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Factors affecting egg mass in the Pallid Swift *Apus pallidus*

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In order to understand the sources of egg mass variation in the Pallid Swift, we weighed 142 eggs (0.1 mg accuracy) from 1990 to 1993 in a colony in north-west Italy. The observed variability was related to laying order and laying date, but was not influenced by the wing length or mass of the parents. Food abundance in the days preceding egg laying did affect egg mass, but the variation was small with respect to the average egg mass. As previously reported for the Common Swift, the last (third) egg laid had the smallest mass. The heaviest eggs were laid early in the season. As there is no seasonal decrease in aerial insect abundance, this trend may be because high quality parents lay earlier in the season. The mass of the egg positively influenced nestling weight at age 20 days. We have analysed to what extent egg mass per se *affected chick survival.*

Within species, chick mass often increases with egg size. For example, in some asynchronously hatched birds[1–3] the last-laid egg weighs the least and hatches last; the chick usually grows more slowly than its siblings and has a lower survival rate. In general, when variation exists within a clutch, larger eggs give rise to heavier chicks at hatching, which have an increased probability of survival in the first few days.[4] However, many other variables can influence chick growth and survival (e.g. quality of the parents and the territory, weather conditions, sibling competition, date of laying, etc.) and may obscure the egg-size effect at the time of fledging. In fact, few studies demonstrate an effect of egg size *per se* on survival at fledging.[5] In the Common Swift *Apus apus*, it has been shown that the great mortality of chicks hatched from last eggs is due to failure in competition for food with older, larger siblings and not specifically to the lesser amount of nutrients in the third egg.[3] O'Connor,[3] in line with Lack's hypothesis[6] of brood reduction as an adaptation to unpredictable food supplies, supposed that the relative sizes of swift eggs within the clutch are adjusted to optimize sibling competition. He also showed that in England the most variable egg sizes occur early in the season (May) when weather conditions are unpredictable, whereas late in the season (June), when atmospheric conditions are more stable, a more constant egg weight is recorded.

During reproduction, aerial feeders such as swallows and swifts are especially sensitive to weather conditions, as on cold and wet days they face a dramatic decrease in their food, i.e. aerial arthropods.[7] Other bird studies have detailed not only the effects of weather conditions on egg mass but, more directly, those of food availability, with a correlational approach[4,7,8] or an experimental approach.[9,10]

This study aimed to assess the relative importance of some sources of egg mass variation in the Pallid Swift, namely: (a) laying order, (b) the wing length and mass of the parents, (c) food availability in the days preceding egg laying and (d) the date of laying. Furthermore, egg mass has been correlated with the weight of the chicks in the middle of the nesting period (20 days after hatching).

METHODS

The research was conducted in north-west Italy during the breeding season from 1990 to 1993. The Pallid Swifts nest in a colony (17–19 pairs)

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located on the external wall of an old building, in the town of Carmagnola (details in ref. 11). Nest cavities were easily reached and inspected from inside the building through the internal wall, which was modified for observations by insertion of a removable window at the rear of each nest cavity. Laying dates were ascertained by daily nest inspection. Eggs were measured with a Mettler analytical balance (accuracy 0.1 mg) on the day of laying when adults were not at the nest. Each chick was marked with a numbered metal ring and weighed at 20 days of age. The parents were marked by means of a small spot on the back created by a decolourizing paste. To avoid nest desertion, we applied the paste before egg laying. We ascertained the sex of each parent by observing egg laying. Ringing and measurement (wing length and mass) of the adults took place at the end of the breeding season, after the fledging of the first young in each nest.

In 1991 and 1992, the abundance of aerial arthropods (mainly insects) was quantified daily by collection in a suction trap located 2 km from the colony. The captures by the suction traps are known to be similar up to a distance of 80 km,[12] a range probably rarely exceeded by the foraging swifts in the laying period. The daily volume of trapped insects was measured to the nearest 0.05 cm^3 by immersion in a graduated cylinder.

