Bird Study

ISSN: 0006-3657 (Print) 1944-6705 (Online) Journal homepage: www.tandfonline.com/journals/tbis20

Determinants of reproductive success in the Hoopoe *Upupa epops*, a hole-nesting non-passerine bird with asynchronous hatching

M. Martín-Vivaldi, J.J. Palomino, M. Soler & J.J. Soler

To cite this article: M. Martín-Vivaldi, J.J. Palomino, M. Soler & J.J. Soler (1999) Determinants of reproductive success in the Hoopoe *Upupa epops*, a hole-nesting non-passerine bird with asynchronous hatching, Bird Study, 46:2, 205-216, DOI: 10.1080/00063659909461132

To link to this article: https://doi.org/10.1080/00063659909461132

Bird Study (1999) **46,** 205–216

Determinants of reproductive success in the Hoopoe *Upupa epops*, a hole-nesting non-passerine bird with asynchronous hatching

MANUEL MARTÍN-VIVALDI*, JOSE JAVIER PALOMINO, MANUEL SOLER *and* JUAN JOSÉ SOLER *Department of Animal Biology and Ecology, Science Faculty, University of Granada, E-18071 Granada, Spain*

Factors affecting success of individual clutches and reproduction in the Hoopoe Upupa epops *were studied over five years in a colour-ringed population in Granada, southern Spain. Pairs initiated between one and three breeding attempts per season (including replacement clutches), but only 19% laid a second clutch after raising one successful brood. Seasonal productivity ranged from none to eight fledglings. The pairs that laid a second clutch obtained slightly greater productivity than those that did not, although the differences were not significant, and productivity was not correlated with the number of attempts initiated. Apparently, the reason that these differences were not greater, was the higher predation rate suffered by second and replacement clutches. Predation accounted for 55% of nest losses, although two other major causes were nest desertion and death of females in the nest (17% each). The modal laying date of first clutches in the population was close to the date when the productivity of first clutches was higher. This suggests that, for most individuals, the costs of early laying exceed the benefits of obtaining two broods due to differences in quality between them. Successful clutches produced one to six fledglings (mean 2.97) and the proportion of eggs per clutch that failed to produce fledglings in these successful clutches was very high (49%). Most losses in successful clutches were due to death of chicks, which normally died very young and in a sequence determined by the hierarchy in the brood due to complete hatching asynchrony. The number of chicks fledged was positively correlated with the amount of food carried to the nest by parents. The patterns of nestling mortality and food delivery suggest that the Hoopoe is a brood reduction strategist that reduces 'optimistic' clutch sizes by selective starvation of the youngest chicks through extreme hatching asynchrony.*

Avian reproductive success depends on the number of successful breeding attempts and on the number of fledglings produced in each successful attempt.[1] The first of these two components is affected mainly by nest predation causing complete nest loss.[2] The predation rate is mainly determined by the type of nest used, with hole-nesting species suffering lower predation rates than open-nesters.[3] This fact has been used to explain why hole-nesting birds tend to invest in just one or two large clutches instead of several small ones.[4,5] However, although high predation rates are clearly associated with many broods per year and small clutches, and the type of nest used is an important correlate of these differences,[6] non-excavator hole-nesting species are outliers in this relationship, with larger clutches and more broods per season than expected.[6] Martin suggested that the cause of this special reproductive pattern of non-excavator species is the

*Correspondence author.
Email: mvivaldi@goliat.ugr.es

scarcity of suitable nest-holes, which makes them reproduce with greater effort when they secure a nest.[6]

The productivity of a successful clutch is limited primarily by the number of eggs laid and the number of these eggs that parents are able to rear. When food availability is predictable, birds normally adjust clutch size to the number of nestlings that the pair is able to feed,[7,8] because eggs that ultimately fail to fledge chicks waste energy. Therefore, in those species which lay 'realistic' clutches, the productivity of a clutch is mainly limited by clutch size. However, when the availability of food during the nestling period is unpredictable at laying, birds are believed to lay 'optimistic' clutches, where productivity is not limited by the number of eggs, but by the number of chicks that the parents can adequately feed.[7,9] Hatching asynchrony in birds was first viewed as a way to facilitate the adjustment of an optimistic clutch to the number of young that the pair is eventually able to feed, avoiding waste of investment in the smallest chicks that would die anyway if food was scarce (brood reduction hypothesis[7]).

For example, in the Jackdaw *Corvus monedula*, a brood reduction strategist in which chick deaths are frequent (62.8% of chicks[10]), 43.7% of deaths occur in chicks less than five days old, which is only 5% of biomass produced in the brood.[11] The brood reduction hypothesis has received experimental support in some cases,[12–14] but not always, and a number of non-exclusive alternative hypotheses have recently been proposed as functional explanations for hatching asynchrony (reviewed in refs 15 and 16).

The Hoopoe *Upupa epops* (Coraciiformes) is a hole-nesting species in which the male provides the female with all the food while she is incubating, and all the food for her and the chicks during the first seven or eight days of the nestling period (normally soil invertebrates, one item per trip) (pers. obs).[17] When nestlings are older, both male and female carry food, but it is mainly the female that feeds the young after receiving the prey from the male[17] (pers. obs.). Hoopoes use a wide variety of hole nests,[17] although most are located in trees below 3 m in height (pers. obs.),[17] being accessible to predators such as small mammals, lizards and snakes. Nestlings develop an active anti-predator defence consisting of the production of a bad-smelling fluid from oil-glands and copious ejection of liquid faeces towards a predator.[17] Hoopoes normally lay eggs with an interval of 24 hours and only rarely 48 hours and start incubation from the first or second egg. The eggs normally hatch at intervals of 24 hours, producing complete hatching asynchrony,[18–20] although for the African subspecies, completely synchronous hatching has been described.[21] Studies of the breeding biology of this species in the Palearctic are scarce and, except for one case in which breeding success in the field is reported,[22] have focused on breeding density, type of nest used or habitat selection,[23,24] or breeding behaviour of birds in captivity.[20] These studies were not based on colour-ringed individuals, and they therefore cannot evaluate seasonal breeding success (sometimes first and second clutches are laid in different nest-holes, and consecutive clutches laid in a nest can be from two different pairs, pers. obs.).

