Increase of parental effort in experimentally enlarged broods of Pallid Swifts

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Abstract: Variation in parental effort of Pallid Swifts (*Apus pallidus*) was investigated for 3 years in a colony in northwestern Italy. The masses of adults and of bolus loads brought to chicks were monitored by electronic balances inserted under nests, and feeding rates were monitored by video cameras. Fluctuations in daily food availability were measured with an insect-suction trap. Manipulation experiments on broods originally consisting of three chicks were performed to increase (four chicks) or reduce (two chicks) adult effort, with the aim of determining if parents tend to allocate food primarily to themselves or to their offspring, and if mass loss in adults results from reproductive stress or from adaptive programmed anorexia. With the enlargement of brood size, mean bolus mass remained constant, but the visitation rate increased significantly. Daily food abundance did not influence the amount of food allocated to chicks (neither time spent foraging nor the bolus mass changed), but positively influenced the mass of adults, which showed large daily variations. These results indicate that parents tend to invest constantly in offspring, at their own expense when food is scarce. Our data lend support to the cost of reproduction hypothesis instead of adaptive anorexia, since adults lose mass mainly in the brooding period, when demand is highest, and always regain mass when prey availability is greater.

Résumé : Les variations de la contribution des parents à l'élevage ont été étudiées pendant 3 ans chez le Martinet pâle (*Apus pallidus*) au sein d'une colonie du nord-ouest de l'Italie. La masse des adultes et celle des boules d'insectes rapportés aux oisillons ont été mesurées au moyen de balances électroniques installées sous les nids et les taux d'alimentation ont été estimés par des caméras vidéo. Les fluctuations dans la disponibilité quotidienne de nourriture ont été évaluées au moyen d'un piège à insectes à succion. Des manipulations expérimentales des couvées de trois oisillons ont été entreprises pour augmenter (quatre oisillons) ou diminuer (deux oisillons) la contribution des parents de façon à pouvoir déterminer si les parents répartissent leur nourriture de façon à favoriser leurs oisillons ou à se favoriser eux-mêmes, et si la perte de masse enregistrée chez les adultes résulte du stress relié à la reproduction ou d'une anorexie évolutive déterminée par la sélection. Après augmentation du nombre d'oisillons, la masse moyenne des boules d'insectes reste la même, mais la fréquence des visites augmente significativement. L'abondance quotidienne de la nourriture n'influence pas la quantité de nourriture allouée aux oisillons (ni le temps consacré à la quête de nourriture, ni la quantité de boules d'insectes ne changent), mais influence la masse des adultes qui subit d'importantes variations quotidiennes. Ces résultats indiquent que les parents investissent continuellement dans l'élevage de leur progéniture, à leurs propres dépens quand la nourriture est rare. Nos données supportent l'hypothèse du stress relié à la reproduction plutôt que celle de l'anorexie évolutive, puisque les adultes subissent des partes de masse surtout au cours de la période d'élevage, alors que la demande est maximale, et reprennent la masse perdue lorsque la disponibilité des proies est plus grande.
[Traduit par la Rédaction]

Introduction

The most influential developments in life-history theory suggest that efforts devoted to present reproduction may reduce future survival and fecundity (Williams 1966). According to almost all applications of optimization theory, this trade-off can be measured in terms of costs and benefits. Attempts to determine the costs of reproduction range from assessment of mortality in populations of marked individuals (Newton 1989; Clutton-Brock 1988) to physiological measures of

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energy expenditure, as by the doubly labelled water technique (Bryant 1989). Changes in body mass may be reliable indicators of costs incurred during reproduction (Nur 1984). In vertebrate homeotherms, body mass loss is frequently utilized as an indicator of depletion of reserves during incubation, lactation, or feeding of the young. However, an adaptive hypothesis of mass loss in birds has been proposed (Freed 1981; Norberg 1981); birds should lose mass, by means of programmed anorexia before the peak of chick-rearing demands, in order to be lighter and improve the efficiency of their feeding flights.

As Williams's (1966) theory of optimum reproduction states, parents should allocate energy between themselves and their offspring to maximize lifetime reproduction. Thus, short-term decisions concerning food delivery during repro-

duction should influence long-term prospects of survival and fecundity of both parents and progeny. The decision to diminish or to increase parental effort in difficult circumstances should depend proximately on critical physiological conditions, and a threshold of resource exhaustion is conceivable (Calow 1979).

It is now widely accepted (Partridge 1989) that only experiments using brood manipulation can thoroughly expose some of the cost of reproduction. In fact, confounding variables can obscure data from a correlational approach; for example, a positive relationship between reproductive performance and survival of adults has been proved (Hogstedt 1981; Ricklefs and Hussell 1984), and this relation would reflect intrinsic variation in individual quality (Pettifor et al. 1989). Concerning food availability, many theoretical models have tried to simulate the optimal parental effort in a resource-fluctuating environment (Gillespie 1977; Kacelnik 1988); on the other hand, ornithological research has clearly revealed a relationship between natural or experimental fluctuations in food availability and variations in breeding parameters such as laying date and clutch size (Daan et al. 1989; Martin 1987).

