Predation by Afrotropical Asilidae (Diptera): an analysis of 2000 prey records

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Two thousand afrotropical asilid prey records, databased by the Natal Museum, are analysed. The key orders of arthropods preyed upon are, in order of importance, Hymenoptera, Diptera, Coleoptera, Orthoptera, Hemiptera, and Lepidoptera, that together accounted for 96 % of records. Insect families with sufficient data to warrant special mention are: Coleoptera (Scarabaeidae), Diptera (Asilidae, Bombyliidae, Calliphoridae, Muscidae, Tabanidae, Tipulidae, Syrphidae, Tachinidae, Empidae), Hemiptera (Cicadidae, Cicadellidae, Lygaeidae, Pentatomidae, Cercopidae), Hymenoptera (Formicidae, Apidae, Halticidae, Megachilidae), Orthoptera (Acrididae). Asilid genera with sufficient data to warrant special attention, are: Apocleinae (*Alcimus, Dasophrys, Neolophonotus, Philodicus, Promachus*), Dasypogoninae (*Pegesimallus*), Laphriinae (*Lamyra, Nusa, Stiphrolamyra*), Laphystiinae (*Hoplistomerus, Trichardis*), Leptogastrinae (*Euscelidia, Lasiocnemus*), Stenopogoninae (*Acnephalum, Daspletis, Gonioscelis, Microstylum, Rhabdogaster, Scylaticus*), Trigonomiminae (*Damalis*). A number of genera appear to be specialist feeders – *Scylaticus* on Hemiptera, *Lasiocnemus* on Araneida, *Hoplistomerus* on Scarabaeidae and *Bana* on *Apis mellifera*. Female asilids generally outnumber males 1.5 to 1 in records of prey capture, but the extent of this imbalance varies from one subfamily to another.

Key words: Afrotropical, Asilidae, prey analysis.

INTRODUCTION

Asilidae, robber flies or assassin flies, are an important group of predators in all zoogeographical regions. This study is confined to data relating to the Afrotropical Region. Considerable attention has been given to the taxonomy of afrotropical taxa, and many species have been described since the appearance of the *Catalogue of the Diptera of the Afrotropical Region.* In that catalogue, Oldroyd (1980) listed 1114 species in 104 genera. These numbers have now increased to 1511 species in 126 genera, showing increases of 26 % and 18 % in the number of species and genera, respectively. This makes the family the most species rich within the afrotropical dipterous fauna. Because they are both predaceous and often abundant insects, knowledge of all aspects of their biology is of importance in our understanding of arthropod communities in general. Such knowledge impacts on the management and conservation of major components of our biodiversity. The accumulation of 2000 prey records for afrotropical robber flies is therefore significant and has prompted this analysis.

Potentially useful information relating to the prey of robber flies is scattered throughout the mass of published information relating to the family and those groups they prey upon. Unfortunately, it mostly takes the form of isolated prey records that are difficult to gather for analysis and verification. It was therefore considered more useful to study data catalogued in museum collections where specimens are readily available for subsequent study. The Natal Museum's collection, together with the detailed list of prey published by Hobby (1935), has already resulted in a number of useful analytical studies (Londt 1990, 1991, 1993, 1995, 1999).

While these studies, together with the information presented in this paper, extend our knowledge of asilid biology, many questions pertaining to their feeding and nutrition remain unanswered. For example, the adaptive significance of predation by the male sex remains unexplained. Asilidae are unique among the Diptera in that adults of both sexes are highly effective predators, as are the larvae. Does the adaptation allow females to mature their ovaries, if this has not already taken place during the larval and pupal instars, and allow extended survival for both sexes in places where other suitable nutrition, *e.g.* nectar, is either absent or in limited supply? It is well-known that asilids display both great diversity and abundance in arid regions, and in grasslands, where nectar-

producing plants are often in short supply. Does resource-partitioning take place? The wide intraspecific range in both body size and feeding behaviour certainly allows a great range of invertebrate food to be consumed in a wide range of microhabitats. Do feeding ranges overlap? And, if they do, what is the degree of 'competition' that this would inevitably produce? Is it this 'competition' that explains both inter- and intraspecific predation of asilids upon other asilids? It is clear that far more research needs to be undertaken before answers to these intriguing questions will be found. All that can be undertaken with confidence is an analysis of available prey records. Perhaps the information will stimulate further research activity.

MATERIAL AND METHODS

Natal Museum asilid collection and database

Since commencing taxonomic research at the Natal Museum in 1976, my fieldwork has focused on the collection of Asilidae. This endeavour has included the collection of prey items whenever these were encountered. Specimens observed to be feeding on or carrying prey were mostly obtained by hand-netting. Prey items were pinned together with the individual predators involved. Each prey item is usually double mounted using a minuten pin secured to a card, polyporous strip or piece of polyethylene foam and pinned below the predator. Occasionally (older records) prey has been pinned on the same pin below the predator, while in some instances, when the prey is small or fragile, it has been placed in a cellulose pill-capsule and pinned below the predator. Every effort has been made to keep the predator and its prey as closely associated as possible so as to avoid subsequent separation or confusion. Specimens are stored within the museum's taxonomically arranged collection of Asilidae, so the tracing of specific prey items may sometimes prove time-consuming.

