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PREY ITEMS OF THE BLACK SWIFT (*CYPSELOIDES NIGER*) IN COLORADO AND A REVIEW OF HISTORICAL DATA

KIM M. POTTER,^{1,4} CAROLYN GUNN,² AND JASON P. BEASON³

ABSTRACT.—The Black Swift (*Cypseloides niger*) was first discovered in Colorado in 1880, yet information on prey items taken by this species in Colorado is very rare. We collected and identified prey items of Black Swifts from three breeding locations in Colorado during August over a seven-year period (2006–2012) and identified 5,371 insects representing 10 orders and 54 families. We compare our data with historical Black Swift prey item information from other locations in North America. These data indicate that Black Swifts forage on a wider array of insect taxa and sizes than previously reported in other parts of its range. Received 7 October 2014. Accepted 31 December 2014.

Key words: Black Swift, *Cypseloides niger*, diet, insects, prey.

Diet is an important component of a species' life history. Species whose diets are specialized are potentially more vulnerable to population declines and extinction than those with generalist diets (Krebs and Davies 1993, McKinney 1997). Identifying species and populations at higher extinction risk is important for developing conservation strategies in relation to current and expected environmental changes. Given that Black Swifts (*Cypseloides niger*) are a long-lived species with a low reproductive rate (Wiggins 2004), food availability may be a significant factor in regulation of their population growth. Understanding the prey composition in the diet of Black Swifts will provide a baseline for understanding how they might react to future environmental disturbances including climate change and habitat loss.

Black Swifts, like other swifts, feed exclusively on aerial insects that originate from various aquatic and terrestrial habitats. Previous studies reported that Black Swifts are specialized foragers concentrating on lipid-rich winged ants, or alates (Foerster 1987, Marín and Stiles 1992, Holroyd 1993, Marín 1999, Rudalevige et al. 2003). It has also been suggested that the breeding of Black Swifts in southwestern Canada and the western US is timed to the swarming period of alate ants which represent a concentrated food source found in dispersed patches (Holroyd and Jalkotzy 1986, Marín 1999). Black Swifts ingest prey items for two reasons. They consume prey for their own

energy and nutritional needs; these insects are completely swallowed and enter the stomach where they undergo digestion. Black Swifts also collect prey items that are stored in the esophagus in the form of one or more boluses which enable the birds to forage at long distances from their breeding colonies during the day and carry large amounts of prey back to their single nestling (Collins 1998, Collins and Peterson 1998).

The only published historical information on Black Swift prey items for Colorado appears as a note by Drew (1882) who examined 10 birds collected near Howardsville (San Juan County) in 1880 and 1881. He reported that the birds had their crops filled with Ephemeroidea, at that time a recognized broad taxonomic grouping of mayflies (Ephemeroptera). Over the next 125 years, researchers in California, Washington, and Mexico collected stomach contents or regurgitated boluses of Black Swifts. Results of these previous studies along with unpublished data are listed in Table 1. Collectively, the historical data indicates that Black Swifts consumed representatives of more than 83 families of insects representing 12 orders (Homoptera has been combined with Hemiptera), supporting Rathbun's (1925) assertion that "nothing in the nature of aerial insect life is rejected by this bird." O. A. Knorr (pers. comm.) theorized that Black Swifts will take any airborne insect and that airborne ant alates constitute only a small portion of an ant population and their nuptial flights are very brief.

Observations of Black Swift diet outside the US include those made by Holroyd (1993) who collected droppings of adult and nestling Black Swifts in Alberta, Canada that contained digested but identifiable insect parts apparently all representing alate ants. Stiles and Negret (1994)

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TABLE 1. Comparison of invertebrate prey items captured by Black Swifts, quantified and listed by Order.

Prey Items:	Colorado		California		Washington		Mexico			
	Sources:	Levad ^a 2004–2005	Drew 1882	Dixon 1935	Foerster 1987	Marín 1999	Rudalevige et al. 2003	Archived data 1891–1938 ^b	Davis 1931	Collins & Landy 1968
		%	%	%	%	%	%	%	%	%
Orders										
Aranacea						<1		<1		
Blattodea						<1		8		
Coleoptera						<1		5	1	
Diptera		25				1		10		
Ephemeroptera		25	100					2		
Hemiptera					1	2		17		
Homoptera ^c						5				
Hymenoptera		50		100	99	91	95	56	99	100
Isoptera						<1		<1		
Lepidoptera						<1		<1		
Neuroptera						<1		<1		
Psocoptera						<1		<1		
Tricoptera								1		
Sample Type ^d /Number:		B/2	B/10 ^e	S/1	B/2	B/10	B/4	S/22	B & S/1	B/2
Specimens (n)		Unknown	Unknown	~100	289	1,180	206	2,013	Unknown	276

