

Effects of glucose-supplemented diets on food intake, nymphal development, and fecundity of glucose-averse, non-glucose-averse, and heterozygous strains of the German cockroach, *Blattella germanica*

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Abstract

Life history parameters were determined for glucose-averse (*glu/glu*), wild-type (*glu+/glu+*) and heterozygous (*glu/glu+*) genotypes of *Blattella germanica* (L.) (Blattodea: Blattellidae) fed diets supplemented with glucose. *Glu/glu* nymphs consumed less glucose-supplemented diet, gained less weight, developed slower and had a lower rate of survival than *glu/glu* nymphs fed the same diet without added glucose, or *glu+/glu+* and *glu/glu+* fed either diet. Prior to formation of the first oötheca, female *glu/glu* consumed less glucose-supplemented diet per day than *glu+/glu+* and *glu/glu+*, which presumably delayed egg case production. Oötheca-bearing *glu/glu* and *glu/glu+* females consumed less glucose-supplemented diet than *glu+/glu+* females. Despite a difference in female total diet intake, there was no effect of diet or genotype on fecundity. However, the intrinsic rate of increase (*r*) for *glu/glu* on unsupplemented diet was less than that of *glu+/glu+* and *glu/glu+*, suggesting that individuals with both *glu* alleles may be at a selective disadvantage in environments lacking diets containing glucose plus a toxicant.

Introduction

Recently, Silverman & Bieman (1993) identified a field-collected strain of glucose-averse *B. germanica* which were believed to have evolved in response to toxic baits containing glucose. Cockroaches of this strain (T-164) avoided glucose-agar mixtures in favor of plain, nutritionally inert agar despite 48 h of prior food deprivation. Cockroaches heterozygous for glucose-aversion responded to 1 M or greater glucose solutions similarly to homozygous glucose avoiders. Glucose-averse cockroaches were subsequently collected from other locations over a broad geographic range (Silverman & Ross, 1994).

Carbohydrates, particularly simple sugars, frequently enhance diet intake in insects (Bernays, 1985), and several mono and di-saccharides stimulate feeding in cockroaches (Tsuji, 1965). Studies on the nutritional requirements of cockroaches indicated that diets with >50% carbohydrate promoted optimal development (Cohen *et al.*, 1987; Forgash, 1958), and defined diets for the German cockroach, *Blattella germanica*

(L.) have included high levels of glucose as the carbohydrate source (House, 1949; Gordon, 1959; 1968). Despite its apparent dietary benefit to cockroaches, there is some evidence that glucose may have deleterious effects on insects. Bedoyan *et al.* (1992) discovered that development of *Manduca sexta* larvae was slowed and modification of the immune protein scolexin occurred following ingestion of excess glucose.

There would appear to be a selective advantage of glucose-aversion in environments containing glucose-toxicant mixtures. Less obvious is aversion to dietary glucose in response to some deleterious effect directly linked to this metabolic fuel. The work reported here was conducted to determine whether a nutritionally complex diet supplemented with glucose adversely affected nymphal development, reproduction, and survival of a *B. germanica* strain (Orlando normal) which recognizes glucose as a feeding stimulant. Nymphal cockroaches require food for growth, and adult females are highly dependent on food during each cycle of oöcyte maturation; egg cases are not produced if females fail to feed (Kunkel, 1966). Consequent-

ly, the response of glucose-averse and heterozygous nymphs and adults to diets supplemented with glucose in the absence of alternate diet and the developmental and reproductive consequences of this response were assessed. Although glucose is widely distributed within the habitat of *B. germanica*, there are many foods without it. If glucose were harmful to *B. germanica* then glucose-aversion alleles would enjoy a selective advantage, unless there were linkage to a deleterious trait(s). Therefore, the fitness of glucose-averse and heterozygous *B. germanica* fed a diet not supplemented with glucose was also assessed to understand whether a discernible genetic load was conferred by this trait.

Materials and methods

Cockroach strains. The following strains of *B. germanica* were used in the course of the experiment: *glu+/glu+*, a laboratory strain (Orlando normal) maintained for >40 years without exposure to insecticides, including insecticidal baits; *glu/glu*, a strain developed from cockroaches collected from an apartment (T-164) in Gainesville, FL which rejected an insecticidal bait containing glucose and which was maintained in the laboratory in the continuous presence of 2% hydramethylnon bait (Clorox Co., Pleasanton CA) with 11.8% D-glucose and alternate food without glucose (Purina dog chow [Ralston Purina, St. Louis MO]) for 18 months (ca. 5–9 generations) prior to the experiment; *glu/glu+*, an F₁ population obtained by crossing *glu/glu* males with *glu+/glu+* females.