There are currently 2001 prey records in the Natal Museum's computerized asilid prey database. These have been assembled from two sources (a) material in the museum's collection (1503 records), and (b) the records (498) published by Hobby (1935). One of Hobby's records provides no identification of the asilid predator and so it has been excluded from this study. Each database record consists of information captured in 12 separate fields providing data about both the predator and prey item as follows:

Place of collection (3 fields named – Country, Province, Locality). The name of the country of origin is recorded, and, for South African records only, the provincial name. Under 'Locality' a brief statement, taken from the specimen's label, is provided. The Natal Museum has a separate and detailed database for the general asilid collection which provides additional information should this be required.

Identity of predator (4 fields named – Subfamily, Genus, Species, Sex). The identity is provided as accurately as possible and the gender of the predator recorded. All identifications of predators were either undertaken or checked by the author.

Identity of prey item (4 fields named – Order, Family, Prey, Det). All prey items are identified to Order and Family level, with a few exceptions. More precise identification, where available, or other information about the prey, is recorded in the 'Prey' field. The name of the person providing the prey determination is recorded under Det. The majority (1269) were identified by the author, most only to family level.

Catalogue number (1 field named – Cat No). Every pair of specimens (predator and prey) has been assigned a unique number (recorded on a green label attached to the predator's pin).

Geographical coverage

Records (number in brackets) are from the following countries: Botswana (5), Ghana (6), Ivory Coast (16), Kenya (23), Lesotho (3), Malawi (27), Mauritius (1), Namibia (63), South Africa (1328), Swaziland (18), Uganda (1), Zimbabwe (508), country unknown (1). Coverage is best for the southern parts of Africa, where most fieldwork has been undertaken, and for which good published information is available, *i.e.* the Zimbabwe records published by Hobby (1935).

ANALYSIS OF ASILIDAE AND THEIR PREY

Representation

All ten afrotropical asilid subfamilies are represented. The number of prey items recorded for each (Table 1) appears to mirror the relative individual species richness of these groups as recorded in an unpublished, updated version of the 1980 afrotropical catalogue of taxa posted on the World Wide Web (*www.geller-grimm.de*). Especially high numbers of prey records for the Apocleinae probably relates to the abundance of individuals.

Table 1. The arthropod prey of the afrotropical subfamilies of Asilidae. Abbreviations: Apo = Apocleinae, Asi = Asilinae, Das = Dasypogoninae, Lar = Laphriinae, Lay = Laphystiinae, Lep = Leptogastrinae, Omm = Ommatiinae, Ste = Stenopogoninae, Sti = Stichopogoninae, Tri = Trigonomiminae. Dominant data are presented in bold face.

Prey order	Total no.	Asilidae subfamily									
	%	Apo	Asi	Das	Lar	Lay	Lep	Omm	Ste	Sti	Tri
Araneida	16	4	0	3	0	0	**6**	0	2	0	1
	0.8	0.3	0	3.1	0	0	**42.9**	0	0.7	0	0.6
Archaeognatha	1	1	0	0	0	0	0	0	0	0	0
	0.1	0.1	0	0	0	0	0	0	0	0	0
Coleoptera	294	118	2	16	11	**22**	0	2	**107**	1	15
	14.7	9.7	5.9	16.3	9.4	**81.5**	0	18.2	**35.1**	14.3	9
Diptera	457	**316**	**17**	25	27	1	3	**5**	44	**4**	15
	22.0	**25.9**	**50.0**	25.5	23.1	3.7	21.4	**45.5**	14.4	**57.1**	9
Ephemeroptera	1	0	1	0	0	0	0	0	0	0	0
	0.1	0	2.9	0	0	0	0	0	0	0	0
Hemiptera	191	103	4	7	11	0	1	2	43	1	19
	9.6	8.4	11.8	7.1	9.4	0	7.1	18.2	14.1	14.3	11.4
Hymenoptera	**527**	244	5	**40**	**57**	4	2	1	65	1	**108**
	26.4	20.0	14.7	**40.8**	**48.7**	14.8	14.3	9.1	21.3	14.3	**64.7**
Isoptera	24	14	0	3	0	0	0	0	5	0	2
	1.2	1.1	0	3.1	0	0	0	0	1.6	0	1.2
Lepidoptera	163	142	5	3	4	0	1	1	7	0	0
	8.2	11.6	14.7	3.1	3.4	0	7.1	9.1	2.3	0	0
Mantodea	2	0	0	0	0	0	0	0	2	0	0
	0.1	0	0	0	0	0	0	0	0.7	0	0
Mecoptera	3	2	0	1	0	0	0	0	0	0	0
	0.2	0.2	0	1.0	0	0	0	0	0	0	0
Neuroptera	25	24	0	0	0	0	0	0	1	0	0
	1.3	2.0	0	0	0	0	0	0	0.3	0	0
Odonata	4	2	0	0	0	0	0	0	2	0	0
	0.2	0.2	0	0	0	0	0	0	0.7	0	0
Orthoptera	280	245	0	0	7	0	0	0	27	0	1
	14.0	20.1	0	0	6.0	0	0	0	8.9	0	0.6
Psocoptera	6	0	0	0	0	0	1	0	0	0	5
	0.3	0	0	0	0	0	7.1	0	0	0	3.0
Thysanoptera	1	0	0	0	0	0	0	0	0	0	1
	0.1	0	0	0	0	0	0	0	0	0	0.6
Trichoptera	2	2	0	0	0	0	0	0	0	0	0
	0.1	0.2	0	0	0	0	0	0	0	0	0
Undetermined	3	3	0	0	0	0	0	0	0	0	0
	0.3	0.2	0	0	0	0	0	0	0	0	0
Total no. &	2000	1220	34	98	117	27	14	11	305	7	167
Percentage	100.6	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Some species of *Neolophonotus* may be particularly well represented. High prey number recorded for the Trigonomiminae is a consequence of a special effort made to sample the prey of *Damalis* species in KwaZulu-Natal. The relatively low prey number for the Leptogastrinae can be attributed to their physically small size. These often tiny and mostly grass-inhabiting asilids are commonly swept from vegetation and hence not actually seen in the act of feeding.

