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Influence of weather conditions on pallid swift Apus pallidus breeding success

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The reproductive ecology of three colonies of pallid swift in a warm continental climate (Piedmont, NW-Italy) was studied over a ten years period. About 60% of the clutches were laid in late May and June, but continued until late August and September, when some females laid a second clutch. Clutch size and the mean number of fledged young decreased progressively from spring to autumn.
Laying dates were influenced by rain and temperature: unfavourable weather conditions during May induced most females to postpone egg laying until June. Clutch size was not related to the rain or temperature parameters considered.
These observations differ from the findings about the common swift studied in cool temperate areas, where a very short stay in the breeding colonies does not allow a delay in laying, and spring weather conditions therefore have a strong influence on clutch size. There are also differences about the effect of weather on chick rearing. In warmer climates, typical of our colonies, fledging success is hindered both by too dry or too rainy seasons, even if these situations very rarely occur and the three-egg clutch is always the most productive. In colder climates the breeding success of the common swift depends primarily on the climatic conditions of May, and in bad weather a two-egg clutch is more productive than a clutch of three. In summary, the annual breeding success of the pallid swift appears little influenced by weather changes, due to a lesser impact of adverse conditions in Southern climates and the possibility, for this species, of shifting the laying period in response to a temporary worsening of climatic conditions.

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Introduction

Several factors are known to influence both the length of the breeding season and clutch-size of birds (Perrins and Birkhead 1983). Among them, geographical and ecological factors such as latitude (Wyndham 1986, Kulesza 1990) and climate (Lack 1947, Immelman 1971, Murphy and Haukioja 1986) play a fundamental role, although other factors, such as taxonomy and body size (Saether 1985) must also be taken into account.

In swifts (Apodiformes), latitude influences the length of the breeding season: the number of broods in a year increases from species living at high latitudes to those breeding in tropical areas (Lack 1954). Taxonomy (Lack and Lack 1951) and colonial habits (Hogstedt 1980) could be other factors in maintaining a remarkably constant clutch size (two or three eggs) throughout the group. Climate, on the other hand, has been considered as the main factor affecting swift reproduction.

According to Lack and Lack (1951), the most productive clutch size of the common swift *Apus apus* (2 or 3 eggs) is dependent on weather conditions. In fine-weather years in England the parents can successfully raise three young, while in poor weather conditions the

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Table 1 Number of first and second clutches in the three pallid swift colonies in different years

		First clutches (no nests)	Second clutches (no nests)	*Not condidered (no nests)
Carmagnola	1978	10	–	1
	1979	9	–	–
	1983	16	5	–
	1984	13	10	–
	1985	8	–	–
	1986	7	–	3
	1987	12	–	–
	1988	16	–	–
	1989	17	–	–
	1990	19	2	1
Torino	1987	58	25	4
	1988	70	25	12
	1989	27	9	4
	1990	50	5	7
Saluzzo	1984	27	13	1
	Total	351	95	33

* This column reports clutches laid in the first half of August or in an unknown period

foraging efficiency of the adults decreases to a considerable extent they are unable to provide sufficient food for three chicks and, as a result, fewer young are raised from clutches of 3 eggs than from clutches of 2 These findings were compared to those from another long-term population study of the same species carried out in Switzerland (Weitnauer and Lack 1955), where summer is normally much finer and warmer The breeding success was generally higher in clutches of three eggs and accordingly most females (67%) laid 3 egg clutches The comparison was also extended to another species, the alpine swift (*Apus melba*) where three-egg clutches were most successfull, and 66% of the females laid clutches of this size In this species clutch size and number of young fledged were not related to the weather in May (Lack and Arn 1947)

The pallid swift *Apus pallidus* shares with the alpine swift a Mediterranean distribution, but differs from it in breeding habitat. the pallid swift nests in cliffs along the Mediterranean coast and in urban areas up to 46° of latitude – N Italy, S Switzerland – (Boano 1979, Lardelli and Lardelli 1987), while the alpine swift, less common in urban areas, colonizes sea – but also mountain – cliffs The pallid swift breeds between May and October, and many females lay a second clutch in autumn (Boano and Cucco 1989, but see Thibault et al 1987).