Most studies on reproductive success of non-excavator hole-nesting species have been performed with populations breeding in nest-boxes. Nestboxes may modify the ecological constraints suffered by populations that use natural holes, mainly reducing the risk of predation and affecting clutch size,[25–27] and therefore may alter at least two important components of breeding success. Therefore, for investigating reproductive success in wild populations it is better to study those breeding in natural holes. Due to the difficulty of locating and inspecting these cavities, such studies are scarce and the incidence of predation underestimated.

We investigated the factors determining individual variation in seasonal reproductive success in a colour-ringed population of Hoopoes breeding in natural nest-holes. The aim was to answer the following questions. (1) Which breeding variables explain seasonal reproductive success? (2) How does the laying of second clutches affect breeding success? (3) What are the main causes of complete clutch loss? (4) What are the determinants of clutch productivity? (5) Do Hoopoes lay realistic or optimistic clutches? (6) How does parental feeding effort influence breeding success? (7) How does asynchrony affect the pattern of chick mortality?

MATERIALS AND METHODS

Study area

The study was carried out from 1991 to 1995 in several areas near Granada (southern Spain), situated around the base of the northern watershed of the Sierra Nevada mountains. One of them, the Corvales Reserve (35 ha), is part of a valley at 800–950 m asl with a mosaic of crops and non-cultivated areas. The rest are gullies or irrigated crops situated in the Hoya de Guadix, a high-altitude basin at 900–1100 m asl, and are separated by open plains cultivated with dryland cereals in which Hoopoes are very scarce. Because of their qualitative similarities and proximity, the different areas have been combined in the analyses. We worked only in Corvales in 1991, in five areas in 1992 and in seven in 1993–95. The number of breeding pairs found in the study area each year were 4 in 1991, 16 in 1992, 23 in 1993, 25 in 1994 and 29 in 1995.

General field procedures

The different areas were visited at least once per week during the breeding season, from early February to the end of July. Most individuals were caught in mist-nets before laying or while feeding chicks. They were individually colour-ringed and provided with numbered aluminium rings (Spanish Institute for Nature Conservation, ICONA). The nest entrance was always too small to allow manual examination. For this reason, nest contents was examined through the nest entrance. When the cavity was straight, we illuminated it with a small bulb tied to a wire. When it had angles, we used a thin periscope provided with a light, a tube, a prism and a convergent lens. We inspected nests at least weekly in order to detect failures, but more frequently during the critical periods: egg laying, hatching and fledging.

When nestlings were 19–21 days old we opened the nests in order to ring them, take body measurements and record unhatched eggs and dead chicks (adults do not remove them from the nest). Five nests were also opened before this age (between 8 and 13 days old) and nestlings ringed and measured, in order to determine the influence of the position in the size hierarchy on the probability of chick mortality. When nests were in piles or walls of stones, we opened them by removing some stones, when they were in trees we cut a hole with a saw and when they were in rocks we used a hammer and chisel. Whenever possible we did not alter the nest entrance while opening the nest. After ringing chicks, the nests were restored by replacing removed stones, cut wood fragments (sticking them with glue), or rock fragments (fixing them with clay), and hiding joints with glue and soil. The nests were opened at midday, because this is the period with low feeding activity and few visits by people. We also opened failed nests to remove eggs, dead chicks or dead females. None of the nests was deserted as a consequence of this manipulation.

We took four measurements from nestlings: tarsus-length, maximum wing-length (both following Svensson's method[28]), bill-length from the tip to the distal edge of the nostrils, and mass. We used dial callipers for tarsus- and bill-lengths (accurate to 0.01 mm), a ruler with a stop at zero for the wing-length (accurate to 0.5 mm) and a spring balance for mass (accurate to 0.5 g). Chicks in a brood were assigned a position in the size hierarchy according to both bill- and wing-length, because both body parts increase continuously during the nestling period. When there was a discrepancy in the relative size of these two measurements between two chicks, we used that with the greatest percentage difference.

Chicks found dead were aged according to size and plumage development. Unhatched eggs were opened to check if they were fertilized (presence of embryo) or infertile.

Breeding variables

We studied the following breeding variables. (1) Laying date, defined as the day when the first egg was laid, assuming that one egg was laid daily.[18,19] When the nests were found after clutch completion, laying date was estimated by subtracting 17 days (mean and mode of the incubation period, see Results) from the hatching date of the first chick. When analysing laying date, annual variation was controlled for by subtracting the median laying date for that year. (2) Clutch size, defined as the maximum number of eggs in the nest during incubation. Hoopoes do not remove dead chicks or unhatched eggs before fledging, and if the first

inspection occurred during the nestling period, clutch size was estimated by summing the number of unhatched eggs, and dead and live chicks. (3) Incubation period, estimated as the number of days between laying and hatching of the first egg. (4) Nestling period, estimated as the number of days between hatching of the first egg and fledging of the last chick. These two last parameters were analysed using only the nests where laying date, hatching date and fledging date were recorded with a maximum error of one day. (5) Brood size at hatching, defined as the maximum number of nestlings observed during inspection of the nest after all chicks should have hatched. When this brood size plus unhatched eggs did not equal clutch size, the missing individuals were considered to have hatched, died very young and decomposed in the nest. (6) Number of fledged young, defined as the number of nestlings ringed that were not found dead in successful nests after fledging. (7) Hatching success, defined as brood size at hatching divided by clutch size in nests that survived until hatching. (8) Fledging success defined as the number of fledged young divided by brood size at hatching in nests that survived until fledging. (9) Nesting success, defined as the number of young fledged divided by clutch size in nests that survived until fledging. On the other hand, (10) the proportion of eggs hatched and (11) young fledged, include clutches and broods that did not survive until hatching or fledging. (12) Productivity, defined as the number of fledglings produced over the whole breeding season.

