Effect of food availability on nestling growth and fledging success in manipulated pallid swift broods

M. Cucco and G. Malacarne

Department of Sciences and Advanced Technologies, University of Torino, via Cavour 84, I-15100 Alessandria, Italy

(With 5 figures in the text)

Growth rate and fledging success were assessed in natural and manipulated broods of the pallid swift *Apus pallidus*. Daily measurements of chick mass, wing length, and insect abundance allowed us to examine the short-term variation of chick growth in relation to food availability.

The number of fledged nestlings increased with brood size. Wing length and body mass were slightly but significantly smaller in larger broods, and the nestlings of enlarged broods needed longer to fledge. We discuss how these differences could influence survival after fledging.

Hatching asynchrony caused a significant difference in growth among siblings, and the difference between the oldest and youngest chick was greater in larger broods.

Chick growth was independent of daily food availability. We suggest that this was due to an increased effort of the parents at their expense, when food availability was poor.

The ability of this species to raise an additional chick is in line with most findings on birds, but partially in contrast with results for the common swift in which, at least during poor seasons, the additional nestling caused an increased mortality and lowered the reproductive success.

Introduction

Lack (1947) suggested that clutch size in birds depends on the number of young that can be raised in a reproductive season. Natural selection should favour those parents that rear the highest number of offspring that are able to survive long enough to reproduce. In nidicolous birds, according to Lack's theory, the ultimate factor limiting brood size is parents' ability to feed their young. Lack's hypothesis can explain average clutch size, while naturally occurring variation within a species may reflect individual differences in parental ability to care for the young (Perrins & Moss, 1974; Pettifor, Perrins & McCleery, 1989) or differences in habitat quality (Drent & Daan, 1980; Hogstedt, 1981). However, several studies do not support Lack's hypothesis, since experimental increases of brood size lead to higher productivity than in control broods (review in Dijkstra *et al.*, 1990). To account for this contradiction, Williams (1966) and Charnov & Krebs (1974) developed the concept of trade-off between current parental investment and future reproductive effort; individuals favoured by natural selection are those which optimize the allocation of resources between themselves and their offspring. Later, Kacelnik & Cuthill (1990) suggested that, in central-place foragers, the allocation of food between parents and young should maximize the sum of current brood productivity plus the residual reproductive value of the parents.

Many difficulties arise, however, when one attempts to measure reproductive trade-offs in birds. For example, only in long-term studies of individually marked populations is it possible to elucidate fully the effects of brood manipulation on adult survival and fecundity. The measure of

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lifetime reproductive output is equally difficult to assess, since offspring dispersal and recruitment of young are often difficult to quantify.

This ecological approach can be integrated with a physiological one (Calow, 1979), by studying short-term behavioural and physiological responses of adults to increased parental effort. In addition, some physiological parameters also allow estimation of chicks' prospects of survival. Among these, chick mass at fledging is considered a reliable estimate of future survival (Magrath, 1991).

Theoretical and empirical studies (Gillespie, 1977; Kacelnik, 1988) have shown that seasonally fluctuating resources influence the evolution of parental life-history traits. Lack (1954), for example, proposed that asynchronous hatching is an adaptation of birds that have a long nestling period and exploit an unstable food supply. The existence of contradictory results, however, has stimulated alternative explanations (review in Magrath, 1991). On a shorter time-scale, parents are expected to respond to sudden changes in resources with short-term economic decisions (Dunbar, 1984; Kacelnik, 1988), which influence, in the longer term, both adult and chick survival (Jones, 1987; Martins & Wright, 1993a; Cucco & Malacarne, 1995).

Aerial-feeding birds are good subjects for the study of both long- and short-term changes in energy allocation, because their food resource (insects) is relatively easy to quantify, by means of nets or suction traps (Bryant, 1975; Quinney & Ankney, 1985), and its distribution is temporally and spatially unpredictable, both from hour-to-hour and over longer time periods. Prey availability greatly influences the reproduction of aerial feeders. For example, in the tree swallow *Tachycineta bicolor* and the house martin *Delichon urbica*, both clutch size and laying date were found to be positively correlated with food abundance (Bryant, 1975; Hussell & Quinney, 1987). In the swallow *Hirundo rustica,* chicks and parents were heaviest when aerial insects were plentiful (Jones, 1987). In the pallid swift *Apus pallidus*, we observed that daily variation in parental mass is related to the daily abundance of food. Furthermore, in experimentally enlarged broods, the parental cost of reproduction appears to be increased since adults lose more mass (Cucco & Malacarne, 1995).

