Digestive efficiency of a generalist avian feeder, the Cape White-eye (*Zosterops pallidus*)

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Abstract

Digestive processes determine whether the particular diet of a bird is utilized efficiently and whether energetic demands are met. Assimilation efficiency is often used as an index of whether a diet is digested optimally. Studies on the digestive processing of generalist feeders are scarce. Cape White-eyes *Zosterops pallidus* have a diverse diet of fruit, nectar and insects. The nutrient contents of these three diets vary considerably and require quite different digestive processing. This study compared the digestive efficiencies of Cape White-eyes on these three diets by measuring transit times and assimilation efficiency. Cape White-eyes lost body mass significantly when fed fruit, while they maintained and gained body mass on nectar and mealworm diets, respectively. Assimilation efficiency varied significantly between the three diet types (nectar > mealworms > apples). When given a choice of diets, Cape White-eyes selected the diet, which was most efficiently digested and yielded the greatest energetic reward. Diet preference trials further showed that Cape White-eyes regulated daily energy intake. Assimilation efficiency depends on the accessibility of nutritional contents of a diet. Cape White-eyes did not maximize assimilation efficiency. Instead, they adjusted transit time to maximize the rate of energy gain per gram of food in order to maintain energy balance.
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1. Introduction

Digestive processes determine whether food is utilized efficiently and whether energetic demands are met (Place and Stiles, 1992; Afik and Karasov, 1995). Digestive efficiency is an important measure when determining nutrient utilization of organisms (Witmer, 1999). Intake rates, transit time and assimilation all contribute to the efficiency of digestion of a diet (Sibly, 1981; Afik and Karasov, 1995). According to the reaction rate model (Sibly, 1981; Martinez del Rio and Karasov, 1990), there is a trade-off between the rate of digesta processing and the thoroughness of digestion (Levey and Karasov, 1992; Karasov, 1996).

As different food types differ considerably in their nutritional composition and energy yield, food choice is important. Most avian species are described as either frugivorous, insectivorous or nectarivorous although whether this is obligatory or facultative is usually omitted. Nectar and fruit pulp contain varying amounts of sucrose, glucose and fructose (Baker and Baker, 1983). However, fruit is usually low in nutrients but high in bulk (Levey and Karasov, 1989). Insects are composed predominantly of protein and lipids.

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Frugivores generally have high energetic demands, small gut volumes and short gut retention times (Levey and Karasov, 1989). They are often described as inefficient nutrient assimilators (Martinez del Rio et al., 1989; Karasov and Levey, 1990; Levey and Karasov, 1989, 1992, 1994). However, Witmer (1999) found four frugivorous species that efficiently absorbed fruit sugars. This efficiency, however, was dependent on the sugar concentration in the fruit pulp. As fruit contains a high level of water, faster rates of passage are necessary for sufficient energy gain when fruit has a low concentration of sugars (Witmer, 1996). The predominate sugar in fruit is glucose which may be easily assimilated by passive movement through the intestine (Martinez del Rio et al., 1992). Nectar, because of its sugar composition is easily assimilated and has a relatively fast transit time (Richardson and Wooller, 1990). An insectivorous diet of low carbohydrate and high protein content requires longer processing and transit time leading to a longer gut length (Richardson and Wooller, 1986). Increased dietary substrate levels, or increased protein and fat, tend to increase digesta retention time (Karasov, 1996).

Frugivores might be unable to increase their retention time to accommodate more nutrient-rich diets, and might extract less energy than insectivores from an insectivorous diet (Levey and Karasov, 1994). Likewise, insectivores with a long retention time might be unable to process enough bulky food in order to stay in energy balance (Levey and Grajal, 1991; Levey and Karasov, 1994). The low protein content of fruit leads to a protein deficit in a frugivorous bird's diet (Izhaki, 1992). Gut lengths or widths may change to permit a dietary switch or feeding rates may increase to maximize protein intake (Levey and Karasov, 1989; Karasov, 1996; Witmer, 1998a). American robins (*Turdus migratorius*) and Yellow-rumped warblers (*Dendroica coronata*) switch from eating fruits in fall to insects in spring (Karasov and Levey, 1990; Afik and Karasov, 1995). The switch in diet takes place over a period of time enabling the gut to increase or decrease in length or width to accommodate and efficiently assimilate the respective diet.

