

Patterns of food allocation between parent and young under differing weather conditions in the Common Swift (*Apus apus*)

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Abstract – Brood sizes were manipulated to promote different levels of parental effort in the Common Swift (*Apus apus*). The two years in which these brood size manipulations were carried out differed with regard to weather conditions. Data were collected on a visit by visit basis to reveal changes in parental and chick body mass, the mass of prey delivered and the estimated mass of parental self-feeding. This provided a powerful method for testing hypotheses regarding parental investment decision concerned with optimal allocation strategies between parents and young and how these can be affected by resource conditions. When weather conditions were “good” (warmer and sunnier), parents did not have to lower their own self-feeding to increase the amount of food delivered to larger broods as they did when conditions were “bad” (cold and wet). Only in “good” weather conditions did parents suffer no mass loss as a result of increased parental effort, and incur no increased costs from raising larger broods. In addition, “good” weather conditions meant that fledging mass in larger broods was similar to that in smaller broods, which suggests that a reduction in the survival chances of fledglings from larger broods only occurred in “bad” weather conditions. The differential allocation responses shown in both years are discussed in terms of parental strategies to cope with increased brood demands.

Introduction

The trade-off between present and future reproductive success is central to life-history theory (Williams 1966, Charnov and Krebs 1974, Stearns 1976, Ricklefs 1977, Calow 1979). However, such trade-offs have proved difficult to quantify in the field, and in fact positive relationships between reproductive performance and adult survival are often recorded instead (Kluyver 1971, Bryant 1979, Högstedt 1981, Smith 1981, Ricklefs and Hessel 1984), which usually reflects inherent differences in individual quality (Perrins and Moss 1975, Pettifor *et al.* 1989). It is widely accepted that the effect of this phenotypic variation in individual quality should be overcome using experimental manipulation (Askenmo 1979, De Steven 1980, Bell 1984, Partridge and Harvey 1985, 1988, Nur 1988, Smith *et al.* 1988, Orell and Koivulla 1988, reviews in: Reznick 1985, Reznick *et al.* 1986, Bell and Koufopanou 1986, Nur 1988). However, even experimental studies are not problem free, either because monitoring adult survival and recruitment of young has its limitations or because environmental conditions can affect reproductive costs. If conditions are favourable, costs are likely to

be small or absent, whilst if conditions are harsh costs may be high (Nur 1988). Therefore, assessments of costs of reproduction over a number of seasons may be necessary in order to infer a selective consequence in terms of life-history.

It is normally assumed that parental investment decisions operate in the long-term with parents trading levels of care in the present breeding attempt against breeding success in the future (Trivers 1972). This is probably because most theoretical treatments of parental investment deal with the problem as one of evolutionary trade-off and there is a tendency to ignore the possibility that such trade-offs can operate over behavioural time-scale within a breeding attempt (Lima and Dill 1990, see also Martins and Wright 1993a,b). One example of a behavioural trade-off which can be expected to have life-time consequences is the way in which breeding birds must divide the food they gather between themselves and their offspring. Benefits gained from delivering food to the young have to be traded-off against the need of the parent to feed and maintain its own physical condition, and retain a chance of survival to future breeding attempts (reviews in: Partridge and Harvey 1985, 1988, Reznick 1985, Nur 1988) or retain future

fecundity (Gustafsson and Pärt 1990). The parental allocation of resources should therefore be optimized between present and future reproductive attempts so as to maximize life-time reproductive success (Kacelnik and Cuthill 1990).

By manipulating brood size and therefore the levels of parental effort in the Common Swift (*Apus apus*) we aimed at investigating the resulting changes in parental foraging strategy. The allocation of food between parent and young was directly assessed on a visit by basis using the load mass delivered, the calculated energetic cost of the feeding trip and the changes in adult mass during that trip. Conditions differed considerably in the two years in which brood size manipulations were carried out in the swift study colony. This offered an unique opportunity to look at the effects of resource availability on the patterns of parental investment and food allocation. The aim of this paper is therefore to investigate the changes in foraging strategy of parents feeding manipulated brood sizes under different conditions and to evaluate the associated costs in terms of adult body mass loss.

