

## FACTORS INFLUENCING BIRD FORAGING PREFERENCES AMONG CONSPECIFIC FRUIT TREES<sup>1</sup>

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**Abstract.** The rates at which birds visit fruiting individuals of *Allophylus edulis* (Sapindaceae) differ substantially among trees. Such avian feeding preferences are well-known, but usually involve fruits and trees of different species. Factors controlling avian preferences for particular trees in a population of conspecifics are generally undocumented. To address this issue, I attempted to correlate rates at which individuals birds and species fed in trees of *Allophylus* with 27 fruit or plant characteristics. Birds that swallow fruits whole were considered separately from those that feed in other ways. Plant characters were selected on the basis of their potential influence on feeding efficiency or predation risk, assuming that birds would select feeding trees so as to maximize the net rate of energy or nutrient intake and to minimize predation. Correlations were found between feeding visits by some groups of birds and percent water in the pulp, milligrams of mineral ash in the pulp, and crop size. No character was correlated with feeding visits by all groups of birds in both years of the study. The correlations with water and mineral ash are unexplained and may be artifacts. The correlation with crop size may represent a tactic to minimize predation.

**Key words:** *Allophylus edulis*; foraging; frugivorous birds; fruit; fruit crop; patch preference; predation.

### INTRODUCTION

*Allophylus edulis* (St. Hil.) Radlk., or Cocú, is found in subtropical and temperate forests in Paraguay, Brazil, Uruguay, Argentina, and Bolivia (Lopez et al. 1987). In Paraguay, the fruits of this small sapindaceous tree are eaten by at least 26 species of birds (Appendix), but these birds do not visit trees with equal frequency. Observations revealed that both rates of bird visitation and numbers of species visiting differed substantially among fruiting individuals. That trees vary in their attractiveness is not surprising, since birds routinely show preferences for different types of fruits (Turček 1963; Herrera 1981; van der Pijl 1982; Moermond and Denslow 1983, 1985; Levey 1987a, 1987b; Moermond et al. 1987). It is more surprising that the birds expressed preferences for individual plants among a population of synchronously fruiting conspecifics, a less well-known behavior (but see Howe and De Steven 1979; Howe and Vande Kerckhove 1979, 1980; Manasse and Howe 1983). In addition, the tree preferences exhibited by the individuals and species feeding on *Allophylus*, were fairly uniform, which was not expected given

en the taxonomic, morphological, and behavioral diversity of species involved (Foster 1987).

To address these issues, I documented the rates at which birds and bird species fed in different trees of *A. edulis* and then determined the degree to which feeding visits were correlated with 27 fruit or plant characteristics. Characters were selected on the basis of their potential influence on foraging efficiency or predation risk. I hypothesized that birds would select feeding trees so as to maximize net rate of energy (or nutrient) intake (Stephens and Krebs 1986) within the confines imposed by the need to avoid predators (e.g., Milinski and Heller 1978, Heinrich 1979, Howe 1979, Sih 1980). I considered birds that swallow fruits whole and disperse seeds separately from opportunists that remove the fleshy fruit pulp but leave the seed in or under the tree. Because birds in these groups feed in different ways, plant characteristics should differ in their importance to each group.

Among the plant characteristics considered were several measures of fruit and seed size and weight. Such characteristics influence the size of the reward available to a disperser, the likelihood that a given fruit can be manipulated in the bill or swallowed (Wheelwright 1985, Foster 1987), the number of fruits that can be swallowed in a single feeding bout, and feeding rate (Foster 1987).

<sup>1</sup> Received 23 August 1989. Final acceptance 18 June 1990.

I also considered: (1) energy and nutrient content of the pulp, which determine the reward per unit pulp ingested, and, thus, the numbers of fruits required to meet daily energy and nutrient needs; (2) degree of infestation with seed parasites, because parasites can affect nutrients available to birds and the palatability of fruit (Manzur and Courtney 1984); and (2) crop size, which may influence the number of visitors to given fruit trees through its effect on immediate fruit availability and predation potential (Howe and De Steven 1979; Howe and Vande Kerckhove 1979, 1981; Manasse and Howe 1983; Martin 1985; Davidar and Morton 1986; Murray 1987).

### STUDY AREA AND SPECIES

The study was conducted in the forest adjacent to El Tirol (ca. 55°47'W, 27°11'S, elevation 170–260 m), Dpto. Itapua, Paraguay, from 1978 to 1983. Data presented here are primarily from 1978 and 1980. The area is described in Smith and Foster (1984).

*Allophylus edulis* occurs in moderate densities (dbh  $\geq$  5 cm, ca. 15/ha) in undisturbed forest at Tirol, but is abundant (ca. 213/ha) in early to medium-aged stands of second growth (Foster, unpubl. data). The species also grows well in the open and is often spared when land is cleared because of the popularity of its fruit among humans.

Trees of *A. edulis* flower in August at Tirol, with ripe fruit appearing as early as mid-September. Fruiting within the population is highly synchronous, although trees with larger crops retain fruit for longer periods. Fruit is available for approximately 5 weeks, with a large peak during weeks 2 through 4. Fruits are bright, shiny red drupes borne on axillary racemes. The fruits are roughly cylindrical, with diameter generally exceeding height. Each fruit contains a single, somewhat laterally flattened, drop-shaped seed.

### METHODS

#### BIRD OBSERVATIONS

Rates of bird visitation were recorded at six trees in 1978 and eight in 1980 (six the same in both years). Seven of the trees were located in a 26 m  $\times$  110 m area, and the eighth tree (no. 11) ca. 750 m away. In 1978 and 1980 12 hr of tree observation for each tree were distributed approximately evenly between 06:00 and 18:00. In 1978 only, each tree was observed for an addi-

tional 8 hr between 06:00 and 10:00 and 15:00 and 18:00, for a total of 20 hr. Observations were made on clear warm days, using 7  $\times$  35 or 8  $\times$  40 binoculars. Observers recorded the species and, if possible, the length of the visit. Birds were included in the analyses only if they fed.