Most work to date on how digestive efficiency and digesta transit differs between diets has been done using bird species that specialize on certain diets. Few studies have focussed on how digestive efficiency and digesta transit differs between diets within the same bird species.

The *Zosteropidae* are described by Franke et al. (1998) as the third largest family of nectarivores in southern Africa. The Cape White-eye (*Zosterops pallidus*), however, is not a specialist nectarivore but rather a generalist feeder selecting various proportions of arthropods, nectar and fruit (Skead, 1967; Maclean, 1985). Consequently, we investigated the digestive efficiency and digesta transit of this generalist avian feeder. We hypothesized that Cape White-eyes are efficient nutrient assimilators irrespective of diet type. We predicted that digestive efficiency would be high and the transit rate rapid irrespective of diet type. We also hypothesized that Cape White-eyes show preference when given a choice, for diets that gave them the highest gross energy (GE) reward in terms of the highest ratio of assimilable energy to diluting factors.

2. Materials and methods

2.1. Capture and maintenance

During April 2000, twenty Cape White-eyes were caught in mist nets and walk-in traps near Pietermaritzburg, South Africa (29°30′S, 30°30′E) under permit from KwaZulu-Natal Wildlife. Birds were colour ringed on capture and released here following the experiments. Bird body mass was recorded at capture and weekly, thereafter, to monitor any mass changes during the experimental period.

Cape White-eyes were kept in groups of two to three in bird cages ($90 \times 30 \times 45$ cm^3). They were maintained on a 12:12 light dark cycle at 25 °C in a constant environment room. Birds were fed a mixed diet of nectar (Pick'n' Pay Choice Concentrated Fruit Punch, Pick'n' Pay South Africa and Horlicks, Beecham South Africa), apple pieces (variety Granny Smith) and insects (mealworms, *Tenebrio molitor* and fruit flies, *Drosophila* spp.). Birds were acclimatized to captivity for a month before trials were conducted.

During the experimental period, birds were held individually in cages ($90 \times 30 \times 45$ cm^3) with a central partition. Removable trays lined with heavy aluminum foil were placed in each half of the cage to facilitate faeces removal. Birds were left for approximately 14 h (16:30–06:30) to acclimatize to the cages. Water was offered ad libitum overnight but removed prior to trials. Birds were food

deprived overnight in order to ensure a post-absorptive state prior to experimentation.

Cape White-eyes were weighed in the morning before 06:00 prior to experimentation and again after 18:00 in the evening. Three food types were used. Artificial nectar consisted of a 20% sucrose solution, approximating the sugar concentration and composition of some local floral nectars visited by Cape White-eyes (Franke et al., 1998; Jackson et al., 1998). Feeders used during nectar experiments were modified 50-ml burette tubes calibrated at 0.1-ml intervals. Fruit was offered as sections of apple attached to a perch. *Tenebrio molitor* larvae were provided as the insectivorous diet and were placed in petri dishes on the floor of the cage.

2.2. Transit time and digestive efficiency on a single diet type

Passage of food through the digestive tract was measured by transit time, the time to first appearance of food items in excreta (Witmer, 1998b). Ten Cape White-eyes were chosen randomly for transit time experiments. The same ten birds were used in respective fruit, insect and nectar only trials. At 06:00, a measured amount of the particular diet type, injected with red food colourant (Moirs, R.S.A.), was offered to each of the birds. Time was recorded when birds first started to feed and again on first appearance of the coloured dye in the excreta. Birds would not feed on mealworms injected with dye and, therefore, the first appearance of chitin in the faeces was taken as the indicator of transit time.

