



Effects of nicotine on the digestive performance of nectar-feeding birds reflect their relative tolerance to this alkaloid



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ARTICLE INFO

Article history:

Received 13 May 2015

Received in revised form 20 July 2015

Accepted 28 August 2015

Available online 6 September 2015

Keywords:

Apparent assimilation efficiency

Bird pollinators

Foraging behaviour

Gut transit time

Secondary metabolites

ABSTRACT

The paradox of secondary metabolites, toxic defence compounds produced by plants, in nectar and fruits is well known. Deterrence of feeding by nectarivorous and frugivorous birds is better understood than the effect of these chemicals on the digestive performance of birds. Digestive parameters such as transit time and sugar assimilation are important in assessing nutrient utilization and deterrence may be related to post-ingestive effects involving these parameters. Nectar and many fruits contain mainly sugars and water, and avian consumers compensate for low sugar content in their diet by increasing food intake: this may also increase their intake of secondary metabolites. We investigated how the alkaloid nicotine, naturally present in nectar of *Nicotiana* species, influences compensatory feeding and digestive performance of nectar-feeding birds. High nicotine concentration negatively affected compensatory feeding and apparent assimilation efficiency of white-bellied sunbirds *Cinnyris talatala* and Cape white-eyes *Zosterops virens*; but nicotine slowed gut transit time only in the latter species. In contrast, food intake and digestive performance of dark-capped bulbuls *Pycnonotus tricolor* was unaffected by nicotine up to a concentration of 50 μ M. Bulbuls are primarily frugivorous; hence, they are more exposed to secondary metabolites than sunbirds and possibly white-eyes. Because their diet is richer in toxins, frugivorous birds may have evolved more efficient detoxification strategies than those of specialist nectar-feeding birds.

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1. Introduction

Despite the clear role of floral nectar and fruit pulp as a nutritional reward to attract pollinators and seed-dispersing animals, little is known about the adaptive significance, if any, of secondary metabolites in nectar and fruits. Several hypotheses, not all mutually exclusive, have been put forward to explain the puzzling presence of those compounds in attractive substances (Herrera, 1982; Cipollini and Levey, 1997a; Adler, 2000). It is still debated if the presence of these toxic compounds is a pleiotropic consequence of plant chemical defence strategy (Eriksson and Ehrlé, 1998; Strauss et al., 2002; Manson et al., 2012). Alternatively, secondary metabolites could attract effective pollinators or seed dispersers while repelling nectar and pulp robbers (Stephenson, 1982; Cipollini and Levey, 1997a; Johnson et al., 2006). It has been shown that secondary metabolites in nectar could benefit plant reproduction if pollinators move more frequently between flowers (Kessler et al., 2008; Thomson et al., 2015). Similarly, secondary metabolites in fruits could increase passage time of seeds through the digestive system of frugivores and hence the distance of seed dispersal (Murray et al., 1994; Cipollini and Levey, 1997a; Wahaj et al., 1998).

Alkaloids are one of the major groups of secondary metabolites in plants, distributed widely in angiosperm roots, leaves and fruits, and many are toxic and bitter-tasting (De Luca and St Pierre, 2000; Wink, 2003; Schoonhoven et al., 2005). Deterrent effects of alkaloids on nectar and fruit consumers are well documented. Nicotine, naturally present in *Nicotiana* nectar, deters hummingbirds, sunbirds and white-eyes (Tadmor-Melamed et al., 2004; Kessler et al., 2012; Lerch-Henning and Nicolson, 2013). Steroid alkaloids, occurring as glycoalkaloids in ripe *Solanum* spp. fruits (Heftmann, 1983), are toxic to many frugivorous birds (Cipollini and Levey, 1997b; Levey and Cipollini, 1998). However, some birds are surprisingly tolerant to the presence of alkaloids. Capsaicin, an alkaloid-like compound found in chilli, reduces food consumption in mammals but not in birds; curve-billed thrashers *Toxostoma curvirostre* are not deterred by the presence of capsaicin in artificial fruits (Tewksbury and Nabhan, 2001). Mealworms injected with quinine deter European starlings *Sturnus vulgaris*, but the proportion of prey eaten depends on factors such as variability in the injected dose and the size of undefended prey, demonstrating that birds are able to manage the ratio of toxin to nutrients ingested (Halpin et al., 2013; Barnett et al., 2014).