Since *glu/glu* and *glu/glu+* both rejected ≤ 0.5 M glucose (Silverman & Bieman, 1993), it was necessary to determine whether selection with the glucose-containing hydramethylnon bait eliminated *glu/glu+* from the T-164 stock colony. The susceptibility of *glu+/glu+*, *glu/glu+* and *glu/glu* to the hydramethylnon bait was assessed by placing 20 males of each genotype (4 replicates) in containers with bait, dog chow, water and harborage (folded 5 cm diam filter paper). Mortality was assessed daily and LT₅₀'s and LT₉₀'s were calculated for each genotype.

Environmental conditions during insect rearing and experimentation were 27 °C, 50% r.h., and a L12:D12 photoperiod. Experiments were conducted in 0.5 liter glass jars (cage) containing a water vial, harborage and diet. A thin film of petroleum jelly/mineral oil (2:1) was applied along the inside rim to prevent insect escape. Although stock colonies were reared on dog chow, insects used in experiments were fed either

a standard diet of ground Purina #5012 Rat Chow, or rat chow supplemented with 18% D-glucose w/w (Sigma Chemical Co., St. Louis, MO) when it was learned that rat chow promoted greater growth and development of *B. germanica* than dog chow (Cooper & Schal, 1992a). Unsupplemented rat chow contained 0.3% w/w glucose. This level of glucose in rat chow was not detected by either *glu+/glu+* or *glu/glu* genotypes, as determined by a paired-comparison feeding assay. Glucose-supplemented diets were prepared by grinding 82 g of rat chow pellets, then adding 100 ml of 1 M glucose (18 g). Exactly 100 ml of diH₂O was added to the ground, unsupplemented rat chow. Both diets were mixed thoroughly and aliquoted into 34 cm³ plastic cups. The diets were dried at 60 °C to a constant weight (48 h).

Diet intake and development of immature cockroaches.

One to 3 day old nymphal *B. germanica* were collected from hatched oöthecae of each strain and groups of ten were confined in a cage. Nymphs of each genotype received either a rat chow or rat chow plus glucose diet. There were 10 replicate cages (100 nymphs) for each genotype-diet combination. Cages were examined daily, and dead nymphs were removed to reduce cannibalism. The quantity of diet consumed by the 10 nymphs was determined gravimetrically following drying. The remaining diet was weighed 28 days from the beginning of the study, following emergence of the first adult cockroach. Wet weight of the remaining live nymphs was also determined at this time. After weighing, insects were returned to their cages with the diet and adult emergence was monitored daily.

Adult diet intake, fecundity, and longevity studies.

Nymphs used in adult studies were fed whole Purina #5012 Rat Chow pellets. Male and female last instar nymphs were placed into separate containers. Adult eclosion was monitored daily and newly emerged females were placed singly into cages, whereas two newly emerged males were confined in each cage. Diets fed to females were preweighed, then dried and reweighed after each reproductive event, and after death. Females were provided with fresh diets following each oöthecal hatch, and at monthly intervals following production of the last oötheca. Males received fresh diets each month. Females and males of the same genotype and diet experience were mated. Beginning the fourth day after adult emergence, two males were introduced into each female cage for two hours during the photophase. The diet was removed from the

female cage during this period. Males were placed in the female cages each day until viable oöthecae were observed in 10 females per treatment. Males were not reintroduced after production of the first oötheca because one mating is normally sufficient for a female's entire reproductive life (Cochran, 1979). Daily food intake and timing between reproductive events were recorded. Male longevity on glucose supplemented and unsupplemented diets was also determined.

