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Modifications to torula yeast borax-baited traps and their impact on the attraction of tephritid fruit flies (Diptera: Tephritidae)

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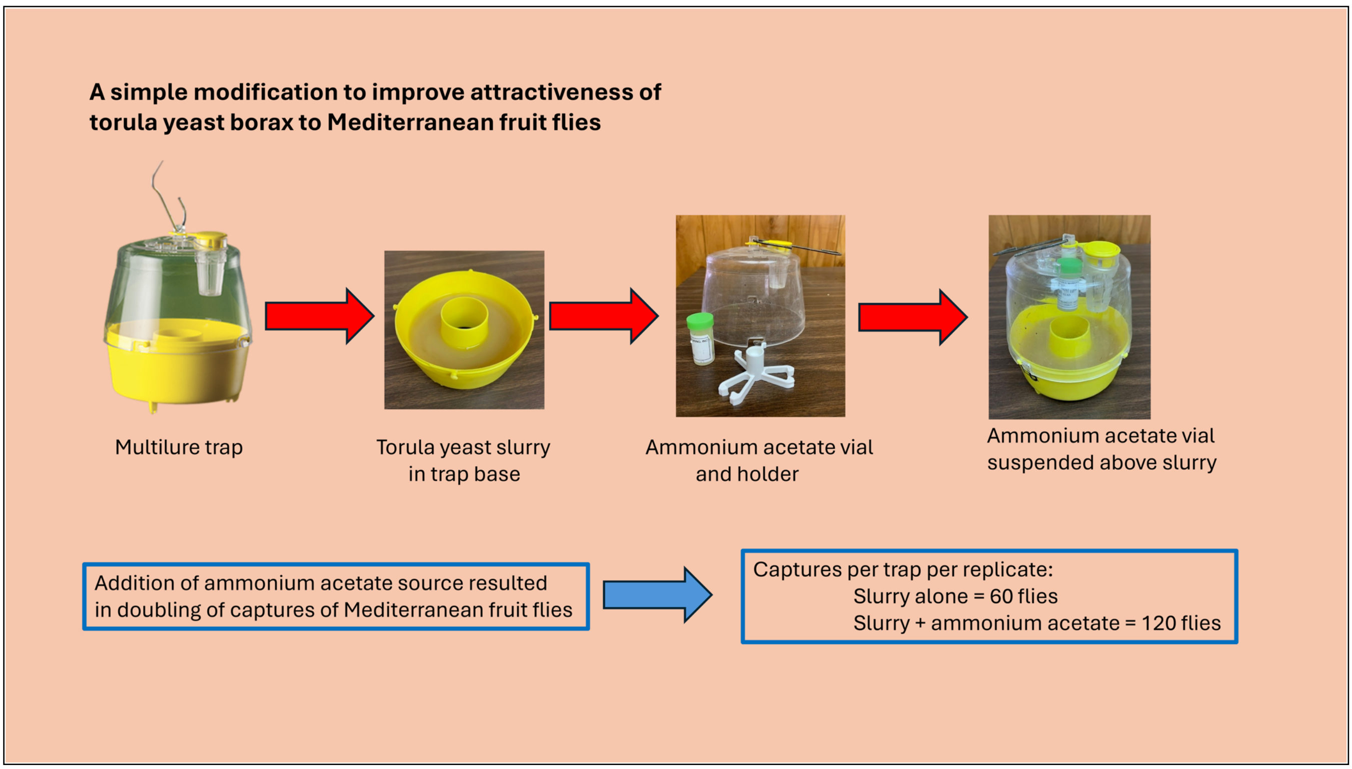
Traps containing food-based attractants are an important component of regional networks operated to detect invasive tephritid fruit flies (Diptera: Tephritidae), which pose a serious threat to fruit and vegetable production worldwide. However, food baits are weak attractants, and there is a critical need to increase their effectiveness. A recent study demonstrated that the addition of ammonium acetate crystals to an aqueous torula yeast borax (TYB, a commonly used food bait) solution significantly increased captures of Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann), and oriental fruit flies, *Bactrocera dorsalis* (Hendel), but not melon flies, *Zeugodacus cucurbitae* (Coquillett). The present study investigated 2 alternative methods for providing ammonium acetate in TYB-baited traps. First, a cylinder containing ammonium acetate was affixed to the inner, upper surface of traps above the standard TYB solution, and this resulted in significantly higher captures of *C. capitata*, but not *B. dorsalis or Z. cucurbitae*, than observed for traps baited with standard TYB. Second, ammonium acetate was incorporated directly into field-ready TYB pellets. However, these had no effect on *C. capitata* and even appeared to repel *Z. cucurbitae*. Two additional modifications were investigated: (i) extra amounts of certain amino acids or (ii) ground brine shrimp were added to TYB. The increased levels of amino acids significantly enhanced captures of *C. capitata* but not *B. dorsalis* or *Z. cucurbitae*. Addition of shrimp powder did not positively influence trap catch for any species. Implications of these results for detection trapping are discussed.

