

# Adaptive contraction of diet breadth affects sexual maturation and specific nutrient consumption in an extreme generalist omnivore

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## Abstract

Animals balance their intake of specific nutrients, but little is known about how they do so when foraging in an environment with toxic resources and whether toxic foods promote adaptations that affect life history traits. In German cockroach (*Blattella germanica*) populations, glucose aversion has evolved in response to glucose-containing insecticidal baits. We restricted newly eclosed glucose-averse (GA) and wild-type (WT) female cockroaches to nutritionally defined diets varying in protein-to-carbohydrate (P : C) ratio (3 : 1, 1 : 1, or 1 : 3) or gave them free choice of the 3 : 1 and 1 : 3 diets, with either glucose or fructose as the sole carbohydrate source. We measured consumption of each diet over 6 days and then dissected the females to measure the length of basal oocytes in their ovaries. Our results showed significantly lower consumption by GA compared to WT cockroaches when restricted to glucose-containing diets, but also lower fructose intake by GA compared to WT cockroaches when restricted to high fructose diets or given choice of fructose-containing diets. Protein intake was regulated tightly regardless of carbohydrate intake, except by GA cockroaches restricted to glucose-containing diets. Oocyte growth was completely suppressed in GA females restricted to glucose-containing diets, but also significantly slower in GA than in WT females restricted to fructose-containing diets. Our findings suggest that GA cockroaches have adapted to reduced diet breadth through endocrine adjustments which reduce requirements for energetic fuels. Our study illustrates how an evolutionary change in the chemosensory system may affect the evolution of other traits that govern animal life histories.

## Introduction

Optimal foraging theory predicts that animals have evolved adaptations to forage optimally in their environment (Stephens & Krebs, 1986; Waldbauer & Friedman, 1991), and optimal foraging has more recently been extrapolated to the intake composition of specific nutrients (Simpson & Raubenheimer, 2012). Thus, a wide range of animals, including herbivores (Simpson *et al.*, 2004; Behmer, 2009), omnivores (Raubenheimer & Jones, 2006; Lee *et al.*, 2008; South *et al.*, 2011;

Jensen *et al.*, 2013), and predators (Mayntz *et al.*, 2005; Jensen *et al.*, 2012), have been shown to forage selectively to balance the intake of multiple nutrients and thereby maximize fitness-determining traits. Nutrient balancing might have to be compromised, however, if some foods in the environment are deterrent or toxic, forcing animals to forage for a balanced nutrient intake while avoiding ingestion of deleterious compounds to survive and perform optimally.

Taste perception and the ability to discriminate phagostimulants from deterrents have most likely evolved to screen potentially nutritious foods against deleterious secondary compounds (Rosenthal & Berenbaum, 1992; Chapman, 1998; Ozaki *et al.*, 2003). The functioning and evolved or intended purpose of deterrents and toxins are therefore fundamentally dissimilar (Behmer *et al.*, 2002). Plant deterrents may be toxins or

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are coupled with toxins, and serve the main purpose of preventing or stopping the consumer from eating. Typically, their function is served long before lethal doses of toxins have been ingested. Toxins used in insecticidal baits, on the other hand, are coupled with phagostimulants to encourage ingestion of lethal doses with the intention of killing the unaware consumer. Whereas nutrient balancing and food deterrence have been studied in herbivorous pests, locusts and caterpillars (Bernays & Raubenheimer, 1991; Raubenheimer, 1992; Simpson & Raubenheimer, 2001; Behmer *et al.*, 2002; Singer *et al.*, 2002), nutrient balancing and performance in relation to toxins have only been investigated very recently (Archer *et al.*, 2014; Shik *et al.*, 2014).

The German cockroach (*Blattella germanica*, Linnaeus) is an extreme generalist omnivore and a widespread pest within human establishments (Schal *et al.*, 1984; Schal, 2011). German cockroaches can therefore theoretically compose a nutritionally balanced diet by foraging selectively from different food objects within a household (Rivault & Cloarec, 1991; Jones & Raubenheimer, 2001). Indeed, German cockroach nymphs have proven exceptionally adept at redressing nutritional imbalances and resuming growth trajectories by selectively compensating for previous nutritional deficiencies after restriction to different individual, nutritionally imbalanced diets (Raubenheimer & Jones, 2006).

Provisioning of toxic baits in the environment of German cockroaches is often the most efficacious measure of cockroach control (Appel, 1990; Schal & Hamilton, 1990). However, like other pest control measures, baits have selected for the evolution of physiological resistance to toxins used in baits (Schal, 1992; Wang *et al.*, 2004; Gondhalekar & Scharf, 2012), as well as behavioural resistance induced by bait components (Silverman & Bieman, 1993; Strong *et al.*, 1993; Silverman & Ross, 1994; Ross, 1997; Wang *et al.*, 2004). A remarkable feature of formulated synthetic baits is that the toxin is normally coupled with phagostimulatory compounds to promote its ingestion, and sugars, in particular glucose, are used as phagostimulants in multiple bait formulations.

