

## Fledging in the common swift, *Apus apus*: weight-watching with a difference

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(Received 5 July 1995; initial acceptance 11 September 1995;  
final acceptance 18 September 1996; MS. number: 4970)

**Abstract.** Fledging in the common swift involves young having to switch suddenly and completely from the sedentary lifestyle of a nestling to continuous flight with no post-fledging care. Using manipulations of brood size and the contrasting resource conditions in different breeding seasons, I observed fledging under a range of chick states. Poorly fed chicks took longer to fledge, and had lower body mass and short wing length at fledging. Despite this, maximum body mass of nestlings always exceeded those of adults and fledged young. Under all conditions, nestlings lost mass for 1 week prior to fledging, and at fledging they had similar wing loadings. I suggest that in their last days in the nest young swifts use up the fat stores that insured them against irregular parental provisioning as well as losing water from the drying out of feathers. Reductions in body mass associated with increases in wing length before fledging will affect flight efficiency by increasing the lift:drag ratio. This is interpreted as 'slimming' down to the optimal body mass which would improve the lift:drag ratio and set fledgings up for their life on the wing.

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Fledging studies have focused on nest leaving as a result of interactions between parents and offspring. Parents are expected to manipulate nestlings into fledging while nestlings should try to stay in the nest for as long as possible to maximize their survival chances (Trivers 1974). One way parents could force offspring to fledge is by reducing provisioning when they perceive that it is time to terminate parental investment. But it is now known that provisioning is not reduced before nestlings fledge in at least two species of altricial birds, marsh tits, *Parus palustris*, and pied flycatchers, *Ficedula hypoleuca*, and so this mechanism does not appear to be used by all species to manipulate the time of fledging (Nilsson & Svensson 1993). Also, in puffins, *Fratercula arctica*, a species in which provisioning is reduced prior to fledging, experimental artificial feeding at the maximum level provided later in the nestling period did not influence either the age of fledging or body mass at fledging (Hudson 1979).

However, sibling-sibling competition and energetic considerations do play an important role in patterns of fledging (Lemel 1989; Nilsson 1990a;

Nilsson & Svensson 1993). If provisioning to all chicks is adequate, fledging order tends to reflect dominance hierarchy among chicks and as such is related to size and condition. This is a consequence of the highest ranked chick tending to be in the best feeding position in the nest (Bengtsson & Rydén, 1983; Forbes & Ankney 1987; Gottlander 1987) and later closer to the feeding parent. Movements towards the provisioning parent can result in fledging (Nilsson 1990a). However, if provisioning to all chicks is not adequate, the first chick to leave need not be the highest ranked individual but rather an individual in poorer condition (Lemel 1989). Such an individual would benefit by dividing parental attention away from the nests as parents favour fledglings (Lemel 1989; Nilsson 1990a). After one individual has fledged, the dominant nestling must also leave the nest to continue having access to the food brought by the parents, and the rest of the brood soon follows.

Fledging in swifts involves young having to switch suddenly and completely from a sedentary lifestyle to one of continuous flight with no post-fledging care (Lack 1956a). The lack of parental care after fledging suggests that nestlings would not fledge prematurely in order to divide parental attention as in other altricial species. Moreover,

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**Table I.** The brood size manipulation in 1988 and 1989 with number of nests used (*N*)

	Manipulated brood size		
	1	2	3
<b>1988</b>			
Mean lay-date	21.0	19.6	19.3
Mean hatch-date	43.6	42.8	41.3
<i>N</i>	5	5	3
<b>1989</b>			
Mean lay-date	20.0	21.0	20.3
Mean hatch-date	42.2	42.2	41.8
<i>N</i>	5	4	6

the change to a completely air-borne state suggests that attaining proficient flight at fledging is more important for a swift than for other species and it is also possible to argue that this need could reduce conflict between parent and offspring over the amount of care at independence as found in marsh tits (Nilsson 1990b). One should therefore expect fledging decisions in swifts to be determined by age, condition or size.

By randomly manipulating brood sizes and therefore the levels of parental effort in the common swift in two different years in a study on costs of reproduction (see Martins & Wright 1993a, b, 1994) I had the opportunity to observe fledging under a range of chick states. My aim in this paper is to test the prediction that under all circumstances, for a species with no post-fledging care, the fledging decision should be highly fixed. To test this I investigated whether swifts fledge when they reach (1) a certain age, (2) a certain wing length, (3) a certain body mass or (4) a certain size:mass ratio. To test these predictions I investigated the period leading up to and including fledging. For larger experimental broods, I also looked at whether a strong established hierarchy (caused by differences in provisioning) can indeed influence the order in which chicks leave the nest.