The data were analysed with the SYSTAT package. When we found statistical differences in ANOVA, we contrasted categories by post-hoc tests with a Bonferroni correction. We analysed the first, second and third eggs separately when examining correlations with the laying date and the insect abundance. To avoid pseudoreplication, we used mean nest values to investigate the relationship between egg mass and the mean nestling mass, parental mass or wing length.

RESULTS

Egg mass ranged from 2.71 to 4.1 g (N = 142, from 17 two-egg and 38 three-egg clutches). In the three study years we observed only two dwarf eggs, which did not hatch and have been excluded from the analysis. Clutches of two had a mean egg mass of 3.55 g and clutches of three, 3.52 g.

Laying order

In clutches of three (Fig. 1), there was a significant difference between egg mass at laying ($F_{2,108}$= 36.4, P <0.001). The last egg laid weighed less than the first and second eggs (–0.14 g and –0.20 g, respectively); the difference

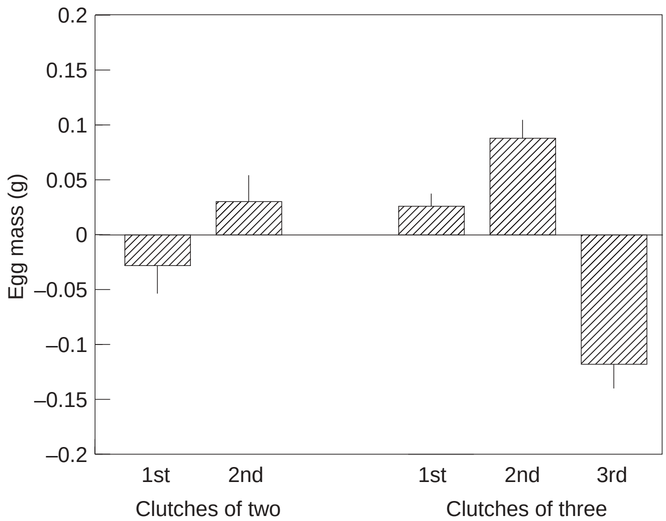

Figure 1. Egg mass in relation to position in the clutch (mean ± sd). Zero represents the average clutch value as calculated separately for each female.

between the first and second eggs was small (+0.06 g) but statistically significant (post-hoc tests; 1 vs. 2: $F_{1,108}$= 6.68, $P < 0.001$; 2 vs. 3: $F_{1,108}$ = 69.7, $P < 0.001$; 1 vs. 3: $F_{1,108}$ = 33.9, $P < 0.001$). In clutches of two (Fig. 1), the second egg was slightly heavier than the first but the difference was not significant ($F_{1,30}$ = 2.86, P = 0.10 ns).

Wing length and mass of the parents

Mean egg mass was not related to the wing length or body mass of either parent (Table 1). There was also no correlation with these variables when the two parents were considered together (i.e. in each pair, the female and male values of mass or wing length were averaged).

Laying date

Egg mass declined through the season (Fig. 2) in each of four study years (ANCOVAs: first eggs: $F_{3,50}$ = 2.1, P = 0.11; second eggs: $F_{3,48}$ = 1.2, P = 0.30; third eggs: $F_{3,29}$ = 1.02, P = 0.40). Pallid Swifts starting in mid-May laid heavier eggs, whereas at the end of June eggs were significantly lighter (first eggs: r = –0.37, n = 55, $P <$ 0.001; second eggs: r = –0.44, n = 53, P < 0.001; third eggs: r = –0.33, n = 34; P < 0.05). The difference between the latest- and earliest-laid eggs represents about 7% of the average egg mass. From a comparison of Figs 2 and 3, it is evident that the seasonal decline in egg mass does not follow the fluctuation in arthropod abundance.

