



Reproduction of the pallid swift (*Apus pallidus*) in relation to weather and aerial insect abundance

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ABSTRACT

The reproductive activity of swifts is affected by seasonal fluctuations of aerial insects which are largely unpredictable, depending day by day on climatic conditions. In this work we investigated whether the parental food provisioning is influenced by hourly fluctuations of insect abundance or if adults maintain a constant feeding rate. We found during each day that the amount of food delivered to nestlings was not related to hourly insect availability. We also verified that daily insect abundance is related to daily minimum and maximum temperature (38% of variability explained) and is unrelated to rainfall. Finally we compared, during different reproductive seasons, the aerial insect abundance and the biomass (eggs and nestlings) produced by adult swifts. Insect abundance was constantly high from June to September and did not precisely match the main period of biomass production (first clutch), which reached a maximum in July.

KEY WORDS: Pallid swift reproduction - Influence of weather - Seasonal changes in food - Daily rhythm of activity - Aerial feeding birds.

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INTRODUCTION

Many swifts and swallows are migratory species that breed in the temperate areas where their food (aerial insects) is abundant in spring and summer but nearly absent in winter. In contrast, the resident aerial feeding species live in tropical areas and rely on a moderate but constant food availability throughout the year (Hails, 1982). In the temperate areas, the aerial plankton is an ephemeral and patchy resource strongly influenced by climatic factors like wind, rainfall and temperature.

The trophic specialization of aerial feeders conditions their behaviour in many ways; for example, to avoid rainy weather, swifts move long distances away from stormy depressions (Elkins, 1983). When food is abundant, aerial feeders prefer to capture larger prey but, when it is scarce, their selectivity sharply decreases (Lack & Owen, 1955; Turner, 1980).

Furthermore, adverse weather conditions delay the dates of laying (Cucco *et al.*, 1992; Gory, 1992), cause a decrease in the clutch size (Bryant, 1975) and egg mass (Ward, 1995; Cucco & Malacarne, in press a) and lead to a reduction in food provisioning to the brood by the parents (Martins & Wright, 1993). A swift nestling can overcome prolonged periods of poor weather through hypothermia, a temporary decrease of body temperature (Koskimies, 1950). However, both in chicks and adults, mortality occurs if adverse climatic situations are prolonged (Lack & Lack, 1951).

The reduction of airborne insects due to rain, wind and low temperatures makes less profitable the restless flights of swallows and swifts; as a consequence, in poor weather conditions, a decrease in the mass of adults is observed (Jones, 1988; Martins & Wright, 1993; Cucco & Malacarne, 1995). When food is scarce the parents are faced with a decision about the allocation of resources: primarily to themselves, at the nestlings' expense, or toward offspring production at the risk of their own survival (Martins & Wright, 1993; Cucco & Malacarne, in press b) and/or reproductive value.

It has been proposed that differences in predictability and abundance of food resources are the cause of a latitudinal gradient in clutch size (Lack, 1968). For example, in tits living in Mediterranean areas the food resources are less abundant than in North Europe, and as a consequence the clutch size is smaller (Blondel *et al.*, 1993). Swifts, compared to other insectivorous birds, were indicated as exceptions, having a reverse gradient with larger clutches in warmer areas. Lack supposed that these differences were due to their peculiar trophic specialization (insects caught on the wing) which should be more unpredictable in northern areas. We studied the pallid swift, a circum-Mediterranean species similar in many aspects to the common swift *Apus apus* (Cucco *et al.*, 1993).

The aims of this work were: 1) to investigate whether the parental food provisioning is influenced by hourly fluctuations of insect abundance or if adults maintain a

constant feeding rate. As observed on a daily basis (Cucco & Malacarne, 1995) parents maintain a constant feeding rate when insect availability decreases; 2) to assess to what extent daily insect abundance is explained by climatic factors; 3) to compare food abundance and the biomass produced (eggs and nestlings) by adult swifts over various reproductive seasons.

We discuss how the patterns of aerial insect abundance at different latitudes may mould adaptive traits in aerial-feeding birds.

MATERIALS AND METHODS

Study area

The study was conducted in the colonies of Carmagnola and Torino (28 km far) NW Italy (45° N lat.). The climate is temperate continental, with a thermal excursion of 23° C and a yearly mean rainfall of 712 mm (Boano & Cucco, 1989). The rainiest months are May and October.