Bird species differ in the ways they handle fruits (described in detail in Foster 1987). Some pluck and swallow whole fruits and carry them away from the tree internally (Type I of Foster 1987; hereafter, swallow feeders or swallowers). Birds of other species remove varying amounts of pulp from a fruit and then drop the seed beneath the tree. Some roll the fruit in the bill, mashing the pulp or cutting it from the seed (Type II of Foster 1987; hereafter, cutters or cut feeders). Other species take bites from fruits that remain attached to the tree or push them against a branch with the bill while removing small pieces of pulp (Type III of Foster 1987; hereafter, biters or bite feeders). Data for cut and bite feeders usually were analyzed separately from those for swallowers. Exceptions were analyses involving dimensions of whole fruits, in which data from birds that must grasp the fruit in the bill in order to feed (swallow and cut feeders) were combined and analyzed separately from those (bite feeders) that do not.

#### FRUIT CHARACTERISTICS

Small branches with fruits were removed from north-, south-, east-, and west-facing sectors of the tree in the height categories of 0–5 m, 5–10 m, and  $>$  10 m, where applicable, using pruners on long poles. Fruits were picked, mixed, and then a random subsample ( $n$ 's in Tables 1, 2) removed for measurement. Fruit length (through the point of attachment) and greatest diameter were measured with calipers to the nearest 0.1 mm. Fruit size was estimated using the formula for the volume of a cylinder ( $V = \pi r^2 l$ ). The seed was removed from each fruit, cleaned, and its greatest length and diameter measured. For each tree observed in 1980 only, 10–30 fruits selected at random and their cleaned seeds were weighed in lots of 10. Average fruit, pulp, and seed weights were calculated for each tree. In 1978, fruits and their cleaned seeds were weighed individually; pulp weight was obtained by subtraction. Seed loads were calculated by dividing wet seed mass by wet fruit mass.

In 1980, a sample of fruit pulp (exocarp + mesocarp) was obtained from each tree for nu-

TABLE 1. Feeding visits by individual birds and species to selected trees of *Allophylus edulis* at El Tirol, and selected characteristics of those trees and their fruits in 1978.

Tree	Total bird feeding visits (x/hr)				Fruit and tree characters							
	Swallowers		Cutters and biters		Fruit size (x)			Seed size (x)		Parasitized seeds		Estimated number of fruits
	Individuals	Species	Individuals	Species	n	Volume <sup>1</sup>	Diameter <sup>2</sup>	n	Diameter <sup>2</sup>	n	Proportion	
7	24 (1.20)	6	6 (0.30)	3	126	480	8.64	126	4.8	158	0.07	30,000
4	13 (0.65)	4	7 (0.35)	2	50	435	8.06	50	4.5	50	0.54	7,000
8	10 (0.50)	4	2 (0.10)	1	126	414	8.19	126	4.9	183	0.10	20,000
11	1 (0.05)	1	16 (0.80)	2	11	278	6.72	25	4.3	25	0.60	10,000
12	1 (0.05)	1	0 (0.00)	0	18	343	7.83	63	4.6	43	0.49	1,000
3	0 (0.00)	0	0 (0.00)	0	100	531	8.91	100	5.7	100	0.59	2,000

<sup>1</sup> Volume = mm<sup>3</sup>.<sup>2</sup> Diameter = mm.

tritional analyses. Pulp was removed with forceps, weighed, and air-dried. Upon return to the laboratory, samples were stored frozen until analyzed, when they were dried in an H<sub>2</sub>SO<sub>4</sub> vacuum desiccator at room temperature, weighed, and homogenized. Subsamples were analyzed for ash, lipid, protein, and trichloroacetic acid (TCA)-soluble carbohydrate contents according to methods outlined in Foster (1977 and references therein). Two to 10 subsamples were subjected to each analysis, and the results averaged. Metabolizable energy content was calculated using the conversion factors of 39.75 kJ/g lipid (= 9.5 kcal), 17.15 kJ/g carbohydrate (= 4.1 kcal) (Paine 1971), and 18.0 kJ/g protein (= 4.3 kcal) (Ricklefs 1974).

#### TREE CHARACTERISTICS

I examined seeds of a randomly selected sample of fruits from each tree and scored them as parasitized (curculionid, lepidoptera, or other insect larvae present; seed remains with insect frass), rotten, or undeveloped. An insect larva generally consumes the entire seed; if a larva dies, the remaining seed rots. Therefore, for the purpose of these analyses, rotten seeds were assumed to have been destroyed by parasites.

Crop size was estimated by counting the numbers of fruits on small branches, then the numbers of small branches per large branch, and finally the number of large branches. Estimates for trees with small crops undoubtedly are more accurate than those for trees with large crops. Nevertheless, these estimates should reflect relative positions of trees when ordered by crop size.

#### ANALYSES

Data were analyzed with Pearson's product moment correlation where specified. Correlations of

rates of bird visits and total numbers of species visiting with fruit and tree characteristics were determined using Spearman's rank correlation analyses, with corrections for ties (Siegel 1956). Plant characters considered included mean, modal, and maximum values of fruit volume, fruit diameter, and seed diameter. Because of the marked similarity of the results, I provide only mean values in the tables. I also analyzed four characters associated with fruit mass, 12 measures of fruit nutrient and energy content, infestation with seed parasites, and crop size. Data from 1978 and 1980 were analyzed separately.

