The Condor 94:912–923

A COMPARATIVE ANALYSIS OF THE NUTRITIONAL QUALITY OF MIXED AND EXCLUSIVE FRUIT DIETS FOR YELLOW-VENTED BULBULS[1]

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Abstract. Yellow-vented Bulbuls (*Pycnonotus xanthopygos*) were fed a mixed diet of four fruit species (*Rhamnus alaternus, Lonicera etrusca, Rubia tenuifolia, Ephedra aphylla*) and diets containing each of these four fruits separately. A mixed-fruit diet proved no more nutritious than a single-fruit diet, and all the birds lost weight at the same rate regardless of diet. Birds fed a mixed-fruit diet assimilated less protein than those fed exclusively on *Rubia* and *Rhamnus* fruits, and assimilated more energy than those fed exclusively on *Ephedra* fruits. The apparent metabolizable energy (AME) in bulbuls fed a mixed diet (0.73) was higher than in those fed on *Rubia* and *Ephedra* (0.69 and 0.61, respectively) but lower than in those fed on *Rhamnus* (0.82). Protein content alone does not explain loss of body mass. However, lack of specific amino acids, or high potassium to sodium ratios, may cause mass loss. In addition, a mixed diet of four fruit species may not prevent the accumulation of secondary compounds to a damaging level resulting in low protein assimilation.

Key words: frugivory; fruit preference; nutrition; Yellow-vented Bulbul; Pycnonotus xanthopygos; *digestion; metabolizability.*

INTRODUCTION

The relationship between plants which produce fleshy fruits and their dispersers is based partially on the nutritional value of the fruit for the disperser. The ability to digest fruit is believed to be an important constraint on the evolution of the interaction between plants bearing fleshy-fruits and frugivorous birds (e.g., Herrera 1984, Jordano 1988, Worthington 1989).

In previous experiments, frugivorous birds of the eastern Mediterranean avifauna were fed on a single fruit species exclusively (Izhaki and Safriel 1989). Although birds ate large amounts of fruit they nevertheless lost mass due to poor nitrogen assimilation. It was assumed that nutrient intake would be better balanced by feeding the birds on several fruit species rather than on a single one, since a mixed diet could increase the possibility of extracting specific nutrients (e.g., Jordano 1988, Mack 1990) and could reduce accumulation of specific secondary compounds (Jordano 1988; Izhaki and Safriel 1989, 1990a; Levey and Karasov 1989).

The Pycnonotidae are well-known frugivores in regions of the Old World such as the Malaysian lowland rain forest (Lambert 1989), scrub and bush-jungle in India (Whistler 1949), eastern Mediterranean scrubland (Izhaki 1986; Izhaki and Safriel 1985, 1991, unpubl. data), mixed date palm-citrus orchards in Iraq (Al-Dabbagh et al. 1987), gardens and palm groves in western Arabia (Meinertzhagen 1954), and the Ethiopian lowland forest and non-forest habitats (Moreau 1972). The northern limit of the distribution of the Pycnonotidae in the Old World is in the Middle East which is populated by the Yellow-vented Bulbul *Pycnonotus xanthopygos.* The bulbul consumes and disperses several fruit species in the Israeli scrublands (Izhaki 1986; Izhaki and Safriel 1985, 1990b, 1991), and is one of the most important frugivorous birds in the Israeli avifauna. In this study, I fed these bulbuls four fruit species commonly available from June to August in the northern parts of Israel (*Rhamnus alaternus, Lonicera etrusca, Rubia tenuifolia, Ephedra aphylla,* unpubl. data). These foods are relatively poor in proteins and lipids, but rich in carbohydrates and water. The profitability of these fruits is reduced by their poor protein and lipid content as well as their indigestible seeds (Herrera 1981, Levey 1986, Jordano 1988).

In the current paper, I investigate the following questions. (1.) Are bulbuls fed on a mixed diet of several fruit species better able to maintain a constant body mass than bulbuls fed exclusively on single fruit species? (2.) Does a mixed fruit-diet improve protein, fat, carbohydrate, mineral and energy digestion? and (3.) Is the choice of a fruit species by birds connected with a particular

[1] Received 17 February 1992. Accepted 10 July 1992.

nutritional or morphological characteristic of the fruit?

METHODS

FEEDING TRIALS

I collected fruits and birds for these trials around the University of Haifa at Oranim campus, Israel (32°43′N, 35°07′E), during the summer and fall of 1989 and 1990. Bulbuls were captured using mist netting and held in individual indoor cages (40 × 50 × 80 cm) fitted with easily cleaned undercarriages. The bulbuls were maintained at room temperature (25° ± 3°C) with artificial light for 12 hr each day in addition to natural sunlight. In captivity, the birds were fed domestic fruits (apples, peaches, grapes, watermelons, and oranges), vegetables (tomatoes, cucumbers, and peppers), eggs, bread, and invertebrates (mealworms and locusts) for several days, until their body mass stabilized, usually after 10–20 days. There was no difference between the birds' mass when captured (37.7 ± 2.6 g) and on the first day of experiment (36.6 ± 2.8 g, paired t-test t_{23} = 1.06, $P > 0.05$).

