

# Gustatory adaptation affects sexual maturation in male German cockroaches, *Blattella germanica*

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**Abstract.** Adaptations to hazardous environmental factors are essential for survival, although they may be maladaptive in conditions where the hazard is absent. In German cockroach (*Blattella germanica* L.) populations, glucose aversion has evolved rapidly in response to glucose-containing insecticidal baits, but little is known about the consequences of this behaviour in the absence of bait. In the present study, glucose-averse (GA) and wild-type (WT) male German cockroaches are restricted to a range of nutritionally defined diets containing either glucose or fructose as the sole carbohydrate source, and time to first expression of courtship is measured by stimulating the male antennae daily with isolated antennae from receptive, 6-day-old females. Glucose-averse males that are restricted to glucose-containing diets mature their courtship responses significantly later than GA males restricted to fructose-containing diets, whereas there is no difference in maturation of courtship responses between GA males restricted to fructose-containing diets and WT males restricted to diets containing either sugar type. Glucose-averse males furthermore respond later to GA female antennae than to WT female antennae, all from 6-day-old females. This suggests that GA females are less sexually stimulating, and the results are also consistent with earlier findings showing that GA females contain less developed oocytes than WT females at this age. These findings demonstrate that an adaptive gustatory mutation conferring protection from a toxin may have comparatively detrimental effects under conditions where the toxin has vanished, both by delaying female sexual maturation and signalling and by delaying male sexual maturation and courtship under conditions where glucose is a major energy source.

**Key words.** Adaptive behaviour, Blattodea, carbohydrate, courtship, developmental cost, fructose, glucose aversion, performance, taste evolution, toxin avoidance.

## Introduction

The extent of genetic adaptation to local environmental conditions is often manifested in individual development and performance (Via, 1984; Pashley, 1988; Stearns, 1989) and honest signals of genetic quality in that environment are widely used by females in sexual selection to assess potential sires (Moore, 1994; Kotiaho *et al.*, 2001; Tomkins *et al.*, 2004; South *et al.*, 2011; Warren *et al.*, 2013). However, an adaptation that is essential for survival in a certain environment may be disadvantageous under other environmental conditions. For example,

adaptations that evolve in response to environmental hazards, such as the presence of a predator or toxin, may be maladaptive under circumstances where the hazard lessens or is absent. Moreover, the presence of such hazards may fluctuate over time and space, potentially imposing opposite selection pressures.

The anthropogenic environment is a rapidly changing landscape, where commensal organisms must adapt to onslaughts by humans as a result of new technologies, chemistries and cultural practices. Antibiotic resistance and pesticide resistance are two of the best understood adaptive responses to anthropogenic selection. The German cockroach (*Blattella germanica* L.) is a common obligatory commensal in human establishments. It is an opportunistic omnivore, and so it experiences strong selection to exploit food sources maximally when they are available. Humans often attempt to eradicate this pest with

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various insecticides, including baits, in response to which German cockroaches have evolved multiple physiological and behavioural adaptations that allow populations to persist despite these interventions (Schal, 1992; Silverman & Bieman, 1993; Strong *et al.*, 1993; Silverman & Ross, 1994; Ross, 1997; Wang *et al.*, 2004, 2006; Gondhalekar & Scharf, 2012). However, interventions are inconsistent in time and space, and, in the absence of insecticidal baits, for example, such adaptations may be maladaptive and cause lower overall fitness compared with non-adapted individuals.

A unique and highly adaptive evolutionary response to glucose-containing insecticidal baits is a behavioural aversion to ingesting glucose (Silverman & Bieman, 1993). This heritable adaptation prevents glucose-averse (GA) individuals from consuming glucose-containing insecticidal baits, whereas non-adapted, wild-type (WT) individuals ingest the bait and die (Silverman & Ross, 1994). This response is particularly fascinating because glucose is a ubiquitous monosaccharide in nature and an important nutrient in the habitat of the German cockroach. Therefore, at the same time as protecting the cockroach from glucose-containing baits, glucose aversion severely limits its access to an important energy source. This trait appears to be controlled by a single major gene and, because it is highly adaptive where glucose is used to stimulate ingestion of insecticide baits, it has spread rapidly within populations (Silverman & Bieman, 1993; Silverman & Ross, 1994). Glucose aversion is found in multiple geographically separated populations, all sharing the same mechanism involving changes in taste neurones: glucose, which normally stimulates sugar-sensitive neurones in taste sensilla, also stimulates bitter-sensitive neurones in GA cockroaches (Wada-Katsumata *et al.*, 2011, 2013). Although they are protected from glucose-containing baits, in the absence of alternative foods, GA cockroaches ingest only small amounts of glucose-containing food and develop at a greatly reduced rate (Silverman, 1995; Silverman & Selbach, 1998; Shik *et al.*, 2014).