We excluded from estimates of breeding success any clutches and pairs in which losses were due to our manipulation (four cases). When one member of the pair disappeared and was replaced by a new individual for the subsequent attempts in the season (six cases), the different attempts were considered to belong to the same pair, because they were always associated with the same nest or breeding site.

We considered a nest to be predated when (1) all eggs or chicks disappeared between two visits, (2) some disappeared and the others were scattered in the nest (eggs), (3) the chicks were found partially eaten, or (4) there were remains of blood and feathers from the female. We considered that a clutch was deserted when the eggs remained in the incubation position without being incubated for several days.

We considered second clutches to be those laid by a pair after a successful first clutch in the same breeding season, and replacement clutches those laid by a pair after a failed one in the same breeding season.

Feeding rates were recorded by making two observations in each breeding attempt, when nestlings were 4–8 and 15–22 days old. The number of visits with food by the male and the female were recorded during a period of 60–90 minutes in the afternoon (between 15.30 and 20.00 hours) by observing the nest entrance from a distance with a telescope, or by recording with a video camera. Each prey carried was assigned a size value of 1, 2 or 3 when it was smaller than a quarter, between a half and a quarter, and larger than half of the adult bill size, respectively. When it was not possible to determine the size of prey, it was assigned as size 2 (mean 1.45 ± 1.65 (sd) prey per nest in first samplings, 1.97 ± 2.63 in second samplings). We used an index of the amount of food carried per hour which was calculated as the sum of the sizes of all prey carried multiplied by 60 and divided by the duration of the sampling in minutes.

Statistical procedures

We used non-parametric statistics because many variables were not normally distributed. However, we used quadratic regressions to describe the relationship between laying date and clutch size, and descriptive statistics are mean ± standard deviations. When correlations used for calculating partial correlations differed in sample size, in order to be conservative we selected the lowest one for the estimation of the level of significance of the partial correlation.

There were no significant differences between years in the breeding variables (Kruskall–Wallis, all ns), except in clutch size of first clutches (Kruskall–Wallis, $H_4 = 13.58$, $n = 73$, $P < 0.01$). For most variables we have therefore pooled data from all years. When studying the relationship between clutch size and laying date, we standardized clutch size for year differences (standardized value = actual value + mean over the whole study period – mean of the year).

We have used breeding data from all pairs in all years except when both members of a pair bred together in different years, to avoid pseudoreplication. However, when one individual changed its partner between two breeding seasons we have used data from both years, because otherwise we would exclude some individuals (the second partner) and thus would lose a part of the breeding population that we try to describe. Nevertheless, when analysing relationships between productivity and feeding effort, only one breeding attempt from each individual was used.

RESULTS

Variation in breeding variables

Hoopoes raised on average less than one brood per season, but initiated between one and three breeding attempts (Table 1). Only 19% of pairs (n = 91) initiated second clutches, and 8% of pairs (n = 89) raised two broods. There were no third clutches. The rest of the attempts were replacements for failed first clutches, and in one case for a failed second clutch.

First, second and replacement clutches did not differ significantly in clutch size or number of fledglings produced (Table 1).

The earliest clutch in any year was initiated on 22 February and the latest one (a second clutch) on 13 June (Table 1), although most first clutches (63.6%) were initiated between 15 March and 15 April.

Many of the clutches (50% of them) had more than six eggs, which was the maximum number of chicks fledged in any brood (Table 1, Fig. 1). An exceptionally large clutch (12 eggs) failed to hatch and was deserted by the female after the eggs should have hatched, although the eggs were fertile and some had embryos in an advanced stage of development. This clutch was unlikely to result from intraspecific brood parasitism, because the eggs were very similar in shape and colour, and because eggs differ considerably between females.

The duration of the whole cycle of a brood was around 44 days (Table 1) and the interbrood interval increased with increasing brood size at fledging in the previous brood (Fig. 2).

Table 1. Breeding parameters for first, replacement and second clutches in the Hoopoe.

	First	*Replacement*	*Second*	*All clutches*	H_2
Number of attempts				1.33 ± 0.54 (92) 1–3	
Number of broods raised				0.78 ± 0.58 (89) 0–2	
Clutch size	6.65 ± 1.24 (71) 4–12	6.82 ± 1.33 (11) 4–9	6.13 ± 1.19 (15) 5–8	6.59 ± 1.25 (97) 4–12	4.29 (97) ns
Fledged young	1.98 ± 1.90 (91) 0–6	0.92 ± 1.38 (12) 0–3	1.27 ± 1.71 (15) 0–5	1.79 ± 1.86 (118) 0–6	
Fledged young successful clutches	3.02 ± 1.53 (60) 1–6	2.75 ± 0.50 (4) 2–3	2.71 ± 1.50 (7) 1–5	2.97 ± 1.48 (71) 1–6	0.18 (71) ns
Laying date (days)	68.3 ± 19.4 (88) 22–122	99.1 ± 16.1 (10) 73–128	113.7 ± 18.2 (17) 67–133		
Relaying interval (days)	11.2 ± 6.9 (16) 1–25				
Incubation period (days)				16.7 ± 1.7 (14) 13–19	
Nestling period (days)				27.1 ± 2.0 (7) 24–30	

Number of breeding attempts and number of broods raised are for the whole breeding season. The number of attempts includes both second and replacement clutches. For laying date, day 1 was 1 February. For the duration of incubation period and nestling period, only data with a maximum error of 1 day have been used. Values are means ± sd and ranges. Sample sizes are in brackets. H_2 = results of the comparison between first clutches, replacement and second clutches (Kruskall–Wallis test).