Prey composition

Data relating to the major groups of Arthropoda preyed upon are presented in Table 1. These results show that 17 different orders of arthropods have been recorded as prey. Two of these are spider taxa, while the rest are insects. Six insect orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera) account for 1912 records, or 96 % of all prey items recorded. Diptera dominate in four asilid subfamilies, Hymenoptera in three, Coleoptera in two, and Araneida in one. A more detailed analysis of each of the asilid subfamilies, and the more significant genera contained within them, is provide below.

Apocleinae

Details are available in Table 1. Three orders Diptera , Orthoptera and Hymenoptera, together make up 66 % of the diet. At subfamilial level the group appears to have catholic feeding behaviour. An analysis of significant genera (those for which there are at least 50 records) is provided below in alphabetical order, with mention of prey families when these are represented by at least 10 records.

Alcimus Loew, 1848 (302 records): Orthoptera (136), Lepidoptera (100), Diptera (34), Hymenoptera (11), Hemiptera (9), Coleoptera (5), Neuroptera (3), Odonata (2), Isoptera (1), Undetermined (1). Significant families making up 74 % of known prey are the Acrididae (133), Asilidae (27), Nymphalidae (24), Lycaenidae (22) and Pieridae (18). Although a species analysis must await a revision of the genus, it is probable that some species specialize on Acrididae, while others prey mainly on day-flying Lepidoptera.

Hobby (1935) records 17 Asilidae of the genus *Pegesimallus* Loew, 1858, being preyed upon by *Alcimus.*

Dasophrys Loew, 1858 (66 records): Diptera (26), Hymenoptera (19), Hemiptera (9), Orthoptera (6), Coleoptera (2), Isoptera (2), Lepidoptera (2). The only family with more than 10 records is the Formicidae (12), with 18 % of prey records. However, this probably does not indicate a preference for ants, but that species of *Dasophrys,* like many other asilids, will take advantage of easily captured and abundant swarming alate formicids. Isolated prey records were published when Londt (1981) revised the genus.

Neolophonotus Engel, 1925 (486 records): Diptera (165), Hymenoptera (110), Coleoptera (69), Hemiptera (49), Orthoptera (29), Lepidoptera (28), Neuroptera (19), Isoptera (9), Araneida (3), Trichoptera (2), Archaeognatha (1), Undetermined (2). The first six listed Orders account for 93 % of the prey. Significant prey families are Apidae (56), Scarabaeidae (50), Bombyliidae (35), Asilidae (32), Tabanidae (18), Muscidae (16), Cicadellidae (14), Syrphidae (13), Calliphoridae (11) and Formicidae (11). The genus appears to have catholic feeding tastes, the first four listed families accounting for 36 % of all prey. Honey bees (*Apis mellifera*) constitute 95 % (53) of the Apidae listed, while 17 of the Asilidae (*i.e.* 53 %) are identified as *Neolophonotus.* Londt (1988), in a revision of the genus, included a brief analysis of prey based on 143 prey items. The number of records currently available allows an intrageneric analysis of species with at least 15 records (Table 2). An analysis of nine species of *Neolophonotus* serves to demonstrate that there may be significant intrageneric differences in diet. Many more prey records would be needed before predilections can be identified with any certainty.

N. abuntius (Walker, 1849): feeds mainly on Diptera and Hymenoptera. The only significant family is the Apidae which accounts for all the hymenopterous records. All these apids are honey bees (*Apis mellifera*).

N. bimaculatus Londt, 1986: feeds mainly on Diptera and Coleoptera. Significant prey families are the Scarabaeidae (21) that represent 84 % of the beetles, Tabanidae (15) that represent 29 % of the flies, Nemopteridae (10) that account for all the lacewings, and possibly the Apidae (all honey bees) (9) and Bombyliidae (9).

N. expandocolis Londt, 1985: feeds chiefly on Hemiptera, Neuroptera and Diptera. Families which may be significant are the Nemopteridae (6) which account for all the lacewings (see comments for Nemopteridae later in this paper), and the Cicadellidae (4) which account for 67 % of the bugs.

Table 2. The composition of prey items recorded for *Neolophonotus* species with at least 15 records. Abbreviations: Arc = Archaeognatha, Col = Coleoptera, Dip = Diptera, Hem = Hemiptera, Hym = Hymenoptera, Iso = Isoptera, Lep = Lepidoptera, Neu = Neuroptera, Ort = Orthoptera, Und = Undetermined specimens. Dominant data is presented in bold face.

Species	Records	Arthropod order									
		Arc	Col	Dip	Hem	Hym	Iso	Lep	Neu	Ort	Und
N. abuntius	38	0	4	**18**	2	10	0	3	1	0	0
N. bimaculatus	118	0	25	**52**	12	14	4	1	10	0	0
N. expandocolis	24	1	1	5	**6**	0	2	1	**6**	1	1
N. hessei	23	0	2	5	4	**11**	0	1	0	0	0
N. louisi	15	0	2	4	0	**6**	0	1	0	2	0
N. rapax	39	0	2	8	2	**17**	0	0	0	9	1
N. robustus	15	0	4	2	2	5	0	0	0	2	0
N. suillus	15	0	**6**	3	1	5	0	0	0	0	0
N. vansoni	15	0	0	**12**	4	0	0	0	0	2	0
Total	302	1	46	109	33	68	6	7	17	16	2

N. hessei Londt, 1986: feeds mainly on Hymenoptera but the Diptera and Hemiptera may prove to be significant. Nine of the hymenopterans are *A. mellifera* making the Apidae (39 %) a significant family.