#### PREDICTIONS AND RESULTS

##### BIRD VISITS

In 1978 (Table 1) and 1980 (Table 2), numbers of individual visits by swallow feeders and by cut and bite feeders differed significantly among trees (swallowers, 1978:  $\chi^2 = 54.69$ ,  $P < 0.001$ ,  $df = 5$ ; 1980:  $\chi^2 = 254.72$ ,  $P < 0.001$ ,  $df = 7$ ; cutters and biters, 1978:  $\chi^2 = 35.75$ ,  $P < 0.001$ ,  $df = 5$ ; 1980:  $\chi^2 = 511.09$ ,  $P < 0.001$ ,  $df = 7$ ). Between years, the total number and rate of bird visits (mean number of bird visits per hour) to the trees observed in 1980 was much greater than in 1978 (Tables 1, 2). Visits by individuals (80 vs. 259), for example, increased by 224%. And, although the rankings of the six trees studied in both years according to the rate of visits by swallowers were similar, they were not significantly correlated ( $r_s = 0.812$ ,  $P > 0.05$ ). Between-year ranks of trees according to visits by cutters and biters also were not significantly correlated ( $r_s = 0.471$ ,  $P > 0.05$ ). Within-year visits by swallow feeders and by cut and bite feeders were significantly correlated in 1980 ( $r_s = 0.936$ ,  $P < 0.01$ ), but not in 1978 ( $r_s = 0.456$ ,  $P < 0.05$ ).

TABLE 2. Feeding visits by individual birds and species to selected trees of *Allophylus edulis* at El Tirol, and selected characteristics of those trees and their fruits in 1980.

Tree	Total bird feeding visits (x/hr)				n	Fruit characters				
	Swallowers		Cutters/biters			Fruit volume <sup>1</sup> (x)	Fruit diameter <sup>2</sup> (x)	Seed diameter <sup>2</sup> (x)	Proportion of para- sitized seeds	Estimated number of fruits
	Individuals	Species	Individuals	Species						
8	55 (4.60)	5	59 (4.90)	7	100	453	8.47	4.7	0.55	25,000
7	14 (1.17)	4	110 (9.17)	5	100	470	8.53	4.6	0.07	25,000
4	4 (0.33)	3	8 (0.75)	5	50	388	7.75	4.3	0.20	7,000
11	2 (0.17)	1	4 (0.33)	2	25	331	7.21	3.9	0.80	4,000
2	1 (0.08)	1	0 (0.00)	0	125	404	7.90	4.4	0.10	10,000
10	1 (0.08)	1	0 (0.00)	0	50	332	7.69	4.3	0.36	1,200
12	1 (0.08)	1	0 (0.00)	0	62	440	8.58	4.3	0.44	750
3	0 (0.00)	0	0 (0.00)	0	50	380	8.01	5.2	0.52	500

<sup>1</sup> Volume = mm<sup>3</sup>.<sup>2</sup> Diameter = mm.

Of the 26 species observed feeding on *A. edulis* at Tirol, three were recorded only in 1978, and six were recorded only in 1980. Only 21 of the species were recorded during the scheduled fruit watches, 14 (nine swallows and five cutters or biters) in 1978, and 18 (8 and 10) in 1980, an increase of 29%.

In contrast to the rate of visits by individuals, the rankings of the six trees studied in both years according to the numbers of swallower species visiting were significantly correlated ( $r_s = 0.896$ ,  $P < 0.05$ ). Between-year ranks of trees according to visits by cut and bite species showed no significant correlation ( $r_s = 0.591$ ,  $P > 0.05$ ). Within-year visits by swallower species and cut or bite species were significantly correlated in 1980 ( $r_s = 0.891$ ,  $P < 0.05$ ), but not in 1978 ( $r_s = 0.773$ ,  $P > 0.05$ ).

#### FRUIT AND SEED SIZE AND MASS

Because fruit and seed size and mass influence the ability of a bird to grasp and manipulate a given fruit in the bill, or to swallow it whole (Wheelwright 1985, Foster 1987), one might predict a negative correlation between the rate of visits by birds that grasp and manipulate the whole fruit with the bill and fruit diameter. In 1978, mean, modal, and maximum fruit diameters for the tree with the largest fruits exceeded these values for the tree with the smallest fruits by 33%, 28%, and 44%, respectively (Table 1). In 1980, greatest values exceeded smallest by 19%, 19%, and 12% (Table 2). Nevertheless, neither numbers of species visiting nor rate of bird feeding visits for swallows alone or for cutters

and biters combined was significantly correlated with any of these measures in either year (all  $P > 0.05$ ).

On the other hand, because swallows may compress the pulp on a fruit before swallowing it, maximum diameter of the seed, which influences swallowing, could be a controlling dimension. Mean, modal, and maximum seed diameters from trees with the largest seeds exceeded those from trees with the smallest seeds by 33%, 16%, and 39%, respectively, in 1978, and by 33%, 39%, and 33%, respectively, in 1980 (Tables 1, 2). Again, however, there were no significant rank correlations between any of these measures and numbers of species visiting nor rate of bird feeding visits.

One might also predict that swallows should prefer fruits with the smallest seed load, which would maximize the absolute amount of digestible material consumed per feeding action. On the other hand, such a preference could reflect a negative correlation with seed size (Howe and Vande Kerckhove 1980, 1981). In contrast, one would expect cutters and especially biters to feed on the largest fruits available. This practice should allow them to take larger and fewer bites, and thus to feed more efficiently.

Volumes of individual fruits varied considerably between years both among trees, and within trees (Tables 1, 2). In 1978, mean fruit sizes for the tree with the largest fruits were 1.9 times larger than those of the tree with the smallest; maximum fruit size was 2.2 times as large. In 1980, the greatest mean and maximum values exceeded the smallest by more than 42% and

TABLE 3. Average wet masses of ripe fruits and fruit parts for selected trees of *Allophylus edulis* at Tirol in 1980.