Fecal analysis of 14 bulbuls captured in Beit Jimal, Judean Hills, Israel, between July and February demonstrated that the birds ate five fruit species (*Rubia tenuifolia, Asparagus aphyllus, Smilax aspera, Rhamnus palaestinus,* and *Pistacia lentiscus*) with an average of 1.4 ± 0.9 fruit species per bird (Izhaki 1986). Fecal analysis of 49 bulbuls captured at Ramat Hanadiv, Israel, between November and January revealed that the birds consumed five fruit species (*Phillyrea latifolia, A. aphyllus, Ephedra aphylla, R. palaestinus, P. lentiscus*) with an average of 1.6 ± 0.7 fruit species per bird (Adar 1991). Two fruit species identified by this analysis and one congeneric species were used in the present study. Because bulbuls are frequently observed eating *Lonicera* fruits around our campus and in other locations in Israel (Izhaki, pers. observ.), this fruit was added to the diet. The data on fecal analyses covers a period of several months, but bulbuls actually consume fewer fruit species over shorter periods of time, depending on availability. Hence, the four fruit species fed to bulbuls in this study represent greater fruit diversity than exists in nature. The four fleshy fruit species (madder, *Rubia tenuifolia*; buckthorn, *Rhamnus alaternus*; joint pine *Ephedra aphylla*; and honeysuckle, *Lonicera etrusca*) used in feeding trials were picked daily from several different plants within each species.

After the bulbuls' mass stabilized, three groups of six different individuals were offered an exclusive diet of one fruit species each, and a fourth group of six birds was offered a mixed diet containing the four fruit species. In each experiment I used six birds picked randomly from the pool of 30 bulbuls. *Lonicera,* however, was too rare in the area for an experiment to use this fruit exclusively. Each type of food was provided *ad libitum* for several days, as well as water *ad libitum,* at 08:00 hours. In the trials using all four fruit species I offered an equal wet biomass of each fruit species placed randomly on the cage floor at 08:00 hours every day.

Each day I measured the total wet mass of the fresh fruit provided, the total wet mass of fruits left uneaten from the previous day's provision, the total wet mass of the excreted seeds, and the total wet mass of the non-seed excreta (for a more detailed description of this procedure see Izhaki and Safriel 1989). The non-seed excreta were oven-dried until they reached a constant mass and reweighed to obtain the dry mass of excreta per day (Qe). I weighed the birds daily at 08:00 hr to determine whether or not to continue the experiment. Trials lasted five to 10 days each. At the end of each trial, the bird was fed on the pre-experiment mixed diet. Its mass was monitored at five-day intervals for an additional 30 days.

NUTRITIONAL ANALYSIS

Many fresh fruits (usually hundreds) were collected from each plant species. Fresh pulp from the fruits were mixed, dried and divided into two samples. These samples of dried pulp from the four fruit species and the dry feces from each experiment were analyzed for lipids, nitrogen, reducing sugars, ash, and several cations (Na, K, Ca, P), according to AOAC (1975) procedures. I estimated protein content of all species except *Ephedra* as total N × 6.25 (Bondi 1987). *Ephedra* is well known for its relatively high content of alkaloids such as ephedrines (Herrera, pers. comm.). Such nonprotein nitrogenous compounds may cause overestimation of protein content when the traditional 6.25 factor is used and so the protein content of *Ephedra* fruits was analyzed separately using Biotronic LC 5000 Amino Acid Analyzer (Moore and Stein 1951). This indicated that the correct conversion factor for *Ephedra* fruits was 4.3, which was close to 4.4, suggested by Milton and Dintzis (1981) for tropical plants. I also measured the sugar content in the fruit juice in the field using a hand refractometer. The caloric content of dry pulps and feces was estimated using the average gross energy equivalents of protein (17.2 kJ/g), fat (38.9 kJ/g) and carbohydrates (17.2 kJ/g, see Karlson 1972).

METABOLIZABILITY COEFFICIENTS

I calculated the Apparent Metabolizability (AM) for each dietary constituent x, AMx by AMx = $(Qi_x - QE_x)/Qi_x$ (Robbins 1983) where Qi_x and Qe_x are the quantity of substance x in the dry consumed feed (intake) and in the dry excreta produced, respectively. Because fecal and urinary wastes cannot be separated in birds I used the term "Apparent Metabolizability" (Robbins 1983, Miller and Reinecke 1984). The Apparent Metabolizable Energy (AME) was calculated by AME = ([GEi][Qi] − [GEe][Qe])/(GEi)(Qi), where GEi and GEe are the gross energy density of the consumed dry food and excreta produced, respectively (Kendeigh et al. 1977).

PROTEIN AND ENERGY REQUIREMENTS

The expected nitrogen intake for maintenance was calculated from the equation, $N_{required} = 0.43$ g N $kg^{-0.75}$ day^{-1} (Robbins 1981, 1983) and nitrogen values were converted to protein by multiplying the correct conversion factor, as described. The expected energy requirements for maintenance were calculated from the equation, $E_{required} = 1.572\ kg^{0.62}$ (Kendeigh 1970).

STATISTICAL ANALYSIS

Two-factor analysis of variance (ANOVA) was used to examine the effects of the four different diets (one mixed and three diets of a single fruit species) and the effects of the trial day (six days) on fruit intake, relative to body mass, and on the number of fruits eaten per day. One-way ANOVA was used to detect the effect of the four diets on mass loss, energy and protein consumption, and metabolizabilities. For this analysis, I pooled the results for each individual over the first six days of the trial. I used the REGWF Multiple *F* test (SAS 1988) as an *a posteriori* test for comparisons of these means. All proportions were arcsine square-root transformed before analysis (Sokal and Rohlf 1981). Values are presented as means ± standard deviations.