Keywords: detection trapping, invasive fruit fly, *Ceratitis capitata*, food bait

Graphical abstract



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Introduction

Many countries that are free of tephritid fruit flies operate trapping systems designed to detect incursions of invasive fruit flies (Epsky et al. 2014), as these pose a serious economic threat to many important agricultural crops (White and Elson-Harris 1992). These surveillance networks rely on both male lures and food-based attractants. Collectively, male lures are considered the more potent attractant, but their effectiveness is limited by their specificity, that is, individual male lures target specific species or genera and as the name implies do not attract females (Tan et al. 2014). Food baits, on the other hand, are weaker attractants but are more generic and attract both sexes of nearly all tephritid species (for exceptions see Sharp and Landolt 1984, Katsoyannos et al. 2000, where the study species showed little or no attraction to proteinaceous food baits), though a female bias is often reported (eg Miranda et al. 2001, Thomas et al. 2008, Leblanc et al. 2010). It is because of this broad attractiveness that food baits are included in fruit fly detection trapping (Food and Agriculture Organization/International Atomic Energy Agency 2018).

After various food baits were tested (eg López and Becerril 1967, Epsky et al. 1994, Duyck et al. 2004), torula yeast (with borax added to prevent decomposition of captured insects, López and Becerril 1967) was identified as an effective attractant (López et al. 1971, Burditt 1982) and emerged as the most widely used food lure in fruit fly trapping programs worldwide (Heath et al. 1995). Although widely used, torula yeast borax (TYB hereafter) solution has a limited period of effectiveness, and international guidelines recommend that the bait be replaced every 1 to 2 weeks (Food and Agriculture Organization/International Atomic Energy Agency 2018). This frequent replacement interval represents a major cost in terms of both materials and human labor, especially for large programs (eg California, United States) that maintain thousands of food-based traps (Vargas et al. 2013). As a result, a synthetic food bait (commercially available as 3C BioLure, Suterra LLC, Bend, Oregon) was developed that consisted of 3 components, ammonium acetate, putrescine, and trimethylamine (Heath et al. 1997). BioLure (and related products based on the same 3 components) has been tested worldwide and generally found to be as attractive as TYB to the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann) (Gazit et al. 1998, Epsky et al. 1999, Miranda et al. 2001), and various *Anastrepha* spp. (Hall et al. 2005, Martinez et al. 2007). Importantly, the synthetic lures were found to retain their attractiveness for intervals of 4 to 12 weeks (Epsky et al. 1999, Martinez et al. 2007, Enkerlin et al. 2025). Given these findings, some trapping programs (eg Florida, United States) have switched from using TYB-baited traps to traps baited with BioLure sachets or an equivalent product (United States Department of Agriculture–Animal and Plant Health Inspection Service 2024a).

While TYB incurs substantial cost associated with frequent rebaiting, synthetic food baits are expensive and may, in certain circumstances, be less cost effective than TYB. Identifying simple modifications that enhance the attractiveness of TYB may will increase the "detection sensitivity" of TYB-baited traps and thus avoid the high costs associated with synthetic food baits. In addition, and just as important, recent studies reported that TYB-baited traps were significantly more attractive to *Bactrocera* and *Zeugodacus* species than BioLure-like baits. Studies conducted in Hawaii (Leblanc et al. 2010, Shelly et al. 2020, 2022, 2023, Shelly and Fezza 2024) repeatedly found that captures of the oriental fruit fly, *Bactrocera dorsalis* (Hendel), and the melon fly, *Zeugodacus cucurbitae* (Coquillett), were significantly greater in traps baited with TYB than those baited with synthetic food baits. Ekesi et al. (2014) reported the same result for *B. dorsalis* in Africa. These findings are particularly important for agriculture in the USA, as incursions of *Bactrocera* spp. and *Zeugodacus* spp. have collectively been much more common than incursions of *Ceratitis* spp. Over the past 20 years, 2,179 adults of *Bactrocera* and *Zeugodacus* species have been collected in detection traps in California and Florida compared to only 400 adults of *Ceratitis* species, a 5.45-fold difference (includes records from approximately 50,000 traps over both states baited with food or male-specific attractants (https://www.aphis.usda.gov/plant-pests-diseases/fruit-flies). This observation justifies, to some degree, the continued use of TYB-baited traps in the United States, and, indeed, California still employs TYB as a core food bait in its state-wide surveillance program (M. Al-Zubaidy, pers. comm.).

Liquid protein baits, including TYB, emit a complex mixture of volatiles resulting from protein degradation via microbial metabolic processes (Gow 1954). Buttery et al. (1983), for example, identified 43 volatile chemicals from PIB-7, a corn-based protein bait, and Morton and Bateman (1981) found 14 common volatiles in the headspace of an enzymatic yeast hydrolysate. Although not all volatiles identified are likely attractive to fruit flies, various authors (McPhail 1939, Biasazin et al. 2018, Lasa and Williams 2021a, 2021b, 2022) suggest that attraction is based on multiple compounds possibly acting individually as well as synergistically. Among these, the production of ammonia via the degradation of amino acids and protein appears critical (Morton and Bateman 1981). In a seminal study, Mazor et al. (1987) demonstrated positive correlations between the release rate of ammonia and captures of *C. capitata* females (see also Bateman and Morton 1981). A similar trend was documented for the Queensland fruit fly, *Bactrocera tryoni* (Froggatt) as well (Bateman and Morton 1981; but see Lasa and Williams 2021b for contrasting results with *Anastrepha* spp.). In addition, the attractiveness of liquid protein was found to increase with increasing pH (Epsky et al. 1993, Heath et al. 1994), presumably reflecting the increased rate of ammonia from more alkaline solutions (Lasa and Williams 2022). The importance of ammonia as a fruit fly attractant is further evidenced by the fact that, to my knowledge, all BioLure-like synthetic food-based baits (eg vial-lures, food cones, and TMA Difusors, Shelly and Fezza 2024, Shelly et al. 2026) contain ammonium acetate as one of the 3 components, which, particularly after absorbing moisture, releases ammonia and acetic acid (National Institute of Health, pubchem.ncbi.nlm.nih.gov/compound/Ammonium-acetate).