In the present study, male GA and WT German cockroaches are restricted to dietary treatments with either glucose or fructose as the sole carbohydrate source across three dietary protein-to-carbohydrate ratios or when given a choice between nutritionally complementary foods. The sexual maturation rate is then estimated as the time to the onset of male courtship in response to a female stimulus. It is hypothesized that male GA cockroaches will show delayed courtship behaviour as a result of slower sexual maturation when restricted to glucose-containing diets, irrespective of dietary protein-to-carbohydrate composition compared with WT males and GA males maturing on fructose-containing diets.

## 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), whereas the WT strain (Orlando Normal) was originally collected in

Orlando and has been maintained as a standard, unselected laboratory culture for more than 60 years (Silverman & Bieman, 1993). Cultures of both strains were maintained in the laboratory on water and rat chow (Purina 5001 Rodent Diet; PMI Nutrition International, St Louis, Missouri) provided *ad libitum*. The diet comprises a protein : carbohydrate (P : C) ratio of approximately 1 : 1.6 and 0.22% glucose, which does not induce aversive feeding behaviour in GA cockroaches (Shik *et al.*, 2014). The GA culture was selected monthly with a custom-made, glucose-containing bait containing 2% of the insecticide hydramethylnon over 2 days to maintain the frequency of glucose aversion coding alleles as close to 100% as possible. Prior to the experiments, cultures of both strains were distributed across four containers (45.7 × 22.8 × 30.4 cm) to reduce the risk of different rearing environment between the two strains, and left unselected for 3 months. The containers were then cleared of adults, and emerging adult males were collected within 24 h of eclosion and individually allocated to dietary treatments in transparent Petri dishes (diameter 100 mm, depth 16 mm). Experimental foods and water were provided *ad libitum* in inverted plastic lids (diets: 15 × 10 mm; water: 25 × 12 mm). Insect rearing and experiments were performed under an LD 12 : 12 h photocycle at 25 ± 2 °C and 35 ± 5% relative humidity.

### Design and procedures

Six nutritionally complete, synthetic foods were produced varying only in protein-to-carbohydrate (P : C) ratio (1 : 3, 1 : 1 and 3 : 1) and in the 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. The six synthetic foods are identical to the diets used by Jensen *et al.* (2015), where full recipes are presented. Because protein and carbohydrate contain approximately the same amount of energy by mass (approximately 16.7 kJ g<sup>-1</sup>), the energy value of the six foods was equal. Upon eclosion, experimental males were weighed to the nearest milligramme and allocated to one of eight dietary treatments ( $n = 20$  males of each strain per treatment). Six of the dietary treatments were no-choice diets where each cockroach was restricted to one of the six synthetic foods, and another two treatments were choice diets where each cockroach was allowed to self-select from the two nutritionally most extreme foods (3 : 1 and 1 : 3), with either glucose or fructose as the carbohydrate component in both foods. Food remained with a male until his first display of courtship.

### Measuring sexual maturation

Before they can court females and mate, males must undergo a period of sexual maturation (Uzšák & Schal, 2013). A sexually mature male responds to a contact sex pheromone on the female or on the female antennae with a species-typical rotation of the body through approximately 180° at the same time as raising his wings (Roth & Willis, 1952; Eliyahu *et al.*, 2009), thus exposing

glands with nuptial secretions on tergal abdominal segments (Nojima *et al.*, 1999). A receptive female then mounts the male's abdomen and feeds on the tergal gland secretion, thus placing herself in a proper position for copulation. Male wing-raising is required for copulation and is therefore the earliest clear indicator that the male is sexually mature and ready to mate. The time until first occurrence of courtship wing-raising was used as a measure of male sexual maturation. Courtship behaviour was assayed by stroking the male antennae vigorously for 30 s with an excised antenna from a 6-day-old adult WT female (Roth & Willis, 1952; Eliyahu *et al.*, 2009). The female antennae were taken immediately before use from live female cockroaches, and each antenna was used for stimulating up to five males (i.e. approximately 3 min) (Uzsák & Schal, 2013). Males from across treatments were lined up at random according to strain and age before testing. If chemical cues on the antennae were diminished with repeated use or if previous males deposited their cues on the antennae, this procedure ensures that these effects are limited and randomized across male treatments. All assays of courtship behaviour were performed 2 h after darkness and initiated after males fed for 3 days on their given diets.

