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**Short Communication**

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**Sex-Specific Food Preferences in the Madagascar Hissing Cockroach *Gromphadorhina portentosa* (Dictyoptera: Blaberidae)**

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*Accepted December 9, 2002; revised June 27, 2002*

**KEY WORDS:** Dictyoptera; Blaberidae; *Gromphadorhina*; food quality; sex specificity; nutrition.

**INTRODUCTION**

For most insects, adult nutrition affects not only survival of individuals but also their reproductive output. In particular, fecundity of females commonly depends on ingestion of protein necessary for egg development, whereas male fertility is not highly protein dependent (Chapman, 1982; House, 1974; Engelmann, 1999). Furthermore, because insects generally are unable to convert lipids to monosaccharides (Bignell, 1981), carbohydrates and proteins serve as primary energy sources in both sexes (House, 1974).

Recent studies reveal that a number of insects exhibit sex-specific differences in feeding behavior that are correlated with adult nutritional requirements. For example, young female tephritid fruit flies (Diptera: Tephritidae) that are protein-hungry are more attracted to odors of protein food baits than to odors of host fruit, whereas males and protein-fed females are attracted more toward fruit odors (Cornelius *et al.*, 2000, and references therein). Female peacock butterflies (*Inachis io*) and Adonis blue butterflies (*Lysandra bellagrus*) prefer floral nectars rich in amino acids, but males discriminate among nectars in favor of sugar content (Erhardt and Rusterholz, 1998; Rusterholz and Erhardt, 2000).

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We hypothesized that adult Madagascar hissing cockroaches, *Gromphadorhina portentosa*, might also exhibit sex-specific dietary preferences driven not so much by their sexual size dimorphism [female *G. portentosa* are 1.4 times heavier than males (Breed *et al.*, 1981; Darmo and Ludwig, 1995; Yoder and Grojean, 1997)], but by sex-associated differences in reproductive investment. Female *G. portentosa* invest heavily in production of large oothecae unlike males that produce small spermatophores (Roth, 1967; Leibensperger *et al.*, 1985), so females of this species, as in some other cockroaches (Cornwell, 1968; Mullins and Cochran, 1987; Clarebrough *et al.*, 2000), likely require substantially more protein in their diets than males. On the other hand, female *G. portentosa* are relatively immobile, whereas males exhibit vigorous, ritualized aggression and hissing toward other males to establish and maintain dominance-based territories in laboratory colonies (Nelson and Fraser, 1980; Breed *et al.*, 1981; Fraser and Nelson, 1984; Clark and Moore, 1994; Clark *et al.*, 1995), so males likely require more energy from carbohydrates to fuel their neuromuscular systems than females. Here we report on sex-specific food preferences for this cockroach when given a binary choice between a low-protein/high-carbohydrate item (raw apple) and a high-protein/high-carbohydrate/high-lipid item (moist dog treat).

## METHODS

### Cockroaches

We used adult male and female cockroaches ( $N = 160$ ) raised in eight laboratory colonies which had been isolated since 1990 in plastic cages ( $50 \times 35 \times 23$  cm) containing a wood-shaving bedding, several inverted cardboard flats for shelter, and *ad libitum* food (Purina Dog Chow) and water. Food and water were monitored weekly and occasionally raw banana, apple, and potato were offered as dietary supplements. All colonies were maintained in our laboratory under an approximate 12:12-h light:dark photoperiod at 23–26°C and ambient humidity.

### Tests of Feeding Preferences

A fully randomized design was used in our experiments. To evaluate the affect of hunger on food choice, we removed the food from four of eight colonies 2 weeks before conducting our tests. [This giant cockroach has a remarkable ability to retain body moisture and adults can survive for more than 1 month without food or water (Yoder and Grojean, 1997).] A total of 10 males and 10 females from each colony was placed singly in an inverted,

translucent plastic jar (9-cm diameter) in the middle of an arena. Each arena consisted of a plastic pan (28 × 21 × 12 cm) lined with a piece of white paper on which the layout of arena floor had been photocopied. The paper layout consisted of two 21-cm-long “end lines” drawn crosswise 7 cm from each end of the sheet, a 9-cm-diameter circle centered on the sheet, and two “plus” marks located 3.5 cm in from each end on the midline of the sheet.

