

Nest attendance, parental roles and breeding success in the Pallid Swift (*Apus pallidus*)

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Abstract. MALACARNE, G., M. CUCCO & G. ORECCHIA (1992): Nest attendance, parental roles and breeding success in the Pallid Swift (*Apus pallidus*). – Vogelwarte 36: 203–210.

Parental behaviour in relation to breeding success in the Pallid Swift has been studied from 1987–1990. Observations at the nest of sexed pairs showed similar roles during incubation, although in the first ten days females incubated more than males. In 36% of pairs a partner incubated significantly more than the other, but more equitable pairs did not have a higher hatching success. Pairs hatching more eggs spent a higher percentage of time for incubation. During chick-feeding, males and females had similar nest visit frequencies. These frequencies were constant in the first month but then declined close to fledging. Pairs raising more chicks had higher feeding rates, but each chick received the same amount of food as chicks in smaller broods. The involvement of the male and the female in feeding young varied within pairs. The higher the pair effort, the higher the breeding success, but more equitable pairs did not have a higher reproductive success. These data are in line with a model of optimal parental investment in biparental species, where a lower effort of a member of the pair is compensated by higher involvement of the partner.

Key words: Pallid Swift (*Apus pallidus*), parental behaviour, nest attendance, breeding success.

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1. Introduction

LACK (1968) stated that birds are mostly monogamous because both sexes enjoy the greatest reproductive success when they share parental duties: food requirements of nestlings make both male and female involvement necessary. Recently, BART & TORNES (1989) summarized the conditions under which male monogamous birds are likely to be of major importance in rearing the greatest number of offspring; the most important point for altricial birds is that the female cannot both incubate and feed the young alone.

A survey of monogamy in birds (WITTENBERGER & TILSON 1980) showed a complex picture due to the lack of special phylogenetical trends and of the difficulty detecting all the ecological factors exerting pressure on male fidelity. Among insectivorous birds, for aerial feeders (Hirundinidae and Apodiformes) the cost of providing food is considerable, since despite a relatively low metabolic cost of flight (HAILS 1979) the continuous hunting of flying insects is potentially expensive in energy terms (WILLIAMS 1988). Thus factors related to feeding ecology could be important in maintaining biparental care in aerial feeding birds. Monogamy is described as the most frequent mating system (LEFFELAAR & ROBERTSON 1986) although the Swallow *Hirundo rustica* at least, is a partial exception to the rule (MØLLER 1985). Data on swifts are more scanty than on martins and swallows. Although feeding visit frequencies are known for many swift species (review in TARBURTON 1986) and pair fidelity is inferred from ringing data on European swifts (LACK 1956; WEITNAUER 1947 for *Apus apus*; BOANO & CUCCO 1989 for *Apus pallidus*; LACK & ARN 1947 for *Apus melba*), there are only qualitative data on parental roles suggesting that both parents share incubation and feed the young.

Within species showing biparental care, potential conflict of interests between sexes can arise (TRIVERS 1972). Whilst the level of investment by each partner may be influenced by many factors, the investment of one partner should influence the contribution of the other. A general prediction from ESS (Evolutionary Stable Strategy) models (WINKLER 1987) is

that, except at very low levels of parental efforts, the optimal response to a reduction in investment by one partner is, for the other, to partially compensate by increasing its effort.

In this work we have examined male and female contributions to parental care of Pallid Swifts, a palaeartic circum-mediterranean species.

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2. Study Area and Colony Size

The Pallid Swift colony under study is in Carmagnola (Piemonte, NW Italy). The climate is continental and specifically defined "sublitoraneo padano" (MENNELLA 1967). Rains are at a maximum in May with a secondary peak in November. From June to late October atmospheric conditions are favourable, with high temperatures and little rain. The study birds nest in an old building in the town's central square. Behavioural observations on marked swifts were carried out in 1987 on 9 nesting pairs (none sexed); in 1988 on 12 pairs (7 sexed); in 1989 on 17 pairs (14 sexed) and in 1990 on 17 pairs (14 sexed). Out of 22 adults ringed in 1988, 16 returned to the colony the next seasons, while out of 30 adults ringed or controlled in 1989, 22 returned to the colony in the 1990. Data on breeding biology at this colony are available in BOANO & CUCCO (1989).

3. Methods

Nests are easily reached from inside the building. The internal nest-wall is well suited for eye or videocamera observations (MALACARNE & GRIFFA 1987). Each nest was lit by a 1 Watt lamp, the least that is sufficient for videocamera recording. Videocameras (Blaupunkt CR 2000S or Panasonic F10) were set in place between 6 and 7 a.m. and they recorded continuously for 8 hours.