To test whether GA males would display courtship behaviour earlier if stimulated with antennae from females of their own strain, a separate experiment was conducted in which GA males fed rat chow were stimulated daily with antennae from either WT or GA females from day 3 post-eclosion until wing raising was observed ( $n = 60$  GA males per female strain). All antennae used were taken immediately prior to use from 6-day-old females, the male sequence was randomized across strain and age, and each antenna was used for stimulating up to five males, as described above.

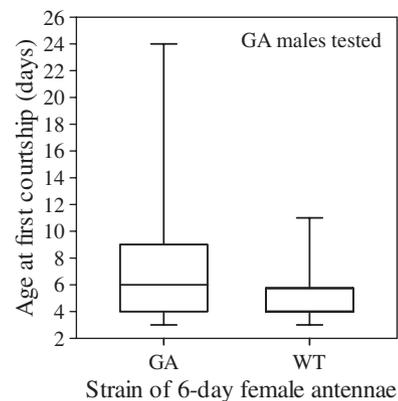
#### Statistical analysis

Animal weights were compared between cockroach strains using *t*-tests. The time to the initiation of male courtship behaviour was analyzed between strains using a proportional hazards test with strain, sugar type and diet as factors, and initial body mass as covariate, followed by proportional hazard tests between strains and sugar types with Bonferroni correction if  $P < 0.05$ . One GA male on glucose-containing diet did not court within 24 days of assays and was excluded from the analysis. A Wilcoxon test was used to test for differences in the time to the onset of courtship between GA males stimulated with antennae from either GA or WT females. All statistical analyses were performed in JMP, version 7.0 (SAS Institute Inc., Cary, North Carolina).

## Results

#### Animal weights

The mass of newly-eclosed GA males was significantly lower than that of WT males ( $42.12 \pm 0.23$  mg versus  $44.56 \pm 0.23$  mg (mean  $\pm$  SE), respectively; *t*-test:  $t_{360} = 54.58$ ,  $P < 0.0001$ ).



**Fig. 1.** Age of adult glucose-averse (GA) male *Blattella germanica* at first courtship when stimulated daily from day 3 with antennae from GA or wild-type (WT) females ( $n = 60$  males per female strain). All female antennae were from females that had matured for 6 days on rat chow after eclosion. Boxes show the median  $\pm$  25th percentiles, and error bars show 95% confidence intervals.

#### Dietary effects on maturation of courtship behaviour

Glucose-averse males displayed courtship behaviour significantly sooner when stimulated with antennae from WT females than when stimulated with antennae from GA females (Wilcoxon:  $\chi^2 = 6.98$ , d.f. = 1, 120,  $P = 0.0083$ ); median age of response to WT female antennae was 4 days post-eclosion, whereas the median age of response was 6 days post-eclosion when stimulated with GA female antennae (Fig. 1). Wild-type female antennae were therefore used for stimulating males of both strains in all subsequent assays.

Significant effects of cockroach strain and sugar type were found, as well as the interaction between strain and sugar type on maturation time until first courtship response (Table 1). Glucose-averse males matured significantly slower when restricted to glucose-containing diets than when given fructose-containing diets (Fig. 2); median age of response when restricted to glucose-containing diets was 5.5 days post-eclosion, whereas the median age of response was 4 days post-eclosion when given fructose-containing diets (Fig. 2). By contrast, WT males matured at a median age of 4 days post-eclosion independent of dietary sugar type (Fig. 2). Dietary composition other than sugar type had no significant effect on male maturation time (Table 1). A significant effect of mass upon eclosion was also found (Table 1), indicating that larger males courted sooner than smaller males.

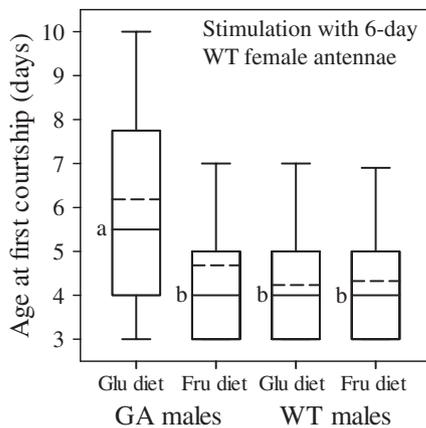
## Discussion

In response to persistent environmental hazards, animals evolve and maintain genetic adaptations, which may turn out to be costly and maladaptive in the absence of the hazards (Carrière *et al.*, 1994; Grassmann *et al.*, 2009). Glucose aversion has evolved in multiple *B. germanica* populations as an adaptive response to anthropogenic selection with glucose-containing toxic baits (Silverman & Bieman, 1993; Silverman & Ross,

**Table 1.** Proportional hazard test on the effects of strain (GA or WT), sugar type (glucose or fructose), diet (3 : 1, 1 : 1, 1 : 3, or choice) and initial body mass of male *Blattella germanica* ( $n = 20$  per strain, sugar type and diet) on the number of days under maturation until first courtship display.