In Carmagnola the pallid swifts nest in a colony (17-19 pairs) located in the external wall of an old garrett in the centre of the town (Cucco & Malacarne, 1995). Observations were carried out in the reproductive seasons from 1989 to 1991. In Torino from 1987 to 1990 we surveyed a colony (30-50 pairs) located in the cavities of blind boxes of a school building in the city centre.

Behavioural observations

Observations of feeding frequencies were made in Carmagnola during the reproductive season of 1990. One day each week, from the end of June to July, we counted parental visits to the 19 nests under observation. In each session we lumped the feedings into four time periods: 1) early morning: 6.00-9.00 a.m.; 2) morning: 9.00-12.00 a.m.; 3) midday: 12.00-3.00 p.m.; 4) afternoon: 3.00-6.00 p.m. There were no feedings before 6 a.m. and we did not take into account those after 6 pm when screaming parties occur around the colony (Mazzotto *et al.*, 1996). Each day we checked the number of chicks in the nests in order to calculate mean feeding per chick.

To compare insect abundance and productivity on a seasonal basis, each two weeks we obtained an index of biomass production of the colonies by weighing eggs and nestlings.

Insects sampling

Aerial insects (Aranaeidae are unimportant in pallid swift diet: Cucco *et al.*, 1993) were monitored by means of a suction trap 12.2 m high, located 2 km from the colony under study in the surrounding farmlands. The trapped insects were dried for two hours and their volume was measured, to the nearest 0.1 cm³, by immersion in a graduated cylinder. Because *A. pallidus* and the suction trap typically caught arthropods in different percentages (more Diptera in the trap: Cucco *et al.*, 1993), the measured volume has been considered merely as an index of aerial insect abundance, useful for comparison among different days. The captures of the suction traps have been shown to be similar up to a distance of 80 km (Taylor, 1973), a range probably rarely exceeded by foraging swifts in the breeding period.

Insects were trapped on a daily basis from April to November. In 1990, in order to compare insect fluctuations and parental feeding rates, on the days when behavioural observations were performed the trap was set to obtain four separate samples per day in the same time periods utilized for behavioural observations.

RESULTS

Parental food provisioning and insect abundance

Aerial insect abundance was highly variable (CV = 108.9%) during the day and was not significantly different ($F_{3,14} = 0.413$, $P = 0.75$, NS) in the four time periods (Fig. 1).

The feeding rate was less variable (CV = 50.4%). The parents fed each nestling on average 0.21 times per hour; insect abundance (Fig. 2) did not correlate with the hourly rhythm of feeding ($r = 0.013$, $N = 18$, $P = 0.96$ NS).

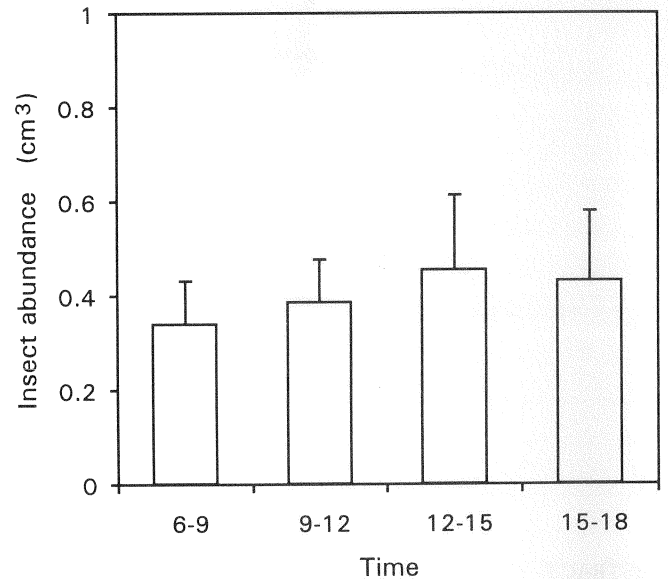


Fig. 1 - Insect abundance (cm³ volume of trapped insects, mean±SE) in relation to time (h).