Aerial-feeding birds (e.g., swifts and swallows) are ideal species in which to monitor variations in parental effort, since during their continuous flights they incur high energy costs and lose mass unusually quickly if they do not feed, as has been detected by electronic balances placed under the nest (Jones 1987a, 1987b; Martins and Wright 1993a, 1993b). Moreover, even if food availability (aerial arthropods) is difficult to manipulate, daily food abundance is relatively easy to quantify by means of net or suction-trap captures (Quinney and Ankney 1985; Bryant 1975; Jones 1987b). For example, Tree Swallows, *Tachycineta bicolor*, and House Martins, *Delichon urbica*, responded rapidly to short-term food increments, laying earlier in the season and increasing the clutch size (Bryant 1979; Hussel and Quinney 1987). In Barn Swallows, *Hirundo rustica*, the mass of both adults and chicks fluctuated daily according to food availability, since parents delivered more food to the brood, and were heavier themselves, when prey was more abundant. Furthermore, sexual differences were detected: when food was scarce, males invested relatively more in self-maintenance and less in the offspring than did females (Jones 1987b).

In this paper, we analyze food allocation between parents and young in normal and experimentally enlarged broods of Pallid Swifts, *Apus pallidus* (Shelley). The masses of bolus loads and variations in mass of the parents were monitored on a visit-by-visit basis using electronic balances under the nests, and daily food availability was assessed by an insect-suction trap. The objectives of the study were (i) to describe short-term variations of parental reproductive effort to reveal whether parents tend to allocate food primarily to themselves or to the chicks, or if food is shared equally; (ii) to determine if the decision is faced in the short term (evident daily variations) or in the longer term (variation over the whole reproductive period); and (iii) to test the prediction of programmed loss of mass against reproductive costs.

Methods

The research was conducted in northwestern Italy during the breeding season, from April to August, in 1990 – 1992. The colony (17 – 19 pairs) is located on the exterior walls of an old building in the town of Carmagnola (240 m asl), about 30 km south of Torino. The area is characterized by a temperate continental climate (Cucco et al. 1992). The nest cavities were easily reached and inspected from inside the building, through an interior wall that was modified for observation.

Clutch and brood sizes

Clutch and brood sizes were ascertained by daily inspections of the nest cavities. Chicks showing regular growth and leaving the nest 40 – 45 days after hatching were considered successfully fledged. All young and nearly all the adults were marked with metal rings from the Italian Ringing Scheme. The daily identification of all individuals nesting in the different cavities was made possible by marking their backs with a small spot created by applying a decolourizing paste with a small brush during the laying period (Malacarne and Griffa 1987). The technique did not appear to affect the natural behaviour of the birds in comparison with that observed in nonmarked individuals in 1987 – 1988.

Behaviour

The behaviour and identity of parents at the nest was monitored by video cameras (Panasonic F10 CCD and Blaupunkt CR 2000S) connected to video recorders. The nests (12 per year) were numbered and the filming procedure was followed a rotation schedule; typically each nest was monitored for 1 day every 4 or 5 days throughout the whole nestling period (40 – 45 days). To avoid disturbance, the video cameras were placed behind the nest, whose rear plywood wall had a rectangular glass window usually covered by a black cloth; once the glass window was removed, the camera lens was placed inside the nest cavity through an opening in the cloth. Moreover, every nest contained a small light bulb (12 V, 1 W) whose intensity was regulated by an adjustable rheostat (Malacarne et al. 1992). Sex was determined by examining the video tapes recorded during laying and identifying which of the two marked parents laid the eggs. The routine methodology provided 8 daily recording-hours (from 07.30 to 15.30) for each recorded nest; subsequently all events (feeding, entering and exiting the cavity) were identified on the video tapes.

At the end of the breeding season, nesting adults were captured and ringed at night. To avoid disturbance and the possibility of nest abandonment, adults were captured when their nestlings were aged 40 days, near the fledging date.

Mass

The mass of each bird was measured when it reached the nest to incubate the eggs (14 pairs) or to feed the young (36 pairs). The cavities had false floors so that electronic balances (AD Salter KE1200A, 0.1 g accuracy, 1200 g capacity) could be placed underneath. Two IBM personal computers were used to read automatically up to four different balances (same rotation schedule as for video cameras) via the RS232 interface. The computers scanned the balances 6 times every second, and recorded data only when there was a change of more than 0.5 g from the previously recorded nest mass. The recorded mass values were later plotted and measured by means of custom-written software.

Bolus mass was calculated by measuring the increase in mass of the chicks – nest – floor complex after parental visits. The nestlings typically defecated in the nest cavity, hence the false floor was provided with 4-cm raised edges to prevent any accidental reduction of the measured mass caused by expulsion of faeces.