There was substantial variation in the length of time taken for fruit to pass through the gastrointestinal tract, even though the amount of food eaten was fairly constant. Transit time depended on the amount of food eaten and also on the amount of time spent feeding. Therefore, the total amount of time spent feeding (from bill contact to swallowing) during the trial was recorded. The trial ended at the first appearance of dye in the excreta.

After the transit time trials, weighed food was left in the cage for the remainder of the day. Every 2 h excreta were removed, and in the case of the apple experiments, fresh food was placed in the cage. Collection of excreta during the respective fruit and mealworm trials involved the scraping of the excreta off the foil and into glass vials. Excreta

during the nectar trials were collected off the foil using a syringe. All samples were frozen at -2 °C. Consumption was quantified at the end of each day by weighing all uneaten food. Controls of each diet were used to estimate evaporative moisture loss from the uneaten food. Mealworms and fruit were measured to 0.01 g. Nectar was measured in ml and converted to grams.

At 18:00, birds were weighed, returned to their maintenance cages and fed the maintenance diet. No birds were used on consecutive days so as to enable them to regain any body mass lost during experiments.

Gross daily energy intake and daily faecal energy loss obtained from the above trials were used to determine apparent energy assimilation efficiency of the respective food types. Food intake was quantified by subtracting the dry mass of each food item remaining from the dry mass of the food item provided each day (by energy content and mass). Apparent assimilation efficiency (%) (AE) of nutrients were calculated using Eq. (1).

$$AE = (GE \text{ of diet eaten} \times GE \text{ of faeces}/GE \text{ of diet eaten}) \times 100 \qquad (1)$$

Total daily assimilated energy was calculated by multiplying daily GE intake by the assimilation efficiency of the respective diets.

2.3. Mixed diet experiments

To determine what quantities of each diet type Cape White-eyes ingest when provided with a selection, mixed food trials were conducted. Individual Cape White-eyes ($n = 20$) were simultaneously offered measured amounts of all three diet types (sections of apple, 20% sucrose solution and mealworms) for a day. Six birds were tested daily. Food was measured (mass and later converted to GE) hourly to determine the proportions of each diet eaten. This was to ascertain whether Cape White-eyes selected particular diet types more on a gram compared to a GE basis. All food intake measurements were corrected for individual body mass (mean body mass for that day) (expressed in g (body mass)$^{-1}$).

2.4. Nutritional analysis

Faeces and diets were oven-dried at 60 °C to determine moisture content and were then analyzed

Table 1

Nutritional composition of dietary items fed to Cape White-eyes in the laboratory trials

Food item	Percentage dry mass	GE/wet mass ($kJ\ g^{-1}$)	Dry mass GE content ($kJ\ g^{-1}$)	Protein[a] (%)	Crude fibre[a] (%)	Fat[a] (%)
Fruit (apple)	12.28	1.89	15.42	0	4.45	0.11
Nectar (20% sucrose)	20	3.29	16.44	0	0	0
Mealworms	38.13	10.26	26.92	43.49	0	40.42[b]

GE: gross energy.

[a] Percentage of dry mass.

[b] Downs and Perrin (1990).

for GE using bomb calorimetry (Animal Science, University of Natal). Mealworms were analyzed for crude protein, while fruit was analyzed for crude fibre and fat. Crude fat analysis of mealworms was obtained from Downs and Perrin (1990).

GE was measured using a DDS Isothermal CP500 bomb calorimeter (AOAC 1990) (Helrich, 1990). The Soxhlet procedure using a Buchi 810 Soxhlet Fat Extractor was used to determine crude fat (920.39 AOAC 1990) (Helrich, 1990). Fat was extracted using solvent petroleum ether and percentage fat was calculated on a gravimetric analysis. Crude protein was determined according to the Dumas Combustion Method using a LECO FP2000 nitrogen analyzer (968.06 AOAC 1990) (Helrich, 1990). Finally, crude fibre content was measured according to the fitted glass crucible method (978.10 AOAC 1990) (Helrich, 1990).