Tree	n	Fruit (g)	Pulp (g)	Seed (g)	Seed load
8	20	0.325	0.265	0.060	0.185
7	20	0.350	0.294	0.056	0.160
4	10	0.304	0.249	0.056	0.184
11	10	0.261	0.226	0.036	0.138
2	30	0.309	0.249	0.060	0.194
10	10	0.272	0.226	0.046	0.169
12	20	0.357	0.307	0.050	0.140
3	10	0.365	0.295	0.070	0.192

31%, respectively. Nevertheless, neither numbers of species visiting nor rate of bird feeding visits for swallower individuals alone, swallowers and cutters combined, or for cutter individuals was significantly correlated with any measure of fruit volume.

Seed loads also varied substantially (greatest value 51% larger than smallest; Table 3), but, along with mean fruit mass, mean pulp mass, and mean seed mass (greatest values ca. 40%, 36%, and 94% larger, respectively, than smallest values; Table 3), showed no significant correlation with the number of species nor rates of individual visits by swallow or cut and bite feeders.

#### NUTRIENT CONTENTS

Energy and nutrient contents of the pulp determine the reward received and, thus, the number of fruits required to meet daily energy and nutrient needs. One would expect birds to eat fruits providing the greatest net intake of energy (or nutrient). Assuming equivalent handling times, this should be manifest as a preference for fruits with the greatest overall energy content (or amount of lipid, which greatly enhances caloric content, or amount of carbohydrate, which is a source of quick energy), or with the greatest amount of a particular nutrient such as protein, which generally is limited in carbohydrate-rich fruits of this type (McKey 1975). If so, then visits by swallowers should be correlated with absolute quantities of any of these substances per fruit, and visits by cut or bite feeders should be correlated with percent composition. Birds swallowing fruits whole, which tend to be "time minimizers" (Schoener 1971, Foster 1987), should feed in trees offering the greatest average reward per fruit. Birds removing pulp in pieces feed relatively slowly (Foster 1987) and should be "en-

ergy maximizers" (Schoener 1971), favoring fruits with the greatest reward per gram of tissue.

Rates of bird feeding visits and total species visits showed no significant correlations (all  $P > 0.05$ ) with percent protein, lipid, or TCA-soluble carbohydrate in the pulp, nor with milligrams of these substances per pulp per fruit, even though differences among trees were sometimes quite large (Tables 4, 5). Likewise, there were no significant correlations with kJ/pulp/fruit nor kJ/ash-free gram dry mass of pulp. Quantities of two other nutrients did show some significant correlations. The rate of feeding visits by swallower individuals was positively correlated with percent water in the pulp ( $r_s = 0.659$ ,  $P < 0.05$ ), accounting for 43% of the variation observed among trees. Rate of visits by cut and bite birds, and species totals did not show this correlation. Also, there were no correlations between visits by any bird group and milligrams water/pulp/fruit.

Rates of feeding visits by swallowers ( $r_s = -0.708$ ,  $P < 0.05$ ) and cut or bite feeders ( $r_s = -0.672$ ,  $P < 0.05$ ), and visits of cut or bite species ( $r_s = -0.677$ ,  $P < 0.05$ ) were significantly negatively correlated with milligrams of mineral ash/pulp/fruit, explaining 50%, 45%, and 46%, respectively, of the variation observed among the trees for visits by each group. In contrast, feeding visits by neither group of species nor individuals were significantly correlated with percent composition of mineral ash (all  $P > 0.05$ ).

#### SEED PARASITES

The presence of parasites in seeds can affect nutrients available to the birds as well as palatability of the fruit (Manzur and Courtney 1984). Testae of seeds infested with weevil larvae are relatively soft and crack under moderate pressure from a fingernail, in contrast to the firm testa of an intact seed. Larvae in such seeds could be susceptible to digestion by birds swallowing the fruits whole. If so, one would predict that these birds should feed preferentially in trees with high infestation rates, to maximize protein or caloric intake. All of the swallower species consume some insects as part of their regular diet (Foster 1987 and references therein). The alternative, that these birds should avoid parasitized seeds, might be expected if these larvae contain noxious substances, but I have no data that bear on this.

Parasite infestation showed extreme variation among trees, ranging from 0 to 80% among 14

TABLE 4. Nutritional composition of pulp of ripe fruits from selected trees of *Allophylus edulis* at Tirol in 1980.

Tree	Water % <sup>1</sup>	Mineral ash % <sup>2</sup>	Protein % <sup>2</sup>	Lipid % <sup>2</sup>	TCA-soluble carbohydrate % <sup>2</sup>	Metabolic kJ/ash-free g dry mass
8	78.4	1.42 (3) <sup>3</sup>	6.72 (2)	0.73 (2)	85.7 (5)	16.42
7	80.6	1.76 (3)	3.66 (3)	0.13 (2)	82.8 (7)	15.18
4	74.4	1.64 (2)	6.35 (2)	0.35 (2)	81.1 (10)	15.45
11	89.9	1.11 (3)	5.63 (3)	0.50 (2)	76.8 (4)	14.53
2	78.3	2.25 (3)	4.94 (2)	0.58 (2)	82.3 (6)	15.55
10	73.8	1.73 (2)	8.24 (2)	0.18 (2)	79.4 (7)	15.43
12	75.1	3.19 (2)	4.37 (2)	0.19 (2)	86.0 (4)	16.12
3	70.7	1.56 (2)	5.42 (2)	0.36 (2)	78.2 (6)	14.75

<sup>1</sup> Percent wet mass.<sup>2</sup> Percent dry mass.<sup>3</sup> Numbers in parentheses indicate numbers of subsamples analyzed.

trees followed over a period of 6 years (Tables 1, 2; Foster, unpubl. data). Despite this variability, no significant correlations of rates of bird feeding visits with proportions of seed parasitized were noted for swallows (or for cut and bite feeders). However, data from feeding experiments with birds in cages (Foster, unpubl. data) indicate that testae of parasitized seed that are swallowed and regurgitated or passed through the avian gut are unaffected, and the contained insect larvae, seemingly unharmed.