In this study, we have monitored, on a daily basis, both food availability and chick growth (increase in mass and wing length) in natural or experimentally manipulated broods of pallid swift.

Aims of the study were: 1) to investigate if the daily changes of mass and wing length in nestlings are affected by food abundance, in a species in which food availability significantly affects parental mass variation; 2) to ascertain whether breeding success, the growth rate, mass and wing length of chicks at fledging, and the duration of the rearing period are affected by brood size. Lack's hypothesis of optimal clutch size would predict that the parents' reproductive success is not enhanced in larger broods, as has been verified in the congeneric common swift *Apus apus* (Perrins, 1964; Martins & Wright, 1993a, b). In this study, we show that fledging success is higher in manipulated broods: this result is discussed in light of the life-history theory and compared with data obtained for other birds.

Methods

The research was carried out from 1987 to 1992 in 2 colonies in north-west Italy (Carmagnola and Torino, 20 km apart). The area is characterized by a temperate continental climate (Cucco *et al.,* 1992). The nest cavities were located on old buildings and were easily reached and inspected from inside the building. Nests were numbered and inspected daily in Carmagnola (17–19 nests per year) and every 2–3 days in Torino (27–70 nests per year).

Pallid swifts usually lay 3 eggs, while clutches of 2 are less frequent and those of 4 or 1 are very uncommon (Cucco *et al.*, 1992). The eggs typically hatch asynchronously, with a delay of 1 day in 2-egg clutches, and of 2 days in 3-egg clutches (Malacarne & Cucco, 1991). In the 2 colonies (Carmagnola and Torino), we considered, respectively, 10 and 19 unmanipulated broods of 1, 27 and 61 of 2, 14 and 23 broods of 3 young. The manipulated nests comprised 6 and 10 increased broods of 4 chicks (created by adding 1 nestling (2–4 days old) to broods of 3 young of similar age) and 6 and 10 reduced broods of 2 chicks (created by removing 1 nestling from broods of 3). The age of the added nestling was intermediate between the oldest and youngest chicks of the recipient brood.

Chicks were individually marked with a metal ring; however, during the first 10 days after hatching, when their tarsus was too small to allow ringing, a small white spot of non-toxic paint was applied to each nestling's skin (random position, on the back). This technique did not appear to affect the natural behaviour of the birds, as compared with that of non-marked animals. The nestlings were weighed to the nearest 0.1 g with a Pesola spring balance, and their wing length was measured by a metal ruler to the nearest mm. Chicks showing regular growth and leaving the nest after 40–45 days were considered successfully fledged.

To determine the relationship between daily nestling growth and daily food abundance, in 1991 and 1992 at the Carmagnola colony, each nestling was measured at 24-h intervals. Measurements took place at 07:00 h, when typically the parents had just left the nest and the feeding of the chicks had not begun. Thus, an increase in a nestling's mass and wing length could be ascribed to the feeding loads brought by the parents on the previous day.

Food resources available to breeding swifts were quantified daily by collecting aerial arthropods with a suction trap (tower, 12.2 m high) located 2 km from the colony in the surrounding farmlands. The trapped insects were dried for 2 hours, then their volume was measured to the nearest 0.1 cc by immersion in a graduated tube. Because the pallid swifts and the suction trap typically caught arthropods in different percentages (more Diptera in the trap, Cucco, Bryant & Malacarne, 1993), the measured volume has been considered merely as an index of aerial insect abundance, useful for comparison among different days. The captures of the suction traps have been shown to be similar up to a distance of 80 km (Taylor, 1973), a range probably rarely exceeded by the swifts in the breeding period.

Statistics: As reported in Thibault *et al.* (1987), growth of nestlings was globally estimated utilizing the logistic equation:

$$y = A/(1 + b*e^{(-kt)})$$

where: y = estimated mass or wing length at age t; A = asymptote, the fledging period value; b and k = estimated growth constants; t = nestling age.