Sexing: Pallid Swifts do not show any morphological dimorphic character. An easy recognition of the female by inspecting which individual is present in the nest is made difficult by the simultaneous presence of both parents during egg laying. For this reason we used a procedure based on the fact that females usually lay the second egg two days after the first one. In the laying period nest cavities were daily inspected and, when the first egg was found in a nest, one of the two parents was marked, the following night, with a white spot on the back (MALACARNE & GRIFFA 1987). Sex was stated two days later by examining the videotapes and detecting which individual laid the second egg.

Incubation: Observations started when the last egg was laid. Incubation period lasts about 21 days. Individual presences at the nests were ascertained by scan samplings (LEHNER 1979), with sample-intervals of 15 min. As Pallid Swift parents usually finished brooding about the 10th day after hatching, the observations continued until this moment (for standardization, 15 days after hatching in each nest). A total of 6839 records has been considered, of which 5525 were from sexed pairs.

Chick feeding: From hatching, we videorecorded each nest (average twice a week) with continuous 8-hour sessions. From the video tapes the feeding episodes were studied and reported on check lists. Slow motion replay allowed us to ascertain the individual involved in 76% (N = 29) of the visits at nests in 1988, while in 1989 the value was 88% (N = 592) and in 1990 it was 97% (N = 980). Sessions ended with the departure of the last fledgling. We have 1601 records of chicks being fed, in 2120 hours.

Equality: An equality index of partner involvement in the case of incubation or chick-feeding was calculated as:

$$E. I. = \frac{N \text{ of records with A individual}}{\text{records with A ind.} + \text{records with B ind.}} \times 100$$

The index ranges from 0 to 100, with 50 meaning absolute equality.

4. Results

The breeding seasons of 1987, 1988, 1989 and 1990 all had fine weather without prolonged periods of rain. Laying dates of the first clutches varied from early May until early July.

38 females (69%) laid 3 eggs and 14 (26%) 2 eggs. Hatching was successful for 86% of the laid eggs; mean fledging success was 1.91 (± 0.14 s. e., $N = 55$) young per nest. We excluded second clutches from the analysis, because only three females laid these clutches (August 1990).

4.1. Incubation and Brooding

Parents covered the eggs in 73.3% of the 6839 observations. There was a marked increase in the time spent incubating after the 5th day following clutch completion, when parents covered the eggs for about 85% of the time. Brooding levels of chicks were similar, and decreased sharply only when the chicks were 1 week old (Figure 1). Parents alternated at the nest regularly. They spent usually one to two hours in continuous incubation and the entrance in the cavity of a partner caused the leaving of the other. There were no differences in the pattern of alternation between morning and afternoon.

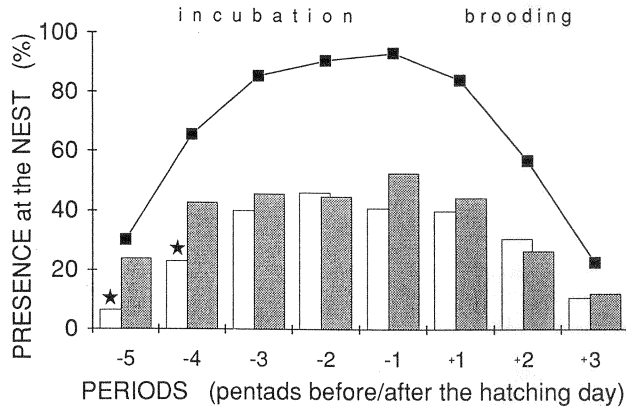


Fig. 1: Presence at nest and sex roles during incubation. ($N = 5525$ observations, 35 pairs). White bars = males, black bars = females, line = males + females. $\star = p < 0.01$, MANN-WHITNEY U-test.

Abb. 1: Prozentuale Antreffquote eines brütenden bzw. hudernden Altvogel (aufgeschlüsselt nach dem Geschlecht) vor und nach dem Schlüpftag. Weiße Säulen = σ , schwarze Säulen = φ , Kurve = $\sigma + \varphi$.

Overall the sexes shared incubation duties almost equally: out of 5525 records (only data of sexed pairs), males were recorded on eggs 1731 times (31.3%) and females 2048 times (37.1%). However, in 19 (35.8%) out of the 53 pairs examined, there was a significant difference (X^2 tests, $p < 0.05$) in individual contribution. Involvement was higher by the male than the female in 5 cases, with the reverse found in 7 cases. Sex was not ascertained in the other 7 pairs showing differences in individual contribution. In Figure 1 a temporal shift in parental nest attendance is shown. Females incubated more during the first ten days (MANN-WHITNEY U-tests: Pentad = -5, $p < 0.02$, $N = 17$ pairs; Pentad = -4, $p < 0.01$, $N = 33$ pairs; Pentad = -3 to Pentad = +3, $p = n. s.$), while male attendance reached female levels later and was maintained during brooding.