After a cockroach was placed in the arena, we positioned a freshly cut, ~1.5-cm cube of raw apple (Yellow Delicious variety) and a similar-sized cube of moist dog treat (Heinz Canine Carry Outs Beef 'n Cheese Flavor) on the “plus” marks on the paper liner. We wore a new pair of disposable latex gloves whenever we handled a cockroach or either food item. After a 5- to 10-min acclimation period, we carefully lifted the plastic jar to release a cockroach when its head was located in the center of the arena. We timed to the nearest 0.1 min how long it took the cockroach to cross either end-line (= response time) and recorded which food item was located nearby (= food preference). If an insect remained in the middle of the arena and did not cross one of the end-lines within 10 min, we classified its food preference as “no response” and terminated the test. We returned cockroaches to their respective colonies when the tests were finished and fed them.

Paper liners were discarded after each test and replaced by new liners before another test was conducted to avoid the possibility of chemical contamination from residual olfactory cues of the sort this species is known to employ during mate choice (Leibensperger *et al.*, 1985). Furthermore, the north–south compass orientation of each arena was randomly varied between tests conducted on our laboratory bench under fluorescent illumination in a room with fully darkened windows.

We obtained information about the nutrient composition of pet foods used in our study by calling the consumer relations department of each manufacturer (Heinz Pet Products and Ralston Purina Company). We acquired comparable information about raw apples from the nutrient database of the Nutrient Data Laboratory in the Agriculture Research Service at the U.S. Department of Agriculture (<http://www.nal.usda.gov/fnic/foodcomp/Data/index.html>). The data are summarized in Table I.

We analyzed our results by AVOVA using the SYSTAT statistical package (Wilkinson, 1989). Subsequently we performed a chi-square analysis to test the hypothesis that the observed frequency of food chosen by cockroaches was independent of their sex (Zar, 1974).

## RESULTS

When released from the inverted jar, most cockroaches began to move their antennae back and forth before they walked out of the central circle

**Table I.** Relative Abundance of Nutrients in Two Food Items Offered to Cockroaches in Preference Tests Compared to the Standard Diet (Dog Chow)<sup>a</sup>

Nutrient	Abundance (%)		
	Standard diet	Raw apple	Dog treat
Water	12	83.9	34.0
Carbohydrate	47.9 (54.4)	15.3 (94.4)	38.2 (57.9)
Protein	21.0 (23.9)	0.2 (1.2)	12.5 (18.9)
Fat	8.0 (9.1)	0.4 (2.5)	7.0 (10.6)
Ash	6.7 (7.6)	0.3 (1.9)	8.6 (13.0)

<sup>a</sup>Values based on dry weight are in parentheses.

toward one side of the arena. Usually a cockroach quickly crossed an end-line and turned toward the nearby food item, whereupon it soon began to feed. Only 6 of 160 cockroaches showed no response in our study. All six non-respondents were females whose extended abdomens suggested that they were very gravid; moreover, they generally kept their antennae pressed to the substrate beneath their bodies. (Presumably all female cockroaches had mated prior to our tests since each colony contained many mature males.) On average a cockroach required 1.6 min from release until it crossed an end-line, but the data were highly variable ( $N = 154$ ,  $SD = 2.28$ , coefficient of variation = 3.29).

Analysis of variance revealed that the type of food chosen (food preference) was significantly associated with sex of the cockroach (Table II). But feeding history (=cockroach condition) and the colony an insect came from (=cockroach colony) were not significant variables. In addition, the time it took for a cockroach to cross an end-line (response time) did not vary significantly with any of the variables we measured and all interaction terms were insignificant ( $P > 0.05$ ).

Because all but one of the aforementioned variables were insignificant, we lumped the data for the cockroaches together by sex and eliminated the six females that did not respond from further consideration. As shown in Table III, there was a highly significant difference between

**Table II.** ANOVA Table for Food Chosen by Madagascar Hissing Cockroaches, *G. portentosa*

Source of variation	df	SS	MS	F ratio	P
Cockroach condition	1	0.310	0.310	1.267	0.262
Cockroach sex	1	9.994	9.994	40.825	0.0001
Cockroach condition * sex	1	0.306	0.306	1.252	0.265
Cockroach colony	3	0.542	0.542	2.214	0.139
Response time	1	0.608	0.608	2.484	0.117
Error	152	37.701	0.245		

**Table III.** Male and Female Madagascar Hissing Cockroaches, *G. portentosa*, Chose Different Foods<sup>a</sup>

Sex	Food item	
	Raw apple	Dog treat
Male	49/33.2	31/46.8
Female	15/30.8	59/43.2

<sup>a</sup>Data are given as observed/expected number of individuals ( $\chi^2 = 26.58$ ,  $N = 154$ ,  $df = 1$ ,  $P < 0.00001$ ).

the food preferences of male and those of female cockroaches. Most male *G. portentosa* (60% of 80 insects tested) chose the raw apple, whereas almost all female *G. portentosa* (80% of 74 animals) chose the moist dog treat.

