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Digestive efficiencies of Cape white-eyes (*Zosterops virens*), red-winged starlings (*Onychognathus morio*) and speckled mousebirds (*Colius striatus*) fed varying concentrations of equicaloric glucose or sucrose artificial fruit diets

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ABSTRACT

Digestive physiology is important for understanding the feeding behaviour of organisms. Specifically, studies on the digestive physiology of frugivorous and nectarivorous birds are important for elucidating their preference patterns in the wild and the selective pressures they exert on fruit pulp and nectar. In this study, digesta transit times and digestive efficiencies of three species of birds, the Cape white-eyes (*Zosterops virens*), red-winged starlings (*Onychognathus morio*) and speckled mousebirds (*Colius striatus*) were investigated on equicaloric glucose or sucrose artificial fruit diets. Three concentrations, approximating the natural range of sugar concentrations in sugary, bird-dispersed fruits were used: low (6.6%), medium (12.4%) and high (22%). Digesta transit times of birds increased with an increase in concentration for all diets but were generally higher on glucose diets. Intake rates, on the other hand, decreased with an increase in sugar concentration. All species of birds failed to maintain a constant assimilated energy intake on glucose diets but mousebirds and white-eyes maintained it on sucrose diets. Apparent assimilation efficiencies of glucose diets for all species were comparable and typical of those found in other frugivorous birds. However, assimilation efficiencies for sucrose diets differed widely with red-winged starlings displaying very low assimilation efficiencies and as a consequence; they lost significant body mass on all sucrose diets. These results demonstrate the importance of digestive physiology in explaining fruit selection patterns in frugivorous birds and how a seemingly trivial physiological trait can have dire ecological consequences.

1. Introduction

Sucrose, glucose and fructose are the three primary sugars in fruit pulp and nectar of plants and their composition varies widely among plant species (Martinez del Rio et al., 1992; Schondube and Martinez del Rio, 2003; Johnson and Nicolson, 2008). Because pollinator and disperser preference is assumed to exert selection pressures on nectar and fruit pulp composition, the variation in sugar composition in plant rewards could be expected to be reflected in the pollinator and disperser assemblages (Martinez del Rio et al., 1992). For nectar, Baker and Baker (1983) postulated a hummingbird-passerine dichotomy with hummingbird-pollinated flowers having sucrose-rich nectar while those of passerine-pollinated plants contained hexose-rich nectar (Baker and Baker, 1983; Baker et al., 1998). Based on this dichotomy, hummingbirds were expected to prefer sucrose-dominant nectar whereas passerines were expected to prefer hexose-dominant nectar (Baker and Baker, 1983). Indeed laboratory studies showed support for the notion with hummingbirds preferring sucrose solutions (Martinez del Rio, 1990; Martinez del Rio et al., 1992) and passerines preferring hexose solutions over sucrose (Martinez del Rio et al., 1988, 1992, Martinez del Rio and Stevens, 1989; Brugger et al., 1993). However, these studies were confounded by that they compared specialized nectarivorous non-passerines with generalized frugivorous/nectarivorous passerines (Franke et al., 1998; Jackson et al., 1998; Brown et al., 2010a). Furthermore, they were conducted on birds from a restricted geographical range (Franke et al., 1998) and assumed that the pattern applies globally. Studies on southern African and Australian specialized nectarivorous passerines have shown that they too digest sucrose as efficiently as hummingbirds and as a result, they prefer sucrose over hexose solutions (Downs and Perrin, 1996; Lotz and Nicolson, 1996; Downs, 1997a; Nicolson and Fleming, 2003a; Fleming et al., 2004, 2008; Brown et al., 2010a). A more recent study by Johnson and Nicolson (2008) showed that nectar of flowers pollinated by specialized nectarivores is characterized by high concentration (15–25%), low volume (10–30 μl) and high sucrose content (40–60% of total sugar). On the other hand, nectar of flowers pollinated by generalized nectarivores is dilute (8–12%), copious (40–100 μl) and sucrose-deficient (0–5%). As a result, they refuted the hummingbird-passerine dichotomy and suggested that a more useful distinction is between generalized and specialized bird-pollination systems (Johnson and Nicolson, 2008).

