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Differences in diet of Common (*Apus apus*) and Pallid (*A. pallidus*) Swifts

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Abstract The diets of Common (*Apus apus*) and Pallid Swift (*A. pallidus*) were compared by faecal and food bolus analysis in a mixed colony in NW Italy. The size of insect-remains increased with age of nestlings in both species. Size (mm) and mean dry mass of insect prey items was greater in the Common Swift. There were also differences in the taxonomic composition of prey: the Common Swift took more aphids in June, and Heteroptera and Coleoptera in July, while the Pallid Swift caught more Acalyptera in June, and Hymenoptera in July . Food balls and faecal analysis agreed in their description of swift diets.
A comparison with aerial arthropod abundance, sampled by suction trap, suggested a positive selection of Hymenoptera and Coleoptera, while Diptera were more frequent in suction trap samples than in the swifts' diets.

Introduction

Aerial feeding birds (e.g. swifts, Apodidae, and swallows, Hirundinidae) are selective in catching their prey, at least during reproduction (Bryant 1973, Hespenheide 1975, Waugh 1979). Larger items than generally available are selected by Swallows *Hirundo rustica*, Sand Martins *Riparia riparia*, House Martins *Delichon urbica* and the Common Swift *Apus apus* (Waugh 1978).
Swifts normally catch insects at higher altitudes than swallows and martins, even when feeding areas overlap, such as during adverse weather (Waugh 1978). Differences in feeding location probably reflect dietary preferences and the flight characteristics as well as the aerial distribution of insects of different types (Waugh 1978).
Of the three generally distributed European species of swifts, the Alpine *A. melba* feeds on moderate-sized arthropods, while the Common and Pallid *A. pallidus* Swifts take both small and moderate size arthropods (Cramp 1985).
Comparison of food preferences amongst species of swifts is difficult because diets can vary geographically. A prevalence of aphids was found in the diet of the Common Swift in Oxford, but this preference varied seasonally. Heterogeneous samples have been detected in the Pyrenees (Glutz and Bauer 1980), Switzerland (Weitnauer 1947) and Italy (Moltoni 1950). Finlayson (1979) in Gibraltar found a large overlap in diet between Common and Pallid Swifts in mixed colonies, even though the latter took a wider range of food including larger prey. A certain degree of niche segregation between the two species is also indicated by structural and behavioural differences: the Pallid Swift has a slighty wider bill and is said to fly lower than the Common, down to 1.5 m (Konig and Konig 1973, Boano 1979, Affre and Affre 1967). This behaviour, however, has only been observed near the colony-sites, where the Pallid Swift usually nests in lower cavities (Cucco and Malacarne 1987), and little is known about the heights of more distant foraging flights.
In this study we analyze by faecal analysis the diets of breeding Common and Pallid Swifts, in order to describe individual differences, seasonal variation, and diet overlap in the two species when there is no geographical segregation.

Methods

The study colony was located in the town of Carmagnola (NW Italy). Both the Pallid and the Common Swifts nested together, in closely spaced (4-5 m apart) cavities situated on the external walls of an old building.
Nestling diets were studied by examining insect remains in faeces produced by the young during their 40-45 days in the nest. In 1991, faeces were collected

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at 15-day intervals, from mid-June to August, in 18 nests of the Pallid and 3 of the Common Swift. On each occasion the cavities were completely cleaned out, in order not to mix faeces from different periods. We analyzed 20 samples, obtained from 4 and 3 individual nests of Pallid and Common Swifts during three 15-days periods, to examine for differences between broods. Another four 15-day samples were obtained by mixing the faeces collected in the same period, from 8, 12, 9 and 10 nests respectively of Pallid Swift: these samples represented the full range of the insects taken by the birds at the colony in the four periods. A further sample from a few nests in Spain (Sevilla Cathedral, 24 June 1979) was also considered for the Pallid Swift.

