State-Dependent Attractiveness of Protein Bait and Host Fruit Odor to *Bactrocera cucurbitae* (Diptera: Tephritidae) Females

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ABSTRACT We evaluated responses of protein-deprived and protein-fed mature (26–30-d-old) female melon flies, *Bactrocera cucurbitae* (Coquillett), to odor of host fruit and of proteinaceous baits by using 1 by 1 by 1-m cages containing nonhost plants. Protein-deprived and protein-fed females were attracted equally to odor of host fruit. For both types of females, odor of cucumber, *Cucumis sativis* L., and cantaloupe, *Cucumis melo* L., was more attractive than odor of tomato, *Lycopersicon esculentum* L. Odor of kabocha, *Cucurbita maxima* Duchesne, was more attractive than the odor of bittermelon, *Momordica charantia* L., but not more attractive than zucchini squash, *Cucurbita pepo* L. In choice tests, protein-fed females preferred cucumber odor over protein odor, whereas protein-deprived flies showed an almost identical response to the two odors. Our findings suggest that some feral host-seeking *B. cucurbitae* females that have fed recently on natural sources of protein and carry mature eggs might bypass proteinaceous baits, reducing the effectiveness of current approaches to melon fly management.

KEY WORDS *Bactrocera cucurbitae*, host odor, protein bait, attraction, physiological state

FOR NEARLY A CENTURY, BAIT sprays containing insecticide have been used to control several different species of tephritid flies, including the melon fly, *Bactrocera cucurbitae* (Coquillett) (Severin et al. 1914, Back and Pemberton 1917, Steiner 1955, Nishida et al. 1957, Roessler 1989, Peck and McQuate 2000, Vargas et al. 2001). The strategy behind bait spray use for tephritid control is simple: the presence of bait in a spray mixture should attract adults to droplets of the mixture, followed by feeding and death (Chambers et al. 1974). Bait sprays should allow a reduction in the proportion of crop or land area receiving spray as well as a reduction in the amount of toxicant compared with broadcast application of insecticide alone in conventional sprays that kill primarily by contact.

Since the 1950s, the standard bait spray for tephritid control has been a combination of Staley's Protein Bait (PIB-7) or a very similar material (Nu-Lure) and malathion (Mangan and Moreno 1995, Moreno and Mangan 2001). Recently, other proteinaceous substances have been investigated as potential replacements for PIB-7 or Nu-Lure, and other toxicants have been evaluated as replacements for malathion (McQuate et al. 1999, Peck and McQuate 2000, Burns et al. 2001, Vargas et al. 2001, 2002). Malathion has been shown to harm several different kinds of beneficial and other nontarget insects (Hoy and Dahlsten 1984, Hoelmer and Dahlsten 1993, Messing et al. 1995). The most prominent candidate replacement toxicants (photoactive insecticidal dyes and spinosad) are more environmentally friendly than malathion. However, these alternative toxicants must be ingested before taking maximum effect, unlike malathion, which has considerable contact toxicity (DowElanco 1994, Mangan and Moreno 1995, Moreno and Mangan 2001). Hence, it is vital to combine them with baits that are highly phagostimulatory and, if possible, also highly attractive.

The issue of attractiveness is especially important when bait sprays are applied to border crops (Howell et al. 1975) or as spot treatments (Nishida et al. 1957) instead of a broadcast manner. In concept, the attractive component of a bait spray mixture could succeed as a lure by drawing tephritid flies searching for either food, mates, or egg-laying sites and relying on a powerful phagostimulant (such as sucrose) to elicit feeding after arrival. To date, attractive stimuli associated with tephritid bait sprays have signaled the presence of food (particularly proteinaceous food) and not other kinds of resources. It is possible that such attractants might be particularly effective in luring protein-hungry flies but less effective in luring flies that have recently acquired substantial protein. Indeed, such is the case with several tephritids, including Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann); apple maggot, *Rhagoletis pomonella* (Walsh); and Mexican fruit fly, *Anastrepha ludens* (Loew) (Robacker 1991; Prokopy et al. 1992, 1993; Robacker and Moreno 1995). One could postulate that protein-