RESULTS

NUTRITIONAL CONTENT OF FRUITS

The four fruit species had a juicy pulp $\bar{x}$ = 70.3% ± 7.8% water content), which was relatively poor in crude protein (4.6% ± 1.6% of dry mass) and rich in carbohydrates (>72% of dry mass, Table 1). However, the pulps of *Rhamnus* and *Ephedra* contained almost twice as much protein as the pulps of *Rubia* and *Lonicera*. The pulp of *Rubia* was relatively rich in lipids but relatively poor in carbohydrates, and had no sugars in its juice (Table 1). This pulp also contained a high concentration of energy (20.1 kJ/g) compared to the mean for the other three fruit species together (16.5 kJ/g). All four fruit species had relatively low protein to energy ratios. While the total ash content was relatively similar among the species it was notable that *Rubia* fruits were exceptional in their low K to Na ratio and their high Ca to P ratio (Table 1).

SEED LOAD

Bulbuls did not regurgitate seeds of the experimental fruit species, but passed them through their digestive tracts undigested. The load of seeds relative to nutritional gain of pulp was expressed by the ratio of seed mass to fruit mass (Table 1). It is notable that *Ephedra* and *Lonicera* had a relatively low seed load (12–13%) compared with the other two species.

FRUIT PREFERENCE

Fruit preference (calculated from pulp consumption) among the four fruit species that were offered simultaneously varied among the individuals but less among trial days (Fig. 1). The average pulp consumption of *Lonicera* and *Ephedra* fruits (39% ± 9%, 32% ± 5%, respectively) was two to three times greater than pulp consumption of *Rhamnus* (13% ± 4%) and *Rubia* (17% ± 6%) fruits. Four individuals (Nos. 3, 4, 5, 6) preferred *Lonicera* fruits while the other two almost ignored them (Fig. 1). One of these two (No. 2) preferred *Ephedra* fruits and the other (No. 1) preferred *Rubia* and *Ephedra* fruits (Fig. 1). Although the birds were relatively consistent in their main preference during the trial, an important part of their diet consisted of the other three fruit species (Fig. 1). It is notable that the birds preferred the two fruit species with the lower seed mass to fruit mass ratio (Table 1).

TABLE 1. Morphological characteristics (Mean ± SD) and nutritional content of the four fruit species fed to bulbuls.

	Rubia tenuifolia	*Rhamnus alaternus*	*Lonicera etrusca*	*Ephedra aphylla*
Morphological characteristics				
Sample size[a]	147	26	52	25
No. of seeds per fruit	1.0 (0)	3.0 (0)	1.86 (1.09)	1.56 (0.5)
Wet fruit mass (g)	0.16 (0.02)	0.26 (0.06)	0.15 (0.03)	0.20 (0.07)
Wet pulp mass (g)	0.10 (0.01)	0.19 (0.06)	0.13 (0.02)	0.18 (0.07)
Seed mass/fruit mass	0.41 (0.04)	0.28 (0.09)	0.13 (0.05)	0.12 (0.07)
Nutritional content				
Water (%)[b]	59.0	72.0	73.0	77.0
Protein (%)[c]	3.2	5.8	3.3	6.1
Fat (%)[c]	18.1	0.7	4.1	0.7
Carbohydrates (%)[d]	72.8	88.5	87.9	83.7
Sugars (%)[e]	0	28.2	20.9	23.1
K (%)[c]	1.77	2.75	3.7	2.73
Na (%)[c]	0.26	0.1	0.29	0.12
Ca (%)[c]	0.92	0.34	0.58	0.29
P (%)[c]	0.02	0.05	0.16	0.11
Ash (%)[c]	5.9	5.0	4.73	6.7
K/Na	6.8	27.5	12.8	22.8
Ca/P	46	6.8	3.6	2.6
Energy (kJ/g dry pulp)[f]	20.1	16.4	17.3	15.7

[a] Number of fruits (a sample of at least 10 fruits from each plant species used in feeding trials).
[b] Percentage of wet pulp mass.
[c] Percentage of dry pulp mass.
[d] Calculated by subtracting the percentages of fat, protein, and ash from 100%.
[e] g/100 g solution of fruit juice.
[f] Calculated by multiplying the amount of fat, protein, and carbohydrates in 1 g dry pulp by their energy contents (see Methods).

BODY MASS CHANGES

Birds on all four diet regimens lost mass steadily during the first seven days of the experiments (Fig. 2). Although the average body mass loss for the entire trial across individuals differed among the four diets (one-way analysis of variance $F_{3,20} = 4.72$, $P = 0.01$) the average body mass loss of birds fed on a mixed diet of fruits (−10.8% ± 6.3%) was not significantly different from that of birds fed on *Rhamnus* (−7.2% ± 3.8%), *Rubia* (−14.2% ± 3.1%), and *Ephedra* (−15.3% ± 2.2%, REGWF Multiple F Test, $P > 0.05$).