Motivated by these findings, Shelly et al. (2025) investigated whether the addition of ammonium acetate crystals to TYB, slurry might increase its attractiveness and, in fact, confirmed higher captures of *C. capitata* and *B. dorsalis* in traps baited with ammonium acetate-supplemented TYB relative to unmodified TYB slurry. Measuring and adding ammonium acetate crystals is a time-consuming procedure, however, and the present study examined 2 methods allowing easier presentation of ammonium acetate with TYB, namely placing an ammonium acetate vial-lure above the TYB slurry and using TYB pellets to which ammonium acetate had been added in production. In addition, the impact of (i) increasing the concentrations of certain amino acids in the TYB and (ii) adding ground shrimp powder to the TYB on fly captures was investigated.

Materials and Methods

Study Site

Field work was conducted in a coffee field (*Coffea arabica* L.; area 65 ha, elevation 90 m) in central Oahu approximately 10 km southeast of Haleiwa, Hawaii. Plants were 2 to 4 m tall and were grown in rows spaced 2 to 3 m apart. Within a row, trunks of the individual plants were separated by 1 to 2 m, and foliage generally overlapped between adjacent plants. In addition to coffee, additional hosts of *C. capitata* and *B. dorsalis*, such as papaya (*Carica papaya* L.), mango (*Mangifera indica* L.), and lychee (*Litchee chinensis* Sonn.) (United States Department of Agriculture–Animal and Plant Health Inspection Service 2024b), were present near the coffee field. Coffee is not a host plant of *Z. cucurbitae*, but hosts, such as bitter melon (*Momordica charantia* L.) and ivy gourd (*Coccinia grandis* L. Voigt), occurred within and adjacent to the study site. As noted, 4 separate experiments were conducted, and the timing, average daily minimum/maximum temperatures, and overall average temperatures (in parentheses) were: experiment 1: July–August 2024, 20.7 °C/28.3 °C (24.2 °C); experiment 2: June–July 2025, 20.1 °C/28.1 °C (24.0 °C); experiment 3: October–December 2024, 18.8 °C/27.2 °C (23.3 °C); experiment 4: February–March 2025, 17. 3 °C/26.3 °C (21.7 °C) (temperature data from Wheeler Army Airfield, Wahiawa, Hawaii, approximately 10 km from the study site).

Traps

All food baits were placed in Multilure traps (Better World Manufacturing Inc., Fresno, California, United States), which are 2-piece, plastic McPhail-like traps (Food and Agriculture Organization/International Atomic Energy Agency 2018). The top portion is clear, while the bottom is bright yellow and holds liquid food bait or preservative (as described below). The bottom of the trap has a central, open invagination through which bait odors are emitted and insects enter. The liquid-filled reservoir acts as the killing mechanism. A wire hanger at the top of the trap is used to suspend the trap from branches of coffee plants.

Food Baits

In all 4 experiments, the standard (control) bait was an aqueous solution of TYB, which is widely used in current tephritid trapping programs (Food and Agriculture Organization/International Atomic Energy Agency 2018). Following accepted protocol, TYB solution was prepared by dissolving 1 TYB pellet (5 g; Better World Manufacturing Inc., Fresno, California, United States) per 100 ml of a water/antifreeze solution (90:10 v:v; SPLASH RV and Marine Antifreeze, [14% propylene glycol] SPLASH Products Inc., St. Paul, Minnesota, United States). The odorless antifreeze was included to reduce evaporation and reduce decomposition of the trapped flies (Food and Agriculture Organization/International Atomic Energy Agency 2018). Individual traps were baited with 300 ml of the TYB solution (ie 3 TYB pellets per trap). According to the manufacturer, TYB pellets were comprised of 50% borax, 45% torula yeast, and 5% excipients (Table 1). Torula yeast is a mixture of nutrients, including proteins, amino acids, carbohydrates, minerals, vitamins, lipids, and nucleic acids (Fanson et al. 2013, Ouedraogo et al. 2017). Proteins comprised approximately 50% of the torula yeast used to formulate the pellets used for the standard TYB bait. TYB was prepared 2 to 3 d before field deployment to allow microbial activity.

Fly captures in TYB-baited traps were compared to captures in traps that contained TYB but modified as follows.

In experiment 1, a thermoplastic cylindrical unit (termed a vial-lure) infused with ammonium acetate (Better World Manufacturing, Inc., Fresno, California, United States) was affixed to the upper surface of a trap containing standard TYB solution. The vial-lure (12 mm diameter; 30 mm height) was held in a transparent plastic carousel affixed to the inner top of the Multilure trap above the reservoir containing the TYB and activated by removing a cap at the base of the vial, thus allowing volatilization. The amount of ammonium acetate contained in a vial-lure is proprietary (Table 1). This treatment is hereafter referred to as AM-VL (denoting addition of ammonium acetate in a vial-lure separate from the TYB solution).