^a Levad, R. G. (unpubl. data).
^b USGS Patuxent Wildlife Research Center (unpubl. data) from specimens collected in western Washington and California (Jun–Sep).
^c Homoptera now combined with the Order Hemiptera.
^d Bolus/esophagus (B), stomach (S).
^e Difficult to determine exact number of stomachs examined.

described Black Swifts in migration near Popayán, Colombia, feeding on large swarms of small beetles represented by two genera of the Scarabaeidae (scarab beetles) and one genus in the Coccinellidae (ladybird beetles). There is no information about Black Swift diet at recently discovered wintering areas in South America (Beason et al. 2012).

This study describes the taxon, number, and size of prey items taken by Black Swifts in Colorado during the latter half of the breeding season. We summarize the prey items captured by Black Swifts during the breeding season as found in previous studies and compare the historical data with our current findings. We examine these data collectively to gain a greater understanding of Black Swifts' diet.

METHODS

We collected regurgitated boluses from Black Swifts during August 2006–2012 at three locations in Colorado, USA: Fulton Resurgence Cave in Garfield County at 39° 49' 09" N, 107° 38' 34" W; Zapata Falls in Alamosa County at 37° 37' 09" N, 105° 33' 11" W; and Box Canyon Falls in Ouray County at 38° 01' 06" N, 107° 40' 44" W. Swifts occasionally regurgitate complete or partial boluses from the upper esophagus during handling. Forty fully or partially regurgitated boluses were retrieved incidentally during mist-netting and banding sessions between 1730 and 2140 hrs MDT as adults were returning to their nests in the evening. All boluses were placed into vials with 70% ethanol and labeled, each vial containing only the bolus contents from a single bird. The distance between the commissures of the beak was measured with dial calipers (Swiss Precision Instruments Inc., Garden Grove, CA, USA) to obtain gape width on 14 adult swifts.

Insects from each bolus were separated and counted, the total length of each insect was measured from apex of the head to apex of the abdomen, and each insect was identified to the lowest practical taxonomic level by B. Kondratieff using available literature and identification guides (e.g., Slater and Baranowski 1978; McAlpine et al. 1981, 1987; Arnett and Thomas 2000; Arnett et al. 2002; Triplehorn and Johnson 2005). Insects in the C. P. Gillette Museum of Arthropod Diversity, Colorado State University (Ft. Collins, CO), were used for comparison. All specimens, depending on size, were measured to the closest tenth of a millimeter with either a transparent

ruler with 10 mm increments or a calibrated ocular micrometer in a 10x eye piece on a Wild M5A stereomicroscope (Leica Microsystems (Schweiz) AG, Heerbrugg, Switzerland).

In this analysis, we reference unpublished data (R.G. Levad, pers. comm.); published data (Drew 1882, Davis 1931, Dixon 1935, Collins and Landy 1968, Foerster 1987, Marín 1999, Rudalevige et al. 2003); archived data from the USGS Patuxent Wildlife Research Center; collective historical data referring to all the above; and data from the current study.

A dominance index (Berger and Parker 1970) was used for comparisons among studies because of the substantial variation in specimen numbers. Insect diversity within a bolus is dependent on bolus size. The Berger-Parker Index is a simple measure of the numerical importance of the most abundant taxa and is represented by: $d = N_{\max}/N$, where d represents dominance of one taxon; N_{\max} is the number of individuals in the most abundant taxon, and N is the total number of individuals in the bolus. The results are presented as a percentage. The index can be used at various taxonomic levels.

RESULTS

We identified 5,371 insects representing 10 orders and 54 families from the 40 boluses we collected (Appendix). Insects were identified to the lowest possible taxonomic level; 164 of insects could be identified to species, 2,371 to genus, 2,554 to family, 281 to order, and 1 to subclass. In our study, insects from four orders made up more than 92% of all prey identified (Fig. 1). Insects from three families made up more than 53% of all prey identified (Fig. 2). Within the Hymenoptera, 95% of individual specimens were represented by the Formicidae. Mean prey size of 5,371 specimens was 6 mm, with a range of 1.5–27.5 mm. All of the prey items larger than 16 mm ($n = 52$) were moths. The gape of Black Swifts ($n = 14$) averaged 15.7 mm for males (range 15.0–17.2 mm, $n = 8$) and 14.8 mm for females (range 13.5–15.6 mm, $n = 6$).