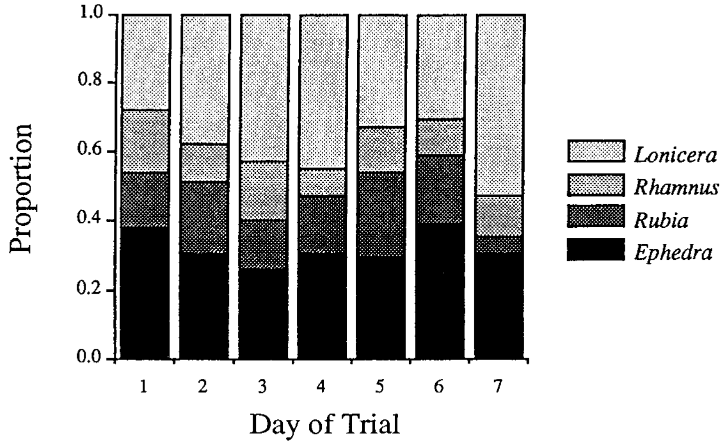
The daily proportion of body mass to pre-experiment body mass depended on the number of days elapsed from the beginning of the trial, as indicated by the regression equations (Fig. 2). There were no significant differences between any pair of regression coefficients in Fig. 2 ($t > 0.1$, $P > 0.1$; Marascuilo and Serlin 1988:623) indicating that there was no difference among diets in the rates of mass loss during the trial.

FRUIT INTAKE RATE

In all four diets the birds gradually increased their fruit intake rate (wet mass of consumed fruits per day/body mass) until the third day of the trial (Fig. 2). Thus, at the beginning of the experiments fruit mass consumption increased each day as body mass decreased. The mean daily rate of fruit intake (across individuals) was significantly dependent on both the type of diet and the day of the trial (Table 2) with the highest values for the *Rubia* diet (1.32 ± 0.20) and much lower values for the mixed fruit diet (0.68 ± 0.09), the *Rhamnus* diet (0.68 ± 0.06), and the *Ephedra* diet (0.56 ± 0.11). The average daily number of fruits consumed was 87 ± 20 for *Rhamnus,* 250 ± 99 for *Rubia,* 102 ± 24 for *Ephedra* and 116 ± 24 for the mixed diet. The number of fruits consumed per day was significantly affected by both the type of diet and the day of trial (Table 2).

PROTEIN AND ENERGY CONSUMPTION

The average protein content of fruit pulps for bulbuls fed on mixed diet (4.6% ± 1.6%) was lower than in exclusive diets of *Rhamnus* and *Ephedra* but higher than in diets of *Rubia* and *Lonicera* (Table 1). Considering the amount of food eaten per day, bulbuls fed on a mixed diet consumed less protein (mg/g body mass per 6 days) than those on the single fruit diets of



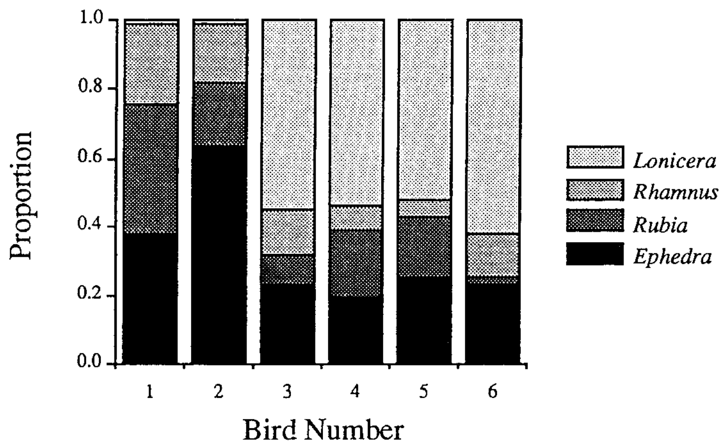


FIGURE 1. Fruit consumption of bulbuls fed a mixed diet of four fruit species during a seven day trial. Proportions are of total pulp's wet mass consumption. The upper figure presents the mean proportions per day and the lower presents the mean proportions per individual over the seven day trial.

TABLE 2. Two-way ANOVA tables for the effect of diet and day of trial on the number of fruits eaten per day, and on fruit intake (total wet fruit mass consumed per day/body mass). Original data were transformed.

Source of variation	df	Mean square	*F*	*P*
Fruit intake				
Diet	3	4.66	166.67	0.0001
Day	6	0.13	4.72	0.0002
Diet × day	18	0.12	4.72	0.0001
Residual	129	0.03		
Number of fruits eaten				
Diet	3	224,457.6	85.46	0.001
Day	6	7,201.4	2.74	0.015
Diet × day	18	1,975.2	0.75	0.75
Residual	135	2,626.5		

Ephedra and *Rubia* (Table 3). In all trials, birds consumed more protein than their expected maintenance requirement according to Robbins (1981, 1983) (Table 3). Bulbuls fed on a mixed diet assimilated less protein than those fed on *Rubia* and *Rhamnus* but more than those fed on *Ephedra* (Table 3). Bulbuls fed on *Ephedra* had a negative protein balance (Table 3).