## METHODS

This study was carried out in 1988 and 1989 in the nestbox colony in the University Museum tower in Oxford, U.K. This swift colony is well established and contains over 60 breeding pairs. It was the site of David Lack's original work on the breeding biology of common swifts (Lack 1954,

1956a, 1964, 1968; Lack & Lack 1951, 1952). The common swift is a long-lived aerial insectivore that flies all of its time outside the nest and has no post-fledging care (Lack 1956a).

In both years, when chicks were 5 days old, I randomly assigned brood sizes of one to three to 15 nests in roughly equal numbers, such that every chick was reared in a nest other than its original one (Table I). This random assignment meant that original clutch size, laying date and hatching date were averaged across the groups. This was done to remove the effects of parental quality on chick body mass and also to standardize body mass variation within nests (no nest occupants are siblings). In 1988, owing to a prolonged cold spell, in two of the five nests with an experimental brood size of three, one chick died early in the nestling phase and these nests were not included in any of the following analyses (but see Martins & Wright 1993a). No significant effects of original clutch size were found in any of the preliminary tests (i.e.  $P > 0.50$ ) and it was therefore not included in any of the following analyses.

I used a system of electronic balances (Ohaus Port-O-Gram, model c501, 500 g capacity, 0.1 g accuracy, Ohaus Scale Europe, Cambridge, U.K.) linked to a BBC model B Microcomputer through a switching device (Smart switch, model V. 24, Inmac, U.K.) in both years to collect data on parental visits and chick body mass during the nestling period (for detailed methods see Martins & Wright 1993b). I weighed each chick to the nearest 0.1 g every day by adding it to the balance. Analyses concerning mean chick masses refer to the period after 12 days of age (i.e. after the exponential growth phase and at the mass asymptote; Lack 1956a). At the end of the nestling period, I also measured the wing length of

the young every day until fledging. Wing length was measured to the nearest 0.5 mm using a stopped wing ruler and taken according to the maximum flattened chord method (see Svensson 1984).

Wing loading ( $N/m^2$ ) is the ratio of weight per unit of wing area. To calculate wing area I used the method described in Pennycuik (1989), where the wing area approximates to twice the sum of the area of a rectangle (corresponding to the ulna, radius, humerus and the secondaries) plus the area of a triangle (corresponding to the carpometacarpus and primaries), the wing length measured being the hypotenuse of the triangle. To estimate the two sides of the rectangle I used six skins held at the University of Oxford Museum. I then estimated the length of these two sides in relation to each specimen's wing length. I calculated the average relative (to wing length) estimate for both sides for all wing measurements at fledging, and was then able to estimate wing area for all fledglings. Using this same method, I could also estimate wing span (m), as twice the total wing length plus the average width of the body. I used wing span (m) for the calculation of power curves. I calculated curves of power consumption against flight speed and estimates of maximum range speed, minimum power speed and maximum effective lift:drag ratio using program 1 from Pennycuik (1989).

For ease of analysis and to avoid pseudoreplication (Hulbert 1984), I performed analyses of variance (ANOVAs) on the averages per nest: I used the GLM procedure from the SAS system statistical package (SAS Institute Inc., Cary, North Carolina). Contrasts were performed within each model and  $F$ -values calculated by dividing the mean sum of squares for the contrast of interest and the mean sum of squares for the error in the model. I performed ANOVAs on variables for the effect of brood size, year and the interaction between these two factors. When brood size year and/or the interaction terms were significant, to locate pair-wise differences, I performed a posteriori contrasts on the pairs of means that were most dissimilar. These contrasts could have been performed for overall steps up in brood size, to examine linear and quadratic terms or between years for each brood size. To be conservative and to reduce the probability of a type I error I considered these contrasts significant only if  $P < 0.01$ .

The meteorological data presented here were provided by the School of Geography, Oxford University and were recorded at the Radcliffe Meteorological Station in Oxford.

