

Sibling competition in asynchronously hatched broods of the Pallid Swift (*Apus pallidus*)

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Parent-offspring interactions during the rearing period were studied in the Pallid Swift, to examine competition for food among nestlings of different ages. We videotaped 1572 feeding events, in 26 nests over a period of 2 years.

Both parents and all chicks, in broods of two or three, were individually marked. Both male and female adults allocated food (insect boluses) with no apparent patterns of preference for any one nestling. Siblings hatched asynchronously and the last born chick obtained less food than the first one. Success in obtaining food was related positively to a nestling's begging activity. The area in the cavity where nestlings waited for parent arrival was not random, but tended to be in sectors close to the nest, where the majority of feeding events occurred ("activity centre").

The observed behaviours have been compared with those of other nidicolous birds with asynchronous hatching and a general pattern emerges: parents are apparently unselective in feeding chicks, and the competitive capacities of siblings in begging and positioning themselves in a proper central area have the largest effect on their ability to obtain food.

KEY WORDS: *Apus pallidus*, sibling competition, parent-offspring interaction, begging behaviour, hatching asynchrony.

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INTRODUCTION

Hatching asynchrony in altricial birds can result in parents favouring older nestlings at the expense of the last born. At first this phenomenon has been considered as a parental strategy for unpredictable periods of food shortage during

the breeding season (brood reduction hypothesis, LACK 1968). Subsequently many other competing hypotheses have been proposed (MAGRATH 1990). The size-differences between the young, from the very start of the nestling period, may lead to the starvation of the late-hatched chick (e.g. MALACARNE & CUCCO 1991). In most cases chick mortality occurs very early, otherwise the late-hatched young compete (intra-brood competition) for a long time with senior siblings to obtain food from the parents. According to the brood reduction hypothesis, parents are expected to discriminate between offspring, favouring large offspring in unfavorable conditions because they are more likely to survive. Similarly, in favourable conditions, female Budgerigars *Melopsittacus undulatus* (STAMPS et al. 1985) and Pied Flycatchers *Ficedula hypoleuca* (GOTTLANDER 1987) feed more to nestlings that are lighter in mass.

When there are very large disparities in size between siblings, cases of direct aggression, sometimes leading to siblicide, have also been reported (review in MOCK et al. 1990). In all colonial siblicidal birds (kittiwakes, boobies, pelicans and egrets), parents remain tranquil during sibling fights, doing nothing to thwart or distract the combatants (SPELLERBERG 1971, DRUMMOND et al. 1986, MOCK 1987). In coots *Fulica atra*, parents usually feed the chick closest to them, apparently regulating proximity by attacking chicks that persistently follow them; on those occasions when they do not feed the closest chick, they usually feed a chick smaller than the one closest to them (HORSFALL 1984). In a number of species, however, parents equalize the distribution of food, feeding the closest chick that is begging actively (RYDEN & BENGSSON 1980, MOCK & PARKER 1986, GOTTLANDER 1987, SMITH & MONTGOMERIE 1991) and sometimes refusing to feed the same nestling more than once in succession (BENGSSON & RYDEN 1981).

It is generally observed that the probability of a nestling being fed when a parent arrives at the nest, is clearly related to begging behaviour. Parents are more likely to feed a nestling that starts to beg earlier, extends its neck higher and holds its beak closer to parent's beak (e.g. LÖHRL 1968, RYDEN & BENGSSON 1980, GREIG-SMITH 1985, STAMPS et al. 1985, PLOGER & MOCK 1986, STAMPS & CLARK 1989, SMITH & MONTGOMERIE 1991). In hole-nesting birds, chicks must also choose the best area of the cavity in which to stay. In the Blue-throated Bee-eater *Merops viridis*, insects are delivered singly to chicks favourably positioned at the front of the nest chamber or in the nest tunnel (BRYANT & TATNER 1990). A proper position can lead to an advantage, because the entrance of the parents into the cavity is extremely rapid and feeding events occur after 1-2 sec. Positioning rules for offspring should depend on parental delivery patterns (MCCRAE et al. 1993). For example, parents could feed the young randomly in the nest cavity, in which case no optimal positioning strategy exists for offspring. However, if the feeding event occurs mainly in a single predictable sector, any chick present there before the parent's arrival would gain an advantage. Alternatively, if parents tend to feed young several times in the same sector, and the sector can sometimes switch during the day, the optimal strategy for the young would be to place themselves in the previously provisioned instead of the average sector of the nest (MCCRAE et al. 1993).

