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Chick mortality and hatching asynchrony in the Pallid Swift *Apus pallidus*

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Abstract — In swifts (Apodiformes), hatching asynchrony has been frequently reported and it has been suggested (Lack, 1947) that it can enhance reproductive success because in favourable conditions an extra chick can be reared, while in poor conditions it can be eliminated (brood reduction hypothesis). In this paper hatching asynchrony is studied in relation to nestling mortality.
A four year study of the Pallid Swift in two Piedmontese (NW Italy) colonies has been conducted. Clutch size and other measures of reproductive success were recorded in 313 nests, either of the first or of the second clutch.
Hatching success and fledging success were similar to those observed in previous years in the same North-Italy area. Mortality increased, both in the first and second brood, in late-laid clutches. Chicks died mainly during the first ten days after hatching.
The most important factor affecting nestling survival was hatching hierarchy: the last hatched, especially in three-egg clutches, experienced higher mortality. Hatching asynchrony was nearly always observed in three-chick broods, and in 75% of the cases in two-chicks broods. In the latter situation, asynchronous and synchronous broods did not differ significantly as to mortality and mass of the fledging birds. It is discussed why in two-chick broods hatching asynchrony did not affect strongly the breeding success, while in three-chick broods the survival value of asynchrony was apparently fully expressed.

Introduction

Nestling birds may differ in size and weight on the first day a clutch is fully hatched mainly because eggs within clutches hatch over a period of several days. This asynchronous pattern of hatching is usually thought to facilitate brood reduction when food supply is unpredictably restricted (Lack 1947). For example, the smaller, weaker chicks of Herring Gulls *Larus argentatus* and Common Terns *Sterna hirundo* that are laid third, survive only when food conditions are exceptionally good (Parsons 1975, Nisbet 1973).
Swifts are aerial feeding birds subjected to shortages and unpredictability in food availability during reproduction. Hatching asynchrony has been explained in the Common Swift *Apus apus* according to the brood reduction hypothesis (Lack, 1956). O'Connor (1979) also described an egg mass asymmetry in this species, the last laid egg being lighter than the others, which enhanced the difference in mass between siblings. However, much of the impact of weight asymmetry on subsequent survival can be mitigated by the ability of young swifts to survive by stopping growth and becoming hypothermic. Koskimies (1950) observed this physiological adaptation during cold and rainy periods, when he showed Common Swift chicks could survive several days of starvation.
Far fewer data are available on hatching asynchrony and brood reduction in the Pallid Swift *Apus pallidus*, a circum-mediterranean species, which has recently extended the Northern boundary of its breeding range to the Alps area, namely the Ticino Swiss Canton (Lardelli 1986, Lardelli and Lardelli 1987). Furthermore, in North Italy, new colonies have been discovered in the Po river basin (Boano 1979, Pulcher and Boano 1984, Gimpel et al. 1986, Bonvicini 1989, Bordonaro et al. 1988).
Aim of this work is to analyze mortality, from egg hatching to fledging, in the first and second clutch of the Pallid Swift. The occurence of deaths in relation to clutch size, egg laying period and age of chicks, is also examined. Finally the role of hatching asynchrony and its adaptative function in brood reduction are discussed.

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Methods

Observations were made in two colonies located in towns of North-West Italy: Torino (260 m asl) and Carmagnola (240 m asl). In Torino Pallid Swifts breed in a school building and utilize window roller or blind boxes as their nest-cavity (150x50x50 cm). Nests are built on the bottom of the boxes or on top of the blinds. We checked 89 nests in 1987, 113 in 1988, 42 in 1989 and 69 in 1990. We inspected the colony every 2-3 days. In Carmagnola the swifts breed in an old building and utilize as nest-cavities the holes existing in its walls. The nests were inspected daily from inside the building. The colony consisted of 12, 16, 17 and 22 pairs in 1987, '88, '89 and '90 respectively. All nestlings were weighed to the nearest 0.1 grams and measured (wing and third-primary length) from hatching to fledging.

The relative difference in nestling mass (RDNM) has been used to classify the broods in two categories: synchronous or asynchronous broods. According to Bryant 1978 we calculated: RDNM = (heaviest chick - lightest chick) / (mean chick mass). Values of RDNM were assessed within the first 5 days of age and we considered as synchronously hatched broods those below the threshold value of 0.15.

At the Torino colony the routine of inspecting the nests once every 2-3 days prevented an accurate determination of hatching asynchrony in some cases. All uncertain records were discarded, hence, for the purpose of the present analysis, we considered 29 synchronously and 274 asynchronously hatched chicks.