An intriguing adaptation that has arisen independently in several wild German cockroach populations is an aversion to ingesting food that contains glucose (Silverman & Bieman, 1993; Silverman & Ross, 1994). The adaptation has evolved rapidly during exposure to insecticidal baits with glucose as a phagostimulant (Silverman & Bieman, 1993). The aversive behaviour of glucose-averse (GA) German cockroaches appears to be controlled by a mutation in a single major gene (Silverman & Bieman, 1993) and was recently discovered to be due to a change in the response of taste neurons on the chemosensory appendages (Wada-Katsumata *et al.*, 2011): glucose stimulates bitter receptor neurons (Wada-Katsumata *et al.*, 2013). In contrast, GA cockroaches readily ingest fructose (Silverman &

Bieman, 1993; Wada-Katsumata *et al.*, 2011, 2013), and if no other food is present over a longer term, they will also ingest small amounts of glucose-containing food (Silverman, 1995; Silverman & Selbach, 1998).

Glucose aversive behaviour is highly advantageous if it prevents the ingestion of toxins that would cause death. However, the adaptation might be costly and a handicap in normal foraging without baits (Silverman, 1995). First of all, rejecting glucose-containing food reduces the overall nutrient availability, specifically for covering energetic requirements. Secondly, rejecting glucose-containing foods might affect the ability to ingest a nutritionally balanced diet, thus forcing the insects to ingest a higher ratio of other nutrients. Glucose aversion might furthermore be linked with physiological costs or adaptations, which might in turn have competitive consequences in the absence of baits if wild-type (WT) individuals reinvade. Mild aversion to a range of mono- and disaccharides has been indicated in a few wild German cockroach populations with long-term exposures to sugar-containing baits (Wang *et al.*, 2004, 2006), and Shik *et al.* (2014) found that GA nymphs given choice ingested less carbohydrate than WT nymphs while they selected a similar protein intake. This was the case even when substituting fructose for glucose, suggesting that glucose aversion might be associated with lower consumption of other sugars as well (Shik *et al.*, 2014).

We applied the *Geometric Framework for Nutrition* (Simpson & Raubenheimer, 2012) to investigate the nutrient balancing behaviour of female GA and WT German cockroaches during sexual maturation, and linked specific nutrient intake to the rate of oocyte development, a measure of the reproductive rate. Specific nutrient intake and sexual maturation were compared between the two strains both when diets contained glucose as the nonprotein energy source and when glucose was substituted with fructose in the diets, or when given a standard rat chow diet. Our findings show slower sexual maturation in GA compared to WT cockroaches and accordingly different specific nutrient consumption by the two strains, even when dietary glucose was replaced with fructose.

## Materials and methods

### Animals and housing

Both strains of German cockroaches were originally collected in Florida. The GA strain (T164) was collected in Gainesville in 1989 (Silverman & Bieman, 1993), and the WT strain (Orlando Normal) was collected in Orlando around 60 years ago and has since been maintained as a standard, unselected laboratory culture (Silverman & Bieman, 1993). Cultures of both strains were maintained in the laboratory on *ad libitum* water and rat chow (Purina 5001 Rodent Diet; PMI Nutrition

International, St. Louis, MO, USA), which contains a P : C ratio around 1 : 1.6 (Shik *et al.*, 2014). The GA culture was selected monthly by adding a glucose-containing, toxic (hydramethylnon) bait to the containers for 2 days, which is sufficient to prevent the establishment of potential accidentally invading WT individuals and maintain the frequency of glucose aversion coding alleles at almost 100%. Prior to experiments, cultures of both strains were distributed across four containers (45.7 cm × 22.8 cm × 30.4 cm) and were left unselected for 3 months. The containers were then cleared of adult animals, and emerging adults were collected daily and distributed to dietary treatments ( $n = 20$  per treatment per strain) within 24 h of eclosion. Experimental cockroaches were held individually in transparent Petri dishes (100 mm diameter × 16 mm). Experimental diets and water were provided *ad libitum* in inverted plastic lids (diets: 15 mm × 10 mm; water: 25 mm × 12 mm). Rearing and experiments were performed in a room at  $25 \pm 2$  °C,  $35 \pm 5\%$  RH, and a 12:12 h L:D regime.

### Experimental design and procedure

We produced six nutritionally complete, synthetic diets varying only in protein-to-carbohydrate (P : C) ratio (3 : 1, 1 : 1, and 1 : 3) and in carbohydrate component (either glucose or fructose), modified from Jones & Raubenheimer (2001). Protein consisted of a 2 : 1 : 1 mixture of casein, bacteriological peptone, and egg albumin, and protein plus carbohydrate constituted 60% of the mass in all diets. Full recipes for the six diets are presented in Table 1.

Upon eclosion to the adult stage, experimental animals were weighed to the nearest milligram and assigned to one of nine dietary treatments ( $n = 20$

cockroaches of each strain per treatment), and were given 6 days to feed. Six of the dietary treatments were no-choice treatments where each animal was restricted to one of the six synthetic diets (Table 1). Cockroaches on these treatments were forced to balance over- and underingestion of protein and carbohydrate relative to each other to maximize performance on the diet, described as the dietary rules of compromise (Raubenheimer & Simpson, 1997), and the variation in protein and carbohydrate intake across dietary P : C ratios shows whether and to what extent the intake of one nutrient is regulated more tightly than that of the other. The treatments furthermore allow for comparison of performance outcomes under the different nutritional imbalances. Two other treatments were choice treatments where each animal was allowed to self-select from the two nutritionally most extreme diets (3 : 1 and 1 : 3), with either glucose or fructose as the carbohydrate component in both provided diets. Such choice treatments show the self-selected, nutrient-specific intake point, and furthermore show whether animals, when given a choice, select an optimally balanced diet that maximizes fitness components compared to performance on the no-choice treatments. In the last dietary treatment, the cockroaches were provided with rat chow.