N. louisi Londt, 1986: feeds mainly on Hymenoptera, but the Diptera are also significant. The Apidae account for 67 % of the hymenopterans and are all honey bees.

N. rapax (Ricardo, 1920): all the records available for this species were published by Hobby (1935), and show the dominant prey order to be the Hymenoptera. The Orthoptera and Diptera are also significant groups. Families that appear to be of importance are the Acrididae (9) which account for all the orthopteran records, the Megachilidae (7) that make up 41 % of the hymenopterans. The Apidae (7), constituting 41 % of the hymenopterans, are mostly honey bees (5).

N. robustus (Ricardo, 1922): although the sample is small, the Hymenoptera and Coleoptera together account for 60 % of the prey. No significant families can be detected.

N. suillus (Fabricius, 1805): together, the Coleoptera and Hymenoptera make up 73 % of the sample. Of significance is the fact that all the beetles belong to the Scarabaeidae, accounting for 40 % of the known diet.

N. vansoni Bromley, 1936: Diptera account for 80 % of the diet and it is interesting that only two families are represented, the Sepsidae (8) and Muscidae (4), strongly suggesting that this asilid preys on insects associated with decaying matter, such as animal dung.

Philodicus Loew, 1848 (183 records): Orthoptera (62), Hymenoptera (47), Diptera (41), Hemiptera (18), Coleoptera (7), Lepidoptera (5), Neuroptera (2), Mecoptera (1). The first three listed orders constitute 82 % of prey. Significant prey families are Acrididae (62), Apidae (20), Asilidae (18) and Cicadidae (10). Acrididae represent 34 % of the diet of *Philodicus.*

Promachus Loew, 1848 (169): Hymenoptera (57), Diptera (49), Coleoptera (30), Hemiptera (15), Orthoptera (11), Lepidoptera (5), Araneida (1), Isoptera (1). The first three listed orders account for 80 % of prey. Significant families are the Apidae (26), Scarabaeidae (21), Asilidae (12) and Acrididae (11). All except two apid records are for *Apis mellifera.*

Asilinae

Although only 34 records are available, the Diptera clearly dominate in the diet of the Asilinae in general, making up 50 % of recorded prey (Table 1). Other insect orders representing more than 10 % of the diet are the Hymenoptera, Lepidoptera and Hemiptera, but the low numbers do not inspire confidence.

The best generic data relate to *Caenoura* Londt, 2002, and *Valiraptor* Londt, 2002, each with eight records, and both appear to mirror observations made at the subfamily level.

Dasypogoninae

The dominant prey orders represented in the

diet of the Dasypogoninae are the Hymenoptera, Diptera and Coleoptera, accounting for 83 % of prey items (Table 1). As all the data available for the subfamily relate to *Pegesimallus,* the information provided above applies at both taxonomic levels.

Pegesimallus Loew, 1858 (98 records): the genus has fairly catholic feeding habits. Although the Tipulidae (18) represent the only significant prey family and constitute 18 % of the total prey number, it should also be noted that the Scarabaeidae (8) constitute 50 % of the recorded Coleoptera and the Apidae (7) represent 18 % of the Hymenoptera. All seven apids are honey bees (*Apis mellifera*). Further comment on the feeding on tipulids is provided later in this paper. Of interest is the relatively high number of Araneida (3) which represent 19 % of all spiders recorded. *Pegesimallus* is obviously capable of catching wingless prey. Although spiders are incapable of flight, they can dangle from silk threads and jump into the air, and so such prey may also have been collected in 'flight'. Fifty-three (57 %) records relate to *P. pedunculatus* (Loew, 1858), a commonly encountered species in the vicinity of Pietermaritzburg (KwaZulu-Natal). Londt (1980) revised the genus and included comments on prey records from his suburban garden. *Pegesimallus,* is the genus most preyed upon by other asilids with 41 records.

Laphriinae

The dominant prey order represented in the diet of the Laphriinae is the Hymenoptera accounting for 49 % of prey (Table 1). Together with the Diptera these insects form 72 % of the diet. Data suggest that within these insect orders the Laphriinae are generalists; the largest prey family is the Halictidae (10), constituting a mere 9 % of the total diet. Significant genera are given attention alphabetically below.

Lamyra Loew, 1851 (12): Hymenoptera (10), Diptera (2). Hymenoptera constitute 83 % of prey. All records pertain to *Lamyra gulo* (Loew, 1851), the most widespread and commonly collected species in the genus (Dikow & Londt, 2000). Although Dikow & Londt (2000) briefly discuss the prey of *Lamyra,* there are too few records to indicate predilections within the Hymenoptera. Although two dipterans were preyed upon, it is interesting that *Stiphrolamyra* Engel, 1928, resembles an aculeate wasp, and a *Promachus* bears a superficial resemblance to a bee. As *Lamyra* is regarded as a wasp mimic, an understanding of this mimicry in relation to its hymenopteran diet would be of interest.

Laxenecera Macquart, 1838 (37): Hymenoptera (15), Diptera (9), Orthoptera (5), Coleoptera (4), Hemiptera (4). There does not appear to be any predilection. Thirty-one (84 %) records relate to the feeding of *Laxenecera albicincta* Loew, 1852, a commonly encountered bee-like southern African species.

