Methods of Assessing Dietary Intake: A Case Study from Wedge-capped Capuchins in Venezuela

Introduction

Many socioecological models are founded upon variance in foraging success (see, for example, Wrangham, 1980). It is widely recognized that what an animal eats may have a profound impact upon other facets of its ecology and social behavior, such as ranging patterns (Isbell, 1991), group size (Janson, 1988; Terborgh and Janson, 1986), rates of aggression (Janson, 1985; Whitten, 1983), and frequency of allomothering (McKenna, 1979).

Despite their importance, precise measures of food intake tend to be elusive. A few studies have successfully used analyses of fecal samples (Goodall, 1977; Tutin and Fernandez, 1993) or stomach contents (Charles-Dominique, 1974; Gautier-Hion, 1980; Hladik, 1977). However, most investigations have relied solely upon observations to estimate intake. Two methods are commonly employed. First, researchers have assessed the proportion of total feeding time that subjects devote to ingesting different types or species of foods (Chapman and Fedigan, 1990; Chivers, 1977; Garber, 1993; Hladik, 1977; Janson, 1985; Kinzey, 1977; Klein and Klein, 1977; Milton, 1980; Norconk, 1996; Richard, 1977; Robinson, 1986; Rodman, 1977; Strier, 1991; Terborgh, 1983). Second, studies have noted the proportion of feeding bouts in which subjects exploit different species or types of foods (Defler and Defler, 1996; Fossey and Harcourt, 1977; O'Brien and Kinnaird, 1997; Oates, 1977; de Ruiter, 1986; Sussman, 1977; Waser, 1977).

While these methods provide an initial assessment of diet, they may not accurately indicate the quantity of different foods ingested (Clutton-Brock, 1977; Durland and Gaulin, 1987; Hladik, 1977). Those foods that are consumed rapidly may be underestimated; those that require more time to gather and process may be overestimated. For example, five minutes of gathering and feeding on ripe fruits will likely result in greater food intake than will five minutes of foraging for insects. Even different animals feeding in the same tree may have different rates of harvest and therefore intake. Such disparities are rarely accounted for in simple measurements of time spent feeding. Only under the most auspicious viewing conditions can measures of gross food intake me made (Gaulin and Gaulin, 1982; Hladik, 1977; Miller, 1996; Stacey, 1986; Watts, 1988). Without them, however, inter- and intraspecies comparisons are likely to be flawed (Baron, 1992).

The work presented here provides a case study of three methods of dietary assessment. Based upon a two-year investigation of a population of wedge-capped capuchins (*Cebus olivaceus*), diet was estimated by three different methods. (1) Daily activity budgets were used to indicate the proportion of time devoted to foraging for plant versus animal matter. (2) Feeding records showed the frequency with which subjects fed on plant versus animal matter. (3) Estimates were made of the actual volume of plant versus animal food consumed. A comparison of results will demonstrate the disparate pictures of diet that these three measures provide.

Methods

The Subjects

Wedge-capped capuchin monkeys (*Cebus olivaceus*) are small-bodied platyrrhines native to Venezuela, the Guyanas, Surinam, and northern Brazil (Wolfheim, 1983). They are opportunistic foragers, relying heavily upon ripe fruit and invertebrate matter, but also occasionally exploiting young leaves, seeds, and vertebrate prey (Robinson and Janson, 1987; see also Miller, in press). Group size is variable, with assemblages as small as eight and as large as 50 (Robinson, 1988a, 1988b; Miller, 1991, 1992). The species is best known from studies by John Robinson and his colleagues at Hato Masaguaral (Fragaszy, 1990; O'Brien, 1991; Robinson, 1981, 1984, 1986, 1988a, 1988b; de Ruiter, 1986; Srikosamatara, 1987; Valderrama *et al.*, 1990). More recent research at Hato Piñero, which lies some 60 km northwest of Hato Masaguaral, has supplemented our understanding of this species' socioecology (Miller, 1996, 1998, in press, and in review, a and b). The subjects for this investigation were two groups of capuchins, one large (LG = approximately 36 animals) and one small (SG = approximately 16). Both were fully habituated to observer presence within three meters. (For greater detail on this species or these groups, see Miller, 1992, 1996.)

The Study Site

The research was carried out at Hato Piñero, a nature reserve in the *llanos* of Venezuela, owned and operated by the Fundación Branger. Because the capuchins have experienced no molestation (e.g., through hunting or habitat destruction) for nearly 50 years, they were easily habituated. The vegetation is a mosaic of open grassland and semideciduous dry tropical forest. The climate is seasonal, with approximately 200 mm per month of rainfall during the wet season (May through October) and 30 mm per month during the dry season (November through April). Many tree species drop their leaves in the dry season, and so viewing during these months is excellent. In the wet season, however, the foliage is dense, making accurate observation more difficult. The study site is a 270 ha plot in the middle of several thousand hectares of contiguous forest. There are approximately 45 km of trails forming a grid of 125 x 125 m sections. (For greater detail on the study site, see Miller, in press.)