Methods

This study was carried out in 1988 and 1989 in the nest-box colony in the University Museum tower in Oxford, U. K. This swift colony is well established and contains over 60 breeding pairs and was the site of David Lack's original work on the breeding of common swifts (Lack 1954, 1956, 1964, 1968; Lack and Lack 1951, 1952). The Common Swift is a long-lived aerial insectivore that spends all of its time outside the nest flying and has no post-fledging care. It is therefore an excellent species for the study of costs of reproduction during the nestling phase. Data for the 1988 breeding season, a season in which resources were limiting, was presented separately elsewhere (Martins and Wright 1993a, b). The data analyses presented here are concerned with investigating the year effect in a combined years data set. Adults were sexed by identifying the females during laying. Due to a high sensitivity to disturbance at this stage, females were marked on the head with hydrogen peroxide using a long brush (Malacarne and Griffa 1987). Parent birds were caught in the nest boxes at the end of each breeding season when they were weighed and given sex-specific colour rings. In both years, when chicks were at the age of five days, brood sizes of one to three were randomly assigned to 15 nests in roughly equal numbers, such that every chick was reared in a nest other than its original nest (Table 1). In 1988, due 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 and Wright 1993b). There were no statistically significant differences between the three groups before the manipulation in either lay-date or hatch-date for either of the two breeding seasons (1988: $F_{2,10}=0.32$, $P=0.73$; $F_{2,10}=0.32$, $P=0.74$; 1989: $F_{2,12}=0.13$, $p=0.88$; $F_{2,12}=0.04$, $P=0.96$ respectively). It should be noted that 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.

Table 1. The brood size manipulation in 1988 and 1989 with number of nests used (n).

	MANIPULATED BROOD SIZE		
	1	2	3
1988			
mean lay-date	21.0	19.6	19.3
mean hatch-date	43.6	42.8	41.3
n	5	5	3
1989			
mean lay-date	20.0	21.0	20.3
mean hatch-date	42.2	42.2	41.8
n	5	4	6

A system of electronic balances (Ohaus Port-O-Gram, model c501, 500g capacity, 0.1g 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.) were used in both years to collect data on parental visits during the nestling period (for detailed methods see, Martins and Wright 1993a). In 1988, adults were weighed each day when feeding chicks on the balance, making it possible to sex the birds on most days on the basis of differences in body mass between the parents. In 1989, at hatching, small magnets were glued to one parent's colour ring and a system of micro-switches (Martins 1992) and magnet-detectors (Hall-plate detector: for specifications see Stevens 1984) were used to record visits to the nest and to sex the visiting parent bird. All chicks were individually weighed every day by hand using the same balance set-up. Analyses concerning mean chick masses and mean mass of the heaviest chick refer to the period after 12 days of age (i.e. after the exponential growth phase and at the mass asymptote; Lack 1956). Using this set-up, parental mass on arrival and departure could be derived from the extra mass of the nest during a visit, and the differences in these corresponded to the

mass of the food bolus brought to the chicks. Faecal sacs were not considered in these calculations since they are usually left in the nest by the adults (Lack and Lack 1952). Using the data in this form, other variables could also be derived, such as time spent in the nest-box, the length of time of each feeding trip (i.e. time of round trip) for each sex and the parental mass gained or lost during these feeding trips.

In order to calculate how much each parent fed itself (in terms of grams of fat when away from the nest, an estimate was needed of the energy spent per hour of foraging flight. Since, 1 BMR costs 1.57 KJ per hour, with active flight estimated at 12 BMRs, this gives a cost of flight in swifts of 18.84 KJ per hour (Dolnik and Kinzhewskaja 1980). Although energy can be obtained from other forms of metabolic products, it is usually accepted that birds primarily use fat (Berger and Hart 1974, Griminger 1986). So, if the amount of metabolizable energy obtainable from a gram of fat is believed to be around 37.7 KJ per gram (Blem 1990), dividing by the cost of flight means that a swift could fly for two hours using one gram of fat, using 1.38×10^{-4} grams of fat per second in active flight.

“Self-feeding” can then be calculated as the total energetic cost of that flight trip plus the adults body mass change for that trip (as in equation 1).

$$S = (T * C * 1.57 / 3600 * E) + W \quad (\text{eq.1})$$

where S is the estimated amount of self-feeding in g;

T is time of a foraging trip in seconds;

C is the cost of flight in BMRs;

E is the energy obtainable from a gram of food in $\text{KJ} \cdot \text{g}^{-1}$; and $1.57/3600$ is the cost of 1 BMR in swifts in $\text{KJ} \cdot \text{sec}^{-1}$. Self-feeding is therefore not the mass of insects in the gut, but the mass of fat assimilated. The rates of assimilation of insects as energy stores and of conversion of fat into energy are not known for swifts, but are assumed in this paper to be the same for every bird. Therefore, costs of assimilating food into energy and vice-versa are not included here. The use of such a method for estimating self-feeding are not of consequence here and are fully discussed elsewhere (Martins 1992, Martins and Wright 1993a).

It is important to emphasise that the random assignment of brood sizes as an experimental design and the form of data collection used here standardises for any effect of weather on foraging conditions between brood sizes within the same year. The effect of weather conditions on the foraging strategies can therefore be assessed by contrasting the two breeding seasons, 1988 and 1989.

For ease of analysis and to avoid pseudo-replication (Hulbert 1984), multiple analysis of variance (MANOVAS) were performed on the averages per

bird or per nest as appropriate. It is important to point out that for all measures of parental effort (per bird) and chick mass (per nest), the within subject variation (i.e. within nests and birds) are not of concern here and therefore averages are an unbiased statistics to use.