2.5. Statistics

Comparisons between the three diets, initial and final body mass and between hours, were done using repeated-measures analysis of variance (RMANOVA) with STATISTICA (Statsoft, USA). *T*-tests were performed to determine whether there

was a significant difference between initial and final body mass on a particular diet. Multiple *t*-tests with Bonferroni adjustments were used to determine the position of the significance between the transit times of the three diets.

3. Results

3.1. Diet composition

The three diets offered varied in GE and preformed water content (Table 1). Fruit had the highest preformed water content and lowest GE content. In contrast, mealworms had the lowest preformed water content but highest GE content.

3.2. Body mass

Initial and final body mass of Cape White-eyes differed significantly according to diet type (RMANOVA, d.f. = 3, 27; $F = 9.06$; $P < 0.05$; Table 2). Body mass declined significantly on the single fruit diet treatment. Birds maintained body mass when fed only nectar. They gained body mass significantly both on the mealworm only trial and the mixed diet trial. Cape White-eyes gained more than 9% body mass on the mealworm only and

Table 2

Daily initial and final body mass (mean ± S.E.) of Cape White-eyes during the respective single diet trials ($n = 10$) and the mixed diet trial ($n = 20$)

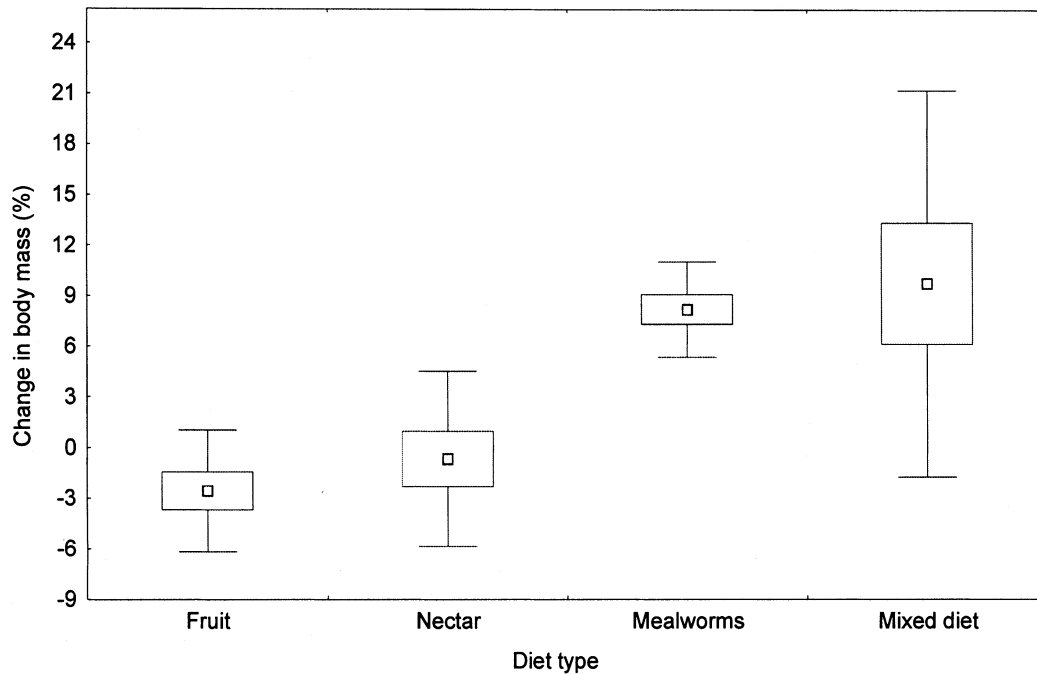| Diet	Initial body mass (g)	Final body mass (g)	*T*-test
Fruit (apple)	10.62 ± 0.33	10.34 ± 0.33	$t = 2.298$, $P > 0.05$
Nectar (20% sucrose)	10.68 ± 0.21	10.61 ± 0.28	$t = 0.398$, $P > 0.065$
Mealworms	10.19 ± 0.23	11.02 ± 0.23	$t = -9.147$, $P < 0.05$
Mixed diet (apple, 20% sucrose + mealworms)	10.35 ± 0.14	11.50 ± 0.24	$t = -2.667$, $P < 0.05$

Fig. 1. Percentage change in body mass of Cape White-eyes over the day on nectar, apples and mealworms, respectively.

mixed diet treatments, respectively, maintained body mass on the nectar only diet and lost on average 3% body mass on the fruit only diet (Fig. 1).