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Conventional ecological wisdom predicts that the selection of a particular diet by an organism should be based on its ability to digest it (Martinez del Rio, 1990; Lotz and Schondube, 2006). While there is constancy in digestive abilities of birds for hexose sugars, their ability to digest sucrose differ markedly, with significant ecological consequences (Martinez del Rio et al., 1988; Schondube and Martinez del Rio, 2003; Lotz and Schondube, 2006). A number of birds lack sucrase, the enzyme responsible for breaking down sucrose to glucose and fructose (Martinez del Rio et al., 1988, 1989; Martinez del Rio and Stevens, 1989; Martinez del Rio and Karasov, 1990; Karasov and Levey, 1990; Martinez del Rio, 1990; Malcarney et al., 1994; Gatica et al., 2006; Bizaare et al., 2012; Brown et al., 2012). As a result, these birds show an aversion to sucrose as it causes osmotic diarrhoea (Martinez del Rio et al., 1988; Brown et al., 2012). It has been confirmed that the lack of sucrase is restricted to a single lineage, the Sturnidae-Muscicapoidea (Lotz and Schondube, 2006; Gatica et al., 2006; Bizaare et al., 2012; Brown et al., 2012). However, even species with significant sucrase activity prefer hexose solutions as they do not digest sucrose efficiently enough to maintain energy balance on it (Martinez del Rio et al., 1989; Martinez del Rio, 1990). This has been attributed to their fast passage rates which does not allow for sufficient exposure time of food to the digestive enzymes (Martinez del Rio et al., 1992). Therefore the preference for sucrose and lack thereof in birds is not only a function of sucrase activity but depends on the interplay between retention time, sucrose hydrolysis, and glucose and fructose uptake (Martinez del Rio, 1990).

Sugar type and concentration are important determinants of sugar preferences in birds because they affect digestive efficiency and rate of food processing (Schondube and Martinez del Rio, 2003). In the wild, sugar type and concentration in nectar and fruit show considerable variation even at small temporal and spatial scales (Levey, 1987). Therefore sugar selection in birds likely depends on both composition and concentration which suggests that in order elucidate factors affecting sugar preference in birds, these factors should be examined simultaneously (Nicolson and Fleming, 2003a). Indeed, studies that have examined these attributes simultaneously have shown that they have a synergistic effect. Specialist nectarivores generally prefer hexose at low concentration, no preference at intermediate levels and sucrose preference at high concentrations (Schondube and Martinez del Rio, 2003; Fleming et al., 2004, 2008; Lotz and Schondube, 2006; Brown et al., 2010a). Generalized nectarivores, on the other hand, prefer hexose solutions at low concentrations and show no preference or hexose preference at high concentrations (Brown et al., 2010b; Odendaal et al., 2010). Napier et al. (2013) suggested that sucrase activity drives the concentration-dependent sugar preference patterns in birds. They showed that specialized nectarivores (which have high sucrase activity) tend to select hexose only in the most dilute solutions while occasional nectarivores (which have low sucrase activity) select hexose up to higher concentrations (Napier et al., 2013). The general hexose preference at low concentrations has been attributed to short transit times at this concentration causing sucrose hydrolysis to limit energy delivery rate (Napier et al., 2013).