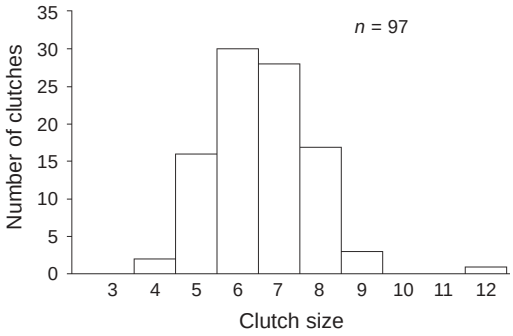

Figure 1. Frequency distribution of different clutch sizes.

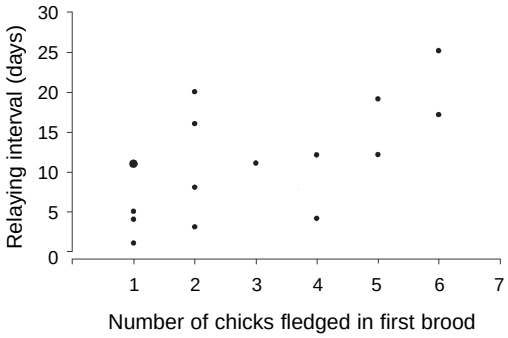

Figure 2. Relationship between the number of fledglings raised by pairs in the first brood and the time (days) between the fledging date of first brood and the laying date of the second clutch (Kendall $\tau = 0.49$, $n = 16$, $P < 0.008$). Points of double size include two cases.

Determinants of breeding success

Mean seasonal productivity per pair was less than three fledglings (Table 2). Pairs that started laying first clutches early in the season tended to have greater productivity than those starting to lay later (Fig. 3a). However, although starting early tended to increase the possibilities of laying a second clutch (Fig. 3b), pairs that laid a second clutch did not produce significantly more fledglings than those which did not lay one after a successful first clutch (pairs with one clutch: 3.1 ± 1.40, $n = 43$; with two clutches 4.2 ± 3.08, $n = 15$; Mann–Whitney *U*-test, $z = -0.58$, ns). Nevertheless, pairs that were successful in the second clutch produced more fledglings (7.00 ± 1.83, $n = 7$) than pairs which reared only one brood (2.89 ± 1.40, $n = 55$) (Mann–Whitney *U*-test, $z = -3.76$, $P < 0.0002$). Although hatching success was very high, more than 40% of chicks that hatched in successful nests died (Table 2).

Both the number of chicks fledged from individual clutches and clutch size tended to decrease with laying date (number of fledglings, successful clutches: Kendall $\tau = -0.21$, $n = 69$, $P < 0.02$; clutch size, all clutches: Kendall $\tau = -0.18$, $n = 92$, $P < 0.02$). However, a quadratic regression provided a better fit (Fig. 4a & 4b). The maximum values for the number of fledglings and clutch size were not at the beginning of the laying period but around laying date 0

Table 2. Different measures of breeding success for first, replacement, second and all clutches.

	First	*Replacement*	*Second*	*All clutches*
Proportion of hatched eggs	0.76 ± 0.37 (65)	0.40 ± 0.52 (10)	0.67 ± 0.44 (11)	0.71 ± 0.41 (86) 0–1
Hatching success	0.92 ± 0.13 (54)	1.00 ± 0.00 (4)	0.93 ± 0.10 (8)	0.92 ± 0.13 (66) 0.4–1
Proportion of fledged young	0.47 ± 0.30 (52)	0.47 ± 0.06 (4)	0.45 ± 0.33 (8)	0.47 ± 0.30 (64) 0–1
Fledging success	0.57 ± 0.23 (43)	0.47 ± 0.06 (4)	0.52 ± 0.30 (7)	0.56 ± 0.23 (54) 0.14–1
Nesting success	0.52 ± 0.23 (43)	0.47 ± 0.06 (4)	0.48 ± 0.26 (7)	0.51 ± 0.23 (54) 0.13–1
Productivity				2.34 ± 2.24 (89) 0–8

Productivity is for the whole breeding season. Proportion of hatched eggs and fledged young includes both clutches that hatched and fledged successfully and those that did not. Hatching, fledging and nesting success include only clutches that survived until hatching (hatching success) and fledging (fledging and nesting success). Values are means ± sd, plus ranges for all clutches. Sample sizes are in brackets.

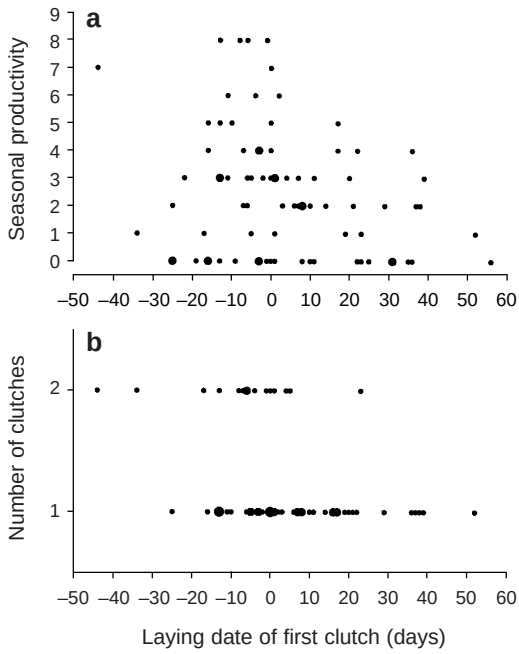

Figure 3. Relationship between (a) number of young fledged in the season (seasonal productivity) and laying date of the first clutch (all pairs: Kendall $\tau = -0.17$, $n = 82$, $P < 0.03$; successful pairs: Kendall $\tau = -0.24$, $n = 59$, $P < 0.01$) and (b) number of clutches laid (without including replacement clutches) and laying date of the first clutch for pairs that were successful in their first breeding attempt (Kendall $\tau = -0.27$, $n = 57$, $P < 0.003$). Points of increasing size represent 1, 2 and 3 cases, respectively.