The difference between the measured and estimated values (relative mass or relative wing length) was then used in the statistical tests. To allow comparison between broods in 2 distinct periods (initial and final nestling period), we performed separate ANOVAs on mean wing length and mass at day 20 (initial) and at day 40–45 (fledging age), respectively. Pairwise comparisons between ANOVA categories were performed using post-hoc multiple comparison tests with Bonferroni correction.

To avoid pseudoreplication, each nest contributed a single measurement (brood mean) to the assessment of mean values for the different brood sizes. The relative differences in nestling mass (Bryant, 1978) and wing length were used to describe the extent of the size hierarchy within broods (Relative difference = (oldest chick value − youngest chick value)/mean chick value).

The analyses presented in the **Results** have also been performed separately for each year in order to estimate the effect of this factor on the parameters considered. However, for the sake of brevity, the separate statistics are not presented in this paper, since we did not find any difference between the years of study (Cucco, 1992).

The data were analysed using the Systat package (Wilkinson, 1985).

	Parameters			
	A	b	k	N
Mass	41.98 ± 0.17	7.83 ± 0.42	0.245 ± 0.006	2033
Wing length	175.6 ± 0.83	12.12 ± 0.18	0.122 ± 0.001	2018

Results

Mass and wing length increase in relation to brood size

The patterns of daily growth of nestling pallid swifts is well explained by a logistic curve (equation in **Methods**). Asymptotic values, growth constants, and initial values, as estimated by the Nonlin procedure in Systat, are reported in Table I. The period of regular increase is from 1–20 days of age for the mass (Fig. 1), and from 5–35 days of age for the wing length (Fig. 2). The fledging period values were reached at 30 days of age for the mass, while the wings continued to increase in length until the last days of the nest period, at age >40 days.

Initial growth (period with linear increase, age = 20 days): nestlings growing in larger broods had a smaller mass and wing length (Table II). The reduced and natural broods of two did not differ in wing length ($F_{1,98} = 0.08$, $P = 0.93$ ns) or mass ($F_{1,98} = 0.012$, $P = 0.91$ ns). Brood size affected the relative difference between oldest and youngest chick (Table II), with larger broods (3 or 4 chicks) having the greatest difference.
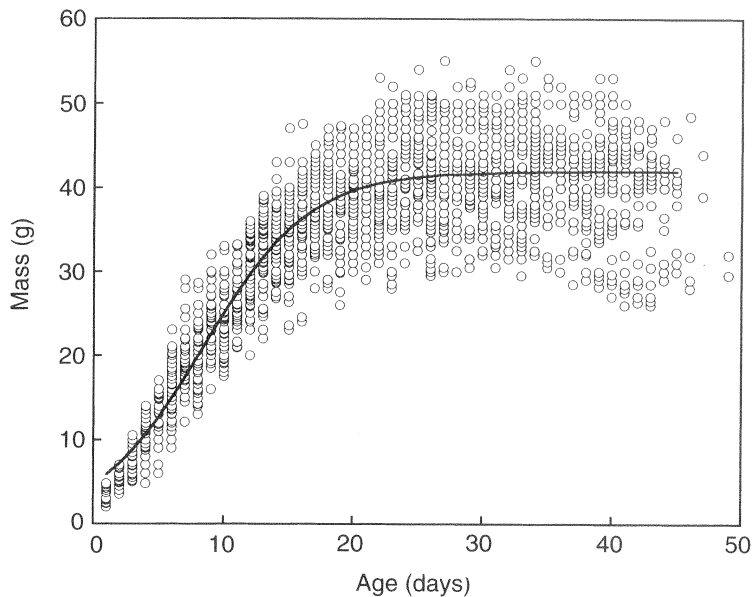