Table 1. Composition of the different food baits used in the field experiments

	TYB standard	AM-VL	AM-TYB	AA-TYB	SP-TYB
Experiments	1, 2, 3, 4	1	2	3	4
TYB components:					
Amount (g) (% total)					
Borax	7.50 (50)	7.50 (50)	3.72 (31)	10.0 (55)	6.0 (37.5)
Torula yeast	6.75 (45)	6.75 (45)	5.04 (42)	6.4 (36)	9.0 (56.25)
Excipients	0.75 (5)	0.75 (5)	2.04 (17)	—	—
Supplements:					
Amount (g) (% total)					
Ammonium acetate	—	+++	1.20 (10)	—	—
Amino acids	—	—	—	1.6 (9)	—
Ground shrimp	—	—	—	—	1.0 (6.25)
—					
Total bait amount (g)	15.0	15.0	12.0	18.0	16.0

Data were supplied by the manufacturers and represent total amounts per trap. See text for methods used to prepare and dispense the baits. Symbols: +++ denotes present in unknown amount; — denotes absence.
AA-TYB, amino acids added to TYB; AM-TYB, ammonium acetate incorporated directly into TYB; AM-VL, ammonium acetate presented in vial-lure separate from TYB; SP-TYB, shrimp powder added to TYB; TYB, torula yeast borax.

In experiment 2, 10% (w: w) ammonium acetate was added to TYB pellets during production (Süsbin S.A., Mendoza, Argentina). Each ammonium acetate-enhanced TYB pellet had a total mass of 4 g, with borax, torula yeast, excipients, and ammonium acetate constituting 1.24, 1.68, 0.68, and 0.4 g, respectively. For the trials, traps were baited with 3 such pellets (Table 1). This treatment is referred to as AM-TYB (denoting incorporation of ammonium acetate directly in the TYB pellets). As with the standard TYB, AM-TYB was prepared 2 to 3 d before field use.

In experiment 3, the treatment bait was prepared using torula yeast supplemented with additional amounts of particular amino acids. The bait was dispensed as a powder from 2 biodegradable plastic pouches (10.2×8.8 cm) each of which contained 5.0 g of borax, 3.2 g torula yeast, and 0.8 g supplemental amino acids (Table 1). Torula yeast contains most of the proteinogenic amino acids (Morton and Bateman 1981, Ouedraogo et al. 2017, Espinoza et al. 2023), but levels of only certain amino acids were enhanced, namely valine, leucine, isoleucine, threonine, methionine, phenylamine, lysine, histidine, arginine, and tryptophan. The levels of increase for the different amino acids are proprietary. This product is under development by Better Worlds Manufacturing, Inc. (Fresno, California, United States) and is here referred to as AA-TYB (denoting addition of enhanced amino acid levels to TYB). Three hundred milliliters of a water/antifreeze solution (90:10 v:v; SPLASH RV and Marine Antifreeze, SPLASH Products Inc., St. Paul, Minnesota, United States) was placed in the reservoir of each trap.

In experiment 4, the standard TYB was modified via the addition of ground brine shrimp, *Artemia salina* (Linnaeus) (Anostraca: Artemiidae) obtained from My Corazón Mexicano (Fort Collins, Colorado). Protein content was approximately 50%. The bait was dispensed as a powder from 1 biodegradable plastic pouch (10.2×8.2 cm) that contained 6.0 g borax, 9.0 g torula yeast, and 1.0 g ground shrimp (no excipients were included; Table 1). Thus, the borax and shrimp-supplemented torula yeast comprised 38% and 62% of the powder, respectively. This product is under development by Better Worlds Manufacturing, Inc., and is here referred to as SP-TYB (denoting addition of ground shrimp to TYB). Three hundred milliliters of a water/antifreeze solution (90:10 v:v; SPLASH RV and Marine Antifreeze, SPLASH Products Inc., St. Paul, Minnesota, United States) was placed in the reservoir of each trap.

Trapping Protocol: Released *C. capitata*

Aside from experiment 3, trapping was conducted when the abundance of wild *C. capitata* was low, consequently data were gathered using released insects. Nonirradiated, nondyed pupae were obtained from the California Department of Food and Agriculture (CDFA) facility in Waimanalo, Hawaii, which mass-rears a *tsl* genetic sexing strain for a Sterile Insect Technique program operated in California. Male and female pupae (40 ml per sex×56 pupae per ml ≈ 2,240 pupae per sex) were placed in separate screen-mesh cages (30 cm cubes). Based on CDFA quality control measurements, which follow international guidelines (Food and Agriculture Organization/International Atomic Energy Agency/United States Department of Agriculture 2019), for flies used over all release dates, the average adult emergence rate was 85%, and 78% of these adults were, on average, flight-capable (ie 40 mL of pupae yielded 1,485 flight-capable adults per sex or 2,970 total flies). Neither emergence rate ($H = 3.2$, $df = 2$, $P = 0.20$) nor flight ability ($H = 1.7$, $df = 2$, $P = 0.42$) varied significantly among flies used in experiments 1, 2, or 4 (Kruskal–Wallis test). Emerged flies were maintained at 23 to 25 °C and 55% to 70% relative humidity under a 14:10 (L:D) photoperiod and were provided food (a 3:1 mixture of sugar and protein hydrolysate) and water ad libitum. Adults were held until 4 d of age at which time they were taken to the field and released.