In this paper the behaviour of nestlings and parents during feeding visits is described in an aerial feeding bird, the Pallid Swift *Apus pallidus*, a Mediterranean species showing within-brood differential growth rates (MICELA 1991). The aim of this work is to investigate in detail the feeding of young and to examine: (i) whether parents feed their young selectively and (ii) how nestling begging behaviour influences food distribution and intra-brood conflict.

METHODS

The research was conducted in Piedmont (Northern Italy) during the breeding season, from April to August, in 1989-1990. The colony (17-19 pairs) was located on the external walls of an old building, in the town of Carmagnola (240 m a.s.l.), about 30 km South from Turin. The area is characterized by a temperate continental climate (Cucco et al. 1992). The nest cavities were modified for observation from inside the building, through the internal wall.

Our sample includes 12 and 14 broods in 1989 and 1990, respectively. There were two nestlings in 5 nests and three in 7 nests in 1989; one nestling in 1 nest, two in 6 nests and three in 7 nests in 1990.

The feeding events were recorded daily — in two (1989) or three (1990) different nests — with video cameras (Panasonic F10 CCD and Blaupunkt CR 2000S) connected to video tape recorders. Every nest was numbered and the filming procedure was made following a rotation schedule, therefore typically each nest was monitored for 1 day every 4-5 days throughout the whole (40-45 days) nestling period.

To avoid disturbance, the video cameras were placed behind the nest, whose back plywood wall had a rectangular glass window usually covered by a black cloth; the camera lens was placed against the glass through an opening in the black cloth (MALACARNE & GRIFFA 1987); moreover every nest had a small bulb (12 v, 1 w), whose luminous intensity was regulated by an adjustable rheostat. To detect both the existence of preferred sectors inside the nest-cavity and the possible monopolization of this area by certain nestlings, the image of the base area of the breeding cavity (seen by the television camera and displayed on a monitor screen) was subdivided into 25 sectors, in a 5×5 grid with the nest being in the middle (Fig. 1).

We have 1572 records of chicks being fed with total 2080 hr. In a few cases (9.2%) it was impossible to detect which nestling was fed. All those uncertain records were discarded from the analysis, so the recordings covered an effective period of 744 hr in 1989, and 1144 hr in 1990.

To allow individual recognition each parent was marked on the back with a little white spot, using a hair decolourizing paste applied by means of a small brush during the laying period (MALACARNE & GRIFFA 1987). Adults were sexed by examining videotapes recorded during egg laying to detect which individual was producing the egg. Nestlings were similarly marked with feather spotting; during the first 2 weeks, when the chicks are largely naked, a small white spot of non-toxic paint was directly applied on each nestling's skin (random position, on the back). Neither technique appeared to affect the natural behaviour of the birds, in comparison to non-marked birds observed in 1987-1988.

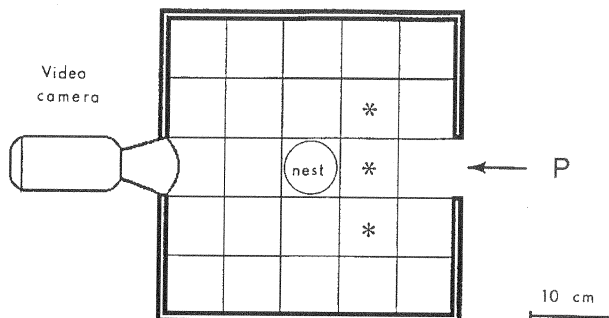


Fig. 1. — Top view of the 5×5 grid subdivision of the nest-cavity. The arrow points to the cavity hole through which the parents (P) entered; in the different nests the most utilized sector (activity centre) was one of the three squares indicated by asterisks.