Compared to these deterrent effects of alkaloids on foraging behaviour, there is little information concerning the post-ingestive effects of these toxins on nectar and fruit consumers. Studies on frugivorous birds have used different time scales, methods of exposure, species

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and secondary metabolites, thus making it difficult to draw general conclusions. In addition, frugivorous birds consume different diets and their digestive traits vary correspondingly (Witmer and Van Soest, 1998). This can be illustrated by examples of studies in which retention time was measured. Murray et al. (1994) found that fruits of the family Solanaceae contained laxative chemicals that reduced seed retention time, while in contrast glycoalkaloids had a significant constipative effect on cedar waxwings *Bombycilla cedrorum*, increasing seed retention time (Wahaj et al., 1998). Emodin, an anthraquinone present in fruits of the family Rhamnaceae, was found to increase gut retention time and food assimilation of yellow-vented bulbuls *Pycnonotus xanthopygos* (Tsahar et al., 2002, 2003); thus, the naturally low emodin concentration in fruits increases digestibility for these frugivorous birds (Tsahar et al., 2003).

Sugars such as sucrose, glucose and fructose are the main nutrients in nectar and fruits (Martínez del Rio et al., 1992; Baker et al., 1998) and their efficient digestion depends in part on passive absorption by the paracellular pathway, especially in small birds and bats (Caviedes-Vidal et al., 2007; Napier et al., 2008; Karasov et al., 2012). This could be disadvantageous for consumers if fruits and nectar contain hydrophilic secondary metabolites, because they will be easily absorbed by the paracellular route (Diamond, 1991; Karasov et al., 2012). In addition, nectar sugar concentration is highly variable (Martínez del Rio et al., 2001; Nicolson, 2002) and specialist nectar-feeding birds are able to accurately regulate daily energy intake by varying their food intake according to the sugar content of nectar (Nicolson and Fleming, 2003). However, if diluted nectar contains secondary metabolites, it imposes an additional challenge to specialist nectarivores, since their increased nectar intake means the inevitable ingestion of a greater amount of toxins, if supplementary food sources are not available. Hence, we are interested in understanding whether compensatory feeding is subject to limitations imposed by alkaloids, especially for specialist nectar-feeding birds consuming nutrient-dilute diets.

Our interest in nicotine has an ecological basis because this alkaloid is present in nectar of many *Nicotiana* (Solanaceae) flowers at concentrations between 0 and 42 μM (Adler et al., 2012; Kessler et al., 2012). Despite the presence of nicotine in nectar, many *Nicotiana* species are pollinated by hummingbirds and moths (Raguso et al., 2003; Kaczorowski et al., 2005) and sunbirds consume nicotine in the nectar of invasive *Nicotiana glauca* in South Africa and Israel (Tadmor-Melamed et al., 2004; Geerts and Pauw, 2009). Assessment of the nicotine tolerance of nectar-feeding birds showed that generalist bulbuls tolerated much higher nicotine concentrations than sunbirds and white-eyes (Lerch-Henning and Nicolson, 2013). There is a single study focusing on the physiological effect of alkaloids on a nectar consumer: nicotine and anabasine, both present in nectar of *N. glauca* flowers, reduced gut transit time of Palestine sunbirds *Nectarinia osea* by 30–42% and their sugar assimilation efficiency by 9–17%, compared with the control, alkaloid-free diet (Tadmor-Melamed et al., 2004).