In the field, the flies were released from a central point, and traps were placed equidistantly along the circumference of a circle of 25 m radius. Twelve standard TYB-baited traps alternated with 12 AM-VL-baited traps in experiment 1 and 12 SP-TYB-baited traps in experiment 4 (ie 24 traps total per experiment, with ≈7 m separating adjacent traps). Owing to a limited supply of AM-TYB pellets, 6 standard TYB-baited traps alternated with 6 AM-TYB-baited traps around the circle (ie 12 traps total, with ≈13 m separating adjacent traps; experiment 2). In all experiments, traps were deployed immediately before insect release between 7 AM and 8 AM. To release flies, the 2 cages (1 per sex) were placed on the ground at the center of the circular plot. Females were released 15 to 20 min before males. For both sexes, the hinged top was opened, and the flies exited on their own volition. After 20 to 30 min, the cages were tapped gently to induce flight in the remaining flies. Traps were collected 2 d after deployment. The liquid was poured through a sieve to retain the catch, and samples were returned to the laboratory to identify and count the flies. The positions of standard and treatment baits were switched between successive replicates to minimize potential spatial effects on captures. For experiments 1 and 4, 1 release (replicate) was performed weekly over 6 consecutive weeks, while releases were conducted weekly for 5 consecutive weeks for experiment 2.

Trapping Protocol: Wild *C. capitata*

Experiment 3 was conducted during the peak fruiting period of coffee on Oahu and targeted wild *C. capitata*. For this experiment, 1 standard TYB-baited trap and 1 AA-TYB-baited trap were placed in each of 10 different rows of coffee (ie 20 traps total per replicate). Within a row, the traps were separated by 12 to 16 m, and rows with traps were spaced approximately 15 m apart. Traps were placed at the same sites over all replicates, with the positions of the treatments switched between successive replicates. Traps were deployed at 9 AM and 10 AM and operated for 7 d over 6 consecutive weeks. Collected traps were processed as described above.

Trapping *B. dorsalis* and *Z. cucurbitae*

The trapping experiments targeted *C. capitata*, but wild *B. dorsalis* and *Z. cucurbitae* were sometimes captured in sufficient numbers for statistical analysis. Specifically, data for *B. dorsalis* were included for experiments 1 and 3, while data for *Z. cucurbitae* were included for all 4 experiments.

Statistical Analysis

Initially, for all species analyzed for a particular experiment, the sex ratios of captured flies (presented as % females) were compared between the 2 baits tested in each experiment using data pooled over all replicates. With 1 exception, these comparisons were drawn on a trap-by-trap basis, with analysis restricted to those traps that captured at least 8 individuals of a given species during a replicate. Sex ratios between treatments were compared using the Mann–Whitney test (test statistic U). The low numbers of *Z. cucurbitae* flies captured in experiment 4 precluded the Mann–Whitney test and instead sex ratios of the 2 baits were compared to a χ^2 test using total numbers of females and males captured over all traps and all replicates. As will be shown, sex ratios did not differ significantly between food baits for any species in any experiment, consequently female and male data were pooled for subsequent analysis.

For each experiment, captures with TYB vs. modified TYB bait were compared using a 2-tailed, paired t-test based on the total captures per bait for a particular trapping period ($df = 5$ for experiments 1, 3, and 4; $df = 4$ for experiment 2). In all cases, the raw data or $\log_{10}$ transformed data were normally distributed (Shapiro–Wilk test), and variances were homogeneous (Brown–Forsythe test). Statistical tests were performed and graphs prepared using SigmaPlot 15.0 software (Grafiti LLC, Palo Alto, California, United States).

Results

Experiment 1—TYB vs. AM-VL

For *C. capitata*, sex ratios (% females) did not differ significantly between Multilure traps baited with TYB (average = 71%, $N = 72$) or AM-VL (average = 72%, $N = 72$; $U = 2{,}447.0$; $P = 0.56$). This same result was found for *B. dorsalis* (TYB: average = 69%, $N = 22$; AM-VL: average = 70%, $N = 28$; $U = 284.5$, $P = 0.65$) and *Z. cucurbitae* (TYB: average = 35%, $N = 53$; AM-VL: average = 33%, $N = 51$; $U = 1{,}223.0$, $P = 0.40$).

Based on data combined for the sexes, AM-VL-baited traps captured significantly more *C. capitata* than TYB-baited traps ($t = 5.0$, $P = 0.004$; Fig. 1). In contrast, captures did not vary significantly between these 2 baits for *B. dorsalis* ($t = 0.09$, $P = 0.93$) or *Z. cucurbitae* ($t = 0.12$, $P = 0.91$; Fig. 1). Over both treatments, 73% (2,160/2,970) of the flies released were recaptured in this experiment.

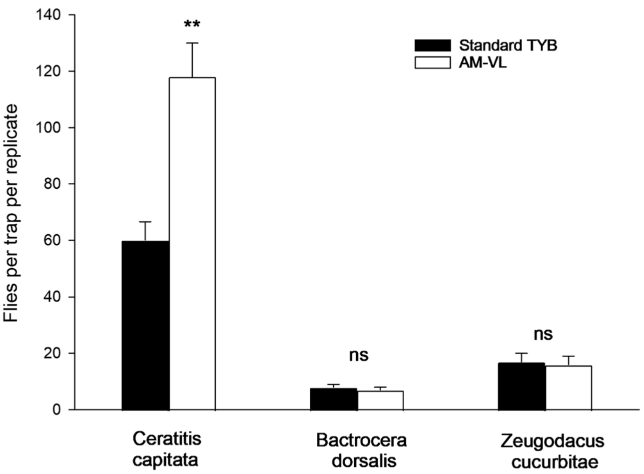

Fig. 1. Captures (sexes combined) of *C. capitata*, *B. dorsalis*, and *Z. cucurbitae* in traps baited with standard TYB alone or standard TYB plus an ammonium acetate-containing vial-lure (AM-VL, experiment 1). Bar heights represent average captures (±1 SE) per trap over 6 replicates. *C. capitata* were released from the center of the circular plot, while data for the other species represent wild flies. Statistical result: $^{**}P < 0.01$; ns, not significantly different.