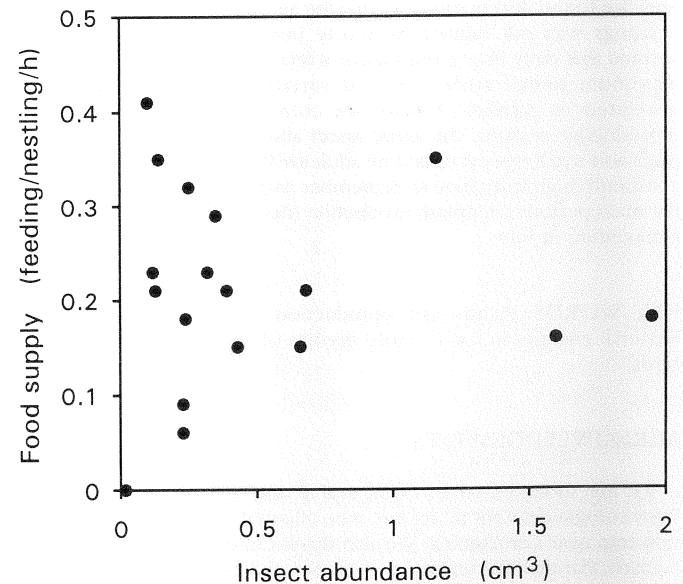


Fig. 2 - Parental food supply to nestlings (feeding · nestling⁻¹ · hour⁻¹) in relation to insect abundance.

Influence of climatic factors on insect abundance

Figure 3 shows the relationship between maximum (Tmax) or minimum (Tmin) daily temperatures and daily insect abundance during the whole six-month reproductive period. Both temperatures were correlated with arthropod abundance; more insects were present as the temperature increased. A second-order regression explains 38.4% of the variation for the Tmax (equation: $y = 0.00212 x^2 + 0.0104 x + 0.143$, $r = 0.620$, $N = 171$, $P < 0.001$) and 38.6% of the variation for Tmin (equation: $y = 0.00339 x^2 + 0.0563 x + 0.161$, $r = 0.622$, $N = 171$). When the same relationships were considered for a shorter period (two months), the variation explained was high in spring (May-June) and autumn (September-October) while in summer (July-August) it was con-

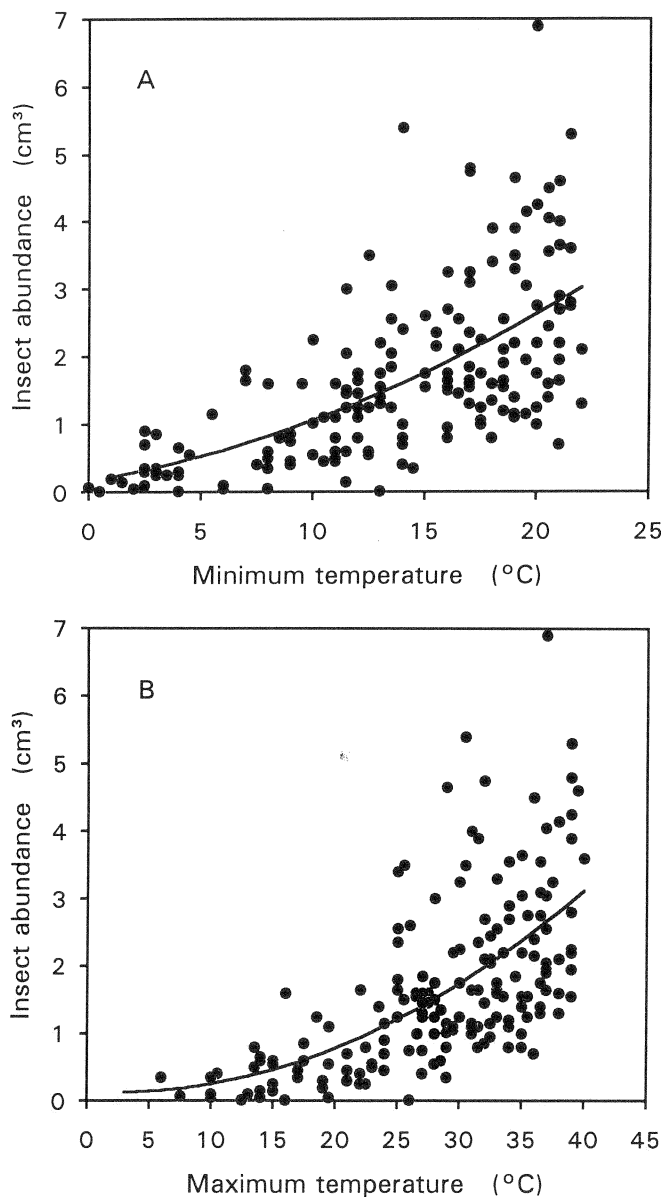


Fig. 3 - Influence of minimum (A) and maximum (B) temperature on insect abundance.