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fed flies might be more attracted to the odor of host fruit in spite of the presence of abundant bait spray droplets in the local habitat. This hypothesis has yet to be evaluated critically for *B. cucurbitae.*

B. cucurbitae was discovered in Hawaii by Clark in 1898 (Back and Pemberton 1917) and has since become a major pest of vegetable crops, including melons, cucumbers, squash, and tomatoes. Although much is known about the ecology of *B. cucurbitae* (Nishida 1953) and although proteinaceous bait sprays have been used since the 1950s in Hawaii (Nishida et al. 1957), little is known about the behavior of *B. cucurbitae* in response to odor of hosts or odor of proteinaceous food (including baits). Nishida and Bess (1950) reported that gravid females moved into cultivated fields from outlying border areas, presumably in response to host odor, during the morning and returned in the evening. In Nishida's report immature female flies were observed primarily in vegetation of the border areas. Nishida (1958) also found that *B. cucurbitae* responded more positively responsive to certain species of nonhost plants (used as resting sites) than to sprays of yeast hydrolysate.

Two experiments were conducted to assess *B. cucurbitae* response to protein bait and fruit odor. In experiment 1, we attempted to identify attractive host fruit odors to use in experiment 2. In our second experiment, we directly compared responses of female *B. cucurbitae* of two different physiological states (protein-fed and protein-deprived) to odor of the most attractive fruit of the first experiment and GF-120 fruit fly bait (Dow AgroSciences, Indianapolis, IN). Overall, our goal was to determine if protein-fed females would still respond to attractive protein bait in the presence of host odor.

Materials and Methods

Flies. All *B. cucurbitae* females used here were of the F2 generation. Parental generation flies originated from infested fruit of papaya, *Carica papaya L.,* collected beneath fruiting trees on the island of Hawaii. F1 generation flies were allowed to oviposit into ripe papaya, which were then surrounded with moistened fruit fly diet (Vargas 1989) to provide larvae a substrate on which to develop. Insects pupated in dry sand from which they were sieved and removed. After eclosion, adults were held in groups of ≈100 females and 100 males for 26–30 d at 25 ± 1°C, 60% RH, and 13-h natural daylight in 30 by 30 by 30-cm laboratory cages to permit mating. After eclosion, flies were divided into two physiological groups. Protein-deprived flies were provided continuously with both sucrose and water. Protein-fed flies were given sucrose, enzymatic yeast hydrolysate, and water ad libitum. Dissections revealed that average loads of fully developed eggs for these two types of females at times of testing (26–30 d after eclosion) were 0.0 ± 0.0 and 16.0 ± 10.3 (mean ± SD) mature eggs per female, respectively (n = 15 females per type).

Bioassays. All trials were carried out in 2001 from 0900 to 1500 hours in 1 by 1 by 1-m wood-frame cages covered with 16-mesh black nylon screen. Screening on two opposite walls of each cage was held in place by Velcro to permit temporary lifting of these walls and entry into the cage. Five potted nonfruiting, nonhost coffee, *Coffea arabica* L., plants were positioned on the floor of each cage, with one plant near each corner and one in the center. Each plant had ≈40 leaves that were rinsed with water and dried thoroughly before use. The canopy of each plant extended to within ≈15 cm of each of the nearest walls of the cage. Each cage was placed on a rotating platform on top of a one meter high wooden table. The cages and tables were placed in a greenhouse whose roof and sidewalls were covered with partially translucent plastic panels that gave diffuse light within the greenhouse. Temperature in the greenhouse ranged from 22 to 32°C and varied with sunlight and cloud cover. Wind speed into the area where cages were was 0–1 km/h.

In both experiments we hung a single uncovered petri dish (10 mm in depth by 35 mm in diameter) horizontally on one branch of each of four separate coffee plants inside a cage. A different treatment was contained in each of these four dishes. Positions of treatments in the trees were randomly assigned for each replicate. Immediately after treatment introduction, a 25-ml clear-plastic cup was used to gently transfer six arbitrarily selected females from a holding cage onto the foliage of the center coffee plant. A positive response occurred when a female alighted on any part of a petri dish or its contents, after which it was removed gently with an aspirator and replaced with a new protein-deprived or protein-fed female. After two consecutive trials (requiring ≈45 min in total), all odor sources were renewed.

