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THE DIETS OF NEOTROPICAL TROGONS, MOTMOTS, BARBETS AND TOUCANS[1]

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Abstract. Although membership in broad diet categories is a standard feature of community analyses of Neotropical birds, the bases for assignments to diet categories are usually not stated, or they are derived from anecdotal information or bill shape. We used notations of stomach contents on museum specimen labels to assess membership in broad diet categories ("fruit only," "arthropods only," and "fruit and arthropods") for species of four families of birds in the Neotropics usually considered to have a mixed diet of fruit and animal matter: trogons (Trogonidae), motmots (Momotidae), New World barbets (Capitonidae), and toucans (Ramphastidae). An assessment of the accuracy of label data by direct comparison to independent microscopic analysis of actual stomach contents of the same specimens showed that label notations were remarkably accurate. The specimen label data for 246 individuals of 17 species of Trogonidae showed that quetzals (*Pharomachrus*) differ significantly from other trogons (*Trogon*) in being more frugivorous. Significant differences in degree of frugivory were found among various *Trogon* species. Within the Trogonidae, degree of frugivory is strongly correlated with body size, the larger species being more frugivorous. The more frugivorous quetzals (*Pharomachrus*) have relatively flatter bills than other trogons, in accordance with predictions concerning morphology of frugivores; otherwise, bill morphology correlated poorly with degree of frugivory. An analysis of label data from 124 individuals of six species of motmots showed that one species (*Electron platyrhynchum*) is highly insectivorous, differing significantly from two others that are more frugivorous (*Baryphthengus martii* and *Momotus momota*). An analysis of 135 individuals of 12 species of barbets showed that although "fruit only" predominated among almost all species, arthropods are more frequently recorded in the stomachs of species in the genera *Eubucco* and *Capito* than in *Semnornis*. The highly frugivorous diet of *Semnornis* species is yet another parameter in which they resemble toucans more than New World barbets. Data from 326 individuals of 32 species of toucans showed that the family is remarkably homogeneous in the predominance of fruit in the stomachs of all species. These data suggest that the degree to which toucans prey upon bird eggs and nestlings, and animal matter in general, is overemphasized. Although our data suggest that it is safe to assign toucans to a "fruit only" category in community analyses, such assignments must be taken on a genus-by-genus or species-by-species basis in trogons, motmots, and barbets.

Key words: Diet; guild; Neotropical forest bird communities; Trogonidae; Momotidae; Capitonidae; Ramphastidae.

INTRODUCTION

Quantitative analyses of the diets of most species of Neotropical forest birds are virtually nonexistent. Therefore, classifications of these species into foraging or diet guilds is usually based on bill morphology, anecdotal observations, or extrapolations from nearest relatives; in some studies, the basis for the classification is not stated. Such guild assignments are a frequent and necessary feature of studies of bird communities of Neotropical forest localities (e.g., Orians 1969; Karr 1971, 1990; Terborgh 1980; Faaborg 1985; Bierregaard and Lovejoy 1989; Bierregaard 1990; Blake et al. 1990; Karr et al. 1990; Robinson and Terborgh 1990; Blake and Loiselle 1991), and their accuracy is critical for assessing potential community convergence (Terborgh and Robinson 1986). Only two such studies (Remsen 1985, Cardoso da Silva and Oniki 1988), however, have supported the assignments with analysis of stomach contents and quantitative foraging data from the study site itself.

Because of their heterogeneous diet, five families of Neotropical birds pose special problems for guild assignments: trogons (Trogonidae), motmots (Momotidae), barbets (Capitonidae), toucans (Ramphastidae), and tanagers (Thrau-

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pidae). Isler and Isler (1987) compiled existing data on stomach contents of the tanagers that show that the family is highly heterogeneous with respect to the broad categories of insectivory and frugivory. Some species seem exclusively insectivorous, others exclusively frugivorous, and others have a mixed diet. Diets of most species in the other four families, however, have yet to be analyzed in a comprehensive way. Although many species in these four families have been included as frugivores in compilations of frugivorous birds ranging from world-wide (Snow 1981) to local (Wheelwright et al. 1984) in scope, the degree to which frugivores feed on animal prey is usually unknown. Most community studies (references above) have assigned all species within each of these four families to a single dietary guild, usually the "omnivore" category.

What is the best way to make such guild assignments? Direct observations, such as those presented by Stiles and Skutch (1989), provide valuable information on diet but are usually biased in favor of conspicuous feeding behaviors and large and identifiable prey items. Although biases in digestion rates and poor taxonomic resolution of food items limit the usefulness of stomach contents in describing the diets of birds (Rosenberg and Cooper 1990 and references therein), analysis of stomach or crop contents potentially provides the best data on diet composition at the level of resolution necessary for guild assignments. Although microscopic analysis of the contents can generate quantitative data on diet composition (e.g., Orejuela 1980; Sherry 1984; Rosenberg 1990; Chapman and Rosenberg, 1991), such analyses require considerable time investment and expertise in the identification of diet items. Notations on labels of museum specimens concerning stomach contents typically lack taxonomic precision and do not state relative proportions of components of the contents. These data are also certainly biased against detection of small fragments of arthropods and partly digested fruit pulp. Although inferior to microscopic analysis in many ways, label notations can be used to address questions concerning broad diet categories, such as whether a taxon is largely insectivorous or frugivorous. Analysis of label data can yield novel results, such as the degree of insectivory in hummingbirds (Remsen et al. 1986).

To explore the usefulness of specimen label data for making guild assignments, we first determined the degree of accuracy of label data by direct comparison of label notations of the preparator of the specimen to actual contents determined by an independent observer. Then we used label notations as a first approximation to the question of whether species in four families are insectivorous, frugivorous, or mixed in diet. More sophisticated categorization awaits detailed, year-round studies of foraging behavior and diet, and quantitative, microscopic analyses of the stomach contents themselves.

MATERIALS AND METHODS

Most label data on stomach contents were compiled from the bird collection of the Museum of Natural Science, Louisiana State University. These specimens were collected primarily in Bolivia and Peru during the dry season; a few individuals were collected in Panama and Costa Rica. Some stomach contents from specimen labels from other museums (see Acknowledgments) were also included (primarily from the dry season in Ecuador, Peru, and Brazil, and from Costa Rica). A few stomachs with contents enumerated by Van Tyne (1929), Wagner (1944), Wetmore (1968), and Bourne (1974) were also included. Using adults only, each specimen's notation was categorized as follows: (1) arthropods only; (2) fruit only, including seeds, fruit skins, or pulp; (3) mixture of arthropods and fruit; (4) unidentifiable vegetable matter; or (5) unidentifiable "mush." Presence of vertebrate remains was also noted.

