

Survival rate and mate fidelity in the Pallid Swift *Apus pallidus*

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Abstract - Survival and fidelity both to the mate and to the nest were studied in a colony of Pallid Swifts in Piedmont (NW Italy). An overall adult survival rate of 75%, as estimated by the Jolly-Seber and related methods, was found in the whole colony. Females and males showed no differences in survival rate; the mean life span as an adult was 3.61 years. Adult breeding birds showed a wide range of strategies: some were faithful to the nest cavity or to the partner for many years, but a considerable percentage of birds changed cavity and/or partner year after year. Compared with other European species of swifts, the Pallid Swift seems to be characterized by slightly lower survival and less intense mate and nest fidelity.

Introduction

Long term studies of colonial birds have shed light on many aspects of life-history and mating system theories (Newton 1989). Among the pioneering studies, Lack's work on population dynamics has had a major impact. In this view (Lack 1954, 1966), mortality and its relation to ecological factors play a critical role in the regulation of animal numbers.

In ornithology, mortality (or survival) estimates have traditionally been derived from analyses of ring recoveries (i.e. recoveries of marked birds, usually found dead, made by the general public from a large geographic area: Haldane 1955, Brownie *et al.* 1985). Currently, they are also being derived from analyses of recaptures or resightings of live marked birds (i.e. recaptures of marked birds, usually made at a local study area) in association with proper stochastic open-population models (Cormack 1964, Nichols *et al.* 1981, Seber 1982, Clobert *et al.* 1985, Pollock *et al.* 1990).

A major problem in estimating mortality from capture-recapture studies at a local site arises from the possibility of permanent emigration: if a significant part of the population, although alive, does not return to the sampling site in the subsequent sampling times, then mortality estimates will be positively biased. Thus bird species known to be strongly philopatric are more suitable for investigation by this last method. In any case estimates derived from capture-recapture

experiments have to be regarded as minimal survival values.

Survival estimates arising from local studies are valid for a clearly defined population, which is not the case in large-scale recovery studies. At such a local scale other biological phenomena can also be easily studied, thus providing good opportunities to test hypotheses of ecological and methodological interest (Clobert *et al.* 1985).

Long-term studies of Holarctic swifts have been extant since the middle of the century. In particular, the Common *Apus apus* and Alpine *A. melba* Swifts have been extensively studied (Lack 1956, Weitnauer 1947, Arn 1960, Koskimies 1950), whereas there are no such long term studies of the more southern Europe Pallid Swift *A. pallidus*. This last species differs from the other two mainly in one aspect of its reproductive biology, the laying of a second clutch, which occurs in about 30% of the pairs nesting in spring (Cucco *et al.* 1992). As result, the laying period is protracted until very late in the season; eggs are found in September and chicks are fed for the whole of October and sometimes November (Boano and Cucco 1989). A survey of European swift studies (data from Cramp 1985) shows that *Apus* species are long-lived and survival, calculated on ring recoveries, is high. It ranges in the Common Swift from 84% (Oxford) to 76% (other areas in Britain), while in the Alpine Swift survival is 79% (Switzerland). First-year swifts are much less likely to survive than adults; their

survival rate is only 24% in the Alpine Swift, and similar values have been reported for the Common Swifts. The only study of survival in a Pallid Swift colony was in Gibraltar (Finlayson 1979), where a lower rates have been found (74% survival in adults and 33% in first-year birds).

Adult European swifts are well known to be highly philopatric, so they are suitable for survival analysis by capture-recapture experiments. Partners in a pair have been found together for 12 years. Fidelity has been demonstrated both to the nest-cavity and to the previous partner. Also in the Pallid Swift, marked fidelity to colony and nest site have been described (Finlayson 1979).

In this paper we summarize 17 years of observations in a colony in Piedmont (NW-Italy). Data are reported on colony consistency, survival rate and mate fidelity.

Methods

The study was carried out from 1976 to 1992 in the town of Carmagnola (NW-Italy). The climate in the area is continental and specifically defined as "sub-litoraneo Padano" (Mennella 1967). Rainfall reaches one peak in May and another in November. From June to late October the weather is generally favourable, with warm temperatures and few rainy days.