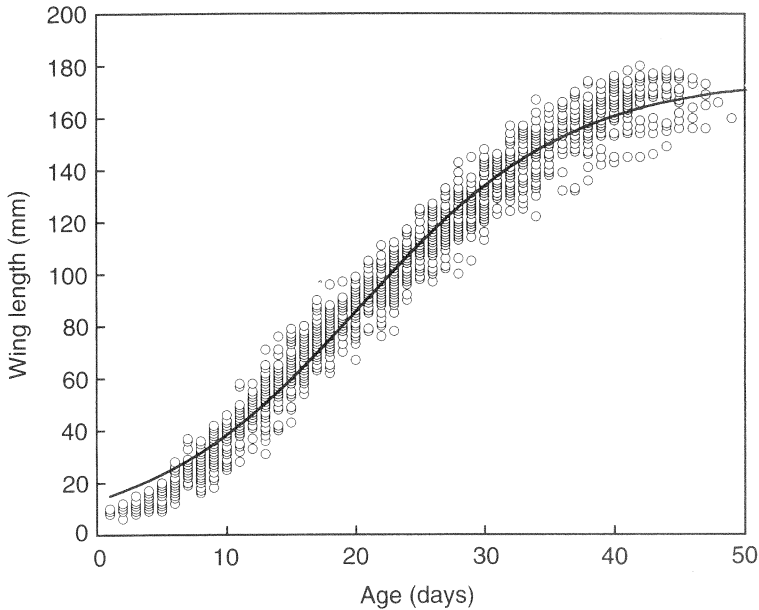FIG. 1. Body mass growth curve of nestling pallid swifts.

FIG. 2. Wing length growth curve of nestling pallid swifts.

End of growth (period when asymptotic values were reached, age > 40 days): nestlings growing in larger broods had a smaller mass and wing length at fledging (Table III). The reduced and natural broods of two did not differ in wing length ($F_{1,27} = 0.55$, $P = 0.46$ ns) or mass ($F_{1,98} = 0.007$, $P = 0.94$ ns). Brood size affected the relative difference between oldest and youngest chick (Table III), with larger broods (3 or 4 chicks) having the greatest difference.

The mean brood values for both wing length and mass at fledging ranged ±6% with respect to the average expected values (Table I). For both parameters, the largest intra-brood difference (oldest vs. youngest chick in the brood of three) was ±7% of the expected fledging value.

TABLE II

*Comparison of mass and wing length in different brood sizes (age = 20 days). Mean deviations from expected values are reported; * = manipulated broods*

	Brood size					ANOVA	
	One	Two	Two*	Three	Four*	F	P
Relative mass (g)							
Brood mean	+ 3.096	+ 0.236	+ 0.296	−1.524	−2.104	5.7	0.01
S.E. (N)	0.735 (29)	0.509 (88)	1.123 (16)	0.545 (37)	1.102 (16)		
Relative difference in nestling mass		0.024	0.028	0.189	0.150	14.1	0.01
S.E. (N)		0.010 (88)	0.027 (16)	0.015 (37)	0.025 (16)		
Relative wing length (mm)							
Brood mean	+ 4.95	−0.50	−0.41	−1.45	−2.58	4.9	0.01
S.E. (N)	1.42 (29)	1.12 (88)	2.03 (16)	1.15 (37)	2.35 (16)		
Difference oldest-youngest chick		0.026	0.026	0.101	0.035	6.1	0.01
S.E. (N)		0.010 (88)	0.027 (16)	0.015 (37)	0.025 (16)		

TABLE III

Comparison of mass and wing length in different brood sizes (age > 40 days). Mean deviations from expected values are reported; * = manipulated broods

	Brood size					ANOVA	
	One	Two	Two*	Three	Four*	F	P
Relative mass (g)							
Brood mean	+3.91	+1.21	+1.25	−3.81	−2.55	7.7	0.01
S.E. (N)	0.71 (29)	0.75 (88)	0.85 (16)	1.1 (37)	0.91 (16)		
Relative difference in nestling mass		0.026	0.018	0.185	0.062	35.3	0.01
S.E. (N)		0.018 (88)	0.020 (16)	0.035 (37)	0.021 (16)		
Relative wing length (mm)							
Brood mean	+6.84	+2.84	+1.14	−8.06	−2.56	7.3	0.01
S.E. (N)	0.58 (3)	1.61 (19)	1.51 (16)	3.20 (11)	1.7 (16)		
Difference oldest-youngest chick		0.028	0.030	0.102	0.047	19.5	0.01
S.E. (N)		0.019 (19)	0.021 (16)	0.029 (11)	0.027 (16)		