Effect of glu on biotic potential. Reduced fitness is recognized as a possible consequence of pesticide resistance (Georghiou & Taylor, 1977; Roush & McKenzie, 1987). Inheritance of the *glu* allele may place an individual at a fitness disadvantage. Since both nymphal development time and fecundity affect rates of population increase, and ultimately fitness, both parameters were used in the equation $r = (\log_e R_o) / T$ to compare genotypes, where r = the intrinsic rate of increase, R_o = net replacement rate (number of daughters per female), and T = mean generation time (Andrewartha & Birch, 1954). Because the first progeny produced during the adult life span have the greatest impact on population growth (Lewontin, 1965; Price, 1975), R_o was based on nymphs from the first oötheca, assuming a 1:1 sex ratio (Ross, 1991; Cochran & Ross, 1961). Values for T were obtained by randomizing female emergence times (col 5 of Table 2) and adding each of the first 10 emergence times to each row in column 4 (days to first oötheca) plus column 7 (days for first oötheca hatch) of Table 3. In the above studies insects were not offered a diet choice. *Glu/glu* and *glu/glu+* cockroaches present in environments where food choices are available would most likely select diets low in or lacking glucose. Consequently, r was calculated for each strain fed diets not supplemented with glucose to determine whether glucose-averse genotypes might be at a selective disadvantage relative to non-glucose-averse genotypes in the absence of dietary constraints.

Nymphal and adult parameters were analyzed using Two-way Analysis of Variance (ANOVA) and One-way ANOVA with Fisher's LSD test for mean separation (BBN Software Co., 1988).

Results and discussion

Purity of T-164 (glu/glu) stock colony. Bioassay of *glu+/glu+*, *glu/glu+* and *glu/glu* with baits containing 2% hydramethylnon and 11.8% glucose, in the

presence of dog chow, revealed the following LT₅₀'s and LT₉₀'s (95% CI): *glu+/glu+* LT₅₀ 2.91 (2.61–3.21) days, LT₉₀ 4.74 (4.32–5.19) days; *glu/glu+* LT₅₀ 5.75 (5.03–6.56) days, LT₉₀ 10.64 (9.48–11.94) days; *glu/glu* LT₅₀ 22.20 (18.12–27.20) days, LT₉₀ 46.30 (33.26–64.44) days. Although bait (glucose) aversion differed significantly for each genotype, as indicated by non-overlapping confidence intervals, the closer response of *glu/glu+* to *glu+/glu+* indicated that continuous exposure of T-164 *B. germanica* to glucose-containing hydramethylnon baits over several generations probably produced a pure *glu/glu* population.

Diet intake and development of immature cockroaches. There were significant strain ($F = 25.58$; $df = 2, 59$; $P = 0.00001$) and diet ($F = 19.08$; $df = 1, 59$; $P = 0.0001$) differences in nymphal diet intake. Although glucose-supplemented diet was consumed, *glu/glu* nymphs had the lowest intake over a 28 day period (17.3 mg) (Table 1). Since male *glu/glu* rejected a 1 M glucose solution, even after 48 h of food deprivation (Silverman & Bieman, 1993), incorporation of the same glucose concentration within a complex diet (rat chow) may have partially masked its deterrence to *glu/glu*. *Glu/glu* nymphs were provided the non-choice, 18% glucose-rat chow diet continuously and may have altered their feeding pattern to ingest small amounts frequently, rather than consuming fewer but longer meals of a non-deterrent diet. Characteristics of phytophagous insect feeding behavior such as meal duration, total time spent feeding and amount eaten are altered when fed plants containing deterrents (Schoonhoven *et al.*, 1992), and some herbivorous animals will ingest small quantities of plant material to allow time for detoxification of deleterious allelochemicals (Slansky, 1992). Although *glu+/glu+* and *glu/glu+* consumed the same quantity of glucose-supplemented and unsupplemented diet, nymphs fed a glucose-supplemented diet achieved a lower wet weight gain than nymphs on unsupplemented diet ($F = 92.00$; $df = 1, 59$; $P = 0.00001$), which was expected given that glucose is converted primarily to energy rather than biomass (Dadd, 1985). *Glu/glu* gained less weight than either *glu+/glu+* or *glu/glu+* on unsupplemented diet and were ca. 50% of the mass of the other strains when fed a glucose-supplemented diet. The conversion of food to biomass (wet weight) was affected by both strain ($F = 22.92$, $df = 2, 59$; $P = 0.00001$) and diet supplement ($F = 61.01$; $df = 1, 59$; $P = 0.00001$). Weight gain in *glu/glu* fed a glucose-supplemented diet was not correlated with diet consumption ($r = 0.38$, $P > 0.05$), indicating that

