ACTA THERIOLOGICA
Vol. 27, 21: 283—293, 1982

A Test of the Validity of Two Currently Used Methods of Determining Bat Prey Preferences

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Rabinowitz A. R. & Tuttle M. D., 1982: A test of the validity of two currently used methods of determining bat prey preferences. Acta theriol., 27, 21: 283—293 [With 3 Tables & 3 Figs.]

Direct field observations were made of foraging gray bat (*Myotis grisescens*, Howell 1909) over an east Tennessee Reservoir. Conclusions from these observations differed markedly from results of analyses of feces and culled insect remains from beneath the bats' roosts. This led to an investigation of the validity of the latter techniques. In a single blind experiment, captive gray bats were fed a variety of kinds of insects, and their feces were examined to determine meal composition. Results were strongly biased in favor of beetles and against mayflies, the observed preferred prey. Sources of bias in such analyses and relevant literature on determination of food preferences, especially in insectivorous bats, are discussed.

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I. INTRODUCTION

Bat foraging behavior is a subject of much current interest. Prey preference studies of insectivorous bats have been based upon examination of stomach contents (Pine, 1969 ; Easterla & Whitaker, 1972 ; Whitaker, 1972 ; Kunz, 1974 ; Bradbury & Vehrencamp, 1976 ; Whitaker *et al.*, 1977 ; Bauerova, 1978 ; Whitaker & Mumford, 1978 ; Black, 1979), fecal pellets (Hamilton, 1933 ; Coutt *et al.*, 1973 ; Black, 1974 ; Husar, 1976 ; Anthony & Kunz, 1977 ; Bauerova, 1978 ; Bonaccorso, 1979 ; Fenton & Thomas, 1980 ; Whitaker & Findley, 1980) or culled insect fragments (Poulton, 1929 ; Ross, 1961 ; Nyholm, 1965 ; Hill & Morris, 1971 ; Wilson, 1971 ; Fenton, 1975 ; Krauss, 1978 ; LaVal & LaVal, 1980). Unfortunately, however, little information is available regarding the relative validity and potential biases of these techniques.

Belwood and Fenton (1976) found that mayflies fed to captive little brown bats (*Myotis lucifugus* LeConte, 1831) were unidentifiable when passed in feces, and Davies (1977) emphasized the potential biases resulting from use of fecal analysis where soft-bodies or otherwise differentially digestable prey types were involved. Yalden & Morris (1975), for these reasons, doubted the validity of fecal analysis in determining prey preferences of bats.

Clearly, further evaluation is required. In the present study we fed a variety of insects to gray bats (*Myotis grisescens* Howell, 1909) and in a single blind experiment, compared conclusions based on standard fecal analysis techniques with the bats' known meals. We also present conclusions based on feces collections and on culled insect fragments from beneath a maternity roost and discuss biases based upon our observations of the bats foraging behavior.

2. METHODS

Two postlactating female gray bats were mist netted at 2100 hours during evening emergence from a maternity cave located 0.5 km from the Norris Reservoir in eastern Tennessee on June 28 and 29, 1978. They were hand fed in an attempt to test the validity of fecal analysis. The first bat readily ate 274 mayflies (*Stenacron pallidum*) while the second was fed the following variety and numbers of insects in order, as listed (body lengths in mm): *Lepidoptera, Arctiidae, Halisidota* (18), 1; *Ephemeroptera, Heptageniidae, Stenacron pallidum* (8—11), 20; *Lepidoptera, Noctuidae* (16), 1; *Coleoptera, Carabidae* (10, 1; *Diptera, Tipulidae* (8), 1; *Ephemeroptera, S. pallidum* (8—10), 5; *Diptera, Chironomidae* (4—6), 8; *Trichoptera* (4), 3; *Coleoptera, Carabidae* (4), 1; *Lepidoptera, Arctiidae, Halisidota* (18), 1.

Moth wings and the elytra of the largest beetle were entirely discarded by the bat, but elytra of the smaller beetle were only partially avoided. Only the thorax of the first moth was eaten while all but the wings and the posterior end of the abdomen of the second were accepted. Both wings of the tipulid fly were discarded. Mayfly wings also were discarded when possible, but many mayflies (due to our capture technique) were dead with wings stuck to their bodies in a manner that made rejection difficult or impossible.

Both bats were caged in individual containers for 21 hours before being released, and all fecal pellets were collected and examined. In order to avoid potential bias, the bats were fed by Tuttle and the feces sent to Rabinowitz, who did not know what the bats had eaten.