Table 1 shows variability among pairs in the time spent at the nest. Curiously at 2 nests parents were present in less than 5% of our diurnal samples but the eggs hatched successfully. Pairs spent more time incubating three eggs than other clutch-sizes (Table 2). Pairs incubating more eggs did not have more equitable distribution of duties (Table 2).

Table 1: Mean percentage time spent on incubation by Pallid Swift pairs (evaluation of scan samplings with sample – intervals of 15 min.).

Tab. 1: Prozentuale Antreffquote eines brütenden Altvogels bei Registrierung in 15-Min.-Intervallen.

(% records with parent at nest)	Presence at the Nest					Total
	0–20	20–40	40–60	60–80	80–100	
Number of pairs	4	2	4	13	32	55

Table 2: Presence at the nest and equality of incubation for different clutch sizes.

Tab. 2: Prozentuale Antreffquote eines brütenden Altvogels und Partnerbeteiligung (Gleichheits-Index) in Beziehung zur Gelegestärke.

Group	Eggs		Nests (N)	Presence at the Nest (% samples with parent)		Equality of Incubation (equality index)	
	Laid	Hatched		Mean	S. E.	Mean	S. E.
A	3	3	26	80.5	3.3	39.2	1.6
B	3	2	8	72.9	6.9	38.7	4.7
C	2	2	13	49.0	6.7	33.1	4.0
D	3	0/1	4	59.8	19.1	34.1	7.9
	2/1	0/1	3	48.6	13.8	26.9	13.5

Presence at nest: KRUSKAL-WALLIS χ^2 -test = 15.6; df = 3; $p < 0.001$

group A vs. C: MANN-WHITNEY U-test = 46; d.f. = 1; $p < 0.001$

group A vs. D: MANN-WHITNEY U-test = 40; d.f. = 1; $p < 0.05$

all other comparisons: MANN-WHITNEY U-tests; $P = n. s.$

Equality of incubation: KRUSKAL-WALLIS χ^2 -test = 2.28; df = 3; $p = n. s.$

4.2. Feeding of chicks

Feeding rates of Pallid Swifts ranged from 0.67 to 2.34 (trip*nest⁻¹*hour⁻¹). The number of feeding trips was slowly decreasing from hatching until the 45th day, when chicks were near fledging (Figure 3). Parents, in the first ten days, generally fed chicks and then brooded them for about 5–30 minutes. As with brooding, feeding roles show a broad equality between males and females. Out of 1601 videorecords of feeding events, we were able to ascertain the sex involved in 1392 cases. On the whole, 738 (53%) were performed by males and 654 (47%) by females. This equality in feeding rate was maintained throughout the rearing period (Statistics on 23 pairs, WILCOXON tests: n. s.; N = 9 sampled pentads per pair).

Feeding rates increased with brood size. Pairs successfully rearing more young, visited the nest more frequently (Figure 2; SPEARMAN Rank test, $r_s = 0.085$, N = 27, $P < 0.001$). This trend was maintained throughout the rearing period (Figure 3; Student t test significant for each 5-days period, exception in the first pentad). Each nestling, in broods of 2 or 3 young (Figure 4), received on average the same number of feeding visits (t-test for each pentad; $p = n. s.$; exceptions in the first and the fifth pentads).

The breeding success of the 27 pairs considered was not related to their equality in feeding roles (SPEARMAN rho = 0.03, n. s.).

Out of 55 pairs examined we found only one nest abandonment after the hatching of the eggs. This was by a female and led to breeding failure.

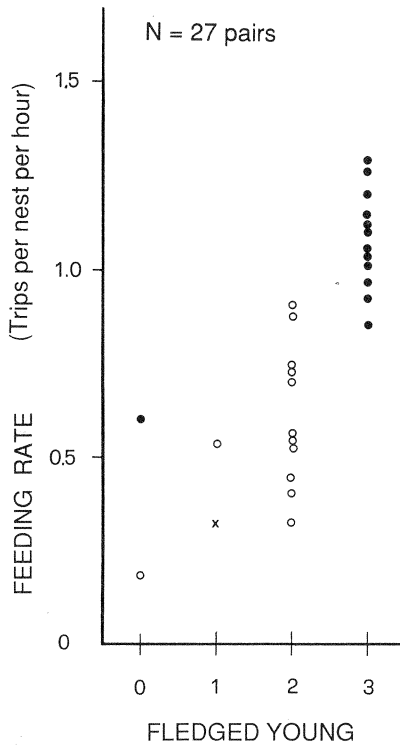


Fig. 2:
Feeding rate in relation to fledging success.
x = 1-young broods, o = 2-young broods,
● = 3-young broods.