Frugivorous birds have been poorly studied with regards to the effects of sugar type and concentration on their digestive efficiencies (Wilson and Downs, 2011). Fruits are broadly categorized into two groups based on their carbohydrate and lipid content (Izhaki, 1992). Energy-dilute fruits are characterized by high water and carbohydrate content and low fibre and lipid content whereas nutrient-dense fruits have high lipid content, variable protein content and low water and carbohydrate content (McKey, 1975; Moermond and Denslow, 1985; Downs, 2008). Studies of fruit characteristics from diverse ecosystems suggest that the majority of fruits are nutrient-dilute (Herrera, 1987; Witmer, 1998). Compounding the dilution of nutrients in fruits is the high seed mass (up to 50% of total dry fruit mass, Moermond and Denslow, 1985) which takes up gut space that could be occupied by fruit pulp (Levey and Grajal, 1991; Murray et al., 1993; Stanley and Lill, 2002). This suggests that in order for frugivores to maintain energy balance on fruits, they should consume a large number of fruits and process them rapidly or select only nutrient-rich fruits (Worthington, 1989; Levey and Karasov, 1989). However, since the fruiting phenology of fruiting trees is highly seasonal and fruit shortages frequently occur, being selective cannot fully solve the dilemma faced by frugivores (Worthington, 1989). Therefore the ability to process large amounts of low quality fruits rapidly can allow avian frugivores to maintain energy balance during periods of low fruit abundance (Worthington, 1989).

Digestive efficiency is a measure of how well organisms extract nutrients from food (Levey and Karasov, 1992) and determines whether energetic demands are met (Brown and Downs, 2003; Downs, 2008). The reaction-rate model suggests a trade-off between the rate at which food is processed in the gut (passage rate) and the extent to which food is digested (digestive efficiency) (Levey and Karasov, 1992; Afik and Karasov, 1995; Downs, 2008). Frugivorous birds have high energetic demands, small gut volumes and fast passage rates (Levey and Karasov, 1989; Karasov and Levey, 1990). As a result, they are considered to be poor at assimilating energy (Karasov and Levey, 1990). However, compelling evidence has accumulated to suggest that frugivores do not have inherent fast passage rates but they modulate retention time according to the time required for the complete digestion and assimilation of food (Levey and Karasov, 1992; Afik and Karasov, 1995; Witmer, 1998, 1999; Witmer and van Soest, 1998). Furthermore, digestive efficiencies of sugars by frugivores have been found to be as high as those of hummingbirds when fed sugars of high concentration (Worthington, 1989; Witmer, 1998, 1999; Witmer and van Soest, 1998). The low digestive efficiencies reported in other studies could therefore be attributed to the low concentration of sugar used resulting in low digestive efficiency (Witmer, 1999).

The aim of this study was to determine whether sugar type and concentration affects fruit selection in birds. Three frugivorous bird species (Cape white-eye, *Zosterops virens*, red-winged starling, *Onychognathus morio* and speckled mousebird *Colius striatus*) were used for this study. These species are indigenous and locally abundant especially along the eastern coast of KwaZulu-Natal (Hockey et al., 2005). In this region, about 233 plant species are known to be dispersed by birds (Pooley, 1993). Although fruiting is seasonal, some plants (57–63) fruit in winter, suggesting that fruits are available throughout the year (Pooley, 1993). Because the foraging behaviour of frugivores have consequences for the process of seed dispersal, examining sugar preferences in frugivores may play a role in understanding the link between the distribution of frugivores and their food plants by determining precisely which fruits are being selected (Ally, 2010). Equicaloric glucose or sucrose artificial fruit diets of varying concentrations were used in this study. Due to a lack of sugar composition of South African fruits, the artificial fruit diets used were based on those developed by Witmer (1998) for North American birds. These diets were chosen because they (1) they allowed us to compare our findings to those of other studies and (2) they controlled for the effect of seeds and secondary compounds, factors that affect digestion (Bairlein, 1996; Cipollini and Levey, 1997). We hypothesized that sugar type and concentration would affect digestion in these species. We thus predicted that (1) birds would have slower digesta transit times as sugar concentration increased; (2) birds would reduce intake rates as sugar concentration increased to maintain a constant energy flux and (3) birds would show high apparent assimilation efficiency regardless of sugar type (Martinez del Rio and Karasov, 1990; Lotz and Nicolson, 1996; Witmer, 1999).

2. Materials and methods

2.1. Study species and maintenance

Cape white-eyes ($n = 9$), red-winged starlings ($n = 6$) and speckled mousebirds ($n = 6$), kept at the Animal House of the University of