Food resources

Food resources available to the breeding swifts were quantified daily by collecting aerial arthropods in a suction trap (a 12.2 m high tower) located 2 km from the colony in the surrounding farmland. The trapped insects were dried for 2 h and their volume was measured to the nearest 0.1 cm^3 by immersion in a graduated cylinder. Because the percentages of different types of arthropods caught by *A. pallidus* and the suction trap typically differed (more Diptera were caught in the trap; Cucco et al. 1993), the measured volume is considered merely an index of aerial insect abundance, useful for comparisons among days. Captures in the suction traps have been shown to be similar up to a distance of 80 km (Taylor 1973), a range probably rarely exceeded by foraging swifts during the breeding period.

Manipulation

Apus pallidus females usually lay two or three eggs, and clutches of one or four are uncommon (Cucco et al. 1992). We considered eight unmanipulated clutches of two and six clutches of three eggs in order to monitor mass variations in incubating adults. During the nestling period, six increased broods of four chicks (created by adding one 2- to 4-day-old nestling to broods of three young of similar age) and six reduced broods of two (created by removing one nestling from broods of three young) were experimentally formed. On the whole, in the nestling period we considered 2 natural broods of one, 16 (10 natural and 6 experimental) broods of two, 12 natural broods of three, and 6 experimental broods of four young.

In preliminary analyses, none of the parameters considered differed between reduced and natural broods of two, therefore these broods were combined and in the present study will be presented together.

Self-feeding

To calculate the allocation of food (measured in grams of fat) eaten by the parents when away from the nest, we needed an estimate of the energy spent per hour of foraging flight. Following Lyuleeva (1970) and Hails (1979) we assumed that 1 basal metabolic rate (1 BMR) costs 1.22 kJ · h^{-1}, with active flight estimated at 5.4 BMR, so the cost of flight in swifts is 6.6 kJ · h^{-1}. Since the amount of metabolizable energy obtainable from 1 g of fat is approximately 37.7 kJ (Blem 1990), 0.175 g of fat is required for 1 h of flight.

From the relation

$$\text{mass variation} = \text{self-feeding} - \text{flight cost}$$

self-feeding (the amount of food that the parents allocated to themselves) can be calculated as the total energy cost of a flight (in grams) plus the change in adult body mass for the trip. Martins and Wright (1993a) fully discuss some sources of bias when estimating flight costs, such as differences in

adult body mass, assimilation of insects, and metabolic conversion of food, measured as fat, into energy.

Statistics

The analyses presented in the Results were also performed separately for each sex and year to estimate the effect of these two factors on the parameters considered. However, we did not find (Cucco 1992) any difference between females and males, or between the 3 years of study; thus, for brevity, these preliminary analytical statistics are not presented here.

The data were analyzed using the SYSTAT package (Wilkinson 1985). All means are presented ± standard deviation.

Results

Feeding frequency, bolus load mass, and brood size

The visitation rate (Fig. 1a) was significantly different in relation to brood size ($F_{[3,32]}$ = 25.7, P < 0.01). The number of visits increased significantly with increasing brood size, the higher values being reached by adults rearing the experimental broods of 4 chicks.

The bolus mass was, on average, 1.35 g (±0.44, N = 895). Mean bolus mass (Fig. 1b) did not differ significantly between brood sizes ($F_{[3,31]}$ = 0.755, P = 0.53).

Food delivery per brood (Fig. 1c) differed between brood sizes ($F_{[3,28]}$ = 11.4, P < 0.01), with a significant increase in relation to the number of chicks, although the difference between brood sizes of three and four was not significant (contrast term $F_{[1,28]}$ = 2.71, P = 0.11). The overall increase in food delivery appears to have been the result of an increase in visiting rate, with little variation in bolus size.

Food delivery per chick (Fig. 1d) also varied between brood sizes ($F_{[3,28]}$ = 3.44, P < 0.04); in spite of the increased effort of the parents, there was a significant decrease in food per chick with increasing brood size.

Foraging time and food abundance

The time spent foraging outside the nest (Fig. 2) was not significantly related to insect abundance (Table 1). When the effect of brood size was removed, mean bolus mass also did not differ (Table 1) in relation to food abundance (Fig. 3).

The foraging trips usually lasted from 30 min to 2 h; parents rarely foraged for less than 30 or more than 120 min on one trip (10.9% of cases, N = 274). Bolus mass increased with time spent foraging (Table 1), but not proportionally: a doubling of the time caused only an increase of about 20% in bolus mass (Fig. 4).