Abb. 2:
Fütterrate (pro Nest und Stunde) in Beziehung
zum Ausfliege-Erfolg.
(x = 1 Junge, o = 2 Junge, ● = 3 Junge).

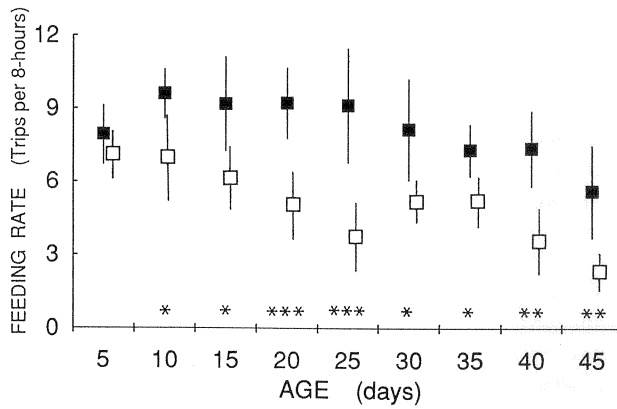


Fig. 3: Feeding rate per brood in relation to nestlings age. (Mean number of feeding trips per nest \pm s. e.; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$). □ = 2-young broods. ■ = 3-young broods.

Abb. 3: Fütterrate pro Brut in Beziehung zum Nestlingsalter (□ = 2 Junge, ■ = 3 Junge).

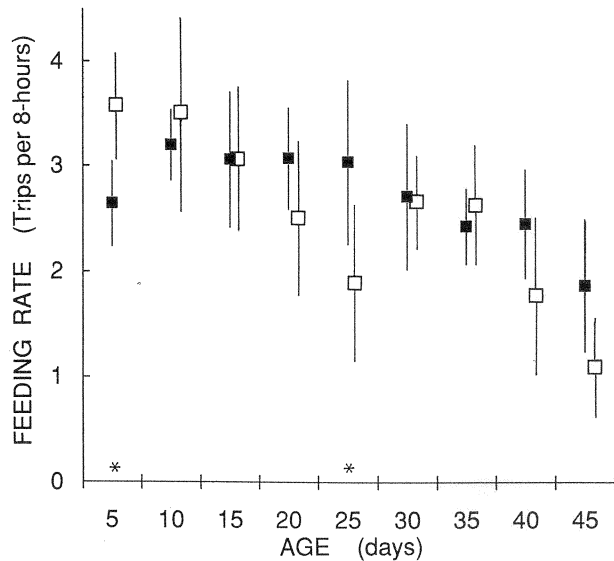


Fig. 4: Feeding rate per chick in relation to nestlings age. Mean number of feeding trips per chick ± 2 s. e.; * = $p < 0.05$; □ = 2-young broods, ■ = 3-young broods.

Abb. 4: Fütterrate pro Nestling in Beziehung zum Nestlingsalter (□ = 2 Junge, ■ = 3 Junge).

5. Discussion

Hatching and breeding success in our Pallid Swift population was similar to those reported in previous years (BOANO & CUCCO 1989) and for other Palearctic swifts (CRAMP 1985).

Attendance during incubation is often low in warm climates (e. g. for Hirundinidae and Apodidae: MOREAU 1939) and we report two cases of very infrequent incubation, at least during the day, that resulted in normal hatching success. In contrast, in the Common Swift cases of eggs left uncovered for six hours have been considered exceptional (LACK & LACK 1952).

The greater time spent incubating by pairs with three eggs vs. other clutch sizes, could be due to the presence of good quality parents both investing considerably in cares, or it simply reflects the difficulties of heating the clutch of three eggs.

Male/female similar contribution in incubation agrees with previous qualitative descriptions in *A. pallidus* (FINLAYSON 1979), *A. apus* (LACK & LACK 1951, PELLANTOVA 1975), *A. melba* (ARN 1950) and the majority of swifts (TARBURTON 1986), even if in the Pallid Swift we observed that females spent time on incubation earlier than the males. Hatching success, on the other hand, was not strictly related to equality in incubation, suggesting a compensatory effect of a partner when the other is neglectful.