Insect remains in faeces were identified with a binocular microscope, by examination of the wing shape and venation. Identification was made to the order, suborder or family level (Colyer and Hammond 1968, Chinery 1973, 1986) according to the frequency of items and the feasibility of classifying them merely on wing pattern. The size of prey was assessed by measuring intact wing lengths to the nearest millimetre. On average, 149 insects were identified and measured in each sample considered.

Individual insect masses were calculated from wing lengths using the allometric winglength equation: $Y=X^b/D$, where Y=dry weight (mg), X= winglength (mm), b and D are coefficients, different for each taxonomic group of insects, as reported by Turner (1980, 1982).

Another analysis of the taxa eaten by nestlings of Pallid Swifts was obtained in the same colony in 1989-90, using 34 boluses regurgitated by nestlings. In this case the size of prey was not measured.

The availability of insects from different taxa in the area surrounding the colony was estimated by counting the items collected daily from a suction-trap (12.2 m high, captures made during 15/16 days for each half-month period) of the Italian network for aphid control, located in Carmagnola, 3 km North of the study colony.

Results

Sizes of insects and age of nestlings

The size of insects caught throughout the breeding season by Pallid and Common Swifts is shown in Figure 1. In both species we observed an increase in the size of prey correlated with the age of the nestlings, the insects being smaller at the beginning of the rearing period. Differences were statistically significant (Table 1) comparing prey sizes over the first 15-days of age with sizes in the following 15-day period, from either the same nest (A - G) or mixed group of nests. In contrast, at each nest, sizes were similar when comparing the last two 15-day periods (Figure 1, t values ranging from 0.10 to 1.89, P=n.s. for all comparisons).

On the whole, different pairs were similar in the size of selected food items. The size of insects caught in different nests, but in the same period with nestlings of the same age, did not differ between birds of the same species (Figure 1; t tests, P= n.s.). Partial exceptions were found only in two cases for a Pallid Swift nest, which had smaller sizes in the 16-30 June and 16-31 August periods than otherwise, and in one case for a Common Swift nest, where sizes were larger on 1-15 July (t tests, $P<0.05$). The size of insects in Pallid Swift faeces from Sevilla, Spain, did not differ from those found at the same time of year in NW Italy (Figure 1, t=1.95, P=n.s.).

Insects-sizes in the two species

The distribution of insect sizes in the faeces of Pallid and Common Swifts is shown in Figure 2. The frequency distribution was different in the three 15-

Table 1. Comparison of prey-size in the first and second 15-days periods of rearing.

Nest		First period		Second period	t	N	p
Common Swift	- Nest A	16-30 June	vs.	1-15 July	5.02	272	<0.01
	- Nest B	16-30 June	vs.	1-15 July	2.80	294	<0.01
	- Nest C	1-15 July	vs.	16-31 July	1.64	297	<0.01
Pallid Swift	- Nest D	16-30 June	vs.	1-15 July	4.77	373	<0.01
	- Nest E	16-30 June	vs.	1-15 July	5.75	294	<0.01
	- Mixed	16-30 June	vs.	1-15 July	3.34	277	<0.01
	- Nest F	16-31 July	vs.	1-15 Aug.	2.71	272	<0.01
	- Nest G	16-31 July	vs.	1-15 Aug.	2.58	374	<0.01

Table 2. Comparison of mean prey-size (mm) in the Pallid and Common Swift in 1991 (NW Italy).

Period	Pallid			Common			Statistic	
	Mean	(S.D.	N)	Mean	(S.D.	N)	t	p
16-30 June	3.37	(1.86	713)	3.78	(1.69	388)	3.60	0.01
1-15 July	4.12	(2.07	491)	4.36	(217	363)	1.64	0.10
16-31 July	3.72	(1.85	687)	4.25	(2.04	337)	4.16	0.01