### Hierarchy and Order of Fledging

I analysed hierarchies among chicks for broods of three only. The reason for this is that brood size is a strong factor in reducing the food delivered per chick (Martins & Wright 1993a) and it is therefore an example of worsening conditions. I calculated position in the brood hierarchy as the number of days (from chick age 12 until the first chick fledged) that each chick occupied the top body mass position for each nest. Each hierarchical position was therefore associated with a given percentage of the total number of days of the nestling period. In an attempt to control for independence, I ran regressions of the percentage (arcsine transformed) on hierarchical position for each nest separately. I then examined the effect of the different years (1988, 1989) by running an ANOVA on the mean slopes per year. Therefore, if a strong hierarchy was established, chick 1 would occupy the top position more often than expected by chance alone and the resulting slope would be negative. On the other hand, if a hierarchy was not established, a shallow or non-existing slope would be expected.

## RESULTS

### Experimental Design

There were no statistically significant differences between the three groups of nests assigned to the three brood sizes in either lay-date or hatch-date for either of the two breeding seasons (1988:  $F_{2,10}=0.32$ , NS;  $F_{2,10}=0.32$ , NS; 1989:  $F_{2,12}=0.13$ , NS;  $F_{2,12}=0.04$ , NS, respectively).

### Weather Conditions

A summary of the weather conditions during the swift nestling periods in 1988 and 1989 was presented in Martins & Wright (1994). I analysed the meteorological data for the period from the first chick hatching until the last fledging day of experimental nests in both years. The nestling reared period in 1988 was significantly colder, less

sunny and more windy than 1989. Furthermore, these 2 years represented the two extremes of a distribution of mean maximum temperatures for swift nestling feeding periods for the 44 years (1947–1990) for which data on swifts are available (1988: 19.05°C; 1989: 24.08°C; Martins & Wright 1994). It is known that the higher the maximum temperature the better the conditions for breeding swifts (Lack 1956a; Martins & Wright 1994), so I interpret the difference in mean maximum temperature between these 2 years as a good indicator of differences in food supply.

### Tests of Predictions

#### At fledging

The age at which chicks fledged increased significantly with brood size (Fig. 1a:  $F_{2,22}=4.55$ ,  $P<0.05$ ; linear contrast term:  $F_{1,22}=8.87$ ,  $P<0.01$ ), and chicks tended to fledge at an older age in 1988, but this difference was not quite significant ( $F_{1,22}=3.70$ ,  $P<0.1$ ). Mean fledging mass decreased with manipulated brood size (Fig. 1b:  $F_{2,22}=6.80$ ,  $P<0.01$ ; linear contrast term:  $F_{1,22}=13.05$ ,  $P=0.001$ ), and the mean fledging mass was higher in 1989 than in 1988 ( $F_{1,22}=7.98$ ,  $P=0.01$ ). The interaction term was not significant, showing that the effect of brood size was similar in both years ( $F_{2,22}=1.54$ , NS). When years were contrasted within brood sizes, chicks from broods of three were found to fledge at a significantly higher body mass in 1989 than in 1988 (contrast year within brood size 3:  $F_{1,22}=8.63$ ,  $P<0.01$ ). Mean chick wing length at fledging tended to decrease with brood size, but this trend only approached significance (Fig. 1c:  $F_{2,22}=3.08$ ,  $P<0.1$ ; linear contrast term:  $F_{1,22}=3.27$ ,  $P<0.1$ ). Year had a very strong and significant effect on wing length, with chicks fledging in 1989 having longer wings than chicks in 1988 ( $F_{1,22}=15.71$ ,  $P<0.001$ ); again the interaction term was not significant ( $F_{2,22}=2.74$ ,  $P<0.1$ ). The main difference between years was the significantly shorter mean wing length in 1988 for brood size 3 (contrast years within brood size 3:  $F_{1,22}=16.18$ ,  $P<0.001$ ), contrast terms were not significant for broods of 1 or 2 (contrast year within brood size 1:  $F_{1,22}=1.57$ ; NS; contrast year within brood size 2:  $F_{1,22}=2.09$ , NS). When wing length was tested for a brood size effect for 1989 alone, no differences at the time of fledging were found ( $F_{2,12}=0.07$ , NS). Wing loading at fledging