Nusa Walker, 1851 (10): Diptera (5), Lepidoptera (3), Orthoptera (2). The Diptera constitute 50 % of prey, and, although numbers are small, three of them are Tabanidae. It appears that *Nusa* is exceptional within the subfamily in not feeding predominantly on hymenopterans. A few additional prey records are included in Londt's (2006) revision of the genus.

Stiphrolamyra Engel, 1928 (26): Hymenoptera (20), Coleoptera (3), Diptera (2), Hemiptera (1). Hymenoptera represent 77 % of prey items. Although a wide range of hymenopteran families are represented, the Halictidae (5) may be of significance. Species of this genus also resemble aculeate wasps, and so the predilection for hymenopteran prey may be biologically significant. Londt (1983a) published a few prey records and briefly discussed predation by the genus.

Laphystiinae (27 records)

Coleoptera represent 81 % of prey (Table 1). As only two genera are represented and show divergent and specialized feeding, they are treated separately below.

Hoplistomerus Macquart, 1838 (23): Coleoptera (22), Diptera (1). Coleoptera represent 96 % of the diet. The significant family is the Scarabaeidae (21) which alone constitute 91 % of all records. Species of the genus specialize on dung-frequenting insects and individuals are usually encountered perched on dung awaiting the arrival of prey. A number of the available prey records were collected during a systematic survey carried out by G. Bernon to establish ecological information relating to dung beetles. Apart from dung beetles, records include dung-frequenting Hydrophilidae (1) and Muscidae (1), the fly being iridescent green in colour and thus resembling some dung beetles.

Trichardis Hermann, 1906 (4): although there are only four prey records, all belong to the Hymenoptera. The records consist of Halictidae (3) and Pompilidae (1); as species of *Trichardis* are usually

found resting on the ground (Londt 1994) a predilection for ground-nesting hymenopterans is possible.

Leptogastrinae (14 records)

Spiders constitute 43 % of the prey records (Table 1). Records are only available for two genera, and both warrant separate discussion below. Although *Leptogaster* Meigen, 1803, is the largest genus in the subfamily, there are no prey records. This is probably due largely to the small size of these mostly grass-inhabiting species, and the fact that they are usually sampled by sweeping vegetation, prey being dropped as a result of the disturbance caused during capture.

Euscelidia Westwood, 1850 (10): Diptera (3), Araneida (2), Hymenoptera (2), Hemiptera (1), Lepidoptera (1), Psocoptera (1). As the majority of records are for *E. procula* (Walker, 1849) (9), the broad representation of prey groups shown can only suggest that this species has a fairly catholic diet. Dikow (2003) records the prey of two species (*E. brunnea* (Loew, 1858), *E. procula*).

Lasiocnemus Loew, 1851 (4): Araneida (4). The genus deserves special mention as all prey records are spiders. All records also pertain to *L. lugens* collected in Swaziland. The spiders have been tentatively identified as belonging to the Oxyopidae. The author observed these asilids flying around the umbelliferous flowering heads of plants growing to a height of about a metre. The asilids were seen 'searching' the flower heads for prey and hovering above victims before rapidly swooping down and capturing the spiders. Although the data suggest highly-specialized feeding, more records are required to confirm this.

Ommatiinae (11 records)

Although Diptera represent 45 % of prey, data are insufficient to allow meaningful comment (Table 1). All records have been ascribed to the genus *Ommatius* Wiedemann, 1821, but the group requires taxonomic revision and so this may be erroneous.

Stenopogoninae (305 records)

Recorded prey consist of Coleoptera, Hymenoptera, Diptera and Hemiptera together account for 85 % of all prey (Table 1). The Coleoptera dominate by forming 35 % of the diet. Apart from the most significant genera, *Microstylum* Macquart, 1838 (123) and *Gonioscelis* Schiner, 1866 (74), a few other genera for which there are at least ten records will be briefly discussed below as the Stenopogoninae is particularly rich in genera.

Acnephalum Macquart, 1838 (14): Coleoptera (7), Hemiptera (5), Diptera (1), Hymenoptera (1). The Coleoptera and Hemiptera constitute 85 % of prey items. Of possible significance is that the Coleoptera include four Scarabaeidae.

Daspletis Loew, 1858 (24): Hymenoptera (8), Diptera (6), Lepidoptera (4), Hemiptera (3), Orthoptera (2), Araneida (1). The data suggest a catholic diet. A few isolated prey records were published by Londt (1983b).

Gonioscelis Schiner, 1866 (74): Coleoptera (51), Hymenoptera (11), Diptera (5), Hemiptera (4), Isoptera (2), Lepidoptera (1). The Coleoptera dominate and account for 24 % of all prey records, while the Scarabaeidae (38) constitute the largest family (75 %) within this order. No other significant insect families can be identified. Londt (2004), who revised the taxonomy of the genus and included information on prey, supported a suggestion that the enlarged fore-femora found in *Gonioscelis* might assist in feeding on hard-bodied insects like beetles. *Gonioscelis maculiventris* Bigot, 1879, is represented by 25 databased prey records, and so is worthy of separate analysis. Prey consists of Coleoptera (22), Hymenoptera (2) and Diptera (1). All the beetles, which make up 88 % of the diet, are Scarabaeidae and most have been identified as belonging to the flower-visiting Rutellinae. For an additional comment on predation by *G. maculiventris* see Londt (2004).