MANOVAS were performed using the GLM procedure from the SAS system statistical package (SAS Institute Inc, Cary, NC). 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. MANOVAS were performed on variables for the effect of brood size, year and the interaction between these two factors. Statistical contrasts for each overall step up in brood size, linear and quadratic terms, and also between years for each brood size were performed. In the same model, within year contrasts were also performed on the overall brood size effect and whether this effect was linear or quadratic. For brevity, such contrasts are presented only if they are of particular interest.

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

Results

Weather Conditions

A summary of the weather conditions during the swift nestling periods in 1988 and 1989 is given in Table 2. All analyses were performed on the meteorological data for the period from the first chick hatching until the last fledging day of experimental nests in both years. The nestling rearing period in 1988 was significantly colder, less sunny and more windy than 1989.

The mean maximum temperature for the years of 1947 to 1990 ($n=44$) was calculated for the equivalent period (i.e. when adults swifts should have been providing food to the chicks, in this case estimated as the period between the 7th June and 31st July) is given in Fig. 1. The average maximum temperature for all years (excluding 1988 and 1989) was 20.75 ± 3.70 °C (mean \pm s.d.). The years of 1988 and 1989, shown in the graph, are both within one standard deviation of the mean. These two years therefore represent the two extremes of the distribution of mean maximum temperatures for swift nestling feeding periods in these past 44 years.

Table 2. Summary of the weather conditions during the swift nestling periods in 1988 and 1989. Rainfall, maximum and minimum temperature refer to the period 09:00 - 03:00 GMT. Wind speed and humidity are collected at 09:00 GMT. Sample sizes are 49 and 53 days for 1988 and 1989 respectively.

	1988		1989		t	P
	mean	se	mean	se		
maximum temperature (°C)	19.05	0.36	24.08	0.56	-7.43	<0.001
minimum temperature (°C)	11.19	0.30	13.16	0.37	-4.03	<0.001
rain (mm)	2.07	0.60	0.98	0.38	1.54	0.125
sunshine (hours)	4.70	0.64	8.97	0.61	-4.79	<0.001
humidity (%)	78.61	1.67	69.24	1.66	3.97	<0.001
wind speed (knots)	9.65	0.69	7.96	0.74	2.04	0.044

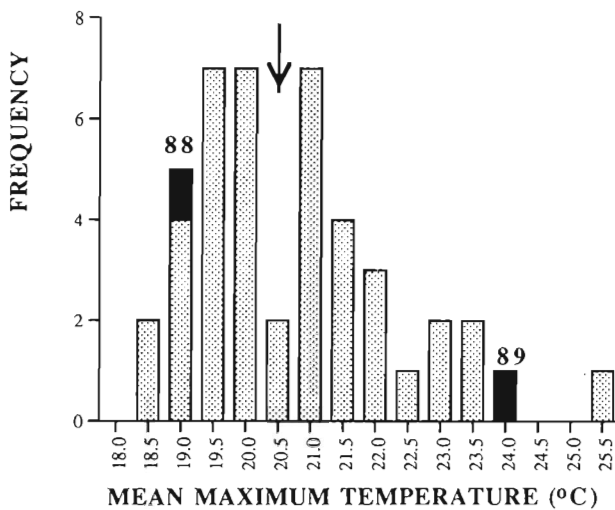


Figure 1. Mean maximum temperature distribution for the months of June and July (when swifts usually have chicks in the nest) for the years from 1947 to 1990 ($n=44$). The position for 1988's and 1989's mean maximum temperature are shown in dark. The arrow points at the average mean maximum temperature for these 44 years (88 and 89 excluded).

Parental Effort

Nests with more young were visited more often by the parents (Fig. 2A: $F_{2,14}=4.69$, $P=0.014$). Overall, the number of visits was the same for the two years ($F_{1,44}=0.08$, $P=0.782$), and the brood size effect was not significantly different between years (interaction term: $F_{2,44}=1.05$, $P=0.357$). When broods of different sizes were contrasted overall, it becomes clear that the brood size effect was the result of a significant increase in visits between brood size 1 and 2 only (contrast 1 vs 2: $F_{1,41}=8.26$, $P=0.006$; contrast 2 vs 3: $F_{1,14}=0.19$, $P=0.667$; linear contrast term $F_{1,41}=4.88$, $P=0.032$). The increase in number of visits within

1988 was significant (contrast brood size within 88: $F_{1,44}=4.66$, $P=0.014$) and although it was not quadratic in form it approached significance (linear contrast for 88: $F_{1,41}=3.68$, $P=0.061$; quadratic contrast for 88: $F_{1,44}=3.60$, $P=0.064$). For 1989, there was no effect of brood size on the number of visits (contrast brood size within 89: $F_{1,44}=0.79$, $P=0.458$).