Data Collection and Analysis

Preliminary observations were made from April 1989 to May 1990. During this time, focal groups were chosen, and subjects were habituated and identified. Intensive data collection took place from June 1990 to June 1991. The

study groups were followed on an opportunistic basis, with efforts made to gather data during all months of the year and all hours of the day. Data were collected in focal animal samples of 30 s duration. All samples in which viewing was obscured or interrupted were discarded. No subject was observed more than once per half-hour. Observations focused on adult females, but efforts were made to sample all age-sex classes. The emphasis on the activities of adult females might introduce a bias to accurate measures of mean food intake per individual. However, the same data set was used for all three methods of dietary assessment, and thus the analysis presented here should be largely unaffected by this inequity. This study is based upon 485 hours of observation, 265 with the large group and 220 with the small group. In this time, 3841 behavior samples were obtained.

Among the data collected with each focal animal sample, the following are pertinent to this analysis: (1) the time, (2) the subject's activity, operationally defined as *feeding* (gathering and ingesting plant matter), *foraging* (actively searching for and ingesting animal matter), *moving* (moving from one place to another without also foraging or engaging in some other activity), *moving and foraging* (moving along while also searching for prey), *resting* (e.g., sitting, lying down, sleeping), or *social behavior* (e.g., playing, fighting); (3) the type of any food item ingested (plant or animal, and species if known); and (4) the number of items ingested (e.g., of individual fruits, or bites of a very large fruit). (For greater detail on data collection and analysis, see Miller, 1996.) These data were used to assess diet in the following ways.

Daily activity budgets: The proportion of time subjects devoted to feeding on plant matter was indicated by the percentage of time spent *feeding*. Ingestion of animal matter occurred during both *foraging* and *moving and foraging* time, therefore these categories were combined. Daily activity budgets were assessed as mean values, averaging across groups, subjects, days and times, with analysis controlling for the influence of diurnal activity patterns. (For greater detail, see Miller, 1996.)

Frequency of use: Each focal animal sample included an assessment of the food type consumed, which allowed estimation of the frequency with which subjects exploited each different species (Miller, in press). For the purposes of this analysis, all data points (for all subjects over all days and times of observation) were grouped and simply stratified by plant versus animal matter.

Volume ingested: Data collection included precise evaluation of the quantity of food items each subject ingested during each sample (in numbers of fruits or numbers of bites). From there, simple estimates of volume ingested per sample were made. These data were then used to extrapolate the mean volume (averaged across subjects, days and times of observation) of plant and animal food eaten per day.

The volume of each plant food item was estimated from its dimensions, minus any large seeds which were known to be discarded. Animal foods were more difficult to identify and quantify. Their volumes were estimated based upon the category into which they fell: Small prey items were those which were eaten in a single bite, such as termites licked off of a tree limb or small grubs picked out of a twig; medium items were those which were eaten in one to two bites, such as spiders or flying arthropods; large items, such as cicadas or grasshoppers, could usually be identified and their volumes were estimated accordingly. (For greater detail, see Miller, 1996 and in review, a.)

Results

Data analysis required considerable averaging (e.g., across subjects, group sizes, seasons) and therefore the following values must be considered as approximations. Nevertheless, it is clear that the three means of assessing dietary composition yielded three significantly different results.

Daily activity budgets: Based upon the proportion of time spent *feeding*, the subjects devoted approximately 17% of their daily activity budgets to collecting and ingesting plant matter. The time engaged in *foraging* was 19%, and *moving and foraging* was 22%, for a total of 41% of the day spent seeking, capturing and consuming prey items. Another way to look at these data is that, of total time spent feeding, 29% was devoted to plant matter and 71% to animal matter. For further reference, mean time spent *moving* was approximately 15% of the day; *resting*, 25%; and *social behavior*, 2%.

Frequency of use: Of the samples accumulated, 1312 recorded the subject feeding, 673 (51%) on plant food and 639 (49%) on animal matter.

Volume ingested: The subjects consumed, on average, approximately 2000 cc of food per day. Of this, roughly 1300 cc (65%) were plant matter and 700 cc (35%) were animal matter.

Discussion and Conclusions

This analysis clearly demonstrates that different methods of dietary evaluation can yield dramatically different results. The percentage of feeding time exploiting different food types suggests that these subjects consumed 29% plant matter and 71% animal matter. However, as a quantitative measure of food intake, this method is weak. *Feeding* represents only the time spent actually harvesting and ingesting plant food, but does not indicate the time spent moving from tree to tree. Conversely, *moving and foraging* includes not only harvesting and ingesting animal foods, but also travel time between "patches". Thus, this method tends to underestimate the intake of plant foods and overestimate animal foods. In order to make the measures more congruent, the time spent acquiring plant foods might also include time traveling between patches. In this case, *moving* might be added to *feeding*, for a total of 32% of the daily activity budget, or 44% of total feeding time (leaving 56% of feeding time to animal matter). However,

moving surely serves purposes other than food location, such as traveling to water sources or sleeping sites, and thus, this simply introduces further error.