Diet intake was measured as the difference between diet provided and diet remaining after 6 days of feeding. Before and after feeding, foods were dried in an oven at 38 °C for at least 3 days and weighed to the nearest 10 µg. Specific nutrient intakes were then calculated by multiplying dry mass intake with the proportion of each specific nutrient in the ingested diet (Table 1).

### Measuring sexual maturation

The cumulative oocyte development at the end of the experiment was used as a measure of sexual maturation in the females (Schal *et al.*, 1993; Uzsák & Schal, 2012). All cockroaches receiving dietary treatments were dissected 6 days post-eclosion, and the lengths of three basal oocytes were measured with an eyepiece micrometer in a dissecting microscope. Oocyte lengths were also measured in 20 females from both strains within 24 h upon eclosion. The average of the three oocyte lengths was used as the individual measure for analysis. All basal oocytes of the German cockroach mature synchronously, so there was little variation among the three oocytes within a female.

### Statistical analyses

Animal weights were compared between the two strains using *t*-tests. Overall effects of strain, dietary P : C ratio, and sugar type on dry mass intake, protein intake and carbohydrate intake were first analysed using a multivariate analysis of covariance (MANCOVA)

**Table 1** Ingredient compositions of the six artificial diets.

Ingredients (per 100 g)	P : C ratio		
	3 : 1	1 : 1	1 : 3
Protein (g)*	45.00	30.00	15.00
Casein (g)	22.50	15.00	7.50
Peptone (g)	11.25	7.50	3.75
Albumin (g)	11.25	7.50	3.75
Glucose or fructose (g)	15.00	30.00	45.00
Cellulose (g)	27.00	27.00	27.00
Agar (g)	9.00	9.00	9.00
Cholesterol (g)	0.55	0.55	0.55
Linoleic acid (mL)	0.55	0.55	0.55
Salt mixture (g)†	2.50	2.50	2.50
Vitamin mixture (g)‡	0.46	0.46	0.46

P, protein; C, carbohydrate.

\*Includes casein, peptone and albumin.

†Wesson's salt mixture.

‡Vanderzant modification vitamin mixture.

test with initial body mass as covariate. To analyse the influence of strain, dietary P : C ratio and dietary sugar type on the consumption of each dietary component (dry mass, protein, and carbohydrate) separately, the MANCOVA was followed by a three-way analysis of covariance (ANCOVA) with initial body mass as covariate. Oocyte lengths at 6 days were analysed similarly using a three-way ANCOVA with strain, dietary P : C ratio and dietary sugar as factors and initial body mass as covariate. Dietary P : C ratio was not included as a factor in analyses involving choice. Dry mass, protein and carbohydrate intakes, as well as oocyte lengths, were compared between individual treatment groups using Student's *t*-tests. Student's *t*-tests were chosen because we are equally interested in similarities and differences between treatment groups, and the variables in two groups can be described as either similar or different with good confidence. Because dietary protein plus carbohydrate content was constant in all diets, significant differences in dry mass intake across dietary P : C ratios within strain and dietary sugar type indicate significant differences in total nutrient (protein plus carbohydrate) intake and therefore whether the intake array is significantly different from a slope of  $-1$ . We further tested this using Levene's tests, which reveal whether there was more variation in the consumption of one nutrient than the other across dietary P : C ratios, and thereby whether the intake of one nutrient was regulated significantly more tightly than that of the other when feeding on imbalanced diets, and we calculated the coefficient of variation ( $CV = \sigma/\mu$ ) for the intake of protein and carbohydrate within each strain and dietary sugar type. We also compared consumption of each of the two diets in the choice treatments with paired *t*-tests to determine whether the cockroaches consumed more of one nutrient than the other. In all statistical tests, differences were considered to be significant if  $P < 0.05$ . Dietary rules of compromise were analysed and discussed following Raubenheimer & Simpson (1997). All statistical analyses were performed in JMP 7.0 (SAS Institute Inc., Cary, NC, USA).

## Results

### Animal weights

The weight of females entering the experiments averaged  $61.85 \pm 0.36$  mg (mean  $\pm$  SE) for the GA strain and  $62.17 \pm 0.36$  mg for the WT strain and did not differ significantly between the two strains across treatments (*t*-test:  $t_{400} = 0.38$ ,  $P = 0.54$ ) or within any treatment ( $P > 0.26$ ).