The routine methodology provided eight daily recording-hours (from 07:30 to 15:30) for each recorded nest; subsequently all feeding events were located on the videotapes, and saved on backup video cassettes. Later, a slow motion replay allowed us to record the feeding schedule, in addition to general notes (date, elapsed time, temperature, meteorological conditions). For each parental visit we recorded: (1) time of the parent's arrival; (2) sex of the parent; (3) time of the feeding event; (4) begging intensity score (see below); (5) location of the nestlings and location of the parent in the 5×5 grid; (6) which nestling received food.

Because nestling behaviour changed notably during development, we distinguished a first growth stage (age < 15 days), when the nestlings had closed eyes, largely naked bodies and did not move out of the nest, from a second growth stage (age > 15 days), when chicks moved freely throughout the nest cavity. Three levels of begging intensity were considered: low, medium and high:

a) Low begging intensity: unbroken sleep, condition of torpor and subsequent reactions only to parent's direct stimulation (age < 15 days). Low interest at the arrival of the parent, absence of vocal peeping and remaining in the same position occupied before parent's arrival (age > 15 days).

b) Medium begging intensity: moderate peeping (lasting less than 10 sec), neck-raising and beak-opening, alternating with moments of stasis with the head on the nest edge or on a sibling's back (age < 15 days). Acute peeping, wing vibration, pecking the white region on the parent's throat and head, turning round and round (age > 15 days).

c) High begging intensity: intense peeping, head raising with constant beak-opening, for several (> 10) seconds (age < 15 days). Frenetic movement inside the cavity and active pursuit of the parent, wing beating and insistent pecking (age > 15 days).

The age-rank of the siblings in each brood was ascertained by daily inspections of the nests and by measuring the wing-length and mass of the individually marked nestlings. The eggs in the study nests typically hatched asynchronously, with a delay of 1 day in two-egg clutches, and 2 days between first and last egg in three-egg clutches (MALACARNE & CUCCO 1991).

To avoid pseudoreplication, we analyzed only mean values for each nest. Percentage values (for feedings and sector preferences) were arcsin transformed when performing ANOVAs (FOWLER & COHEN 1990).

RESULTS

In broods of two or three chicks, the oldest chick obtained more feedings overall than siblings (Fig. 2). The differences however are slight, and reach statistical significance only when comparing first and last chicks in broods of three (ANOVA $F_{1,33} = 6.84$, $P = 0.013$).

The success in obtaining food depended largely on the degree of begging activity, particularly when nestlings were aged more than 15 days. In the first period after hatching, when chicks were blind and less mobile, parents fed the nestling even with a low begging level. During the whole nest period there was no overt aggression between siblings, but in the last days the begging of older nestlings was so frantic during parent visits that they frequently ran over each other. With a low begging level (Fig. 3), chicks obtained less food compared with both medium and high begging levels (ANOVA $F_{2,27} = 14.8$, $P = 0.014$). There were no differences in obtaining food comparing medium and high begging levels (Fig. 3). For all the begging scores, feeding *per capita* is higher during the first 15 days because in this period the parents, on each visit to the nest, allocated food to more than one chick (51% of feeding events). Later a bolus was always given to only one chick and the individual success in being fed decreased.

The activity levels of chicks (Fig. 4) in the three age categories (first, second or third) did not differ (Kruskall-Wallis ANOVA $H = 0.052$, $P = 0.95$, NS).

Female and male parents did not concentrate their effort on different chicks within the brood. The percentage of feedings given by female or male to the three age-categories of nestlings was not different (ANOVA $F_{1,46} = 0.07$; $P = 0.78$, NS).

Generally both parents fed their young in a preferred area of the nest, located in one of the three sectors between the nest and the cavity entrance ("activity centre"). Accordingly, mobile nestlings awaited parent arrivals in this cavity sector (Table 1). Out of the 25 sectors considered in each cavity, 16 (64%) were peripheral and less occupied by young than the contiguous sectors (36%) of the central area: the choice of the sector was not random, in both nests with three and two chicks (Table 1).