Errors such as these can be ameliorated by taking data in very long focal animal samples (Altmann, 1974) or in delineating behavioral categories that allow fine discrimination between activities (Chivers *et al.*, 1984). However, the nature of capuchin foraging, in which various activities are carried out simultaneously, makes it difficult to discern accurately the proportion of the daily activity budget devoted to acquiring different foods. This is probably true for most primate species. Therefore, estimates of food intake via foraging time, while straightforward in principle, are complicated in practice, and are likely to lead to inaccurate measures of intake.

According to the proportion of feeding bouts focused on the major food types, these subjects consumed 51% plant matter and 49% animal matter. However, this method also provides dubious measures of dietary intake, particularly if the data are collected in long samples. Because of different rates of locating and processing food items, one observation of prey consumption represents lower food intake than does one observation of fruit consumption. A five-minute focal animal sample in which a single grasshopper was consumed would count as one use of animal matter; a five-minute sample in which 25 fruits were eaten would count as one use of plant material. The two samples would, however, clearly represent different amounts of food ingested. Thus, this method also tends to overestimate the importance of invertebrate matter and underestimate the proportion of plant matter in the diet. This bias can be ameliorated by collecting data in very short scans (Altmann, 1974).

A volumetric assessment surely provides a more accurate measure of dietary intake, and also serves to support the evaluations of the other two methods. By volume, these subjects consumed approximately 65% plant matter, which is higher than the 29% indicated by time and 51% by frequency of use. Animal matter represented 35% of intake, lower than the 71% by time and 49% by frequency of use.

Volumetric estimates , such as those made here, may also be subject to bias if viewing conditions vary for different activities, for example, if subjects feeding on fruit are easy to see but obscured from view while foraging for prey items (Harcourt and Stewart, 1984). Thus, viewing conditions may play a large role in determining the optimum length of focal animal samples and whether or not accurate estimates of intake can be made.

Volumetric assessments are especially valuable because they facilitate precise analyses of nutrient intake. Various studies have collected samples of foods exploited by their subjects and, by combining accurate data on feeding with chemical analyses of each food's nutritional composition, have been able to produce remarkably detailed profiles of dietary intake (see, for example, Altmann *et al.*, 1987; Barton *et al.*, 1993; Rogers *et al.*, 1990). This type of analysis is necessary for determining, for example, the role of plant phytochemistry in food choices of different species or individuals (Davies *et al.*, 1988; Mowry *et al.*, 1996). Accurate measures of diet are essential for testing the hypothetical relationships between food intake and social variables such as group size, age and sex class, and social ranking.

In conclusion, quantitative measures of food intake, such as volume or fresh weight, are extremely important. However, a complete assessment of feeding activity is perhaps best obtained by employing several different methods of data collection and analysis simultaneously. Each method offers insight into a different aspect of the subjects' feeding activities. For example, a comparative approach may reveal the relative importance of different food types to the subjects' well-being. As a case in point, the volumetric data alone from this study might indicate that protein (in the form of animal matter) is of lesser importance than is carbohydrate (in the form of plant matter), given that the food volumes were 35% and 65% respectively. However, the majority of feeding time is devoted to foraging for prey. This suggests that protein is an essential component of the diet, so important, in fact, that it receives significant time and energy expenditure. This relationship comes to light only through a comparison of different measures of feeding and diet.

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Cambios en la Actividad de Juego en Infantes y Jóvenes de Mono Aullador (*Alouatta seniculus*)

Abstract: Play behavior is an important factor for the normal development of young animals in different species. Some authors argue that the frequency and duration of play depend only on chance. I observed the play behavior of the young members of a howler monkey troop for four months in the Tinigua National Park (Colombia). The results suggest that among the individuals of the same troop there is a pattern in which solitary play always appears before social play. There were no significant differences in the duration of play among individuals of the same age.

Introducción

Juego es cualquier actividad improvisada y compuesta por variaciones de acciones motoras y de comunicación, las cuales se presentan en contextos diferentes a donde estas acciones específicas aumentarían el éxito reproductivo del individuo (Fagen, 1993). El juego así definido, es considerado como una actividad de especial importancia para el desarrollo de las relaciones sociales y de las capacidades motrices y de comunicación de ciertas especies.

En primates y carnívoros el juego es parte importante del proceso de aprendizaje y socialización durante el periodo sensible, que tiene lugar en las edades tempranas de cada individuo (Sackett y Ruppenthal, 1973; Mendl, 1988). Pese a su importancia, parece no existir un patrón rígido en la duración y frecuencia de la actividad de juego dentro de cada una de las especies que lo practican. Según Lee (1983) tanto el tiempo como la frecuencia del juego dependen únicamente de las oportunidades que se le presenten a cada individuo para practicarlo antes de llegar a la edad adulta.

Este trabajo sugiere la existencia de un patrón general en la duración media de las sesiones de juego social y solitario de los infantes (*Alouatta seniculus*) de una misma tropa y en la aparición secuencial de dos condiciones generales