### Nutrient balancing under no-choice conditions

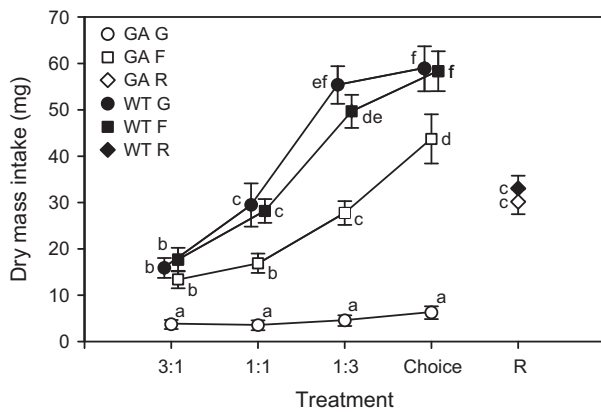
The overall consumption of dry mass, protein and carbohydrate by individual cockroaches under no-choice

conditions was highly affected by their strain, the dietary P : C ratio and the dietary sugar type, as well as interaction effects (Table 2). When analysing the dependent variables separately, dry mass intake (Fig. 1) and carbohydrate intake (Fig. 2) were both highly dependent on all three factors (Table 3). Overall, females of both strains consumed more food when restricted to diets with higher carbohydrate content (Fig. 1, Table 3). Carbohydrate intake was therefore generally very high by cockroaches restricted to carbohydrate-rich diets (Fig. 2, Table 3), except by GA females restricted to glucose-containing diets which had very low consumption on all diets (Fig. 1). In contrast, protein intake (Fig. 2) depended on strain and dietary sugar type, but was not overall significantly affected by dietary P : C ratio (Table 3). This shows that cockroaches of both strains regulated protein intake tightly and were not willing to increase protein consumption in order to ingest more carbohydrate when restricted to protein-rich diets (Fig. 2). In particular, WT females regulated protein intake very tightly across P : C ratios and ingested very high amounts of carbohydrate on protein-poor diets (Fig. 2, Table 4). Protein regulation was less pronounced but also highly significant in GA females restricted to fructose-containing diets (Fig. 2, Table 4), which on average only consumed half as much carbohydrate compared to the WT females when fed the high carbohydrate diet (Fig. 2). In contrast, GA females restricted to glucose-containing diets did not prioritize the consumption of one nutrient over the other but rather regulated the total intake of the two nutrients (Fig. 2, Table 4). The significant interactions between strain and P : C ratio and between strain, P : C ratio and sugar type on dry mass

**Table 2** MANCOVA tests, with initial body mass as the covariate, testing for the effects of strain (GA or WT), dietary P : C ratio (3 : 1, 1 : 1, or 1 : 3), sugar type (glucose or fructose), and their interactions on overall differences in dry mass intake, protein intake and carbohydrate intake at 6 days of feeding after eclosion. P : C ratio is not included as a factor under choice conditions.

Condition	Factor	d.f.	Pillai's trace	<i>F</i>	<i>P</i>
No-choice	Strain	2		95.54	< 0.0001
	P : C	4	0.827664	80.13	< 0.0001
	Sugar	2		8.98	0.0002
	Strain $\times$ P : C	4	0.539649	41.94	< 0.0001
	Strain $\times$ sugar	2		15.23	< 0.0001
	P : C $\times$ sugar	4	0.092717	5.52	0.0002
	Strain $\times$ P : C $\times$ sugar	4	0.153902	9.46	< 0.0001
	Initial body mass	2		1.75	0.1761
	Choice	Strain	2		42.33
Sugar		2		11.40	< 0.0001
Strain $\times$ sugar		2		9.30	0.0003
Initial body mass		2		0.07	0.9281

GA, glucose-averse cockroaches; WT, wild-type cockroaches.

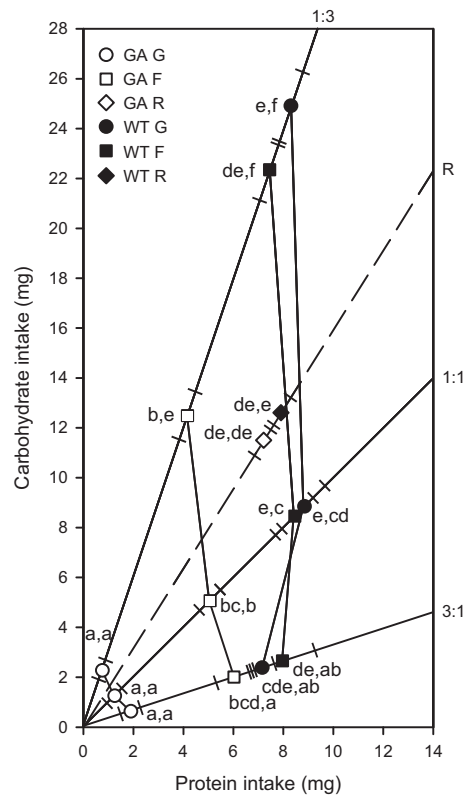


**Fig. 1** Dry mass intake (mean ± SEM) on all dietary treatments. The ratios on the x-axis are P : C. Different letters indicate significant differences (Student's *t*-test:  $P < 0.05$ ). GA, glucose-averse cockroaches; WT, wild-type cockroaches; G, glucose-containing diets; F, fructose-containing diets; R, rat chow.

intake (Table 3) furthermore indicate that GA and WT females used different rules of compromise when balancing over- and underingestion of protein and carbohydrate, and in particular that GA females used different rules of compromise depending on sugar type (Fig. 2, Table 4).