Additional fecal samples were collected from three gray bats trapped as they returned from foraging, with mayfly remains matted in their fur, and from beneath the maternity roost.

Samples were baked for 12 hours at 100°C, then softened for microscopic analysis in a solution of 4 parts Photoflo rinsing solution (Eastman-Kodak Co., Rochester, New York 14650, U.S.A.), 1 part 70% ethanol, and 1 part distilled water (Anthony & Kunz, 1977). Each pellet was then transferred to a dish of 70% ethanol and carefully teased apart with the aid of a dissecting scope (45×). All insect fragments isolated from the feces were compared with reference material obtained through pulverization of insects caught in blacklight and sticky traps at gray bat foraging sites. Fragments were identified to order and, when possible, to family. Since it is believed that each fecal pellet of an insectivorous bat contains the remains of either one large insects or a number of smaller ones (Coutts *et al.*, 1973), one insect per pellet was assumed unless the number of eyes, legs, or wings recovered exceeded 2, 6, or 4 respectively (only 2 wings allowed for

Dipterans). In this way approximations of the proportions of each taxonomic grouping could be made.

Culled insect parts were collected from beneath both maternity and temporary roosts in the cave. These were counted, sorted, and identified to order and, when possible, to family.

3. RESULTS

The first of the two hand fed bats produced 33 fecal pellets. Ten of these were randomly chosen for examination. Although several mayfly wings were easily recognized, no other identifiable mafly remains were found (Table 1). Dipteran remains were from several less than 2 mm long individuals that accidentally stuck to the mayflies during hand feeding. The second bat produced 8 fecal pellets from which 75 insect fragments were identified (Table 2). Table 3 provides a comparison of the results of standard fecal analysis on these pellets with the actual percent of insects eaten.

Table 1

Results of fecal analysis for hand fed bat number 1. Pellet numbers not in order of defecation.

Pellet No.	Size (mm)	Order	No./Kind identifiable parts
1	.78	*Ephemeroptera*	3 *Ephemeroptera* wings
2	.60	—	nothing identifiable
3	.75	—	nothing identifiable
4	.46	—	nothing identifiable
5	.70	*Ephemeroptera*	3 *Ephemeroptera* wings
6	.76	*Ephemeroptera*	2 *Ephemeroptera* wings
		Diptera	2 *Diptera* leg pieces
7	.54	—	nothing indentifiable
8	.61	—	nothing indentifiable
9	.89	*Ephemeroptera*	4 *Ephemeroptera* wings
10	.54	*Ephemeroptera*	1 *Ephemeroptera* wing

The three bats returning from foraging were selected because they had fed upon mayflies, as indicated by mayfly remains matter in their fur. Analysis of their 30 fecal pellets indicated the following prey proportions: *Diptera* (46.9%), *Coleoptera* (43.8%), *Lepidoptera* (6.2%), and *Ephemeroptera* (3.1%).

Analysis of 100 fecal pellets from beneath the maternity roost indicated the relative dietary preference shown in Figure. The overwhelming majority of Dipterans identified were of the family *Chironomidae*. All *Homoptera* were of the family *Cicadellidae*. Coleopteran fragments included the families *Platypodiadae*, *Carabidae*, and *Scarabaeidae*. Tick species which parasitize gray bats were present in the feces as whole body forms but were not included in gray bat food preference data.

Table 2

Results of fecal analysis for hand fed bat number 2. Pellet numbers not in order of defecation.

Pellet No.	Size (mm)	Order	No./Kind identifiable parts
1	.75	*Ephemeroptera*	7 *Ephemeroptera* wing pieces
		Coleoptera	4 *Coleoptera* leg pieces
			3 *Coleoptera* eletrya pieces
2	.58	*Ephemeroptera*	8 *Ephemeroptera* wing pieces
		Coleoptera	3 *Coleoptera* leg pieces
			2 *Coleoptera* eletrya pieces
		Diptera	1 *Diptera* leg
		Trichoptera	1 *Trichoptera* wing piece
3	.78	*Ephemeroptera*	2 *Ephemeroptera* wing pieces
		Coleoptera	2 *Coleoptera* eletrya pieces
4	.63	*Ephemeroptera*	4 *Ephemeroptera* wing pieces
		Coleoptera	1 *Coleoptera* leg piece
		Diptera	3 *Diptera* leg pieces
			2 *Diptera* head pieces
5	.52	*Coleoptera*	7 *Coleoptera* leg pieces
			7 *Coleoptera* eletrya pieces
		Trichoptera	1 *Trichoptera* wing
6	.98	*Ephemeroptera*	1 *Ephemeroptera* wing
		Coleoptera	1 *Coleoptera* leg
			2 *Coleoptera* eletrya pieces
		Diptera	2 *Diptera* leg pieces
7	.28	*Diptera*	1 *Diptera* body piece
		Lepidoptera	many scales
8	1.49	*Ephemeroptera*	2 *Ephemeroptera* wing pieces
		Coleoptera	2 *Coleoptera* leg pieces
			1 *Coleoptera* antenna
		Diptera	2 *Diptera* leg pieces
		Lepidoptera	many scales
			75 identifiable fragments