Table 1. Diet consumption (\pm SD) and weight gain of nymphal *B. germanica*

Genotype	18% Glucose Supplement	N	Diet	Wet Wt	Gain/
			Consumed (mg)	Gain (mg)	Consumed
<i>glu+/glu+</i>	Yes	88	24.6 \pm 2.03b	24.7 \pm 4.00b	1.0 \pm 0.10b
	No	91	25.2 \pm 2.28b	29.0 \pm 3.07c	1.2 \pm 0.05c
<i>glu/glu+</i>	Yes	93	23.4 \pm 1.55b	23.4 \pm 2.11b	1.0 \pm 0.10b
	No	95	25.3 \pm 1.86b	29.8 \pm 4.03c	1.2 \pm 0.12c
<i>glu/glu</i>	Yes	70	17.3 \pm 4.06a	12.4 \pm 2.13a	0.7 \pm 0.16a
	No	87	22.8 \pm 1.29b	23.7 \pm 1.44b	1.0 \pm 0.05b

Column means followed by the same letter are not significantly different ($P=0.05$; Fisher's LSD test).

Table 2. Mean survivorship (\pm SD) and duration of nymphal stadia of *B. germanica*

Genotype	18% Glucose Supplement	% Adults	Days to adult	
			Male	Female
<i>glu+/glu+</i>	Yes	85 \pm 7.07b	41.7 \pm 2.62ab	41.4 \pm 4.53b
	No	86 \pm 5.16b	40.9 \pm 2.35a	40.1 \pm 3.27ab
<i>glu/glu+</i>	Yes	88 \pm 6.32bc	42.8 \pm 3.17bc	43.0 \pm 4.18c
	No	94 \pm 9.66c	40.5 \pm 1.80a	39.2 \pm 1.38a
<i>glu/glu</i>	Yes	58 \pm 13.98a	58.6 \pm 6.42d	56.1 \pm 4.49d
	No	85 \pm 10.27b	44.3 \pm 2.89c	43.7 \pm 3.83c

Column means followed by the same letter are not significantly different ($P=0.05$; Fisher's LSD test)

food to biomass conversion in *glu/glu* was affected by glucose, thereby providing a possible metabolic explanation for the origin of glucose-aversion behavior. Bedoyan *et al.* (1992) reported that excess dietary glucose, but not fructose, slowed the development of *M. sexta* larvae, possibly by altering immune system function. Diet consumption and utilization studies to determine the efficiency of biomass (dry weight) conversion in *glu+/glu+* and *glu/glu* are in progress.

Nymphal survival to the adult stage was strain ($F=21.41$; $df=2,59$; $P=0.00001$) and diet ($F=20.40$; $df=1,59$; $P=0.00001$) dependent. Excess dietary glucose significantly reduced *glu/glu* nymphal survival (Table 2). Both male ($F=208.58$; $df=2,233$; $P=0.00001$) and female ($F=163.91$; $df=2,260$; $P=0.00001$) *glu/glu* nymphs developed slower than either *glu+/glu+* or *glu/glu+* when fed rat chow or glucose-supplemented rat chow. There are many examples of reduced growth rates and viability of immature insecticide resistant arthropods (Ferrari & Georghiou, 1981; Roush & Plapp, 1982) including German cockroaches (Ross, 1991). Glucose-supplemented diets retarded *glu/glu* and *glu/glu+*

male ($F=187.50$; $df=1,233$; $P=0.00001$) and female ($F=158.25$; $df=1,260$; $P=0.00001$) development (Table 2).

Adult diet intake, fecundity and longevity. Both strain ($F=59.04$; $df=2,47$; $P=0.00001$) and diet ($F=7.01$; $df=1,47$; $P=0.01$) affected the duration of the adult emergence – first oötheca interval. *Glu+/glu+* and *glu/glu+* produced oöthecae 10–11 days after the imaginal molt, and excess dietary glucose did not affect the time to oötheca formation (Table 3). *Glu/glu* females took ca. 1.5-fold longer to produce an oötheca than the other genotypes on unsupplemented diet and ca. 2-fold longer on glucose-supplemented diet, thereby accounting for the significant interaction between strain and diet ($F=9.75$; $df=2,47$; $P=0.0003$).