**Nutrient balancing under choice conditions**

The overall consumption of dry mass, protein and carbohydrate by individual cockroaches under choice conditions was highly affected by strain and dietary sugar type, as well as their interaction (Table 2), and all three dependent variables were highly dependent on both factors as well as the interaction when analysed separately (Table 3). WT females ingested similar amounts of protein and carbohydrate when the dietary sugar was glucose or fructose, and therefore regulated to the same intake point regardless of sugar type (Fig. 3). GA females given a choice between complementary fructose-containing diets, however, ingested similar amounts of protein as the WT females but significantly less carbohydrate (Fig. 3). The intake ratio of the GA females was therefore more protein biased than that of the WT females (Fig. 3), and total consumption was lower (Fig. 1). The selected P : C ratios of WT females and of GA females given a choice between fructose-containing diets were all significantly more carbohydrate biased than 1 : 1 (Fig. 3), however, which shows a significant preference for eating more carbohydrate than protein. In contrast, GA females given a choice between glucose-containing diets, in addition to ingesting significantly less of both protein and carbohydrate, selected a P : C ratio that was even more protein biased and not significantly different from 1 : 1 (Fig. 3).



**Fig. 2** Ingestion (mean ± SEM) of protein and carbohydrate under no-choice conditions. The slopes of the solid lines show the C : P ratios of the artificial diets, and the P : C ratio of each diet is given by the end of each line. The slope of the dashed line shows the C : P ratio of rat chow. Standard errors follow the nutritional composition of the ingested foods. Different letters indicate significant differences in protein or carbohydrate intake, respectively, separated with a comma (Student's *t*-test:  $P < 0.05$ ). GA, glucose-averse cockroaches; WT, wild-type cockroaches; G, glucose-containing diets; F, fructose-containing diets; R, rat chow.

**Dietary effects on oocyte development**

Oocyte lengths at 6 days post-eclosion depended on both strain and dietary sugar type, and their interaction, under both no-choice and choice conditions (Table 3). Oocytes in WT females were of similar lengths within dietary P : C ratios regardless of sugar type, but were significantly larger than the oocytes in GA females within all dietary treatments (Fig. 4). Furthermore, oocyte lengths in GA females were highly dependent on the sugar type in the diets (Table 3, Fig. 4), and oocytes in GA females restricted to glucose-containing diets were not significantly longer than oocytes measured within 24 h after eclosion and had therefore not developed significantly over the 6-day experiment (Fig. 4). Dietary P : C ratio affected oocyte development significantly within both strains with

**Table 3** Three-way ANCOVA tests, with initial body mass as the covariate, testing for the effects of strain (GA or WT), dietary P : C ratio (3 : 1, 1 : 1, or 1 : 3), sugar type (glucose or fructose), and their interactions on the univariate differences in dry mass intake, protein intake, carbohydrate intake and oocyte length at 6 days of feeding upon eclosion. P : C ratio is not included as a factor under choice conditions.

Condition	Dependent variable	Factor	d.f.	F	P
No-choice	Dry mass intake	Strain	1	178.39	< 0.0001
		P : C	2	67.55	< 0.0001
		Sugar	1	17.75	< 0.0001
		Strain × P : C	2	27.92	< 0.0001
		Strain × sugar	1	29.10	< 0.0001
		P : C × sugar	2	0.48	0.6180
		Strain × P : C × sugar	2	3.73	0.0254
		Initial body mass	1	2.60	0.1081
	Protein intake	Strain	1	117.94	< 0.0001
		P : C	2	0.99	0.3744
		Sugar	1	16.68	< 0.0001
		Strain × P : C	2	1.83	0.1622
		Strain × sugar	1	20.15	< 0.0001
		P : C × sugar	2	0.66	0.5185
		Strain × P : C × sugar	2	0.12	0.8913
		Initial body mass	1	3.45	0.0644
	Carbohydrate intake	Strain	1	191.44	< 0.0001
		P : C	2	214.01	< 0.0001
		Sugar	1	14.72	0.0002
		Strain × P : C	2	65.99	< 0.0001
		Strain × sugar	1	30.32	< 0.0001
		P : C × sugar	2	2.72	0.0681
		Strain × P : C × sugar	2	9.68	< 0.0001
		Initial body mass	1	1.52	0.2191
	Oocyte length	Strain	1	256.89	< 0.0001
		P : C	2	59.83	< 0.0001
		Sugar	1	10.34	0.0015
		Strain × P : C	2	29.38	< 0.0001
Strain × sugar		1	4.64	0.0322	
P : C × sugar		2	1.08	0.3402	
Strain × P : C × sugar		2	1.70	0.1849	
Initial body mass		1	1.54	0.2154	
Choice	Dry mass intake	Strain	1	-7.74	< 0.0001
		Sugar	1	4.22	< 0.0001
		Strain × sugar	1	4.34	< 0.0001
		Initial body mass	1	-0.26	0.7974
	Protein intake	Strain	1	-5.79	< 0.0001
		Sugar	1	3.31	0.0014
		Strain × sugar	1	4.13	< 0.0001
		Initial body mass	1	-0.33	0.7387
	Carbohydrate intake	Strain	1	-8.51	< 0.0001
		Sugar	1	4.56	< 0.0001
		Strain × sugar	1	4.27	< 0.0001
		Initial body mass	1	-0.20	0.8399
	Oocyte length	Strain	1	-8.15	< 0.0001
		Sugar	1	3.15	0.0024
		Strain × sugar	1	2.63	0.0104
		Initial body mass	1	0.29	0.7749

