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 character-
istics 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
(Cram 1985).

Comparison of food preferences amongst species of
swifts is difficult because diets can vary geographi-
cally. 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 slightly wider bill and is said to
fly lower than the Common, down to 1.5 m (Konig
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, Chimney 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-

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

<table>
<thead>
<tr>
<th>Nest</th>
<th>First period</th>
<th>Second period</th>
<th>( t )</th>
<th>( N )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common Swift</td>
<td>- Nest A</td>
<td>16-30 June</td>
<td>vs.</td>
<td>1-15 July</td>
<td>5.02</td>
</tr>
<tr>
<td></td>
<td>- Nest B</td>
<td>16-30 June</td>
<td>vs.</td>
<td>1-15 July</td>
<td>2.80</td>
</tr>
<tr>
<td></td>
<td>- Nest C</td>
<td>1-15 July</td>
<td>vs.</td>
<td>16-31 July</td>
<td>1.64</td>
</tr>
<tr>
<td>Pallid Swift</td>
<td>- Nest D</td>
<td>16-30 June</td>
<td>vs.</td>
<td>1-15 July</td>
<td>4.77</td>
</tr>
<tr>
<td></td>
<td>- Nest E</td>
<td>16-30 June</td>
<td>vs.</td>
<td>1-15 July</td>
<td>5.75</td>
</tr>
<tr>
<td></td>
<td>- Mixed</td>
<td>16-30 June</td>
<td>vs.</td>
<td>1-15 July</td>
<td>3.34</td>
</tr>
<tr>
<td></td>
<td>- Nest F</td>
<td>16-31 July</td>
<td>vs.</td>
<td>1-15 Aug.</td>
<td>2.71</td>
</tr>
<tr>
<td></td>
<td>- Nest G</td>
<td>16-31 July</td>
<td>vs.</td>
<td>1-15 Aug.</td>
<td>2.58</td>
</tr>
</tbody>
</table>
Table 2. Comparison of mean prey-size (mm) in the Pallid and Common Swift in 1991 (NW Italy).

<table>
<thead>
<tr>
<th>Period</th>
<th>Pallid</th>
<th>Common</th>
<th>Statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (S.D.) N</td>
<td>Mean (S.D.) N</td>
<td>t</td>
</tr>
<tr>
<td>16-30 June</td>
<td>3.37 (1.86) 713</td>
<td>3.78 (1.69) 388</td>
<td>3.60</td>
</tr>
<tr>
<td>1-15 July</td>
<td>4.12 (2.07) 491</td>
<td>4.36 (2.17) 363</td>
<td>1.64</td>
</tr>
<tr>
<td>16-31 July</td>
<td>3.72 (1.85) 687</td>
<td>4.25 (2.04) 337</td>
<td>4.16</td>
</tr>
</tbody>
</table>

Days periods considered (16-30: $\chi^2=59.6$, d.f.=8, P<0.01; 1-15 July: $\chi^2=31.7$, d.f.=8, P<0.01; 16-31 July: $\chi^2=38.9$, 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: $\chi^2=79.9$, d.f.=7, P<0.01; 1-15 July: $\chi^2=20.4$, d.f.=7, P<0.01; 16-31 July: $\chi^2=28.0$, 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: $\chi^2=68.1$, d.f.=5, P<0.01; 1-15 July: $\chi^2=33.4$, d.f.=5, P<0.01; 16-31 July: $\chi^2=59.6$, d.f.=8, P<0.01; 1-15 July: $\chi^2=12.3$, 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>
<thead>
<tr>
<th>Taxon</th>
<th>16-30 June</th>
<th>1-15 July</th>
<th>1-31 July</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ephemeroptera</td>
<td>12.4</td>
<td>5.9</td>
<td>5.5</td>
</tr>
<tr>
<td>Odonata</td>
<td>0.4</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>2.5</td>
<td>2.0</td>
<td>2.5</td>
</tr>
<tr>
<td>Heteroptera</td>
<td>26.5</td>
<td>12.2</td>
<td>25.2</td>
</tr>
<tr>
<td>Homoptera</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Aphidae</td>
<td>3.3</td>
<td>3.3</td>
<td>3.3</td>
</tr>
<tr>
<td>Cicadellidae</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Pseudococcidae</td>
<td>2.0</td>
<td>2.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Planoceridae</td>
<td>0.2</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Psocidae</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Neompharidae</td>
<td>0.4</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Tipulidae</td>
<td>0.4</td>
<td>0.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Nematocera</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Tipulidae</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Nematocera</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Acalyptrae</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Sepedidae</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Siphunculidae</td>
<td>3.1</td>
<td>3.1</td>
<td>3.1</td>
</tr>
<tr>
<td>Syrphidae</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>6.0</td>
<td>6.0</td>
<td>6.0</td>
</tr>
<tr>
<td>Araneidae</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Other</td>
<td>6.0</td>
<td>6.0</td>
<td>6.0</td>
</tr>
</tbody>
</table>