The colony is situated in an old building and, during the study period, we observed a yearly average of 13 pairs (min 7, max 19, Figure 1). The nests were easily reached and inspected from inside the building. Nest-cavities were numbered (N=22) and inspected almost fortnightly (from 1976 to 1986) or daily (from 1987 to 1992). From 1987, all young and nearly all the adults

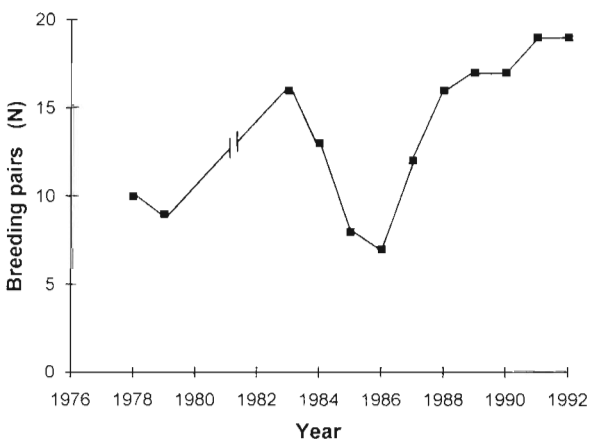


Figure 1. Number of first clutches observed in the Carmagnola study colony.

were marked with metal rings of the Italian Ringing Scheme; before 1987 ringing effort was not so intensive.

Nest and mate fidelity

The Pallid Swift typically lays a first clutch in May-June, and some females lay a second clutch in August-September (Boano and Cucco 1989). In this paper we will only analyze nest and mate fidelity in the first clutches, because the adults were not regularly captured in autumn during the second breeding period. The identity of the individuals nesting in the different cavities was ascertained by capturing the adults at night. To avoid disturbance and the possibility of nest-abandonment, the captures of adults took place when their nestlings were at an age of 40 days, which is near the fledging date. Birds were immediately released after the usual ringing operations and measurements of wing length and weight.

Sex of the adults was ascertained only in the years from 1987 to 1992. In this period the breeding Pallid Swifts were individually marked by bleaching a few feathers on their back (Malacarne and Griffa 1987), and the behaviour at the nest was monitored by videocameras (Malacarne *et al.* 1992). Sex was determined by examining the videotapes recorded during the days of laying, and detecting which of the two parents laid the eggs.

Breeding parameters

The laying date in each year is influenced by the weather conditions (Cucco *et al.* 1992). In order to investigate differences in the laying date between classes of adults (those that did or did not change nest or mate), and to avoid the effect of weather, we calculated for each year the median date of laying in the colony, and then we calculated for each female the difference between her laying date and the median date for that year (i.e. the number of days earlier or later than the median).

Means and standard deviations were calculated on logtransformed values, when necessary, in order to correct for the errors caused by non-normal distributions (Fowler and Cohen 1992).

Clutch and brood sizes were ascertained from 1987 to 1992 by daily inspections of the nest-cavities. Chicks which exhibited regular growth and left the nest after 40-45 days, were considered successfully fledged.

Survival rate

Demographic parameters were estimated using the Jolly-Seber and related stochastic models (Jolly 1965, Seber 1965, Brownie *et al.* 1985, Pollock *et al.* 1990).

These models include parameters for both survival (s) and capture probabilities (p). Survival probability is the probability that a bird which is alive during the period i will still be alive and in the sampling area during the period $i+1$. As with all capture-recapture sampling, the complement of survival probability estimates ($1-s$) includes both mortality and permanent emigration.

Capture probability is the conditional probability that an individual will be caught during period i , given that the individual is alive and in the relevant area at the time of sampling. Survival estimates based on these models differ from estimates which equate survival and recapture rates, because the models explicitly include the possibility that an individual is alive and in the population being sampled, but simply not caught. In contrast, methods which equate survival and recapture rates require the assumption that capture probability is 1, and they yield unbiased estimates of survival only in the very unusual condition in which every marked animal still in the population is actually caught (Nichols and Pollock 1983). Other parameters estimated by the models are the number (N) of birds present in the population in each sample period, and the recruitment (i.e. the number of birds entering the population between sample period i and sample period $i+1$).

