

Notas Breves

FOOD HABITS OF THE ALPINE SWIFT ON TWO CONTINENTS: INTRA- AND INTERSPECIFIC COMPARISONS

DIETA DEL VENCEJO REAL EN DOS CONTINENTES: ANÁLISIS COMPARATIVO INTRA E INTERESPECÍFICO

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SUMMARY.—The prey brought by alpine swifts *Tachymarptis melba* to their chicks in Switzerland, Spain and South Africa included a wide variety of arthropods, principally insects but also spiders. Insects comprised 10 orders and 79 families, the Homoptera, Diptera and Hymenoptera being the most often consumed. The assessment of geographical variation in the diet was complicated by the great variability among the individual supplies of prey. Prey size varied between 1.3 and 29.6 mm, differing significantly in the median prey size of the three populations (5.12 - 8.81 mm) according to the intraspecific variation in size of alpine swifts. In an interspecific comparison, prey size correlated positively with body size in seven species of swifts.

RESUMEN.—Las presas aportadas por vencejos reales *Tachymarptis melba* a sus pollos en Suiza, España y Sudáfrica incluyeron una amplia variedad de artrópodos, principalmente insectos pero también arañas. Entre los insectos, fueron identificados 10 órdenes y 79 familias, siendo Homoptera, Diptera e Hymenoptera los más consumidos. Las variaciones geográficas en la dieta se vieron ensombrecidas por una gran variabilidad entre los aportes individuales de presas. El tamaño de presa varió entre 1.3 y 29.6 mm, oscilando las medianas para cada población entre 5,12 y 8,81 mm. Los vencejos reales mostraron diferencias significativas en el tamaño de sus presas correspondiendo con su variación intraespecífica en tamaño. En una comparación interespecífica, el tamaño de siete especies de vencejos se correlacionó positivamente con el tamaño de sus presas.

Food is one of the most important aspects of the biology of most species. Equally important is the mode of acquisition and behavioural choices of the type and size of poten-

tial prey item (Bertsch and Barreto, 2008). Swifts gather their food entirely on the wing where they selectively sample the array of arthropods (spiders and insects) available in

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the air column. Availability may in turn depend on a variety of factors including prey type and size as well as its flight characteristics (Glick, 1939; Hespeneheide, 1977). Aerial foraging, combined with remote nest sites, has led to a paucity of detailed information on some species of swifts. For those species which have been studied, their diets include a diverse array of prey items (Harrison, 1974; Lack and Owen, 1955; Collins, 1968, 1980; Cramp, 1985; Tarburton, 1986; Lourie and Tompkins, 2000). These studies suggest that potential prey varies in its abundance, and thus availability, both geographically and temporally.

Tropical swifts frequently take prey such as termites (Isoptera) which may be absent from the diet of temperate species (Harrison, 1974; Lack and Owen, 1955; Collins, 1968, 1980; Tarburton, 1986; García del Rey *et al.*, pers.obs.). Year to year, seasonal and perhaps also day-to-day changes in abundance in the air column of some prey types, such as aphids (Aphididae), results in pronounced differences in the magnitude of their occurrence in swift diets (Lack and Owen, 1955; Cucco *et al.*, 1993; García del Rey *et al.*, pers.obs.). Prey size is also important with larger swifts taking, on average, larger prey and having a larger maximum prey size that they consume (Collins, 1980; García del Rey *et al.*, pers.obs.).

To date, those studies which have documented quantitatively both the type and size of prey captured have been all on small or medium-sized swifts (< 50 grams body weight; Collins, 1968, 1980; Tarburton, 1986; Rudalevige *et al.*, 2003; Lourie and Tompkins, 2000; García del Rey *et al.*, pers.obs.). We present here similar information on the kind and size of prey taken by the substantially larger alpine swift *Tachymarptis melba* at three study sites in Switzerland, Spain and South Africa. The predicted outcomes of this study are: (i) that alpine swifts will be shown to take a wide variety of prey types (taxa) as true of other swifts; (ii) that the prey types taken by alpine swifts at the three study sites will show geographic differences;

(iii) that the prey of the alpine swift will be, on average, larger than that recorded for smaller swifts and will include a larger overall range of prey sizes; (iv) that the intraspecific difference in body size of alpine swifts breeding in Europe and South Africa will also be reflected in different sizes of the prey they consume.