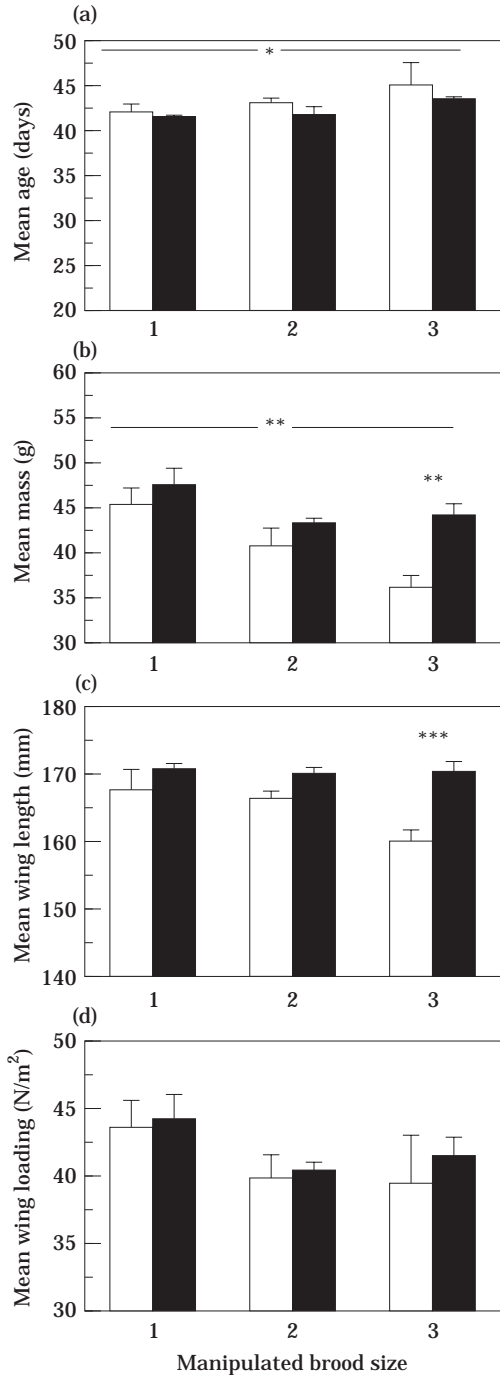
(ratio of force, i.e. weight, to wing area) was not significantly different between brood sizes (Fig. 1d:  $F_{2,22}=2.58$ , NS) or years ( $F_{1,22}=0.43$ , NS), showing that whatever the conditions chicks were reared under, fledging wing loadings were not significantly different.

#### Before fledging

Chicks lost mass before leaving the nest. There was no effect of brood size on the mean mass loss (Fig. 2a:  $F_{2,22}=0.89$ , NS), but chicks lost more mass before fledging in 1989 than in 1988 ( $F_{1,22}=6.08$ ,  $P<0.05$ ). This year difference was mainly due to chicks in broods of three in 1989 losing more mass than chicks from the same brood size in 1988 (contrast year within brood size 3:  $F_{1,22}=9.14$ ,  $P<0.01$ ). At the other two brood sizes there were no significant differences between years (contrast year within brood size 1:  $F_{1,22}=0.02$ , NS; contrast year between brood size 2:  $F_{1,22}=1.46$ , NS). Interestingly, this nestling body-mass loss happened over the same mean number of days for chicks from different brood sizes (Fig. 2b:  $F_{2,22}=0.25$ , NS) and reared in different years ( $F_{1,22}=1.34$ , NS). As with fledging body mass, mean highest body mass attained (before body-mass loss started) decreased significantly with brood size (Fig. 2c:  $F_{2,22}=7.10$ ,  $P<0.01$ , linear contrast:  $F_{1,22}=14.19$ ,  $P=0.001$ ) and was higher in 1989 than in 1988 ( $F_{1,22}=19.61$ ,  $P<0.001$ ) the main difference again being due to chicks from broods of three in 1989 attaining higher body masses than chicks from the same brood size in 1988 (contrast year within broods of 3:  $F_{1,22}=24.78$ ,  $P<0.001$ ), while no differences were found for the other brood sizes (contrast year within brood size 1:  $F_{1,22}=0.44$ , NS, contrast year within brood size 2:  $F_{1,22}=3.24$ ,  $P<0.1$ ). The age, in days, at which these mean highest body masses were attained were not significantly different for the different brood sizes (Fig. 2d:  $F_{2,22}=2.21$ , NS) and showed no year effect either ( $F_{1,22}=0.01$ , NS).