The basic assumptions of the Jolly-Seber model are discussed by Seber (1982), the most important being: (1) every bird present in the population at the time of sampling in period i has the same probability of being captured;

(2) every marked bird present in the population immediately after sampling period i has the same probability of surviving until period $i+1$;

(3) marks are not lost or overlooked;

(4) all emigration is permanent;

(5) the sample is instantaneous (i.e. the sampling time is negligible in relation to the intersample period).

Biased estimates of the parameters of interest may result from any departure from the above assumptions. Unfortunately, heterogeneity among individuals in either survival or capture probabilities likely affects animal populations (Johnson *et al.* 1986). If survival probabilities vary among individuals, then estimates will also be biased. If both capture probabilities and survival probabilities vary among individuals, and are correlated, the captured animals will not be representative of the general population with respect to survival rate. Heterogeneity within a population can arise from several sources, some of which are often associated with a measurable variable such as age or sex. We were forced to study only adult birds because of the very low philopatry of the young. We were, however, able to test sexual differences in survival because most birds were sexed at laying. Our data were collected each year in July (a few in June and August), to satisfy assumption 5.

All the estimates were obtained using the computer programs JOLLY (Pollock *et al.* 1990). These programs provide parameter estimates under the basic Jolly-Seber model (Model A) and other related models which either generalize or further restrict assumptions about capture and survival probabilities (assumptions 1 and 2; Table 1). The programs also provide goodness-of-fit tests and specific tests for individual assumptions. The input format adopted here consists of the capture histories of all the birds, coded with 0 (not captured in the sample period) or 1 (captured at least once in a sample period).

The mean life span as an adult (MLS) was calculated, according to Brownie *et al.* (1985), as: $MLS=1/\log(s)$.

Results

Survival rate

The number of adult Pallid Swift ringed per year was on average 13, for a total of 78 birds.

Table 1. Summary of models provided in the JOLLY computer program.

Models		Definitions
*	**	-
A	st, pt :	standard Jolly-Seber model, permitting time specific capture and survival probability;
B	s, pt :	reduced-parameter model with time specific capture probability, but survival probability assumed to be constant;
D	s, p :	reduced-parameter model with constant capture;
2	st, s^*, pt :	the most general model, similar to model A, but permitting also different survival probabilities for newly ringed birds (s^*) versus previously ringed birds.

* After the notations of Pollock *et al.* (1990).

** After the notations of Clobert *et al.* (1985).

We first consider the survival probabilities of females (N=32) and males (N=21) separately (Table 2). JOLLY's estimate under model A was the only one appropriate for the female data, even though model D would be acceptable, and more precise, for males. The values estimated by model A for the two sexes are 0.88 and 0.85 respectively.

Table 2. Mean adult survival rates of the Pallid Swift under model A (sexed birds).

	<i>s</i>	S.E. (<i>s</i>)	<i>p</i>	S.E. (<i>p</i>)
Females	0.884	0.052	0.815	0.159
Males	0.852	0.056	0.594	0.146

Survival rates and capture probabilities of females and males, compared with the *z* test (Brownie *et al.* 1985), showed no significant differences ($z(s)=0.416$ and $z(p)=1.02$, $P=n.s.$). Therefore, for further analysis we lumped together all the adult recoveries (females and males plus non-sexed birds, N=78). In this case model D is not rejected (Table 3); nevertheless, annual variation in survival rate appears to be very likely for the Pallid Swifts, thus we believe model A (Table 3) better describes survival in our colony. The goodness-of-fit tests ($\chi^2=4.73$, $d.f=4$, $P=0.316$ n.s.) suggest no strong violations of the assumptions of the Jolly-Seber model. The survival rate estimate (0.749) is lower than those calculated for sexed birds; these findings will be discussed below.

The population size estimates are shown in Table 4. The mean number of males was slightly less than that of females, which resulted from the fact that captures were done at the end of the breeding period for each nest, when frequently only one parent spent the night in the cavity.

Table 4. Population size estimates (values calculated by the Jolly program: model D for the whole population and males, model A for females).