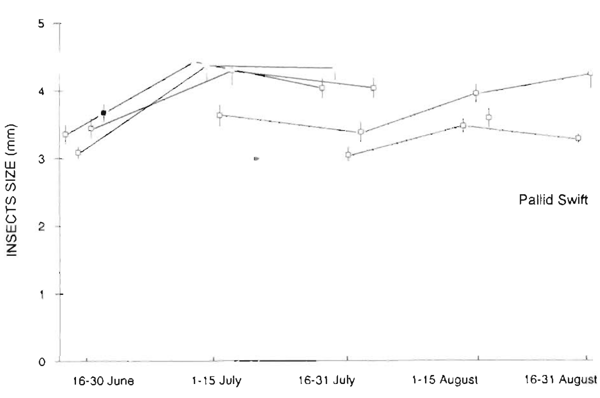
days periods considered (16-30: χ^2=59.6, d.f.=8, P<0.01; 1-15 July: χ^2=31.7, d.f.=8, P<0.01; 16-31 July: χ^2=38.9, d.f.=8, P<0.01). In each period, the prey were smaller in the Pallid Swift (Table 2).
The same result was found when considering the mass of insect prey items (Figure 3): the frequency distribution was different in the three 15-days periods considered (16-30 June: χ^2=79.9, d.f.=7, P<0.01; 1-15 July: χ^2=20.4, d.f.=7, P<0.01; 16-31 July: χ^2=28.0, d.f.=7, P<0.01). Hence, whichever method of size measurement was used, Pallid Swifts were found to take generally smaller prey than Common Swifts.

Differences in taxa

The six principal taxa found in the faeces of Pallid and Common Swifts are shown in Figure 4. A seasonal trend was observed: the Heteroptera were mostly present late in the summer (August) while the reverse was found for the Aphidae. For the other groups seasonal differences were less pronounced. It must also be taken into account that the species of insects contributing to these inclusive categories probably changed during the season.
When comparing the diets of the two species of swifts, the frequency distribution differed significantly between all three 15-days periods (16-30 June:χ^2=68.1, d.f.=5, P<0.01; 1-15 July: χ^2=33.4, d.f.=5, P<0.01; 16-31 July: χ^2=59.6, d.f.=8, P<0.01; 1-15 July: χ^2=12.3, d.f.=5, P<0.03). The Common Swift took more aphids in June, and Heteroptera and Coleoptera in July, while the Pallid Swift caught more Acalyptera in June, and Hymenoptera in July.

Comparison of prey in faeces, food-balls and suction trap.

In Table 3 arthropod percentages obtained from the three different sampling methods are reported. Since the data were collected in different years, detailed comparisons are of limited value. Only the greatest differences between aerial insect availability (suction trap data) and prey ingested (faecal and bolus analysis) are therefore examined. The suction trap samples showed a marked prevalence of Diptera in both years. This taxon occurs in the diet, but is not the most abundant food of swifts. On the contrary, swifts eat large quantities of Hymenoptera, which occur at a low frequency in the suction trap samples. Similarly, Coleoptera, captured in relatively small numbers by the trap, were an important component of the swift's diet, especially when determined from faecal samples. Hemiptera (mainly aphids and leafhoppers) show great fluctuations within and between years in our



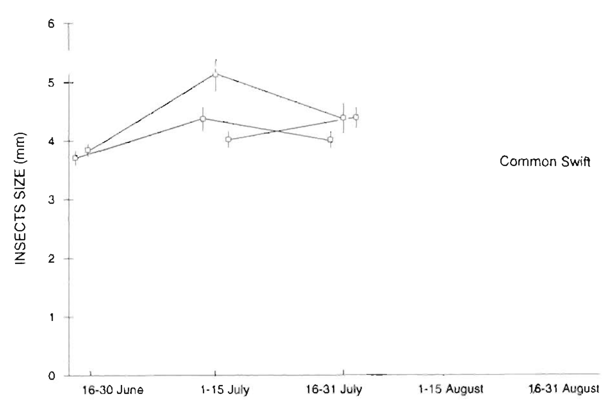


Figure 1. Size of insects (mean ± s.e.) caught in different nests in NW Italy in 1991 (Black square = Sevilla nests, 24 June 1979).