Daily mass variation in adults

The adults showed a high fluctuation in mass, which sometimes varied more than 2 g (5% of adult mass) in a single day. The mass variations were related to daily insect abundance (Fig. 5). In the incubation (Fig. 5a) and brooding (Fig. 5b) periods (end of May – June), the available insects never exceeded intermediate values (about 3 cm^3 · day^{-1}), and in both periods the relation between the two variables was linear (incubation: y = −1.409 + 0.747x, r_{50} = 0.48, P < 0.01; brooding: y = −1.064 + 0.696x, r_{51} = 0.579, P < 0.01). In the nestling period (end of June – July), an increase in mass when insect abundance was high again occurred (Fig. 5c), but did not exceed a threshold value of

Fig. 1. The effect of manipulated brood size on mean parental effort in terms of number of visits per hour (a), bolus mass delivered (b), amount of food delivered per hour to each brood (c) and amount of food delivered per hour to each nestling (d). Vertical lines denote ±SD.
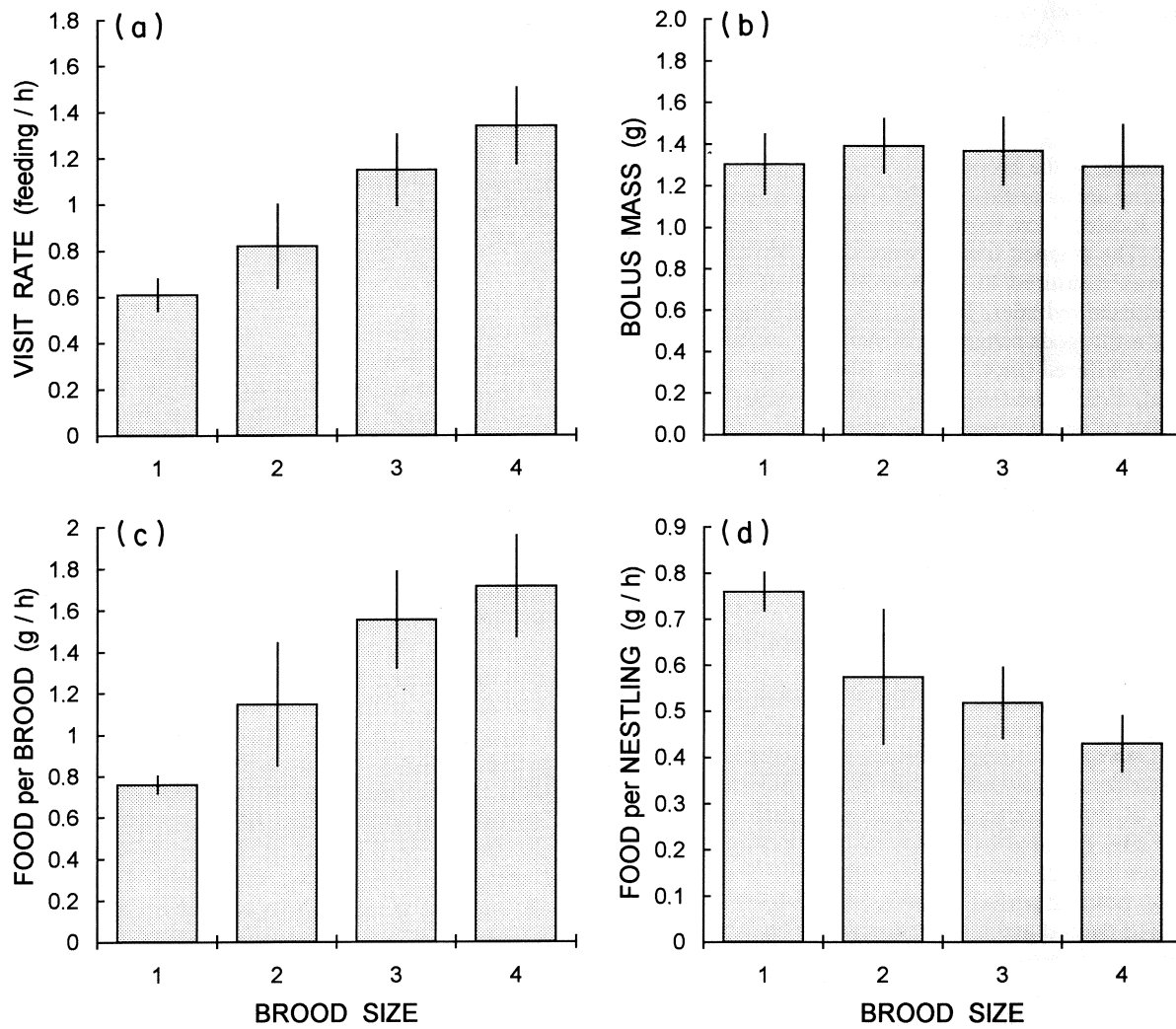