#### Hierarchy and Order of Fledging

There was a strong year effect on the mean slopes of percentage of hierarchy and chick position for broods of three in the 2 study years ( $F_{1,7}=7.95$ ,  $P<0.05$ ; see Methods for explanation). In 1988, when food was apparently



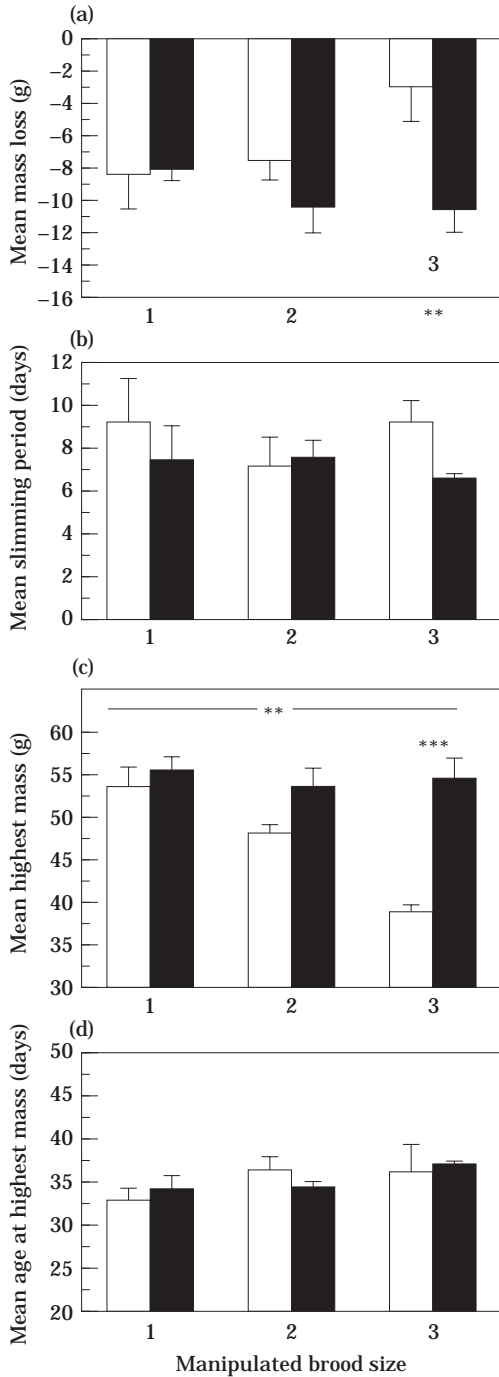
**Figure 1.** Measures of chick condition (+SE) at fledging according to brood size and year. (a) Mean age; (b) mean body mass; (c) mean wing length; (d) mean wing loading. □: 1988; ■: 1989.

**Table II.** Frequency of different orders of fledging in 1988 and 1989

Order of fledging	1988	1989
1 first (1, 2, 3 and 1, 3, 2)	0	4
2 first (2, 1, 3 and 2, 3, 1)	0	2
3 first (3, 1, 2 and 3, 2, 1)	3	0

scarce, a strong hierarchy became established and chick number 1 was the heaviest on most days. In 1989, on the other hand, all chicks spent the same proportion of time at the heaviest position. Thus, the food supply seemed to determine whether a hierarchy among chicks was established. The presence or absence of a hierarchy, being a measure of distribution of food within broods, makes it possible to predict the order of fledging. One would expect that, in a hierarchical set-up, the second or third chick would get less food and might therefore fledge first. In years when there is no tight hierarchy, chicks should fledge as they attain the right wing length to their body mass, which, in good years, tends to happen as they grow older (mainly because they are on average heavier and therefore need longer wings) the order of fledging being therefore age related (chick number 1 first, 2 second, and 3 third). Chick number 3 fledged first in 1988 and the pattern in 1989 was also as predicted, that is, fledging in that year was age related (Table II).

Despite the effect of hierarchy or chick condition on fledging order, fledging should happen only once chicks attain an optimal body mass/size for their life on the wing. If that is the case, fledging sequence should be dependent on wing loading, that is all chicks at fledging should show the same wing loading. However, because order of fledging within broods is not a series of independent events, regressions of order of fledging and wing loading were performed separately for each nest. The mean slopes of order of fledging and wing loading per year were not significantly different from each other (year effect:  $F_{1,7}=1.59$ , NS) showing that although hierarchy determines order of fledging, young swifts fledge only as they attain the right wing loading. This seems to be done by a combination of body mass loss and feather growth prior to fledging.



**Figure 2.** Measures of chick condition (+SE) before fledging according to brood size and year. (a) Mean body-mass loss; (b) mean slimming period; (c) mean highest body mass attained; (d) mean age at highest body mass. □: 1988; ■: 1989.