Year	Population size		Females		Males	
	N	s.e.	N	s.e.	N	s.e.
1988	33.2	4.95	10.0	–	11.3	2.08
1989	45.0	5.09	19.7	2.0	14.8	1.75
1990	38.8	3.55	23.6	5.0	13.1	1.29
1991	47.9	5.94	16.0	–	11.5	1.54
1992	44.4	6.35	–	–	14.1	2.33
Model D mean	41.8	8.52	17.3	–	13.0	2.66
Model A	36.3	3.33				

Table 3. Adult survival rates of the Pallid Swift (all birds).

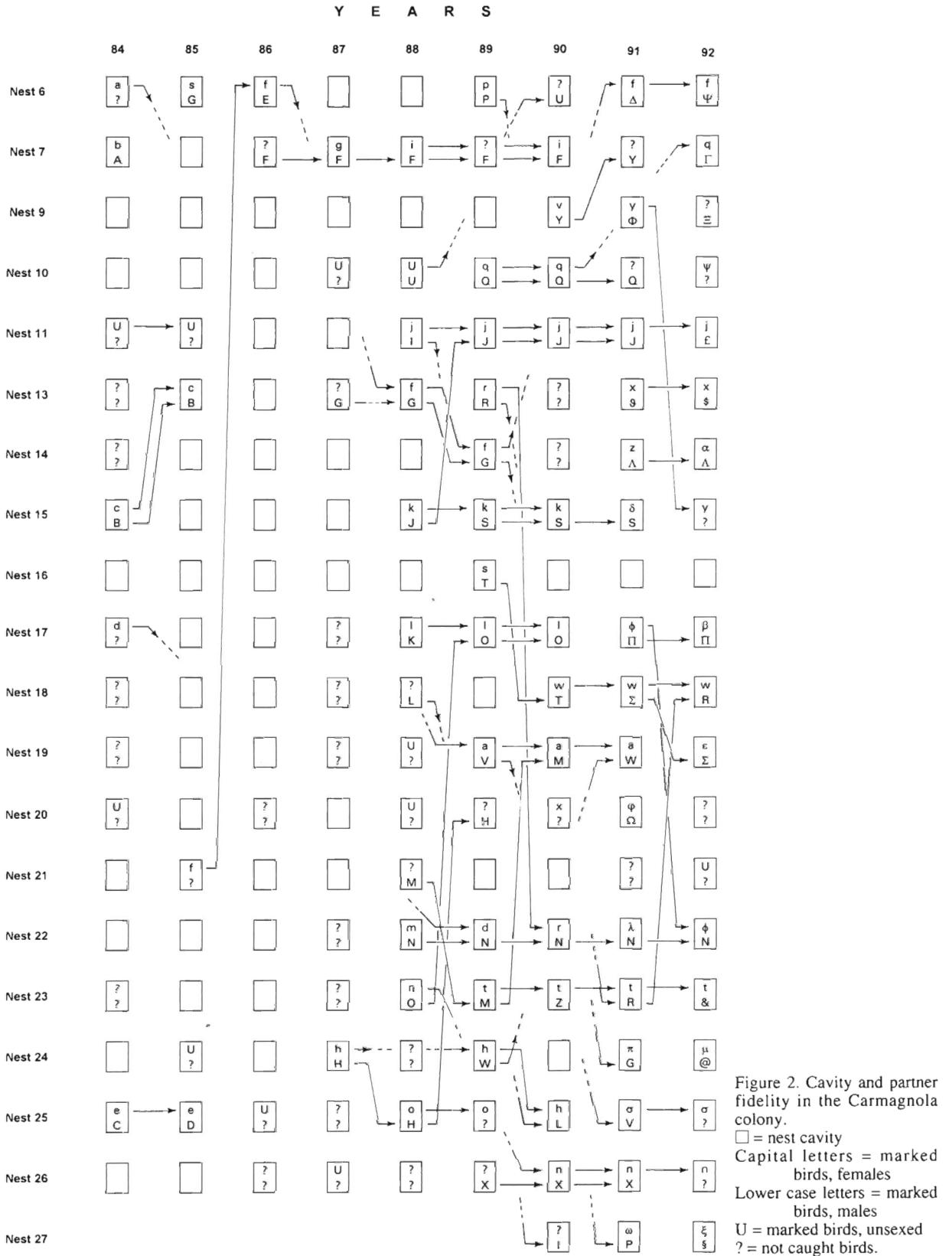
Model D		
<i>s</i> = 0.749		S.E. (<i>s</i>) = 0.050
<i>p</i> = 0.653		S.E. (<i>p</i>) = 0.005
95% conf. interval of <i>s</i> = 0.651-0.846.		
Model A		
Year	<i>s</i>	S.E.
1987	0.754	0.186
1988	0.838	0.105
1989	0.940	0.143
1990	0.500	0.114
Mean	0.758	0.058