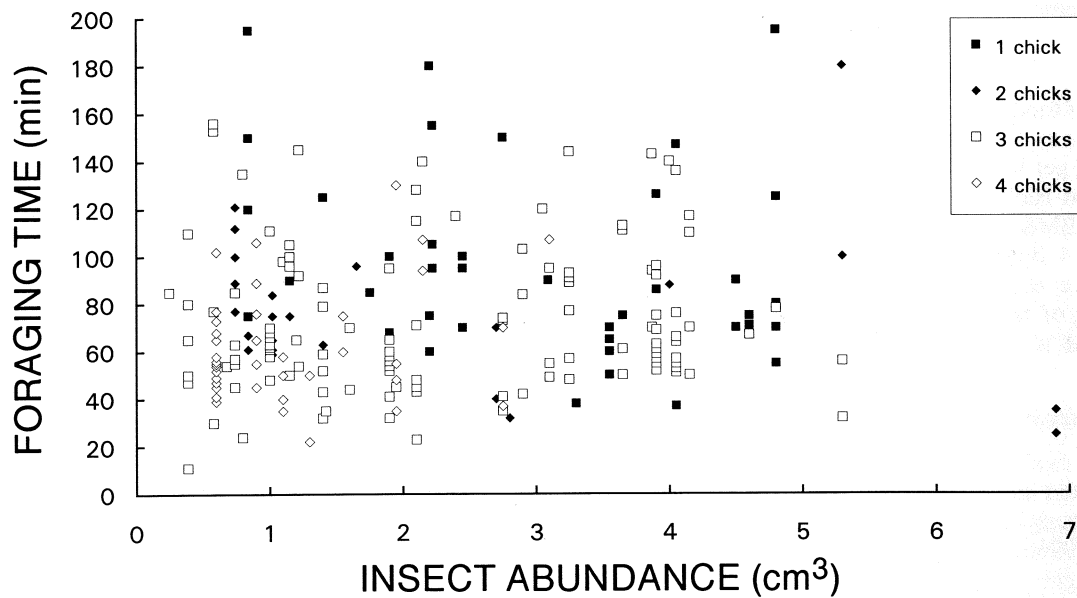**Fig. 2.** Relationship between insect abundance and time spent foraging outside the nest.

Table 1. The effect of insect abundance and brood size on time spent foraging and bolus mass.

Dependent variable	Independent variable	df	F ratio	P	Significance
Foraging time	Insect abundance	1	0.026	0.872	ns
	Brood size	3	4.461	0.005**	
Bolus mass	Insect abundance	1	1.730	0.189	ns
	Brood size	3	0.920	0.431	ns
Bolus mass	Foraging time	1	4.735	0.031*	
	Brood size	3	0.771	0.511	ns

Note: *, $P < 0.05$; **, $P < 0.01$; ns, not significant.

Fig. 3. Relationship between insect abundance and mean bolus mass delivered to nestlings. Vertical lines denote $\pm$SD.

Fig. 4. Relationship between time spent foraging outside the nest and mean bolus mass delivered to nestlings. Vertical lines denote $\pm$SD.
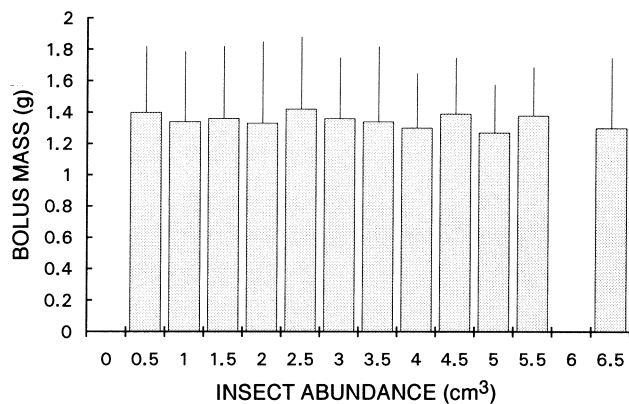
about 1 g, even when the food supply was at a maximum. The relation between the two variables is better explained by a quadratic function than by a linear function ($y = -0.791 + 0.422x - 0.022x^2$, $r_{64} = 0.444$, $P < 0.01$).
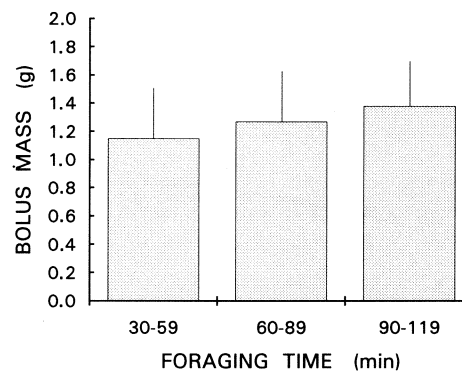
When the whole breeding period is considered (Fig. 5d), it can be observed that intermediate values for food abundance (at least 2 $cm^3 \cdot day^{-1}$) are necessary to maintain adults and to avoid daily decreases in mass.

Brood size affected daily mass variations: the gain in mass was greater in birds rearing smaller broods. However, the differences only approach significance ($F_{[3,157]} = 2.5$, $P = 0.06$, ns), probably on account of the dispersion of the data. On the whole, the amount of variance explained did not exceed 40% (a source of error in the estimated mass changes could be the fact that we could not ascertain when defecation (0.6–0.8 g) occurred; in addition, the estimate of available insects likely introduced some error).

The amount of food that parents allocated to themselves during each trip (i.e., self-feeding; calculated as the variation in mass plus the flight-energy cost during the foraging bout) tended to be higher when time spent outside the nest increased ($r = 0.42$, $N = 20$, $P = 0.06$, ns). However, even if the loads brought to the nestling showed small variations in mass (Fig. 1b), when the mass was larger, self-feeding tended to decrease ($r = -0.51$, $N = 12$, $P = 0.09$, ns).