### Lift and Drag: Cost of Flight

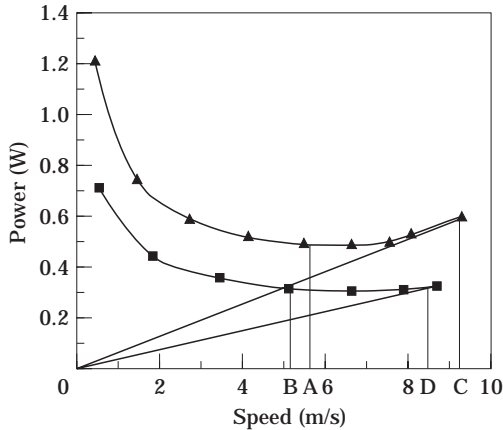
I calculated power curves for a hypothetical fledgling using the extremes shown over the 2 years for fledging body mass and fledging wing span (wing span was kept constant at the overall mean in the first case and fledging body mass was kept constant at the overall mean in the second case). The reductions in fledging body mass were responsible for the highest rate of change in lift:drag ratio (19.5% increase compared with 11.1% increase in lift:drag ratio for increase in wing span). Therefore, larger reductions in the cost of flight would be brought about by reductions in the fledging body mass.

To estimate the possible gain in lift:drag ratio shown by mass loss before fledging, I calculated power curves for the mean highest body mass achieved in all years and for the mean body mass at fledging (wing span held constant at the overall mean). I calculated the resulting change in minimum power speed and maximum range speed, minimum power and maximum range power and for the maximum effective lift:drag ratio in relation to the highest body mass (Fig. 3). The average reduction in body mass before fledging was 13.1 g (24%). This reduction in body mass caused a 9.6% reduction in minimum power speed, an 8.6% reduction in maximum range speed, and a 36.7% reduction in minimum and maximum range power. The maximum effective lift:drag ratio, which is a measure of flight efficiency, was increased by 9.6%.

## DISCUSSION

### Brood Size Manipulation and Food Supply

The increase in food delivery rate with increasing brood size is not proportional to the number of chicks in the nest and so each chick gets less food (Martins & Wright 1993a), especially in years when food is scarce (Martins & Wright 1994). As brood size increased by one chick, chick age at fledging increased by a day. However, in 1988, when food was scarce, chicks from broods of three fledged on average when 2 days older. Brood size had an equivalent effect on fledging body mass and wing length. Also, among broods of three, poorly fed chicks in 1988 fledged at about 80% of the body mass and at about 94% of the wing length of chicks from 1989. Although differing



**Figure 3.** Power curve for a chick attaining the average highest body mass in the nest (0.0545 kg, ▲) and for the same chick fledging, after losing mass, at an average fledging body mass (0.0414 kg, ■). The maximum range speed is given by the tangent to the power curve; minimum power speed is the minimum point on this curve. A denotes the minimum power speed for a chick fledging at the highest body mass, B the minimum power speed for the same chick fledging after losing mass in the nest, C is the maximum range speed for the chick fledging at the highest body mass and D is the maximum range speed for the same chick fledging after losing mass in the nest.

chick feeding conditions created these differences in the fledging pattern no differences were found either for brood sizes or years in the wing loading at fledging. So it seems that, whatever the situation, chicks fledged at the same wing loading.

Mass recession happened over the same number of days whatever the circumstances chicks were in. Also, chicks in different brood sizes lost on average the same amount of mass but year had a significant effect. Chicks reared in 1989 lost more mass than chicks from 1988 and this larger mass loss was mostly because they had attained higher body masses in the nest. The mean age at which the highest body mass was attained was the same for all brood sizes and years. So it seems that, before fledging, all chicks lost mass starting at the same age and over the same amount of time whatever the brood size or year. The extent of this mass recession is dependent only on how well fed they were during the nestling period.

Mass recession in swift and hirundine chicks has been mostly associated proximately with water loss as a result of the integument drying

out (Ricklefs 1968; O'Connor 1977; Bryant & Gardiner 1979). It is possible therefore that its starting point and its duration are determined by the developmental stage at which the integument dries out. If this were the case it could explain why, in this study, mass recession started for all chicks at the same age and lasted for the same length of time. However, the amount of mass reduction can be different for chicks reared in different conditions which suggests that some lipid must be lost. Chicks reared in good conditions are known to have higher levels of lipids (Lack 1956a; Bryant & Gardiner 1979). Also, species that show marked mass recession are also the ones that accumulate large fat reserves during the nestling phase and some of that insurance mass must be lost before fledging (Lack 1968). It is therefore not surprising that it is the chicks that attained higher body mass in the nest that lost the most weight before fledging. However, in spite of mass being lost by desiccation and variable use of fat reserves, while at the same time skeletal, muscle and feather growth was positive, chicks reared under different chick feeding conditions still attained similar wing loadings at fledging.