The diet of alpine swifts in the breeding season was determined by analysis of food boluses brought by different adults to nestlings. Collections were made at three study sites where there have been continuing studies of alpine swifts: (i) Solothurn, Switzerland (Arn-Willi, 1960), (ii) Oliete, Teruel, Spain (Tella *et al.*, 1995, Tella and Jovani, 2000) and (iii) Bloemfontein, South Africa (Colahan *et al.* 1991). Bolus collections were made by M. Dizerins in 1975 (Switzerland), J. L. Tella in 1998 (Spain) and B. Colahan in 1992 and 1994, and Colahan and Collins in 1998 (South Africa). The number of boluses obtained was constrained by the difficult access to nests in the colonies, as it is usual in this cliff-nesting species. All boluses were stored separately in 70 % ethyl alcohol and later examined under a dissecting microscope. Prey items were, when possible, identified to family or superfamily level; head to tail length, excluding antennae or caudal appendages, was measured with an ocular micrometer with measurements rounded to the nearest 0.1 mm. Alpine swifts breeding in Europe are referred to the nominate subspecies *T. m. melba*, while those breeding in Bloemfontein, South Africa, are referable to the smaller *T. melba africanus* (Fry, 1988). Insect taxonomy follows that presented by Scholtz and Holm (1985).

Description of the diet

The three boluses collected in Switzerland contained a total of 228 prey items (22 - 133 / bolus) which were all insects. These included Coleoptera (3), Diptera (108), Hemiptera (5), Hymenoptera (108) and Lepidoptera (4). The

two most numerous prey types were ants (Formicidae) and syrphid flies (Syrphidae) (appendix 1). Prey sizes ranged from 1.7 to 29 mm in body length with an average of 8.81 mm. The smallest item was a shore fly (Ephydriidae); the largest prey items were two crane flies (Tipulidae) which were 28 and 29 mm long.

The eleven boluses collected in Spain contained a total of 1,834 prey items (56 - 445 / bolus) > 99 % of which were insects (appendix 1). Seven orders and 43 families of insects were identified in the boluses with ants (Formicidae, Myrmicinae) and leafhoppers (Cicadellidae) being the most numerous prey types (appendix 1). The prey items ranged from 1.3 to 20.3 mm in body length and averaged 5.98 mm. The smallest item was an aphid (Aphididae); the largest prey item was a long-horned beetle (Cerambycidae).

The ten samples collected in South Africa contained a total of 1,640 prey items and averaged 164 / bolus (range 8 - 235 / bolus) of which > 98 % were insects (appendix 1). Seven boluses averaged 17.1 x 22.6 mm and weighed 1.8 g. Seven orders and 64 families of insects were identified in these boluses with leafhoppers, seed-bugs (Lygaeidae) and aphids being the most abundant prey types (appendix 1). The prey items ranged from 1.3 to 29.6 mm in body length and averaged 5.12 mm. The smallest prey item was an aphid; the two largest prey items (> 29 mm) were a short-horned grasshopper (Acrididae) and a damselfly *Enallagma gloucum* (Coenagrionidae).

As is found in other swifts, the prey items taken by alpine swifts were taxonomically diverse with spiders plus ten orders and 79 families of insects represented in the combined samples (appendix 1). The most diverse prey types were Diptera (25 families), Coleoptera (14 families) and Hymenoptera (13 families). The boluses from Switzerland showed the least diversity which was certainly an artifact of the smaller sample size (3 boluses). In a previous study there, an unspecified number of boluses contained from 11 to 626 prey items (aver-

age 219) including flies (308), beetles (200), aphids (125), wasps (94), ants (2), cicadas (15), lacewings (15), butterflies (2) and spiders (21) as well as wood wasps, drone honeybees and a damselfly (Cramp, 1985). In this study the inter-bolus variation in alpine swift prey items was substantial. Ants were the most abundant prey type in Spain where three boluses had 152 - 252 individuals/bolus, three had < 51 / bolus and ants were completely absent from one bolus. The second most abundant prey type there, leaf-hoppers, were represented by fewer than 10 individuals in six boluses and none in two boluses but had 180 - 182 individuals in each of two other boluses. In South Africa, 113 of 119 aphids, 84 of 217 seed-bugs and 29 of 34 ichneumon wasps (Ichneumonidae) were each present in single boluses. This among-bolus heterogeneity has also been seen in other species of swifts (Collins, 1968; García del Rey *et al.*, pers. obs.).