In this paper we analyze the relationships between weather and laying dates, clutch size, breeding success of the pallid swift at three colonies in northern Italy

Study area and methods

The study was carried out from 1978 to 1990 in three colonies in Piedmont, northwestern Italy Carmagnola, Saluzzo and Torino These towns are situated within 30 km of each other The colonies are all in old buildings, and are relatively small, comprising 10–70 pairs (Table 1) In Carmagnola and Torino nests were easily reached and inspected from inside the buildings, while in Saluzzo they were inspected from the outside by means of a long ladder

Nests were numbered and inspected almost fortnightly (from 1978 to 1986) or daily (from 1987 to 1990) in Carmagnola, every 2–3 d in Saluzzo and Torino In the first study area all young and nearly all the adults were marked with metal-rings of the Italian ringing scheme In Torino all young and a few adults were ringed, no birds were marked in Saluzzo Two clutch-categories have been considered first clutches range from May to end of July, including some replacement laying Clutches ranging from mid-August to October were considered as second clutches (Boano and Cucco 1989), while eggs laid in the first half of August were of incertain status and precautiously excluded from the analysis Chicks regularly checked and leaving the nest after 40–45 d of nest permanence, were considered successfully fledged

The climate in the central part of Piedmont is continental and specifically defined "sub-litoraneo Padano" (Mennella 1967) Rainfall reaches a maximum in May and again in November From June to late October the weather in general is favourable, with high temperatures and few rainy days Meteorological data were obtained from the Bra Museum station (20 km south of Carmagnola) Following Lack and Lack (1951), we considered Temperature· Average maximum temperature (in 15-d periods) Rainy days· Number of rainy days (mm of rain > 1) during the period considered (in 15-d periods)

For clutch-size and laying date we considered temperatures and rains during the 15-d period of eggs deposition For the chick-rearing period (45 d) the three respective 15-d values were considered

Meteorological values in Bra were strongly correlated to values recorded in Torino, for temperature ($r=0\ 95$, 15-d periods $N = 88$, $p < 0\ 001$) and rainfall ($r = 0\ 78$, $n = 88$, $p < 0\ 001$)

Results

Comparison of the colonies in the areas considered

Laying dates

First clutch. Considering the years for which we had data on more than one colony (Table 1), we couldn't detect differences in 1984 (Student's t-test: $t = 1.23$, df

Table 2 Number of pairs laying at different times of the breeding season

Period	Colonies		
	Carmagnola	Saluzzo	Torino
1–15 May	15	0	5
16–31 May	46	0	56
1–15 June	32	10	55
16–30 June	27	12	42
1–15 July	7	3	28
16–31 July	2	2	19
1–15 Aug	2	1	25
16–31 Aug	3	4	36
1–15 Sep	11	5	25
16–30 Sep	4	2	1
1–15 Oct	0	2	2

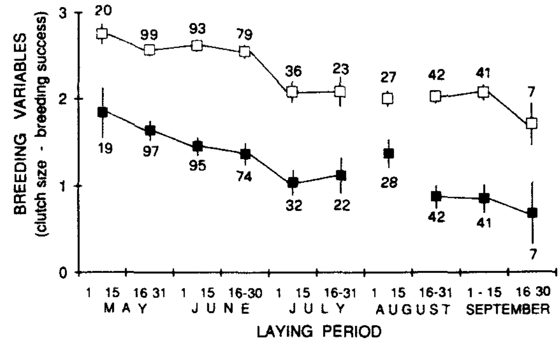

Fig 1 Clutch size and breeding success in relation to laying period □ = mean clutch size + s e ■ = mean fledged young + s e (relative to dates of egg-laying) Figures refer to the number of sampled nests From May to July first clutches From mid-August to September second clutches