GA, glucose-averse cockroaches; WT, wild-type cockroaches.

greater oocyte growth at higher dietary carbohydrate ratio (Fig. 4), except for the oocytes in GA females restricted to glucose-containing diets. However, the oocytes in WT females were progressively longer than

those in GA females at increasing dietary carbohydrate ratio (Fig. 4). The oocytes in WT females given choice were of similar length as those in the WT females restricted to the most carbohydrate-rich diets, but

**Table 4** Coefficient of variation (CV) in protein and carbohydrate intake across dietary P : C ratios within each strain and dietary sugar type under no-choice conditions. Equal variation in protein vs. carbohydrate intake is tested with a Levene's test. Significant differences ( $P < 0.05$ ) show that intake of the nutrient with a lower CV (protein) is regulated significantly tighter than intake of the nutrient with a higher CV (carbohydrate).

	CV protein	CV carbohydrate	d.f.	F	P
GA G	1.28	1.33	1	0.59	0.4444
GA F	0.58	0.86	1	22.32	< 0.0001
WT G	0.57	0.93	1	57.15	< 0.0001
WT F	0.47	0.85	1	42.60	< 0.0001

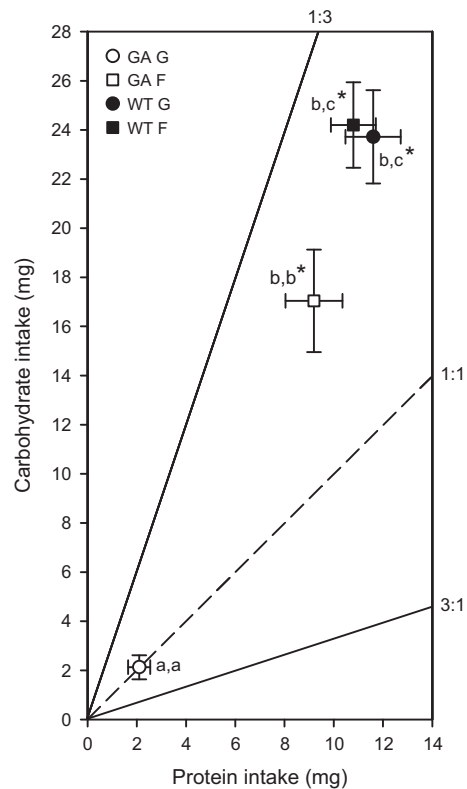
GA, glucose-averse cockroaches; WT, wild-type cockroaches; G, glucose-containing diets; F, fructose-containing diets.

generally longer than in the WT females given rat chow (Fig. 4). In contrast, oocytes in GA females given choice between fructose-containing diets were significantly longer than in GA females restricted to the most carbohydrate-rich, fructose-containing diet, but were of similar length as those in GA females given rat chow (Fig. 4).

## Discussion

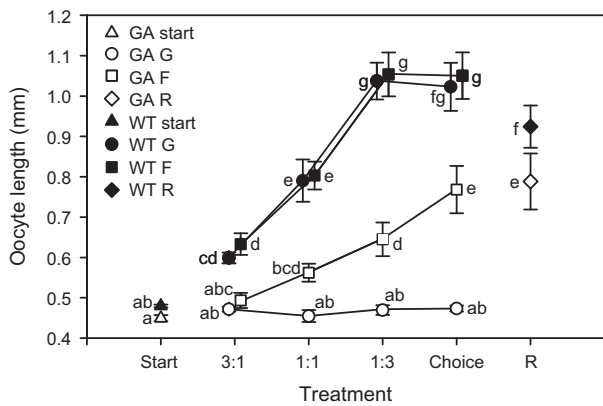
The sensory reception and central nervous system processing of taste stimuli and the associated acceptance or rejection behaviours are subject to strong natural selection (Simpson *et al.*, 1991; Wada-Katsumata *et al.*, 2013), because these processes dramatically affect feeding, subsequent performance and overall fitness. Whereas deterrent avoidance has been studied in relation to nutrient balancing in locusts and caterpillars (Bernays & Raubenheimer, 1991; Raubenheimer, 1992; Simpson & Raubenheimer, 2001; Behmer *et al.*, 2002; Singer *et al.*, 2002), nutrient balancing adaptations in relation to toxins mixed with phagostimulants to promote ingestion of lethal doses have only recently been studied (Shik *et al.*, 2014). Our study shows clear differences in sexual maturation and carbohydrate vs. protein intake balancing between female GA and WT German cockroaches, both in the presence and in the absence of dietary glucose.

