Frequency of Arthropods in Stomachs of Tropical Hummingbirds

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Although flower nectar is the most conspicuous and energetically efficient food source of hummingbirds, it is notably deficient in amino acids and other essential nutrients (Baker and Baker 1975, Hainsworth and Wolf 1976). Therefore, hummingbirds require an additional source of proteins, lipids, and other nutrients. In most or all species, these nutrients are obtained by consuming small arthropods. Yet arthropod-foraging by hummingbirds remains very little studied compared with nectar-foraging (Gass and Montgomerie 1981, Hespenheide and Stiles unpubl. data). The few available time-budget studies of foraging hummingbirds (reviewed by Gass and Montgomerie 1981) indicate that arthropod-hunting constitutes only 2–12% of total foraging time except when nectar is scarce or unavailable. An incubating female Broad-tailed Hummingbird (*Selasphorus platycercus*) consumed only arthropods for about 10 days when nectar was unavailable (Montgomerie and Redsell 1980). Thus, under some field conditions a hummingbird can satisfy energetic as well as nutritional needs by feeding exclusively on arthropods.

The contents of stomachs and crops of collected birds represent an obvious source of dietary information. Because these data are recorded routinely on specimens collected by our institutions, the specimens can provide an indication of the frequency and generality of arthropod-foraging in hummingbirds. Accordingly, we recorded the presence or absence of arthropod remains in the stomachs and crops of 1,629 specimens of 140 species of hummingbirds (41% of the approximately 340 species in the family Trochilidae).

Presence of arthropods in the digestive tract of a specimen indicates only that the bird had recently fed on arthropods; it tells us nothing about the relative frequency of arthropods vs. nectar in the diet. It is well known that different kinds of foods have different digestibilities, rates of gut passage, and detectabilities; nectar and arthropods exemplify this problem in the extreme. Nectar is virtually 100% assimilable (Hainsworth 1974, Hainsworth and Wolf 1972) and is rarely detected in the stomach because it usually passes directly from esophagus to intestine (the openings of these are closely apposed in hummingbird stomachs). Arthropods are extensively digested in the stomach, following only brief storage in the crop. Soft-bodied arthropods, such as most small spiders, may be digested relatively quickly, except for easily overlooked poison claws. Many chitinous insect parts (e.g. wings, head capsules) are easily detectable for considerably longer periods. In this paper we do not record in detail the kinds of arthropods consumed, except insofar as this may affect the frequency of detectable arthropod remains. A detailed study of the arthropod diets and foraging tactics of hummingbirds is in preparation (Hespenheide and Stiles unpubl. data).

The specimens reported here were collected (1) from 1980 to 1985 by personnel of the Museum of Zoology, Louisiana State University (LSUMZ) or (2) from 1971 to 1985 by Stiles and his students. Approximately 70% of all specimens were collected in Bolivia or Peru, 25% in Costa Rica, and the remainder in northwestern Ecuador, Venezuela, or Darién, Panama. Twenty recent specimens of 15 species from Ecuador and Peru deposited in the Academy of Natural Sciences, Phildelphia, also were included. Although specimens were obtained from throughout the year, the sample from Peru and Bolivia is mostly from May through August, the "dry" season. Most (>95%) birds from group 1 above were captured in mist nets, which were checked from dawn to dusk at 3–4-h intervals; the remainder were shot. Birds from group 2 were collected from mist nets checked at least hourly, or were shot, in roughly equal proportions. Stomachs and crops of group 1 birds were scored on specimen labels as containing "insects" (including other arthropods), as containing unidentifiable material, or as being "empty." Group 2 birds were scored in greater detail, but the data were converted to one of the three categories used for group 1 birds. Although not usually recorded on the labels, stomachs that contained arthropods were almost always *packed* with material rather than containing just a trace of parts. Because soft insects and spiders can be digested completely within 3–4 h (Stiles unpubl. data), our sampling procedure for mist-netted birds is conservatively biased against detection of arthropods. Also, many of the stomach contents of group 1 specimens scored as "unidentifiable" were presumably the remains of soft insects and spiders.

Most (1,279 of 1,629, 79%; see Appendix) hummingbird stomachs and crops contained arthropod remains. Individuals of 133 (95%) of the 140 species examined had been feeding on arthropods. Of the 7 species for which arthropods were not recorded, the largest sample size was only 5 individuals.