Table 3. Arthropods of different taxa observed in faeces, food-balls and suction trap in NW Italy.

Taxon	16-30 June					1-15 July				16-31July				1-31 July
	FAECES 1991		SUCTION TRAP		FOOD-BALLS	FAECES 1991		SUCTION TRAP		FAECES 1991		SUCTION TRAP		FOOD-BALLS
	Common	Pallid	1989	1990	Pallid	Common	Pallid	1989	1990	Common	Pallid	1989	1990	Pallid
Ephemeroptera	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odonata	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Orthoptera	-	-	-	-	-	-	-	-	-	-	-	-	-	
Hemiptera Het.	4.4	3.2	0.4	0.5	-	12.4	5.9	5.5	1.9	11.6	12.9	2.4	1.0	8.3
Homoptera														
Aphidae	26.5	12.2	25.2	-	6.2	0.3	1.8	6.7	-	1.5	2.1	0.8	0.3	1.6
Cicadellidae	-	-	2.0	1.7	23.9	-	-	1.0	1.7	-	-	1.3	2.7	22.8
Psyllidae	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Other	2.3	1.7	-	-	-	0.3	1.2	-	-	0.3	0.4	-	-	-
Neuroptera	-	-	0.2	0.1	-	-	-	0.3	0.2	-	-	0.6	0.2	-
Coloeptera	33.8	31.7	6.0	4.6	33.0	37.2	39.7	6.9	6.3	29.7	29.5	15.5	6.6	7.6
Trichoptera	-	-	0.1	0.1	-	-	-	0.1	0.1	-	-	0.1	0.1	-
Lepidoptera	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diptera	-	-	65.2	85.7	17.7	-	-	71.2	72.5	-	-	74.7	47.4	30.2
Nematocera	0.3	-	-	3.2	-	0.3	0.2	-	13.1	-	-	-	37.7	-
Tipulidae	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-
Lonchopteridae	-	0.4	-	-	-	-	-	-	-	-	0.1	-	-	-
Phoridae	0.3	0.3	-	-	-	0.6	0.6	-	-	-	-	-	-	-
Syrphidae	1.8	2.2	-	-	-	0.8	3.6	-	-	0.3	2.5	-	-	-
Acalypterates	10.1	22.3	-	-	-	6.9	3.3	-	-	4.5	5.7	-	-	-
Sepsidae	0.3	0.3	-	-	-	-	0.2	-	-	-	-	-	-	-
Sphaeroceridae	1.3	0.7	-	-	-	-	0.2	-	-	-	0.1	-	-	-
Siphonaptera	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hymenoptera	16.8	21.3	0.6	3.1	15.8	38.0	41.5	7.4	3.4	51.6	43.8	2.3	3.2	23.6
parasitic Hym.	2.3	2.9	-	-	-	3.3	1.4	-	-	0.6	2.8	-	-	-
Araneidae	-	0.1	0.2	0.5	3.3	-	-	0.7	0.5	-	-	0.6	0.3	1.4
Other	-	-	0.1	0.5	-	-	-	0.1	0.4	-	-	1.6	0.4	-
N =	388	713	22165	18253	209	363	495	13102	13416	337	682	13336	21934	5695

Table 3. Arthropods of different taxa observed in faeces, food-balls and suction trap in NW Italy.