Nestling position was not influenced by the location of the previous feeding event. Chicks awaited more in the "activity centre", the sector in which parents delivered most feedings, than in the sector where the previous feeding occurred ($F_{1,12} = 5.2$, $P < 0.05$).

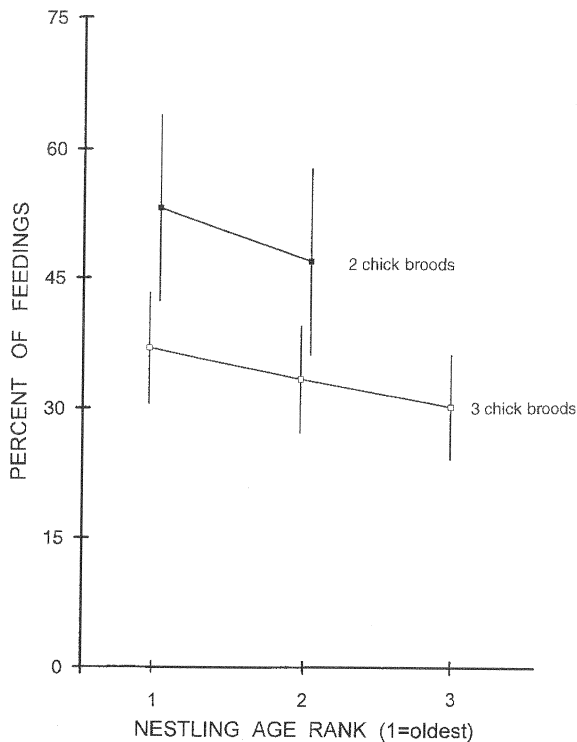


Fig. 2. — Distribution of feedings between nestlings of different ages (mean \pm SE). Two chick broods: ANOVA $F_{1,14} = 1.37$, $P = 0.26$. Three chick broods: ANOVA $F_{2,33} = 3.42$, $P = 0.045$; contrast 1 vs 2: $F_{1,33} = 1.52$, $P = 0.23$; contrast 1 vs 3: $F_{1,33} = 6.84$, $P = 0.01$; contrast 2 vs 3: $F_{1,33} = 1.92$, $P = 0.17$.