| N = 708 | 713 | 716 | 1255 | 1255 | 209 | 363 | 495 | 1302 | 1316 | 357 | 682 | 1236 | 21934 | 5905 |

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

<table>
<thead>
<tr>
<th>Taxon</th>
<th>1-15 August</th>
<th>16-31 August</th>
<th>1-31 August</th>
<th>1-30 September</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FAECES 1991</td>
<td>SUCTION TRAP</td>
<td>FAECES 1991</td>
<td>SUCTION TRAP</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>0.2</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Odonata</td>
<td>-</td>
<td>-</td>
<td>0.2</td>
<td>-</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Hemiptera Het.</td>
<td>34.0</td>
<td>0.8</td>
<td>0.7</td>
<td>62.9</td>
</tr>
<tr>
<td>Homoptera</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Aphidiae</td>
<td>3.3</td>
<td>1.3</td>
<td>0.2</td>
<td>2.4</td>
</tr>
<tr>
<td>Cicadellidae</td>
<td>-</td>
<td>0.9</td>
<td>1.1</td>
<td>1.4</td>
</tr>
<tr>
<td>Psyllidae</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Other</td>
<td>2</td>
<td>-</td>
<td>1.6</td>
<td>-</td>
</tr>
<tr>
<td>Neuroptera</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>18.5</td>
<td>10.9</td>
<td>8.2</td>
<td>19.1</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>-</td>
<td>0.1</td>
<td>0.1</td>
<td>-</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Diptera</td>
<td>-</td>
<td>81.0</td>
<td>39.5</td>
<td>-</td>
</tr>
<tr>
<td>Nematocera</td>
<td>-</td>
<td>-</td>
<td>46.0</td>
<td>-</td>
</tr>
<tr>
<td>Tipulidae</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Lonchopteraida</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Phoridae</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Syrphidae</td>
<td>1.0</td>
<td>-</td>
<td>-</td>
<td>5.2</td>
</tr>
<tr>
<td>Acalyptratida</td>
<td>4.3</td>
<td>-</td>
<td>-</td>
<td>2.3</td>
</tr>
<tr>
<td>Sepsidae</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sphaerocerida</td>
<td>0.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Siphonoptera</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
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<td>34.8</td>
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<td>3.4</td>
<td>7.7</td>
</tr>
<tr>
<td>parasitic Hym.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.7</td>
</tr>
<tr>
<td>Araneidae</td>
<td>-</td>
<td>0.5</td>
<td>0.3</td>
<td>-</td>
</tr>
<tr>
<td>Other</td>
<td>-</td>
<td>2.0</td>
<td>0.3</td>
<td>0.2</td>
</tr>
<tr>
<td>N</td>
<td>509</td>
<td>11689</td>
<td>16832</td>
<td>439</td>
</tr>
<tr>
<td></td>
<td>15959</td>
<td>20736</td>
<td>4437</td>
<td>-</td>
</tr>
</tbody>
</table>

Differences in diet of Common Aphis spira and Pallid Asaphidius Styphi.
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, Hespeneide 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, Hespeneide (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 hymenopte-
rans and excluded spiders (a common occurring 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 (Finlayson 1979, Bigot et al. 1984 for
example) were probably too restricted in this respect.
Finlayson (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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References