There was also considerable geographical variability in the prey types taken by alpine swifts at the three locations. Hymenoptera made up 47.4 and 56.5 % of the prey items in Switzerland and Spain, but only 4.8 % of the items in South Africa (appendix 2). Hemiptera made up 76.1 % of the prey items in South Africa but only 29.2 % in Spain and 2.2 % in Switzerland (appendix 2). Termites (Isoptera), which were prominent in the diets of some tropical swifts (Harrison, 1974; Collins, 1968, 1980; Tarburton, 1986) were represented, in low numbers, only in the alpine swift boluses in South Africa. Fry (1988) reported field observations in the Kasali Mts. in Zaire, where a flock of alpine swifts were "thought to be catching winged termites." In Bloemfontein, alpine swifts have been observed foraging near the colony on a large emergence of termite alates (Colahan, pers. obs.). Mating swarms of these insects are at times utilized by a wide variety of birds, including but not limited to, swifts and swallows (Brooke, 1970; Dial and Vaughan, 1987; Collins, 1999; Korb and Salewski, 2000). Even birds as large as eagles *Aquila* sp., marabou storks *Leptoptilus*

crumeniferus and spotted eagle owls *Bubo africanus* have been observed feeding on termite alates when available (Brown, 1982; Dial and Vaughan, 1987). Such swarms are episodic and thus easily missed or under-represented in limited dietary studies.

Hymenoptera are often numerous in the diets of swifts, including the alpine swift (appendix 2). These range from large lipid-rich winged reproductive ants to much smaller parasitic chalcid wasps (Chalcidoidea and families therein). Ants were prominent in the alpine swift diet in Spain but less numerous in boluses from Switzerland and were nearly absent from boluses collected in South Africa (appendix 1). Honeybees *Apis mellifera* were among the less common prey items taken in Switzerland and South Africa but in both places only drones were taken. Common swifts *Apus apus* and alpine swifts were previously noted to at times consume only drones (Lacey, 1910; Hess, 1927) while Bartels (1931) reported 11 bee stings in an alpine swift's throat indicating that worker honeybees are also taken by these swifts. In South Africa, alpine swifts were reported to be important predators of honeybees at commercial apiaries during cool windy weather in spring (Swart *et al.*, 2001). Under these weather conditions other, more typical, higher flying prey items may have been less available. Similarly, in the Philippines, the purple needletail *Hirundapus celebensis* has been recorded flying low and taking large numbers of both drone and worker honeybees; 162 whole bees or head capsules were found in one swift stomach (Morse and Laigo, 1969).

Considering the substantial among-bolus variation it is difficult to assess properly the differences in the diet among alpine swift populations. Longer term studies based on large samples of boluses are needed to document consistently different dietary habits attributable to geographical shifts in the prey fauna and not just shorter term or localized changes in prey type abundance and availability in this and other swift species.

Variability in prey size

The distribution of prey sizes was wide (1.3 - 29.6 mm) and markedly right-skewed, with most prey falling within the range of 2 - 8 mm (figure 1a). Prey sizes varied among populations (GLM test for log-transformed prey sizes, fixed effect: $F_{2,3698} = 1444.41$, $P < 0.01$) but also strongly among boluses (GLM test for log-transformed prey sizes, random effect: $F_{23,3677} = 62.11$, $P < 0.01$). A generalized linear mixed model testing for differences among populations while controlling for bolus as a random term did not converge, probably due to the low number of boluses. Therefore we calculated median prey sizes for each bolus for testing population effects while avoiding pseudoreplication. Median prey size differed among the three populations (Median test, asymptotic significance $P = 0.004$) in a gradient Switzerland > Spain > South Africa (figure 1b), coinciding with the same gradient in body mass of alpine swifts at the three populations (106.4, 90.4 and 77.9 g respectively, according to Arn-Willi, 1960, Tella *et al.*, 1995; Collins and Colahan, pers.obs.). Differences were also significant between the two last populations for which sample sizes were larger (Median test, exact significance $P = 0.02$).