Because these data were taken by many different preparators who presumably varied in their skills in recognizing food items, the data set is heterogeneous. The specimens were collected from different regions, habitats, and seasons. Sample sizes were insufficient to determine whether these variables contributed to the heterogeneity. For a few species with the largest sample sizes, informal comparisons did not reveal any substantial effects of region, season, sex, or breeding condition. Clearly, the next step is to obtain sample sizes adequate for quantitative comparisons among regions, habitats, and seasons.

Another limitation is the degree of accuracy and resolution of label notations, which seldom contain notations on relative proportions of contents. A single fragment of an arthropod in a stomach full of fruit hypothetically received the same category assignment in our scheme as a stomach with a single fruit fragment in one otherwise full of arthropod remains. It is unlikely that most preparators would have detected small arthropod fragments, such as mandibles, in a stomach packed with fruit seeds or pulp; likewise, most preparators would probably overlook small amounts of fruit pulp or skins in a stomach packed with arthropod parts. Therefore, label data might be biased towards all-fruit or all-arthropod scores unless substantial portions of both components were present in a stomach. Furthermore, misidentifications are possible because portions of certain plant-mimicking arthropods, and soft-bodied portions of arthropods in general, may look like "vegetable matter" or even "fruit pulp." Conversely, certain ribbed, hairy, or spiny fruit coats and seed fragments might appear to be "arthropod" fragments.

To assess the accuracy of label notations of specimens, we compared preparators' notations to an analysis of actual contents for those specimens for which the contents were deposited in the Stomach Contents Collection of the Museum of Natural Science, Louisiana State University. One of us (Chapman) with previous experience in microscopic analysis of stomach contents (Chapman 1991; Chapman and Rosenberg, 1991) examined the contents of 68 individual stomachs of 26 species of the four families to determine relative composition of arthropods and fruit. This analysis was completed without Chapman's knowing what the preparator had written on the specimen's label and before Chapman knew the outcomes of the analyses of the label data. Contents of each stomach were examined using a stereomicroscope (12×). Prey items were sorted into "plant" and "animal" categories, and the relative volume of each was estimated to the nearest 5–10%. We surveyed literature on the diets of species of the four families but do not claim that the survey is exhaustive. We assumed that Stiles and Skutch (1989) have included in their summaries Skutch's many earlier papers on the natural history of Costa Rican trogons, motmots, barbets, and toucans.

Chi-square tests were performed using Statview 512®. Because a large number of multiple pairwise comparisons were performed, we urge great caution in interpretation of levels of statistical significance that we report, and we recommend that the statistical tests be used only to identify comparisons that are *likely* to be biologically meaningful. We set significance levels conservatively a priori at 0.01 rather than the usual 0.05; however, to avoid overlooking trends that might be biologically significant, we mention comparisons for which $P \leq 0.05$. Statistical comparisons excluded species for which sample size was smaller than 10 and excluded stomachs in the "unidentified" categories.

To examine morphological correlates of diet, we recorded bill measurements and body weights from study skins of five adult male specimens of each species from Bolivia or Peru. Unfortunately, insufficient sample sizes of skeletons prevented us from quantifying bill shapes by using bone measurements, which we found to be more repeatable than those from study skins. Bill measurements (length of exposed culmen, width at gape, height of bill at base) followed Baldwin et al. (1931) and were measured to the nearest 0.1 mm with dial calipers. Spearman rank correlations were performed using Statview 512®.

RESULTS

ASSESSING ACCURACY OF LABEL NOTATIONS

Stomach contents of 22 individuals representing six species of *Trogon* were examined microscopically. Of the seven labeled as "arthropods only" by the preparator, four contained 100% arthropods, one 95% arthropods, one 90%, and one 75%. Of the 11 labeled as having a mix of arthropods and fruit or vegetable matter, all contained a mix that ranged from 90% arthropods to only 5% arthropods. Thus, some preparators are apparently capable of detecting the minor component in a stomach when it represents as little as 5% of the volume. Of the four labeled "fruit only," all four contained fruit but all four also contained arthropods, ranging from 10% to 50% of the volume. Of these four, the two stomachs with the highest proportion of arthropods were from specimens prepared by inexperienced preparators. These two stomachs were so densely packed with material that the alcohol in which they were stored was made opaque by dissolved contents, making accurate identification of the contents difficult. The effect of using label data is, as we predicted, to under-represent the mixed category of diet. However, arthropods were detected by preparators in all but four (18%) of the 22 stomachs that contained arthropods, and fruit was detected in all but three (17%) of the 18 stomachs that contained fruit.

Stomach contents of 21 individual motmots of three species were examined microscopically. Of the 13 labeled as "arthropods only" by the preparator, eight contained 100% arthropods and five 95% arthropods. Of the six labeled as having a mix of arthropods and fruit or vegetable matter, five contained a mix that ranged from 20 to 80% arthropods. The other contained arthropods only. This mistake was the only one in our entire analysis in which the preparator recorded an item in the contents that we could not find in the stomachs; it is also possible that the fruit component listed, "seeds," may have been lost in the transfer of contents to a vial. Of the two labeled "fruit only," one contained 100% fruit and the other 90% fruit and 10% arthropods. As with trogons, the effect of using label data is to under-represent the mixed category of diet. However, arthropods were overlooked in only one (5%) of the 20 stomachs that contained arthropods. Fruit was missed in five (39%) of the 13 stomachs that contained fruit, but the contents of these stomachs averaged only 5% fruit by volume.

Only nine barbet stomachs of five species were available for microscopic analysis. One was labeled as having only arthropods, and this stomach actually contained 40% arthropods and 60% fruit. Two labeled as having mixed contents both contained fruit and insects, one with only 5% arthropods by volume. Of the six labeled as having only fruit or vegetable matter, three contained 100% fruit, two contained 25% arthropods, and one, 50% arthropods. The latter was prepared by the same person who prepared the "arthropods only" specimen above that actually contained 60% fruit (and this same person prepared a toucan specimen labeled as having an "empty" stomach for which the fruit-packed contents were saved). Consequently, we deleted all of this person's label data from the data-base below except for those specimens for which we could corroborate the label data by microscopic analysis.

Stomach contents of 16 individual toucans representing 12 species were analyzed microscopically. Two of these were labeled as having only birds in their stomachs, which we confirmed. One was labeled as having only unidentified vegetable matter, and this was 100% fruit. The other 13 were labeled as having fruit only; we confirmed this for all 13. Thus, we detected no errors in scoring of labels of our sample of toucans.