The aim of this study was to investigate whether the presence of nicotine in artificial nectar influences compensatory feeding and digestive performance of nectar-feeding birds (one specialist, the white-bellied sunbird *Nectarinia talatala*, and two generalists, the Cape white-eye *Zosterops virens* and the dark-capped bulbul *Pycnonotus tricolor*). Although bulbuls and white-eyes are both considered generalist nectarivores, they respond differently to the presence of nicotine in nectar; white-eyes are deterred at low concentrations while bulbuls tolerate this alkaloid (Lerch-Henning and Nicolson, 2013). Therefore, we expect that the negative post-ingestive effects of nicotine will be less in bulbuls than in the other two species, reflecting their nicotine tolerance. We asked: (i) Does nicotine affect the ability of nectar-feeding birds to compensate for changes in nectar sugar concentrations? (ii) Does nicotine adversely affect their digestive performance, namely, gut transit time and sugar assimilation efficiency? and (iii) Is the effect of nicotine less pronounced in bulbuls than in sunbirds and white-eyes?

2. Material and methods

2.1. Study species

White-bellied sunbirds were mist-netted in Jan Celliers Park, Pretoria, South Africa during the nonbreeding season of 2011 ($n = 9$) and 2012 ($n = 9$); mean body mass (\pm SE) was 8.07 ± 0.24 g. Cape white-eyes were captured with the same method at the National Botanical Gardens in Pretoria during the nonbreeding season of 2011 ($n = 7$) and 2012 ($n = 9$); mean body mass (\pm SE) was 10.63 ± 0.13 g. Dark-capped bulbuls were caught with spring traps at the experimental farm of the University of Pretoria during the nonbreeding season of 2012 ($n = 6$) and 2013 ($n = 2$); mean body mass (\pm SE) was 37.43 ± 1.03 g. All birds were released at the place of capture after experiments were completed.

Birds were kept in outside aviaries covered with shade-cloth ($9 \times 5.5 \times 1.8$ m for sunbirds and white-eyes; $12 \times 6 \times 2$ m for bulbuls), during acclimation to captivity and between experiments. Two weeks before an experiment, birds were moved to individual cages ($30 \times 42 \times 46$ cm for sunbirds and white-eyes, and $36 \times 45 \times 90$ cm for bulbuls) in a climate-controlled room maintained at 20 ± 2 °C on a 12:12 h light/dark cycle, where dawn and dusk were simulated with 0.5 h of dimmed light before and after the full light period that started at 0800 h. The cages contained wooden perches and water baths. The maintenance diet, in both aviaries and cages, consisted of a 0.6 M sucrose solution with a nutritional supplement for protein, vitamins and minerals (Ensure®, Abbott Laboratories, Johannesburg, South Africa). In addition to the artificial nectar, white-eyes and bulbuls received seasonal fruits such as papaya, apple and banana, as well as moistened ProNutro® cereal (Becketts CNR, Wadeville, South Africa). Sugar solution and water for the small birds and bulbuls were presented in 20 ml and 60 ml inverted stoppered syringes, respectively. Maintenance diet, water and fruits were renewed daily and presented *ad libitum*.

2.2. Experimental design

Trials were carried out with different test diets (sucrose solutions with or without nicotine), all prepared in advance and frozen until used. We mixed nicotine-containing solutions at 0.5, 5 and 50 μM (Sigma-Aldrich, (–)-nicotine, N3876). All birds were tested with all test diets (12 for compensatory feeding and 4 for gut transit time and sugar assimilation efficiency) and the sequence of the test diets for each individual bird was randomised. During trials, white-eyes and bulbuls did not receive fruits or cereal and between trials at least one day of maintenance diet followed for all birds. Food intake (g) was recorded by weighing the feeders (± 0.1 mg, Mettler Toledo AG-64, Microsep Ltd., Johannesburg) before and after a trial. Plastic cups containing liquid paraffin (to avoid evaporative loss) were placed beneath feeders to correct food intake for possible spillage. The cups were weighed at the same time as feeders.

2.3. Compensatory feeding

Birds were presented with diets containing nicotine at different concentrations (0, 0.5, 5 and 50 μM) in three sucrose concentrations (0.25, 0.5 and 1 M); each nicotine concentration was presented in each sucrose concentration, hence birds were presented with a total of 12 test diets and a water feeder. Due to possible side bias (Franke et al., 1998), the position of the test diet and the water feeder was switched every 1.5 h. The duration of the experiment was 6 h, from 0800 h until 1400 h. Food intake (g) was converted to sugar intake (g in 6 h) using the sucrose concentrations, molar mass of sucrose and density of sucrose solutions.

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