The average energy content of the mixed pulps in bulbuls fed on a mixed diet (17.38 ± 1.93 kJ/g dry mass) was lower in birds fed on *Rubia,* higher than in birds fed on *Rhamnus* and *Ephedra* and similar to that in bulbuls fed exclusively on *Lonicera* fruits (Table 1). Accounting for the amount of pulp eaten per day, bulbuls on a mixed diet consumed less energy (kJ/g body mass per

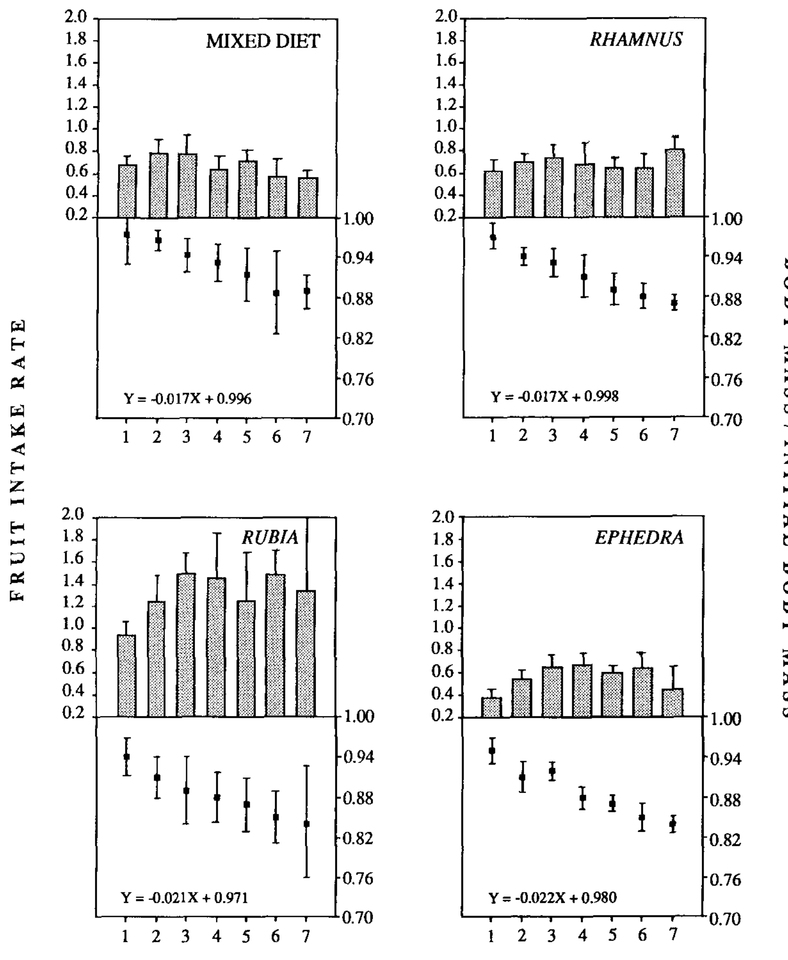


FIGURE 2. The rate of body mass loss (bottom) and fruit intake rate (top, pulp consumption/body mass) of bulbuls during the first seven days of feeding trial of a mixed fruit diet and three diets of a single fruit species. The regression equations of body mass loss are also given.

day) than birds fed on *Rubia,* more energy than birds eating only *Ephedra,* and same amount of energy as birds fed on *Rhamnus* fruits (Table 3). However, in all diets birds consumed more energy than expected based on their daily requirements (Kendeigh 1970). Bulbuls fed on *Rubia* consumed 3.6 times more energy than their daily requirements and assimilated significantly more energy than those fed on the other three diets (Table 3). Bulbuls fed on *Ephedra* consumed only 8% more energy than required (Table 3).

APPARENT METABOLIZABILITY (AM)

Bulbuls fed a mixed diet of fruits had a significantly higher AME than those fed an exclusive diet of *Rubia* and *Ephedra* but lower than those fed on *Rhamnus* (Table 4).

The average dry matter metabolizability in birds consuming a mixed diet was significantly higher than in those fed on *Ephedra,* lower than those fed on *Rhamnus* but with no difference from those fed on *Rubia* (Table 4). The AM of dry matter of birds fed on a mixed diet decreased during the trial (average AM for the first three days of the trial was 0.76 and for the next three days was 0.66, paired t-test, $t_5 = 7.72, P < 0.001$). This pattern was not detected when birds were fed on exclusive diets of one fruit species (paired t-test for the three trials, $P > 0.1$).

Apparent metabolizabilities for birds eating the mixed fruit diet were in the range of values for birds fed on the exclusive diet of one fruit species (Table 4). Birds fed a mixed fruit diet had a lower AM for protein than those fed an exclusive diet

TABLE 3. The requirements of protein and energy for the maintenance of bulbuls vs. consumption when fed a mixed diet and single fruit diets. One-way ANOVA tests for the differences among different diets were executed on arcsine square-root transformed proportions. The results of REGWF multiple F test ($P < 0.05$, SAS 1988) among diets are indicated in each row by the superscripts a–d: a > b > c > d. $n = 6$ bulbuls for each diet. The results are pooled from the first six days of the trials. Standard deviations are in parentheses.

	Diet				
	Mixed	*Rhamnus*	*Rubia*	*Ephedra*	F
Protein consumption (mg per 6 days/g body mass)	39.27 (3.96)^{b}	46.31 (8.22)^{b}	59.65 (6.12)^{a}	42.40 (4.87)^{b}	13.36*
Protein consumption/ expected protein intake‡	1.04 (0.10)^{c}	1.30 (0.15)^{b}	1.57 (0.18)^{a}	1.67 (0.18)^{a}	19.90*
Protein assimilation (mg per 6 days/g body mass)	3.60 (5.89)^{b}	24.27 (7.36)^{a}	24.84 (5.84)^{a}	−45.61 (7.52)^{c}	146.37*
Energy consumption (kJ per 6 days/g body mass)	16.10 (2.59)^{b}	13.09 (2.33)^{bc}	37.47 (3.84)^{a}	10.91 (1.25)^{c}	126.19*
Energy consumption/ expected energy intake‖	1.54 (0.24)^{b}	1.33 (0.16)^{bc}	3.55 (0.43)^{a}	1.08 (0.11)^{c}	107.61*
Energy assimilation (kJ per 6 days/g body mass)	11.66 (1.62)^{b}	10.70 (2.15)^{b}	19.09 (2.72)^{a}	6.66 (0.89)^{c}	41.72*