Overall, mean load mass increased linearly with brood size (Fig. 2B: $F_{2,32}=4.24$, $P=0.021$; contrast 1 vs 2: $F_{1,32}=0.07$, $P=0.791$; contrast 2 vs 3: $F_{1,42}=6.05$, $P=0.018$; linear contrast term: $F_{1,42}=7.14$, $p=0.011$) and loads were generally larger in 1989, but the year effect only approached significance ($F_{1,42}=3.69$, $P=0.061$). The interaction term indicates that the increase in the load size in response to an increase in brood size was not significantly different between years ($F_{2,42}=0.007$, $P=0.930$). Within years, the increase in the load mass was not significant in 1988 and it approached significance in 1989 (contrast brood size within 88: $F_{2,42}=1.82$, $P=0.174$; contrast brood size within 89: $F_{2,42}=3.01$, $P=0.060$). However, only for 1989 the linear contrast was significant (linear contrast within 89: $F_{1,42}=5.30$, $P=0.026$).

Food delivery rate also increased significantly with brood size (Fig. 2C: $F_{2,42}=7.67$, $P=0.001$; linear contrast term $F_{1,42}=14.61$, $P<0.001$). Although there was a consistent trend for greater food delivery rates in 1989, this was not statistically significant when years were compared ($F_{1,42}=2.47$, $P=0.124$), and the interaction between brood size and year was not significant ($F_{2,42}=3.73$, $P=0.691$). Within years, there was also an increase in the food delivery rate with brood size (contrast brood size within 88: $F_{2,42}=4.30$, $P=0.020$; contrast brood size within 89: $F_{2,42}=3.73$, $P=0.032$), which was linear in both years (linear contrast for 88: $F_{1,42}=7.71$, $P=0.008$; linear contrast for 89: $F_{1,42}=7.45$, $P=0.009$).

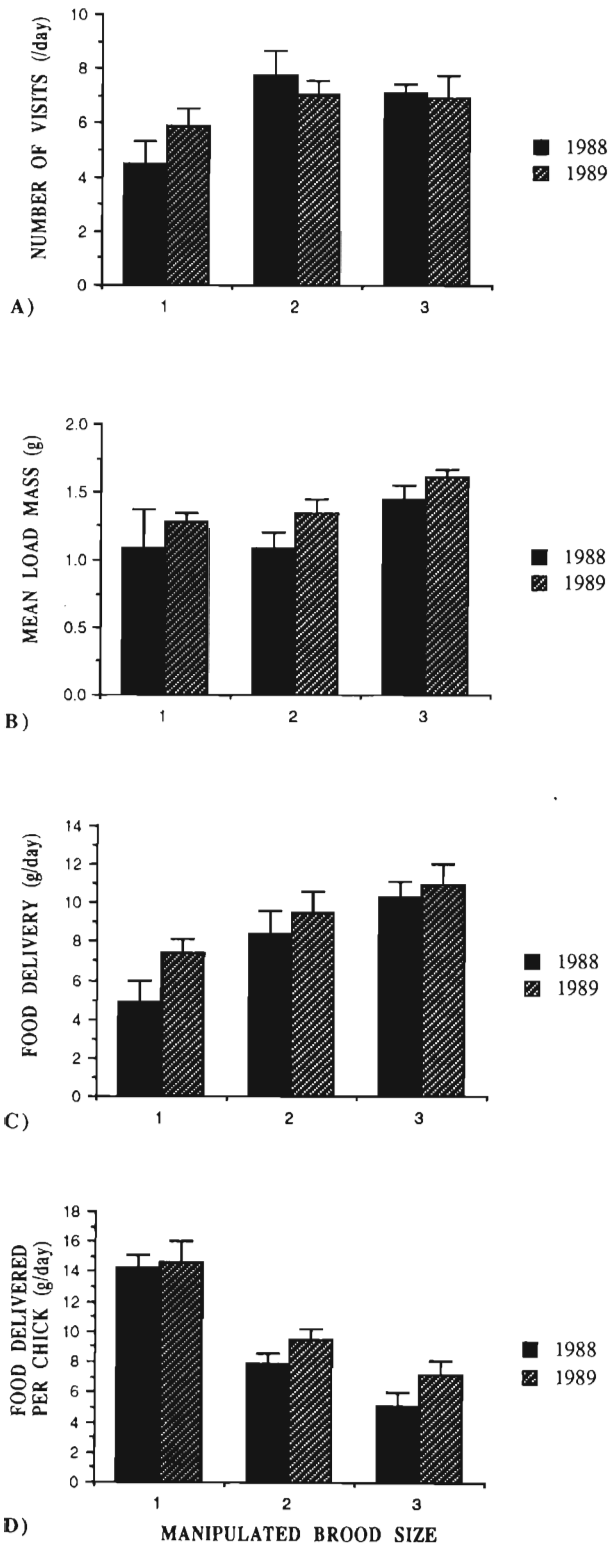


Figure 2. The effect of manipulated brood size on mean parental effort in both years (+SE) in terms of: A) number of visits per day; B) load mass delivered; C) food delivered per day per bird; and D) food delivery per chick per day.