DISCUSSION

Black Swifts in the current study captured a wide array of insect taxa (Appendix). Our results differ from previous reports indicating that Black Swifts are specialized foragers, preying primarily on alate ants (Formicidae). The great variety of aerial prey taken by Black Swifts in Colorado

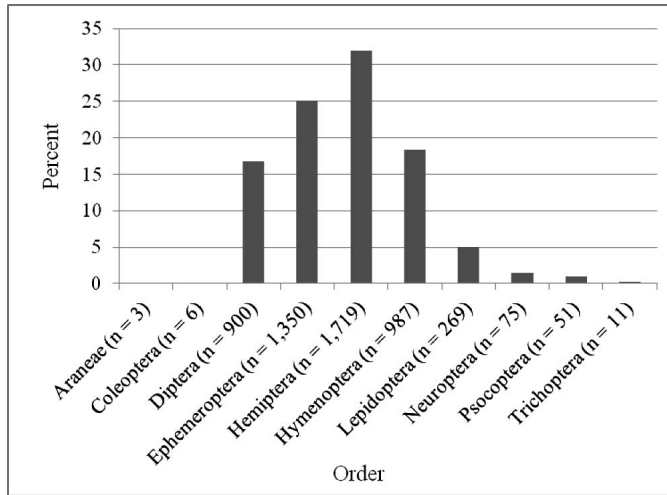


FIG. 1. Arthropoda Orders represented in the present study.

during the chick-rearing period is consistent with the diversity of prey captured by other species of swifts (Collins et al. 2009, Garcia-del-Rey et al. 2010, Collins and Thomas 2012).

Black Swifts opportunistically seek out large swarms of air-borne insects (Knorr 1961, Marín 1999). **Hespenheide (1975) hypothesized that large swifts, because of their potentially greater foraging range, may specialize in the exploitation of local concentrations of single species of insects in mating or dispersal swarms, especially ants, but also**

termites (Isoptera) and other orders when present.

Previous studies (Dixon 1935, Collins and Landy 1968, Foerster 1987, Marín 1999, Rudalevige et al. 2003, R.G. Levad, unpubl. data) indicated that Hymenoptera, specifically alate ants, dominated prey items in boluses or stomach contents. Our data demonstrate that Black Swifts do not exclusively target dense alate ant nuptial flights.

In our study, there was little evidence of exclusive swarm feeding in which the majority of contents of a single bolus from an individual

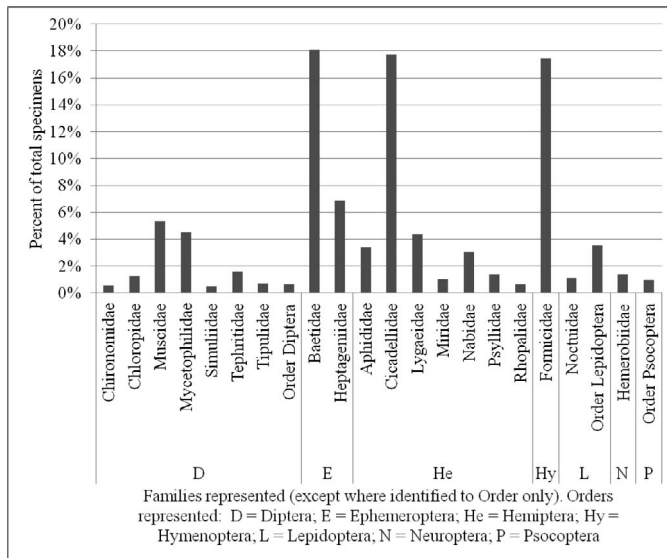


FIG. 2. Insect Families represented in the present study (only Families with >0.5% shown).