* = $P < 0.001$.
‡ Expected nitrogen intake was calculated by 0.43 g N $kg^{-0.75}$ day^{-1} (Robbins 1983) converted to protein by multiplying by 6.25 (Bondi 1987) for mixed diet, *Rhamnus* and *Rubia* and by 4.3 for *Ephedra* (see Methods).
‖ Expected energy intake was calculated according to Kendeigh (1970).

of *Rhamnus* and *Rubia* but higher than those fed on *Ephedra* (Table 4). Birds fed on *Ephedra* experienced a negative balance of proteins, fats, Na, Ca, and P (Table 4). Although negative balances were not observed for the other diets (except for phosphorus in the mixed diet), relatively low AMs were found for various components in different diets (Table 4).

DISCUSSION

The results of recent studies of the nutritional value of fruits to frugivorous birds indicate that

TABLE 4. Apparent metabolizable energy (AME) and apparent digestibilities of several pulp constituents (AM) consumed by bulbuls. One-way ANOVA tests for the differences between birds fed mixed diets and those fed a single fruit diet were executed on arcsine square-root transformed proportions. The results of REGWF Multiple F test ($P < 0.05$) among diets are indicated in each row by the superscripts a–d: a > b > c > d. $n = 6$ bulbuls for each diet. The results are pooled from the first six days of the trials. Standard deviations are in parentheses.

	Diet				
	Mixed	*Rhamnus*	*Rubia*	*Ephedra*	F
AME‡	0.73^{b} (0.03)	0.82^{a} (0.02)	0.69^{c} (0.02)	0.61^{d} (0.03)	73.44*
AM‖					
Dry matter	0.71^{b} (0.02)	0.83^{a} (0.03)	0.72^{b} (0.01)	0.63^{c} (0.03)	82.48*
Carbohydrates	0.78^{b} (0.01)	0.85^{a} (0.03)	0.78^{b} (0.01)	0.78^{b} (0.02)	16.99*
Proteins	0.03^{b} (0.22)	0.55^{a} (0.11)	0.41^{a} (0.07)	−1.21^{c} (0.15)	176.12*
Fats	0.61^{a} (0.08)	0.26^{a} (0.10)	0.53^{a} (0.04)	−1.25^{b} (0.79)	28.26*
Ash	0.34^{b} (0.06)	0.59^{a} (0.09)	0.59^{a} (0.04)	0.02^{c} (0.08)	82.77*
Na	0.61^{a} (0.18)	0.35^{b} (0.18)	0.74^{a} (0.05)	−1.18^{c} (0.21)	167.82*
K	0.52^{b} (0.18)	0.97^{a} (0.01)	0.55^{b} (0.02)	0.07^{c} (0.07)	87.55*
Ca	0.31^{b} (0.13)	0.62^{a} (0.08)	0.66^{a} (0.03)	−0.27^{c} (0.12)	112.32*
P	−0.55^{c} (0.75)	0.22^{b} (0.11)	0.77^{a} (0.08)	−1.73^{d} (0.18)	46.25*

* = $P < 0.001$.
† (Energy consumed − energy excreted)/energy consumed.
‡ (Constituent × consumed − constituent × excreted)/constituent × consumed.

most birds are unable to subsist on an exclusive diet of fruits (Berthold 1976; Bairlein 1987; Herrera 1984; Izhaki and Safriel 1989, 1990a; Levey and Karasov 1989; but see Walsberg 1975; Holthuijzen and Adkinsson 1984; Jordano 1988; Studier et al. 1988; Worthington 1989). In this and another study (Levey and Karasov 1989) where a mixed fruit diet was presented, the birds lost mass (but see Holthuijzen and Adkisson 1984). The rate of body mass loss (Fig. 2) for birds fed on a mixed fruit diet did not differ from that for birds fed on a single fruit diet.

THE PROTEIN DEFICIENCY OF FRUITS

The average low protein content (4.6%) of the four fruit species used in this study does not differ substantially from those of other regions such as the Iberian Peninsula (5.1% ± 3.8%, $n = 92$ [Herrera 1987]), southern England (6.1% ± 5.4%, $n = 28$ [Snow and Snow 1988], central Sweden (5.2% ± 3.8%, $n = 31$ [Eriksson and Ehrlen 1991]), central Illinois (5.1% ± 2.3%, $n = 20$ [Johnson et al. 1985]), Washington (5.3% ± 3.4%, $n = 18$ [Piper 1986]) and Hawaii (7.0% ± 3.5%, $n = 22$ [Sakai and Carpenter 1990]). Furthermore, it is likely that the actual available protein for birds is even less than these values since pulps may contain non-digestible nitrogen, such as in secondary compounds (Milton and Dintzis 1981; Sedinger 1990; and see Methods).