Food abundance in the days preceding egg laying

The daily insect abundance was highly variable: data for 1991 are shown in Fig. 3, and similar variability was found in 1992. As Pallid

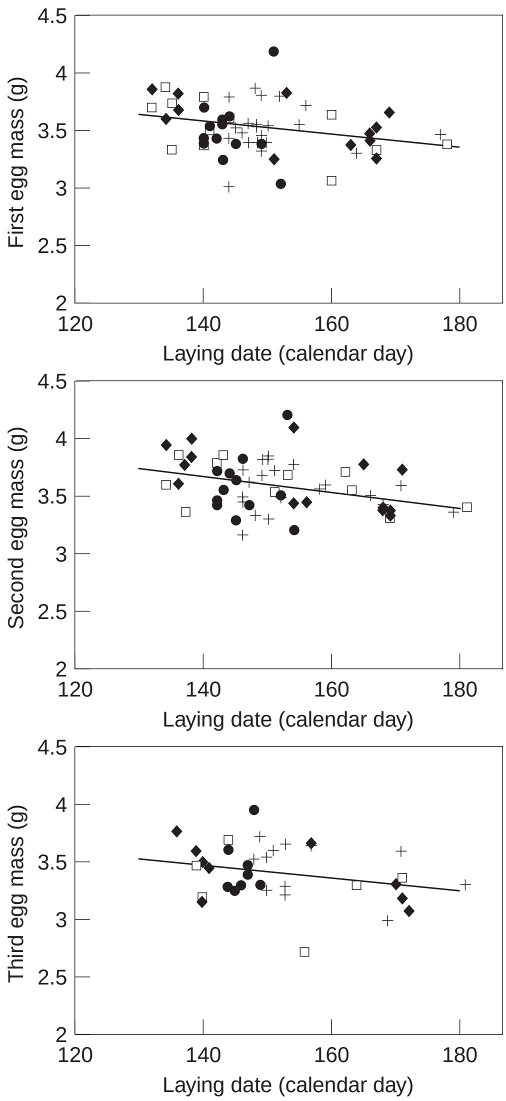

Figure 2. Egg mass in relation to laying date. From top to bottom, the fitted lines have the equations: $y = 4.395 - 0.00578x$; $y = 4.663 - 0.00704x$; $y = 4.237 - 0.00546x$. ❏ = 1990; + = 1991; ◆ = 1992; ● = 1993.

Table 1. Relation between mean egg mass and parental wing length and mass

Variable	*Parent*	r	N	P	
Wing length	Female	0.04	26	0.85	ns
Wing length	Male	0.01	28	0.95	ns
Wing length	Female + male	0.05	24	0.84	ns
Mass	Female	0.19	28	0.40	ns
Mass	Male	0.24	27	0.28	ns
Mass	Female + male	0.08	24	0.75	ns

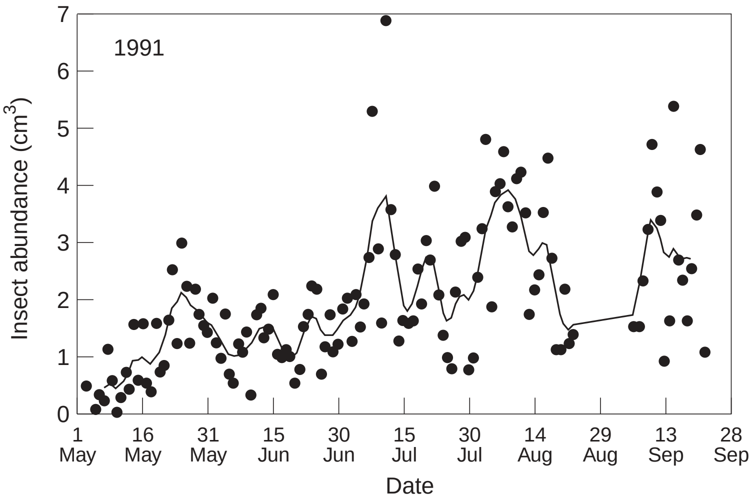

Figure 3. Daily variation in food abundance in 1991 (insects collected by suction trap).