Long-term mass variation in adults

The mass of each adult *A. pallidus* varied during the season. To illustrate the variation in mass between the different reproductive periods without considering the absolute individual mass, we rescaled the measured values in relation to the adult mass recorded on the days of hatching (considered to be zero), immediately before brood manipulation (Fig. 6).

Adult body mass was highest at the beginning of the breeding season, then decreased by about 2 g in the 2 weeks prior to egg laying. In this prelaying period, the swifts were engaged in pair formation or bond reinforcement, nest building or nest rearrangement, and nest-cavity defence. Aerial carousels in the immediate proximity (<50 m) of the colony site are frequently performed (Malacarne et al. 1987), as are vocal duets (Malacarne and Cucco 1990).

There was no difference in body-mass variation between pairs incubating 2 and 3 eggs ($t = 1.02$, df = 12, $P = 0.33$). No clutches of 1 or 4 eggs were observed in the colony.

Adult body mass remained constant during the 3 weeks of incubation (Fig. 6), during which parents spent half of their daylight time at the nest, with the partners alternating their presence.

In the brooding period, parents were engaged in both warming and feeding the young, and in this 2-week period there was a sharp decrease in body mass. Brood size significantly influenced mass loss ($F_{[3,22]} = 3.28$, $P = 0.04$); the largest decrease was shown by birds rearing the experimental broods of 4 young (Fig. 6).

In the last 3 weeks of rearing, when parents fed the chicks but brooding did not occur, brood size did not affect the variation in mass ($F_{[2,29]} = 1.78$, $P = 0.19$). By the time of fledging, the parents had lost almost 3 g relative to their hatching-period mass, regardless of the brood size.