Microstylum Macquart, 1838 (123): Coleoptera (38), Orthoptera (24), Diptera (20), Hemiptera (20), Hymenoptera (14), Isoptera (2), Odonata (2), Lepidoptera (1), Mantodea (1), Neuroptera (1). Although the first four listed orders make up 83 % of records, the genus appears to be catholic in its choice of prey. The genus, however, needs revision, and so it is not possible at present to analyse the prey of any one species to see if specialization takes place at this taxonomic level. Significant prey families are the Scarabaeidae (30), Acrididae (24), Asilidae (16), and Cicadidae (12).

Rhabdogaster Loew, 1858 (14): Hymenoptera (9), Diptera (2), Araneida (1), Hemiptera (1), Isoptera (1). The Hymenoptera make up 64 % of prey records. Of these the Formicidae (7) represent 78 %. These ants are all winged alates, and so it can be assumed that this is a case of opportunistic feeding.

Scylaticus Loew, 1858 (10): Hemiptera (7), Diptera (1), Hymenoptera (1), Mantodea (1). The Hemiptera constitute 70 % of prey records. This appears to be the only asilid genus to prey heavily on Hemiptera. Of possible significance is that there are four Lygaeidae (2 nymphs) in the sample. Londt (1992a) published isolated prey records and commented on feeding habits based on eight prey records.

Stichopogoninae (7 records)

While there are only seven recorded prey items the majority are diperans, making up 57 % of the total (Table 1). Six of the records are for the dominant genus *Stichopogon* Loew, 1847, while one is for *Clinopogon* Bezzi, 1910. Species of *Stichopogon* are small and this might account for the paucity of prey records.

Trigonomiminae (167 records)

The dominant order is the Hymenoptera, with 65 % of all records (Table 1). All but four of the prey records relate to *Damalis* Fabricius, 1805, some species of which may be commonly encountered in grassland habitats in KwaZulu-Natal. Apart from this genus, to be dealt with separately below, there is only one other in the subfamily, *Rhipidocephala* Hermann, 1926. Species of this genus are tiny, which probably explains the low number of recorded prey (4).

Damalis Fabricius, 1805 (163): Hymenoptera (107), Hemiptera (19), Coleoptera (15), Diptera (13), Psocoptera (5), Isoptera (2), Araneida (1), Thysanoptera (1). The dominant prey order is the Hymenoptera representing 66 % of prey records. While numbers are not high, some degree of specialization appears in the Coleoptera and Hemiptera. Staphylinidae (10) make up 67 % of the beetles while the Cicadellidae (7) and Lygaeidae (7) each account for 37 % of the hemipterans. As far as the Hymenoptera are concerned, Formicidae (100) make up the bulk of records (93 %). These ants are invariably winged alates and 72 have been identified generically as *Solenopsis* Westwood, 1841. It is difficult to determine whether alate ants are the preferred prey, or whether the predators are merely taking advantage of swarming alates. Such feeding is probably opportunistic, but as the *Damalis* species involved (*D. femoralis* Ricardo, 1925) is active in late summer when ants commonly disperse, the timing of their emergence may be linked. Londt (1989) briefly analysed 65 prey records, while Londt (1991), provided observations on the biology of *D. femoralis* with a detailed analysis of recorded prey items, concluding that the species has a 'wide range of acceptable prey' and suggesting that it is catholic in its feeding habits.

ANALYSIS OF ARTHROPOD ORDERS CAPTURED BY ASILIDAE

Table 1 provides a list of the prey orders utilized by afrotropical asilids. A more detailed examination of the data, identified at familial level provides further insights into which groups are most likely to be preyed upon. Orders for which there are at least 20 records are dealt with alphabetically below.

Coleoptera (294 records)

Although representatives of some 17 families are documented in the database, the Scarabaeidae (185) clearly dominate and constitute 63 % of records. Other families worthy of brief mention are the Staphylinidae (16), Cerambycidae (8) and Chrysomelidae (8).

Scarabaeidae (185): the identification of scarabaeid prey below family level has only partly been undertaken, and so detailed discussion can not be provided. However, it is clear that two major groups are involved – those species associated with dung and those that visit flowers. The major asilid predators of dung-visiting scarabs are laphystiine species of *Hoplistomerus*. Available records are for two species *H. nobilis* Loew, 1858 (19) and *H. serripes* (Fabricius, 1805) (2). Flower-visiting scarabs, belonging chiefly to the subfamily Rutellinae, form an important part of the diet for a number of asilid genera including *Gonioscelis, Microstylum, Neolophonotus* and *Promachus,* all discussed earlier in this paper. While taxonomic revisions are required for both *Microstylum* and *Promachus,* it is possible to identify the following species of *Gonioscelis* and *Neolophonotus* as significant predators of flower-visiting scarabs – *G. maculiventris* Bigot, 1879, *N. bimaculatus* Londt, 1986.

Diptera (457 records)

Some 35 families of Diptera are recorded as prey of Asilidae; Asilidae (127), Bombyliidae (66), Calliphoridae (38), Muscidae (37), Tabanidae (26), Tipulidae (23), Syrphidae (22), Tachinidae (17) and

Empidae (10). Brief comments relating to the predation of these families follow. Apart from the Asilidae, specific identifications of prey Diptera have not been made.

Asilidae (127): it is of interest that the Asilidae form 28 % of the dipteran prey of Asilidae. This observation prompted a separate analysis (Londt 1995), based on 101 records. The more important asilid genera involved as predators of other asilids are *Neolophonotus* (32), *Alcimus* (27), *Philodicus* (18), *Microstylum* (16) and *Promachus* (12). All but *Microstylum* belong to the Apocleinae. Asilid genera most commonly recorded as prey are *Pegesimallus* (41) and *Neolophonotus* (21).