We pooled the above results from the three families (Trogonidae, Momotidae, Capitonidae) that had species with mixed diets to derive overall indices for the true presence of minor components in stomachs labeled as either arthropods only or fruit only. The mean percent of arthropods (by volume) in the 21 stomachs labeled as having only arthropods is 97%, a reassuringly high figure. The mean percent of fruit (by volume) in the nine stomachs labeled as having only fruit was 82%. Inclusion of the 13 toucans labeled as "fruit only" improves the mean percent to 92%. These are our best estimates of the true percentages of the major components for stomach contents labeled as exclusively arthropods or fruit. In both cases, the representation of the minor component of the contents was less than 25% in all but 2 (5%) of the 43 stomachs. For the 20 stomachs labeled as having mixed contents, seven were 50:50 by volume, the mean deviation from 50:50 was 21%, and the mean percentages were 52% arthropods and 48% fruit. We are unable to determine whether these figures represent fairly the skills of preparators who were not included in our analysis, but we have no reason to expect that those from other institutions differed in their proficiency from those in our sample, which included many novice preparators. Therefore, we recommend that the "arthropods only" and "fruit only" categories in Tables 1–4 be translated roughly as "usually 90–100% arthropods/fruit."

Because missing minor components in mixed-content stomachs underestimates the true number of stomachs in the "arthropods and fruit" category, use of label data exaggerates differences between species if all three categories (two "only" and a "mixed") are treated as equivalents in a contingency-table analysis. However, our analysis also shows that stomachs scored as having "only" one or the other component have much more imbalanced proportions (average 9:1) than the average stomach scored as "mixed" (average 1:1; one average deviation from mean produces proportions of 7:3 and 3:7). Therefore, retaining all three categories in an analysis can be justified as reflecting real differences between average proportions in "mixed" vs. "only" stomachs.

For the three species of trogons and one motmot for which we had the largest samples of stomachs analyzed microscopically, we were able to compare statistically the data from our direct examination to our specimen-label data for these same species. For this comparison, we considered the "arthropod-only" and "fruit-only" categories from labels equivalent to "arthropods $\geq$ 90%" and "fruit $\geq$ 80%," following from our previous comparison above of label data to microscopic examination for these three families. Label data did not differ significantly from data from microscopic examination (Chi-square, $P <$ 0.05) for any of the four species (*Trogon collaris* $P = 0.90$, $\chi^2 = 0.216$; *T. melanurus* $P = 0.91$, $\chi^2 = 0.19$; *T. viridis* $P = 0.58$, $\chi^2 = 1.09$; *Electron platyrhynchum* $P = 0.84$, $\chi^2 = 0.34$).

All five stomach samples labeled as "unidentified plant or vegetable matter" by the preparator were determined to be fruit. Although flower-eating has been reported for some species of toucans (Riley and Smith 1986), fruit is the only vegetable material likely to be consumed by most species in the four families. Therefore, we added those samples identified by the preparator as unidentified plant or vegetable matter (3 individual trogon stomachs, 0 motmots, 5 barbets, and 26 toucans) to the "fruit-only" category in our analyses of label data below.

TROGONIDAE

Trogons as a family are typically considered to have a mixed diet of fruit and arthropods (e.g., Wetmore 1968, Meyer de Schauensee 1970, Eisenmann 1985, Hilty and Brown 1986) or primarily fruit (Fjeldså and Krabbe 1990). Snow's (1980, 1981) tabulations of specialized frugivorous birds of the Neotropics included all Trogonidae but noted that the diets were supplemented by insects.

We were unable to find many quantitative data to support these assertions for most species. On the basis of stomach contents, Wetmore (1968) reported that five species in Panama (*Trogon massena, T. melanurus, T. viridis, T. collaris,* and *T. rufus*) had mixed diets, as did Haverschmidt (1968) for four species in Surinam (*T. melanurus, T. viridis, T. rufus,* and *T. violaceus*). Haverschmidt reported at least one small lizard (Teidae) taken by *T. viridis*. Stiles and Skutch (1989) noted that 10 species in Costa Rica (*Pharomachrus mocinno, T. massena, T. clathratus, T. bairdii, T. melanocephalus, T. elegans, T. collaris, T. aurantiiventris, T. rufus,* and *T. violaceus*) all had mixed diets, based primarily on foraging observations. They also noted that three of the largest species (*P. mocinno, T. massena, T. clathratus,* ate small vertebrates (i.e., small frogs and lizards) and that *T. collaris* was more insectivorous than other trogons. Howe (1982) found that *T. massena* in Panama was an important disperser (11% of all fruits dispersed) of the fruits of the tree *Virola surinamensis*. Wheelwright's (1983) detailed study of the diet of *Pharomachrus mocinno* indicated that adults were almost exclusively frugivorous, with the animal portion of food items primarily delivered to nestlings. Kantak (1979) observed 392 visits by *T. citreolus* to five species of fruiting trees, especially *Ehretia tinifolia*, in Campeche, Mexico. Eguiarte and Martínez Del Rio (1985) found that *T. citreolus* was almost exclusively frugivorous, at least during the dry-season study period, when only two observations of insectivory were obtained in 20 days of observations. Wheelwright et al. (1984) reported that *T. aurantiiventris* was "commonly observed" feeding on the fruits of *Hasseltia floribunda* and "uncommonly" or "occasionally" on the fruits of another 14 species of plants in montane Costa Rica. The association of certain *Trogon* species with foraging monkeys (*T. massena* and *T. rufus* [Stott and Selsor 1961, Boinski and Scott 1988]), whose prey-flushing behavior is used by the trogons, indicates that some species have specialized arthropod-searching behavior.