Few significant regional differences were detected between samples of the same species; therefore, data from all areas were pooled in the Appendix. The main exceptions were several species of hermits (Phaethorninae: genera *Glaucis* through *Eutoxeres*). In stomachs of these species arthropods occurred with

TABLE 1. Percentage of individual nonhermit hummingbirds feeding on arthropods in six humidity-elevation categories. Species found in more than one category (see Appendix) were not included.

Humidity-elevation category	Percent arthropods	No. of birds	No. of species
Humid montane	86.3	401	26
Humid foothills	79.9	313	32
Humid lowlands	78.4	176	17
Semihumid lowlands	95.8	24	8
Arid highlands	92.0	50	11
Arid lowlands	93.5	46	9

TABLE 2. Chi-square values for pairwise comparisons of arthropod-feeding frequency between nonhermit hummingbirds in different humidity-elevation categories.[a] HM = humid montane, HF = humid foothills, HL = humid lowlands, SL = semihumid lowlands, AH = arid highlands, AL = arid lowlands.

	HM	HF	HL	SL	AH	AL
HM	—	5.24*	5.61*	1.81	1.28	1.89
HF		—	0.15	3.69	4.21*	4.95*
HL			—	4.08*	4.75*	5.50*
SL				—	0.38	0.16
AH					—	0.08
AL						—

[a] * = $P < 0.05$.

significantly lower frequency in South American than in Costa Rican birds [pooled samples of all hermits, 60% for South America ($n = 231$) vs. 78% for Costa Rica ($n = 138$); $\chi^2 = 12.26$, df = 1, $P < 0.001$]. We suspect that the discrepancy beween South American and Costa Rican samples is due to a difference in specimen-collecting techniques, which is relevant in the case of hermits because they take a much higher proportion of soft-bodied spiders than do most nonhermits (Hespenheide and Stiles unpubl. data). Nonhermits take more hard-bodied insects that persist longer in the gut. The time that netted hummingbirds remained entrapped prior to collection was on average 3-4 times longer for the South American birds. The time of day of collection may be another contributing factor. Most hermits are lek species that may commence lek activity before feeding, following a dawn flight between roost and lek (cf. Stiles and Wolf 1979). By opening nets at dawn, South American workers might well have captured a number of hermits that had not yet fed. By contrast, virtually all netting to collect hummingbirds in Costa Rica commenced at least 1 h after dawn, and it was more likely that the birds had fed before being collected.

Because hermits and nonhermits take different kinds of arthropods, a comparison of frequency of arthropod feeding is problematical. The bias resulting from more rapid digestion of arthropods in hermits' stomachs is minimized in the Costa Rican sample. Arthropods occurred less frequently in hermits' than nonhermits' stomachs (78% for hermits; 85% for nonhermits, $n = 312$), but the difference was significant only at the 0.10 level ($\chi^2 = 3.66$, df = 1). The difference was highly significant in the South American sample (60% for hermits; 83% for nonhermits, $n = 930$; $\chi^2 = 57.01$, df = 1, $P < 0.0001$), but, as discussed above, we believe this to be largely an artifact of the longer time South American birds spent in nets before being collected.

Perhaps the most interesting pattern to emerge from the data on nonhermits (see Appendix) is a relationship between the elevation and humidity of the collecting areas and the proportion of stomachs containing arthropods. Species were assigned to one or more of six humidity-elevation categories. The data on nonhermits are summarized by humidity-elevation category in Table 1. The null hypothesis that the probability of a stomach containing arthropods would be the same for birds in the six different habitats was rejected ($\chi^2 = 17.33$, df = 5, $P < 0.01$). Results of pairwise comparisons between birds in different categories are shown in Table 2. In general, the cooler or drier an area, the more likely a bird was to have arthropods in its stomach. Arthropods were most frequent in the stomachs of hummingbirds of arid or semihumid areas. Within humid areas, montane hummingbirds more often had consumed arthropods than had lowland species (Table 1). These relationships obtained in Costa Rican and in South American samples (except that no arid regions exist in Costa Rica). Because the two samples are large and were gathered independently, we think the relationships reflect differences in hummingbird feeding patterns between environments.

The differences may reflect variation between environments in availability and quality of nectar and arthropods. Dry tropical forests support relatively few species of hummingbird-pollinated flowers compared with wetter areas (Stiles 1981), and hummingbirds in dry areas may make relatively greater use of arthropods to meet energetic needs. Nevertheless, the energetic importance of good nectar supplies is indicated by the facts that dry-forest hummingbird communities contain relatively few species and show low morphological and behavioral diversity compared with wet-forest communities (Stiles 1981). It is less clear why the frequency of arthropod consumption should increase with elevation. There is evidence that nectar from highland areas tends to be more dilute than that of lowland flowers (Hainsworth and Wolf 1972, Wolf et al. 1976). Arthropod consumption may help highland hummingbirds survive cold nights by providing a longer-lasting source of energy than nectar. Data on time budgets of foraging birds and seasonal and daily fluctuations in resource availability in different areas would be required to test hypotheses suggested by differences in frequency of arthropod consumption.