siderably lower (Table I). Rainfall occurred on 135 days out of the 660 sampled. When only the rainy days were considered (Fig. 4) the quantity of insects trapped was not related to the amount of rain (Table II). Also after a correction for a temperature interaction, we could not detect an effect of rainfall ('r' tests for correlation in the three years, Tmax and Tmin considered separately: $0.08 < P < 0.94$, NS).

The seasonal pattern of insect abundance was similar in the three years sampled (Fig. 5). The volume of trapped insects increased after April and fluctuated around high values from June to September. A peak abundance was observed in June 1989, in July 1990 and July-August 1991. Only in November did the decline in insect abundance lead to negligible daily quantities of insects.

There were considerable differences among years in insect abundance: 1990 was a very productive year, while 1989 and 1991 were poorer. The coefficients of variation (CV) of monthly insect volumes (Fig. 5d) indicate that spring and fall are the more variable and unpredictable periods for food availability, while summer shows the least variation.

Food abundance and biomass in the colonies

The biomass produced (eggs plus nestlings) and food abundance were not precisely matched throughout the reproductive seasons (Fig. 6). The biomass peak occurred in mid-July when food abundance was high but not at its maximum (this occurred 15-20 days later). In August, the volume of trapped insects was still at very high levels but

TABLE I - Relation between insect abundance and temperature.

Variable	Months	r	N	P
Tmax	May-June	0.581	58	<0.001
	July-August	0.363	54	<0.01
	September-October	0.549	47	<0.001
Tmin	May-June	0.476	58	<0.001
	July-August	0.210	54	0.12
	September-October	0.561	47	<0.001

TABLE II - Relation between insect abundance and rainfall.

Variable	Year	r	N	P
Rain	1989	0.235	45	0.12
	1990	0.024	56	0.86
	1991	0.140	34	0.43

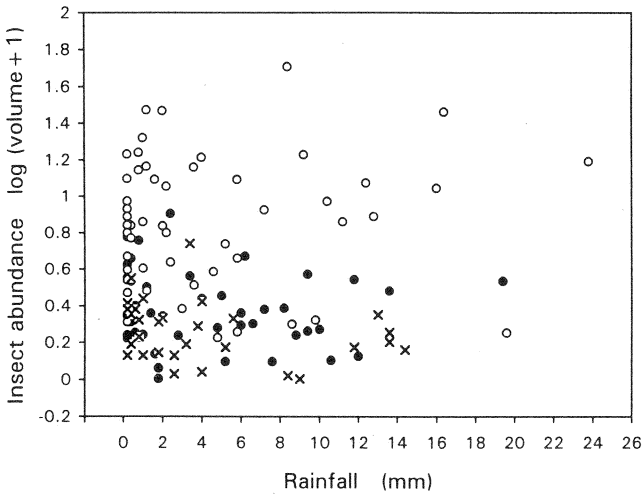


Fig. 4 - Rainfall (mm · day⁻¹) and insect abundance [log(Volume + 1)] in three different years (solid circles, 1989; open circles, 1990; crosses, 1991).

biomass production decreased sharply. The pallid swifts (adults and young fledged) were no more observed around the colonies in August and this suggests that they did not utilize fully the amount of food available in this period. Only the pairs engaged in substitution clutches

and those that started a second clutch (second clutches were observed mainly in the Torino colony) frequented the colonies. The second broods occurred late in the season (most biomass was produced in October) and, even if biomass production increased when insect availability showed a regular decrease, the nestlings took advantage of the insects available before their disappearance in late November.

DISCUSSION

Parental food provisioning and insect abundance

In this study we observed that chick feeding frequency during the day was not influenced by the abundance of food. A similar independence was inferred by Lack & Owen (1955) for the common swift *Apus apus* at Oxford, where the daily activity was not in tune with the estimated peak of food. Moreover the uniform pattern of nest-flights in the house martin *Delichon urbica* during the rearing period did not follow food fluctuations in normal weather conditions (Bryant, 1975).