Experiment 2—TYB vs. AM-TYB

For *C. capitata*, sex ratios (% females) did not differ significantly between Multilure traps baited with TYB (average = 73%, $N = 28$) or AM-TYB (average = 72%, $N = 27$; $U = 325.5$, $P = 0.38$). This same result was found for *Z. cucurbitae* (TYB: average = 23%, $N = 25$; AM-TYB: average = 25%, $N = 12$; $U = 257.5$, $P = 0.34$).

Based on data combined for the sexes, there was no significance difference in captures of *C. capitata* between TYB- and AM-TYB-baited traps ($t = 0.68$, $P = 0.67$; Fig. 2). In contrast, significantly higher numbers of *Z. cucurbitae* were captured in TYB-baited traps than in AM-TYB-baited traps ($t = 32.7$, $P \leq 0.001$; Fig. 2). Over both treatments, 10% (300/2,970) of the flies released were recaptured in this experiment.

Experiment 3—TYB vs. AA-TYB

For *C. capitata*, sex ratios (% females) did not differ significantly between Multilure traps baited with TYB (average = 72%, $N = 56$) or AA-TYB (average = 71%, $N = 59$; $U = 2{,}447.0$, $P = 0.66$). This same result was found for *B. dorsalis* as well (TYB: average = 83%, $N = 53$; AA-TYB: average = 81%, $N = 52$; $U = 1{,}294.0$, $P = 0.59$) and *Z. cucurbitae* (TYB: average = 29%, $N = 16$; AA-TYB: average = 31%, $N = 26$; $U = 191.0$, $P = 0.66$).

Based on data combined for the sexes, AA-TYB-baited traps captured significantly more *C. capitata* than TYB-baited traps ($t = 4.0$, $P = 0.009$; Fig. 3). The same result was found for *Z. cucurbitae* as well ($t = 19.3$, $P < 0.001$), whereas captures did not vary significantly between the 2 baits for *B. dorsalis* ($t = 0.33$, $P = 0.75$; Fig. 3).

Experiment 4

For *C. capitata*, sex ratios (% females) did not differ significantly between Multilure traps baited with TYB (average = 70%, $N = 58$) or TYB-SP (average = 67%, $N = 47$; $U = 1{,}146.5$; $P = 0.16$). For *Z. cucurbitae*, sex ratios were compared between treatments using total female and male counts

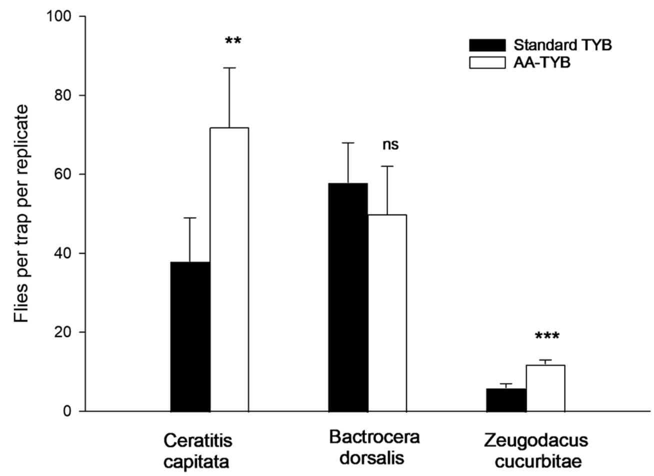

Fig. 2. Captures (sexes combined) of *C. capitata* and *Z. cucurbitae* in traps baited with standard TYB alone or ammonium acetate-enhanced TYB (AM-TYB; experiment 4). Bar heights represent average captures (±1 SE) per trap over 5 replicates. *C. capitata* were released from the center of the circular plot, while data for *Z. cucurbitae* represent wild flies. Statistical result: $^{**}P < 0.01$; $^{***}P < 0.001$; ns, not significantly different.

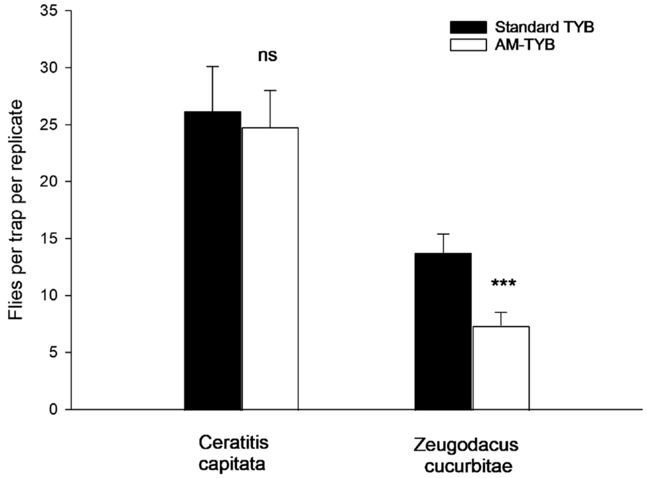

Fig. 3. Captures (sexes combined) of wild *C. capitata*, *B. dorsalis*, and *Z. cucurbitae* in traps baited with standard TYB alone or standard TYB with supplemental amino acids (AA-TYB, experiment 2). Bar heights represent average captures (±1 SE) per trap over 6 replicates. Statistical result: ***$P < 0.001$; ns, not significantly different .