Although significant habitat-related variation in feeding patterns apparently exists, we emphasize our general finding that almost all tropical hummingbirds *routinely* feed on arthropods. The percentage of stomachs and crops containing arthropods was high in all habitats, ranging from 78% to 96% among nonhermits. Among hermits, which specialize on soft-bodied spiders that are digested rapidly, the value obtained from the Costa Rican sample (78%) represents our best estimate. The data indicate that most hummingbirds, at any given moment during the day, are digesting arthropods. From this it may be inferred that most hummingbirds feed on arthropods on a daily basis, and probably at regular intervals throughout the day.

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APPENDIX. Stomach and crop contents of hummingbirds. The number of individuals in each of three categories (AR = arthropods present; E = empty; 0 = contents unidentifiable) is given, and for those species with $n > 9$, the proportion of individuals with arthropods is given in parentheses. H-E refers to humidity-elevation categories: HL = humid lowlands, under 1,000 m elevation; HF = humid foothills, 1,000–2,500 m; HM = humid montane, 2,500–3,600 m; SL = semihumid, subtropical lowlands, under 1,500 m; AL = arid lowlands, under 2,000 m; AH = arid and semiarid highlands, above 2,000 m; X = does not fit other categories. For species collected in more than one H-E category, the first category listed is the one in which most specimens were taken.

Species	AR	E	0	H-E
Glaucis aenea	25 (0.76)	6	2	HL
G. hirsuta	15 (0.68)	7	0	HL
Threnetes leucurus	12 (0.50)	12	0	HL
T. ruckeri	17 (0.74)	5	1	HL
Phaethornis yaruqui	0	2	2	HL
P. guy	10 (0.48)	11	0	HF
P. syrmatophorus	0	3	0	HF
P. superciliosus	90 (0.75)	27	3	HL, HF

APPENDIX. Continued.

Species	AR	E	0	H-E
P. hispidus	8 (0.53)	7	0	HL
P. bourcieri	3	2	0	HL
P. philippii	3	5	1	HL
P. koepckeae	8 (0.40)	12	0	HF
P. pretrei	0	0	3	SL
P. subochraceus	4	1	1	SL
P. ruber	1	1	0	HL
P. griseogularis	0	1	0	X
P. longuemareus	12 (0.67)	6	0	HL
Eutoxeres aquila	14 (0.61)	9	0	HF
E. condamini	23 (0.77)	7	0	HF
Androdon aequatorialis	1	0	0	HF
Doryfera johannae	11 (0.73)	4	0	HF
D. ludoviciae	16 (0.89)	2	1	HF
Phaeochroa cuvierii	3	0	0	AL, HL
Campylopterus largipennis	21 (0.81)	5	0	HF
C. hemileucurus	6	1	0	HF
C. villaviscensio	16 (0.76)	5	0	HF
Eupetomena macroura	2	0	0	SL
Florisuga mellivora	20 (0.83)	4	0	HL
Colibri delphinae	8	0	0	HF
C. thalassinus	6	0	0	HM
C. coruscans	14 (0.82)	2	1	AH, HM, HF
Anthracothorax prevostii	5	0	0	AL
A. nigricollis	4	0	0	HL
Chrysolampis mosquitus	1	0	0	SL
Klais guimeti	1	1	0	HL
Lophornis adorabilis	3	0	0	HL
Popelairia popelairii	1	0	0	HL
Discosura conversii	2	0	0	HF
Chlorostilbon aureoventris	9	0	0	SL
C. canivetii	5	1	0	AL
C. stenura	2	0	0	AH
Thalurania furcata	65 (0.76)	19	1	HF, HL
T. colombica	27 (0.73)	10	0	HL
Panterpe insignis	25 (0.93)	2	0	HM
Hylocharis eliciae	5	1	0	HL
H. chrysura	2	1	0	SL
Chrysuronia oenone	13 (0.72)	5	0	HF
Goethalsia bella	0	5	0	HF
Polytmus guainumbi	5	0	0	SL
Leucippus baeri	3	0	0	AL
L. chlorocercus	4	0	0	HL
Taphrospilus hypostictus	2	0	0	HF
Amazilia chionogaster	13 (0.93)	1	0	AH
A. viridicauda	3	3	0	AH, HF
A. fimbriata	3	0	0	HL
A. amabilis	5	3	0	HL
A. rosenbergi	2	0	0	HL
A. boucardi	4	1	0	X
A. decora	10 (0.83)	2	0	HL
A. saucerrottei	12 (0.86)	2	0	AL, AH
A. tobaci	1	0	0	SL
A. edward	3	0	0	HF, HL
A. rutila	4	1	0	AL
A. tzacatl	14 (0.82)	3	0	HL
A. amazilia	4	0	0	AL
Eupherusa eximia	1	2	0	HF
E. nigriventris	4	3	0	HF
Elvira chionura	4	1	0	HF
E. cupreiceps	8	1	0	HF