Two clutch categories have been considered: FIRST CLUTCHES, whose laying dates range from May to end of July and can include some substitution clutches; and SECOND CLUTCHES, laid from mid-August to October. A few cases (N = 26 nests) of clutches laid in the first half of August, when both first and second clutches could be found (Boano and Cucco 1989), were not considered in the analysis. Chicks were regularly checked and those which left the nest after 40-45 days of age were considered to have normally fledged.

Results

Pallid Swift females laid fewer eggs in the second clutch than in the first one. Average clutch sizes were 2.44 ± 0.76 eggs/nest (N = 265) and 2.03 ± 0.53 eggs/nest (N = 65) respectively. More than half the first clutches were of three eggs. A smaller number of females laid two eggs and few laid one egg. In the 1987-90 period, only 19.7% of the females started a second clutch.

Average hatching success was 72.1% and there were no differences between the first and second clutches (Table 1; $\chi^2 = 0.51$; df = 1; n.s.).

Average fledging success was 77.7% (Table 2). On the whole, the chicks in the second clutches showed a slightly higher mortality than those born in the first one (Table 2; $\chi^2 = 3.56$, df = 1, $P<0.10$). There were no differences in mortality rate between different brood sizes (Table 3; $\chi^2 = 2.27$; df = 2, n.s.).

Figure 1 shows the percentage of chicks that died in each half-month period in relation to the number of individuals (chicks of all the different ages) alive in the nests in the same period. Mortality during the reproductive period followed a seasonal pattern (Figure 1). There was a summer peak at the end of July corresponding to the chicks hatched after the second part of June. Furthermore, mortality had an autumn peak at the end of October affecting chicks hatched after the second half of September. In both the first and second clutches, mortality was lower in early broods, while it increased in late ones.

Mortality during development showed a progressive decline with increasing age (Figure 2). The majority of deaths occurred in the first ten days, then

Table 1 - Egg failures in the nests of the Pallid Swifts.

CLUTCH	NUMBER OF EGGS Total	Hatched	Lost	HATCHING RATE
First	475	346	129	72.8%
Second	163	114	49	69.9%

Table 2 - Mortality of young in first and second broods.

BROOD	NUMBER OF YOUNG Total	Fledged	Dead	MORTALITY
First	346	276	70	20.2%
Second	115	82	33	28.7%

Table 3 - Mortality of young in relation to brood size.

BROOD SIZE	NUMBER OF YOUNG Total	Fledged	Dead	MORTALITY
1 young	33	18	15	45.5%
2 young	219	127	92	42.0%
3 young	342	217	125	36.5%

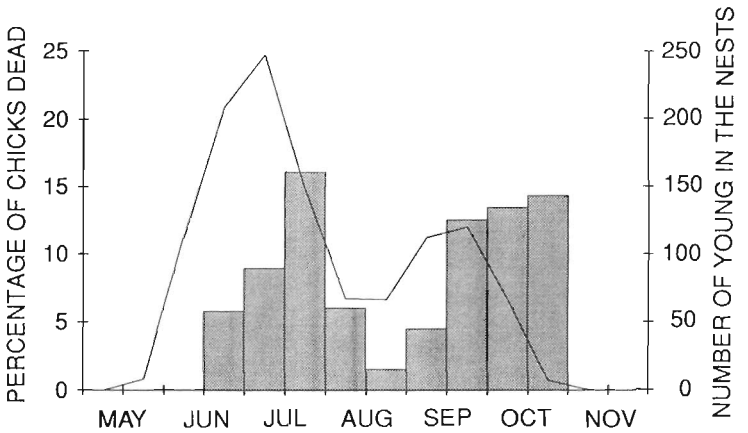

Figure 1 - Number of nestlings and percentage of chicks which died during the reproductive period. (Total number of chicks in all nests. Dotted area = % chicks which died; — = chicks alive).

decreased to 9% in nestlings older than one month. Dead chicks were found inside the nest in the early days of development; older chicks (>10 days), were able to move about and fell out of their nest-cavity. Mortality also showed a marked pattern in relation to hatching order (Figure 3). In three-chick broods the last hatched was most likely to die ($\chi^2 = 13.6$; df = 2; P<0.01). The majority of these observations came from the first clutch (spring-summer), as Pallid Swifts rarely lay three eggs in the second clutch (autumn). In two-chick broods, the second chick was more likely to die than the first one, but the statistical test (Binomial test) does not reach significance (P<0.10). The majority of these records came from the second clutches, where 2 eggs are commonly laid. Two cases of 4 chicks in a brood have been recorded and in both of them the last hatched chicks died. Hatching asynchrony was the rule in both colonies: it was observed in 90.4% of the broods. Cases of hatching synchrony were detected almost exclusively (93.3%) when two eggs per nest hatched successfully; we observed only one instance of a nest where three eggs hatched on the same day. For this reason, comparisons of the occurrence of synchrony and chick survival in synchronous vs. asynchronous nests are reported only for the two-chick broods. The first and the second broods did not differ as to the percentage of asynchronous nestslings, (73.1 and 83.3% respectively; N = 88; $\chi^2 = 1.27$; df = 1; P = n.s.).