Bombyliidae (66): asilid genera most commonly found feeding on bombyliids are *Neolophonotus* (34), *Philodicus* (9), *Promachus* (9) and *Alcimus* (5), all members of the Apocleinae. Of the *Neolophonotus, N. bimaculatus* (9) account for 26 % of records.

Calliphoridae (38): asilid genera most commonly found feeding on calliphorids are *Neolophonotus* (13), *Promachus* (8) and *Dasophrys* (7), all Apocleinae.

Muscidae (37): of the 12 asilid genera recorded feeding on muscids, only *Neolophonotus* (16) has more than four records.

Tabanidae (26): of the 26 tabanids recorded as prey, 18 (69 %) were captured by *Neolophonotus,* 15 (83 %) of these records being ascribed to *N. bimaculatus.* Tabanids, however, only account for 13 % of the known diet of this species.

Tipulidae (23): all but five tipulid prey records are for *Pegesimallus* (18), and all of these pertain to *P. pedunculatus* (Loew, 1858). Tipulidae, however, account for only 18 % of the recorded prey of *Pegesimallus.* Almost all the *P. pedunculatus* records were collected in a suburban garden where tipulids were common and probably associated with the lawn, suggesting opportunistic feeding.

Syrphidae (22): syrphids are preyed upon by *Neolophonotus* (13), *Philodicus* (4), *Promachus* (3) and *Laxenecera* (2). While the samples are small, *N. bimaculatus* (5) and *N. abuntius* (4) account for 69 % of the *Neolophonotus* records.

Tachinidae (17): of the eight genera recorded feeding on tachinids, *Neolophonotus* (5) and *Promachus* (5) are the most significant.

Empididae (10): seven asilid genera are recorded feeding on empidids, *Damalis* (3) being the most significant genus. These *Damalis* records are all for *D. femoralis.*

Hemiptera (191 records)

Of the more than 20 families recorded as prey, the following, with more than 10 records, are considered significant – Cicadidae (37), Cicadellidae (31), Lygaeidae (30), Pentatomidae (24) and Cercopidae (11). The preponderance of homopterans may be relevant. These families, as asilid prey, are briefly discussed below.

Cicadidae (37): although a number of these specimens have not been identified, *Melampsalta* Kolenati, 1857 (16) and *Stagira* Stäl, 1861 (3) are genera databased. Asilid genera with at least five cicadid records are *Microstylum* (12), *Philodicus* (10), *Alcimus* (5) and *Promachus* (5).

Cicadellidae (31): most of the cicadellids require specific identification. Eleven genera of asilids have been recorded feeding on them, of these *Neolophonotus* (14) and *Damalis* (7) are the most significant. Six of the *Damalis* records relate to *D. femoralis.*

Lygaeidae (30): Most of the lygaeids require specific identification. Of the 10 asilid genera that have been recorded feeding on lygaeids, three have at least five records – *Damalis* (7), *Neolophonotus* (6) and *Philodicus* (5), and make up 60 % of records.

Pentatomidae (24): almost all the pentatomids require specific identification. 12 asilid genera have been recorded feeding on pentatomids and *Neolophonotus* (5) is the most significant.

Cercopidae (11): none of the cercopids are identified below family level. Seven asilid genera are recorded feeding on cercopids, none with more than two records.

Hymenoptera (527 records)

As shown in Table 1 the Hymenoptera are the most significant prey order, with 26 % of all records, 40 prey items still requiring familial identification. However, those that have been identified to family level indicate that the following are the most significant families; Formicidae (160), Apidae (148), Halictidae (28) and Megachilidae (28). Formicidae and Apidae dominate with a combined 58 % of all hymenopterous records. The four families listed above are given separate attention below.

Formicidae (160): although only 61 % of the ants are recorded as being alates this is certainly an underestimation as many records exclude this kind of information. The percentage is probably well over 90 %. Of those that have been identified at subfamilial level (107) the Myrmicinae (93)

dominate the Ponerinae (10) and Formicinae (4), accounting for 87 % of the sample. Seventy-seven records bear the generic name *Solenopsis*. The asilid genera considered to be significant ant-eaters are: *Damalis* (99), *Dasophrys* (12) and *Neolophonotus* (11). Ants form 93 % of the diet of *Damalis,* 18 % in *Dasophrys,* and only 2 % of the prey of *Neolophonotus.*

Apidae (148): of the apids, 117 (79 %) records relate to honey bees (*Apis mellifera*), updating earlier work on predation of honey bees (Londt 1993). Thirteen asilid genera are recorded feeding on honey bees, but only seven have five or more records *i.e. Neolophonotus* (53), *Promachus* (24), *Philodicus* (8), *Pegesimallus* (7), *Microstylum* (6), *Alcimus* (5) and *Bana* Londt, 1992 (5). The dietary proportion that honey bees represent in these asilid genera is generally low – *Neolophonotus* (11 %), *Promachus* (14 %), *Philodicus* (4 %), *Pegesimallus* (8 %), *Microstylum* (5 %), *Alcimus* (2 %) with the exception being *Bana* (56 %). This monotypic genus, represented only by *B. apicida* Londt, 1992, appears to mimic honey bees (Londt 1992b).