Data from 246 specimen labels from 17 species (Table 1) support the assignment of *Trogon* species to a mixed diet category. Although our sample sizes for quetzals (*Pharomachrus*) are small, their stomach contents are more frequently devoid of arthropods than are those of other trogons ($\chi^2 = 34.10$, $P < 0.0001$). Therefore, we recommend that quetzals be assigned to the "frugivore" category in community analyses. There are also differences among *Trogon* species in the degree of frugivory. *Trogon melanurus* differs significantly from *T. collaris* ($\chi^2 = 12.10$, $P = 0.0024$), *T. personatus* ($\chi^2 = 18.87$, $P < 0.0001$), *T. rufus* ($\chi^2 = 12.10$, $P = 0.0024$), and *T. curucui* ($\chi^2 = 15.64$, $P = 0.0004$) in having a higher proportion of stomachs scored as "fruit only"; *T. melanurus* also shows the same trend compared to *T. viridis* ($\chi^2 = 5.98$, $P = 0.05$), *T. surrucura* ($\chi^2 = 8.70$, $P = 0.0129$), and *T. violaceus* ($\chi^2 = 8.81$, $P = 0.012$). The tendency of *T. melanurus* to be more frugivorous parallels its more quetzal-like plumage and body size relative to most other trogons. Not only is *T. melanurus* larger than are most other trogons, but it (and its presumed sister taxa *T. massena* and *T. comptus*) are more quetzal-like in plumage in lacking tail-barring

TABLE 1. Stomach contents of 244 individuals of 17 species of trogons and quetzals (Trogonidae). The figures refer to the percent of the individuals examined whose stomach contents fall in that particular category.

Species	Arthropods only	Arthropods and fruit	Fruit only	Unident. "mush"	n
Pharomachrus moccino	—	—	100%	—	1
Pharomachrus antisianus	—	—	100%	—	1
Pharomachrus auriceps	—	12.5%	87.5%	—	8
Pharomachrus pavoninus	—	11.1%	88.9%	—	9
Trogon citreolus	20.0%	20.0%	60.0%	—	5
Trogon massena	66.7%	33.3%	—	—	3
Trogon melanurus	21.1%	50.0%	29.9%	—	38
Trogon comptus	42.9%	42.9%	14.3%	—	7
Trogon clathratus	—	—	100%	—	1
Trogon viridis	41.4%	20.7%	37.9%	—	29
Trogon elegans	100%	—	—	—	1
Trogon collaris	56.0%	16.0%	12.0%	16.0%	25
Trogon personatus	72.7%	13.6%	13.6%	—	22
Trogon rufus	59.3%	14.8%	22.2%	3.7%	27
Trogon surrucura	64.3%	21.4%	14.3%	—	14
Trogon curucui	52.8%	44.4%	—	2.8%	36
Trogon violaceus	57.9%	26.3%	15.8%	—	19
Mean, all species with $n \geq 5$	40.7%	24.5%	33.0%	1.9%	$\Sigma = 246$

and prominent white chest bands. We predict that larger sample sizes of stomachs for *T. massena* and *T. comptus* will show that they are also more frugivorous than are most other trogons. Among the remaining species of trogons, another relatively large-bodied species, *Trogon viridis*, also has significantly higher proportions of stomachs with fruit as contents than does *T. curucui* ($P = 0.0002$) and shows the same trend compared to *T. personatus* ($P = 0.014$).

Given the marked differences in the degree of frugivory among species in the Trogonidae, one might predict that these differences would show the morphological correlates of frugivory found in other bird groups, namely relatively wider gapes and flatter and shorter bills for species that are more frugivorous (Snow 1973, Karr and James 1975, Traylor and Fitzpatrick 1982, Herrera 1984, Fitzpatrick 1985). This is particularly so because trogons use aerial maneuvers for taking fruit (Moermond and Denslow 1985). However, Moermond and Denslow (1985) predicted that bill shape among species that were frugivorous were more likely to be associated with differences in fruit-handling behavior than degree of frugivory. They proposed that the relatively larger bill of *T. massena* compared to *P. mocinno* is associated with the former's eating of large fruit piecemeal rather than swallowing them whole as in *P. mocinno*.

We quantified bill shape and bill dimensions relative to body mass (weight) for nine species of Trogonidae for which sample sizes of stomach contents and body weights were relatively large. Our qualitative impression that bill shapes of trogonids are similar was supported by analysis of ratios between three linear dimensions (length, width at gape, and depth {height}), all of which showed small differences among the nine species. The differences among species shown in Figure 1 are maximally inflated by having small ranges of values on the axes; addition of species other than trogons to the analysis condenses the cloud of points represented by the Trogonidae to a tiny ball in three-dimensional space. Even so, the two species of quetzals (*Pharomachrus*) have bills with smaller dept-to-width and depth-to-length ratios than do any of the seven species of trogons (*Trogon*). This supports the prediction that species that are more frugivorous should have flatter bills. However, we found no correlation (Spearman rank, $P \geq 0.05$) between any of the three ratios and any combination of diet categories (arthropods only, fruit only, arthropods only + arthropods-and-fruit, fruit only + arthropods-and-fruit; percentages taken from Table 1). Several correlations were close to the conventional level of statistical significance, most notably "depth-to-length" with "fruit only + arthropods and fruit" ($r = -0.56$, $P = 0.055$). These trends were driven

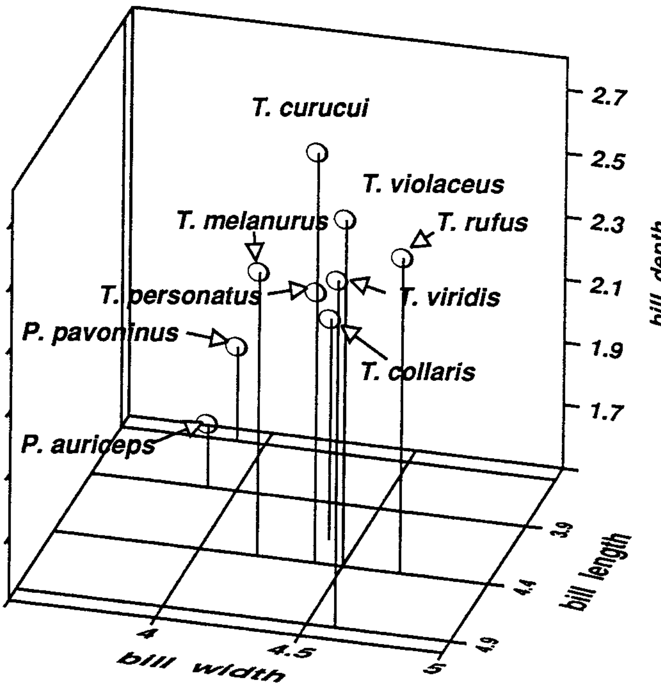

FIGURE 1. Relative bill widths, bill lengths, and bill depths for nine species of Trogonidae (*Pharomachrus* and *Trogon*).

by the differences in flatness of bills of quetzals vs. trogons and the higher degree of frugivory for the quetzals. When quetzals were removed from the analysis, most trends disappeared completely. However, one significant correlation emerged: "length-to-width" with "fruit only + arthropods and fruit" ($r = 0.81$, $P = 0.023$). The correlation, however, was opposite of predictions: the most frugivorous species (*T. melanurus* and *T. viridis*) had relatively longer bills.