Table 3

Summary of insects hand fed to bat number 2 and conclusions of fecal analysis. Mayfly wings are excluded from fecal analysis results.

Insect Orders	Actually Fed			Analysis Conclusions	
	Number	% of Total	% of Biomass	Number	% of Total
Ephemeroptera	25	59.6	60.3	0	0
Coleoptera	2	4.8	3.5	7	43
Trichoptera	3	7.1	1.4	2	13
Lepidoptera	3	7.1	26.9	2	13
Diptera	9	21.4	7.9	5	31

Identification of culled fragments indicated the food choices shown in Figure 2. These proportions were based on numbers of fragments belonging to any one order. All *Lepidoptera* identified belonged to the families *Noctuidae* or *Geometridae*. Dipteran remains were of the family *Tipulidae*. Coleopteran fragments included the families *Scarabaeidae* and *Carabidae*.

The results may be compared with the relative availability of insect orders at this gray bat colonies' foraging sites, as indicated by sticky trap capture (Fig. 3).

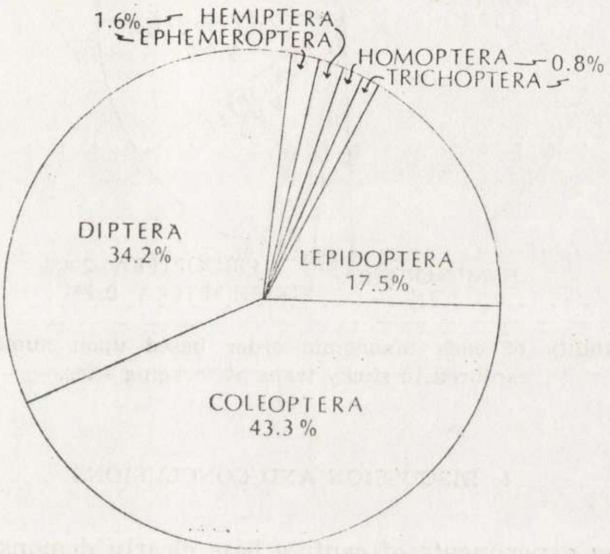

Fig. 1. Per cent of each taxonomic order found in fecal analysis.

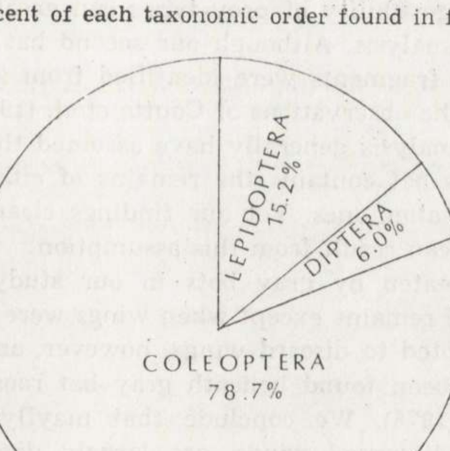

Fig. 2. Per cent of each taxonomic order as indicated by culled insect fragments.

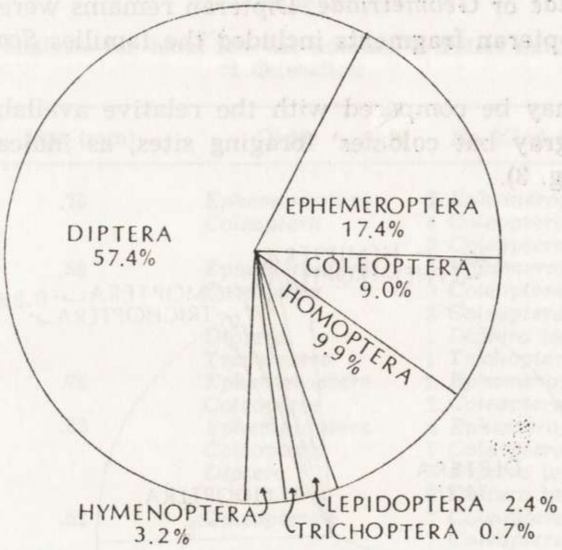

Fig. 3. Availability of each taxonomic order based upon numbers of insects captured in sticky traps at foraging sites.