Mass recession could have been a consequence of parents manipulating young to fledge. However, data on adult mass loss available for the period before fledging reveals that in 1988 and for broods of three, adults reverted to feeding themselves when their body mass was reduced to a certain level (Martins & Wright 1993a, b). This was interpreted as a response to an increase in the perceived risk of starvation and/or predation (as in Lima & Dill 1990). It is expected that this behaviour produced an overall reduction in provisioning in that year. Since this 'reverting to feeding self' did not happen in 1989, it is difficult to explain this behaviour as a mechanism to manipulate young to fledge.

Mass recession during the initiation of sustained flight has also been shown in an experiment with juvenile pipistrelle bats, *Pipistrellus pipistrellus* (Hughes et al. 1995), bats with very different experimental growth regimes all converging to precisely the same body mass at the same time. Furthermore, the bats' wing loading decreased with age until levelling off after the time of sustained flights. Hughes et al. argued that the mass the bats reached was probably the optimum for pipistrelle bats at that particular age and learning to fly: possibly a compromise between

sufficient support structures, muscle output, reserve fuel and on the other hand carrying the minimum excess payload.

### **Hierarchy and Order of Fledging**

The order of fledging was associated with the establishment of a strong hierarchy and was therefore closely determined by chick condition. When food was abundant, the order of fledging was age related, older chicks fledging first. It is possible that this fledging order in fact reflects the need to attain the correct wing length for their body mass. This can happen by one or both of two processes: feather growth or mass loss. The high feeding rates shown for 1989 (Martins & Wright 1994) are reflected in the fact that, although chicks reared under good conditions are younger at fledging than the ones reared in a poor year, they are also bigger and heavier. In years when food is scarce, low feeding rates determine the establishment of strong hierarchies among siblings and the second or third chicks might fledge first (Lack 1956b, this study). Although fledging first for swifts is not associated with gaining access to the providing parent it might reflect the need to escape from the nest to avoid sibling competition. Swift fledglings start foraging immediately and could therefore achieve a higher net energy gain outside the nest. Therefore, it is also possible that subdominant nestlings would leave the nest to have a higher net energy budget by foraging for themselves. Studies on nest leaving order in other species have shown both patterns. In marsh tits the order of fledging reflects a size hierarchy, the long-winged chicks fledging first and the others soon following (Nilsson 1990a). For great tits the fledging order correlates negatively with body mass (Lemel 1989), the second chick fledging first to gain parental attention. Nilsson (1990a) discussed the difference between these two species in terms of a possible relaxed parent-offspring conflict in marsh tits and argued that the increased benefits to chicks that fledge earlier in the season makes it important for chicks to leave the nest as early as possible. However, I suggest that the willingness to leave the nest is in fact due to differences in chick condition. Such differences in the pattern of fledging would therefore be dependent on the effect of resource conditions on the establishment of hierarchy through sibling competition. The fact that post-fledging care is available for both marsh tits and great tits makes it possible to fledge and

also to receive care outside the crowded competitive nest. For swifts, a species where the fledging order is not confounded by post-fledging care, I was able to show that both patterns occur when food supply differs.

For swifts differences in hierarchy can also determine the order of leaving the nest. However, the lack of post-fledging parental care and the need to be on the wing continuously from fledging make it impossible for swifts to leave the nest before some form of flight efficiency is attained. This can be seen in the behaviour of chicks on the last days in the nest. During this period, the chick closest to fledging will sit on the edge of the nest entrance (Lack & Lack 1952) but it will not beg or be fed when the parent visits. During this period it is completely oblivious to the parents or the other chicks and, within a day or two, the chick will just leave the nestbox (Lack 1956a). The next young to leave will do so from 1 to 6 days after the first and it will also spend some time by the entrance prior to departure (Lack & Lack 1951). If, on the other hand, a chick has been suffering from strong competition from its siblings it would have lost some body mass already and the process of nest leaving would be shorter than in other cases. These 'starving' chicks are known to leave within a day of sitting by the entrance.