Swifts always lay in the morning, only insect abundance on the days before laying is likely to affect egg mass. There was no relationship between residual egg mass (i.e. mass value after correction for date) and the volume of insects captured in the suction trap on the single previous day ($P > 0.05$ for each egg category). However, when the cumulative insect volume of the two previous days was considered (Fig. 4), the correlation was significant for the second- and third-laid eggs (first eggs: $r = -0.164$, $n = 30$, $P = 0.40$ ns; second eggs: $r = 0.393$, $n = 30$, $P < 0.02$; third eggs: $r = 0.386$, $n = 21$; $P < 0.05$). The influence of food abundance was less than that of the seasonal decline: the eggs differed only by about 0.7% of the average egg mass per cm^3 variation in the daily insect abundance.

Chick mass in relation to egg mass

The residual mass of each clutch (i.e. the residual difference between the expected and the observed mean value in each nest) and the mean nestling mass of the corresponding brood (at age 20 days) were considered (Fig. 5). Nestling mass increased with residual egg mass both in broods of two ($r = 0.77$, $n = 6$, $P < 0.02$) and three ($r = 0.42$, $n = 20$, $P < 0.03$).

Laying date affected both egg and nestling mass, but a partial correlation analysis (coefficient of determination = 0.34) showed that the effect of laying date accounted for only 15.6% of the variability (partial $r = 0.22$). Egg mass was the more important correlate (partial $r = 0.53$), accounting for 84.4% of the variation in nestling mass.

DISCUSSION

Swifts have a small egg mass relative to the size of the adult. However, since their eggs contain more yolk than other nidicolous birds of comparable size, newly hatched swifts have more total lipid.[13]

In the Pallid Swift, as in the Common Swift,[3] the laying order influences egg mass, the third egg being lighter than the first and second ones, and the second egg weighing slightly more than the first.

Egg mass influenced the weight of nestlings at age 20 days, when typically the chicks reach the fledging mass value.[14] However, especially in the next 20 days of the nestling period, individual growth rates can vary erratically, so that the growth curve is poorly defined,[13] and there is typically a decrease in mass at the end of the nestling period.[14] Thus egg mass probably has little, if any, influence on chick mass at fledging. Moreover, it is unknown to what extent mass at fledging conditions the future prospect of survival, as young swifts do not return to the natal colony.[15,16] The high mortality of the junior swift chicks is probably due primarily to hatching asynchrony and not specifically to the slight difference in egg mass.[3]

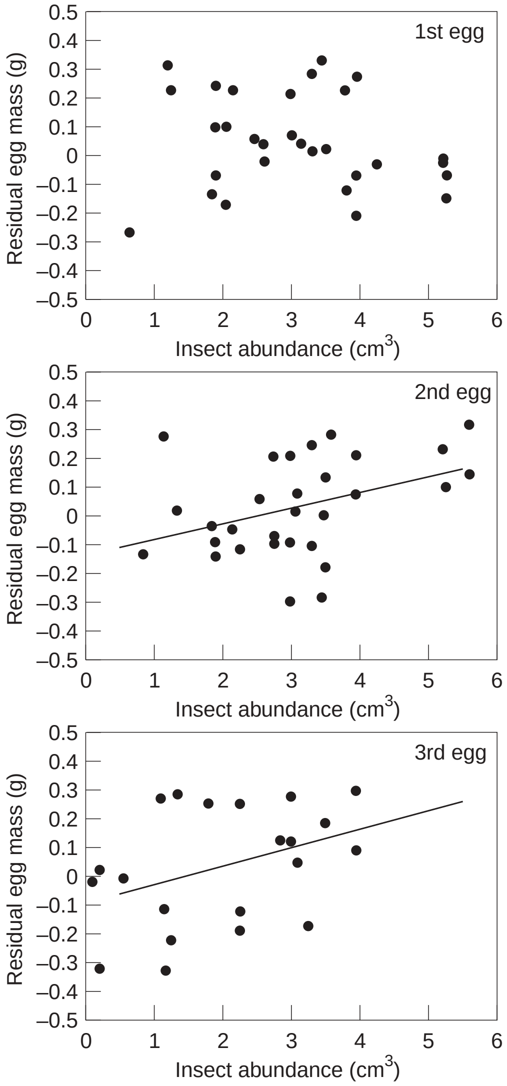

Figure 4. Relationship between abundance of food in the two days before laying and residual egg mass (i.e. mass value after correction for the reported seasonal decline). The fitted lines have the equations: $y = -0.142 + 0.0552x$; $y = -0.0947 + 0.0637x$.