We suspect that the differences in bill shape between the two genera reflect differences in degree of frugivory. However, among the variably frugivorous species of *Trogon,* bill shapes show little evidence of differences that might be interpreted as adaptations associated with diet differences. We cannot resolve whether differences in diet are too small to exert selective pressure on bill shapes, whether bill shapes within *Trogon* are phylogenetically constrained, or whether larger sample sizes of individuals and species within *Trogon* might reveal subtle but statistically significant differences.

We also compared relative lengths, widths, and depths of bills by dividing the absolute measurements by the cube-root of body mass (as an index of body size). As with the previous analysis, the relative dimensions were all similar among the nine species. However, the two quetzals have relatively smaller bills in all three dimensions than do the seven trogons (Fig. 2). Thus, the differences in relative bill size between *P. mocinno* and *T. massena* found by Moermond and Denslow (1985) applies to a broader range of species in both genera. Whether the differences between the two genera are related to food-handling differences as suggested by Moermond and Denslow cannot be determined without data on fruit-handling techniques of the nine species in this analysis.

The strongest relationship between diet and morphology in the Trogonidae appears to be that large-bodied species are more frugivorous than small-bodied species. Correlations between body mass and all four diet categories and their combinations (arthropods only, fruit only, arthropods only + arthropods-and-fruit, fruit only + arthropods-and-fruit; percentages taken from Table 1) are all statistically significant (Spearman rank, $P = 0.011$ to 0.026), although multiple tests of the same data set must be regarded cautiously. The highest correlation is between body mass

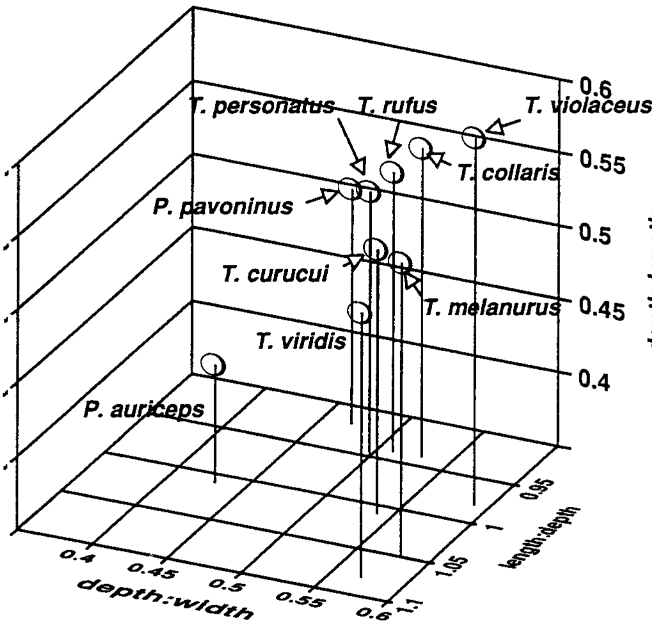

FIGURE 2. Ratios of bill dimensions for nine species of Trogonidae (*Pharomachrus* and *Trogon*).

and "% arthropods only" (Fig. 3). Although no statistically significant correlations remain once the analysis is restricted to *Trogon* species, the two largest species, *T. melanurus* and *T. viridis,* are more frugivorous than the five other species, which are all similar in body mass. The correlation within *Trogon* between body mass and "% arthropods only" is reasonably strong ($r = -0.61$, $P < 0.068$) given the small sample size. Therefore, it is doubtful that the relationship between body mass and frugivory is strictly due to a phylogenetic effect, namely greater frugivory in quetzals. We have no plausible hypothesis to explain the apparent relationship between body size and

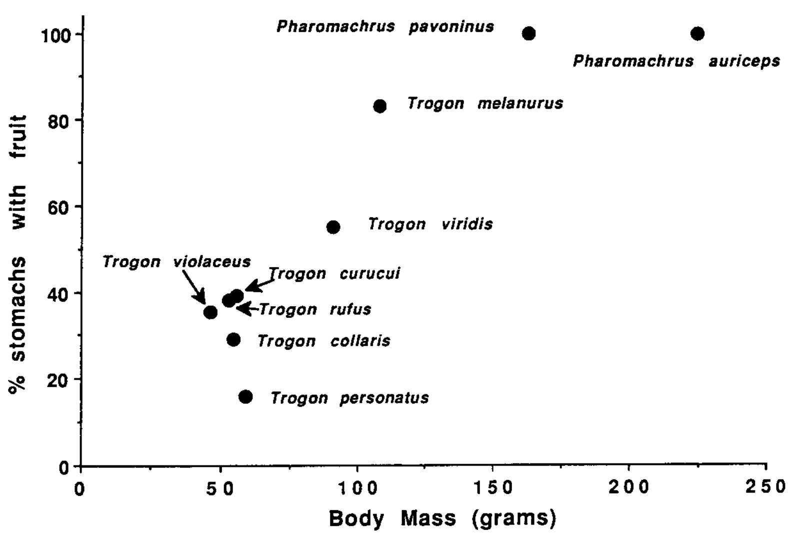

FIGURE 3. Relationship between body weight (mass) and percent of stomachs examined that included fruit in contents for nine species of Trogonidae.

TABLE 2. Stomach contents of 118 individuals of 6 species of motmots (Momotidae). The figures refer to the percent of the individuals examined whose stomach contents fall in that particular category.

Species	Arthropods only	Arthropods and fruit	Fruit only	Unident. "mush"	n
Hylomanes momotula	100%	—	—	—	6
Aspatha gularis	100%	—	—	—	1
Electron platyrhynchum	96.4%	3.6%	—	—	28
Eumomota superciliosa	100%	—	—	—	2
Baryphthengus martii	45.7%	22.9%	31.4%	—	32
Momotus momota	61.5%	21.2%	15.4%	1.9%	52
Mean, all species with $n \geq 5$	76.0%	11.9%	11.7%	0.5%	$\Sigma = 124$

frugivory. We also note that our selection of species of Trogonidae includes only those species characteristic of lowland tropical rainforest and the Andes, although seven of the nine species are widely sympatric in Amazonia. It is possible that inclusion of other species of trogons found in areas with greater seasonality of resource availability would affect the above analyses.