Among the factors that influence daily feeding rates in the pallid swift, brood size is most important; daily food abundance does not influence the daily visit rate of a pair (Cucco & Malacarne, 1995).

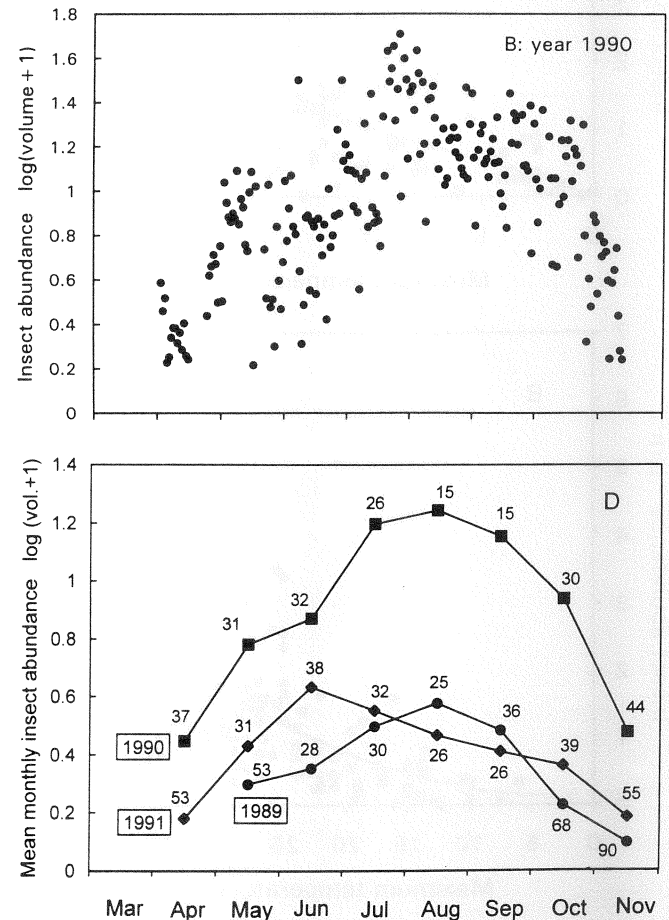
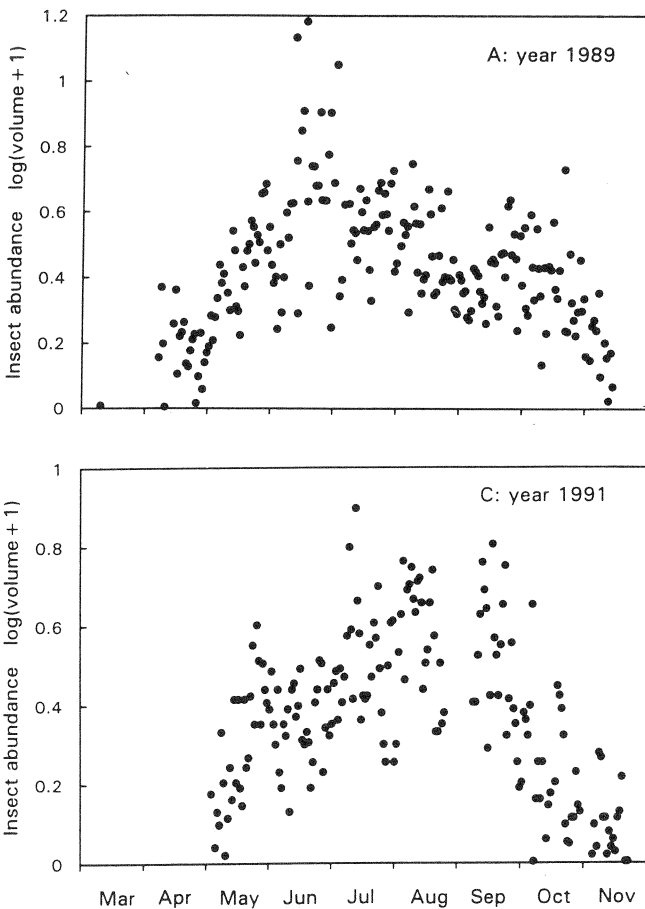


Fig. 5 - Seasonal patterns of trapped insect quantities in three different years (A, B, C), and monthly variability (D); line, mean monthly insect abundance; numbers, coefficients of variation).