Food delivery per chick ($\text{g} \cdot \text{day}^{-1}$) decreased significantly with brood size (Fig.2D: $F_{2,22}=37.01$, $P<0.001$; linear contrast term: $F_{1,22}=68.50$, $P<0.001$). Although there was a tendency for food delivery per chick to be higher in 1989, this difference is not statistically significant ($F_{1,22}=2.77$, $P=0.110$). Also, the interaction term indicates that the response to brood size was not significantly different between years ($F_{2,22}=0.46$, $P=0.638$). The decrease in the food delivery per chick was significant and linear in both years (contrast brood size within 88: $F_{2,22}=20.73$, $P<0.001$; contrast brood size within 89: $F_{2,22}=16.96$, $P<0.001$; linear contrast for 88: $F_{1,22}=35.73$, $P<0.001$; linear contrast for 89: $F_{1,22}=33.15$, $P<0.001$).

Chick mass

Mean chick mass decreased with manipulated brood size (Fig. 3A: $F_{2,22}=12.83$, $P<0.001$; linear contrast term: $F_{1,22}=24.89$, $P<0.001$), and tended to be higher in 1989 than in 1988, with this difference closely approaching significance ($F_{1,22}=4.21$, $P=0.052$). Although mean chick mass tended to decrease with brood size in 1988 and not in 1989, the interaction term was not significant (interaction term: $F_{2,22}=2.65$, $P=0.093$). However, when years are contrasted within

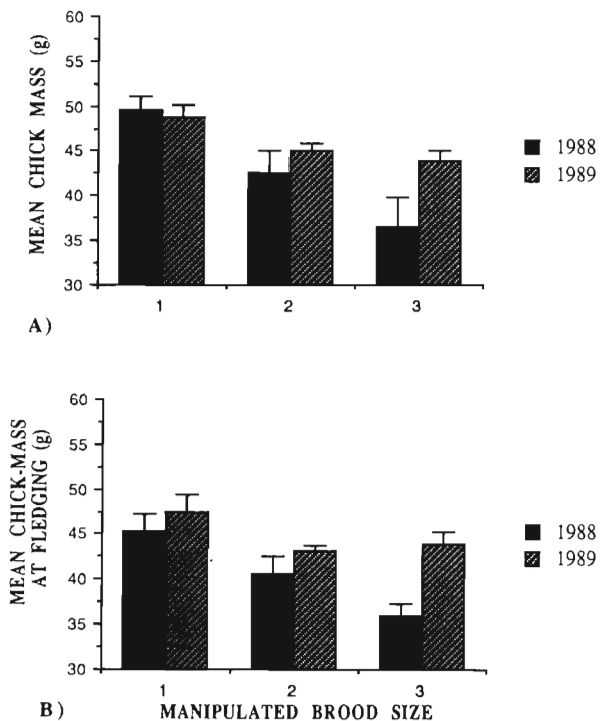


Figure 3. The effect of manipulated brood size in both years (+SE) on: A) mean chick mass; B) mean fledging mass.

brood sizes, mean chick mass was significantly higher in 1989 than in 1988 for broods of three, but not for brood size 1 and 2 (contrast year within brood size 1: $F_{1,22}=0.11$, $P=0.738$; contrast year within brood size 2: $F_{1,22}=0.88$; $P=0.357$; contrast year within brood size 3: $F_{1,22}=7.73$, $P=0.011$). Within years, the brood size effect was present for 1988 only (contrast brood size within 88: $F_{2,22}=11.65$, $P<0.001$; contrast brood size within 89: $F_{2,22}=2.35$, $P=0.119$).

Fledglings

Mean fledging mass decreased with manipulated brood size (Fig. 3B: $F_{2,22}=6.80$, $P=0.005$; linear contrast term: $F_{1,22}=13.05$, $P<0.001$), and mean fledging mass was higher in 1989 than in 1988 ($F_{1,22}=7.98$, $P=0.010$). The interaction term was not significant, showing that the effect of brood size was similar in both years ($F_{2,22}=1.54$, $P=0.237$). However, 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: $F_{1,22}=8.63$, $P=0.007$). Within years the brood size effect was present and linear for 1988 only (contrast brood size within 88: $F_{2,22}=5.71$, $P=0.010$; linear contrast for 88 only: $F_{1,22}=11.13$, $P=0.003$; contrast brood size within 89: $F_{2,22}=1.77$, $P=1.193$).