The sizes of the prey items taken by alpine swifts at all three study sites were substantially different from those of related swifts. Alpine swifts took larger prey items than the six smaller *Apus* species for which quantitative data are currently available, thus arising a positive relationship between body mass and prey size of swifts (GLM, effect of body mass $F_{1,11} = 16.88$, $P = 0.026$ while controlling for species identity as random term: $F_{6,11} = 1.59$, $P = 0.38$; figure 2). Alpine swifts also took a greater range of larger prey items with the largest prey items being > 20 mm, or twice the maximum prey size taken by the smaller *Apus* species. It has been suggested several times that larger swifts, as alpine swifts and mottled swifts *T. aequato-*

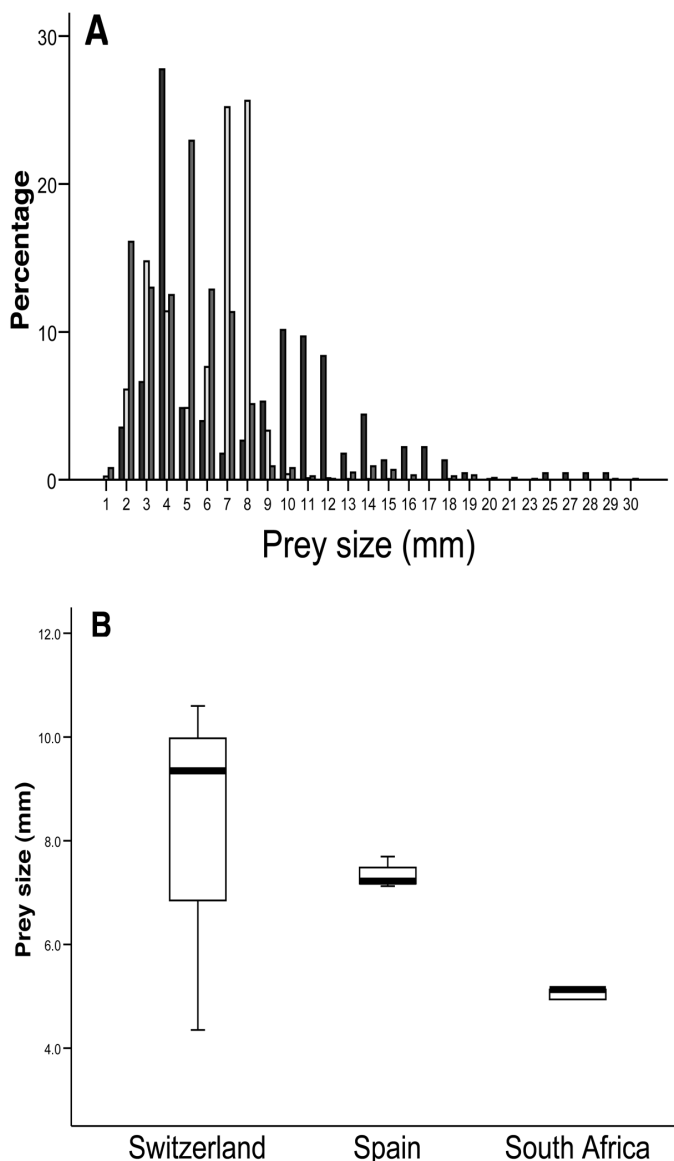


FIG. 1.—Variability in prey size of alpine swifts. A) Distribution of prey sizes taken in Switzerland (white bars, $n = 228$), Spain (black bars, $n = 1,834$) and South Africa (grey bars, $n = 1,640$). B) Variability in prey size among populations based on within-bolus median prey sizes from Switzerland ($n = 3$ boluses), Spain ($n = 11$) and South Africa ($n = 10$). Inter-bolus medians and quartiles are represented.