### **Mass Recession: Costs and Benefits**

The effect of losing body mass is essentially to reduce minimum power speed and maximum range speed and also to reduce the minimum power and maximum range power. These changes resulted in an increase in the flight efficiency (lift:drag ratio) by 9.6%. These results suggest that for young swifts leaving the nest, gains in flight efficiency might be more important than the loss in flight speed. Norberg (1981) has argued that mass loss for adult birds provisioning young would be advantageous as it would reduce flight costs. The data on swifts suggest that mass loss in juvenile birds that are about to undertake sustained flights might also be adaptive. Juvenile bats also lose mass (see review in Kunz 1987; Hughes et al. 1995); by the time they undertake sustained flights their wing loading has fallen to the extreme lower end of possible adult values. A hypothetical flight performance model of pre-volant juveniles showed that the cost of flight was particularly low

during the flight learning period which overlaps with the mass recession period. Hughes et al. (1995) argued that the system was tuned so that the power and optimum wing beat frequencies were close to adult levels by the time the juvenile begins to fly, but the cost of flight was lower thus facilitating first flights.

Changes in body mass can also affect agility and manoeuvrability (see Aldridge 1986; Norberg 1990; Hedenström 1992). First, there is a direct increase in the power to weight ratio which is important in manoeuvres such as initiating rapid climbs, accelerating, stopping, etc. Second, if these reductions in body mass are associated with increases in wing length, the force that must be provided by the wings to turn the bird can counterbalance its body mass and improve both agility and manoeuvrability. However, there is little empirical evidence for such changes in manoeuvrability and they are all associated with an increase in body mass rather than a decrease. Blem (1975) has shown that house sparrows, *Passer domesticus*, with added weights were easier to catch in a net, which may reflect a decrease in manoeuvrability. Aldridge & Brigham (1988) found that an addition of artificial loads (5–30% of body mass) significantly reduced the ability of *Myotis yumanensis* to negotiate an obstacle course. Also, more recently, Witter et al. (1994) has shown that decreases in aerial manoeuvrability were associated with within-natural-range increases in body mass in the European starling, *Sturnus vulgaris*. I suggest therefore that reductions in body mass in young swifts are achieved to improve lift:drag ratio or the cost of flight and to improve manoeuvrability.

Reductions in body mass are also responsible for reducing flight speed, both minimum power speed and maximum range speed (but see Hughes & Rayner 1991). Changes such as these would improve foraging efficiency but could have some negative implications for migration (Pennycuik 1975; Alerstam & Lindström 1990) and maybe for escaping predators (Witter & Cuthill 1993). For migration, reductions in flight speed could reduce the possible distance travelled (Alerstam & Lindström 1990). However, it is possible that young swifts do not migrate straight after fledging as was suggested before (Lack & Lack 1951), but spend some time around the colony before leaving and before migrating. Fledglings' wings were significantly shorter than adults' wings ( $t_{89}=8.50$ ,

$P<0.001$ ), so it is possible that the wing would carry on growing after leaving the nest (for bats that is the case, Hughes et al. 1995). This also supports the idea that foraging considerations would come before migration, and therefore, that manoeuvrability would be immediately more important than flight speed. It is also important to add that an increase in manoeuvrability, owing to reductions in wing loading, would have a beneficial effect on predator avoidance (Witter & Cuthill 1993). Newly fledged swifts are known to be taken by hobbies, *Falco subbuteo* (Klass 1953), which can outfly swifts. So, if an attack is detected, manoeuvrability is likely to be of the utmost importance in escaping.

How would the young swifts 'know' of their wing to body mass ratio to time fledging accordingly? Young swifts exercise their wings in the nest (Lack & Lack 1952). When they are about 4 weeks old, they do a form of 'press-up', the wing being partly extended and pressed down on the floor, taking the weight, while the body is raised until both it and the feet leave the floor altogether. At first, the young bird cannot sustain this position and merely hops up and down, but after a few days it can hold the body clear of the ground for a second or two. This time increases steadily until, just before fledging, the chicks are able to hold this position for 10 s or more. I suggest that, unlike wing flapping exercises when birds are clearly training the wing muscles, one possible function of press-ups might be to check on body mass to wing length ratio. Once they can hold position for a certain amount of time, the young are ready to fledge.

## ACKNOWLEDGMENTS

I am indebted to Gareth Jones for the idea for this paper (during my D.Phil. Viva at Oxford!). Thanks to Jon Wright for providing constructive feedback and also for coming up with the amusing title. The aerodynamics section benefited from discussions with Adrian Thomas. Tim Benton provided some 'life-saving' stats advice. Matthew Evans, David Bryant, Peter Hudson, Mark Witter and Jan-Åke Nilsson read and commented on early drafts of the manuscript. This study was supported by a CNPq scholarship (Brazil) and an Overseas Research Scheme grant.

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