With the exception of GA females fed glucose-containing diets, the rule of compromise used by the cockroaches in our experiment strongly supports the theory that omnivores eat until their protein requirements are covered but do not overingest large amounts of protein (Fig. 2), known as the protein leverage hypothesis (Sørensen *et al.*, 2008; Jensen *et al.*, 2013). It is becoming increasingly clear that protein has a deleterious effect if present at a high ratio in the diet, with reduced lifespan as a consequence (Lee *et al.*, 2008; Maklakov *et al.*, 2008; Schmehl *et al.*, 2014; Solon-Biet *et al.*, 2014). This effect might be particularly pronounced in



**Fig. 3** Ingestion (mean  $\pm$  SEM) of protein and carbohydrate under choice conditions. The slopes of the solid lines show the C : P ratios of the two provided choice diets, and the P : C ratio of each diet is given by the end of each line. The dashed line indicates an intake ratio of 1 : 1, which would result from equal consumption from the two choice diets. Different letters indicate significant differences in protein or carbohydrate intake, respectively, separated with a comma (Student's *t*-test:  $P < 0.05$ ). Asterisks indicate P : C intake ratios that were significantly more carbohydrate biased than 1 : 1 (paired *t*-tests,  $P < 0.0001$ ). GA, glucose-averse cockroaches; WT, wild-type cockroaches; G, glucose-containing diets; F, fructose-containing diets.

cockroaches (Haydak, 1953; Hamilton & Schal, 1988), which are adapted to low protein availability and do not possess mechanisms to excrete excess and potentially toxic nitrogenous waste compounds such as urates and uric acid (Cochran & Mullins, 1982; Cochran, 1985). Instead, the German cockroaches, and most other cockroaches, efficiently preserve nitrogen via special mechanisms, including storage and recycling of nitrogenous waste compounds through symbiosis with bacteria (*Blattabacterium cuenoti*) in specialized cells located in the fat body (Sabree *et al.*, 2009; Patiño-Navarrete *et al.*, 2014). The different rule of compromise applied by GA cockroaches restricted to glucose-containing diets – consuming equal mass independent of P : C ratio – might therefore reflect eating to a constant combined intake of two deterrent nutrients: glucose through gustatory deterrence (Wada-Katsumata *et al.*,



**Fig. 4** Oocyte lengths (mean  $\pm$  SEM) at eclosion and after feeding on the dietary treatments. The ratios on the x-axis are P : C. Different letters indicate significant differences (Student's *t*-test:  $P < 0.05$ ). GA, glucose-averse cockroaches; WT, wild-type cockroaches; G, glucose-containing diets; F, fructose-containing diets; R, rat chow.

2011, 2013), and protein through post-ingestive feedback mechanisms signalling nutrient-specific satiety (Simpson *et al.*, 1991).

Whereas GA cockroaches had very low food intake when restricted to glucose-containing diets, they also had lower consumption than WT cockroaches when glucose was replaced with fructose (Fig. 1). The present study thus provides the first solid evidence that glucose aversion may be linked with lower consumption of other sugars as well. Shik *et al.* (2014) similarly recorded lower fructose consumption by GA than WT nymphs when given a choice of fructose-containing diets. As fructose is a highly effective phagostimulant and no fructose aversion has been detected in sensitive gustation assays with this GA strain (Silverman & Bieman, 1993; Wada-Katsumata *et al.*, 2011, 2013), lower fructose intake should not be viewed as a dislike of fructose but more likely as a reduced sugar consumption rate possibly due to lower energy requirements associated with the slower oocyte development. Moreover, fructose-to-glucose isomerization would require conditions involving enzymatic processes which would not likely occur under our experimental conditions.

It is often observed that consumption is higher in animals that are given dietary choice than in animals restricted to single diets (Raubenheimer & Jones, 2006; Jensen *et al.*, 2012; Rho & Lee, 2014). This likely occurs because choice continually stimulates feeding to rebalance nutrients while ingesting a low ratio of the nutrient that has reached satiety (Rho & Lee, 2014). Such reduced stimulation to feed relative to choice conditions might explain why GA females had low consumption when restricted to single, fructose-containing diets (Fig. 1), but ingested enough when given choice to achieve similar oocyte development as when given rat

chow (Fig. 4). The relatively low consumption but high oocyte development by females given rat chow (Fig. 1) can be explained by satiated protein intake (Fig. 2) and the fact that rat chow also contains substantial amounts of lipid, which on a mass basis contains more than twice the amount of energy found in protein and carbohydrate.

The slower sexual maturation rates by GA females recorded in the present experiment correspond well with earlier experimental data on juveniles, which showed that nymphal development was slower in GA nymphs than in WT nymphs fed rat chow (Silverman, 1995); however, slower growth by GA nymphs was only seen on glucose-containing but not fructose-containing diets by Shik *et al.* (2014). As oocyte development is highly correlated with carbohydrate intake, the lower sugar intake by GA females would limit the availability of substrate to synthesize lipids for the oocytes, which in insects typically consist of 30–40% lipid (Ziegler & Van Antwerpen, 2006). Lower rates of sugar consumption might have an adaptive advantage by reducing the likelihood of ingesting lethal toxin doses, if baits are ingested at low levels as dietary supplements. Furthermore, ingesting low doses of toxin would select for various mechanisms of physiological resistance to toxicants (Georghiou, 1972), and glucose aversion may therefore provide a behavioural mechanism that promotes the evolution of physiological resistance to toxins in baits. However, if no toxic bait is present, the GA adaptation is a significant handicap that is likely to reduce overall fitness, and the GA strain would therefore be expected to be inferior under competitive conditions in the absence of toxic bait (Silverman, 1995; Shik *et al.*, 2014).