[Variabilidad en el tamaño de las presas de vencejos reales. A) Distribución del tamaño de presa en Suiza (barras blancas, $n = 228$ presas), España (barras negras, $n = 1.834$) y Sudáfrica (barras grises, $n = 1.640$). B) Variabilidad en el tamaño de presa entre poblaciones atendiendo a las medianas obtenidas de los bolos alimenticios como unidad muestral en Suiza ($n = 3$ bolos), España ($n = 11$) y Sudáfrica ($n = 10$). Se representan las medianas entre bolos y sus cuarteles.]

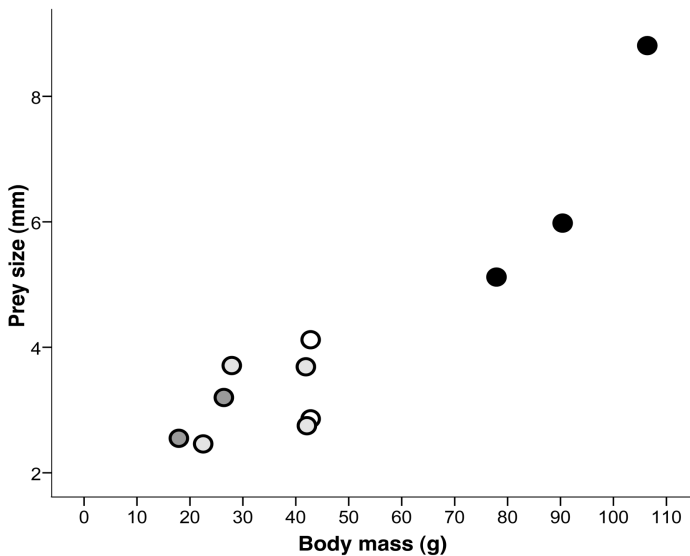


FIG. 2.—Relationship between prey size and body mass of swifts from Genus *Apus* and *Tachymarptis* (formerly *Apus*). Same symbols correspond to populations of the same species (black dots: *T. melba*; dark grey dots: *A. pallidus*; white dots: *A. apus*). Species and data sources are: *A. affinis*: Collins, pers.obs.; *A. unicolor*: García del Rey *et al.*, pers.obs.; *A. barbatus*: Collins, pers.obs.; *A. horus*: Collins, 1980; *A. pallidus*: Cucco *et al.*, 1993; *A. apus*: Collins, pers.obs., Cucco *et al.*, 1993; *T. melba*: this study.

[Relación entre el tamaño de presa y el peso corporal de siete especies de vencejos de los géneros *Apus* y *Tachymarptis* (anteriormente *Apus*). Los mismos símbolos corresponden a poblaciones de la misma especie (puntos negros: *T. melba*; gris oscuro: *A. pallidus*; blancos: *A. apus*). Las especies y el origen de los datos son: *A. affinis*: Collins, obs. pers.; *A. unicolor*: García del Rey *et al.*, obs. pers.; *A. barbatus*: Collins, obs. pers.; *A. horus*: Collins, 1980; *A. pallidus*: Cucco *et al.*, 1993; *A. apus*: Collins, obs. pers., Cucco *et al.*, 1993; *T. melba*: presente estudio.]

rialis, probably take larger prey than smaller species (Lack and Owen, 1955; Collins, 1968, 1980; Brooke, 1973; Tarburton, 1986; García del Rey *et al.*, pers.obs.). The data presented here provide the first quantitative confirmation of what has previously been mostly assumption.

The sizes of the prey items taken by alpine swifts (figure 1) and most other swifts studied to date shows a sharply skewed distribution with the smaller modal size probably reflecting the greater abundance of smaller prey (< 5 mm) in the air column (Glick, 1939). The larger prey items (> 7 mm) are less abundant (Lack and Owen, 1955) but may be preferred when

available. This is suggested here by the secondary peak in the prey sizes taken by alpine swifts in Switzerland (figure 1a). This peak consisted entirely of 8.5 - 17.5 mm long syrphid flies which made up 23 % of one bolus and 70 % of another. Syrphid flies were both smaller in size and less often taken by alpine swifts in Spain and South Africa (appendix 1). In Spain, a similar secondary peak in the number of large prey items (figure 1a) was made up almost entirely of winged reproductive ants (Myrmicinae) which were particularly abundant in two of the eleven boluses.