#### FRUIT CROP

In this study, trees were generally equivalent to a foraging patch. Patch richness is a function of crop size, as is patch detectability given the bright, conspicuous color of the fruits against the green foliage. Thus, an appropriate hypothesis is that bird visits are positively correlated with crop size. On the other hand, predation risk can also be a function of crop size leading to alternative hypotheses about how this character may influence tree choice in frugivores. Predators (particularly

bird hawks such as *Micrastur*; Howe and Vande Kerckhove 1979, 1981) may use conspicuous fruit crops to locate prey concentrations. Thus, an appropriate alternative hypothesis is that small birds or birds with long feeding bouts should avoid trees with large crops or shorten bout length.

Crop sizes varied considerably among trees and between years (Tables 1, 2). Nevertheless, ranks of the six trees studied in both 1978 and 1980 were significantly correlated ( $r_s = 0.912$ ,  $P < 0.05$ ), as were tree ranks of a larger sample of trees over 6 years (Foster, unpubl. data). Surprisingly then, rank correlations of frequencies of bird visits with this character differed between years. For 1980, rates of feeding visits were significantly positively correlated with crop size, accounting for more than 71% of the variation observed in visits by swallows ( $r_s = 0.847$ ,  $P < 0.01$ ), and more than 60% of the variation in visits by cut and bite birds ( $r_s = 0.778$ ,  $P < 0.05$ ). Similarly, the significant positive correlations of crop size with swallower species visiting ( $r_s = 0.868$ ,  $P < 0.01$ ), and with cut and bite species

TABLE 5. Average nutritional content of pulp of single ripe fruits from selected trees of *Allophylus edulis* at Tirol in 1980.

Tree	Water (mg)	Mineral ash (mg)	Protein (mg)	Lipid (mg)	TCA-soluble carbohydrate (mg)	Metabolic kJ/pulp/fruit
8	208	0.81	3.84	0.42	49.1	0.93
7	237	1.01	2.09	0.07	47.3	0.85
4	185	1.05	4.05	0.22	51.8	0.97
11	203	0.25	1.28	0.11	17.5	0.33
2	195	1.21	2.67	0.31	44.4	0.82
10	167	1.02	4.88	0.11	47.0	0.90
12	231	2.43	3.33	0.15	65.6	1.19
3	209	1.35	4.68	0.31	67.5	1.26

visiting ( $r_s = 0.752$ ,  $P < 0.05$ ) explained more than 75% and 56% of the variation observed in bird visits. In contrast, no significant correlations were found for 1978.

In both years, a few bird species accounted for most of the visits. Together, two species made 65% of the visits by swallows in 1978, and 73% of these visits in 1980 (*Thraupis sayaca*, 38% and 51%; *Turdus rufiventris*, 27% and 22%). Four cut or bite species made 87% of the visits by this group in 1978 (*Trichothraupis melanops*, 30%, *Tangara seledon*, 23%; *Coryphospingus cucullatus*, 17%; *Dacnis cayana*, 17%), and three species, 80% of the visits in 1980 (*Euphonia violacea*, 29%; *Chlorophonia cyanea*, 28%; *E. chlorotica*, 23%). The cut and bite feeders are especially small, averaging 22 g or less (Appendix), and these also were among the species with the longest feeding bouts (Foster 1987). Thus, birds, particularly the small, slow feeders, did not avoid trees with large crops. Nevertheless, these species and the two swallower species generally foraged in dense vegetation or on the underside of the crown (Foster 1987), presumably the safest areas of the tree.

All visits recorded for *T. sayaca* and *T. rufiventris* were to trees 4, 7, and 8, i.e., to trees with crops estimated at 7,000 fruits or more (Tables 1, 2). Visits by the cut and bite species listed in the previous paragraph were to trees 4, 7, and 11 in 1978, and in 1980, to trees 4, 7, and 8, again, all trees with crops estimated at 7,000 fruits or more. The trees with the next most numerous crops in 1978 and 1980 had ca. 2,000 and 4,000 fruits, respectively. It may be that a crop must exceed 4,000 fruits or, perhaps, up to 7,000 to attract these species. An anomalous observation during the study was the single bird visit recorded in 1980 for tree 2, which had an estimated crop of 10,000 fruits.

## DISCUSSION

### ENERGY AND NUTRIENTS

Feeding visits showed significant correlations with only two of the 12 nutrient and energy characteristics considered, milligrams ash/pulp/fruit and percent composition of water, which will be discussed below. The absence of correlations with the other 10 characters, which agrees with the findings of Manasse and Howe (1983), could indicate that birds are unable to distinguish differences in pulp composition (Sorensen 1981;

Howe 1983, 1986). This differs from the findings of Levey (1987b), however, who showed that six species of frugivorous birds distinguished among foods differing in sugar content by as little as 2%, and Duncan (1960a, 1960b) who suggested that birds were attracted to fleshy fruits by their taste. I had anticipated that birds should prefer fruits containing the greatest amounts of protein, lipids, or, perhaps, carbohydrates. If these hypotheses were correct, I also expected visits by swallows to correlate with milligrams of any of these substances per fruit, and visits by cutters and biters to correlate with percent composition. The lack of such correlations may indicate that the important components were not assayed, for example, specific minerals such as calcium or magnesium. Alternatively, differences in the substances assayed may not be important because the fruits are abundant, readily available, and accessible, because nutrient levels exceed some minimum threshold, or, in some instances, because differences among trees were insignificant (e.g., lipids, Tables 4, 5).

On the other hand, I can offer no explanation for the observed negative correlations of visitation rate with milligrams of mineral ash per fruit. The result could be an artifact reflecting a negative relationship between the quantity of minerals in each fruit and crop size, but the latter two quantities were not significantly correlated (Pearson's  $r_{1,2} = -0.313$ ,  $df = 6$ ,  $P > 0.05$ ). Although only milligrams of mineral ash showed any significant correlations with visit frequencies, nearly all the relationships between visit frequencies and milligrams of nutrients and available energy were negative.