Food allocation between parent and young on a visit by visit basis

As can be seen from Figure 4 the trend found in 1988 for parents to allocate less to themselves with an increase in brood size (Martins and Wright 1993a) was also present to a lesser extent in 1989. However, mean self-feeding in 1989 was not significantly different for broods of different sizes ($F_{2,17}=0.42$, $P=0.666$). When years were combined, no brood size effect was found on the mean self-feeding (Fig. 4: $F_{2,32}=1.48$, $P=0.243$), and there was no significant effect of year ($F_{1,32}=1.10$, $P=0.302$) and no significant interaction effect between the two ($F_{1,32}=0.15$, $P=0.865$). In fact there was a tendency for a linear decrease in self-feeding for years combined, but this trend also not significant (linear contrast term: $F_{1,32}=2.95$, $P=0.096$). Within years, the effect of brood size was also non-significant (contrast brood size within 88: $F_{2,32}=0.90$, $P=0.418$; contrast brood size within 89: $F_{2,32}=0.62$, $P=0.542$).

In 1989, the negative relationship between mean self feeding and mean load mass was significant (Fig. 5: $r=-0.088$, $P=0.168$), suggesting that in that year birds did not consistently trade-off the food delivered with their own feeding. This result

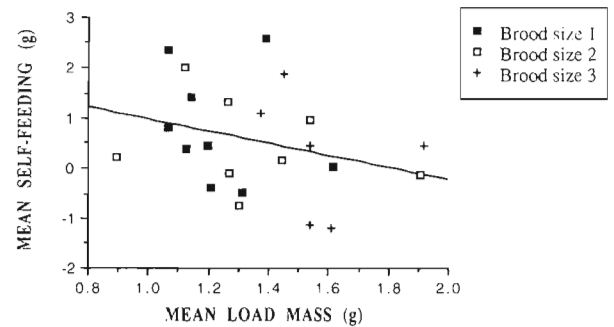


Figure 4. The effect of manipulated brood size on mean self-feeding by parents (+SE) in 1988 and 1989.

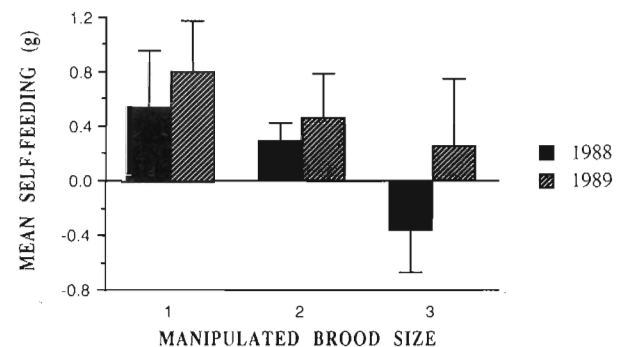


Figure 5. The relationship between mean load mass delivered and mean self-feeding over the whole nestling period in 1989, with the three manipulated brood sizes. Points are means per bird.

also holds when the data are analysed within birds. Regressions of load mass on self-feeding were performed for each bird separately, and a MANOVA was performed on the slopes from the regression equations. The constant term was not significant ($F_{1,15}=0.37$, $P=0.552$) showing that the slopes were not different from zero, i.e. that there was no overall relationship between load mass and self-feeding and that there was no effect of brood size ($F_{2,15}=0.28$, $P=0.759$).

Mean total amount of food collected also did not differ significantly for the three different brood sizes ($F_{2,33}=0.02$, $P=0.980$). Also, although there was an increase in the total amount of food collected between years this difference was not statistically significant ($F_{1,33}=1.76$, $P=0.193$). Within years, total amount of food collected was also non-significant for different brood sizes (contrast brood size within 88: $F_{1,33}=0.02$, $P=0.981$; contrast brood size within 89: $F_{1,33}=0.14$, $P=0.868$).

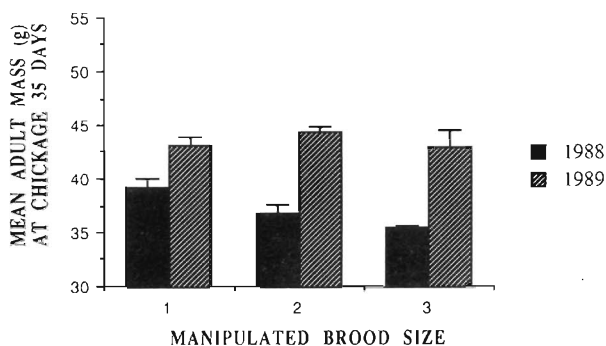


Figure 6. The effect of manipulated brood size on mean adult mass (+SE) in 1988 and 1989.

Adult body mass

Mean adult body mass at the end of chick feeding was also not significantly different for manipulated brood sizes (Fig. 6: $F_{2,38}=1.47$, $P=0.244$), but parents in 1989 were significantly heavier than parents in 1988 ($F_{1,38}=48.9$, $P<0.001$). Although the interaction was not significant ($F_{2,38}=2.07$, $P=0.140$), contrasts between years for each brood size were significant (contrast year within brood size 1: $F_{1,38}=8.19$, $P=0.007$; contrast year within brood size 2: $F_{1,38}=23.92$, $P<0.001$; contrast year within brood size 3: $F_{1,38}=18.15$, $P<0.001$) showing that within each one of the brood sizes parent birds weighed more in 1989 than in 1988. Therefore, an increase in the parental effort resulted in decreased body mass in only one of the breeding seasons.