There was a strain effect on both total diet consumption ($F=15.31$; $df=2,47$; $P=0.00001$) and daily consumption ($F=21.21$; $df=2,47$; $P=0.00001$) within the interval between the imaginal molt and production of the first oötheca. Females with one or both *glu* alleles consumed the most diet during the interval, however, on a daily basis *glu/glu* females consumed the least

Table 3. Diet consumption by female *B. germanica* and event duration within the first two reproductive cycles

Genotype	18% Glucose Supplement	Emerge-Oötheca I				Oötheca I - Hatch I				Hatch I - Oötheca 2				Oötheca 2 - Hatch 2		
		n	Diet			Days	Diet			n	Diet			Diet		
			Consumed (mg)	C/D*	(mg)		Consumed (mg)	C/D*	(mg)		Consumed (mg)	C/D*	(mg)	Consumed (mg)	C/D*	
<i>glu+/glu+</i>	Yes	9	10.1a	44.1ab	4.4bc	21.6a	37.1c	1.7c	9	5.7a	48.5a	8.6a	20.2a	28.0c	1.4b	
	No	10	10.8a	41.9a	3.9ab	21.4a	48.3c	2.3c	9	5.8a	51.7ab	9.0a	20.4a	23.4c	1.1b	
<i>glu/glu+</i>	Yes	10	10.4a	54.0b	5.2c	21.8ab	19.7ab	0.9ab	9	7.4b	71.6bc	9.5a	20.2a	8.0a	0.4a	
	No	10	10.1a	55.0bc	5.4c	22.0ab	24.7b	1.1b	9	7.9b	60.6abc	8.0a	19.6a	22.0bc	1.1b	
<i>glu/glu</i>	Yes	10	21.1c	65.7c	3.2a	23.1c	8.9a	0.4a	8	9.9b	81.4c	8.6a	20.3a	2.1a	0.1a	
	No	10	14.7b	52.8b	3.8ab	22.5bc	24.1b	1.1b	10	7.6b	68.7bc	9.2a	20.3a	11.1ab	0.5a	

Column means followed by the same letter are not significantly different ($P=0.05$; Fisher's LSD test).

* Diet consumed per day.

Table 4. Female *B. germanica* total diet consumption, fecundity and longevity

Genotype	18% Glucose Supplement	Total diet			Total		Diet consumed per day (mg)
		Consumed (mg)	No. Oöthecae	Nymphs/Oötheca	nymphs	Longevity (Days)	
<i>glu+/glu+</i>	Yes	424.1b	4.3a	36.8a	158.8a	190.9ab	2.3b
	No	396.1ab	3.5a	40.1a	137.0a	178.6ab	2.2b
<i>glu/glu+</i>	Yes	447.6b	3.5a	34.9a	118.6a	235.2b	1.9ab
	No	374.9ab	3.2a	37.9a	123.3a	191.1ab	2.0ab
<i>glu/glu</i>	Yes	287.6a	2.9a	35.5a	100.5a	169.6ab	1.8a
	No	348.3ab	3.8a	36.2a	136.4a	153.0a	2.3b

Column means followed by the same letter are not significantly different ($P=0.05$; Fisher's LSD test).

(Table 3). Since glucose diets were consumed, aversion to glucose by non-gravid *glu/glu* females was apparently modulated by hunger cues. For oöthecal production to occur, females must feed (Kunkel, 1966); females feed intensively prior to egg case formation (Cochran, 1983; Hamilton & Schal, 1988) which corresponds with rapid oöcyte development (Roth & Stay, 1962). When fed protein-deficient diets *B. germanica* oöcyte growth is retarded and the preoviposition period is prolonged, though total diet consumption during this period is comparable to that of females provided normal diets (Cooper & Schal, 1992b; Schal *et al.*, 1993). As the duration of any developmental event increases, the cost of maintenance (energy production) increases as well. Therefore, *glu/glu* consumed more of a glucose-supplemented diet because they spent more time in the preoviposition stage though they ate less per day. In lepidopterous larvae, juvenile hormone influences the feeding center in the CNS stimulating food intake (Sieber & Benz, 1978; Muraleedharan & Prabhu, 1981). Peak juvenile hormone release in isolated *B. germanica* females occurs 10 days after

the start of the first gonotrophic cycle (Gadot *et al.*, 1989). Diet quality affects both JH release and oöcyte growth in female *B. germanica*, both directly through the role of the nutritional milieu on corpora allata activation and indirectly through brain disinhibition of the corpora allata (Schal *et al.*, 1993). Although JH affects the ovarian cycle in *B. germanica* and the ovarian cycle modulates feeding, there is no direct evidence that JH regulates feeding (C. Schal, pers. comm.). There is also evidence of habituation and sensory adaptation to plant-derived antifeedants in several phytophagous insects (Schoonhoven, 1982). Feeding on a glucose-supplemented diet by glucose-averse female cockroaches may be explained by either or both of these processes.