Taxon	1-15 August FAECES 1991 Pallid	1-15 August SUCTION TRAP 1989	1-15 August SUCTION TRAP 1990	16-31 August FAECES 1991 Pallid	16-31 August SUCTION TRAP 1989	16-31 August SUCTION TRAP 1990	1-31 August FOOD-BALLS Pallid	1-30 September SUCTION TRAP 1989	1-30 September SUCTION TRAP 1990	1-30 September FOOD-BALLS Pallid
Ephemeroptera	0.2	-	-	-		-	-	-	-	-
Odonata	-	-	-	0.2	-	--	-	-	-	-
Orthoptera	-	-	-	-	-	-	-	-	-	-
Hemiptera Het.	34.0	0.8	0.7	62.9	0.6	0.4	-	0.1	0.4	1.0
Homoptera										
Aphidae	3.3	1.3	0.2	-	2.4	0.4	60.8	9.3	16.9	1.5
Cicadellidae	-	0.9	1.1	-	1.4	0.4	-	0. 3	0.6	80.4
Psyllidae	-	-	-	-	-	-	-	-	-	-
Other	2	-	-	1.6	-	-	-	-	-	-
Neuroptera	-	0.4	0.1	-	0.5	0.1	-	0.1	0.1	-
Coloeptera	18.5	10.9	8.2	19.1	9.0	8.2	22.0	2.2	2.9	0.2
Trichoptera	-	0.1	0.1	-	0.8	0.4	-	2.0	1.7	-
Lepidoptera	-	-	-	-	-	-	-	-	-	-
Diptera	-	81.0	39.5	-	79.5	48.4	4.6	70.5	62.6	4.8
Nematocera	-	-	46.0	-	-	34.3		-	17.1	-
Tipulidae	-	-	-	-	-	-	-	-	-	-
Lonchopteridae	-	-	-	-	-	-	-	-	-	-
Phoridae	-	-	-	-	-	-	-	-	-	-
Syrphidae	1.0	-	-	5.2	-	-	-	-	-	-
Acalypterates	4.3	-	-	2.3	-	-	-	-	-	-
Sepsidae	-	-	-	-	-	-	-	-	-	-
Sphaeroceridae	0.8	-	-	-	-	-	-	-	-	-
Siphonaptera	-	-	-	-	-	-	-	-	-	-
Hymenoptera	34.8	2.0	3.4	7.7	3.6	6.0	1.7	4.1	5.2	7.3
parasitic Hym.	2.8	-	-	0.7	-	-	-	-	-	-
Araneidae	-	0.5	0.3	-	0.5	0.6	1.7	1.2	0.6	1.1
Other	-	2.0	0.3	0.2	1.7	0.6	-	1.2	0.8	-
N =	509	11689	16832	439	8705	13633	1151	15959	20736	4437