Protein deficiency has been suggested as a factor explaining the body mass loss and nitrogen imbalance in cage experiments (Moss and Parkinson 1975, Berthold 1976, Bairlein 1987, Levey and Karasov 1989, Sedinger 1990). Birds may cope with this protein shortage either by switching to insectivory (e.g., Morton 1973, Berthold 1976, Foster 1978, Levey and Karasov 1989) or by increasing their rate of fruit intake (but see Johnson et al. 1985, Bairlein 1987) and gut passage rate as long as high digestion efficiency is maintained. This second solution probably evolved in manakins (Worthington 1989) but was undetected in several temperate species where short retention times actually decrease fruit digestion (Izhaki and Safriel 1989, Levey and Karasov 1989). The main problem might not be the protein shortage per se, but the relatively high ratio of energy to protein in pulps. This results in the fulfillment of energy demands before protein demands (Ricklefs 1976, Foster 1978, Sibly 1981, Jordano 1988). However, the protein requirements for maintenance of frugivorous birds, and the requisite protein content of fruits to satisfy these demands, are not yet clear. Robbins (1981, 1983) provides a general equation for nitrogen intake required for nitrogen balance. However, several frugivorous birds, including bulbuls, consume more protein than expected but assimilate less protein than required according to Robbins' equation (Izhaki and Safriel 1989, Levey and Karasov 1989). Relatively low protein digestion was noted in this study as well (Table 4). Thus, the low protein content of the fruits was not compensated for by an increase in efficiency of protein digestion. However, a mixed fruit diet improved the birds' ability to digest and assimilate more protein as compared with an exclusive diet of *Ephedra* but not exclusive diets of *Rubia* and *Rhamnus* (Table 3).

It is notable that the average protein content of fruits required for nitrogen balance is not significantly different from the average protein content leading to protein imbalance (Table 5, $t_{16} = 0.77$, $P > 0.5$). However, because the data include results of experiments undertaken in different conditions and from birds of different regions (temperate and tropical), this conclusion must be viewed with caution. Nevertheless, the data indicate that the protein content alone tells us little about the ability of birds to subsist on fruits. *Ephedra* fruits with a relatively high protein content (Table 1) were the only ones which caused a negative protein balance (Table 3). Bairlein (1987) reported that the frugivorous *Sylvia borin* fed on an artificial diet that was very low in protein (2.4% wet mass) lost weight immediately at the beginning of the trial, but later maintained a constant mass. Costa's Hummingbirds (*Calypte costae*) can maintain their body mass on only 1.5% protein in their diet (Brice and Grau 1991). Low protein diets in these cases may be tolerable if birds can consume and digest a large volume of food. However, these observations may indicate that a factor other than protein concentration per se may regulate body mass loss in bulbuls.

Fruit pulp may lack some specific amino acids (Parrish and Martin 1977, Mack 1990, Sedinger 1990) and birds may actually select their diets on the basis of their amino acid contents (e.g., Murphy and King 1989). In arils of *Aglaia* species that were analyzed, only two species contained arginine, two species contained cystine and none contained histidine (Pannell and Koziol 1987). There are no data on the amino acid

TABLE 5. The ability of frugivorous bird species to maintain a positive nitrogen balance as a function of pulp protein content.

Bird species	Fruit species	Protein content of fruit pulp (% dry mass)† Positive N balance	Negative N balance	Reference
Phainopepla nitens	*Phorandedron californicum*	7.5		Walsberg 1975
Sturnus vulgaris‡	*Cornus racemosa*		6.1	Levey and Karasov 1989
	Viburnum dentatum			
	Vitis sp.			
Turdus migratorius‡	*Cornus racemosa*		6.1	Levey and Karasov 1989
	Viburnum dentatum			
	Vitis sp.			
Manacus vitellinus	*Heliconia latispatha*	8.5		Worthington 1989
	Psychotria deflexa	8.1		
	Hasseltia floribunda		7.1	
	Psychotria horizontalis		6.3	
	Byrsonima crassifolia		5.1	
	Anthurium brownii		2.6	
Pipra mentalis	*Anthurium clavigerum*	8.3		Worthington 1989
	Hasseltria floribunda		7.1	
	Psychotria marginata	6.3		
	Psychotria horizontalis		6.3	
Pycnonotus xanthopygos	*Rhamnus alaternus*	3.3		Present study
	Rubia tenuifolia	3.2		
	Ephedra aphylla		6.1	
	A mixed diet of the three species above and *Lonicera etrusca*‡	4.6		
Bombycilla cedrorum‖	*Crataegus phaenopyrum*	9.2		Studier et al. 1988
Mean ± standard deviation		6.6 ± 2.3	5.9 ± 1.4	

† Nitrogen converted to protein by multiplying by 6.25 except for *Ephedra*, where the 4.3 factor was used (see Methods).
‡ A diet of mixed fruit species, the value of protein content is the average for these fruit species.
‖ Data for free living birds.

contents of the pulps in the present study, but if bulbuls suffered from a shortage of amino acids when fed a single species of fruit they did not improve amino acid balance when fed a mixed diet.

Several fruit species congeneric with those used as food in my trials (*Rhamnus lycioides, Rubia peregrina, Lonicera periclymenum*) contain secondary compounds (such as glucosids, anthrones, saponins) in their ripe pulp (Jordano 1988). Secondary compounds in pulps may reduce the availability of protein in the diet and the activity of digestive enzymes (Feeny 1969; Swain 1979; Robbins 1983; Robbins et al. 1987; Bernays et al. 1989; Izhaki and Safriel 1989, 1990a; Levey and Karasov 1989; but see Mack 1990; Sedinger 1990). A bird possibly can shift from one fruit to another to avoid ingesting too high levels of a single secondary compound (Jordano 1988, Levey and Karasov 1989, Mack 1990). This is similar to the behavior suggested for herbivores. They may tolerate a small amount of secondary compounds. After consuming this amount they move to another species (Freeland and Janzen 1974). It is possible however, that frugivorous birds have evolved mechanisms of detoxification (Herrera 1985). For example, the relatively large livers found in starlings might help them to detoxify secondary compounds (Moermond and Denslow 1985).