Two *glu/glu* females provided the glucose-supplemented diet were observed mating 17 days after the imaginal molt and a third was observed mating 25 days after the molt. These 3 females produced viable oöthecae 4 days after mating. A *glu/glu* female on unsupplemented diet mated 11 days after emergence and also produced an oötheca 4 days later. Durbin &

Table 5. Longevity of male *B. germanica* genotypes on glucose-supplemented and unsupplemented diets

Genotype	Survival (days) on diet (mean \pm SD)	
	Glucose	No glucose
<i>glu+/glu+</i>	115.1 \pm 38.35b *	87.3 \pm 32.12a
<i>glu/glu+</i>	116.0 \pm 42.35b	117.9 \pm 38.56b
<i>glu/glu</i>	88.3 \pm 38.05a	84.7 \pm 26.30a

Column means followed by the same letter are not significantly different ($P=0.05$; Fisher's LSD test). Row with * indicates significant difference (t -test; $P=0.05$).

Cochran (1985) reported that mating in *B. germanica* was delayed when females were deprived of food for up to 12 days immediately following the imaginal molt, however, the time to oötheca production was unaffected. Furthermore, withdrawal of food from the females after mating also did not effect the period between mating and oötheca production. Oöcyte maturation and sex pheromone production in *B. germanica* are maximal 5 to 10 days into the first gonotrophic cycle, and starved females accumulated little cuticular pheromone (Schal *et al.*, 1990). Since female pheromone production and receptivity, and oöcyte maturation are JH-dependent and deficient diets and starvation affect JH synthesis and release by the corpora allata (Gadot *et al.*, 1991; Burns *et al.*, 1991; C. Schal, pers. comm.), these events may be delayed until sufficient nutrients are accumulated thereby postponing courtship and mating. Hamilton & Schal (1988) noted excess consumption of low protein diets by *B. germanica* females prior to mating, apparently to compensate for the reduced diet quality. Though it may appear that females with both *glu* alleles were at a disadvantage by delaying mating until adequate resources had been procured, males mate repeatedly (Ueda *et al.*, 1969). Since a 1:1 male:female ratio is approximately maintained in *B. germanica* populations (Ross, 1991; Cochran & Ross, 1961), mating opportunities should not be lost. Although not measured, the significantly greater consumption of the glucose-supplemented diet by *glu/glu* during the first oötheca production period may have occurred between mating and oötheca production. An alternate explanation for the apparent disparity between high glucose diet consumption and delayed oötheca production (delayed mating) in *glu/glu* may be that females were paired with males of the same genotype fed the same diet type. Therefore, a male's ability to mate successfully may have been impaired by linkage of *glu* with a deleterious trait related to mating, or perhaps nutrient

reserves needed to complete spermatophore transfer were insufficient. *Glu/glu* males were observed wing raising within minutes after the initial pairing with females (5 days), so apparently receptivity to female-produced pheromone was not diminished.

An effect of strain on incubation time for the first oötheca was evident ($F=13.16$; $df=2,47$; $P=0.00001$), with oöthecae from *glu/glu* females requiring more time to hatch than the other strains (Table 3). The amount of diet consumed by females bearing the first oötheca was affected by both strain ($F=24.93$; $df=2,47$; $P=0.00001$) and diet ($F=11.10$; $df=1,47$; $P=0.002$). Heterozygotes and homozygous glucose-avoiders consumed significantly less diet than homozygous glucose-accepting females, and *glu/glu* on a glucose-supplemented diet consumed less than 0.5 mg per day. Female *B. germanica* feed infrequently and consume little while carrying an egg case (Cochran, 1983; Hamilton & Schal, 1988). Since oöcyte development was completed for the first oötheca and not initiated prior to formation of the second oötheca, nutritional requirements were relatively low. Consequently, aversion to glucose was not overridden by diet procurement needs.

Production of the second oötheca was slower in the *glu/glu+* and *glu/glu* strains ($F=14.17$; $df=2,47$; $P=0.00001$) independent of diet. There was a strain effect on diet consumption during this interval ($F=11.17$; $df=2,47$; $P=0.0001$), however, the quantity of diet consumed per day by each strain on either diet did not differ. More diet was consumed per day prior to the production of egg case 2 than for egg case 1, especially in *glu/glu* and *glu/glu+* on glucose-supplemented diets. *B. germanica* females use 90% of accumulated reserves for the production of each oötheca (Kunkel, 1966). Since consumption of glucose-supplemented diets by *glu/glu* and *glu/glu+* was very low during the prolonged oötheca 1 incubation period, energy reserves may have been excessively depleted, thereby necessitating intake of additional nutrients for the second gonotrophic cycle. As was true for oötheca 1, diet consumption by females bearing the second oötheca was less in individuals with the *glu* allele, particularly when provided a glucose-supplemented diet (Table 3).

