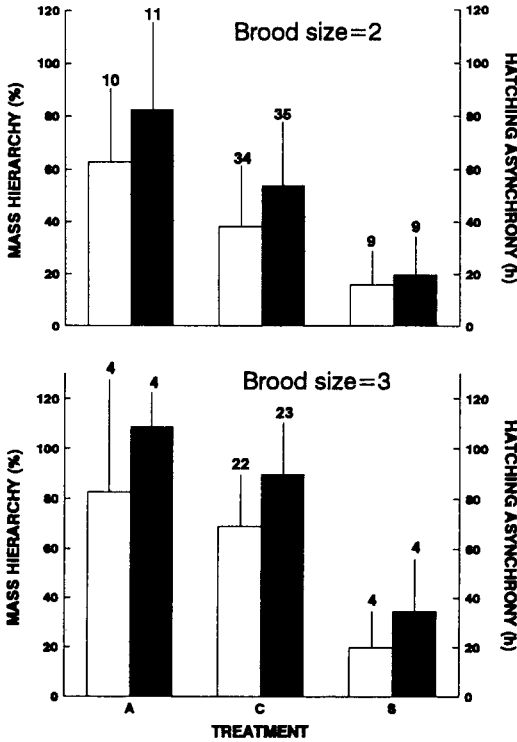
FIGURE 1. Hatching asynchrony (black bars) and mass hierarchy (white bars, weight difference between first and last hatched chicks in a brood as percentage of the average weight of all the chicks in the brood measured on the day of hatching of last chick) in two- and three-chick broods of Black Kites. Means ± SD, sample sizes above bars. Data for experimental asynchronous (A), control (C), and experimental synchronous (S) broods.

used when suggested by scatter plots. This fit was made by multiple regression analyses that included the dependent variable and its square power, and using the conditional sum of squares to assess if the square power significantly increased the variance explained by the model (Sokal and Rohlf 1981).

RESULTS

The mean duration of the hatching process was estimated from 11 eggs for which I observed the first (1) and last (6) hatching stages. Mean duration was 47.8 ± 9.1 hr (range 30.0–68.7 hr). Usually two days elapsed between the observation of first hatching clues and the observation of a hatched chick. Table 1 shows the 288 hatching observations made during 1988 and 1989. During 1987 I did not distinguish between stages

2 and 3 and I did not measure the diameter of the hole, so I have not included these data for the estimates. I assumed that the relative duration of each hatching stage was proportional to its frequency of observation (Table 1; Stokland and Amundsen 1988). To estimate the duration of hatching of each egg, every observation of a hatching stage was considered to be at the midpoint of the whole duration of that stage (Stokland and Amundsen 1988). The time of hatching was estimated to the nearest hour by using seven "correction factors" (Table 1). For example, an egg seen in stage 3 was estimated to hatch 26.8 hr later. For 1987 data, the same method was used, but summing the durations of stages 2 and 3 and those of stages 4A and 4B.

Hatching asynchrony was clearly different between control and experimental nests (two-chick broods: $F_{2,52} = 15.77$, $P < 0.001$; three-chick broods: $F_{2,28} = 15.6$, $P < 0.001$) (Fig. 1). Chick mass hierarchy was positively correlated with hatching asynchrony (Fig. 2) and varied significantly between control and experimental nests (two-chick broods: $F_{2,50} = 9.25$, $P < 0.001$; three-chick broods; $F_{2,27} = 8.1$, $P = 0.0018$; Fig. 1). Chick mass hierarchy was higher in three- than in two-chick broods ($F_{1,81} = 15.2$, $P < 0.001$) and varied significantly between years ($F_{2,80} = 4.54$, $P = 0.014$), but was not affected by laying date ($r = -0.16$, $P = 0.15$, $n = 83$) or breeder experience ($F_{1,81} = 0.58$, $P = 0.46$). The residuals from the regression of chick mass hierarchy on hatching asynchrony did not vary with brood size ($F_{1,81} = 0.09$, $P = 0.76$) or year ($F_{2,80} = 0.87$, $P = 0.42$). Consequently, the relationship between chick mass hierarchy and brood size or year must be a collateral effect of the variation of hatching
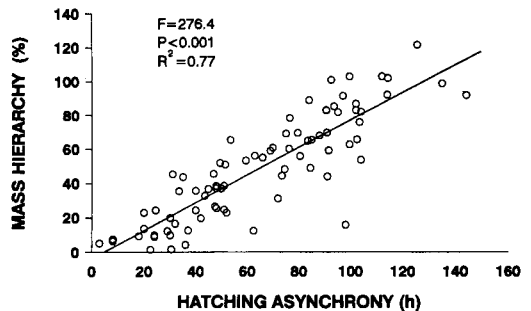