The significant interaction between strain and P : C ratio on oocyte length at 6 days shows that dietary P : C ratio affected the resulting oocyte lengths less in GA than in WT females, also when no glucose was present. This effect is at least partially due to the fact that the oocytes in the GA females were smaller than those in the WT females upon eclosion (Fig. 4). Lower levels of oocyte maturity and development in the GA strain, as well as slower growth in nymphs (Silverman, 1995), might be explained by inherently lower levels of juvenile hormone, which is known to regulate growth and oocyte development in cockroaches and other insects (Engelmann, 1983; Schal *et al.*, 1993, 1997; Goodman & Cusson, 2012). In *Pardosa* wolf spiders, specific nutrient balance in the prey had lower effect on growth in a slow-growing species compared to a sympatric fast-growing species, and the slow-growing species was therefore less dependent on consuming a balanced diet than the fast-growing species (Jensen *et al.*, 2011). Underlying endocrine signals affecting nutrient-specific dietary choice were recently indicated in cricket (*Gryllus firmus*) lines that were selected to develop into phenotypic morphs with different life



history trade-offs (Clark *et al.*, 2013). These crickets selected specific protein vs. carbohydrate compositions that matched the nutritional requirements of the genetically selected phenotype. Slower growth and sexual maturation rates in GA cockroaches, possibly controlled through the endocrine signalling system, might thus be an adaptation that makes GA cockroaches more adapted to nutritional stress by reducing the demand for carbohydrate and increase the chance of survival and successful reproduction if glucose-free energy sources are scarce.

Similar to GA cockroaches restricted to glucose-containing diets, locusts decreased consumption as tannic acid concentration increased in the diet (Raubenheimer, 1992; Simpson & Raubenheimer, 2001), except that the intake reduction by GA cockroaches fed glucose-containing diets was much larger. This can probably be explained by differences in gustatory responses to tannic acid and glucose (as deterrents), due to the differences in the coupling of these deterrents with post-ingestive toxins. Whereas tannic acid is mildly deterrent to locusts and signals low food quality, glucose is an exceptionally potent deterrent to GA cockroaches signalling the presence of highly toxic insecticides (Silverman & Bieman, 1993; Silverman & Ross, 1994).

Although the response of GA cockroaches is driven by gustatory deterrence and is therefore not directly toxin-induced, the feeding response to glucose-containing diets by GA cockroaches is highly comparable to the feeding response observed in animals that are infected with a toxin-producing pathogen. Infected animals typically reduce consumption rate (Exton, 1997; Ayres & Schneider, 2009; Adamo *et al.*, 2010). They furthermore tend to self-select a higher protein ratio, typically by reducing carbohydrate intake more than protein intake (Lee *et al.*, 2006; Povey *et al.*, 2009, 2013), and the relatively higher protein intake is speculated to support immune functioning by supplying amino acids for enhanced phenoloxidase activity and encapsulation response. The higher ratio of protein selected by GA cockroaches given choice of glucose-containing diets (Fig. 3) might similarly provide proteins for the production of enzymes to break down toxins, which under the evolved conditions would be coupled with glucose in baits, by up-regulating the expression of detoxification genes (Schmehl *et al.*, 2014). Interestingly, cabbage looper (*Trichoplusia ni*) larvae from a line with evolved resistance to toxic bacteria (*Bacillus thuringiensis*) had lower intake and growth compared to a susceptible strain when restricted to diets of variable P : C ratios (Shikano & Cory, 2014). Resistant larvae furthermore consumed less carbohydrate but similar amounts of protein when given a choice, similar to the pattern observed for GA females given fructose-containing diets in our experiment. This indicates that pathogens and toxins induce the same feeding response, possibly because their functioning and

effect on the host body are highly comparable, and that an increased protein intake ratio reduces the sensitivity to toxins and other environmental stressors (Archer *et al.*, 2014). However, the equal ingestion of protein and glucose by GA cockroaches given choice of glucose-containing diets could also occur if the cockroaches minimized the relative consumption of either deterrent nutrient (Bernays *et al.*, 1994).

In conclusion, glucose aversion appears to also affect the consumption of other carbohydrates such as fructose and to be associated with slower growth and sexual development, thereby prolonging time to reproduction. Glucose aversion is therefore a highly advantageous adaptation in the presence of toxic, glucose-containing baits, but would be a handicap in competition with WT cockroaches in situations where no toxic bait is present. Our study suggests that a lower requirement for carbohydrate to support development could be an adaptive advantage in GA cockroaches if glucose-free energy sources are scarce, and that by selecting for the GA trait, baits maintain cockroaches at slower developmental rates and thereby lower population growth. We furthermore propose that glucose aversion might facilitate the evolution of physiological resistance to toxins by reducing the intake from sugar-containing baits below lethal doses, and point out the interesting parallel between the feeding of GA cockroaches to that of insects infected with a toxic pathogen. Whether glucose aversion is an ancestral trait that originally evolved in response to glucose-linked allelochemicals in plant-derived detritus (Shik *et al.*, 2014) remains to be investigated.

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## Conflict of interest

The authors have no conflict of interest to declare.

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