3.3. Single diet experiments

On the single diet treatments Cape White-eyes ingested more nectar than fruit or mealworms on a weight basis (nectar > fruit > mealworms; Table 3). Although a smaller mass of mealworms was ingested, it provided the greatest GE intake (Table 3). Birds assimilated similar amounts of energy when fed nectar and mealworms, respectively, while very little energy was assimilated on the fruit diet (Table 3).

Apparent energy assimilation efficiency for each diet treatment varied significantly (RMANOVA,

$F = 100.33$; d.f. $= 9$; $P < 0.05$). Apparent energy assimilation efficiency was highest for nectar ($x \pm$ S.E. $= 88.6 \pm 2.6\%$) and lowest for fruit ($40.3 \pm 3.9\%$). Mealworms had an apparent assimilation efficiency of $64.5 \pm 2.6\%$.

Body mass of Cape White-eyes did not change over the period of the transit time trials. There was no significant difference between the initial mass of birds on each diet (RMANOVA, d.f. $= 2$, 18; $F = 3.293$; $P > 0.05$) and, therefore, transit times were not standardized for body mass.

Transit time was shortest for mealworms and longest for fruit with nectar intermediate. However, transit time varied within a diet treatment according to amount eaten and percentage of time spent feeding. Measured transit times were, therefore, standardized for GE intake and amount of time

Table 3
Daily intake in grams and GE and total GE assimilated by Cape White-eyes during the respective single diet trials (mean $\pm$ S.E.; $n = 10$)

Diet	Intake in grams g/g body mass	Gross energy intake kJ/g body mass	Gross energy assimilated kJ/g body mass
Fruit	0.67 ± 0.04	1.25 ± 0.06	0.50 ± 0.03
Nectar	0.73 ± 0.10	2.40 ± 0.32	2.14 ± 0.28
Mealworms	0.32 ± 0.04	3.30 ± 0.41	2.13 ± 0.27

Table 4
Gross energy intake, intake rate, measured transit time and corrected transit time of single diets of apple, nectar and mealworms, respectively of Cape White-eyes in the laboratory (mean ± S.E.; $n = 10$)

Diet	Gross energy intake (kJ)	GE intake rate (kJ/% feeding)	Transit time (min)	Standardized transit time (min/kJ)
Fruit (apple)	2.85 ± 0.37	12.62 ± 2.67	33.99 ± 9.09	2.99 ± 0.47
Nectar (20% sucrose)	1.21 ± 0.38	15.83 ± 3.29	13.56 ± 2.22	1.39 ± 0.41
Mealworms	2.68 ± 0.32	43.56 ± 6.13	11.72 ± 1.42	0.30 ± 0.04

spent feeding. This correcting factor (GE intake rate) was calculated by dividing the GE intake by the percentage of time spent feeding. Standardized transit time was, therefore, calculated by dividing measured transit time by GE intake rate. This gave the time taken for 1 kJ of food to pass through the digestive tract.

Standardized transit time varied significantly between diets (RMANOVA, $n = 10$; $F = 18.942$; $P < 0.05$; Table 4). Diets with a higher water content and lower energy content moved through the gut at a slower rate than more concentrated diets. Fruit passed through the gut slower than both nectar ($t = 3.447$; d.f. = 9; $P < 0.016$; after Bonferroni adjustment) and mealworms ($t = 5.989$; d.f. = 9; $P < 0.016$; after Bonferroni adjustment). Nectar transit time was slower than for mealworms ($t = 2.705$; d.f. = 9; $P < 0.016$; after Bonferroni adjustment). More dilute foods were retained longer in the digestive tracts.