(median laying date, Fig. 4a & 4b). The modal laying date of first clutches was in the interval of ten days around laying date 0 (Fig. 4c) and was therefore very close to the time with maximum productivity of first clutches.

Nest failure

A large percentage of clutches failed, nest predation being the main cause, although desertion and death of females in the nest (not due to predation) were also relevant causes (Table 3). There was no difference in the proportion of second (46.7%) and replacement clutches (50%) that were preyed upon (Yates corrected chi-square, ns), but both were more frequently depredated than first clutches (16.4%; second clutches, Yates corrected chi-square $\chi^2_1 = 5.42$, $P < 0.03$; replacement clutches, Yates corrected chi-square $\chi^2_1 = 5.42$, P

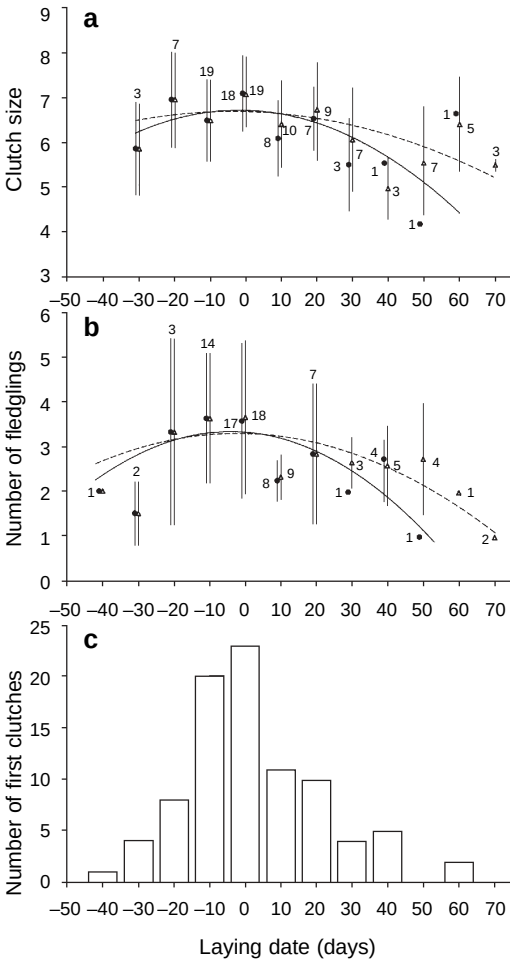

Figure 4. Mean clutch size (a) and mean number of fledglings produced per successful clutch (b) for 10-day periods throughout the breeding season (means ± sd bars). The lines show the quadratic regressions of clutch size and number of fledglings on laying date using as data the actual laying date of individual clutches. Open triangles and dotted lines include all clutches; solid circles and solid lines are first clutches only. The numerals are sample sizes; the vertical lines are standard deviations. The quadratic equations, with the level of significance of quadratic coefficients in parentheses, were: (a) clutch size: all clutches $y = 6.71 - 0.0016(x) - 0.000274(x^2)$, $r = 0.34$, $n = 92$, $P < 0.001$, ($t = -1.62$, $P = 0.11$); first clutches $y = 6.74 - 0.0018(x) - 0.000602(x^2)$, $r = 0.36$, $n = 68$, $P < 0.003$, ($t = -2.34$, $P < 0.03$); (b) number of fledglings: all clutches $y = 3.31 - 0.0015(x) - 0.000427(x^2)$, $r = 0.33$, $n = 69$, $P < 0.01$, ($t = -1.83$, $P = 0.07$); first clutches $y = 3.34 - -0.0059(x) - 0.000756(x^2)$, $r = 0.31$, $n = 58$, $P < 0.02$ ($t = -1.96$, $P = 0.06$); (c) distribution of the laying dates of first clutches.

Table 3. Frequency of the different causes of nest failure for first, replacement, second, and all clutches.

Cause of failure	*First*	*Replacement*	*Second*	*All clutches*
Deserted	7(23)	1(12.5)	0(0)	8(17)
Predated	13(42) + 2*	6(75)	7(87.5)	26(55) + 2*
Clutch	1	3	3	7
Brood	11 + 2*	2	3	16 + 2*
Unknown phase	1	1	1	3
Female died	7(23)	1(12.5)	0(0)	8(17)
Starved	2(6)	0(0)	0(0)	2(4)
Other	2(6)	0(0)	1(12.5)	3(7)
Total failed	31(34)	8(67)	8(53)	47(40)
Total number of clutches	91	12	15	118

The number of failed clutches that were due to each cause is shown, with the percentage in parentheses. 'Other' includes a first clutch flooded, one in which the chicks died simultaneously perhaps due to cold weather, and a second clutch in which nestlings were found outside the nest with wounds, but none was eaten. Of the eight deaths of females in the nest, five were during incubation, one during laying, one during hatching of eggs and one in the nestling period.
*Besides complete losses, two broods suffered partial predation.