= 38, n s) and 1987 (t=1 31, df=68, n.s), but significant differences occurred in 1988 (t = 2.2, df = 83, p < 0 05), 1989 (t = 4 0, df = 43, p < 0 01) and 1990 (t = 3 3, df = 67, p < 0 01) The comparison between Torino and Carmagnola colonies, on the whole, shows a difference in laying dates In Carmagnola, pallid swifts lay (on average, end of May) earlier than in Torino (mid June) (Table 2, χ^2 = 25 7, df = 5, p < 0 001)

Second clutch In the Carmagnola colony rather few females laid a second clutch, and only in four of the ten years checked This prevents definitive conclusions and do not allow a statistical analysis However, the observations suggest earlier date of deposition in Torino (second half of August) than in Carmagnola (first half of September)

Clutch size

First clutch There were no differences in the size of clutches in the three colonies (Table 3, t-tests. n s) Their means were remarkably similar, ranging from 2 41 eggs/nest (Torino) to 2 56 (Saluzzo) through Carmagnola, 2 51 Comparisons for the five years with more than one colony sampled confirm this uniformity (1984 t=1 64, df=38, n s , 1987· t=1 29, df=67, n.s., 1988 t=0 7, df=83, n.s , 1989. t=1 6, df=42, n s., 1990 t=1 33, df=65, n.s).

Second clutch There were no differences among the three colonies (Student's t tests n s.) The majority of females laid two eggs Carmagnola 66%, Saluzzo 77%, Torino 73%

Fledged young

First brood Considering the matched years, we found no differences between colonies in 1984 (t=1 14, df=38, n s), in 1987 (t=0 72, df=62, n s) and in 1988 (t=0 10, df=72, n.s), while in 1989 (t=2 08, df=38, p<0 05) and 1990 (t=2 47, df=73, p<0 02) there were more fledged young in the Carmagnola than in Torino On the whole, more young fledged in Carmagnola colony than Torino (Table 3, t=1 96, df=248, p<0 05) Breeding success of the Saluzzo' colony was lower but did not differ from the other two colonies because of the small sample.

Second brood The small samples and/or the differences in sampled years don't allow a comparison between colonies

Clutch size and fledged young in relation to laying dates

There was a clearcut decrease in clutch size as the breeding season proceeded (Fig 1). More than 60% of the females laid eggs in late May and June and these

Table 3 Productivity in the three pallid swift colonies First broods

Colony	Eggs laid					Fledged young				
	1	2	3	4	Mean	0	1	2	3	Mean
Carmagnola	11	49	85	0	2 51	47	19	53	29	1.43
Saluzzo	1	10	16	0	2 56	10	5	7	5	1 26
Torino	32	61	102	6	2 41	45	49	66	26	1 39
Total	44	120	203	6	2 46	102	73	126	60	1 40

Table 4 Correlation between mean laying period and weather parameters

Parameter	Period	Corr coeff	p
Rainy days	16–30 April	0 368	n s
	1–15 May	0 299	n s
	16–31 May	0 543	0 05
Mean Temperature	16–30 April	0 347	n s
	1–15May	−0 467	n s
	16–31 May	−0 513	0 05

females had a bigger clutch size Clutches in late July were mainly replacement-clutches. The second clutches were concentrated in late August and in first half of September and accounted for c 20% of the total eggs laid

A declining trend was also observed for fledged young (Fig. 1) The progressive decrease was interrupted only in late July, when substitution clutches enhanced the average fledging success The low fledging success of the last autumnal breeding period is notable

Correlation between climatic conditions and annual reproductive parameters

The statistical analysis has been done only for the first clutch To few data are available to draw definitive conclusions on the second clutch Considering each colony as a distinct sample, we obtained 14 values for the ten year period considered A very low breeding success was detected only in 1985, due to a sudden and unexplained abandonement of the colony of Carmagnola by all the parents during the course of the nesting period For this reason, 1985 has been excluded from these statistical analyses

Laying dates

Rainfall and temperature in May influenced the laying dates of the first clutch Good weather conditions during May allowed the females to lay the first clutch, while prolonged rains and cold temperatures delayed egg deposition to June Considering each year in each colony separately (N=14), an inverse relationship between laying date and temperature in the second half of May was found (Table 4). On the other hand, an increase in the number of rainy days in May was correlated with a delay in laying (Table 4). The previous climatic conditions (rains and temperature of end April) did not influence the timing of egg deposition (Table 4). The values tested for correlation were scattered, so significant correlations only explain c. 30% of the variability observed. As reported above, another source of variability was represented by the differences in the colonies themselves. In Torino, on the whole, the dates are delayed when compared to Carmagnola.