3.4. Mixed diet experiment

Total daily intake of each diet type during the mixed diet treatment was calculated on a gram and GE basis and compared to the intake during the single diet experiments (Table 5). Interestingly, similar amounts of nectar were consumed both on the single diet and the mixed diet treatments, while less apple and mealworms were consumed on a mixed diet. Cape White-eyes ingested significantly different amounts of each diet type on a gram basis (RMANOVA, d.f. = 2, 38; $F = 101.64$; $P < 0.05$; $n = 20$) and energy basis (RMANOVA, d.f. = 2, 38; $F = 70.87$, $P < 0.05$; $n = 20$). Total mass intake and GE intake of each diet showed that Cape White-eyes have a preference hierarchy (nectar > mealworms > apple).

Mean daily GE intake during the mixed diet trial was 4.08 ± 0.24 kJ g^{-1} body mass ($x \pm$ S.E.; $n = 20$). There was no significant difference in GE intake of the three diet types offered in the mixed diet experiment (RMANOVA, d.f. = 2, 32; $F = 0.75$; $P > 0.05$; $n = 20$). However, a Scheffe test showed that energy intake from fruit was significantly lower. There was a significant difference in GE intake on an hourly basis (RMANOVA, d.f. = 8, 152; $F = 21.44$; $P < 0.05$; $n = 20$) and the combination of diet and time of day (RMANOVA, d.f. = 16, 304; $F = 1.95$; $P < 0.05$; $n = 20$).

There was a significant difference in total energy intake per hour over a period of 9 h (RMANOVA, d.f. = 8, 152; $F = 2.79$; $P < 0.05$; $n = 20$). However, on performing multiple t-tests with Bonferroni adjustments, it was found that there was no significant difference in GE intake over the 9 h. It must

Table 5
Daily intake of nectar, mealworms and apples (mean ± S.E.) of Cape White-eyes during single diet trials ($n = 10$) and mixed trials ($n = 20$)

Diet	Single g/g body mass	Single kJ/g body mass	Mixed diet g/g body mass	Mixed diet kJ/g body mass
Fruit (apple)	0.67 ± 0.04	1.25 ± 0.06	0.08 ± 0.02	0.18 ± 0.03
Nectar (20% sucrose)	0.73 ± 0.10	2.40 ± 0.32	0.70 ± 0.08	2.75 ± 0.23
Mealworms	0.32 ± 0.04	3.30 ± 0.41	0.12 ± 0.01	1.15 ± 0.24
Total			1.03 ± 0.07	4.08 ± 0.24

be noted that prior to Bonferroni adjustment there was a significant difference between the hour 08:00 to 09:00 and 14:00 to 15:00 ($t=2.12$; d.f.$=$ 19; $P<0.05$). The hour 08:00 to 09:00 was immediately after the hour of gorging caused by birds being in a post-absorptive state. There was also a peak in energy intake in the hours prior to the dark phase.

4. Discussion

Digestive efficiency is not necessarily associated with high assimilation efficiency but with maximizing the rate of energy gain. Diet selection, therefore, plays an extremely important role in determining whether a bird meets its energetic requirements. Preference for certain food types above others is likely to correspond with the birds' ability to digest each diet type (Karasov, 1990). Specialist feeders display a variety of gut structures that accommodate the efficient utilization of specific diets (Karasov, 1990). Generalists, however, do not have gut adaptations that ensure the efficient utilization of all diets. It appears, therefore, that Cape White-eyes should rely on behavioural characteristics to stay in energy balance. The interactions of transit time, daily intake and assimilation efficiency ensure that Cape White-eyes balance their metabolic requirements.

4.1. Apparent assimilation efficiency

Apparent assimilation efficiency may best be defined as 'the proportion of a nutrient digested and absorbed upon passage through the digestive system' (Witmer, 1998b). It, therefore, not only requires optimal breakdown of nutrients but also good absorption efficiency.

Apparent energy assimilation efficiency of Cape White-eyes was highest for nectar (88.6%), then mealworms (64%) and lowest for fruit (40.3%). Although assimilation efficiency of nectar was high in Cape White-eyes it was still much lower than specialist nectarivores (Downs, 2000). The lower assimilation efficiencies of both the mealworm and fruit diet may be a consequence of indigestible material in the diets (chitin and polysaccharides in cell walls) (Van Tets and Nicolson, 2000; Castro et al., 1989). This would have contributed to the GE content of the diet and faeces, and the lower assimilation efficiency.