The estimated population of the colony was about 40 individuals (Table 4), a value which is greater than the sum of sexed females and males because each year some swifts were captured but could not be sexed.

The mean life span as an adult was 3.46 years. The Pallid Swifts can nest for the first time at the age of two as indicated by two cases of birds ringed as nestlings, and retrapped during reproduction. Longer pre-reproductive periods of three to four years have been reported for the Common Swift (Perrins 1971) and cannot be ruled out for Pallid Swift as well.

Nest-cavity fidelity

Adults did not show a strong fidelity to the nest cavity: on average 29.2% of the birds that were present and alive the following year changed cavity (Figure 2). There was no significant difference between females (36.3%) and males (27.3%) in the number of birds changing nest sites ($\chi^2=0.70$, $d.f.=1$; $p=n.s.$). The greatest nest fidelity was exhibited by two females and one male which utilized the same



cavity for at least five years, even though their partner changed during this period.

There was a difference in laying date between birds which changed cavity or did not (Mann-Whitney test: $U=258$, $N=60$; $p<0.036$). Laying occurred 2 days earlier than the median date in birds nesting in the same cavity, but 0.5 days after the median date in birds which changed nest-cavity (Figure 3).

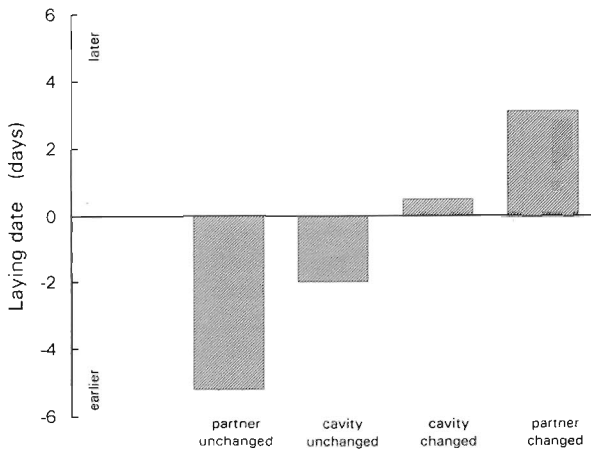


Figure 3. Median laying dates in birds changing or not changing the mate or the cavity.

The clutch size did not vary ($U=120$, $N=30$, $p=n.s.$) between females changing (2.7 ± 0.48 eggs) or not changing (2.9 ± 0.31 eggs) the cavity (Figure 4). A similar result was found ($U=68$, $N=28$, $p=n.s.$) in the comparison of the females paired either to males that changed (2.8 ± 0.41 eggs) or did not change (2.9 ± 0.35 eggs) the cavity. In comparison to the previous year, there was a slight, but not significant, increase in the clutch size both for cavity-changing and non-changing females ($+0.17$ and $+0.29$ eggs, respectively; $U=46$, $N=19$, $p=n.s.$), and in females paired either to cavity-changing or non-changing males ($+0.21$ and $+0.29$ eggs, respectively; $U=52$, $N=21$, $p=n.s.$).