MOMOTIDAE

Motmots as a family are considered to have a mixed diet of arthropods, fruit, and small vertebrates (Meyer de Schauensee 1970), with fruit often relegated to a supplemental category (Skutch 1985a, Hilty and Brown 1986, Stiles and Skutch 1989). Few quantitative data support these assertions. Snow's (1980, 1981) tabulations of specialized frugivorous birds of the Neotropics did not include any motmots. Wetmore (1968) reported that inspection of a few samples of stomach contents of two species (*Hylomanes momotula* and *Electron platyrhynchum*) revealed only insects, whereas two other species (*Baryphthengus martii* and *Momotus momota*) also included a wider variety of invertebrates, vertebrates (lizards, 1 small bird, 1 small fish), and some fruit. Haverschmidt (1968) reported that stomach contents of *M. momota* included fruit, mollusks, Coleoptera, and Orthoptera. Smith (1975) found that hand-reared *Eumomota superciliosa* showed an innate avoidance to snake-shaped models with patterns simulating those of venomous coral snakes whereas most other snake models were attacked; this implies that snakes are a regular component of this species' diet. Stiles and Skutch (1989) reported that (1) *Hylomanes momotula* ate primarily invertebrates, mostly arthropods; (2) *E. platyrhynchum* and *Eumomota superciliosa* ate mostly arthropods but also some small vertebrates (frogs, lizards, snakes); and (3) *B. martii* and *M. momota* ate arthropods and other invertebrates, small vertebrates, and fruit. They also reported that *B. martii* captured fishes and crabs in the manner of a kingfisher. Wheelwright et al. (1984) found that *M. momota* was "commonly observed" feeding on the fruits of two species of *Ficus* and "uncommonly" or "occasionally" on the fruits of seven other species in montane Costa Rica. Orejuela's (1980) analysis of the diets of two motmot species, the most thorough analysis of stomach contents of any neotropical birds to date, showed that both *E. superciliosa* and *M. momota* were predominantly insectivorous throughout the year. Fruit formed only 3.4% and 8.6% of the diet by volume, respectively, and reptiles only 0.9% and 0.1% by volume. Coleoptera and Orthoptera were important taxa in both species' diets, as was Hymenoptera in the diet of *E. superciliosa*. McDiarmid et al. (1977) observed that *E. superciliosa* regularly visited the tree *Stemmadenia donnell-smithii* for fruit, but this supplied only about 3% of daily energy requirements. Scott and Martin (1984) found that *E. superciliosa* was a regular visitor to at least three species of fruiting trees in Yucatan, Mexico. Wendelken and Martin (1987) observed that *E. superciliosa* and *M. mexicanus* were frequent consumers of fruit of the tree *Guaiacum sanctum* in arid Guatemala. Howe (1982) found that *B. martii* was an important disperser (17% of all fruits dispersed) of the fruit of the tree *Virola surinamensis* in Panama.

Our data from 124 specimens of six species of motmots (Table 2) suggest that two species, *H. momotula* and *E. platyrhynchum*, are largely or completely insectivorous, whereas two others, *B. martii* and *M. momota*, have mixed diets. In concert with previously published information, but in contrast with community studies that typically assign all members of the family to a single diet category, we recommend different assignments to diet categories of these two pairs of species. *Electron platyrhynchum* differs significantly from *Baryphthengus martii* (χ^2 = 18.7, P = 0.0001) and *Momotus momota* (χ^2 = 11.0, P = 0.004) in having a greater proportion of stomachs lacking any fruit. Although Orejuela (1980) found that *M. momota* was primarily insectivorous in the Yucatan near the northern extreme of its distribution, our data suggest that fruit forms a more important diet constituent elsewhere. We urge caution in guild assignments for several other species about which little or nothing is known of diet.

With only three species of motmots with adequate sample sizes of stomachs, inferences concerning morphology are of limited value. We note that *E. platyrhynchum* has the flattest bill of the three species (depth-to-width and depth-to-length ratios 0.47 and 0.22, respectively, vs. 0.76 and 0.34 for *B. martii* and 0.83 and 0.33 for *M. momota*). It also has the smallest bill depth relative to cube root of body mass (2.1, vs. 2.5 and 2.8 for *B. martii* and *M. momota,* respectively) and the largest bill width relative to body mass (4.4, vs. 3.3 for both other species). Because this species is the least frugivorous of the three, its flat bill is counter to the predictions concerning degree of frugivory for other groups (see references under Trogonidae). The wide and flat bill shape of *E. platyrhynchum* is similar to that of several species of tyrannid flycatchers, especially those in the genera *Todirostrum* and *Platyrinchus,* that are completely insectivorous and make sallies to foliage to capture arthropods (Fitzpatrick 1980). Hilty and Brown (1986) and Stiles and Skutch (1989) reported that *E. platyrhynchum* also makes sally-strikes to foliage for large arthropods and small vertebrates. However, they also reported similar foraging behavior for *B. martii* and *M. momota.* More detailed observations on the foraging behavior (and nest-tunnel digging behavior?) of these species is needed before meaningful interpretations of the differences in bill shapes of these motmots can be made.

The apparent relationship between larger body size and increasing degree of frugivory found in the Trogonidae may also exist in the Momotidae. For the four species with more than five stomach samples (Table 2), the larger the body size (mass), the higher the degree of frugivory, as measured by "fruit" + "arthropods and fruit." Clearly, a larger sample size of species is needed before such a relationship can be confirmed for the Momotidae.

CAPITONIDAE

New World barbets are reported to eat fruit and insects (Meyer de Schauensee 1970, Hilty and Brown 1986) or primarily fruit supplemented by insects (Wetmore 1968, Stiles and Skutch 1989). Snow's (1980, 1981) tabulations of specialized frugivorous birds of the Neotropics included all Capitonidae, without mention of insects as even a supplement to the diet.

Few quantitative data are available to support these assertions. Wetmore (1968) found that the stomachs of *Capito maculicoronatus* contained mainly fruit, whereas those of *Eubucco bourcieri* contained a higher proportion of arthropods. Haverschmidt (1968) found that *C. niger* had a mixed diet of fruit and arthropods. Stiles and Skutch (1989) reported that *E. bourcieri* fed primarily on arthropods, whereas *Semnornis frantzii* was primarily frugivorous. Wheelwright et al. (1984) found that *S. frantzii* was "commonly observed" feeding on the fruits of 11 species of plants and "uncommonly" or "occasionally" on the fruits of another 19 species in montane Costa Rica. Remsen and Parker (1984) and Rosenberg (1990) reported that several *Capito* and *Eubucco* species exhibit specialized arthropod-searching behavior, namely the regular searching of curled dead leaves suspended above ground for the arthropods that use them as refuges.