Experiment 1. We evaluated the response of protein-fed and protein-deprived females to host fruit (host fruit groups 1 and 2) odors. Replicate tests were conducted for both physiological state and odor type simultaneously to control for environmental variation. Thus, at any one time observers were watching two cages (≈1.5 m apart) with the same fruit odor: one with protein-starved and one with protein-fed flies. Between replicates treatment sets and fly types were randomly moved among the cages. Tests were conducted over a period of 4 d. On days 1 and 3, both states were tested for response to host fruit group 1. On days 2 and 4, both states were tested for response to host fruit group 2.

Host fruit treatments were randomly assigned to two groups for testing. The three host fruits evaluated in host fruit group 1 were zucchini squash, *Cucurbita pepo* L.; kabocha pumpkin, *Curcurbita maxima* Duchesne; and bittermelon, *Momordica charantia* L. The three host fruit odors evalutated in host fruit group 2 were cantaloupe, *Cucumis melo* L.; cucumber, *Cucumis sativis* L.; and tomato, *Lycopersicon esculentum* L. All fruits are grown commercially on Hawaii Island, all were picked ripe within 2 d of testing, and all were stored at 3°C when not in use. Skin and flesh of each fruit were crushed thoroughly 3 min before evaluation (exceptions were cantaloupe and kabocha pumpkin,

whose skins were not included). A plastic petri dish (10 mm in depth by 35 mm in diameter) was filled with 4 g of crushed material of a single fruit, to which 0.1 μl of green vegetable dye was added to standardize the color of each material as dark green. Twelve droplets of water (10 μl each) were applied to a leaf disc (white sapote, *Casimiroa edulis* Llave & Lex) placed in a petri dish as a control treatment to determine whether response to fruit juice was due to thirst. Each trial lasted 16 min. After each fly alighting as well as after 4, 8, and 12 min the entire cage was rotated clockwise 90° to compensate for potential directional effects of sunlight and airflow on directional tendencies of foraging flies.

Experiment 2. Response of female *B. cucurbitae* of both physiological states was examined when flies were given a choice between host fruit juice and protein bait. For a protein bait we used GF-120 fruit fly bait, a product currently widely used in Hawaii for areawide control of melon fly. We chose cucumber as the fruit odor for these trials, because the largest number of flies arrived to it in experiment 1. Trials were conducted simultaneously in two cages. One cage received protein-deprived females and the other protein-fed females. Twelve small droplets (10 μl each) of liquid pressed from freshly crushed cucumber were applied ≈3 min before evaluation to the surface of a 3-cm (diameter) disc of a white sapote leaf that was placed in a plastic petri dish (10 mm in depth by 35 mm in diameter). Each cage received a treatment set consisting of two diagonally opposite petri dishes containing 12 droplets of Dow GF-120 (10 μl each) and two diagonally opposite petri dishes containing droplets of cucumber juice. Each trial lasted 12 min and each cage was rotated 90° after 3, 6, and 9 min.

Statistical Analysis. Experiments 1 and 2 were analyzed as a split-plot design where the main plots were different physiological states of flies in cages and the subplots were odor sources in petri dishes. In experiment 1, a GLIMMIX.SAS macro was used to fit a generalized linear mixed model. This allowed for use of Poisson-distributed count data. The mixed model included both fixed and random effects: physiological state and odor source are fixed effects, whereas date, state × date, state × odor source × date, and replicates within date are random. Errors were adjusted for underdispersion, i.e., variances were smaller than expected for the Poisson distribution (Littell et al. 1996). Tukey's adjustment for multiplicity was used for multiple comparisons. For both experiments 1 and 2 a probability level of $P \leq 0.05$ was used as the significance criterion. In experiment 2, means for each physiological state were subjected to analysis of variance (PROC GLM, SAS Institute 1999). The means were compared using the least significant difference (LSD) test at the $P = 0.05$ level (SAS Institute 1999). Only replicate trials where a response was obtained were included in the analysis in experiments 1 and 2.