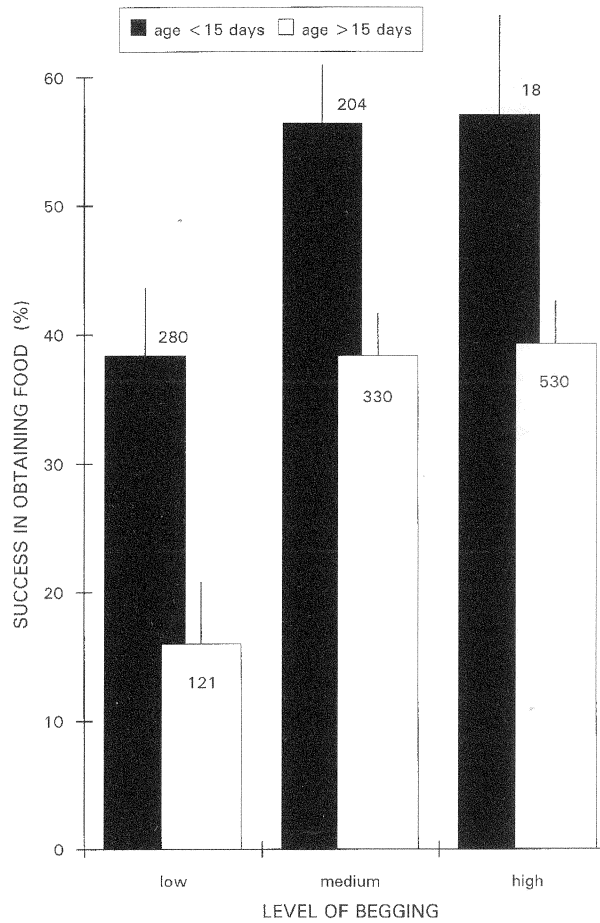


Fig. 3. — Success in obtaining food in relation to the level of begging (mean \pm SE, $n = 12$ nests). Figures report the number of feedings observed. Age < 15 days: ANOVA $F_{2,25} = 2.32$, $P = 0.10$; contrast 1 vs 2: $F_{1,25} = 2.34$, $P = 0.13$; contrast 1 vs 3: $F_{1,25} = 4.18$, $P = 0.05$; contrast 2 vs 3: $F_{1,25} = 0.64$, $P = 0.43$. Age > 15 days: ANOVA $F_{2,27} = 14.8$, $P = 0.001$; contrast 1 vs 2: $F_{1,27} = 23.6$, $P = 0.001$; contrast 1 vs 3: $F_{1,27} = 24.5$, $P = 0.001$; contrast 2 vs 3: $F_{1,27} = 0.83$, $P = 0.84$.

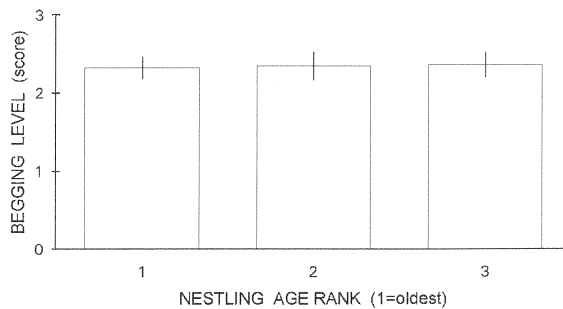


Fig. 4. — Begging level in nestlings of different ages (mean \pm SE, $n = 12$ nests).

Table 1.
Sectors chosen by nestlings while waiting for parent arrival.

Area in the cavity		Observations per sector \pm SD	
Zone	Number of sectors	2 chick broods (n = 6)	3 chick broods (n = 7)
Activity centre	1 (4 %)	45.3 \pm 9.8	30.9 \pm 5.7
Adjacent	8 (32%)	3.3 \pm 1.1	5.2 \pm 1.2
Far (non-adjacent)	16 (64%)	1.8 \pm 0.3	1.7 \pm 0.7
Statistics		$F_{2,15} = 112.3, P < 0.001$	$F_{2,18} = 152.1, P < 0.001$

DISCUSSION

In this study a pattern of parental non-selective chick feeding was observed. This situation has been observed in the majority of the species so far examined (exceptions are noted in the Introduction). The probability that an individual received food was related to indices of begging. This suggests that food distribution is largely regulated by sibling begging and their ability in obtaining the best feeding position, as reported in other species (LÖHRL 1968, BENGTTSSON & RYDEN 1981, GOTTLANDER 1987, SMITH & MONTGOMERIE 1991).

The spread of weight among nestlings may explain the correlation found between age rank and food obtained. Indications of an increasing competitive differential between nestlings with increasing asynchrony in hatching has also been found in many passerine birds (BENGTTSSON & RYDEN 1981, GREIG-SMITH 1985, GOTTLANDER 1987). This competition among nestlings is expected to be exacerbated when food is scarce, for example during critical environmental conditions. In our study period prolonged bad weather conditions did not occur and the last-hatched young, in general, survived and recovered from its initial handicap in mass.

This study reveals for the Pallid Swift the importance attached to nestlings placing themselves in an optimal position in the nest cavity, in order to be fed. The likelihood of being fed differed considerably among different sectors of the cavity. Similar position-related feeding differences have been found in the Blue-throated Bee-eater (BRYANT & TATNER 1990), Jackdaw *Corvus monedula* (LOCKIE 1955), Great Tit *Parus major*, Blackbird *Turdus merula*, Fieldfare *Turdus pilaris* (RYDEN & BENGTTSSON 1980), Song Sparrow *Melospiza melodia* (REED 1981), Stonechat *Saxicola torquata* (GREIG-SMITH 1985), Pied Flycatcher (GOTTLANDER 1987) and American Robin *Turdus migratorius* (MCCRAE et al. 1993).

Our observations do not indicate that the chicks adjust their position in relation to the last feeding event. The most efficient tactic is to occupy a near-average position (the activity centre) consistently, and to compete with siblings through intense begging.

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