Stomach contents data from 135 individuals of 12 species (Table 3) show that "fruit only" is the predominant condition for stomachs of all but one species of barbet in our sample, which includes 12 of the 13 recognized species. Although species in the genus *Semnornis* tend to be more frugivorous than those in the genus *Capito,* which likewise are more frugivorous than those in the genus *Eubucco,* the differences between genera using a pooled sample of all species in each genus are significant for *Capito* vs. *Eubucco* (χ^2 = 13.8, P = 0.001) and *Semnornis* vs. *Eubucco* (χ^2 = 9.6, P = 0.0084), but not for *Semnornis* vs. *Capito* (χ^2 = 2.2, P = 0.34). Because arthropods have yet to be recorded in the limited sample size of stomachs of either *Semnornis* species, we recommend that these two species be placed in the "frugivore" category, whereas *Capito* and *Eubucco* species be classified in a "fruit and arthropods" category. The only interspecific

TABLE 3. Stomach contents of 135 individuals of 12 species of New World barbets (Capitonidae). The figures refer to the percent of the individuals examined whose stomach contents fall in that particular category.

Species	Arthropods only	Arthropods and fruit	Fruit only	Unident. "mush"	n
Capito aurovirens	12.5%	—	87.5%	—	8
Capito maculirostris	—	—	100%	—	3
Capita squamatus	—	22.2%	77.8%	—	9
Capito quinticolor	—	—	100%	—	4
Capito niger	7.3%	9.8%	80.4%	2.4%	41
Capito dayi	14.3%	—	85.7%	—	7
Eubucco richardsoni	25.0%	37.5%	37.5%	—	16
Eubucco bourcieri	6.3%	12.5%	81.3%	—	16
Eubucco tucinkae	—	40.0%	60.0%	—	5
Eubucco versicolor	18.1%	—	81.8%	—	11
Semnornis ramphastinus	—	—	100%	—	10
Semnornis frantzii	—	—	100%	—	5
Mean, all species with $n > 5$	10.4%	10.3%	79.0%	0.3%	$\Sigma = 135$

comparison that was statistically significant was the more insectivorous *Eubucco richardsoni* vs. the widely sympatric and more frugivorous *Capito niger* ($\chi^2 = 11.0$, $P = 0.004$). Other comparisons that showed trends in the direction of our 0.01 significance level involved *E. richardsoni* of lowland forests vs. the possibly more frugivorous *E. bourcieri* ($\chi^2 = 6.4$, $P = 0.041$) and *E. versicolor* ($\chi^2 = 8.2$, $P = 0.017$) of montane forests.

Prum (1988) proposed that, based on morphology, *Semnornis* is more closely related to toucans than it is to other New World barbets. In concordance with this hypothesis, the stomach contents data show that the diets of *Semnornis* species are more similar to those of toucans (next section) than they are to *Capito* or *Eubucco* species. Furthermore, *Semnornis ramphastinus* and toucans in the genus *Andigena* share a combination of plumage characters (black crown, bronzy-olive back, gray throat or breast, and gray tail) that is unique within the toucans and barbets, and they share an Andes-only distribution. *Semnornis ramphastinus* and two species of *Andigena* also share a bill pattern, yellowish base with blackish tip, found in no other barbets or toucans. That bill-snapping in barbets and toucans was reported by Hilty and Brown (1986) only in *S. ramphastinus* and in two species of toucans (*Andigena*) may also be relevant. These similarities between *S. ramphastinus* and *Andigena,* as well as the relatively large bill of *S. ramphastinus,* are so striking that they are reflected in the scientific and English names ("Toucan Barbet").

Of the recent analyses of the phylogeny of the Piciformes, none mentioned direct comparison between *Andigena* and *Semnornis.* Prum (1988) studied both species of *Semnornis,* but *Andigena* was not mentioned specifically. Swierczewski and Raikow (1981) studied *S. ramphastinus* but not *Andigena.* Lanyon and Zink (1987) studied *Andigena,* but *Semnornis* tissue was not then available. Simpson and Cracraft (1981) did not present a complete list of taxa studied; neither genus was mentioned.

RAMPHASTIDAE

As a family, toucans are considered to be primarily frugivorous, with diets supplemented by large insects, small vertebrates, and the eggs and nestlings of other birds (Meyer de Schauensee 1970; Wetmore 1968; Snow 1980, 1981; Skutch 1985b; Hilty and Brown 1986; Stiles and Skutch 1989). Few quantitative data are available to support these assertions. Wetmore (1968) observed that five species in Panama (*Aulacorhynchus prasinus, Pteroglossus frantzii, Selenidera spectabilis, Ramphastos sulfuratus,* and *R.* [*ambiguus*] *swainsonii*) were mainly frugivorous, but had evidence that all but *S. spectabilis* were also nest-robbers. He also found large insects in the stomachs of *R. sulfuratus,* and flower filaments in the stomachs of *R. swainsonii.* Riley and Smith (1986) observed that *A. prasinus* also regularly ate whole flowers, and Riley (1986) stated that the fruit and arthropods fed to nestling *A. prasinus* were also common in the diets of adults. Wagner (1944) found only vegetable matter in eight stomachs of *A. prasinus.* Haverschmidt

TABLE 4. Stomach contents of 326 individuals of 32 species of toucans (Ramphastidae). The figures refer to the percent of the individuals examined whose stomach contents fall in that particular category.

Species	Vertebrates only	Arthropods only	Arthropods and fruit	Fruit only	Unident. "mush"	*n*
Aulacorhynchus prasinus	3.5%	—	—	96.5%	—	29
Aulacorhynchus haematopygus	—	—	—	100%	—	4
Aulacorhynchus derbianus	—	—	—	100%	—	15
Aulacorhynchus huallagae	—	—	—	100%	—	3
Aulacorhynchus coeruleicinctis	—	16.7%	—	83.3%	—	6
Pteroglossus viridis	—	—	—	100%	—	6
Pteroglossus inscriptus	—	—	—	100%	—	18
Pteroglossus bitorquatus	—	—	—	100%	—	12
Pteroglossus flavirostris	—	5.6%	—	94.4%	—	18
Pteroglossus araccari	—	—	—	100%	—	6
Pteroglossus castanotis	—	16.7%	—	83.3%	—	6
Pteroglossus pluricinctus	—	—	25.0%	75.0%	—	4
Pteroglossus torquatus	—	—	—	100%	—	16
Pteroglossus frantzii	—	—	—	100%	—	2
Pteroglossus sanguineus	—	—	—	100%	—	4
Pteroglossus beauharnaesii	—	—	—	100%	—	9
Baillonius bailloni	—	—	—	100%	—	5
Selenidera maculirostris	—	—	—	100%	—	4
Selenidera nattereri	—	—	—	100%	—	2
Selenidera reinwardtii	7.1%	—	—	89.3%	3.6%	28
Selenidera culik	—	—	—	100%	—	1
Selenidera spectabilis	—	—	20.0%	80.0%	—	5
Andigena hypoglauca	—	—	—	100%	—	14
Andigena laminirostris	—	—	—	100%	—	8
Andigena cucullata	—	—	—	100%	—	8
Ramphastos dicolorus	—	—	—	100%	—	2
Ramphastos vitellinus	3.9%	—	—	96.1%	—	26
Ramphastos brevis	—	—	—	100%	—	1
Ramphastos sulfuratus	—	—	19.2%	80.8%	—	26
Ramphastos toco	—	11.1%	44.4%	44.4%	—	9
Ramphastos tucanus	—	—	13.0%	87.0%	—	23
Ramphastos ambiguus	—	—	—	100%	—	6
Mean, all species with $n \geq 5$	0.7%	2.5%	3.0%	93.5%	0.3%	$\Sigma = 326$