APPENDIX. Continued.

Species	AR	E	0	H-E
Microchera albocoronata	5	0	0	HF, HL
Chalybura buffonii	1	3	0	X
C. urochrysia	30 (0.81)	7	0	HL
Lampornis hemileucus	5	1	0	HF
L. calolaema	14 (0.93)	1	0	HF
L. castaneoventris	3	0	0	HM
Adelomyia melanogenys	17 (0.81)	4	0	HF
Urosticte benjamini	1	0	0	HF
Phlogophilus harterti	1	0	0	HF
Polyplancta aurescens	8 (0.53)	6	1	HL
Heliodoxa rubinoides	6	0	0	HF
H. leadbeateri	36 (0.86)	6	0	HF
H. jacula	8 (0.73)	3	0	HF
H. schreibersii	7 (0.70)	3	0	HL, HF
H. gularis	3	1	0	HF
H. branickii	2	1	0	HF
Eugenes fulgens	6	0	0	HM
Oreotrochilus melanogaster	2	0	0	AH
O. estella	7	0	0	AH
O. adela	2	0	0	AH
Patagona gigas	3	0	0	AH
Aglaeactis cupripennis	2	1	0	AH
A. aliciae	1	0	0	AH
A. castelnaudii	17 (0.77)	5	0	AH, HM
A. pamela	0	1	0	HM
Lafresnaya lafresnayi	6	2	0	HM
Pterophanes cyanopterus	19 (0.90)	2	0	HM
Coeligena coeligena	18 (0.82)	4	0	HF
C. torquata	30 (0.88)	4	0	HM, HF
C. bonapartei	1	0	0	HM
C. lutetiae	6	0	0	HM
C. violifer	86 (0.88)	12	1	HM
Ensifera ensifera	9 (0.90)	1	0	HM
Boissonneaua matthewsii	6	2	0	HM, HF
Heliangelus spencei	2	1	0	HM
H. amethysticollis	35 (0.90)	4	0	HM
H. strophianus	2	0	0	HM
H. regalis	1	1	0	HF
Eriocnemis luciani	3	1	0	HM
E. mosquera	1	0	0	HM
E. alinae	9 (0.75)	3	0	HF
Haplophaedia aureliae	1	1	0	HF
Ocreatus underwoodii	5	1	0	HF
Lesbia nuna	1	0	0	AH
Sappho sparganura	10 (0.83)	2	0	AH
Ramphomicron microrhynchum	7	0	0	HM
Metallura phoebe	3	0	0	AH
M. odomae	3	0	0	HM
M. theresiae	1	0	0	HM
M. aeneocauda	21 (0.84)	4	0	HM
M. eupogon	51 (0.77)	15	0	HM
M. tyrianthina	40 (0.83)	8	0	HM
Chalcostigma ruficeps	4	2	0	HM
C. olivaceum	1	0	0	HM
C. stanleyi	2	0	0	HM
Aglaiocercus kingi	3	2	0	HF
Schistes geoffroyi	7	0	0	HF
Heliothryx barroti	6	0	0	HL, HF
H. aurita	1	0	0	HL
Heliomaster constantii	10 (0.91)	1	0	AL
H. longirostris	2	0	0	SL, HL

APPENDIX. Continued.

Species	AR	E	0	H-E
H. furcifer	2	0	0	SL
Thaumastura cora	4	0	0	AL
Calliphlox mitchellii	0	1	0	HL
C. bryantae	1	0	0	HF
C. amesthystina	1	0	0	SL
Myrtis fanny	4	0	0	AL
Myrmia micrura	4	0	0	AL
Acestrura mulsant	5	0	0	HM, AH, HF
Selasphorus scintilla	4	0	0	HF, HM
S. flammula	6	0	0	HM