Fructose constitutes a large proportion of the fruit diet in this study (Fourie et al., 1991). There has been very little research done on fructose assimilation in avian frugivores (McWhorter and Martinez del Rio, 2000). Fructose is transported by a distinct transporter (GLUT5; Rand et al., 1993). Lower fructose uptake may be a consequence of lower densities or absence of this transporter. Jackson et al. (1998) found that fructose was not rapidly metabolized, suggesting that there is a possibility that apparent assimilation efficiency of fructose in Cape White-eyes is low.

The low assimilation efficiency of fruits may be a consequence of low concentrations of sugars in the fruit (Witmer, 1999). It is possible that there is a threshold water level above which digestion and assimilation efficiency decline. The more concentrated the nutrients are in a diet, the greater the chance of contact with enzymes and the absorptive surface of the digestive tracts. Dilution of a diet with water results in higher intake rates and lower digestive efficiencies (Witmer, 1998a). Specialist frugivores are often able to regulate daily intake rates to maintain constant rates of energy assimilation (Witmer, 1998a). But below a threshold of food digestibility, energy assimilation is progressively depressed by digestive limitations such as gut volume and processing rate (Witmer, 1998a).

4.2. Transit time

Transit time is the rate at which diets are passed through the gastrointestinal tract and is thought to be associated with nutrient absorption (Witmer, 1998a). Food intake and transit time may be constrained by the ability of the animal to process nutrients contained in diluted. In Cape White-eyes transit time was highly variable, but was shortest for mealworms and longest for fruit, with nectar intermediate. Transit time varied within a diet treatment according to amount eaten and percentage of time spent feeding. Standardized transit times (time taken for 1 kJ of food to pass through the digestive tract) again showed that fruit passed through the gut slower than both nectar and mealworms, respectively. More dilute foods were retained longer in the digestive tracts of Cape White-eyes.

Generally, a protein or lipid-rich diet requires longer processing time to accommodate for digestion of complex molecules leading to longer transit times (Levey and Grajal, 1991; Fuentes, 1994;

Karasov, 1996). However, in the present study this did not occur, mealworms passed through the digestive tract at an extremely rapid rate. Aqueous components of a meal are emptied from the stomach at faster rates than lipids (Roby et al., 1989). Indigestible chitin may have been passed through the gut with the aqueous portion of the mealworm diet, while lipids and protein might have been processed a lot slower.

Specialist nectarivorous birds appear to have digestive features to optimally digest the nutrients in their diet. They may be able to change intake rate and passage rate according to the concentration of the nutrients in the diet (Witmer, 1998a). Cape White-eyes, along with most other nectarivorous passerines in southern Africa, show preference for sucrose-based nectars (Downs and Perrin, 1996; Franke et al., 1998). A preference for sucrose is likely based on the energy yield per molecule (twice that of equimolar solutions of glucose) (Downs and Perrin, 1996; Jackson et al., 1998). Fast passage rates do not provide the necessary processing time for complex substrates such as sucrose, which has to be hydrolyzed first, before being assimilated (Martinez del Rio et al., 1992). The intermediate transit rate of nectar in Cape White-eyes, however, possibly reflects the complex interaction between energy release and yield of the food type.

Specialist frugivores generally have short guts adapted to processing fruit fairly rapidly (Levey and Karasov, 1989). This may be an adaptation to a fruit diet with low sugar concentrations. Nonspecialist frugivores with longer gut transit times would likely find sugary diets unprofitable as it would take too long to process bulky, nutritionally poor meals (Sorensen, 1984; Levey and Karasov, 1992). This may result in animals feeding on these particular diets entering a state of negative energy balance. (Worthington, 1989; Courtney and Sallabanks, 1992). Cape White-eyes lost body mass when fed fruit only, suggesting that they could not meet their energy requirements solely on a sugary fruit diet.