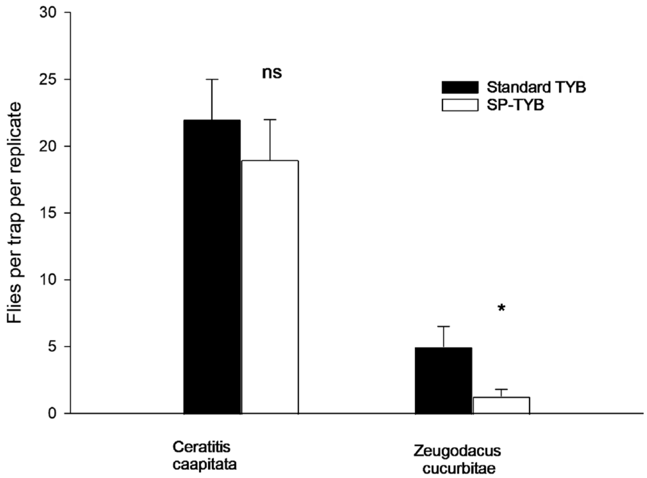

Fig. 4. Captures (sexes combined) of *C. capitata* and *Z. cucurbitae* in traps baited with standard TYB alone or standard TYB with supplemental shrimp powder (SP-TYB, experiment 3). Bar heights represent average captures (±1 SE) per trap over 6 replicates. *C. capitata* were released from the center of the circular plot, while data for *Z. cucurbitae* represent wild flies. Statistical result: *$P < 0.05$; ns, not significantly different.

over all sampling periods in a χ^2 test. Sex ratio (% females) did not vary between TYB-baited traps (75/347 = 22%) and SP-TYB-baited traps (23/96 = 24%; χ^2 = 0.24, $P = 0.62$).

Based on data combined for the sexes, there was no significance difference in captures of *C. capitata* between TYB- and SP-TYB-baited traps ($t = 0.92$, $P = 0.40$; Fig. 4). In contrast, significantly higher numbers of *Z. cucurbitae* were captured in TYB-baited traps than in SP-TYB-baited traps ($t = 3.15$, $P = 0.03$; Fig. 4). Over both treatments, 17% (504/2,970) of the flies released were recaptured in this experiment.

Discussion

Recognizing the high cost of synthetic food-based attractants, a previous study (Shelly et al. 2025) investigated whether the addition of ammonium acetate crystals to TYB slurry, a less expensive and still widely used food bait, might increase its attractiveness. This modification indeed significantly boosted captures of *C. capitata* in 3 separate experiments. The same result was observed for *B. dorsalis* as well, although this species was included in only a single experiment. Findings for *Z. cucurbitae* were inconsistent: the addition of ammonium acetate crystals increased captures of this species in only 1 of 3 field tests. These results prompted the present study, which again examined the impact of supplementing TYB with ammonium acetate, this time using 2 different time-saving methods, namely placement of an ammonium acetate-containing vial in the trap and use of TYB pellets with ammonium acetate added during the manufacturing process.

Placement of an ammonium acetate vial-lure in traps increased attractiveness for *C. capitata* similar to the addition of ammonium acetate crystals in the slurry (Shelly et al. 2025). However, whereas ammonium acetate crystals previously increased trap captures in the single experiment involving *B. dorsalis*, the vial-lures did not enhance catch of this species. Likewise, in the present study, the vial-lures had no effect on captures of *Z. cucurbitae*.

Although not measured in the present study, adding ammonium acetate to Captor 300, a hydrolyzed protein bait used to monitor *Anastrepha* spp. in Mexico, or torula yeast is known to significantly increase the release of ammonia (Lasa and Williams 2021a, 2021b, 2024). Based on these observations and the present results along with Shelly et al. (2025), it appears that increased release of ammonia from TYB slurry increases attraction of *C. capitata* but has little or no effect on *B. dorsalis* or *Z. cucurbitae*. While recognized as an attractant (Mazor et al. 1987), the attractiveness of ammonia is apparently modulated by the presence of protein-derived odors (Lasa and Williams 2021a, 2021b). Thus, it is possible that the addition of ammonium acetate lowered or interfered with the response *B. dorsalis* and *Z. cucurbitae* to the TYB bait. Interestingly, the interspecific variation in response noted here to ammonium acetate-enhanced TYB mirrors that observed regarding the attractiveness of TYB (or other liquid protein baits) relative to synthetic 3C BioLure food baits. That is, in general, *C. capitata* shows equal or greater attraction to 3C BioLure than TYB or other liquid protein baits (eg Heath et al. 1997, Gazit et al. 1998, Epsky et al. 1999, Katsoyannos et al. 1999, Miranda et al. 2001, Cristofaro et al. 2007, Espinoza et al. 2007, Jang et al. 2007, Grout et al. 2011, Enkerlin et al. 2025). In contrast, *B. dorsalis, B. oleae*, and *Z. cucurbitae* are more attracted to TYB or other protein baits than 3C BioLure (Mwatawala et al. 2006, Cristofaro et al. 2007, Quilici et al. 2007, Katsoyannos et al. 2007, Leblanc et al. 2010, Ekesi et al. 2014, Shelly et al. 2022, Shelly and Fezza 2024, Enkerlin et al. 2025). Data are scant, but available measurements indicate that the release rate of ammonia is much higher for 3C BioLure than torula yeast: release rates of 200 to 300 µg/h were reported for BioLure-type dispensers (Robacker and Bartelt 1996, Heath et al. 2007) compared to <10 µg/h for torula yeast solutions (Lasa and Williams 2021a). Thus, the relatively low attraction of *Bactrocera* and *Zeugodacus* spp. to synthetic food-baits may reflect repulsion to high ammonia levels and/or the absence of odors produced via microbial degradation of liquid protein baits.