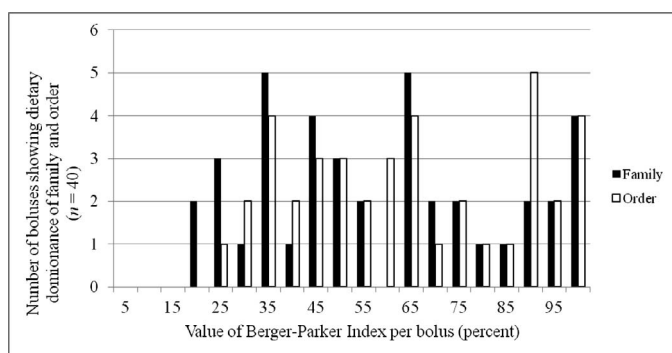


FIG. 3. Histogram of dietary dominance per bolus from current study.

swift was represented by a single insect species. The only published criterion for determining that a bird has fed on a swarm was proposed by Hespeneide (1975); he chose the arbitrary rule of > 20 insects of a single insect species in gut contents of each bird. However, this criterion was applied to birds weighing one-third that of the Black Swift and based on the number, not percentage, of insects within a bolus; therefore, we have not used this criterion. Figure 3 illustrates that individual boluses in our study contained a wide range in dominance of any one type of insect, whether evaluated at the family or order level. In contrast, Figure 4 shows the degree of dominance in the collective historical data in which a greater number of bolus/stomach contents were dominated by one order or family.

Prey size may be important in selective capture by Black Swifts, as has been suggested for other Cypseloidinae swifts (Marín and Stiles 1992). In our study, 41% of prey measured were in the 7–10 mm length range, falling well within the range of sizes measured in other studies (Fig. 5). However, 40% of prey in our study were in the 3–5 mm length range which can be attributed to a large number of leafhoppers (Cicadellidae; 26 of 40 boluses contained members of this family); this pattern is not found in historical data. A comparison of three studies from California measuring prey size from 16 Black Swift boluses showed an overall length range of 1.8–14.5 mm: Foerster (1987) recorded mean prey lengths of 9.9 and 10.2 (two boluses, $n = 289$), Marín (1999) recorded 7.4 mm as an average prey length (ten boluses, $n = 1,154$), and Rudalevige et al. (2003) recorded mean prey length of 9.5 (four boluses, $n = 206$). Esophageal contents from two Black Swift specimens in Veracruz, Mexico, showed

a mean prey length of 8.7 mm with a range of 2.0–12.0 mm ($n = 276$; Collins and Landy 1968). These sizes may represent either insects that tend to swarm, insects small enough to be carried by atmospheric conditions, or preferential choice of the swifts. Studies suggest other swift species selectively choose their prey by size taking the largest available items whenever possible (Lack and Owen 1955, Hespeneide 1975, Chantler 2000).

Swift body size may play a role in size of prey captured (Collins and Landy 1968). In seven species of swifts other than Black Swifts, prey size correlated positively with body mass (Collins et al. 2009). Collins (1980) observed that smaller swifts appear to take a smaller range of food items than larger swifts. Hespeneide (1975) hypothesized that size is the most important characteristic of the prey of birds and that differences in the taxonomic composition of diets reflect differences in preferences for prey size. Given the variation in size of insects within families, it is difficult to draw conclusions about whether Black Swift prey items are preferentially captured based on taxa versus size.

Swifts' large gape allows them to swallow prey whole in flight (Jones et al. 2012). Information collected on gape width in this study relates well with Marín (1997) who showed the gape width of 14 adults measured at Lawler Falls, California, as having a mean width of 16 mm (SD = 0.92 mm). He also measured the gape width of seven nestlings from hatching to fledging at approximately day 50; by day 20, most chicks had a gape width approximating that of the adults.

The areas Common Swifts (*Apus apus*) search for food varies with weather, feeding higher in the air column on fine days and low over water on wet and windy days, probably because terrestrial

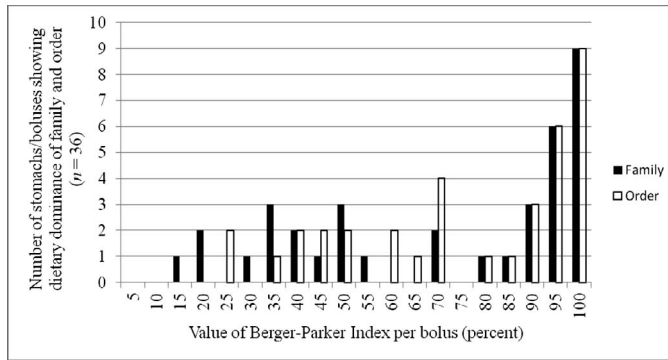


FIG. 4. Histogram of dietary dominance per bolus from collective historic data.

insects rarely take off in poor weather or descend to the ground (Lack and Owen 1955). The same authors suggest that Common Swifts select smaller size insects in poor weather when large species are unavailable. Koskimies (1950) reported that Common Swifts fly around and away from local showers and thunderstorms and at times make large-scale movements to avoid rain belts of oncoming cyclones which contain fewer aerial insects. At times, Black Swifts forage close to the ground or water capturing emerging insects, especially during inclement weather (Lord 1866, Drew 1882, Bendire 1895, Swarth 1922, Rathbun 1925, Burleigh 1929, Bent 1940, Urdvardy 1954, Chantler 2000).