Results

Experiment 1. Table 1 summarizes the mean number of responding females by physiological state and by replicate for host group 1 ($n = 28$) and host group 2 ($n = 36$). Over the entire test for host group 1, 34.5% of the protein-fed and 36.8% of the protein-deprived females responded to odor; for host group 2, 40.0% of the protein-fed and 37.3% of the protein-deprived females responded to odor.

Table 1. Mean number of protein-starved and protein-fed *B. cucurbitae* females responding to all treatments in host fruit groups 1 ($n = 28$) and 2 ($n = 36$)

Host fruit group	Physiological state of female	Mean	Lower interval	Upper interval
1	Protein-fed	0.49a	0.24	0.82
	Protein-deprived	0.59a	0.31	0.95
2	Protein-fed	0.65a	0.41	0.96
	Protein-deprived	0.59a	0.36	0.88

Physiological state means followed by 95% confidence intervals. Mean values for each host fruit group followed by the same letter are not significantly different at the $P < 0.05$ level as determined by interaction contrasts.

In host fruit group 1, the fixed effect of odor source ($F = 12.02$; df = 3, 8.32; $P = 0.002$) was significant (Table 2). The fixed effects of physiological state and the interaction of physiological state and odor source were not significant. Zucchini and bittermelon were both equally attractive and zucchini was significantly more attractive than water ($P < 0.05$).

In fruit group 2, odor source ($F = 19.88$; df = 3, 9.06; $P = 0.0003$) was highly significant (Table 2). Physiological state and the interaction of physiological state and odor source were not significant. Both cucumber and cantaloupe were equally attractive and significantly ($P < 0.05$) more attractive than tomato or water. The mean response to tomato and water was not significantly different.

Experiment 2. Among the 242 females released across 33 replicates, 9.1% of protein-fed and 10.9% of protein-deprived females responded to the odor of fruit or protein (Table 3). In tests of protein-fed flies odor source was significant ($F = 13.62$; df = 1, 28; $P = 0.001$). Protein-fed flies were significantly ($P < 0.05$) more attracted to the odor of cucumber than to Dow GF-120. The effect of odor source was not significant

Table 2. Mean number of *B. cucurbitae* females (both states combined) responding to treatments in host fruit groups 1 ($n = 28$) group 2 ($n = 36$)

Host fruit group	Odor source	Mean	Lower interval	Upper interval
1	Kabocha	1.64a	0.96	2.63
	Zucchini	0.65ab	0.28	1.20
	Bitter melon	0.44bc	0.13	0.89
	Water	0.00c	−0.18	0.26
2	Cucumber	1.71a	1.10	2.53
	Cantaloupe	1.30a	0.81	1.98
	Tomato	0.30b	0.07	0.63
	Water	0.00b	−0.16	0.23

Odor source means followed by 95% confidence intervals. Mean values for each host fruit group followed by the same letter are not significantly different at the $P < 0.05$ level as determined by interaction contrasts.

Table 3. Mean no. of protein-fed (n = 15) and protein-deprived (n = 18) *B. cucurbitae* females responding to cucumber or protein odor

Physiological state of female	Odor source	Mean	Lower interval	Upper interval
Protein-fed	Cucumber	1.05a	0.52	1.86
Protein-fed	Dow GF-120	0.26b	−0.02	0.71
Protein-deprived	Cucumber	0.70a	0.29	1.33
Protein-deprived	Dow GF-120	0.69a	0.28	1.32

Physiological state and odor source means followed by 95% confidence intervals. Values in each physiological state followed by the same letter are not significantly different at the 0.05 level, LSD test, PROC GLM (SAS Institute 1999).

with protein-deprived flies, which showed an almost identical response to cucumber and Dow GF-120.

Discussion

In our first fruit experiment, odor of kabocha pumpkin was significantly more attractive than odor of bitter melon. In the second fruit experiment, cucumber and cantaloupe were significantly more attractive than tomato. In our second experiment, there was an equivalent level of attraction of protein-deprived females to odor of host fruit or protein bait. However, protein-fed females showed a 4-fold greater level of attraction to host fruit odor over protein.