(1968) found only fruit in the stomachs of six species in Surinam (*S. culik, P. aracari, P. viridis, R. vitellinus, and R. tucanus*). Bourne (1974) found that *R. tucanus* was primarily frugivorous but also ate insects and occasionally bird eggs or lizards. Stiles and Skutch (1989) observed that six species in Costa Rica (*A. prasinus, P. torquatus, P. frantzii, S. spectabilis, R. sulfuratus,* and *R. {ambiguus} swainsonii*) were primarily frugivorous, but all took some arthropods; all but *P. frantzii* were recorded eating small vertebrates (lizards and snakes), and all but *S. spectabilis* were recorded eating birds' eggs or nestlings. Van Tyne (1929) found that 19 of 24 stomachs examined of *R. sulfuratus* contained only fruit, with the remaining five containing some animal matter as well as fruit; in only two cases did the animal matter "constitute as much as half of the stomach contents." Howe (1977) found that three species, *R. {ambiguus} swainsonii, R. sulfuratus,* and *P. torquatus,* were among the most frequent consumers of the fruit of the tree *Casearia corymbosa* in Costa Rica. Howe (1981) found that *R. {ambiguus} swainsonii* was the most important disperser (43% of all fruits dispersed) and that *P. torquatus* was the second-most important disperser (17%) for the tree *Virola sebifera* in Panama. Howe (1982) likewise found that *R. {ambiguus} swainsonii* was the most important disperser (42% of all fruits dispersed) for *V. surinamensis* in Panama and that *R. sulfuratus* was also an important disperser (11% of all fruits dispersed). In montane Costa Rica, Wheelwright et al. (1984) found that *A. prasinus* was "commonly observed" feeding on the fruits of 58 species of plants and "uncommonly" or "occasionally" on the fruits of another 37 species, and that *R. sulfuratus* was "commonly observed" feeding on the fruits of eight species of plants and "uncommonly" or "occasionally" on the fruits of another eight species. Kantak (1979) observed 404 visits by *R. sulfuratus* and 148 visits by *P. torquatus* to five species of fruiting trees, mainly to *Ehretia tinifolia,* in Campeche, Mexico. Mindell and Black (1984) observed two *R. {ambiguus} swainsonii* hunting a lizard together in a manner that suggested specialized cooperation.

Given the broad diets reported for toucans, we were surprised to find that the vast majority of toucan stomachs showed no trace of animal prey (Table 4). Of the 326 stomachs of 32 species examined, only 18 individuals (5.5%) of 8 (25%) species contained arthropods and only four individuals (1.2%) of three species (9.4%) contained vertebrate remains (egg shell fragments in one; unidentified vertebrate in one; birds, probably nestlings, in the other two, a pair collected in the same shot). In only one species, *R. toco,* does "fruit only" compose less than 75% of the stomach samples. This species is also the only toucan restricted to open, nonforested areas (Haffer 1974), where perhaps the year-round supply and diversity of fruit is lower than in forests.

These results imply that the proportion of animal material, especially vertebrate, in the diet is quite small and that visual observations are perhaps biased towards detecting animal prey, especially nest-robbing activities made conspicuous by the mobbing behavior of the victims. Perhaps the animal portion of the food items recorded by visual observations for toucans are primarily those items to be delivered to their nestlings, which presumably require a higher proportion of protein in their diets. An alternative hypothesis (T. W. Sherry, in litt.) is that because our stomach samples are mostly from the dry season, which is typically a period of minimum breeding activity, they do not reflect the true, year-round degree of carnivory in toucans. Nevertheless, until year-round diet dictate otherwise, our data suggest that toucans be included in the frugivore category for purposes of community analyses. Their stomach samples are remarkably homogeneous with respect to broad diet categories; there were no statistically significant differences among any species or genera of toucans in proportions of fruit vs. animal matter in stomachs. If the differences in shape and size in the bills of toucans reflect diet differences (Short 1985), such differences are not evident at this crude level of resolution.

GENERAL DISCUSSION

Although label data from museum specimens provide only a crude view of a species' diet, they appear useful in assessing membership in broad diet categories. Unfortunately, most museum specimens do not have such data on their labels, and many species, particularly from Middle America and southeastern Brazil, are represented by small sample sizes. We urge collectors to inspect carefully the contents of crops and stomachs of all specimens, and to record these data on the labels. More valuable still is preservation of these contents and their deposition in a museum collection, as is done at the Museum of Natural Science, Louisiana State University (see Rosenberg and Cooper 1990).

The detection of several statistically significant differences among the species and genera examined implies that the obvious limitations of categorical label data do not preclude discovery of trends. In the Trogonidae, for example, species range from the highly frugivorous quetzals to some trogons that are highly insectivorous (*T. personatus*), and this gradient is associated with a gradient in body size, with the largest species tending to be more frugivorous than the smallest species. In the Momotidae, at least two species are highly insectivorous, whereas two others have a high fruit component in the diet. Although all species of barbets examined are primarily frugivorous, differences in degree of frugivory among some genera are significant. Therefore, in all three families, blanket assignment of species to diet categories based solely on family membership, a practice widely used in current research on community ecology of Neotropical forest birds, is incorrect. Conversely, for the toucans, a family-wide assignment to a single category appears to be justified, but not to the "omnivore" category to which they are assigned by many authors. All species examined are highly frugivorous, more so than indicated by the literature.

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