It has been suggested that breeding of Black Swifts in southwestern Canada and the western US is timed to the swarming of alate ants in August and early September (Holroyd and Jalkotzy

1986) or July (Marín 1999). Nesting phenology for this species varies throughout North America (Wiggins 2004). A study of the nesting phenology of Black Swifts at a colony in Colorado over an 11 year period indicated a long breeding season, with egg laying from 19 June to 16 July and fledging from 31 August to 7 October (Hirshman et al. 2007). Although Chapman (1954) found highest densities of alate ants on western US mountaintops to occur in July and August, this is not adequate evidence to support the hypothesis that Black Swifts time their breeding to swarming Formicidae as much of the breeding season is outside peak Formicidae swarming activity. Numerous factors determine timing of Black Swift breeding including latitude, elevation, and nest site conditions (e.g., microclimate, temperature and humidity regimes, and inundation of nest niches by spring runoff).

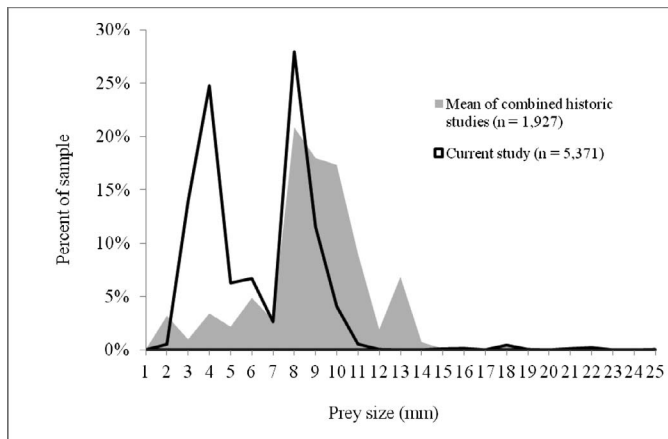


FIG. 5. Distribution frequency of mean Black Swift prey lengths for the current study compared with combined historic data that includes Collins and Landy 1968, Foerster 1987, Marín 1999, and Rudalevige et al. 2003.

Swifts are among the most aerial of birds, spending most of the day on the wing in search of their arthropod prey (Rudalevige et al. 2003). Long slender wings and a streamlined body design with low drag allow swifts to fly at high speeds (Henningsson et al. 2010), giving them the maneuverability to take insects that are not on a direct flight line (Lack and Owen 1955). This maneuverability allows them to use weather patterns to pursue pockets of concentrated aerial insects (Udvardy 1954) while avoiding those areas where insects are scarce (Lack and Owen 1955). Black Swifts are capable of carrying a large mass of food in the esophagus for provisioning the chick, as opposed to a small bolus carried in the mouth, as in the Chaeturinae and Apodinae swifts (Collins 1998).

Availability of prey is probably affected by weather patterns, time of season, time of day, local insect abundance, type of surrounding terrestrial habitat from which insects emerge, and other temporal and spatial influences. Flight ability of prey, prey density, digestibility, and prey size may also play a role in the choice of one prey type over another. Stochastic events such as local emergence of reproductive stages of species in the vicinity of foraging Black Swifts and other parameters could explain the disparity between our data and that of other studies. Because Black Swifts normally forage high above the canopy, data from the collected specimens may be biased toward insects taken while the swifts were foraging at lower altitudes during inclement weather. **How far Black Swifts forage from their nesting colonies in search of prey could affect types of prey captured, but foraging distance is unknown; previously reported distances of 40 km (Boyle 1998, Lowther and Collins 2002) and 24 km (Roberson and Collins 2008) could not be confirmed.** It is unknown whether there are differences in the prey items adults capture for their own feeding versus bolus contents intended for chick provisioning, which might produce different results (Marín 1999). Rapid digestion of some stomach contents, such as soft-bodied insects, might escape counting in a sample (Hespenheide 1975).

