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Suboptimal nutrient balancing despite dietary choice in glucose-averse German cockroaches, *Blattella germanica*

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ABSTRACT

Insects have evolved fine-tuned gustatory and post-ingestive physiological mechanisms that enable them to self-select an optimal composition of macronutrients. Their ability to forage optimally among multiple food sources and maximize fitness parameters depends on their ability not only to taste and perceive the nutritional value of potential foods but also to avoid deleterious components; the strength of such avoidance should reflect the severity of the perceived hazard. In German cockroaches (*Blattella germanica*), glucose aversion has evolved in some populations in response to anthropogenic selection with glucose-containing insecticidal baits. In four feeding treatments, we gave newly eclosed glucose-averse female cockroaches free choice to feed from two artificial, nutritionally complementary foods varying in protein and carbohydrate composition, with glucose or fructose as the sole carbohydrate source in either food. After 6 days of feeding, we measured diet consumption and the length of basal oocytes as an estimate of sexual maturation. The females did not compromise on their aversion to glucose in order to balance their protein and carbohydrate intake, and experienced lower sexual maturation rates as a consequence. Nutrient specific hunger via feedback mechanisms, and adjustments to gustatory sensitivity thus do not override the deterrence of glucose, likely due to strong selection against ingesting even small amounts of toxin associated with glucose in baits. In the absence of baits, glucose aversion would be expected to incur a fitness cost compared to wild-type individuals due to lower overall food availability but also to larger difficulty in attaining a nutritionally balanced diet.

1. Introduction

A wide range of animals, spanning from herbivores to omnivores and predators, have been shown to forage optimally for specific nutrients when allowed to compose a balanced diet from nutritionally complementary food sources (Behmer, 2009; Fanson et al., 2009; Lee et al., 2008; Jensen et al., 2012, 2013; Raubenheimer and Jones, 2006; Simpson et al., 2004, 2015). In particular, omnivores that scavenge in nutritionally heterogeneous environments are faced with the challenge of composing an overall balanced diet from food sources that may vary widely in nutritional composition, quality and availability. In order to do so, animals have evolved highly sensitive chemosensory and internal feedback mechanisms that enable them to sense what specific nutrients they need, and to be stimulated to consume them (Simpson and Raubenheimer, 1993, 1996; Simpson et al., 1991). However, little is known about how the evolution of optimal nutrient balancing mechanisms interacts with mechanisms of deterrence and toxin avoidance, which function to prevent the ingestion of lethal or deleterious compounds.

The effects of food deterrents on nutrient balancing are relatively well studied in herbivorous insects (Behmer et al., 2002; Bernays and Raubenheimer, 1991; Hägele and Rowell-Rahier, 1999; Raubenheimer, 1992; Simpson and Raubenheimer, 2001; Singer et al., 2002), but nutrient balancing and performance in relation to potentially lethal toxins has only been investigated very recently (Archer et al., 2014; Schmehl et al., 2014; Shik et al., 2014). Whereas deterrents typically stop the forager from eating before detrimental toxin doses are ingested (Chapman, 2013; Ozaki et al., 2003), toxins that are coupled with phagostimulating nutrients to disguise their taste and facilitate consumption would require highly sensitive gustatory reception capabilities.

The German cockroach (*Blattella germanica* Linnaeus) is an extreme generalist omnivore and a widespread pest in human establishments, where it is apparently able to compose a nutritionally balanced overall diet from various food objects within a household (Jones and Raubenheimer, 2001; Schal, 2011; Schal et al., 1984). German cockroach nymphs have been shown to grow slower when restricted to nutritionally deficient or imbalanced

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diets, and to have a high capacity to rebalance overall nutrient intake and resume growth trajectories when a complementary food appears (Raubenheimer and Jones, 2006). One of the most successful measures of cockroach population control is the use of toxic baits, in which toxins are coupled with phagostimulants to facilitate the ingestion of lethal toxin doses (Appel, 1990; Schal and Hamilton, 1990). However, selection with baits has led to evolution of physiological resistance to the toxins used in baits (Gondhalekar and Scharf, 2012; Schal, 1992; Wang et al., 2004, 2006), as well as behavioral resistance to bait components (Ross, 1997; Strong et al., 1993; Wang et al., 2004, 2006).

An intriguing adaptation that has evolved rapidly in multiple German cockroach populations in response to insecticidal baits containing glucose as phagostimulant is a strong aversion to ingesting glucose (Silverman and Bieman, 1993; Silverman and Ross, 1994). This is in particular interesting because glucose is a ubiquitous and metabolically important nutrient in nature. The adaptation appears to be controlled by a mutation in a single major gene (Silverman and Bieman, 1993), and was recently discovered to be due to a change in the response of taste neurons in the chemosensory appendages (Wada-Katsumata et al., 2011): glucose, which normally stimulates sweet gustatory receptor neurons, in addition strongly stimulates bitter receptor neurons in glucose-averse cockroaches (Wada-Katsumata et al., 2013). In contrast, fructose and other sugars are readily ingested (Silverman and Bieman, 1993; Wada-Katsumata et al., 2011, 2013). If no other food is available over a longer term, however, glucose-averse cockroaches will ingest small amounts of glucose-containing food (Shik et al., 2014; Silverman, 1995; Silverman and Selbach, 1998).