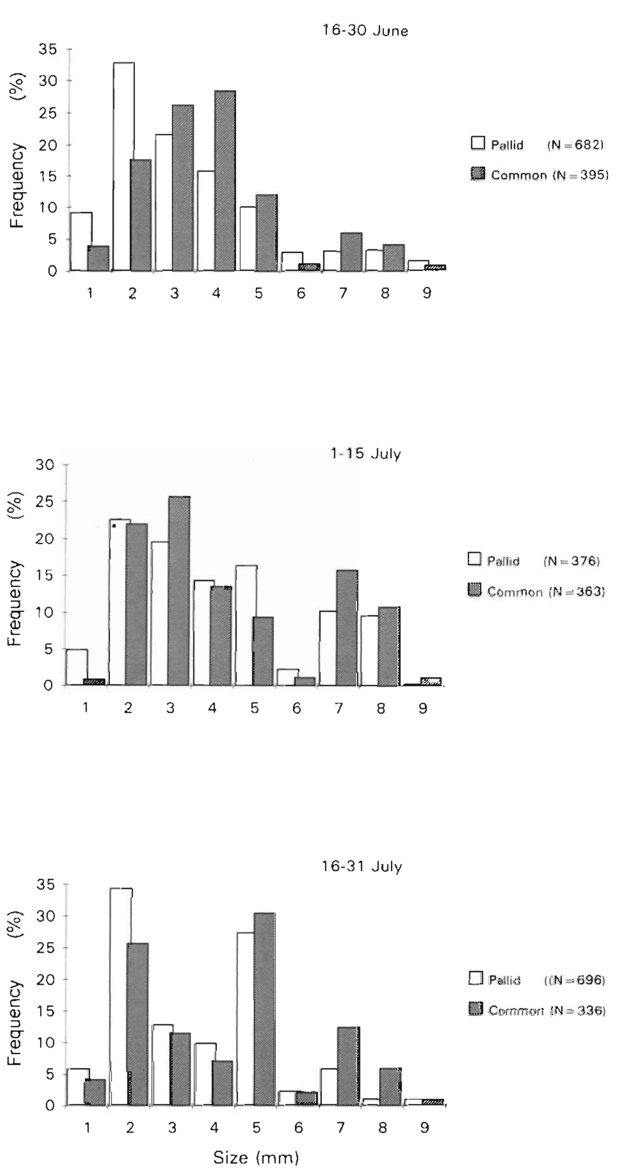


Figure 2. Size of insects caught by Common and Pallid Swifts in different periods in 1991 (NW Italy). Size denotes length of intact wings.

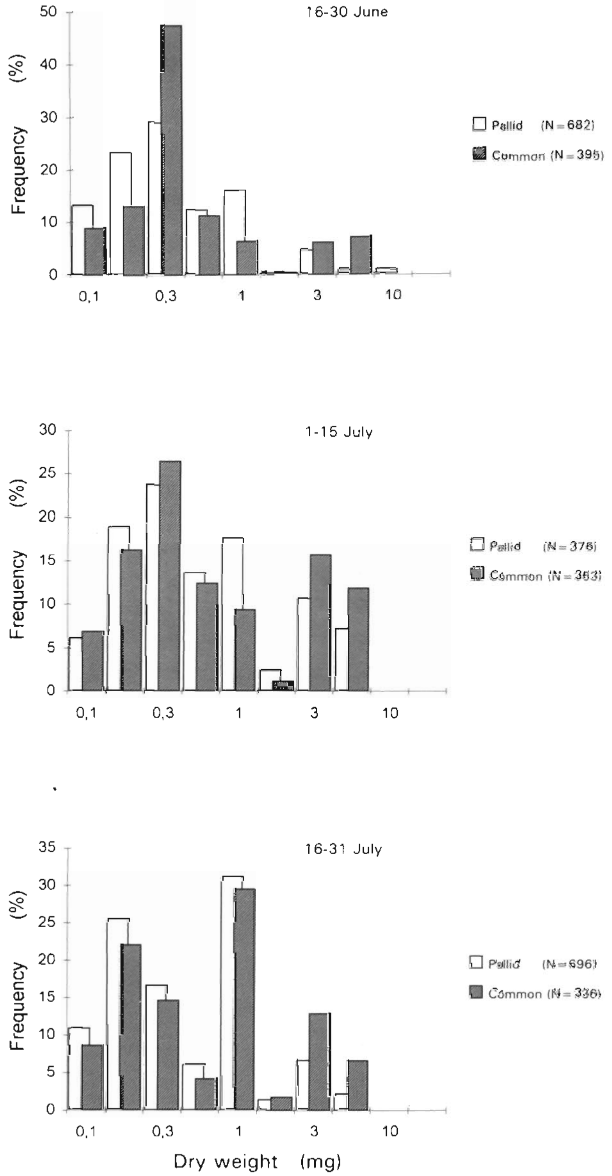


Figure 3. Mass of insects caught by Common and Pallid Swifts in different periods in 1991 (NW Italy).

study-area (Caciagli *et al.* 1989). Accordingly, they seem to appear randomly in the swift diets. On average, however, they seem to be positively selected, since these taxa appear more often in boluses and faeces than in the suction trap.