CONSERVATION IMPLICATIONS

The Black Swift has been identified as a species of conservation concern in every western North American state and province in which it nests. The western US Forest Service regions have designated it as a Sensitive Species, defined as a species for which there is a population viability

concern as evidenced by a current or predicted downward trend in population numbers or habitat capability that would reduce a species' existing distribution. The National Audubon Society, American Bird Conservancy, and the Partners in Flight North American Land Bird Conservation Plan all list Black Swift as a Watch List Species.

Roberson and Collins (2008) reported that the entire coastal population in California has been in recent severe decline. Johnston's Canyon in Banff National Park, Alberta, Canada, which hosted 4 to 12 nests between 1972 and 2004 has dropped to one nest from 2005–2013 (JPB, unpubl. data).

These population declines emphasize the necessity to further understand basic food, foraging, and habitat requirements of the Black Swift and the need to address potential habitat threats. Changes in habitat or global climate change could threaten the connection between insects and the Black Swifts' ability to forage.

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APPENDIX. Prey items taken by Black Swifts in Colorado in August 2006–2012.

Prey taxon (Subclass, Order, Family, and lowest taxonomic level identified)	%	n
Acari	0.02	1
Araneae	0.04	2
Coleoptera	0.11	6
Anthicidae (<i>Notoxus</i> sp.)		1
Carabidae (<i>Bembidion</i> sp.)		1
Curculionidae		3
Staphylinidae		1
Diptera	16.76	900
Agromizidae		3
Anthomyiidae		1
Calliphoridae		9
Cecidiomyiidae		18
Chironomidae		29
Chloropidae		67
Culicidae		23
Dolichopodidae		4
Empididae		14
Muscidae		286
Mycetophilidae		243
Phoridae		3
Scathophagidae		1
Sciaridae		3
Simuliidae (<i>Simulium</i> sp.)		28
Syrphidae (4 <i>Toxomerus</i> sp.)		9
Tachinidae		1
Tephritidae (11 <i>Neotephritis</i> sp., 21 <i>Trupanea</i> sp.)		84
Therevidae		1
Tipulidae		37
Identified to Diptera only		36
Ephemeroptera	25.13	1350
Baetidae (885 <i>Callibaetis</i> sp. ^a and 86 <i>Baetis</i> sp.)		971
Ephemerellidae (2 <i>Drunella</i> sp., 7 <i>Ephemerella</i> sp.)		9
Heptageniidae		370
Hemiptera	32.00	1719
Anthocoridae		2
Aphididae		183
Aradidae		5
Berytidae (<i>Neoneides muticus</i>)		1
Cercopidae		5
Cicadellidae		953
Corixidae (<i>Sigara</i> sp.)		4
Lygaeidae (234 <i>Nysius</i> sp.)		236
Miridae (<i>Lygus</i> spp.)		54
Nabidae (<i>Nabis alternatus</i>)		164
Pentatomidae		3
Psyllidae		74
Rhopalidae (<i>Arhyssus</i> sp.)		35
Hymenoptera	18.38	987

APPENDIX. Continued.

Prey taxon (Subclass, Order, Family, and lowest taxonomic level identified)	%	n
Braconidae		19
Chalcidoidea		13
Formicidae (708 <i>Formica</i> sp. female and 222 <i>Formica</i> sp. male alates and 7 male Formicidae alates)		937
Ichneumonidae		18
Lepidoptera	5.01	269
Gelechiidae		14
Noctuidae (<i>Euxoa</i> sp.) ^b		60
Pyrilidae		1
Tortricidae		4
Identified to Lepidoptera only		190
Neuroptera	1.40	75
Chrysopidae		1
Hemerobiidae		74
Psocoptera	0.95	51
Trichoptera	0.21	11
Hydropsychidae (<i>Hydropsyche</i> sp.)		4
Hydroptilidae		1
Limnephilidae		1
Rhyacophilidae (<i>Rhyacophila</i> sp.)		3
Identified to Trichoptera only		2

^a High numbers of *Callibaetis* sp. in boluses of swifts from Zapata Falls may be a result of birds feeding over the wetlands adjacent to the falls.

^b Presence of Noctuidae (*Euxoa* sp. and other adult moths) in moderately high numbers in some boluses is probably due to availability of these crepuscular and nocturnal moths near dusk when the swifts are still actively feeding.