4. DISCUSSION AND CONCLUSIONS

Our feeding experiments of captive bats clearly demonstrate the fact that differential digestibility of prey types can greatly bias conclusions drawn from fecal analysis. Although our second bat was hand fed only two beetles, beetle fragments were identified from seven of eight fecal pellets. Following the observations of Coutts *et al.* (1973), those who have relied upon fecal analysis generally have assumed that each fecal pellet of an insectivorous bat contains the remains of either one large insect or a number of smaller ones. Yet our findings clearly demonstrate the potential bias that can result from this assumption.

Mayfly species eaten by gray bats in our study area rarely were identifiable in fecal remains except when wings were eaten. Captive gray bats clearly attempted to discard wings, however, and discarded mayfly wings often have been found beneath gray bat roosts at several other localities (Tuttle, 1976). We conclude that mayfly body parts, other than the usually discarded wings, are largely digested and rendered unidentifiable in the feces, as already reported by Belwood & Fenton (1976). This is a serious bias when using fecal analysis as a tool for ascertaining gray bat prey preference.

When the results of analysis of feces and culled insect fragments from beneath the roost are compared with the availability of the different taxonomic orders captured at foraging sites, this study indicates that gray bats are beetle and moth strategists, with mayflies ranking very low in order of preference. The same is true even for bats that clearly had fed upon mayflies. However, such a conclusion is in direct opposition to the findings of Tuttle *et al.* (in manscript), who showed this same colony of gray bats to be highly selective in their choice of foraging territories, favoring locations where mayflies were exceptionally abundant. Numerous observations using night vision scopes and photographic techniques confirmed the importance of mayflies as a major gray bat food source.

Although some insects have solid structures such as jaws, head capsules, and leg segments that remain recognizable even after being chewed and swallowed, many groups of soft bodied insects may be almost completely, digested, leaving little or no detectable remains in the feces (Yalden & Morris, 1975). Yalden and Morris, for example, note that in Hamilton's (1933) study of 2,200 fecal pellets, beetles predominated among the groups recognized, with the decreasing proportion of other groups closely paralleling their decreasing hardness and durability. Accordingly, most bats that have been reported to specialize on particular insect groups are believed to be beetle and/or moth specialists (*e.g.* Black, 1972, 1974, 1979 ; Fenton *et al.*, 1977 ; Husar, 1976 ; Whitaker, 1972 ; Ross, 1961 ; Kunz, 1974). In the light of our results it is tempting to question how many other studies have suffered from the same biases that led to such a conclusion erroneously in this study.

As noted by Yalden & Morris (1975), most studies of bat prey preference are additionally biased by the fact that compared proportions are based on insect numbers rather than on their biomass or nutritional contribution to bat diets. This is effectively demonstrated in our study where it is seen that mere counts of individuals are deceptive. While moths constituted only 7% of our hand fed bat's meal, based on a count of numbers (as is often the case in fecal analysis), moths actually accounted for 27% of the meal based on biomass (calculated according to Bradbury & Vehrencamp, 1976). This misrepresentation can be seen with other insects as well (Table 3).

Further bias of fecal analysis probably results from the fact that gray bats sometimes feed continuously at feeding territories for several hours before returning to their roosts. During this time, rapid, in-flight digestion and defecation occur (Tuttle *et al.*, in manuscript). Thus the relatively few insects caught in the woods en route back to the cave probably show up in inordinately large numbers in fecal pellets collected in the cave or from bats entering the cave. In the woods, coleopterans and lepidopterans were by far the most numerous insects taken at light traps, whereas the same light traps caught mainly dipterans and ephemeropterans at over-water feeding territories.

Analysis of insect remains culled from beneath roosts is of questionable reliability as well. Gray bat roosts where mayfly remains have been found are all located in caves adjacent to rivers or reservoirs. We believe that the absence of mayfly remains under roosts of this colony is due to the distance of the colony's cave from the Norris Reservoir Mayflies probably were eaten long before arrival of bats at the maternity cave, and culled insect fragments from beneath roosts there simply represented the forest insects occasionally caught by bats en route to the cave. Furthermore, the largest insects were most likely to be carried to roosts in the cave, and were the most likely to be discovered in our search. Such forest insects undoubtedly represented a very small fraction of these bats' total diet.