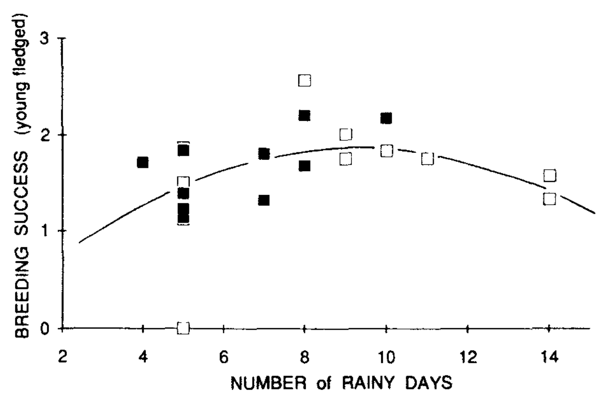

Fig 2 Relation between the pallid swift breeding success (first broods) and number of rainy days □ = May clutches ■ = June clutches Each square corresponds to a single year and colony value

Clutch size

There were no correlations between climatic conditions and clutch size The mean clutch size in different years was not correlated with the respective mean temperatures (r=-0 30, N=14, n s) or number of rainy days (r=-0 15, N=14, n s)

Fledged young

Breeding success varied from 1 14 to 2 56 young/nest in the ten years considered In order to evaluate a relationship with weather conditions we considered each year for each colony separately Analysis was limited to May and June, the most utilized periods for laying, and year with small samples were excluded No significant linear relationships was found between number of rainy days (Fig 2) or temperature (Fig 3) the and number of

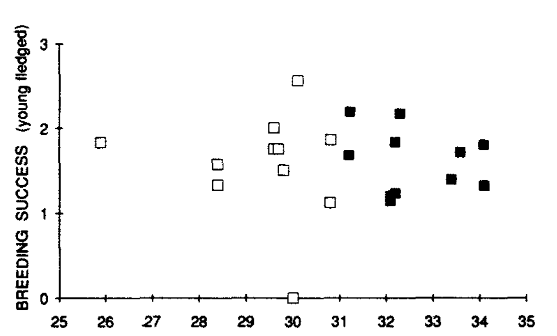

Fig 3 Relation between the pallid swift breeding success (first broods) and mean temperature □ = May clutches ■ = June clutches Each square corresponds to a single year and colony value

Table 5 Breeding success in relation to clucth size in first and second cluthes

Clutch size	Number of young fledged											
	First clutches						Second clutches					
	0	1	2	3	N	mean	0	1	2	3	N	mean
1	19	17	–	–	36	0 47	11	1	–	–	12	0 08
2	25	26	45	–	96	1 21	30	13	24	–	67	0 91
3	35	26	70	59	190	1 80	4	3	6	1	14	1 29
4	2	1	2	1	6	1 33	–	–	–	–	–	–

fledged young A second order regression between number of rainy days and breeding success was, however, statistically significant ($p<0$ 03, $N=21$, $r=0$ 57) The optimum value corresponds to 9 rainy days in the 45 d of chicks rearing, while lower or higher rates of rainfall are seen to correspond to lower breeding success However, this correlation explained only 33% of the variability in the number of young fledged

Clutch size and number of young fledged

During the first laying period a majority of females (58%) produced three eggs (Table 5), and this class is more productive than the two-eggs clutch ($t=4$ 72, $df=284$, $p<0$ 01) Only six females in the ten years studied laid four eggs The mean number of fledged young per pair was 1 4 in the first broods