## DISCUSSION

Based on the manner in which the cockroaches moved their antennae and walked toward a food item, we think that they were using instantaneous comparison of antennal chemoreceptor inputs and direct chemo-orientation (Bell, 1984) to nearby (<10 cm) odorous food in the arena.

To our surprise we found that food-deprived cockroaches located a food item in the arena as quickly as those having constant access to food (dry dog chow). Initially we thought that the food-deprived cockroaches would respond more quickly than those that were fed *ad libitum*, regardless of food items chosen. A possible explanation for our observations is that adult *G. portentosa* fed dry dog chow *ad libitum* might actually be hungry because they are chronically undernourished. Studies on growth, development, and reproduction in the German cockroach, *Blattella germanica*, show that dry dog chow is a low-quality diet because the steam extrusion process used to form kibble creates a hard-baked exterior that serves as a barrier to feeding and the heat damages or degrades proteins and other nutrients contained in the diet (Cooper and Schal, 1992a,b). Hence, if these results for German cockroaches are extended to Madagascar hissing cockroaches, then the reason why both of our treatment groups responded with comparable latencies to food was because both were deprived of certain key nutrients, which might even have been somewhat sex-specific. Perhaps if we had used rat chow as a standard laboratory diet, as recommended for the German cockroach (Cooper and Schal, 1992a,b), then *G. portentosa* in the "well-fed" treatment might have shown longer response latencies.

When designing our tests we thought that almost all *G. portentosa* might prefer raw apple to the moist dog treat because the fresh fruit is very different

from the regular diet of dry dog food, and as we have often observed in laboratory colonies, cockroaches are aroused by and attracted to the fruity odor, so they quickly locate and consume sliced apples. The fact that only 42% of cockroaches (49 males and 15 females) went to raw apple in our tests was much below the expected response level. The strong preference of female cockroaches (80%) for the moist dog treat was the major cause of this outcome.

Our results suggest female *G. portentosa* may be protein-hungry throughout most of their adult lives, as they repeatedly produce large oothecae, giving rise in them to a strong preference for foods rich in amino acids. In contrast, males of this species may tend to select carbohydrate-rich foods because they expend much energy engaging frequently in agonistic and other social interactions, but contribute little to reproduction (Leibensperger *et al.*, 1985; Clark and Moore, 1994; Clark *et al.*, 1995).

Cockroaches and other animals, including humans, are able to self-select a suitable diet given a variety of nutrient choices. The physiological and biochemical processes that regulate feeding behavior are understood sufficiently that one may construct a speculative model to explain our results (Engelmann, 1999; Cohen *et al.*, 2002; and references therein). Perhaps male *G. portentosa* have moderate to high levels of the neurotransmitter octopamine but low levels of serotonin in the brain and other tissues, causing them to feed preferentially on carbohydrate-rich foods. In contrast, female *G. portentosa* in the egg maturation and egg incubation periods possibly have high levels of octopamine and moderate to high levels of serotonin in their brains, so they would be stimulated to feed mostly on foods high in protein and lipids. Once the eggs are mature, feeding may be inhibited temporarily by neural output from the uterus until the ootheca is partially extruded, rotated 90°, and retracted into the membranous brood sac for incubation in this ovoviviparous cockroach.

It is reasonable to ask whether our results apply to wild *G. portentosa* in native Madagascar habitats. Unfortunately very little is known about the details of diets and microhabitats selected by free-ranging cockroaches except for the domestic species (Mullins and Cochran, 1987). For instance, Clarebrough *et al.* (2000) recently compared diet selection in feral and cultured American cockroaches, *Periplaneta americana*. They found that feral males consume a synthetic diet having more protein than cultured males because feral males allocate more ingested nitrogen preferentially to accessory sex glands that form the spermatophore. Proteinaceous secretions in the spermatophore are a form of paternal reproductive investment in this species: the additional protein donated by feral males is consumed by feral females and used by them to produce larger oothecae having more larger offspring than cultured *P. americana*. Because the spermatophore in

*G. portentosa* is small, the reproductive investment of nutrients by male Madagascar hissing cockroaches seems unlikely in any habitat, so we suspect the sexual difference in diet selection reported here may also prevail in the wild.

### ACKNOWLEDGMENTS

We thank Mary Jackson, Richard Daniel, and Jon DeHaven for care of the insects used in this study. We appreciate the technical assistance of Mary Jackson in preparing the manuscript and the comments of three anonymous reviewers that greatly improved the paper. Much of this work was performed as part of a junior high school science project (E.M.T.).

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