Water was the only substance showing a significant correlation with feeding visits in terms of percent composition of pulp, and then only for swallows. Water content influences the texture of the fruit pulp and, thus, the ease with which it can be removed from the seed. Some minimum percentage of water may be required to achieve this textural threshold. Ease of removal could be more important for birds that swallow fruits whole and must maximize the return per unit of ballast carried; cutters and biters, in contrast, can move to the next fruit when removal of pulp from a seed becomes difficult. High water content might also be preferred if water dilutes contained secondary compounds, which may affect the extent to which birds can feed in trees of a given species (Izhaki and Safriel

1989). More likely, the significant correlation between tree ranks for crop size and percent composition of water ( $r_s = 0.659$ ,  $P < 0.05$ ), strongly suggests that the correlation of feeding visits with percent water is an artifact. Increased water content might also reflect increased ripeness, although I noted no differences among trees in degree of ripeness of fruits sampled for analysis.

#### SIZES AND MASSES OF FRUITS AND SEEDS

Sizes and masses of fruits and seeds are of potential importance in feeding because they influence available reward and handling costs (Martin 1985). The lack of any significant correlations between visits and 13 size or mass measures undoubtedly reflects the small size of the fruits relative to the rictal widths and tip gapes of the swallows and cutters, which generally exceeded mean and maximum fruit diameters (Wheelwright 1985, Foster 1987).

The absence of a preference by swallows for fruits with the smallest seed load contrasts with the findings of Herrera (1981) and Howe and Vande Kerckhove (1980, 1981, but see Manasse and Howe 1983). However, selectiveness of birds studied by Howe and Vande Kerckhove (1980, 1981) decreased as the abundance of fruit increased, suggesting that birds were less concerned with "quality" when presented with "quantity" (Howe 1983). The lack of significant correlations of visits by swallows with either seed load or absolute amount of pulp may reflect the great abundance of available fruits or the lack of problem with ballast, given the small size and mass of the seeds. Birds often eat fewer fruits than the maximum number that they have been observed to swallow at one time (Foster, unpubl. data).

It is more surprising that the cutters and biters did not select trees whose fruits had the greatest amounts of pulp, although this has been shown in other studies (Howe and Vande Kerckhove 1980). The absence of significant correlations suggests that fruit size is unimportant, at least if it exceeds some minimum threshold. In fact, in 1978 more cut and bite feeders visited tree 11 than any other, yet it had the smallest fruits of all trees considered (Table 1). Because fruits are so abundant, these birds have the opportunity to move from fruit to fruit and always maximize bite size. Such behavior could explain the apparent inefficiency with which they remove pulp from the seed (Foster 1987).

#### SEED PARASITES AND FRUIT CROP

Birds feeding on *A. edulis* do not appear to come into direct contact with the seed parasites and thus are unaffected by their presence or absence. Crop size, in contrast, clearly influences the frequency of bird feeding visits to this species. The correlation between these factors is not entirely unexpected. Several studies have demonstrated that bird visits increase with increasing crop size (e.g., Davidar and Morton 1986 and references therein; Murray 1987). Trees with limited amounts of fruit may simply be overlooked by foraging birds or may not provide sufficient overall reward to attract avian dispersers (Howe and Estabrook 1977, Stapanian 1982, Manasse and Howe 1983). By feeding only in the trees with the largest crops, birds can reduce their likelihood of visiting a tree where no food is available, especially toward the end of the fruiting season. The near absence of inter- and intraspecific aggression among birds visiting *Allophylus* (Foster 1987) makes it unlikely that low use of small-crop trees is due to fruit defense or interference from more dominant species (Howe 1981, Howe and Vande Kerckhove 1981).

Although crop size influences patch (= tree) richness, and net rate of food gain is of paramount importance to the welfare of an individual, organisms can maximize food gain only within the limits imposed by the need to avoid predators or cope with physical aspects of the environment (e.g., Milinski and Heller 1978, Heinrich 1979, Sih 1980, Grubb and Greenwald 1982, Schultz 1983, Martin 1985, Holbrook and Schmitt 1988). Thus, although the hypothesis that birds avoid trees with large crops because of increased predation risk is not supported, crop size could still exert its most significant impact on bird visitation rates through its influence on predation. Rather than engaging in predator avoidance, birds might capitalize on group-associated benefits. If sufficient birds are attracted to a given tree, even as members of a noncooperative, coincidental assemblage, individuals may benefit from the collective vigilance of their fellow foragers (Powell 1985, Munn 1986) or from reduced likelihood of capture through selfish herd and confusion effects (Hamilton 1971, Krebs and Davies 1981). In such cases one would expect birds to be attracted to trees where other birds are feeding. This could explain the apparent threshold of crop size required to attract these

species. Birds should congregate in trees with the largest fruit crops (trees which also generally have the largest crown volumes and densest foliage; Foster, unpubl. data) to minimize interference competition for food and numbers of agonistic encounters. Such interactions were noticeably absent among birds feeding in *Allophylus* (Foster 1987).

Although the strongest relationship between birds visits and any tree character was with size of the fruit crop, the connection is not totally satisfying because of the absence of a significant correlation in 1978, even though the most common visitors did frequent trees according to crop size. This lack of a significant statistical relationship may reflect nothing more than the much smaller number of visitors in 1978, even with crop sizes similar to 1980, suggesting in addition, the existence of a preferred alternative food source. *Allophylus edulis* produces large numbers of small fruits that are relatively low in nutrients, a syndrome characteristic of species that attract a large pool of opportunistic "generalist" frugivores (McKey 1975, Howe and Estabrook 1977). As such, *A. edulis* may not command the loyalty of bird visitors if more attractive alternatives are available. A variety of other species with bird-dispersed fruits reproduce during the *Allophylus* fruiting season (e.g., Foster 1985). I do not have data on the abundance and nutritional contents of these fruits. However, several of the species are members of families (e.g., Lauraceae, Meliaceae, Araliaceae) or genera (e.g., *Trichilia*) that include species known to be particularly rich in nutrients (Foster and McDiarmid 1983 and references therein).