FIGURE 2. Effect of hatching asynchrony on the development of mass hierarchy (defined as in Fig. 1) in broods of Black Kites. Linear regression line shown (y = −3.8 + 0.81x).
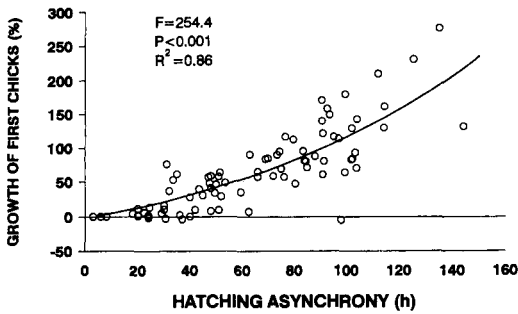
FIGURE 3. Effect of hatching asynchrony on percentage of weight increase of first hatched chicks of Black Kites during the hatching period. Quadratic regression line shown (y = 0.41x + 0.007x²).

asynchrony between brood sizes ($F_{1,84} = 21.1$, $P < 0.001$) or years ($F_{2,83} = 3.6$, $P = 0.03$). Residuals from the ANOVA of hatching asynchrony on brood size did not vary between years ($F_{2,83} = 1.1$, $P = 0.35$).

Growth of first-hatched chicks during the hatching period varied from -4.8% to 275% ($\bar{x} \pm SD = 65.7 \pm 58.9$), and was strongly correlated with hatching asynchrony. A quadratic equation best fit the data (partial F for the square term = 16.3, $P < 0.001$; Fig. 3). Growth of first-hatched chicks was highly correlated with chick mass hierarchy ($r = 0.92$, $P < 0.001$, $n = 83$).

There was no significant correlation between chick mass hierarchy and egg mass hierarchy ($r = 0.14$, $P = 0.2$, $n = 80$), even when considering only synchronous nests ($r = -0.05$, $P = 0.86$, $n = 13$). A stepwise regression analysis was performed with chick mass hierarchy as dependent variable and hatching asynchrony, growth of first-hatched chicks and egg mass hierarchy as independent variables. All three factors significantly entered the model, which explained 90% of the variance of chick mass hierarchy (Table 2). Egg mass hierarchy only entered the model after removing the effects of growth of first-hatched chicks and hatching asynchrony. Its contribution to explained variance was only 1%.

To estimate the growth rate of first-hatched chicks during the hatching period, the ratio "mass increase of first chicks during the hatching period/hatching asynchrony" was calculated. The only variables apparently affecting the growth rate of first-hatched chicks during the hatching period were laying date ($r = -0.23$, $P = 0.035$, $n = 83$) and daily biomass ($r = 0.24$, $P = 0.032$). There was a marginal effect of brood size ($F_{1,81} = 3.1$, $P = 0.08$, slower growth in two-chick broods) and no significant effects of year ($F_{2,80} = 2.3$, $P = 0.11$), breeder experience ($F_{1,81} = 0.31$, $P = 0.59$), rainfall ($r = -0.14$, $P = 0.21$, $n = 83$) or temperature ($r = -0.02$, $P = 0.88$, $n = 83$).

DISCUSSION

Chick mass hierarchy was strongly dependent on the growth of first chicks during the hatching period and on hatching asynchrony. The growth of first-hatched chicks was related to hatching asynchrony by a quadratic equation (Fig. 3), probably due to the logistic shape of growth curves in birds. As hatching asynchrony increases, it is more likely that the oldest chick will reach the phase of linear growth before the last chick hatches. This could also explain why hatching asynchrony had an effect independent from that of growth of first-hatched chicks in a multiple linear regression analysis.