Discussion

Trophic specialization occurs in many communities of aerial feeding birds (Bryant 1973, Waugh 1978, Hespheneide 1975). Food partitioning is obtained partly as a result of different foraging heights, as shown in the study of a British swallow and swift community (Waugh 1978). However prey diversity is also the product of food selection. In fact when the four aerial feeders (*Hirundo rustica, Delichon urbica, Riparia riparia* and *Apus apus*) living in Britain used the same air space, they reduced competition by increasing the difference in size of the prey they took (Waugh 1978). Moreover, Hespheneide (1975) in a

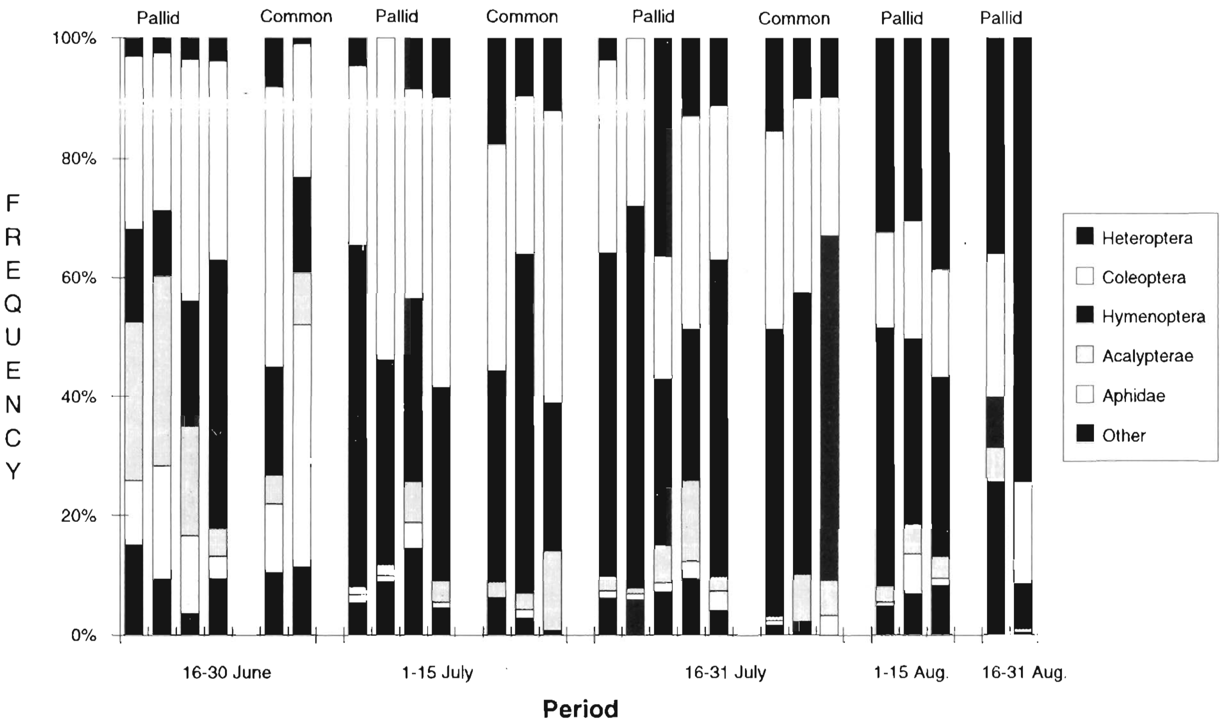


Figure 4. Percentage of insects of different taxa in Common and Pallid Swifts in 1991 (NW Italy). Each column refers to a different nest or group of nests. Common Swifts had left the study area by August.

study of the diets of two swifts and a swallow in a tropical area, found different proportions of taxonomic groups were not explained by preferences alone. He concluded that insect flying agility was important for selection of some prey types and avoidance of others.

The Common and the Pallid Swift show great morphological, ecological and behavioural similarities and breed sympatrically in some Mediterranean areas. Finlayson (1979) showed, on the basis of a small sample from Gibraltar, some diet differences in the two species. The Pallid Swift included big insects (Odonata, Lepidoptera >12 mm) in its prey while the Common Swift never exceeded this size threshold. The Common Swift selected swarms of social hymenopterans and excluded spiders (a common occuring prey type in England, Owen and Le Gros 1954), while the Pallid Swift took both these arthropods as well as many Hemiptera. Our results confirm the existence of diet differences between the two species, but tend to the opposite conclusions about preferred prey sizes. The faecal analysis has shown that insects eaten by the Common Swift are significantly larger in size. On the whole, in our analysis, the Pallid Swifts ate more Dipterans and Hymenopterans, while the Common Swift ate more Aphids and Coleopterans.