The number of young successfully fledged was not significantly different (mean values ranging from 2.3 to 2.5 young/nest) between females who changed or did not change the cavity ($U=70$, $N=26$, $p=n.s.$), nor between females paired either to males who changed or did not change the cavity ($U=39$, $N=22$, $p=n.s.$). In comparison to the previous year, there was a slight, but not significant, increase in the breeding success both in cavity-changing and non-changing females ($+0.25$ and $+0.86$ young/nest, respectively; $U=49.5$, $N=19$, $p=n.s.$), and in females paired either to cavity-

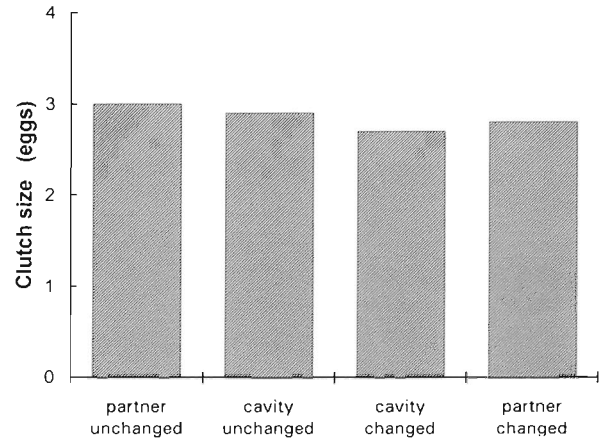


Figure 4. Mean clutch size in birds changing or not changing the mate or the cavity.

changing or non-changing males ($+0.29$ and $+0.86$ young/nest, respectively; $U=58$, $N=21$, $p=n.s.$).

Mate fidelity

Adults did not show a high fidelity to their mates: on average the partner was changed by 58.3% of the birds whose partner was present and alive the following year (Figure 2). The greatest mate fidelity was exhibited by a pair of birds found together for three years. The opposite was shown by a male who, in the period 1985-92, nested successively in 5 different cavities and paired with 4 different females. Mate fidelity was not correlated to cavity-fidelity: in only one case, a bird that changed cavity moved together with the partner of the previous year, while in the remaining cases the mate of the previous year either did not change cavity or moved to a different one (Figure 2).

There was a significant difference in laying date between birds with changed or unchanged mate (Mann-Whitney test: $U=46.5$, $N=34$; $p<0.04$). On average, layings occurred 5.2 ± 1.0 days earlier than the median date in birds with unchanged mate, and 3.1 ± 1.1 days later than the median date when the mate was changed (Figure 3).

The clutch size was not significantly different ($U=59.5$, $N=29$, $p=n.s.$) between females who changed (2.8 ± 0.43 eggs) or did not change (3 eggs) mate from the previous year (Figure 4). Furthermore, the number of young successfully fledged was not different (mean values ranging from 2.8 to 3 young/nest) between females who changed or did not change mate ($U=49$, $N=24$, $p=n.s.$). In comparison to the previous year, there was a slight, but not significant, increase in the breeding success both in

mate-changing and non-changing females (+0.25 and +0.86 young, respectively; $U=49.5$, $N=19$, $p=n.s.$).

Discussion

Our estimates of survival in the Pallid Swift are based on the assumption that the adults show strong breeding philopatry. This is in accord with our observations (very many breeding adults have been recaptured year after year) and with all the long-term studies of European swift populations conducted to date (Cramp 1985).

The Pallid Swift survival rate calculated in this study does not differ from the estimates from Gibraltar. Adult survival in the three European swifts (Table 5) ranges from 74% to 85%. Pallid Swift values suggest that this species may suffer a higher mortality than its congeners. The estimated average life span of the Pallid Swift as adult (3.61 years) is, in consequence, lower than the values calculated for the Common Swift (3.64-5.73 years). On the other hand, given the considerable observed degree of variation between years, we believe that the aggregate standard error computed by the program and reported here may substantially underestimate the true uncertainty.

We did not find a sex difference in survival rate. This is in accord with some studies on birds in Britain (Dobson 1987), and on other colonial birds (e.g. Fulmar *Fulmarus glacialis*, Dunnott and Ollason 1978; Laysan Albatross *Diomedea mutabilis*, Fisher 1975; Short-tailed Shearwater *Puffinus tenuirostris*, Wooller *et al.* 1989). Sexual differences, however, have been shown in a few species in Britain (Dobson 1987, Coulson and Wooller 1976), and in another aerial feeder, the House Martin *Delichon urbica* (Bryant 1979).