In swifts, brood reduction occurs at the expense of the last-born chick,[3] which usually dies in the first days after hatching. It is supposed that this differential mortality is in part due to sibling competition for insect balls delivered by the parents. The last-born chick hatches two days later, is smaller and weaker than the siblings and is less competitive in obtaining food.[11]

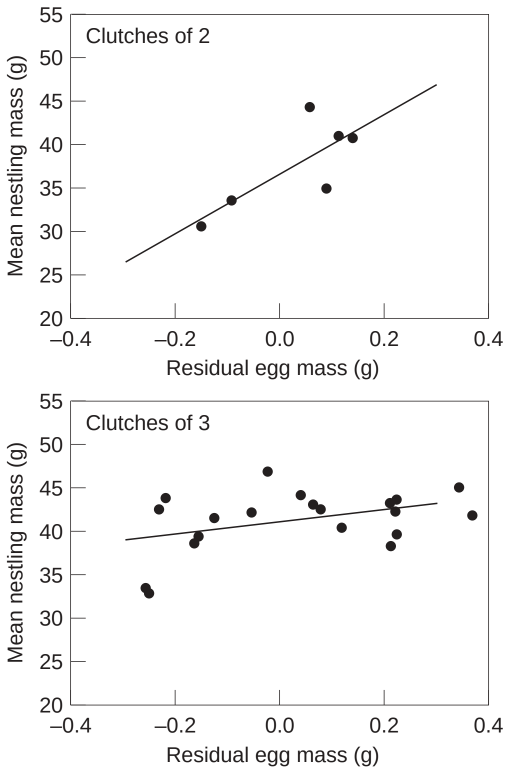

Figure 5. Mean nestling mass (at age 20 days in each brood) in relation to residual egg mass (i.e. difference between the expected and the observed mean value in each clutch). The fitted lines have the equations: $y = 36.7 + 34.4x$; $y = 41.1 + 7.02x$.

This study reveals that egg size is not related to parental morphological characteristics, as found in most studies.[8] In our research, a significant relationship between food abundance in the two days before laying and egg mass was observed only for the second and third eggs. We suggest that food abundance is more likely to influence the second and third eggs because, during the production of the first egg, laying females deplete the reserves accumulated during several days, whereas for the formation of the following eggs the females have to rely mainly on the food available in the two days prior to laying.

A short-term effect of food availability on egg mass has been detected in many species,[4,9,10] but its effect on aerial-feeding birds is more controversial: in the House Martin, Bryant found no correlation between egg mass and food conditions, but rather a reduced number of eggs laid in times of food shortage;[7] in the Swallow, larger eggs with a higher nutrient content were laid in favourable environmental conditions.[8] Similarly, in the Common Swift, the fact that in bad weather the laying interval increases and egg size is reduced is indirect evidence of the effect of food availability.

When parental quality is accounted for, egg mass does not vary with laying date in the majority of birds,[5,7,8] although sometimes there is a seasonal increase due to a rise in temperature in spring.[4] In a few species, differences have been reported from year to year;[5] in the Common Swift, the annual variation has been found only early in the season (the eggs being smaller in rainy years), whereas later in summer there is constancy in egg size.[3] In the Pallid Swift we found a decrease in egg mass with laying date in all three study years. Among the different factors that could produce a seasonal decline of egg mass, we can exclude a seasonal reduction in food availability, because from June to July there are high insect levels in our study area. Therefore, egg size decline is more probably related to the quality of parental behaviour: in the same study colony, we have shown that early breeders are those faithful to the nest cavity and to the partner[16] and that birds laying earlier have a higher fledging success.[17] In the only other species reported to exhibit seasonal decline in egg mass, the Manx Shearwater *Puffinus puffinus*,[5] there is little indication of a clear correlation with laying date. The major factor is that younger females, who produce smaller eggs, tend to lay later, while females with breeding experience form larger eggs and lay them earlier.

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