Halictidae (28): the halictids require specific identification. Eleven asilid genera are recorded feeding on them, but numbers are too low for meaningful comment, although they account for 15 % of the diet of *Stiphrolamyra.*

Megachilidae (28): nine asilid genera are recorded feeding on megachilids, *Philodicus* (9) and *Neolophonotus* (7) being most significant. Although all records for *Neolophonotus* are for *N. rapax* (Ricardo, 1920), megachilids account for only a tiny proportion of the diet of *Neolophonotus* (1 %). Six of the records for *Philodicus* relate to *P. swynnertoni* Hobby, 1933, but the megachilids constitute a tiny part (3 %) of the diet of the genus.

Isoptera (24 records)

The identified termites are represented by Termitidae (10), Hodotermitidae (9) and Kalotermitidae (2). Three are described as workers and so it is assumed the balance are alate reproductives. Ten genera of asilids are recorded feeding on termites, the most significant being *Neolophonotus* (9). The fact that alate termites frequently fly at night may account for the relative paucity of records, the Asilidae being diurnally active.

Lepidoptera (163 records)

Over 50 of the lepidopterans remain unidentified at familial level, and these are mostly small moths needing the attention of a specialist. Current data for butterflies (86) is as follows: Lycaenidae (26), Nymphalidae (25), Pieridae (23), Hesperiidae (5), Papilionidae (5) and Satyridae (2). Significant asilid genera (with at least five records) feeding on butterflies are: *Alcimus* (73) and *Neolophonotus* (8). *Alcimus* records include Nymphalidae (24), Lycaenidae (22), Pieridae (18), Papilionidae (5) and Hesperiidae (4). As there have been few additions since Londt's (1999) paper, no further comment is necessary.

Neuroptera (25 records)

Neuropteran records are made up of Nemopteridae (18), Chrysopidae (3), Ascalaphidae (2) and Myrmeleontidae (2). Domination by the Nemopteridae (72 %) is the result of a focused study of the predation of these lacewings by asilids (Picker, Leon & Londt 1991, 1992). The asilids preying on neuropterans are – *Neolophonotus* (19), *Alcimus* (3), *Philodicus* (2) and *Microstylum* (1). The dominant genus, *Neolophonotus,* accounts for 76 % of all records, and two species, *N. bimaculatus* Londt, 1986 (10) and *N. expandocolis* Londt, 1985 (6), are most significant.

Orthoptera (280 records)

Five orthopteran families are represented in the asilid prey database. As the Acrididae account for the vast majority they are treated separately.

Acrididae (269): the acridids completely dominate (96 %) orthopteran records. Twelve asilid genera feed on acridids, but the most significant are *Alcimus* (136), *Philodicus* (62), *Neolophonotus* (29), *Microstylum* (24) and *Promachus* (10): *Alcimus,* with 51 % of all records, clearly dominates, although *Philodicus* (23 %) is also an important group. Although *Alcimus* needs taxonomic revision, 119 records have been ascribed to *A. setifemoratus* Hobby, 1934 (all Hobby 1935 records). The genus appears to specialize in Orthoptera and Lepidoptera, and specialization may occur at a species level. Also of significance is that all the *Philodicus* records relate to *P. swynnertoni* Hobby, 1933 (Hobby 1935).

ASILID GENDER ANALYSIS

Most published studies show that female asilids are more commonly encountered feeding than males (Londt 1990, 1991, 1995, 1999). Comparisons using current data, resolved at subfamily level, are

Table 3. A comparison of the prey of male and female Asilidae.

Asilidae subfamily	Male		Female		Gender unknown		Total
	No.	%	No.	%	No.	%	no.
Apocleinae	549	45.0	663	54.3	8	0.7	1220
Asilinae	13	38.2	21	61.8	0	0	34
Dasypogoninae	30	30.6	68	69.4	0	0	98
Laphriinae	41	35.0	76	65.0	0	0	117
Laphystiinae	11	40.7	16	59.3	0	0	27
Leptogastrinae	2	14.3	12	85.7	0	0	14
Ommatiinae	2	18.2	9	81.8	0	0	11
Stenopogoninae	84	27.5	221	72.5	0	0	305
Stichopogoninae	1	14.3	6	85.7	0	0	7
Trigonomiminae	60	35.9	107	64.1	0	0	167
Total	793	39.7	1199	60.0	8	0.4	2000

presented in Table 3. In every instance there were more females than males. While data for the family as a whole show that for every male there are 1.5 females, this relationship may be different for individual subfamilies. Comparative figures arranged in order of the degree of difference are: Apocleinae 1:1.2, Laphystiinae 1:1.5, Asilinae 1:1.6, Trigonomiminae 1:1.8, Laphriinae 1:1.9, Dasypogoninae 1:2.3, Stenopogoninae 1:2.6, Ommatiinae 1:4.5, Leptogastrinae & Stichopogoninae 1:6.0. While little confidence can be placed in the data for the last three subfamilies, because of low sample sizes, some of the other observed differences may be significant. The acceptable extremes appear to be the figures provided for the Apocleinae, where females only outnumber males by 1.2 to 1, and those given for the Stenopogoninae where the difference is much greater at 2.6 to 1. A factor that might contribute to observable differences is the relative size difference between males and females. Although measurements have not been taken, in many instances, males are generally smaller than females, and so are probably less visible during collecting expeditions, resulting in the collection of fewer individuals with prey. However, to counter this possibility, in a study of *Damalis femoralis,* Londt (1991) demonstrated that although males were marginally larger than females, females were more frequently captured with prey. Although the reasons for the disparities shown above have not been ascertained, it appears that females require more food than males and so the most likely explanation is that they require the added nutrition to complete the maturation of their ovaries.

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