The occurrence of synchrony had little effect on the survival of nestlings: mortality was slightly higher in synchronous vs. asynchronous broods (Table 4; $\chi^2 = 2.82$; df = 1; P<0.10).

There were no differences in mean mass of chicks near fledging (35 to 40 days old). Mean mass was 45.8 grams (±9.14 s.d.; N = 12) for synchronous nestlings, and 45.4 grams (±7.2 s.d.; N = 153) for asynchronous nestlings (t = 0.18; d.f. = 163; P = n.s.).

Discussion

The present findings on reproductive success of the Pallid Swift are similar to those reported for previous years in the same North-Italian area (Boano and Cucco 1989) but differs greatly from the mortality observed in a Gibraltar colony (Finlayson 1975). There, the percentage of hatched chicks that died before fledging was 39.5% in first clutches and 53.6% in second ones; these values were more than twice as high as those reported in our study area or

Table 4 - Occurrence of asynchrony and mortality in synchronous and asynchronous broods.

BROOD	BROOD SIZE 2 chicks		BROOD SIZE 3 chicks		MORTALITY	PERCENTAGE OF NESTLINGS
	Total	dead	Total	dead		
Synchronous	26	8	3	1	31.0%	9.6%
Asynchronous	106	19	168	42	28.5%	90.4%

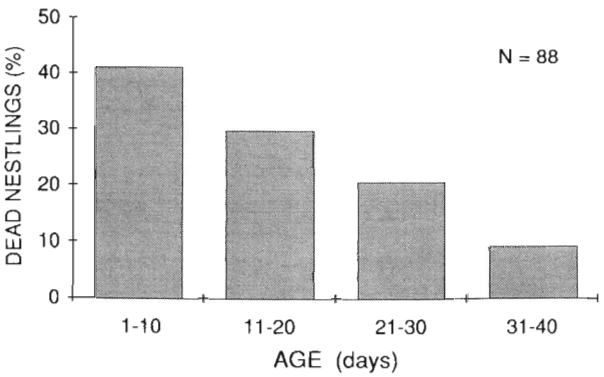

Figure 2 - Nestling mortality in relation to age.

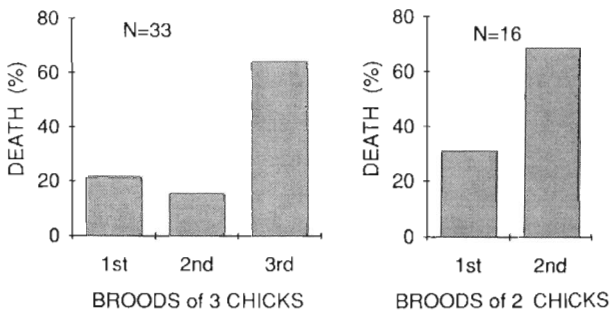

Figure 3 - Mortality in relation to hatching hierarchy.

in colonies of Corse (Thibault et al. 1987; only first clutches laid). The differences observed could be due to local ecological factors in the three areas, or to the diversity in weather conditions between the years when the observations were made.

A seasonal trend commonly observed in other bird species (Perrins 1970) emerges: mortality is lower, in both first and second clutches, in early laid clutches. Early hatched nestlings (June or September, respectively) had a lower mortality than those hatched later (July or October). Similarly in the House Swift *Apus affinis* (Razack and Naik 1968), mortality differed between early and late clutches. In our study area in autumn the weather gets colder and rainy, and days get shorter. Thus, a decrease in reproductive output may be expected during the second brood period. In the Pallid Swift populations studied, a decrease in mean number of fledged young was observed: this occurred mainly through the laying of smaller-sized clutches. Mortality increased slightly in autumn, thus playing a minor role in reproductive success adjustment. In the double-clutched House Swift, Razack and Naik (1968) found a reversed seasonal trend in clutch size, because of reversed weather conditions. In their tropical area, first clutches were laid during the dry season and were smaller than the second ones, laid in the wet season.