## CONCLUSIONS

Rates of bird visits to fruit trees were significantly correlated with only a few of the 27 fruit and tree characters considered. Given these inconclusive and rather negative results, it is tempting to suggest that most of the characters considered are of minimal importance to the birds, or that the birds do not forage in an optimal way (Stephens and Krebs 1986). However, such firm conclusions would be imprudent at this time. Given the small sample of trees, the use of composite feeding visits by many species of birds, and the sometimes small intertree differences, meaningful choices by birds may have gone undetected. Nevertheless, I can envision a hierarchy of importance among foraging parameters, with each

optimized within the limits defined by the parameters above it. Importance of parameters and their positions in the hierarchy would be dynamic, reflecting immediate environmental conditions, as would realizable levels of optimization for each parameter (e.g., see Martin 1985, Holbrook and Schmitt 1988). Organisms could simultaneously optimize several parameters, or could "let the less important slide while focusing on the more critical" (Myers 1983, p. 218).

The results from this study could be indicative of such a dynamic situation. If neither time nor energy is critical during the *Allophylus* fruiting period (generally these birds spend a great deal of time "loafing" at this season; Foster, pers. observ.), then, indeed, the birds may be letting these—in the immediate, short-term—less important nutritional parameters "slide" in the face of the more important parameter of predation.

## ACKNOWLEDGMENTS

Miguela and Armando Reynaers kindly allowed me to work at Tirol. E. W. Schupp provided assistance and entertainment in the field, and L. A. Hayek, patient advice concerning statistical analyses. J. Lawrence, S. Smith, H. Waskins, and Mr. and Mrs. Hugo Beckers helped in other ways. B. M. Beehler, L. Emmons, J. Oldemeyer, U. Safriel, D. White, D. Wilson, and an anonymous reviewer commented critically on earlier drafts of the manuscript. Financial support for this research was provided by the Museum of Vertebrate Zoology, University of California, Berkeley, and the U.S. Fish and Wildlife Service. I thank these individuals and institutions for their generous support.

## LITERATURE CITED

- DAVIDAR, P., AND E. S. MORTON. 1986. The relationship between fruit crop size and fruit removal rates by birds. *Ecology* 67:262-265.
- DUNCAN, C. J. 1960a. Preference tests and the sense of taste in the feral pigeon (*Columba livia* var. *Gmelin*). *Anim. Behav.* 8:54-60.
- DUNCAN, C. J. 1960b. The sense of taste in birds. *Ann. Appl. Biol.* 48:409-414.
- FOSTER, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58:73-85.
- FOSTER, M. S. 1985. Social organization and behavior of the swallow-tailed manakin, *Chiroxiphia caudata*. *Natl. Geogr. Soc. Res. Rep.* 17:313-320.
- FOSTER, M. S. 1987. Feeding methods and efficiencies of selected frugivorous birds. *Condor* 89:566-580.
- FOSTER, M. S., AND R. W. MCDIARMID. 1983. Nutritional value of the aril of *Trichilia cuneata*, a bird-dispersed fruit. *Biotropica* 15:26-31.
- GRUBB, T. C., AND L. GREENWALD. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. *Anim. Behav.* 30:637-640.