In conclusion, alpine swift diets include a wide array of arthropod prey taxa, as is true of

most other swifts. Despite of the extreme variation from bolus to bolus and site to site making the assessment of geographical trends in their diet difficult, our results support the prediction of larger swifts taking larger prey than smaller ones in both intraspecific and interspecific comparisons. Further research on prey availability is needed to assess aspects on prey selection by swifts.

ACKNOWLEDGEMENTS.—We thank M. Dizerins for providing the food boluses from Switzerland, J. A. Farrow and R. Waggenstein for help in their analysis, and R. López and J. Blasco for their field work help in Spain. We are indebted to Dr. Denis J. Brothers who provided invaluable family level identifications of the food samples from Spain and South Africa. Analysis of the food samples from Spain and South Africa were completed while the senior author was a Visiting Research Fellow in the Department of Zoology and Entomology at the University of Natal, Pietermaritzburg. Their hospitality and provision of laboratory space and materials was greatly appreciated. F. de Lope and an anonymous reviewer helped to improve the manuscript.

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[Recibido: 04-07-09]

[Aceptado: 07-07-09]

APPENDIX 1 [APÉNDICE 1]

Food of alpine swifts at three locations in Switzerland, Spain and South Africa.
 [Dieta del vencejo real en tres localidades de Suiza, España y Sudáfrica.]

| Order | Family/sup fam. | Switzerland | Spain | So. Africa |
|--------------|-----------------|-------------|-------|------------|
| Orthoptera | Acrididae | | | 3 |
| Coleoptera | Cerambycidae | | 1 | |
| | Bruchidae | | 17 | 4 |
| | Staphylinidae | | 40 | 12 |
| | Chrysomelidae | | 17 | |
| | Anthicidae | | 3 | 2 |
| | Curculionidae | 3 | 17 | 2 |
| | Cucujidae | | | 1 |
| | Scarabaeidae | | 1 | 8 |
| | Elateridae | | 1 | 1 |
| | Carabidae | | 1 | 19 |
| | Cleridae | | | 2 |
| | Coccinellidae | | 2 | |
| | Haliplidae | | | 22 |
| | Dytiscidae | | | 1 |
| Diptera | Empididae | | 4 | 1 |
| | Tipulidae | 4 | | 1 |
| | Lauxaniidae | | 4 | 3 |
| | Dolichopodidae | 1 | 1 | 6 |
| | Drosophilidae | | 1 | 23 |
| | Ephydriidae | 2 | | 3 |
| | Muscidae | | 13 | 25 |
| | Culicidae | | | 1 |
| | Syrphidae | 88 | 10 | 14 |
| | Tabanidae | | | 1 |
| | Chloropidae | 2 | 51 | 27 |
| | Pipiunculidae | | | 1 |
| | Chamaemyiidae | | | 2 |
| | Agromyzidae | | | 1 |
| | Sphaeroceridae | | 4 | 45 |
| | Sciaridae | | | 3 |
| | Tephritidae | | 7 | 3 |
| | Lonchoceridae | | 2 | |
| | Piophilidae | 9 | | |
| | Chironomidae | | | 8 |
| | Calliphoridae | | | 9 |
| | Sepsidae | | 1 | 2 |
| | Clusiidae | | 2 | |
| Heleomyzidae | | 1 | | |
| Phoridae | | 2 | | |
| unidentified | 2 | 2 | 2 | |
| Isoptera | Termitidae | | | 8 |
| Odonata | Coenagrionidae | | | 1 |

APPENDIX 1 [APÉNDICE 1] CONT.