Factor	d.f.	$\chi^2$	<i>P</i>
Strain	1	20.3766	< 0.0001
Sugar	1	4.6152	0.0317
Diet	3	5.5495	0.1357
Strain × Sugar	1	5.7671	0.0163
Strain × Diet	3	0.1905	0.9791
Sugar × Diet	3	1.7344	0.6293
Strain × Sugar × Diet	3	0.8869	0.8286
Initial body mass	1	4.8898	0.0270

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



**Fig. 2.** Adult age at first courtship for male *Blattella germanica* when stimulated daily from day 3 with a female antenna ( $n = 80$  males per strain per sugar type). All female antennae were from wild-type (WT) females that had matured for 6 days on rat chow after eclosion. Boxes show the median (solid) and mean (dashed)  $\pm 25$ th percentiles, and error bars show 95% confidence intervals. All dietary treatments are pooled within strain and sugar type. Different letters indicate significant differences (Bonferroni-corrected proportional hazards:  $P < 0.0083$ ). GA, glucose-averse; Glu, glucose-containing; Fru, fructose-containing.

1994). The GA trait confers a clear selective advantage by enhancing survival in the presence of bait, although this appears to come at a cost because GA juveniles develop more slowly than glucose-accepting conspecifics (Silverman, 1995).

The present study finds that GA German cockroach males mature slower when restricted to glucose-containing diets than when they have access to similar fructose-containing diets (Fig. 2 and Table 1), indicating that GA males have lower fitness in an environment where glucose constitutes an important nutrient source. This is consistent with findings on juvenile growth, which show that GA juveniles develop slower when restricted to glucose-containing diets (Silverman, 1995; Shik *et al.*, 2014), and on GA females, which have slower development of oocytes when restricted to glucose-containing diets during sexual maturation (Jensen *et al.*, 2015). Even a short delay in sexual maturation can have large consequences on fitness, especially in a

colonizer-type invasive species. When just a few juveniles establish a new population in the built environment, the first male to reach sexual maturity might sire all the local progeny. Under this scenario, GA males would be less readily available for mating after eclosion. In addition, slower sexual maturation in GA males may be accompanied by other deficiencies, and females may be able to sense the lower level of adaptation to the environment for GA males compared with WT males (Moore, 1994; South *et al.*, 2011; Warren *et al.*, 2013). This could be mediated by sex pheromones or the general taste, sweetness, concentration or overall amount of the nuptial secretion (Nojima *et al.*, 1999; Kugimiya *et al.*, 2003), which, in addition to lower body mass, might make GA males less attractive to females.

The assays with female antennae showing that GA males are stimulated to court sooner by antennae from 6-day-old WT females than from same-age GA females (Fig. 1) suggest that GA females might be less sexually mature than WT females at 6 days of age. This is supported by the findings of a previous study showing that GA females dissected after 6 days of sexual maturation on rat chow, and on all other diets tested, contain significantly smaller oocytes than WT females matured on the same diet (Jensen *et al.*, 2015). If the level of sexual maturity and readiness to mate is communicated via sex pheromone levels on the female antennae, as is shown in previous experiments on WT females (Schal *et al.*, 1991), this could explain the lower courtship response by males to 6-day old GA females compared with same-age WT females, and GA females at this maturity stage would therefore be deficient in attracting males (Liang & Schal, 1993) and stimulating them to court (Schal *et al.*, 1991).

The detrimental effect of glucose on sexual maturation in GA males documented in the present study is of a smaller magnitude than those measured for juveniles and sexually maturing females (Silverman, 1995; Shik *et al.*, 2014; Jensen *et al.*, 2015). Most likely, males require much less energy and nutrients to sexually mature because male maturation does not involve any morphological or physiological growth such as juvenile body growth and the growth of oocytes, and, for the same reasons, also occurs over a generally much shorter time frame. However, male German cockroaches have a relatively high consumption of carbohydrate-rich foods (Gordon, 1968), and a lack of access to glucose-free food clearly delays sexual maturation in male GA cockroaches and also possibly decreases their attractiveness to females by lowering pheromone levels (South *et al.*, 2011) and/or other sexual signals. In environments where glucose constitutes a major energy source, GA males probably have reduced fitness in the absence of bait as a result of postponed sexual maturation and therefore delayed chances to mate, in addition to a generally smaller body mass and possibly other deficiencies that might affect female choice.

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