< 0.02). There were also differences in the breeding stage at which predation occurred, with almost all happening during the nestling period for first clutches, but more frequently with eggs for second and replacement clutches (Table 3, Fisher exact test with second and replacement clutches combined, $P = 0.021$). These differences were significant even if the second and replacement clutches depredated during an unknown stage were considered to have been depredated during the nestling period (Fisher exact test, $P = 0.033$). The higher predation rate of second and replacement clutches was not due to our manipulation of nests while ringing chicks from first clutches, because in first clutches there were no differences in predation rate between the week before we opened the nests (13.2%, $n = 53$) and the week after we opened them (10.4%, $n = 48$; Yates corrected chi-square $\chi^2_1 = 0.02$, ns).

Egg and chick mortality

In 36.4% of 66 clutches that survived until hatching, some eggs did not hatch. In most cases (27.3% of 66 clutches), only one egg did not hatch, with cases of more than two unhatched eggs being very scarce (3.0% of the clutches). Of 30 unhatched eggs opened, 10 contained embryos (six of them at an advanced stage), 16 did not, and for the other four eggs this could not be detected.

At least one nestling died in most of the successful clutches, and more than one chick in 67% of them (Fig. 5a). Most of the chicks found dead were younger than 10 days (Fig. 5b) and the actual proportion of mortality occurring in young chicks is probably even higher because chicks that die soon after hatching are less likely to be found dead.

Chicks that occupied the last position in the brood size hierarchy at ringing died more frequently after that moment than those in the penultimate position (Fisher exact test $P < 0.02$, $n = 31$) or those in the remaining positions in the hierarchy (Fisher exact test $P < 0.0001$, $n = 57$; Fig. 5c).

Parental feeding effort and breeding success

The number of fledglings produced per successful clutch was correlated with the amount of food carried to the nest, after controlling for brood size at hatching in partial correlations (early stage: Kendall partial $\tau = 0.38$, $n = 17$, $P < 0.04$; late stage: Kendall partial $\tau = 0.31$, $n = 22$, $P < 0.05$). In the early stage, females normally stayed in the nest brooding the chicks and did not carry food. Consequently, the variation in the amount of food carried that produced this effect was exclusively in male feeding effort whereas, in the late stage, both

Figure 5. Patterns of nestling mortality. (a) Distribution of the number of dead chicks in successful broods. (b) Distribution of estimated age of death of chicks found dead in successful nests. (c) Percentage of chicks that died between two consecutive visits to the nests, according to the position occupied in the brood size-hierarchy. When brood size was two (two cases), we considered that there was no penultimate chick. Moreover, we have excluded three penultimate chicks found dead at the same time as the last chick.

parents took part in feeding.

The mass of the largest nestling at 19–21 days did not correlate with the amount of food carried to the nest, after controlling for the number of live young in that age (early stage, Kendall partial $\tau = -0.12$, $n = 16$, ns; late stage, Kendall partial $\tau = 0.02$, $n = 21$, ns).

DISCUSSION

Single-brooded and multi-brooded species show different trends in variation of clutch size through the season: single-brooded species start to lay when the productivity of single clutches is higher and therefore maximize clutch size at the beginning of the breeding season; multi-brooded species have a peak in clutch size later in the season and modal laying dates early before that peak.[1]

Although phenotypic correlations cannot afford strict analyses on optimization and trade-offs between life-history traits,[29] a comparison of the trends shown by a particular species with those typical of single- and multi-brooded ones can indicate which is the common strategy in that species. In the Hoopoe, some clutches were initiated before the date at which first clutches had the greatest productivity, and the largest clutches were not at the beginning of the season, as is common in multi-brooded species.

However, the modal laying date of the population was very close to the dates of maximum productivity for single clutches, which coincides with the period in which the largest clutches were laid, suggesting that most Hoopoes adjust the start of breeding to the maximum productivity of the first clutch. This indicates that, for most individuals, the costs of early laying exceed either the benefits of producing more than one brood or of increasing chances of re-nesting, whereas only for a few individuals of presumably higher quality would it compensate to face these costs. The most important cost involved in this context seems to be the extremely high predation rate suffered by second and replacement clutches, which meant that pairs laying two clutches obtained only slightly higher average productivity than those laying one, and that the number of breeding attempts initiated in the season did not correlate with the production of fledglings.

Besides predation, an important cause of clutch loss was the death of females. The frequency of these deaths was extremely high compared with other species where similar cases have been found.[30] The deaths were not concentrated in one extraordinary year, there were some in every year. We cannot be sure of the causes of the deaths. The three corpses that

we weighed were above the mean body mass of females in the population, only three of the deaths happened after days with bad weather and, except two cases, the feeding rate of males in the period just before the death was not abnormally low. We believe that several different causes could have produced the deaths, including disease, cold weather, starvation and pesticide poisoning.

The primary variable that limits the productivity of a clutch is its size. Clutch size has long been thought to reflect the number of young that the parents can properly nourish.[7,8,31] In the Hoopoe, however, 50% of clutches had more than six eggs, the maximum number of chicks fledged in any successful brood, and only 11.1% of successful clutches had 100% success. Most losses in successful clutches were due to death of nestlings, and the number of surviving chicks was correlated with the amount of food provided by parents. Therefore, females normally lay more eggs than the number of nestlings that the pair is able to feed – that is, clutch size is optimistic.[9] This fact is common to most asynchronously hatching bird species.[7,31]

A number of hypotheses, including the brood reduction hypothesis, have attempted to explain the paradox of hatching asynchrony (reviewed in refs 15 and 16). For some of these hypotheses, brood reduction may be a side effect of an early start to incubation due to causes other than the promotion of selective chick death.[15] Because mortality of small chicks is a detrimental process in these cases, we would expect that it was minimized by parents through compensated investment (in eggs or chicks) in the last hatched eggs.[16] Such compensation has been documented in some species (in chicks by females,[32–34] in eggs[35,36]). However, in the Hoopoe most deaths occurred when the chicks were very young (in our population at least 56% of deaths were of chicks between one and 10 days old; in the study of Kubik,[22] 80% of 19 dead chicks were less than eight days old), a period in which the female remains in the nest and always feeds the nestlings[17] (pers. obs.). In this situation, females could distribute the food among chicks avoiding monopolization by the largest ones. However, if this was the case, most deaths should occur later in the nestling period, when chicks compete for access to the nest entrance and are fed there.