Facultative frugivores have to retain the ability to process both fruit and insects (Levey and Karasov, 1989). Omnivorous avian frugivores with slower food passage rates often select primarily lipid-rich fruits (Fuentes, 1994; Witmer and Van Soest, 1998). The efficiency with which sugars and lipids are digested and assimilated may differ (Lepczyk et al., 2000). Apples used in the present study were not lipid-rich fruits (crude fat contributing only 0.11% to the dry matter content). Slower transit rates of apples in Cape White-eyes may be associated with a longer intestine associated with efficient utilization of lipid-rich diets in the wild.

The present study showed that although Cape White-eyes regularly consume sugary fruits they cannot subsist primarily on them and will require additional nutrients to balance energy requirements.

4.3. Mixed diet

There are few bird species that can eat all types of food (Karasov, 1990). Generalists do not have gut adaptations, which ensure the efficient utilization of all diets. They, therefore, have to increase energy intake by selecting those food types which yield the highest rate of assimilable energy (Worthington, 1989).

When the daily GE intake of Cape White-eyes were converted to GE assimilated, both nectar and mealworm diets had similar values, whereas fruit had a comparatively low value. Cape White-eye body mass change did not parallel assimilation efficiency but rather GE intake, as has been found in frugivores (Witmer, 1998a).

When given a food choice, daily food intake of Cape White-eyes differed significantly between the three diets (nectar > mealworms > fruit) when measured on both a mass and GE basis. Cape White-eyes ingested significantly smaller amounts of fruit than nectar and mealworms when offered the choice of all three diets. More fruit was consumed on a gram and GE basis on the single diet treatment than in the mixed diet treatment. Presumably the birds were increasing food intake to maintain body mass when consuming exclusively fruit. Significantly more nectar was consumed over the day than mealworms. Diet selection may also be based on nutrient requirements of a bird rather than on high assimilation efficiency.

The survival of a particular species requires the adjustment of its feeding behaviour and general activity in a way that ensures that food intake at least offsets energy expenditure (Collins and Morellini, 1979). For a specialist feeder food availability may be a constraint during food shortage. In the wild, nectar availability is a constraint for nectarivores (Downs, 2000). Cape White-eyes

appear to accommodate shortages by having a diverse diet of fruit, nectar and insects.

5. Conclusion

Digestive efficiency in Cape White-eyes was affected by food type. Apparent energy assimilation efficiency of Cape White-eyes was highest for nectar (88.6%), then mealworms (64.5%) and lowest for fruit (40.3%). Furthermore, transit time also varied with food type. Transit time was highly variable, but was shortest for mealworms and longest for fruit with nectar intermediate. Assimilation efficiency is often used as an indicator of optimal digestion of a diet. This may be adequate when studying specialist avian species. However, in generalist species, daily assimilated GE may be a more useful indicator to compare digestive efficiency of different diets. Variation in assimilation efficiencies are largely caused by characteristics of the food (Karasov, 1990). Nutrient accessibility is important in determining the value of the diet to a bird (Worthington, 1989). This is determined by digestive efficiency, which is a function of factors such as food intake, enzyme activity, nutrient absorption and digesta retention time (Levey and Karasov, 1992).

While assimilation efficiency is associated with nutrient composition, rates of assimilation efficiency have been found to be associated with metabolic demand (Witmer, 1998a). Daily GE assimilated was the same for nectar and insects diets. Cape White-eyes, therefore, adjust transit rates to maximize the amount of assimilated energy gained so that energy balance is maintained for most dietary food choices.

An understanding of a bird's adaptations and trade-offs allows one to comprehend the relationship between an animal's diet and its digestive efficiency, and how these, in turn, are related to its ecology and behaviour (Levey and Karasov, 1989). Cape White-eyes have digestive tracts adapted for efficiently digesting complex nutrients. When given a choice of diet types, Cape White-eyes ate all, but in different proportions with greater intake of food types that were digested efficiently and yielded high energetic rewards.

Acknowledgments

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