Unexpectedly, the ammonium acetate-containing TYB pellets did not yield higher captures of *C. capitata* than standard TYB. This may have directly reflected the smaller amount of ammonium acetate added per trap with the modified pellets compared to the addition of ammonium acetate crystals (1.2 g vs. 3 g per trap, respectively). In addition, a limited number of ammonium acetate-enhanced TYB pellets reduced the number of traps deployed per replicate: only 6 AM-TYB traps were deployed per replicate compared to 12 traps with ammonium acetate crystals (Shelly et al. 2025) or 12 AM-VL traps (present study). Also, only 5 replicates were conducted for AM-TYB-baited traps compared to 6 replicates using ammonium acetate crystal- (Shelly et al. 2025) or AM-VL-baited (present study) traps. All these factors may have limited the robustness of the findings related to AM-TYB, and future work will focus on increasing the ammonium acetate dispensed per trap as well as the number of ammonium acetate-enhanced pellets available for deployment.

Supplementing TYB powder with extra amounts of select amino acids significantly increased captures of *C. capitata* and *Z. cucurbitae*, though no effect was observed for *B. dorsalis*. Amino acids have low volatility (Morton and Bateman 1981, Linander et al. 2012), consequently it is unlikely that the increased catch of *C. capitata* or *Z. cucurbitae* reflected a positive olfactory response to the supplemental amino acids per se. Moreover, although some Diptera, including *Drosophila melanogaster* Meigen (Steck et al. 2018) as well as species of Sarcophagidae (Shimada and Tanimura 1981) and Calliphoridae (Shiraishi and Kuwabara 1970), possess receptors sensitive to amino acids, these are gustatory (taste) receptors present in the labellar sensilla. In the present study, the amino acid-supplemented TYB was dispensed from a sachet and hence was not directly available for tasting. Thus, it appears that interactions between the supplemental amino acids and TYB produced an odor more attractive than standard TYB.

In the final experiment, the addition of ground brine shrimp to TYB had no effect on the captures of *C. capitata* and a negative effect on the captures of *Z. cucurbitae*. The slightly "fishy" odor associated with the SP-TYB bait obviously did not enhance attraction to TYB-baited traps.

Among the release-recapture experiments (all save experiment 3), the recapture rates varied markedly. In experiment 1, over 70% of released flies were recaptured, while the corresponding proportions were only 10% and 17% for experiments 2 and 4, respectively (note that the number of traps deployed was halved in experiment 2). Among abiotic factors, temperature might be considered responsible for this variation, but average temperatures were nearly identical between experiments 1 and 2 and differed by only 2.5 °C between experiments 1 and 4. The importance of other factors, such as humidity or wind speed and direction, is unknown, measurements were not taken for these parameters.

Sex ratios of captured flies were similar between treatments for all species for all experiments. Sex ratios were female-biased for *C. capitata* (67% to 72%) and *B. dorsalis* (69% to 83%; ranges over all treatments across all replicates for each species), trends consistent with earlier studies on food baits (eg Leblanc et al. 2010, El-Gendy 2012, Ekesi et al. 2014). In contrast, sex ratios were strongly male-biased for *Z. cucurbitae* (22% to 35%), a finding consistent with prior studies (eg Leblanc et al. 2010, Shelly et al. 2022, Mahmoud et al. 2024). As females require protein for egg production and maturation, this skew toward males in food-baited traps is unexpected and unexplained.

In conclusion, the use of synthetic food-based attractants, such as BioLure, has the potential to greatly reduce expenses incurred by fruit fly trapping programs, primarily owing to their effectiveness over prolonged intervals. Nonetheless, the high cost of such baits may render them unaffordable to small growers or area-wide monitoring programs operating under tight budgetary constraints. However, such baits may be cost-prohibitive, and as a result, less expensive options, such as TYB, will continue to be widely used. Thus, additional research aimed at improving the effectiveness is warranted. The present results show that adding an ammonium acetate dispenser (experiment 1) or boosting the amino acid content of TYB (experiment 3) may increase the attractiveness of TYB-baited Multilure traps to *C. capitata*. Therefore, these modifications should increase the "detection sensitivity" of food-based traps and thus may promote early detection of invasive *C. capitata*, a key factor in reducing costs associated with suppression or eradication (Suckling et al. 2016). However, the present study also showed that the use of ammonium acetate-containing vial-lures did not similarly increase attraction to *B. dorsalis* or *Z. cucurbitae*. Likewise, TYB with enhanced amino acid content resulted in higher captures of *C. capitata* and *Z. cucurbitae* but not *B. dorsalis*. Such interspecific variation illustrates the difficulty of identifying a food bait attractive to all major tephritid fruit fly pest species.

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Author Contributions

Todd E. Shelly (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Visualization [equal], Writing—original draft [equal])

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Conflicts of Interest

The author declares no conflict of interest.

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