| Order | Family/sup fam. | Switzerland | Spain | So. Africa |
|---------------|-----------------|-------------|--------------|--------------|
| Hemiptera | Coreidae | | 7 | 127 |
| | Cicadellidae | 3 | 388 | 612 |
| | Pentatomidae | | | 19 |
| | Berytidae | | | 2 |
| | Miridae | | 24 | 9 |
| | Nabidae | | 34 | |
| | Delphacidae | 1 | | |
| | Alydidae | | | 24 |
| | Cixiidae | 1 | | |
| | Lygaeidae | | 39 | 217 |
| | Fulgoridae | | 3 | 72 |
| | Pyrrhocoridae | | | 2 |
| | Tingidae | | | 4 |
| | Aphididae | | 26 | 119 |
| | Psyllidae | | | 7 |
| | Cercopidae | | 11 | |
| | Aphrophoridae | | | 5 |
| | Notonectidae | | | 36 |
| Hymenoptera | Formicidae | 70 | 1,009 | 11 |
| | Ichneumonidae | 19 | 4 | 34 |
| | Braconidae | | 2 | 5 |
| | Encyrtidae | | 1 | |
| | Bethylidae | | 2 | 1 |
| | Halictidae | | | 2 |
| | Diapriidae | 1 | | |
| | Apidae | 15 | 1 | 9 |
| | Perilampidae | 1 | | |
| | Pteromalidae | 1 | 5 | 1 |
| | Scelionidae | | | 4 |
| | Torymidae | | 1 | 1 |
| | Elasmidae | | | 1 |
| | Chalcidoidea | | | 1 |
| | unidentified | 1 | | 3 |
| Lepidoptera | Hesperiidae | 1 | | |
| | Pieridae | | | 16 |
| | Lycaenidae | | | 1 |
| | Unidentified | 3 | 9 | |
| Neuroptera | Hepialidae | | 1 | 8 |
| | Hemerobiidae | | 29 | |
| Ephemeroptera | Chrysopidae | | 27 | |
| | Unidentified | | 4 | |
| Araneae | Thomisidae | | 1 | 4 |
| | Salticidae | | | 2 |
| | unidentified | | | 13 |
| Totals | | 228 | 1,834 | 1,640 |

APPENDIX 2 [APÉNDICE 2]

Percentage composition of major prey items in the diets of swifts from Genus *Apus* and *Tachymarptis* (formerly *Apus*).

[Porcentaje de los principales tipos de presa en la dieta de vencejos de los géneros *Apus* y *Tachymarptis* (anteriormente *Apus*).]

| Species | <i>A. affinis</i> | <i>A. unicolor</i> | <i>A. horus</i> | <i>A. apus</i> | <i>T. melba</i> | <i>T. melba</i> | <i>T. melba</i> |
|---------------------------|-------------------|--------------------|-----------------|----------------|-----------------|-----------------|-----------------|
| Location | India | Canary Is. | Kenya | England | Switz. | Spain | So. Africa |
| n = | 416 | 12,800 | 396 | 6,301 | 228 | 1,847 | 1,640 |
| Araneae | 1.7 | 2.6 | 6.6 | 1.2 | 0 | 0.1 | 1.3 |
| Hemiptera | 70.0 | 55.5 | 42.9 | 31.0 | 2.2 | 29.2 | 76.1 |
| Diptera | 20.7 | 15.9 | 7.6 | 57.2 | 47.4 | 5.0 | 11.3 |
| Coleoptera | 7.2 | 9.3 | 5.8 | 2.0 | 1.3 | 5.4 | 4.5 |
| Isoptera | 0 | 0 | 19.4 | 0 | 0 | 0 | 0 |
| Hymenoptera | 7.0 | 15.4 | 17.4 | 6.8 | 47.4 | 56.5 | 4.8 |
| Lepidoptera | 0.2 | 0.1 | 0.8 | < 0.1 | 1.7 | 0.5 | 1.3 |
| Ephemeroptera | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 |
| Other orders ^a | 0.2 | 1.1 | 0 | 3.4 | 0 | 3.5 | 0.3 |
| Boluses | 4 | 32 | 2 | 16 | 3 | 11 | 10 |
| Individuals | 416 | 12,800 | 396 | 6,301 | 228 | 1,847 | 1,640 |
| Sources | 1 | 2 | 3 | 1 | 4 | 4 | 4 |

^a Other orders included: Psocoptera, Thysanoptera, Mecoptera, Neuroptera, Odonata and Orthoptera
[Otros órdenes incluyen: Psocoptera, Thysanoptera, Mecoptera, Neuroptera, Odonata y Orthoptera.]

1 C. T. Collins, pers. obs.; 2- García del Rey *et al.*, pers. obs.; 3- Collins, 1980; 4- this study.

[1 C. T. Collins, obs. pers.; 2- García del Rey *et al.*, obs. pers.; 3- Collins, 1980; 4- presente estudio.]