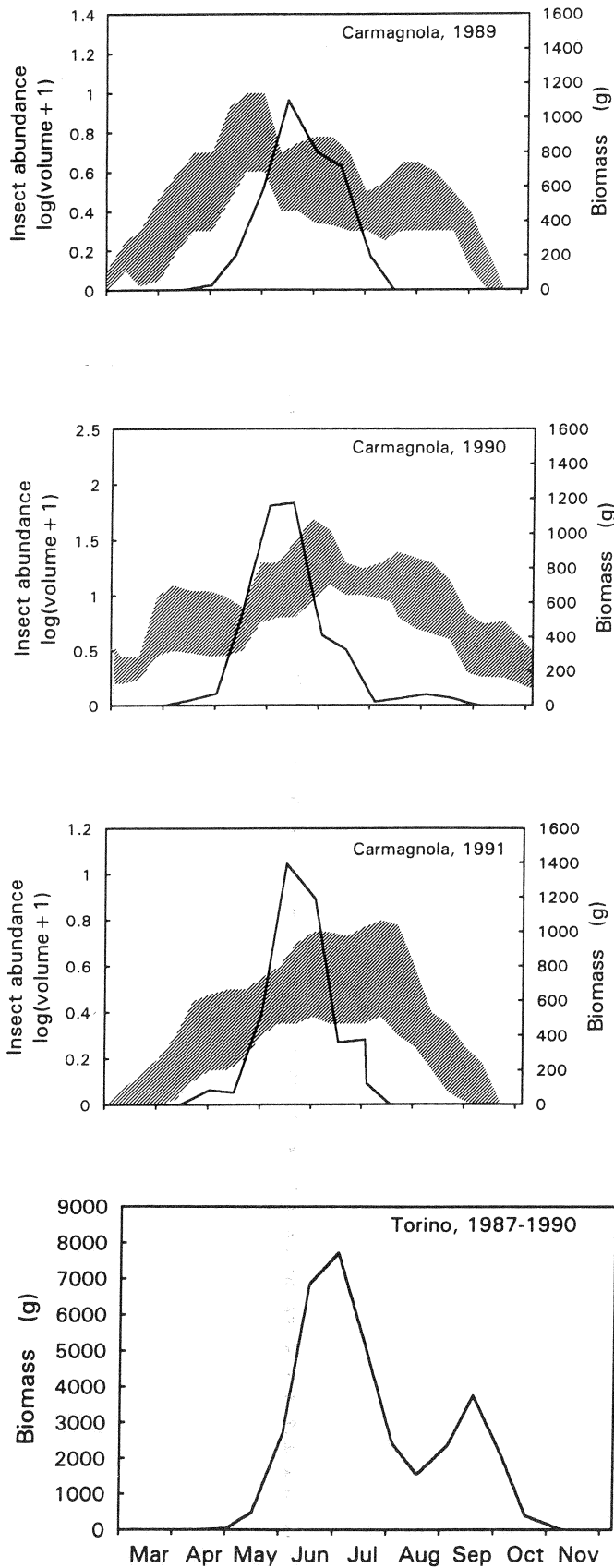


Fig. 6 - Biomass of flying insects and of pallid swifts in different years. Lines represent biomass (cumulated egg and nestling mass) in each colony. The shaded areas encompass the values of trapped insects, as detailed in Figure 5.

The feeding rate of pallid swift parents ensures a constant growth of the nestlings, regardless of the hourly and daily fluctuation of food abundance (Cucco & Malacarne, in press b). When food is scarce the allocation of resources primarily to the nestlings could imply an increased risk of starvation for the parents. A cost of reproduction for parents is also argued by the mass decrease of adults when food is scarce (Cucco & Malacarne, 1995).