We made casual observations of food delivery to chicks in one brood with a clear size hierarchy when the oldest chick was five days old. During one hour of observation the male supplied the female seven times, and the female always fed the largest chick that begged, although the smaller chicks also usually begged. When only the smallest chick begged, the female tried to feed the larger ones, and the smallest one was only fed when she was unsuccessful in this (pers. obs.).

This observation indicates that females do not compensate, but give priority to first-hatched chicks. Moreover, the amount of food carried to the nest was positively correlated with the number of chicks fledged, but not with the body mass of the oldest nestlings, which also indicates that when food is scarce, old chicks are not deprived. Patterns of food delivery biased towards the largest chicks have been described for other species in which brood reduction due to starvation is frequent.[37,38]

The most plausible hypotheses explaining such differential investment in first-hatched chicks are those which postulate that the adaptive significance of hatching asynchrony is facilitation of selective death of the youngest chicks (brood reduction hypothesis,[7] insurance hypothesis[39] and larder hypothesis[40]). For these three hypotheses, parents should not feed the youngest chicks unless larger ones are satiated. However, the larder hypothesis implies that old chicks feed on young ones, which does not happen in the Hoopoe; and for the insurance hypothesis, incubation should start after some minimum basic clutch size has been completed, thus facilitating elimination of last-hatched chicks if they become superfluous, which is not the case (Hoopoes normally start incubation with the first or second egg[17–19]). The brood reduction hypothesis (or some of its variants, as the hypothesis of ensuring chick quality[41]) therefore seems the most valid explanation for hatching asynchrony in the Hoopoe.

Various levels of hatching asynchrony are present in other species of the order Coraciiformes. Bee-eaters *Merops apiaster* have extreme hatching asynchrony, mainly explained by the brood reduction hypothesis, apparently because they feed on large flying insects, a food source unpredictable from day to day, and because the number of helpers in the nest affects chick survival but is not predictable at the time of laying.[42] However, Kingfishers

Alcedo atthis hatch their eggs synchronously,[17] which could be explained because they feed on stable food resources such as fishes, frogs and crayfish. Although Hoopoes feed on insects, these are commonly ground ones that are probably not as unpredictable as flying insects. Nevertheless, Hoopoe chicks show a decline in mass at the end of the nestling period, and at their heaviest stage they reach about 75–85 g[18] (pers. obs.), which is around 20% heavier than the mean body mass of adults in our population (66.2 ± 6.0 g, n = 194, pers. obs.).

Such patterns of nestling growth are in some cases related to resource storage, a character associated with unstable food resources,[43] and have been used as another argument to support the brood reduction hypothesis in Bee-eaters.[42] We believe that the unpredictable character of Hoopoe food supply while breeding is mainly due to the dependence on male provisioning. Although females probably evaluate feeding capacity of males during feeding courtships, the final feeding effort developed by males can probably never be inferred because male condition or interests could vary.[41]

In the Hoopoe, as in Bee-eaters, fledging is sometimes asynchronous within a brood (pers. obs.),[18,20] although it normally takes only between two and four days. Therefore, we cannot exclude the possibility that part of the adaptive value of hatching asynchrony is in avoiding the chance that the whole brood is preyed upon at the end of the nestling period (nest failure hypothesis[35,44]). However, it is so rare that the brood is depredated in those last days, and asynchrony has such a severe effect on the survival of many of the young in the brood, that this selective force is probably of minor importance compared with the unpredictability of the feeding effort by males.

ACKNOWLEDGEMENTS

We are grateful to Catherine M. Lessells, Juan Gabriel Martínez, Anders Pape Møller, Juan Moreno and Juan Carlos Senar for their comments on earlier drafts of the manuscript, Antonio Navarro for permission to work in the Corvales Reserve, Elena Martín-Vivaldi for her help in the translation of some bibliography and Juan Gabriel Martínez for valuable advice during fieldwork and data analyses. Maria del Mar López, José Miguel Marín and Miguel Angel Roldán were of great help in the field. Funds were provided by the DGICYT PB91-0084-CO3-02 research project and by the Consejería de Educación y Ciencia (Becas de Formación del Personal Docente e Investigador (to M.M.V.).