The above biases are not limited to studies of bats that prey on soft-bodied aquatic insects. To varying degrees they affect all studies based upon analysis of feces or culled food remains. Bonaccorso (1979), for example, in a fecal analysis study which included fringe-lipped bats (*Trachops cirrhosus* Spix, 1823) on Barro Colorado Island, Panama, recognized insects and lizard scales but found no evidence of frogs having been eaten. Subsequent direct field observations on the same island demonstrated that *T. cirrhosus* feeds heavily and perhaps mostly on frogs (Tuttle & Ryan, 1981). A more recent study based upon fecal analysis of *T. cirrhosus* in Costa Rica and Panama (Whitaker & Findley, 1980), agreed with Bonaccorso's earlier investigations.

In a study of the racer *(Coluber constrictor)* Fitch (1963) noted that amphibians but not reptiles were digested too completely to be recognized from feces. He stated that "amphibians, lacking indigestible dermal structures were in most instances not represented at all in the scats, since their tissues were more or less completely dissolved by the digestion of the snakes". He further noted that remains of insects previously eaten by amphibians are found in the racer's scats and that, "if not recognized as secondary items, such remains might lead to erroneous conclusions regarding the racer's food". Thus in the above *Trachops* example, unrecognized frogs might actually have contributed insects not caught by the bats.

Although we strongly sympathize with those (*e.g.* Fenton, 1974 ; Howell & Burch, 1974 ; Belwood & Fenton, 1976) who advocate methods which do not necessitate sacrificing studied animals, especially endangered species, it is clear that use of fecal analysis and culled food remains may, and probably has, proved extremely misleading. Stomach analysis results have differed considerably from fecal studies of the same species (Whitaker *et al.,* 1981). Two recent studies of *Myotis lucifugus* at over-water foraging sites, based on stomach analysis (Buchler, 1976) and fecal analysis (Anthony & Kunz, 1977), arrived at very different conclusions regarding the importance of mayflies in the diet of this species. Fitch (1963) in his racer study found that "...items from stomachs included several frogs, whereas amphibians were absent from the much larger sample from scats". It would appear that the severe biases of fecal analysis make stomach analysis the method of choice in determining prey preference, though even the latter technique may be biased, especially if specimens are not collected at their primary foraging areas.

In some abundant animal species this may be an acceptable conclusion. In the case of most bat species, however, stomach analysis studies of any significant size cannot be justified. Study techniques are now available, with the arrival of night vision, acoustical equipment, and radio-telemetry, which should make field observation of bats an increasingly productive endeavor. We believe that these technological advances, combined with inventive use of prey sampling methods, should be emphasized in future research on bat prey preference and bat behaviour. Stomach analysis then can be restricted, when necessary at all, to a verification role requiring only relatively small samples. Whatever methods are chosen, however, it is clear that techniques must be validated and that potential biases must be thoroughly understood and clearly delineated in any discussion of results.

Acknowledgements: We thank Diane E. Stevenson, both for her help in the field and for her editorial advice. J. Ralph Jordan provided much invaluable logistical assistance, and Robert W. Henderson assisted with analysis of feces. Field work was supported contractually by the Division of Forestry, Fisheries, and Wildlife Development, Tennessee Valley Authority.

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Accepted, June 25, 1982.

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PORÓWNANIE METOD OCENY PREFERENCJI POKARMOWEJ U NIETOPERZY

Streszczenie

Bezpośrednie obserwacje terenowe nad odżywianiem się *Myotis grisescens* Howell, 1909 przeprowadzono w rejonie zapory Tennessee. Wyniki tych badań różnią się znacznie od wyników oceniających stosunki pokarmowe poprzez analizę kału i resztek owadów zebranych z miejsc w których nocują nietoperze. Rezultaty te rzutują na wiarygodność innych sposobów szacowania składu pożywienia nietoperzy. W kontrolnym doświadczeniu nietoperze karmiono w laboratorium różnymi gatunkami owadów, a następnie badano ich odchody celem określenia składu pobieranego pokarmu (Tabele 1, 2; Ryc. 1, 2). Stwierdzono, że tym sposobem zostaje zawyżona ilość zjedzonych chrząszczy, a pomniejszony udział jętek (Tabela 3, Ryc. 3). W pracy dyskutuje się źródła różnic w uzyskanych danych oraz rozbieżności w literaturze tyczącej oceny stosunków pokarmowych u owadożernych nie toperzy.