Whereas glucose aversion is highly advantageous in the presence of glucose-containing baits because it prevents intoxication, this adaptation would be expected to be maladaptive in the absence of toxic bait, in particular if glucose-containing foods are a major energy source in the foraging environment. Even in an environment containing glucose-free foods, glucose aversion might be deleterious because individuals might reject nutritionally complementary foods containing glucose which would otherwise enable them to reach their intake target. When given access to nutritionally complementary diets with either glucose or fructose as the sole carbohydrate source in both foods, wild-type German cockroaches reached their protein vs. carbohydrate intake target and maximized oocyte development independently of sugar type (Jensen et al., 2015). In contrast, glucose-averse cockroaches only maximized oocyte development when given nutritionally complementary fructose-containing foods, while consumption and oocyte development were highly suppressed if the foods contained glucose (Jensen et al., 2015). If the presence of glucose in nutritionally complementary foods prevents consumption, glucose-averse individuals foraging in the built environment might thus not be able to reach their nutritional intake target where performance is maximized even though complementary food is available (Jensen et al., 2015; Raubenheimer and Jones, 2006; Simpson et al., 2015). In the situation where glucose-averse individuals have to ingest a glucose-containing food to eat a balanced diet, feedback mechanisms of nutrient specific hunger would have to override the bitter signals from the chemosensory neurons (Simpson and Raubenheimer, 1996; Simpson et al., 1991; Wada-Katsumata et al., 2013), or the cockroaches would have to forage on a diet that is nutritionally imbalanced with the associated costs to performance (Jensen et al., 2015; Raubenheimer and Jones, 2006).

We applied the *Geometric Framework for Nutrition* (Simpson and Raubenheimer, 2012) to analyze the nutrient balancing behavior of glucose-averse female German cockroaches during sexual maturation, and linked specific nutrient intake to the rate of oocyte development. We produced four nutritionally specific, semi-synthetic foods varying in protein-to-carbohydrate ratio with either glucose or fructose as the sole carbohydrate component. We then gave newly eclosed glucose-averse female German cockroaches free choice to compose their diet from single combinations of two nutritionally complementary foods. After 6 days of feeding, we measured cumulative consumption and specific nutrient intake and measured oocyte length as an estimate of sexual maturation. Our results show that females did not balance their intake of protein and carbohydrate from the two foods if one of the foods contained glucose. Failing to ingest a balanced diet incurred a performance cost by slowing the rate of sexual maturation.

2. Materials and methods

2.1. Animals and housing

The glucose-averse German cockroaches used in the experiment originated from the T164 strain which was collected in Gainesville, Florida in 1989 (Silverman and Bieman, 1993), and have been maintained as a laboratory culture on ad libitum water and rat chow (Purina 5001 Rodent Diet, PMI Nutrition International, St. Louis, MO, USA) in transparent plastic containers (45.7 cm × 22.8 cm × 30.4 cm). Before the start of experiments, 400 nymphs were collected from the culture and distributed equally across four plastic containers (18.5 cm × 13.0 cm × 10.0 cm) with ad libitum water and rat chow until eclosion. Adults were collected daily, and newly emerged females were set up in the experiment within 24 h of eclosion. Experiments were performed in a room at 28–29 °C, 25–35% RH, and a 12:12 h L:D regime. Experimental cockroaches were held individually in transparent Petri dishes (100 mm diam × 16 mm), and food and water were provided ad libitum in separate inverted vial caps (foods: 15 mm × 10 mm; water: 25 mm × 12 mm).

2.2. Experimental diets and measuring consumption

We produced four artificial foods differing in protein-to-carbohydrate (P:C) ratio (2:1 or 1:4) and in carbohydrate component (either glucose or fructose), modified from Dussutour and Simpson (2008). Full ingredient lists and compositions of the foods are presented in Table 1. Upon eclosion, experimental animals (*N* = 80) were weighed to the nearest mg and distributed evenly across four dietary treatments, each consisting of free choice to feed on one of the 2:1 foods and one of the 1:4 foods. All foods were dried at 38 °C for 4 days and weighed to the nearest 10 μg before feeding. After 6 days of feeding, the foods were re-collected, re-dried, and re-weighed, and consumption was calculated as the difference in food dry mass before and after feeding. Protein and carbohydrate consumption were calculated respectively by multiplying the proportion of each nutrient group in the foods with the dry mass consumption of the corresponding

Table 1

Ingredient compositions of the four semi-synthetic foods used in the experiment. The numbers in brackets represent the quantity of protein in the respective ingredients. The recipes are modified from Dussutour and Simpson (2008).

P:C ratio	Glucose foods		Fructose foods	
	2:1	1:4	2:1	1:4
Whey protein concentrate (g)	19.3 (16.1)	2.5 (2.1)	19.3 (16.1)	2.5 (2.1)
Calcium caseinate (g)	17.7 (16.1)	2.3 (2.1)	17.7 (16.1)	2.3 (2.1)
Whole egg powder (g)	16.0 (7.8)	16.0 (7.8)	16.0 (7.8)	16.0 (7.8)
Glucose (g)	20.0	48.0	0.0	0.0
Fructose (g)	0.0	0.0	20.0	48.0
Agar (g)	4.0	4.0	4.0	4.0
Vanderzant vitamin mixture (g)	2.0	2.0	2.0	2.0
Methyl 4-hydroxobenzoate (g)	1.0	1.0	1.0	1.0