Influence of climatic factors on insect abundance

In many studies, when a direct measure of food abundance is not available, it is assumed that food availability is related to more easily measured parameters like temperature, rainfall or wind intensity. In a previous study (Cucco *et al.*, 1992) we showed that weather conditions influence pallid swift breeding. The main effect was on laying dates, which were delayed by unfavourable weather in spring (low temperatures and high number of rainy days). After laying, both in delayed and regular years, the mean seasonal temperatures were not correlated with seasonal breeding success. In this study 38% of the variance in daily insect abundance was explained by temperature, while rainfall did not have a significant effect. In a northern climate (Scotland, 56° latitude) Bryant (1975) found that a wide range of environmental variables (daytime temperature, 24-h temperature, daytime rainfall, radiation, hours of sun, wind intensity) explained 50% of the daily variation in flying insects. Interestingly, in both areas the correlation between climatic factors and insect abundance rose considerably when the months were considered separately. In the colder area (Scotland), the highest correlations between environmental parameters (rainfall and radiation) and insect abundance were found in July and August. In this study the correlation between temperature and insect number was higher in May-June and September-October, but decreased in full summer (July-August). Taylor (1963) suggested that in temperate climates a temperature threshold for flying by aerial-plankton would be an important factor determining the rate of trap capture. Above this threshold, insect flight would be relatively independent of temperature. We suggest that this threshold is reached earlier in the season in southern Europe and later in northern areas. In the hot months (July- August) of our continental warm climate, the temperature threshold is greatly exceeded and insect fluctuations are probably caused by other unrevealed factors.

The seasonal pattern of insect abundance found in this study is similar to that described for a cold temperate climate and different from the uniform one sampled in a tropical area (Hails, 1982). Aerial arthropods were abundant from May onward and reached their highest levels in July-August. The decline in insect numbers began in October, but their disappearance occurred only in the last part of November. Compared to the yearly pattern observed in Scotland (Bryant, 1975), insects in Italy are present earlier and decrease later. In both areas (Scotland

and North Italy) large interannual differences in aerial insect abundance are found: poor years alternate with rich years. The monthly values of trapped insects (absolute abundance), in poor and good years, are notably similar in the two areas.

In this study we examined the variations, day after day, of insect numbers, hypothesizing that these variations should be less evident in southern climates than in northern ones. However, monthly coefficients of variation in insect abundance at the two latitudes did not differ markedly, so that smaller fluctuations of food in the southern area cannot be inferred. The influence of unpredictability of resources on reproduction has been investigated in many bird species and it has been proposed that unpredictability can explain differences in clutch size among areas located at different latitudes. For example, clutch size variation in tits has successfully been related to food availability (Blondel *et al.*, 1993). For swifts, Lack & Lack (1951) showed that the clutch size decreases from south to north European areas; however, this latitudinal gradient should not be related to predictability of food, since insect trapping performed in Scotland (Bryant, 1975) and Italy (this study) show similar coefficients of variation.

Food abundance and biomass in the colonies

In this work the insects trapped and the biomass produced by pallid swifts did not covary precisely through the reproductive season. However such a correlation was found in many bird studies; for example, in the great tit *Parus major*, the number of chicks was related to the number of caterpillars available (Perrins, 1991), and in the house martin and the purple martin *Progne subis* there was a close relation between seasonal food availability and the mass of nestlings: insects peak when food demand is highest (Johnston, 1964; Bryant, 1975).

We suggest that in the pallid swift an important role in matching food and biomass output is played by the autumnal second clutch. It follows the period of main biomass production (first clutch) and must occur before the disappearance of insects in late autumn in order to be selectively advantageous. During our study we observed a high intercolony variability in this life-history trait; in the large colonies of Torino, it has always been present (about 30% of pairs), while in smaller colonies like those of Carmagnola it is not present every year (Cucco *et al.*, 1992; Boano & Cucco, 1989). On average the food abundance in October (food demand peak) is still considerable, the chicks (typically two per brood) are well nourished and fat before fledging and the nestlings reared before the first days of November generally succeed in fledging (pers. obs.). Bryant (1975) observed in the house martin that recruitment into the colony population is influenced by food supply also through its effects on the occurrence of second clutches. However, environmental variables influenced the growth of chicks in the second clutch less than in the first one and, as in

our study area, food can still be extremely abundant in this period (September) in Scotland.

More in general, the explanation of the occurrence of the second clutch in birds raises some questions. Besides geographic variations such as the latitudinal gradient of clutch size in tits (Perrins, 1979), the food richness of the habitat and its interseasonal differences surely play a role in the timing and occurrence of the second clutches. In addition other factors such as breeding condition, age and experience must be taken into account (Smith *et al.*, 1987).

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