- HAMILTON, W. D. 1971. Geometry for the selfish herd. 1971. *J. Theor. Biol.* 31:295-311.
- HEINRICH, B. 1979. Foraging strategies of caterpillars. *Oecologia* (Berlin) 42:325-337.
- HERRERA, C. P. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos* 36:51-58.
- HOLBROOK, S. J., AND R. J. SCHMITT. 1988. The combined effects of predation risk and food reward on patch selection. *Ecology* 69:125-134.
- HOWE, H. F. 1979. Fear and frugivory. *Am. Nat.* 114: 925-931.
- HOWE, H. F. 1981. Dispersal of a neotropical nutmeg (*Viola sebifera*) by birds. *Auk* 98:88-98.
- HOWE, H. F. 1983. Annual variation in a neotropical seed-dispersal system, p. 211-227. *In* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick [eds.], *Tropical rain forest: ecology and management*. *Spec. Publ. Br. Ecol. Soc.* No. 2.
- HOWE, H. F. 1986. Seed dispersal by fruit-eating birds and mammals, p. 123-189. *In* D. R. Murrery [ed.], *Seed dispersal*. Academic Press, New York.
- HOWE, H. F., AND D. DE STEVEN. 1979. Fruit production, migration, bird visitation, and seed dispersal of *Guarea glabra* in Panama. *Oecologia* (Berlin) 39:185-196.
- HOWE, H. F., AND G. F. ESTABROOK. 1977. On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* 111:817-832.
- HOWE, H. F., AND G. A. VANDE KERCKHOVE. 1979. Fecundity and seed dispersal of a tropical tree. *Ecology* 60:180-189.
- HOWE, H. F., AND G. A. VANDE KERCKHOVE. 1980. Nutmeg dispersal by tropical birds. *Science* 210: 925-927.
- HOWE, H. F., AND G. A. VANDE KERCKHOVE. 1981. Removal of wild nutmeg (*Viola surinamensis*) crops by birds. *Ecology* 62:1093-1106.
- IZHAKI, I., AND U. N. SAFRIEL. 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54:23-32.
- KREBS, J. R., AND N. B. DAVIES. 1981. *An introduction to behavioural ecology*. Sinauer, Sunderland, MA.
- LEVEY, D. J. 1987a. Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 129:471-485.
- LEVEY, D. J. 1987b. Sugar-tasting ability and fruit selection in tropical fruit-eating birds. *Auk* 104: 173-179.
- LOPEZ, J. A., E. L. LITTLE, JR., G. F. RITZ, J. S. ROMBOLD, AND W. J. HAHN. 1987. *Arboles Comunes del Paraguay*. Peace Corps, Washington, DC.
- MANASSE, R. S., AND H. F. HOWE. 1983. Competition for dispersal agents among tropical trees: influences of neighbors. *Oecologia* 59:185-190.
- MANZUR, M. I., AND S. P. COURTNEY. 1984. Influence of insect damage in fruits of hawthorn on bird foraging and seed dispersal. *Oikos* 43:265-270.
- MARTIN, T. E. 1985. Resource selection by tropical frugivorous birds: integrating multiple interactions. *Oecologia* 66:563-573.
- McKEY, D. 1975. The ecology of coevolved seed dispersal systems, p. 159-191. *In* L. E. Gilbert and P. H. Raven [eds.], *Coevolution of animals and plants*. Univ. Texas Press, Austin.
- MILINSKI, M., AND R. HELLER. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* 275:642-644.
- MOERMOND, T. C., AND J. S. DENSLow. 1983. Fruit choice in neotropical birds: effects of fruit type and accessibility on selectivity. *J. Anim. Ecol.* 52:407-420.
- MOERMOND, T. C., AND J. S. DENSLow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection, p. 865-897. *In* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. S. Buckley [eds.], *Neotropical ornithology*. *Ornithol. Monogr.* No. 36. American Ornithologists' Union, Washington, DC.
- MOERMOND, T. C., J. S. DENSLow, D. J. LEVEY, AND E. SANTANA C. 1987. The influence of context on choice behavior: fruit selection by tropical birds. *Quant. Anal. Behav.* 6:229-254.
- MUNN, C. A. 1986. Birds that cry 'wolf.' *Nature* 319: 143-145.
- MURRAY, K. G. 1987. Selection for optimal fruit-crop size in bird-dispersed plants. *Am. Nat.* 129: 18-31.
- MYERS, J. P. 1983. Commentary, p. 216-221. *In* A. H. Brush and G. A. Clark, Jr. [eds.], *Perspectives in ornithology*. Cambridge Univ. Press, Cambridge.
- PAINE, R. T. 1971. The measurement and application of the calorie to ecological problems. *Annu. Rev. Ecol. Syst.* 2:145-164.
- PIIL, L. VAN DER. 1982. *Principles of dispersal in higher plants*. 3rd ed. Springer-Verlag, New York.
- POWELL, G. V. N. 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the neotropics, p. 713-732. *In* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. S. Buckley [eds.], *Neotropical ornithology*. *Ornithol. Monogr.* No. 36. American Ornithologists' Union, Washington, DC.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds, p. 152-297. *In* R. W. Paynter, Jr. [ed.], *Avian energetics*. *Publ. Nuttall Ornithol. Club* 15.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369-404.
- SCHULTZ, J. C. 1983. Habitat selection and foraging tactics of caterpillars in heterogeneous trees, p. 61-90. *In* R. F. Denno and M. S. McClure [eds.], *Variable plants and herbivores in natural and managed systems*. Academic Press, New York.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York.
- SIH, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041-1043.
- SMITH, A. R., AND M. S. FOSTER. 1984. Chromosome numbers and ecological observations of ferns from El Tirol, Paraguay. *Fern Gazette* 12:321-329.
- SORENSEN, A. E. 1981. Interactions between birds and fruit in a temperate woodland. *Oecologia* (Berlin) 50:242-249.
- STAPANIAN, M. A. 1982. A model for fruiting display:

seed dispersal by birds for mulberry trees. *Ecology* 63:1432-1443.

STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton Univ. Press, Princeton, NJ.

TURČEK, F. J. 1963. Color preferences in fruit- and seed-eating birds. *Proc. XIII Int. Ornithol. Congr.* (1962): 285-292.

WHEELWRIGHT, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66:808-818.

APPENDIX. Species of birds that eat fruits of *Allophylus edulis*, bird weights, and fruit handling methods.<sup>1,2</sup>

Species	x weight (g) ♂♂, ♀♀
<b>Pluck and swallow feeders (Type I)</b>	
<i>Pryoderus scutatus</i>	375, 330
<i>Cyanocorax chrysops</i>	157, 159
<i>Cacicus haemorrhous</i>	102, —
<i>Pitangus sulphuratus</i>	63, 66
<i>Turdus rufiventris</i>	67, 7
<i>Turdus leucomelas</i>	70, 67
<i>Turdus amaurochalinus</i>	63, 63
<i>Myiodynastes maculatus</i>	44, 51
<i>Thraupis sayaca</i>	31, 33
<i>Empidonomus varius</i>	27, 27
<i>Chiroxiphia caudata</i>	23, 23
<i>Zonotrichia capensis</i>	20, 20
<i>Vireo olivaceus</i>	15, 15
<i>Elaenia parvirostris</i>	16, 18
<i>Elaenia albiceps</i>	16, 15
<b>Cut or mash feeders (Type II)</b>	
<i>Tachyphonus coronatus</i>	26, 27
<i>Trichothraupis melanops</i>	20, 22
<b>Push and bite feeders (Type III)</b>	
<i>Tangara seledon</i>	19, 21
<i>Dacnis cayana</i>	16, 16
<i>Coryphospingus cucullatus</i>	15, 15
<i>Euphonia violacea</i>	14, 15
<i>Chlorophonia cyanea</i>	14, 15
<i>Euphonia pectoralis</i>	14, 14
<i>Hemithraupis guira</i>	13, 14
<i>Euphonia chlorotica</i>	12, 13
<b>Feeding method not determined</b>	
<i>Mionectes rufiventris</i>	14, 12

<sup>1</sup> From Foster 1987.

<sup>2</sup> See Foster 1987 for more precise means, sample sizes, and standard deviations.