Growth of first-hatched chicks was the best predictor of intra-brood hierarchies after hatching, while the effect of egg mass hierarchy was negligible (Table 2). Egg mass differences could have a more important effect in synchronous nests (Bryant 1978), as in these nests the effect of hatching asynchrony or growth of first-hatched chicks would be much lower. However, I did not find any significant correlation between chick- and egg-mass hierarchies in synchronous nests. Even in the most extreme cases, differences in egg mass did not seem to have any relevance in the establishment of chick mass hierarchies. This conclusion had also been reached by other au-

TABLE 2. Best multiple regression model for Black Kite chick hierarchy, defined as the difference of weight between the first and the last hatched chick in the day of hatching of last chick, as percentage of the average weight of all the chicks in the brood that day. Independent variables considered were 1) hatching asynchrony, 2) growth of first hatched chicks, and 3) egg mass hierarchy (see Methods for definition of these variables). R^2 values refer to change in explained variance after inclusion of every dependent variable in a stepwise analysis ($n = 80$).

Independent variable	Regression coefficient	F	P	R²
Growth of first chicks	0.33	582.5	<0.001	0.84
Hatching asynchrony	0.31	88.36	<0.001	0.89
Egg hierarchy	0.41	4.12	0.046	0.9

thors (recent reviews in Stokland and Amundsen 1988, Magrath 1992, and Ohlsson and Smith 1994), including some studies on raptors (Poole 1982, Bortolotti 1986). Egg mass differences are relatively small compared to mass differences promoted by hatching asynchronies, even for hatching spreads of relatively short duration. The maximum egg difference recorded was 11 g, a mass difference reached in nests with asynchronies less than 24 hours. On the other hand, the slight mass differences between chicks simultaneously hatched promoted by egg mass differences may be not as important as other factors. During the first hours after hatching, coordination of movements by chicks is still imperfect, and small chicks face problems obtaining food offered by the females during feeding bouts (Viñuela 1991). In a synchronous condition, a slight advantage in coordination of movements could be as important as small size differences (Mead and Morton 1985). The variation of egg mass with laying order has often been related to the establishment of size hierarchies among chicks (Edwards and Collopy 1983, Slagsvold et al. 1984), but my results do not support this idea. A combination of female condition and optimal distribution of resources could better explain intra-clutch egg mass variation in this species (Viñuela 1991).

Brood size and year apparently had an effect on the development of size hierarchies, but this must be due to greater hatching asynchronies of three-egg clutches and year-to-year variation in clutch size. Once the effects of these confounding variables were removed, there was no year-to-year variation in the establishment of chick mass hierarchies, although there was marked year to year variation in weather, food availability, chick mortality and overall growth rates of chicks (Viñuela and Sunyer 1992, Viñuela and Veiga 1992). Also, although breeder experience had an important influence on several variables reflecting breeding performance, such as laying date, clutch size, egg size or chick mortality (Viñuela 1991, 1993), it did not affect the establishment of size hierarchies. Food requirements of recently hatched chicks are relatively small (Ricklefs 1968, O'Connor 1984), and the hatching period lasts only 0–5 days. Thus, it may be difficult to detect significant effects of environmental factors on the growth of first-hatched chicks unless they have a very marked importance, as in the case of laying date (see below). In an opportunist-searcher species, such as the Black Kite, prey delivery rate

to the nests may be very irregular, alternating between overabundance or scarcity during short periods (Viñuela 1991). In fact, estimated daily biomass during the hatching period was highly variable, from no prey found and growth of chicks very slow, to 840 g/day, in nests where prey were as frequent as two rabbits per day, a food supply clearly in excess of the energy requirements of recently hatched chicks.

However, there was a slight, but significant effect of laying date on the growth rate of first chicks during the hatching period. Growth was slower in late broods than in earlier broods. A similar effect of laying date on the overall growth rate of nestlings in this species has been found (Hiraldo et al. 1990, Viñuela 1991). In the study area there is a decrease of food availability during the breeding season (Valverde 1960, Hiraldo et al. 1990, Veiga and Hiraldo 1990). Late laying pairs are mostly inexperienced birds that have poorer hunting abilities or may have imperfect feeding skills (Viñuela 1993). Late laying may be related to low prey delivery rates by males during the pre-laying period (Newton 1979, Daan et al. 1988), and males provide most of the food during the first weeks of the nestling period (Cramp 1980, pers. obs.). So, laying date may reflect simultaneously several constraints on the growth of chicks. This may be the reason why laying date was the only variable, along with daily biomass, that showed a slight effect on intra-brood mass hierarchy, a trait determined mainly by hatching asynchrony, that explained most of the variance in growth of first hatched chicks (86%).

ACKNOWLEDGMENTS

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