REFERENCES

1. Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D. (1993) Seasonal changes in clutch size in British birds. *J. Anim. Ecol.,* **62,** 263–273.
2. Ricklefs, R.E. (1969) An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.,* **9,** 1–48.
3. Alerstam, T. & Högstedt, G. (1981) Evolution of hole-nesting in birds. *Ornis. Scand.,* **12,** 188–193.
4. Lack, D. (1968) *Ecological Adaptations for Breeding in Birds.* Methuen, London.
5. Slagsvold, T. (1982) Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia,* **54,** 159–169.
6. Martin, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.,* **65,** 101–127.
7. Lack, D. (1947) The significance of clutch size. *Ibis,* **89,** 302–352.
8. Murphy, E.C. & Haukioja, E. (1986) Clutch size in nidicolous birds. *Curr. Ornithol.,* **4,** 141–180.
9. Mock, D.W. & Forbes, L.S. (1995) The evolution of parental optimism. *Trends Ecol. Evol.,* **10,** 130–134.
10. Soler, M. (1989) Fracaso reproductor en grajilla (*Corvus monedula*): pérdidas de huevos y mortalidad de pollos. *Ardeola,* **36,** 3–24.
11. Soler, M. (1989) Breeding success and productivity in the Jackdaw (*Corvus monedula* L.) in Granada (Spain). In *Granivorus Birds in Agricultural Landscape* (eds J. Pinowski & D. Summers-Smith), pp. 253–261. INTECO, Warszawa.
12. Magrath, R.D. (1989) Hatching asynchrony and reproductive success in the Blackbird, *Turdus merula*. *Nature,* **339,** 536–538.
13. Hébert, P.N. (1993) An experimental study of brood reduction and hatching asynchrony in Yellow Warblers. *Condor,* **95,** 362–371.
14. Wiebe, K.L. & Bortolotti, G.R. (1995) Food-dependent benefits of hatching asynchrony in American Kestrels *Falco sparverius*. *Behav. Ecol. Sociobiol.,* **36,** 49–57.
15. Stoleson, S.H. & Beissinger, S.R. (1995) Hatching asynchrony and the onset of incubation in birds, revisited. When is the critical period? *Curr. Ornithol.* **12,** 191–271.
16. Stenning, M.J. (1996) Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. *Trends Ecol. Evol.* **11,** 243–246.
17. Cramp, S., ed. (1985) *The Birds of the Western*

Palearctic, Vol 4. Oxford University Press, Oxford.
18. Bussman, J. (1950) Zur Brutbiologie des Wiedehopfes. *Ornithol. Beob.,* **47,** 141–151.
19. Gupta, R.Ch. & Ahmad, I. (1993) On the clutch size, egg laying schedule, hatching patterns and stay of nestlings of Indian Hoopoe (*Upupa epops*). *Geobios,* **20,** 148–150.
20. Löhrl, von H. (1977) Zum Brutverhalten des Wiedehopfs *Upupa epops*. *Vogelwelt,* **98,** 41–58.
21. Skead, C.J. (1950) A study of the african Hoopoe. *Ibis,* **92,** 434–463.
22. Kubik, V. (1960) Beiträge zur Fortpflanzungsbionomie des Wiedehopfes. *Zool. Listy,* **9,** 97–110.
23. Arlettaz, R. (1984) Ecologie d´une population de Huppes, *Upupa epops*, en Valais: répartition spatiale, biotopes et site de nidification. *Nos Oiseaux,* **37,** 197–222.
24. Rehsteiner, U. (1996) Siedlungsdichte und Habitatansprüche des Wiedehopfs *Upupa epops* in Extremadura (Spanien). *Orn. Beob.,* **93,** 277–287.
25. Nilsson, S.G. (1984) The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis. Scand.,* **15,** 167–175.
26. Møller, A.P. (1989) Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? *Oikos,* **56,** 421–423.
27. Purcell, K.L., Verner, J. & Oring, L.W. (1997) A comparison of the breeding ecology of birds nesting in boxes and tree cavities. *Auk,* **114,** 646–656.
28. Svensson, L. (1984) *Identification Guide to European Passerines,* 3rd edn. Stockholm.
29. Lessells, C.M. (1993) The evolution of life-histories. In *Behavioural Ecology. An Evolutionary Approach,* 3rd edn. (eds J.R. Krebs & N.B. Davies), pp. 32–68. Blackwell Science, Oxford.
30. Sealy, S.G., Briskie, J.V. & Biermann, G.C. (1986) Deaths of female passerine birds on their nests while incubating. *J. Field Ornithol.*, **57,** 315–317.
31. Lack, D. (1954) *The Natural Regulation of Animal Numbers.* Oxford University Press, London.
32. Stamps, J., Clark, A., Arrowood, P. & Kus, B. (1985) Parent–offspring conflict in Budgerigars. *Behaviour,* **94,** 1–40.
33. Gottlander, K. (1987) Parental feeding behaviour and sibling competition in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* **18,** 269–276.
34. Mondloch, C.J. (1995) Chick hunger and begging affect parental allocation of feedings in Pigeons. *Anim. Behav.,* **49,** 601–613.
35. Clark, A.B. & Wilson, D.S. (1981) Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.,* **56,** 253–277.
36. Slagsvold, T., Sandvik, K., Rofstad, G., Lorentsen, Ö. & Husby, M. (1984) On the adaptive value of intraclutch egg-size variation in birds. *Auk,* **101,** 685–697.
37. Rydén, O. & Bengtsson, H. (1980) Differential begging and locomotory behaviour by early and late hatched nestlings affecting the distribution of food in asynchronously hatched broods of altricial birds. *Z. Tierpsychol.,* **53,** 209–224.
38. Price, K. & Ydenberg, R. (1995) Begging and provisioning in broods of asynchronously-hatched Yellow-headed Blackbird nestlings. *Behav. Ecol. Sociobiol.,* **37,** 201–208.
39. Cash, K.J. & Evans, R.M. (1986) Brood reduction in the American White Pelican (*Pelecanus erythrorhynchos*). *Behav. Ecol. Sociobiol.,* **18,** 413–418.
40. Alexander, R.D. (1974) The evolution of social behaviour. *Annu. Rev. Ecol. Syst.,* **5,** 325–384.
41. Amundsen, T. & Slagsvold, T. (1996) Lack´s brood reduction hypothesis and avian hatching asynchrony: what´s next? *Oikos,* **76,** 613–620.
42. Lessells, C.M. & Avery, M.I. (1989) Hatching asynchrony in European Bee-eaters *Merops apiaster*. *J. Anim. Ecol.,* **58,** 815–835.
43. O´Connor, R.J. (1978) Growth strategies in nestling passerines. *Living Bird,* **16,** 209–238.
44. Hussell, D.J.T. (1972) Factors affecting clutch size in arctic passerines. *Ecol. Monogr.,* **42,** 317–364.

(MS received 9 October 1997; revised MS accepted 22 June 1998)