A second clutch was laid by c 27% of the females The mean fledging success was 0 87 young per nest, a value lower than the first one ($t=5$ 3, $df=429$, $p<0$ 01) A few females (15%) laid three eggs at this time Their breeding success was higher (Table 5), but not statistically different from that recorded for the 2-egg clutches ($t=1$ 41, $df=79$, n s)

Discussion

In this study we observed a difference in the reproductive phenology of the two more sampled colonies at Carmagnola, in some years, the females laid eggs earlier than in Torino It is difficult to establish if this was related to local differences in weather conditions and/or arthropod abundance The two colonies are relatively near, and swifts are known to move over many km to capture food on the wing (Lack 1956). Other factors, such as demographic composition of the colony (Wooler and Coulson 1977, Pugesek 1987) and physiological condition after migration also could influence breeding success

The pallid swift follows the rule described for aerial feeders, and more generally for breeding birds of the temperate zone (Perrins and Moss 1975), according to which larger clutches are deposited early in the season.

In the common swift (Lack and Lack 1951) and in the house martin *Delichon urbica* (Bryant 1975), clutch size is seen to depend on environmental parameters Lack and Lack (1951) indicated laying-time temperature as a fundamental factor Bryant (1975) did not find a correlation between temperature and clutch size, but the quantity of aphids in May was the closest parameter for explaining this life-history trait In our study we could not find a relationship between clutch size and weather parameters However, a clear relationship was obtained between laying dates and weather considering May temperature and rainfall When May is unfavorable some pairs postpone eggs deposition until the second half of June Compared to the common swift, the deposition dates of our species appear less concentrated in the second half of May, when the majority of the Oxford common swifts deposit eggs. Like the pallid swift, the alpine swift can delay egg-laying in the event of particularly wet and cold May months (Lack and Arn 1947) This appears to be an important difference in the life-history tactics of the Mediterranean breeders vs the cool temperate aerial feeders. Apparently such a shift is possible in the southern species, since the both of them migrate in late summer or autumn. On the contrary, the common swift starts migration at the end of July and cannot postpone laying

Broods reared early in the season are the most successful as observed in other species (Perrins and Moss 1975).

The dependence of pallid swift breeding success on climatic factors seems less strong than that observed in the English (Oxford) populations of the common swift For this species, an 8 yr study (1948–1954) revealed a clear relationship between average maximum temperature during the 6 wk after the hatching and breeding success (Lack 1956). In close agreement with our data, the 15 yr study conducted in Solothurn on the alpine swift shows that a parameter of the year's weather conditions (i.e., the weather in May) is not a good predictor of swift breeding success (Lack and Arn 1947). The common swift populations in Switzerland also seem to be protected against bad weather, since in 9 yr of study (Weitnauer and Lack 1955) breeding success was seen to be affected by the weather only in 1948, when frequent rain was accompanied by severe cold, making the weather much worse than in England a bad weather threshold can be assumed for these populations

In French Mediterranean populations of common swift a rather specific weather-dependency of breeding success has been supposed (Gory 1987), involving a critical influence of strong winds (mistral), a negative effect of hot temperatures on chicks survival and a positive effect of rains, ascribed to the abundance of insect swarming after heavy rains This relationship is consistent with our findings, as pairs with higher breeding success raise young in periods with intermediate rates of rain Prolonged wet or dry conditions seem to hinder offspring survival.

In a tropical double clutched swift, the house swift *Apus affinis* (Razack and Naik 1968), the positive effects of rainfall is even more evident in the second breeding season, when it rains intermittently, the parents can feed three chicks During the first, drier breeding season, rains induce insect swarming only at the beginning of the season and the average clutch size is two

The most productive clutch size of the two Mediterranean species, the alpine and the pallid swift, is invariably three eggs and differs from that of northern populations of *Apus apus*, in which two eggs clutches were more productive in poor weather conditions Most females in both the Mediterranean species lay three eggs On the contrary in the second deposition of the pallid swift, the three eggs in the second clutch is deposited only by 15% of the females It is still unknown to what extent the differences in weather conditions in autumn and the decrease of the light period affect the second clutch size and the relative breeding success

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