Two results reported here must be considered critically: 1) the lower probability of capturing males than females could be due to a higher tendency of

males to fly away from the nest during ringing operations, at night; 2) the higher survival of sexed birds vs the other birds could be due to: (a) a bird which survives for a longer period of time, and thus returns many times to the colony, will be more likely to be sexed than a bird which dies after only one or a few seasons; (b) the presence of immature birds which visit the monitored cavities only a few times. In the Pallid, Common and Alpine Swifts, these first-year non-breeding birds are known to have a lower survival rate than adults (Finlayson 1979, Perrins 1971, Glutz and Bauer 1980).

The estimated size of the colony (c. 20 pairs) is higher than the average values reported in Gibraltar, where 50% of the colonies were of less than 10 pairs (Finlayson 1979), but it is similar to those reported in North Italy (Boano 1979, Boano and Cucco 1988) and France (Yeatman 1976).

Mate and nest fidelity are high in the Common and Alpine Swifts (Weitnauer 1980, Arn 1960), as is the case in the majority of monogamous colonial birds (review in Newton 1989 and Clutton-Brock 1988). Contrary to the current belief (Cramp 1985), Pallid Swifts did not show, in our colony, strong fidelity to the mate or to the nest-cavity.

In birds, pairs showing high mate fidelity have higher breeding success (Coulson and Thomas 1985). This advantage can be due, among other factors, to the breeding earlier in the season of previously matched individuals. In fact, as a rule in the temperate zone, females laying earlier have a higher breeding success (Perrins 1970). Also in the Pallid Swift, there is a tendency to lay larger clutches early in the season (Cucco *et al.* 1992). In this study, faithful pairs initiated egg-laying earlier (on average by about a week), but this was not sufficient to induce significant differences in clutch size, hatching or fledging success compared with non-faithful pairs.

In conclusion, the Pallid Swift has a slightly lower survival rate and lower mate/nest fidelity than the two

Table 5. Estimates of the survival rates (s) in Pallid, Alpine and Common Swift, made with ringing recoveries (a) or recaptures at a breeding colony (b).

	(s)	S.E.	N	locality	years	method	Reference
Pallid	0.74	—	—	Gibraltar	1973-77	—	Finlayson 1979
	0.76	0.06	78	Italy	1976-92	Jolly	This study
Alpine	0.79	—	—	Switzerland	>65	—	Glutz & Bauer 1980
Common a)	0.79	—	—	Britain	1954-66	Haldane	Perrins 1971
	0.76	0.025	111	Britain	1966-78	Haldane	Dobson 1983
	0.808	0.033	—	Britain	1956-76	Brownie MO	Baillie & Green 1987
b)	0.84	—	22	Oxford	1965-66	Haldane	Perrins 1971

other European species of *Apus*. Moreover, considering that the Pallid Swift frequently has two clutches per season (Boano and Cucco 1989), one may say that in a traditional life-history categorization (Pianka 1970) this Mediterranean species seems more "r-oriented" than *Apus apus* and *Apus melba*. In this light, the findings on European swifts seem to contradict the tendency, widespread among birds, for an increase in clutch size and mortality with increasing latitude (Cody 1966).

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Riassunto - In una colonia di Rondone pallido si sono studiati dal 1976 al 1992 i tassi di sopravvivenza e di fedeltà al nido e al partner. Il tasso annuale di sopravvivenza stimato con il metodo Jolly-Seber è pari al 76% e non esistono differenze tra i sessi. La vita media da adulto è stimata in 3.61 anni.

Esiste molta variabilità riguardo alla fedeltà: alcune coppie sono fedeli per più di un anno a partner e cavità di nidificazione, ma molti individui cambiano il sito di nidificazione e/o, in misura ancora maggiore, il partner rispetto all'anno precedente.

In confronto con le altre due specie europee del genere *Apus*, il Rondone pallido appare essere caratterizzato da una sopravvivenza lievemente inferiore e da una minore fedeltà al partner e alla cavità utilizzata per la riproduzione.

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