Mass and wing length increase in relation to insect abundance

In the earlier nestling period, insect abundance did not influence the daily increase in body mass (Fig. 3; r = 0.06, N = 94, $P = 0.56$ n.s.) and in wing length (r = 0.10, N = 94, $P = 0.33$ n.s.). As expected, the daily change in mass was usually an increase (91.5% of cases, N = 94). In a small number of cases (8.5%), there was a decrease in mass, which could be ascribed to diminished parental provisioning on the day.
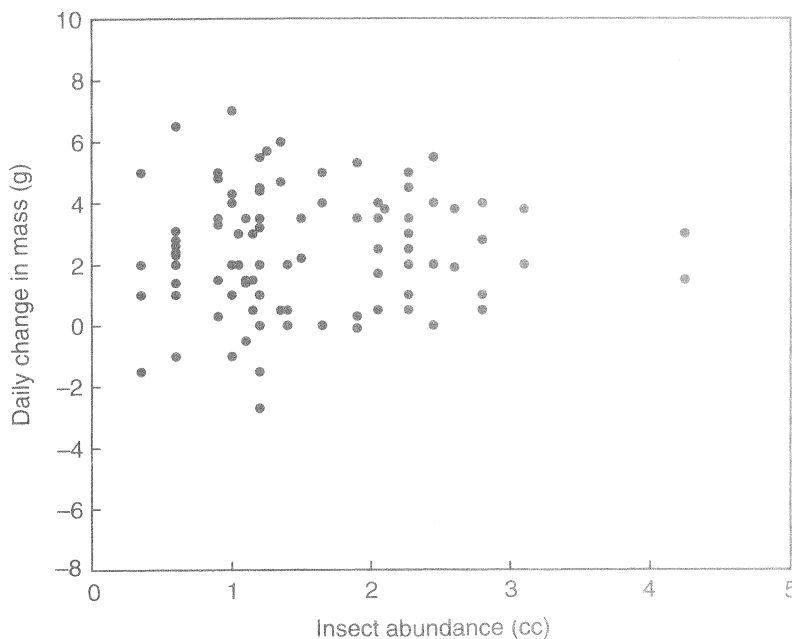

FIG. 3. Relationship between insect abundance and variation in daily body mass of nestling pallid swifts in the first period of nest attendance.
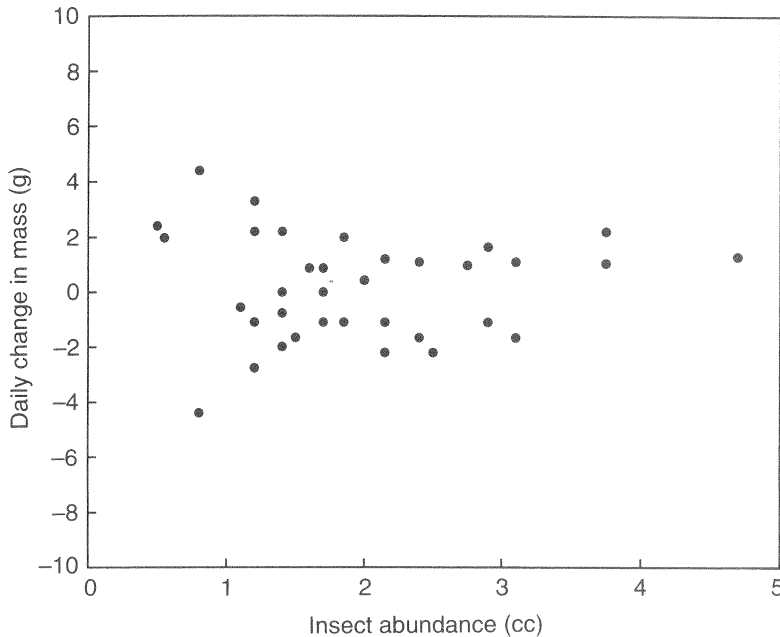
FIG. 4. Relationship between insect abundance and variations in daily body mass of nestling pallid swifts in the last period of nest attendance.

Brood size did not influence the daily increase in mass (ANCOVA $F_{4,88} = 1.75$, $P = 0.146$ ns) or wing length (ANCOVA $F_{4,88} = 1.86$, $P = 0.125$ ns).