THE AME PROBLEM

An interesting finding in this and similar studies (Holthuijzen and Adkinsson 1984, Izhaki and Safriel 1989, Levey and Karasov 1989) are the low AME values. If frugivorous birds accelerate food intake rate to maximize protein intake, they may also reduce the efficiency of energy assimilation (Izhaki and Safriel 1989, Levey and Karasov 1989). Levey and Karasov (1989), however, believed that low AME values were responsible for nitrogen imbalance through catabolism of their body protein to meet energy requirements. Izhaki and Safriel (1989, 1990a), in contrast, suggested that low protein assimilation caused in part by secondary compounds leads to acceleration of the gut passage time and hence to low AME values. Koenig (1991) found that adding tannins to acorn meal eaten by Acorn Woodpeckers (*Melanerpes formicivorus*) decreased AME. It should be emphasized that the low AME values reported by Levey and Karasov (1989) were also found when birds were fed on diets without secondary compounds. However, the main advantage of a mixed fruit over a single fruit diet of *Rubia* and *Ephedra* for bulbuls was their relatively high AME (Table 4). These AME values, though, are still below those expected for frugivorous birds (see Levey and Karasov 1989).

MINERAL DEFICIENCY OF FRUITS

Frugivorous birds may lose mass because of a severe shortage of minerals in pulps (e.g., sodium and potassium). These function with phosphates and bicarbonates to maintain homeostasis, osmotic relationships and optimum pH of the body (Simons 1986, Bondi 1987). Sodium lack may cause an immediate mass loss (Moss and Parkinson 1975). A negative balance of sodium was observed in free-living Cedar Waxwings (*Bombycilla cedrorum*) feeding on Washington Hawthorn fruits (Studier et al. 1988) but not in the bulbuls in this study (Table 4).

There are no data on the mineral requirements of frugivorous birds. The only available data for birds is for domestic forms. Pheasants (*Phasianus colchicus*) and Japanese Quail (*Coturnix coturnix japonica*) need 0.15% sodium in their foodstuff for growth and breeding (National Research Council 1984). The requirements of all domestic animals for sodium are of the order of 0.1%–0.2% of dry matter (Bondi 1987). Thus, if the sodium demands of the bulbuls are of the same order, the sodium content of the four fruit species (0.19% ± 0.1%, Table 1) should fulfill their demands. The four fruit species have a high ratio of potassium to sodium (18 ± 9, Table 1). An extreme predominance of potassium is detected in fruits from other regions, such as the Iberian Peninsula (84 ± 53, n = 72 [Herrera 1987]), Illinois (42 ± 25, n = 20 [Johnson et al. 1985]), and Hawaii (10.5 ± 8.1, n = 22 [Sakai and Carpenter 1990]). Japanese Quail needs a potassium to sodium ratio of 2.7 for growing and breeding (National Research Council 1984). However, animals are able to regulate the level of these two ions, and some can cope with a potassium to sodium ratio as high as 20 (Bondi 1987). It is still unknown if and how this high potassium to sodium ratio is related to the poor physiological state of bulbuls fed on an exclusive diet of fruits with unlimited water.

CONCLUSIONS

This study does not confirm the hypothesis that a mixed fruit diet improves bird maintenance in captivity better than a single fruit diet. Birds apparently have tried to compensate for the low protein levels of the fruits primarily by increasing daily fruit intake. However, because they did not increase the efficiency of protein digestion they lost weight at the same rate, regardless of their diet. Birds selected the fruits with the lowest seeds to pulp load (*Lonicera* and *Ephedra*) and not on the basis of any nutritional attribute. Bulbuls may have consumed large amounts of fruit in order to cope with other pulp attributes such as high energy to protein ratio and high K to Na ratio. I hypothesize that such a high fruit consumption and relatively low digestibility may lead to (1) decreasing AME, (2) imbalance in mineral nutrition and (3) accumulation of secondary compounds to levels that interfere with protein digestion. These factors may lead to body mass loss.

This study does not provide direct evidence for the "secondary compounds hypothesis" and further study on the actual content of secondary compounds in these fruits is needed. An alternative explanation for the bouts of insectivory in frugivorous birds is the shortage of the same free amino acids in all ripe fruit species (Mack 1990, Sedinger 1990). Following this line one needs to analyze the amino acid content of fruits and to compare it with the birds' requirements for maintenance.

ACKNOWLEDGMENTS

I gratefully acknowledge the critical comments of C. M. Herrera, P. Jordano, D. J. Levey, A. L. Mack, U. N. Safriel and J. S. Sedinger, which greatly improved this paper. I would also like to acknowledge assistance from O. Karnieli, H. Kuzik, I. Neeman, and T. Avivi. Nutritional analyses were performed in Miloda Laboratories under D. Izhar's supervision. The study was partly supported by the Carmel Foundation, Israel Ministry of Environmental Affairs, and by an Oranim research grant.

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