Swallows and martins have more variable incubation roles than swifts, since there is a wide range from the Barn Swallow *Hirundo rustica*, where only the female incubates, to House Martins *Delichon urbica* or Bank Swallows *Riparia riparia*, where both sexes incubate although the male does not develop a full incubation patch and does only one third of the incubation (TURNER 1982).

Many swifts and swallows, e. g. the Chimney Swift *Chaetura pelagica* (KENDEIGH 1952, FISHER 1958), the Black Swift *Apus barbatus* (MICHAEL 1927), the White-rumped Swiftlet *Aerodramus spodiopygius* (TARBURTON 1986) and the Tree Swallow *Tachycineta bicolor*

(LEFFELAAR & ROBERTSON 1986), increase their feeding rates with chick age, while in the Pallid Swift we observed a slow decline. Yet, both the present and other papers on the feeding rate did not consider the weight of the food bolus, and these measurements would be necessary to determine the exact quantity of food delivered to chicks.

An increase in feeding rate as a function of brood size has been reported for many aerial feeders, as the Purple Martin *Progne subis* (FINLAY 1971), the Alpine Swift *A. melba* (ARN 1960), the Palm Swift *Cypsiurus parvus* (MOREAU 1941) and the White-rumped Swift *Apus caffer* (MOREAU 1942). Results are inconsistent with regard to the individual food intake in larger and smaller clutches (LEFFELAAR & ROBERTSON 1986). There were no differences in the food per chick in the White-rumped Swiftlet (TARBURTON 1987). On contrast, even though LACK & LACK (1951) observed an increase in number of feeding trips for larger broods of the Common Swift, they found that on average each chick received less food.

On the whole male and female Pallid Swifts fed nestlings at a similar rate. In the White-rumped Swiftlet of Fiji (TARBURTON 1986), where parents feed chick only once each day, similar contributions to feeding nestlings has also been reported. In this respect swifts are similar to the Hirundinidae where equal feeding rates by both sexes have been reported for the House Martin (BRYANT & WESTERTERP 1980), the Barn Swallow (BALL 1982), the Tree Swallow (LEFFELAAR & ROBERTSON 1986), the Purple Martin and the Wire-tailed Swallow *Hirundo smithii* (MOREAU 1947).

Equality in feeding young, however, was not related to the breeding success. As with incubation, we observed variability between pairs and the lower involvement of one partner was compensated by the other.

The data in this study indicate that the total effort is a better predictor of breeding success than the equality of effort by the pair. A general outcome from optimality theory is that, except for very low levels of parental effort, the optimal response to a reduction in investment by one partner is for the other to increase the effort (WINKLER 1987). In accord with this, by experimental lowering one partner's feeding contribution, WRIGHT & CUTHILL (1989) obtained a compensatory increase by the unmanipulated partner in the Starling *Sturnus vulgaris*. The observational data of this study are in line with the experimental data mentioned, since shortfalls by one's mate in the Pallid Swift seems to be compensated by the other. We cannot exclude however that these differences in parental contribution are caused by differences in the quality, age or experience of the parents.

6. Zusammenfassung

Nestanwesenheit, Rolle der Altvögel und Bruterfolg beim Fahlsegler (*Apus pallidus*)

Das Elternverhalten des Fahlseglers in Beziehung zum Bruterfolg wurde in einer Kolonie in Piemont (Norditalien) von 1987–1990 untersucht. Nestbeobachtungen von Paaren mit bekanntem Geschlecht der Partner zeigten eine ähnliche Rollenverteilung beim Brüten, auch wenn in den ersten zehn Tagen die ♀ häufiger brüteten. Bei 36% der Paare brütete ein Partner signifikant häufiger, doch Paare mit ausgeglichener Brutbeteiligung erzielten deshalb keine höhere Schlupfrate. Paare mit mehr Eiern brüteten länger. Während der Fütterungsphase waren ♂ und ♀ gleich häufig am Nest anwesend. Die Anwesenheitshäufigkeit war im ersten Monat konstant; sie nahm ab, wenn die Jungen nahezu flügge sind. Paare mit mehr Jungen fütterten häufiger, doch erhielten diese Jungen die gleiche Menge Nahrung im Vergleich zu Jungvögeln aus kleineren Gelegen. Die Beteiligung der Geschlechter an der Fütterung variierte zwischen den Paaren. Je höher die Leistung des Paares, desto höher war der Bruterfolg. Paare mit ausgeglichener Partnerbeteiligung hatten keinen höheren Fortpflanzungserfolg. Die Ergebnisse stimmen mit dem Modell über die optimale Elternbeteiligung bei biparentalen Arten überein, in dem die geringere Leistung eines der Partner durch eine stärkere Beteiligung des anderen Partners kompensiert wird.

7. References

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