Also, in the last part of the nestling period, insect abundance did not influence the daily variation in body mass (Fig. 4; $r = 0.03$, $N = 34$, $P = 0.87$ n.s.) or in wing length ($r = 0.05$, $N = 34$, $P = 0.78$ n.s.) of the nestlings.

In this period, however, the daily change in mass was almost equally likely to be an increase (55.9% of cases, $N = 34$) or a decrease. Brood size did not influence daily mass variation (ANCOVA $F_{4,28} = 0.91$, $P = 0.47$ ns) or daily increase in wing length (ANCOVA $F_{4,28} = 0.68$, $P = 0.61$ ns).

Reproductive success

Breeding success (Fig. 5a) was significantly higher in larger broods ($F_{4,82} = 18.8$, $P = 0.001$). The length of the nestling period (Fig. 5b) differed significantly with brood size ($F_{3,94} = 6.52$, $P = 0.001$). The efforts of parents rearing smaller broods was less prolonged than those of parents rearing more chicks.

Discussion

In this study, we describe the growth of nestling pallid swifts in natural and manipulated broods. The aerial insect abundance and the mass and wing length variations of chicks were monitored on a daily basis.
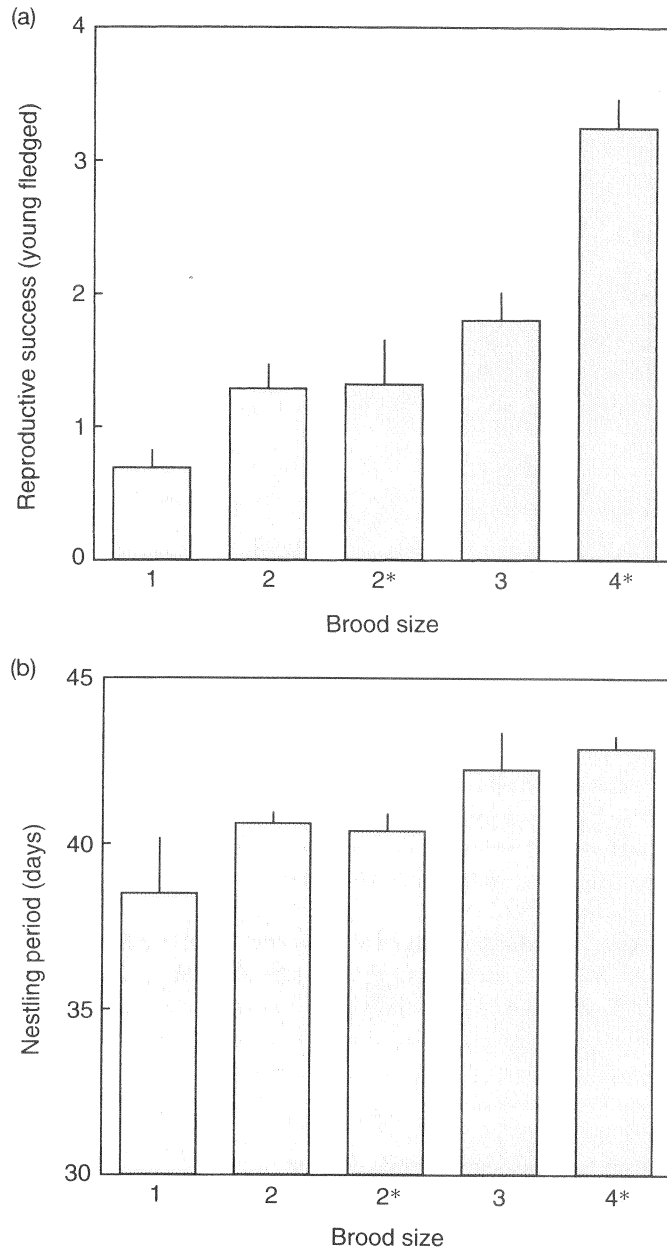
(a)

(b)

FIG. 5. Breeding success (a), and length of the rearing period (b), in relation to brood size (mean ± S.D.).

The average growth of nestlings in our population is very similar to that observed in the same species by Thibault *et al.* (1987) in Corsica and by Finlayson (1975) in Gibraltar.