Intrapatch foraging behavior for host fruit and proteinaceous food has been compared among protein-fed and protein-deprived adults in the tephritids *Bactrocera tyroni* (Froggatt) and *R. pomonella* (Prokopy et al. 1991, 1994, 1995). In those studies, the host fruit were intact and offered visual, olfactory, and contact stimuli. Several studies have been conducted on other tephritid species involving presentation of competing host fruit and proteinaceous food. Prokopy and Vargas (1996) found that the odor of Nu-Lure was significantly more attractive than the odor of coffee fruit to mature-age, protein-deprived females of *C. capitata,* whereas the reverse was true in the case of mature-age, protein-fed females. Robacker (1991) found that Mexican fruit flies deprived of sugar were generally more attracted to the fruit-derived extract 1,8-cineole, ethyl hexanoate, and hexanol (CEH) than to torula yeast. Conversely, Mexican fruit flies deprived of protein were more attracted to torula yeast and bacteria than to CEH. Cornelius et al. (2000) found that protein-fed oriental fruit flies, *Bactrocera dorsalis* (Hendel), in field cages were more attracted to fruit odors than protein odors, but that protein-deprived flies were equally attracted to protein and fruit odors. Here, mature-age, protein-fed female melon flies likewise were significantly more attracted to odor of host fruit (cucumber) than to odor of proteinaceous food, and protein-deprived melon fly females were equally attracted to host fruit and protein odors.

Protein-deprived females were equally attracted to both fruit and protein odor. Conceivably, as in *R. pomonella* (Averill et al. 1988), *B. cucurbitae* females containing partially but not yet fully mature eggs could be just as responsive to host fruit odor as are fully mature females.

Our findings have relevance to current control programs where ground application of bait spray is delivered in the form of swaths or otherwise localized patterns onto border crops or nonhost plants adjacent to cultivated fields of host plants. The intent (after Nishida et al. 1957; Nishida 1958) is to attract (with GF-120) feral *B. cucurbitae* to sprayed sites, where they would ingest the feeding stimulant and spinosad incorporated into GF-120 before entering cultivated fields of hosts. Our present findings, and those of Prokopy et al. (2003), suggest the high probability that some feral females that have recently fed on natural sources of protein and carry mature eggs might bypass the sprayed sites. These flies may proceed to cultivated hosts. However, Nishida (1953) reported that melon fly females might need to feed daily on natural protein sources to reach maximum fecundity. If this is the case, the level of crop protection afforded by protein bait sprays may be proportional to the availability of natural protein in a given area throughout the year. These predictions, however, can only be confirmed by Gf-120 field trials that focus on the collection of fruit infestation data and measure protein availability in the wild.

Little is known about natural sources of protein for *B. cucurbitae* or how these sources would compare in attractiveness to good protein baits. Bird feces have been widely reported as potential sources of natural protein in some species of tephritids (Nishida 1958, Christenson and Foote 1960, Bateman 1972, Hendrichs et al. 1991). Drew et al. (1983) found that *B. tryoni* that were fed bacteria from fruit and leaf surfaces had equal longevity and increased fecundity compared with flies fed traditional yeast hydrolysate and sugar diets. Recent studies by McQuate et al. (2003) have shown that *B. cucurbitae* fed on a diet of corn, *Zea mays* L., pollen and sugar show longevity equal to traditional diets. However, this study showed that fecundity of protein-deprived flies was very low compared with flies fed yeast hydrolysate. The authors predicted that attraction to corn pollen in the field would not likely exceed that to protein bait sprays.

The level of attraction of both protein-fed and protein-deprived flies to host fruit odor further emphasizes the need for growers to remove damaged or fallen fruit that will attract gravid females from adjacent areas and serve as reservoirs for the population in general. Furthermore, future research on identification and isolation of kairomones from fruit juices could be used to increase attraction to baits of gravid female *B. cucurbitae.* This could potentially increase control of melon flies if gravid females are found to be regularly migrating in to agricultural areas from areas with wild hosts. Baits with both fruit and protein odor also may improve traditional efforts to monitor melon fly populations by using McPhail traps.

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