Fig. 5. Relationship between insect abundance and daily change in adult mass during incubation (*a*), brooding (*b*), rearing (*c*), and the entire breeding period (*d*).
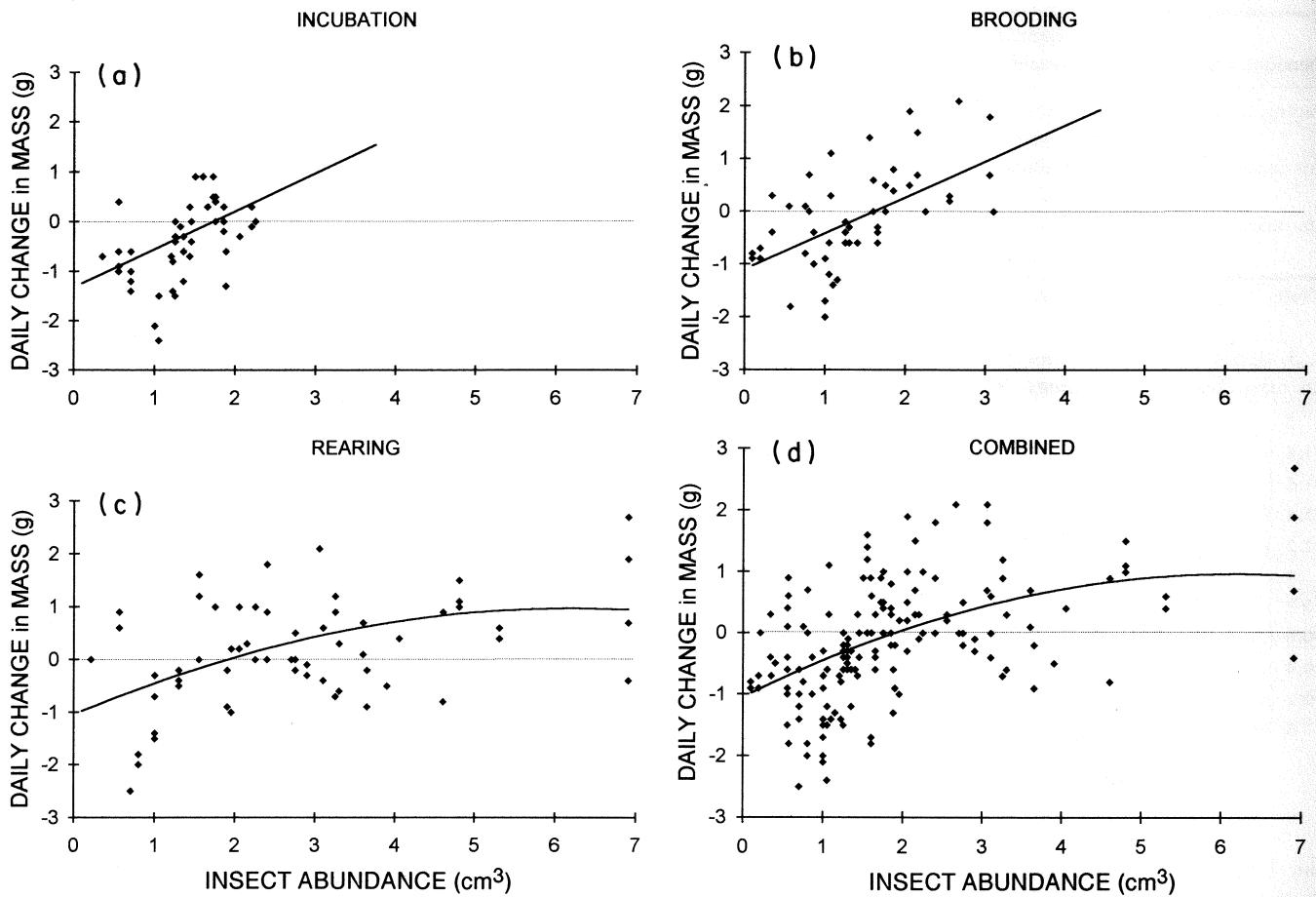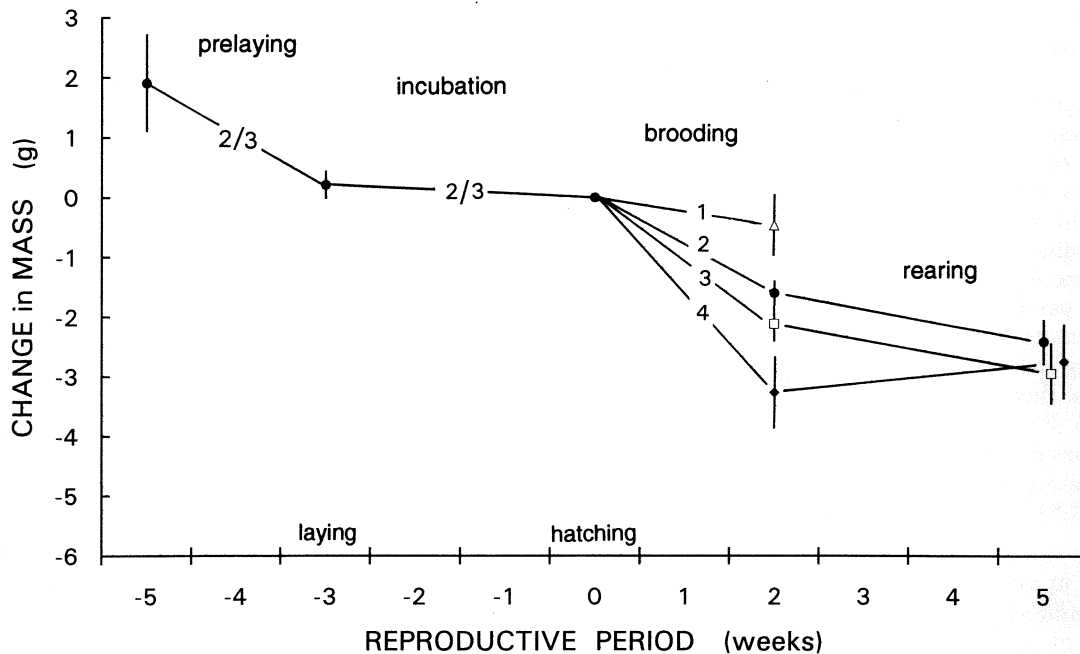

Fig. 6. Patterns of variation in body mass of adults during the breeding season. Masses and dates were standardized relative to each individual's value, as recorded on the days of egg hatching. Values are given as means ± SD. Numbers on the lines indicate clutch and brood sizes. Before the hatching period, no clutches of 1 or 4 eggs were found.

Discussion

From a lifetime perspective, assessment of costs of reproduction in swifts poses some problems. It is difficult to elucidate long-term reproductive trade-offs, since these long-lived species have low mortality rates (Boano et al. 1993) and exhibit small variations in clutch size. As a consequence, very long-term studies are required and large brood manipulations are not realistic. On the other hand, swifts are well suited to the measurement of costs on daily and seasonal bases, because it is easy to monitor their behaviour at the nest, their time-budget activity is simple (continuous flight when foraging and rest in the cavity), and they face unpredictability of food resources, both from hour to hour and over longer time periods.

Feeding frequency and bolus load mass

Many studies of birds point to an increase in the number of feeding visits to larger broods, so the amount of food per capita remains constant (Partridge 1989). However, when very large broods must be reared, a decline in food delivered per nestling is evident in swifts, swallows (Jones 1987b; Jones 1988), and other birds (Nur 1984).

Our brood enlargement caused an increase in the parental feeding rate but, on the whole, a reduction in the amount of food per capita. This was not found in natural broods (Malacarne et al. 1992). Also in Common Swifts, *Apus apus* (Martins and Wright 1993a), larger broods induced an increase in parental effort, though not sufficient to provide the same amount of food per capita as obtained by smaller broods.