Total diet consumed over a female's lifetime was affected by strain ($F=3.14$; $df=2,47$; $P=0.05$); *glu+/glu+* and *glu/glu+* consumed the most and *glu/glu* ate the least of a glucose-supplemented diet (Table 4). Despite a difference in diet consumption, there was no effect on oöthecal production, nymphs per oötheca

or total nymphs per female. Diet affected female longevity ($F=4.61$; $df=1,47$; $P=0.04$) with individuals fed glucose-supplemented diets living longer than females on unsupplemented diets. Although excess dietary glucose prolonged female survival, glucose-supplemented diets were consumed less over the female's lifetime ($F=5.28$; $df=1,47$; $P=0.03$). A strain by diet interaction ($F=5.84$; $df=2,47$; $P=0.006$) was evident, as daily lifetime consumption was significantly higher for *glu+/glu+* with or without supplemental glucose than *glu/glu* on a glucose-supplemented diet (Table 4).

The longevity of male *B. germanica*, paired with the females studied above, was determined. A significant strain effect was identified ($F=7.07$; $df=2,119$; $P=0.001$); males with one *glu* allele had the longest while those with both *glu* alleles had the shortest lifespan (Table 5). Also, *glu+/glu+* males lived longer when their diet was supplemented with glucose. Since diet consumption was not measured, it is not known whether male longevity was affected by the quantity of diet ingested.

Effect of *glu* on biotic potential. The intrinsic rate of increase (r) of *glu/glu* (0.036 ± 0.002 [mean \pm SD] female progeny female $^{-1}$ day $^{-1}$) was significantly less than both *glu+/glu+* (0.041 ± 0.004) and *glu/glu+* (0.042 ± 0.003) ($F=11.18$; $df=2$; $P=0.00001$). Similar r values for *glu+/glu+* and *glu/glu+* indicates that the effects of glucose aversion on fitness were recessive. Roush and Plapp (1982), in describing the fitness of insecticide resistant genotypes, indicated that even though RR and SS may differ in fitness, RS and SS genotypic differences are more important since heterozygotes will be the most common carriers of resistance during its early stage. If the same statement is true for glucose aversion there would appear to be no selective disadvantage to *glu*. The fitness of *glu* is relevant in environments where insects have a diet choice. Therefore, r was calculated for each genotype fed diets not supplemented with glucose since *glu/glu+* and *glu/glu* genotypes would generally reject high-glucose foods in nature when other foods were available. Undoubtedly, *glu/glu* and *glu/glu+* would have a lower r when confined to high glucose diets. It would also be of interest to measure the fitness of *glu/glu* and *glu/glu+* when fed glucose-supplemented diets throughout the insect's entire lifespan, as lower diet consumption by nymphs should affect fecundity. Also, estimates of genotypic fitness based on 'population cage' studies are preferred for insecticide resistance fitness evalua-

tions (Roush & McKenzie, 1987) and would be helpful in determining how competitive the *glu* allele is. The *glu+/glu+* and *glu/glu* strains used in the present study had different geographic origins. Therefore the fitness of *glu/glu+* may have been inflated due to heterosis as was suggested by Ferrari & Georghiou (1981) for heterozygote, temephos-resistant mosquitoes. Furthermore, there is some evidence suggesting that the presence of modifiers improve the fitness of resistance alleles (co-adaptation) (Roush & McKenzie, 1987). No effort was made to backcross *glu/glu+* with *glu+/glu+* to isolate *glu/glu* in a wild-type background, therefore, other loci may have ameliorated the deleterious effects of *glu*.

Although *glu/glu* and *glu/glu+* nymphal development and oöthecal production were delayed, due primarily to reduced diet intake, glucose-supplemental diets were not toxic to *B. germanica*. Therefore, it appears that glucose was not the selective agent in the evolution of glucose-aversion behaviour. A more likely explanation is selection for glucose-averse phenotypes with glucose-linked allelochemicals and/or diets (baits) consisting of glucose plus a toxicant (Silverman & Bieman, 1993).

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