Chicks died mainly during the first 10 days after hatching, out of the 40-45 days spent in the nest. Early death of the young has been reported by Lack and Lack (1951) in the Common Swift. This is in line with the brood reduction hypothesis (Lack 1947): for parents, early chick mortality avoids a waste of time and energy in chick rearing.

In this study the only cause of mortality after the tenth day was from chicks falling out of the nest. A major impact of nest dropping on chick death was reported also in the House Swift (Razack and Naik 1968).

The most important factor affecting nestling survival was hatching hierarchy. In the three-chick broods the last hatched experienced a higher mortality rate, and we found a tendency towards higher mortality of the last hatched in two-chick broods too. The pattern observed in hatching hierarchy is similar to that reported by Bryant (1978) in another aerial feeding bird, the House Martin *Delichon urbica*.

Asynchrony played a strong role in influencing survival of the three-chick broods. These were typically asynchronous and a marked hatching hierarchy was observed. A lesser impact of asynchrony on survival was found in the two-chick broods, where a minority (about 25%) of chicks hatched from synchronous broods. In broods of two, synchronous chicks displayed only a slightly higher mortality than asynchronous ones, the mean weight of asynchronous nestlings was not different

from that of the synchronous ones and asynchrony was less conspicous, since it involved a gap of only one (rarely two) days. On the contrary, in three-chick broods, differences in birth dates usually ranged from two to four (rarely five) days.

It is likely that asynchronous hatching helps to adjust the reproductive output mainly in three-chick broods, while in two-chicks broods the asynchrony is thought to play a minor role. This is because an adequate food supply for a brood of two nestlings may be a poor supply for a brood of three, thus in favourable conditions an extra chick might result in an extra fledged young, while in poor conditions it might be lost. In two-nestling broods, strong asynchrony seems less important, since brood reduction is rarely necessary.

Many hypotheses have been advanced to explain how hatching asynchrony may work to bring about higher breeding success (Magrath 1990). The brood reduction hypothesis (Lack 1954, 1968) predicts that asynchrony will be observed most frequently when food is scarce or variable in supply. This hypothesis fits well with the food and feeding habits of aerial foraging species. However, in the White-bellied Swiflet *Collocalia esculenta*, Bryant and Tatner (1990) found that greater hatching synchrony tended to increase fledging success and proposed that it results in brood reduction only under extremely adverse conditions.

Other explanations have been proposed, and it is now clear (Magrath 1990, Bryant and Tatner, 1990) that no single hypothesis can provide a complete explanation of hatching asynchrony across species. However, the hypotheses are not mutually exclusive and different selective pressures can act on even closely related species which differ in some aspects of their breeding ecology.

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Riassunto — L'asincronia di schiusa è un fenomeno comunemente osservato nei rondoni (Apodiformes) ed è stato suggerito (Lack 1947) che esso sia un adattamento utile per aumentare il successo riproduttivo, permettendo ai genitori di allevare un ulteriore nidiaceo in condizioni climatiche favorevoli, mentre in condizioni climatiche avverse l'ultimo piccolo viene sacrificato (brood reduction hypothesis). In questo lavoro il fenomeno dell'asincronia di schiusa viene studiato considerando le sue relazioni con la mortalità dei nidiacei. Sono state esaminate due colonie di Rondone Pallido situate a Torino e Carmagnola (Italia, NW), misurando nel corso di 4 anni (1987-90) in 313 nidi la dimensione della covata, il numero di giovani involati, il grado di asincronia delle covate e il rango di schiusa dei giovani. Il successo nella schiusa e nell'involo è stato simile a quello rilevato in anni precedenti nella stessa area geografica.
La mortalità dei nidiacei ha raggiunto valori maggiori nelle covate tardive, sia durante la prima che la seconda deposizione annuale. I giovani sono morti prevalentemente durante i primi dieci giorni seguenti la schiusa.
Il fattore più importante nell'influenzare la sopravvivenza dei nidiacei è risultato l'asincronia di schiusa: il giovane nato per ultimo ha maggiori probabilità di morire rispetto ai fratelli. L'asincronia di schiusa è stata osservata in quasi tutte le nidiate di tre piccoli e nel 75% dei casi in quelle da due.
Nei nidi con due giovani non sono state rilevate differenze in mortalità e peso all'involo tra nidiacei sincroni o asincroni. Si suggerisce che in questa situazione il valore adattativo dell'asincronia di schiusa risulti molto ridotto, mentre esso è pienamente espresso nelle nidiate con tre piccoli.

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