There was no brood size effect in parental body mass at fledging when years were combined ($F_{2,31}=0.66$, $P=0.525$), or a year or an interaction effect ($F_{1,31}=0.54$, $P=0.467$; interaction term: $F_{2,31}=0.69$, $P=0.51$). Within years the effect of brood size on adult body mass at fledging was also non-significant (contrast brood size within 88: $F_{2,31}=1.81$, $P=0.180$; contrast brood size within 89: $F_{2,31}=0.03$, $P=0.969$). Therefore, at the end of each season, parent swifts of both sexes weighed the same as each other whatever brood size they raised.

Discussion

Parental effort and brood size

Over the two years, the brood size manipulation created greater food delivery per day in nests with more young. In 1989, when conditions were better in terms of swift feeding, increases in the food delivery rates to larger brood sizes were mostly due to

increases in the load size delivered between broods of 2 and 3. This result differs from 1988 (Martins and Wright 1993a), in which a similar increase in food delivery with brood sizes was mostly due to an increase in number of visits between broods of 1 and 2. It is interesting that the same expected linear increase in food delivery rates with brood size (Bryant and Gardiner 1979, Winkler 1987, Montgomerie and Weatherhead 1988; see reviews in Klomp 1970, Nur 1984a, 1988) occurred in both years, but was achieved in alternative ways as a result of different combinations of increases in the number of visits and in the load mass. This suggests that according to resource conditions, differential parental foraging strategies may exist with regards to how the step-up in feeding effort is achieved in response to increases in brood size, and also that the resulting level of sustained effort seems to be determined by conditions. However, in both years, overall increases in food delivery to the largest brood size seems to have been achieved mainly by increasing the size of the loads delivered (see also analyses in Martins and Wright 1993a). This strategy of returning to the nest only when a large load has been gathered, suggests that parent swifts raising larger broods could be conserving energy by reducing the number of trips and so reducing travel costs. Raising larger broods, even under good conditions, might still be energetically demanding. Further evidence that this might be true comes from the trade-off between load mass and prey quality for boluses delivered to the larger brood sizes in 1989 (Martins 1992, Martins and Wright in prep.).

Although aerial insect prey must have been more abundant in 1989, food delivery rates were still not proportional to the number of chicks in the nest, and delivery rates per chick decreased with brood size. This is the expected pattern seen in many studies (Sibly and Calow 1983, Nur 1984a, b, 1988; Wright and Cuthill, 1990a, b), which reflects parental investment trade-off decision between parental care and future survival to future reproductive attempts.

Chick mass

In 1989, chicks in broods of three were not only as heavy as chicks from other brood sizes during the nestling period, but they also fledged at a similar body mass. Higher fledging masses in that year might have been expected to increase subsequent survival chances and future recruitment rates (Virolainen 1984, Alatalo and Lundberg 1989). This result differs from 1988, when broods of three, might be expected to have had reduced survival chances due to lower fledging mass (Martins 1992, Martins and Wright 1993a). There

fore, parents raising broods of three in 1989 probably produced more recruits into the future breeding population than parents raising one or two chicks (although note that due to the manipulation these chicks were not related to them genetically). The reverse was probably true for broods of three in 1988. Therefore, in years with good feeding conditions, such as in 1989, raising maximum brood-sizes (i.e. three chicks) could enhance a parent's life-time reproductive success, particularly if it did not decrease the parent's chances of future survival. Whilst in poor years, such as 1988, the best strategy may be to raise only two chicks, brood reduction happening then as an adaptive response to conditions (see Martins and Wright 1993b).

Adult body mass and the allocation of food

In 1989, adult swifts raising larger brood sizes did not lose body mass. As a result, they probably did not suffer any increased risk of predation from their higher levels of parental effort as might have occurred in 1988 (Martins and Wright 1993a, b). Therefore, the patterns of parental body mass loss presented here suggest that the costs, from the possible increase in the risk of predation as parental care levels increase, are more likely to happen in years with poor feeding conditions (Martins and Wright 1993a, 1993b).

The patterns of adult body mass loss seem to be due to the differential allocation strategies used by parent birds during the course of the two different nestlings season. Under good resource conditions, the trade-off in food allocation between parent swifts and their young was not as sensitive to the value of the brood as it was under poor conditions. In 1988, the effect of brood size was evident in the way that parent swifts feeding larger broods did so at the expense of their own feeding. The subsequent low parental body mass resulted in periods of exclusive self-feeding in the nestling period and in extreme cases this led to brood reduction (Martin and Wright 1993a, b). Current models of food allocation between parent and young (Kacelnik 1984, Kacelnick 1988, Kacelnick and Cuthill 1990) predict that under very controlled resource conditions optimal allocation is dependent on both the value of the brood and on the rate at which food was being artificially delivered. In the case of abundant food resources, such as in 1989, variables such as the state of parents and young might become more important in predicting the optimal allocation decision. One possible scenario in the situation of food abundance is that parents would adjust their intake to balance their expenditure, whilst delivering the excess to the young. We have shown here that

under good conditions the value of the brood is not a good predictor of the way parent swifts allocate their food and that in such years parents did not seem to incur major costs in raising larger brood sizes.