Some further points have to be considered.

1) Faecal analysis may give different results from those obtained from food-bolus analysis. Different digestibilities of prey may result in under or overestimation of some taxa. For example, particularly large items are often broken down in faeces while smaller more flexible ones survive, so there may be a bias against relatively large items in faecal samples, which would nevertheless appear in food balls. Faecal analysis represents the average diet taken over a certain period. On the other hand, food-ball studies usually utilize items collected over a few hours or days. The previous studies on the Pallid Swift diet (Finalyson 1979, Bigot *et al.* 1984 for example) were probably too restricted in this respect. Finalyson (1979) concluded that dietary differences between the two species exists, on the basis of a sample in June, while more prolonged monitoring could have led to other conclusions, since the overlap between the species is obviously considerable.

2) It is quiet clear that aerial feeders often depend on unpredictable spatio-temporal accumulations of aerial arthropods. Swarming of ants, bees, aphids, termites and ladybird beetles can lead to massive local accumulations of prey and the opportunistic

exploitation of these constantly changing resources induces a very high intraspecific variability in diets (Lack and Owen 1955). This pattern is evident in data from the same nest in different time periods, or even between two close nests on the same day (Malacarne and Cucco 1992).

3) Aerial insectivores forage selectively. In the House Martin, the closest correlation with available food supply was found in the nestlings diet when there was a high relative abundance of large insects, but food selectivity was not associated with changes in the aerial insect diversity (Bryant 1973). It is more difficult, on the basis of the same method, to assess food selectivity in swifts. The proportion of insects eaten by swifts is in general very different from that observed with the suction trap (12.2 m high). This is likely to be due to a difference in the altitude at which swifts and martins forage. It is therefore unlikely that the suction trap catch accurately reflected the insects encountered during foraging, at a great height and over a very wide area.

4) In spite of an obvious diversity in diet composition, there was some constancy in the type of arthropods eaten by swifts. The prey taxa invariably included Hymenoptera, Diptera, Hemiptera (both Homoptera and Heteroptera) and to a lesser extent Coleoptera. Some inconsistencies could be due to a limited sample size. For the Pallid Swift, for example, the unusual importance of Araneae reported in Morocco (Bigot *et al.* 1984) could be due to a very short time over which samples were collected.

The generality of the importance of certain taxa to aerial feeding birds is illustrated by the fact that tropical swiftlets (*Collocalia esculenta, Aerodramus spodiopygius*) mainly eat the same four insect taxa cited above (Hails and Amirudin 1981, Tarburton 1986).

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Riassunto - L'analisi dei resti fecali e dei boli rigurgitati ai pulli ci ha permesso di effettuare un'indagine in contemporanea sull'alimentazione di Rondoni comuni e Rondoni pallidi nidificanti nella stessa colonia. Esiste una buona corrispondenza tra le due metodiche nel descrivere la scelta giornaliera delle prede. Le dimensioni dei residui entomologici aumentano con l'età dei pulli in entrambe le specie. Le dimensione dell'ala e il peso secco delle prede sono risultate maggiori nel Rondone comune. Esistono inoltre differenze nella composizione della dieta: il R. comune cattura più afidi in giugno, eterotteri e coleotteri in luglio mentre il R. pallido ha catturato più ditteri acalipteri in giugno e imenotteri in luglio. Una comparazione giornaliera con gli artropodi aerei disponibili, campionati mediante torre a suzione, suggerisce che i rondoni selezionino positivamente imenotteri e coleotteri, mentre i ditteri sono percentualmente più frequenti nel campione aereo che non nei resti fecali o nei boli.

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