The method adopted by *A. pallidus* to increase effort is slightly different from that observed in *A. apus*, where the number of visits tends to remain constant regardless of brood size while bolus mass increases (Martins and Wright 1993a). In contrast, in *A. pallidus*, bolus mass is constant but feeding rates increase with brood size. In central-place foragers, according to the optimality models (Orians and Pearson 1979; Bryant and Turner 1982), net rates of energy gain will be maximized. In our case, only a slow increase in load is observed with increasing foraging time; thus, longer bouts seem to be less efficient, producing diminishing returns (increased flight-energy costs with a moderate gain in food brought to the nest), but a complete costs—benefits analysis should consider that adults devote more time to self-feeding on long bouts.

We found no relationship between the amount of food delivered to chicks (feeding frequency, bolus mass) and daily food abundance. This finding differs from that reported for another aerial feeder, *H. rustica*, which delivers more food to chicks on days when insects are plentiful (Jones 1987b). In our study species, this discrepancy could reflect higher investment in offspring, at the expense of the parents, when food is less abundant, but could also be explained in part by considering the different weather conditions in the two areas under study. In northern climates, dramatic drops in insect numbers occur within a few days. In our more southern study area, insect abundance fluctuates daily within a smaller range, and parents never face a total absence of food (Cucco 1992). Thus, great variations in bolus mass, correlated with insect availability, are more likely to occur in aerial feeders breeding in northern regions.

Body-mass variations

Adult *A. pallidus* undergo considerable body-mass variations over both short (day) and long (season) periods. The changes depend on daily food abundance and on the amount of food required to raise chicks.

Short term

Allocation of food over a short period is evident from our daily records: when food is abundant adults fatten, and when it is scarce they lose mass. However, parents do not vary the amount of food delivered to chicks, allowing them to grow independently of relative insect abundance (Cucco and Malacarne 1995).

Similar day-to-day variation has been observed in *A. apus* (Martins and Wright 1993a), even though, in the area of study (Oxford), adults seem to be exposed to more adverse weather conditions. In years of poor weather, parents stop self-feeding and their fat reserves are depleted, resulting in a sharp decrease in body mass, and sometimes nestlings are not fed, so brood reduction occurs. In years of good weather, a daily cost of reproduction is still detected, but higher levels of self-feeding occur and the decrease in body mass is less dramatic (Martins and Wright 1993c). The parental behaviour and body-mass variations of *A. pallidus* resemble the physiological and behavioural responses of *A. apus* in years of good weather.

Daily fluctuations of body mass in relation to insect abundance have also been detected in *H. rustica* (Jones 1987b); in this case the chicks are also exposed to adverse weather and lose mass when food is scarce.

Generally, on a short-term basis, adult *A. pallidus* seem more prone to allow daily variations in their own body mass, to provide the advantage of regular growth of the chicks.

Long term

The seasonal decline in the mass of parents follows a trend observed in other birds (Dijkstra et al. 1988). The decrease has its main effects in the first 2 weeks after hatching, when both brooding and rearing requirements must be satisfied. Parental mass does not decrease in the subsequent 3 weeks of rearing, which could be due to a series of factors: freedom from brooding duties, in which each parent was engaged in turn for half of the daylight time (Malacarne et al. 1992); greater availability of insects during the rearing period; and the necessity to avoid further loss of body mass and possible starvation in the event of food scarcity.

It is difficult to know if the loss of mass (an average of 3 g from the mass during the incubation period, or 7% of adult mass) impacts on adult survival. Breeding *A. apus* are more likely to fall prey to Sparrowhawks, *Accipiter nisus*, Barn Owls, *Tyto alba*, Kestrels, *Falco tinnunculus* (Kuhk 1948; Lack 1956), or Hobbies, *Falco subbuteo* (Klass 1953), during cold spells or at the end of the breeding season. Death from starvation has been observed at a mass of about 28 g (Koskimies 1950). In *A. pallidus*, only one adult dropped to a very low value of 34 g, but at that time he abandoned his brood.

When expending greater effort, for natural or enlarged broods, parents lose more mass. Our finding is in accord with that observed in other aerial feeders (Jones 1987b; Martins and Wright 1993a), whereas the results are contra-

dictory when birds in general are considered (Dijkstra et al. 1990), since in many cases a cost in terms of mass loss is not incurred.

Loss of mass is commonly explained as a cost of reproduction, even though an adaptive hypothesis has been proposed; programmed anorexia anticipates the peak demands of nestlings and is useful for more efficient feeding flights (Freed 1981; Norberg 1981; Moreno 1989; Jones 1994). Such an adaptive hypothesis is not supported by our evidence, since the major decrease in mass occurs during, not before, the period of the highest demand, and adults fatten (daily mass variations) as soon as food become abundant.

Finally, the costs incurred by parents rearing enlarged broods could have been increased on account of a prolonged stay in the nest by chicks in the experimental broods (Cucco and Malacarne 1995); this could have further increased parental effort in the reproductive season, and adults could have been exposed for a longer time to the risk of starvation in times of food scarcity.

Acknowledgements

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