The lack of a consistent trade-off between self-feeding and load in 1989 is also interesting when considering that there was no brood size effect in the total amount of food collected by parent birds in that year. It seems that in 1989, although total food collected per foraging bout was also limited, this may not have been due to conditions but some other constraint such as the size of throat pouch or transport costs (Cuthill and Kacelnik 1990).

Parental strategies and associated costs in coping with larger brood demands

Work done on food allocation in parent swifts has so far shown that delivering larger loads seems to be the first strategy used by parent swifts to increase delivery to larger brood sizes and that this is probably due to the lower energetic costs associated with this strategy (Martins and Wright 1993a). This strategy was also evident in the trade-off between the size and the quality of loads delivered, even during the good feeding conditions in 1989 (Martins 1992, Martins and Wright in prep.) When conditions deteriorate, differential allocation between parent and young probably becomes necessary and/or more pronounced, thus resulting in loss of parental body mass. However, if conditions remain poor for longer, and if parents have reached a certain "threshold" in body mass then parents swifts might tend to allocate to themselves mainly and eventually even stop chick feeding, which may or may not, result in brood reduction, depending on the duration of the bad spell (Martins 1992, Martins and Wright 1993a, b).

In 1989, parent swifts showed no resulting decrease in their own chances of survival to breed in the future and no apparent increase in the short-term risk of predation, as in 1988 (Martins and Wright 1993a). So, it seems that foraging conditions appear to determine how big a cost there is to raising a brood of three chicks. It has been also found for other species that fledging success (Virolainen 1984, Alatalo and Lundberg 1989) and/or parental survival (see Högstedt 1981, Murphy and Haukioja 1986) may be also improved in more favourable conditions.

It is possible that a relaxation in the selective disadvantage of rearing a larger brood makes the cost of reproduction less important with respect to the evolution of clutch size. However, years like 1989 are not very common. It is therefore expected that reproductive years such as 1988 would constrain the

system by discriminating against overly large brood sizes. However, it is the feeding strategies used by parents to cope with changes in food conditions that limit the amount of food that can be brought to the chicks. In 1988, the need to increase the amount of food delivered was accomplished by trading-off the amount of food that parent were allocating to themselves on a visit-by-visit basis. In 1989, this trade-off between load and self-feeding was relaxed. So, are parent swifts limited by the amount of food that they can gather for the chicks (Lack 1947, 1968), because they are ultimately limited by how far they can trade-off their own feeding with the load they bring to the chicks on a visit-by-visit basis? Data on food allocation in swift so far seem to suggest that this short-term behavioural decision, in terms of allocation in future and presente reproductive attempts, seems to determine the amount of parental effort expended on a single reproductive attempt thus restricting the number of chicks that can be raised. However, this trade-off is relaxed when resources are abundant permitting larger brood sizes to be raised without major costs.

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Resumo - Manipulações do tamanho de ninhada foram realizadas para promover diferentes níveis de esforço parental Andorinhão Preto (*Apus apus*). Nos dois anos nos quais esta manipulação foi realizada condições climáticas diferiram grandemente. Os dados foram analisados a cada evento de forrageamento em relação à mudanças na massa corporal do adulto visitante e dos filhotes, na massa da bolota de alimento trazida para os filhotes e na massa estimada da quantidade de alimento ingerida pelo mesmo adulto visitante (i.e. "self-feeding"). Tal análise possibilitou o teste de hipótese sobre decisões de investimento parental relativas à estratégias de alocamento ótimo entre pais e filhotes e como estas podem ser influenciadas por diferenças em recursos alimentares. Durante o ano de boas condições climáticas (quente e ensolarado), os adultos não precisaram reduzir a quantidade de alimento coletada para si mesmos para aumentar a quantidade de alimento trazida para as ninhadas maiores como demonstrado anteriormente para anos de condições climáticas ruins (frio e chuvoso). Adultos com ninhadas maiores também não sofreram nenhuma redução de massa resultantes do aumento no esforço parental expandido e aparentemente não sofreram nenhum custo em manterem ninhadas maiores. Além disso, boas condições climáticas possibilitaram que a massa dos filhotes ao deixarem ninhos em maiores ninhadas fosse similar à daquelas provenientes de menores ninhadas sugerindo a não redução nas chances de sobrevivência de filhotes saídos de ninhadas maiores. As respostas diferenciais de alocamento de alimento demonstradas nos dois anos são discutidas em termos de estratégias parentais usadas para alimentar ninhadas maiores.

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