In broods of different size, the growth of nestlings was different, and large broods had lower asymptotic wing lengths and masses. A similar result has been found in the European kestrel *F. tinnunculus* (Dijkstra *et al.*, 1990), while in the American kestrel *Falco sparvierus* (Gard & Bird, 1992) a lower growth rate was not detected in the chicks of larger brood sizes.

The reduced fledging mass could lead to a decreased chance of future survival and fitness, whereas a delay in the time of fledging could increase the survival probability (Perrins, 1965; Gustaffson & Sutherland, 1988). However, for aerial insectivores like the swifts, in which there is no postfledging parental care and most nestlings lose mass before fledging, it is possible that the advantages of prolonged fledging outweigh the dangers of a lower body mass (6% less than the average in our species). It is therefore possible, especially for chicks of smaller broods, that the large fat reserves, which were adaptive while in the nest as insurance against long spells of bad weather, are not useful once in flight and are therefore lost before fledging (Martins & Wright, 1993a). Probably, in the common swift, the delay in fledging of larger broods could also influence survival during their trans-Saharan migratory flight. On the contrary, in the pallid swift, many birds delay their migration until late autumn (Boano & Cucco, 1989), and insects are abundant in late July, when the chicks leave the nest. Thus, the longer nestling period in larger broods is likely to have little impact on survival of the young.

In this study, greater differences in growth between siblings were observed in the larger broods (three or four chicks). The differences occurred both in the period of constant increase and later when asymptotic values were reached. In the pallid swift, hatching asynchrony is the rule in broods of three chicks (Malacarne & Cucco, 1991) and behavioural observations of food distribution among siblings showed that the last-hatched chick obtains less food (Malacarne, Cucco & Bertolo, 1994). Mortality rarely occurred, probably because of the absence of severe weather conditions in the chick-feeding period, and because in larger broods the parents spent more days rearing nestlings until fledging day. When death did occur, it usually was the last-born chick that died (Malacarne & Cucco, 1991).

In our study, fledging success was higher in larger broods. Perrins (1964) found a negative effect of brood manipulation on survival till fledging of common swift nestlings. Fledging success was a function of the yearly weather conditions: good weather allowed higher reproductive success from clutches of three, while poor conditions induced brood reduction and clutches of two were the most productive. Martins & Wright (1993c) recently confirmed the effect of weather conditions; in Oxford in warmer and less rainy seasons, the larger broods were the most productive. Contrary to Perrins (1964), however, brood manipulation did not have a negative effect on survival in fine weather years. Our data are in line with the findings of Martins & Wright (1993b) in good weather conditions, since larger broods led to clearly higher success. On the other hand, brood enlargement experiments have shown that, in the majority of cases, altricial birds are able to rear chicks until fledging (Dijkstra *et al.*, 1990; for aerial feeders Bryant, 1975; De Steven, 1980).

Daily food abundance did not have an effect on nestling growth. This agrees with a study on the common swift (Pellantova, 1981), where no correlation was found between daily air temperature and mean increase in the body mass of the young. Prolonged adverse weather conditions in the reproductive season (rain and low temperatures), however, were able to induce a decrease in nestling mass in the common (Lack & Lack, 1951; Gory, 1987) and pallid (Thibault *et al.*, 1987) swifts. In swifts breeding in some Mediterranean areas (Gory, 1987; Thibault *et al.*,

1987), prolonged strong wind seems to be the most important environmental factor causing starvation and mortality among nestlings. In general, variations in food availability do not influence bird growth rate, unless deficiencies are severe enough to cause starvation (Ricklefs, 1968).

Since benefits gained from delivering food to the young have to be traded-off against the need of the parent to feed itself, it is conceivable that adults lose mass during the higher reproductive effort. In our pallid swift colony, we found that parents rearing enlarged broods lose more mass than controls (Cucco & Malacarne, 1995): this suggests that when adults are faced with greater parental effort they incur some cost of reproduction so as to maintain a quasi-optimal growth of their chicks (this paper). The balance of allocation between offspring or parents seems to be slightly biased towards the offspring. This is an intermediate situation between long-lived species (Sæther, Andersen & Pedersen, 1993; Mauck & Grubb, 1995), who are expected to be biased toward the parents, and short-lived species with a bias towards the offspring (Slagsvold & Lifjeld, 1988, 1990; review in Linden & Møller, 1989).

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