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Paul V Switzer, *Eastern Illinois University*

Patrick C Enstrom, *Eastern Illinois University*

Carissa A Schoenick



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Behavioral Explanations Underlying the Lack of Trap Effectiveness for Small-Scale Management of Japanese Beetles (Coleoptera: Scarabaeidae)

PAUL V. SWITZER,¹ PATRICK C. ENSTROM, AND CARISSA A. SCHOENICK

Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920

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ABSTRACT Traps containing a combination floral and synthetic pheromone lure are used to monitor and manage Japanese beetles, *Popillia japonica* Newman (Coleoptera: Scarabaeidae). One key factor limiting trap effectiveness for beetle control is the “trap spillover” phenomenon, in which the trap attracts beetles without capturing them, resulting in increased damage to surrounding host plants. We investigated the mechanisms underlying trap spillover by conducting two studies in a soybean field in east central Illinois. In the first study, we set up trap stations for 1 d and compared the sex, size, and egg load (for females) of beetles caught in the traps with those on the plants immediately surrounding the trap, downwind of the trap, at lure-only (no trap) stations, and at control areas. Females caught in traps tended to be smaller than those on plants surrounding the traps, and females attracted to the traps had fewer eggs than those downwind or at control sites. We did not find any difference in male characteristics. In the second study, we observed the behavior of beetles initially approaching traps. Upon initial approach, the majority of individuals landed on plants before making contact with the trap, and those beetles that spent an extended time on the leaves tended to be females. Arriving males would occasionally pair with these females on the plants. Overall, traps did not capture a random subset of the beetles present in the field. We hypothesize that trap spillover is a result of arriving females not being as attracted to the precise location of the trap as they are to the general location itself, and of arriving males seeking mates and finding them among these spillover females.

KEY WORDS *Popillia japonica*, fecundity, traps, trap efficacy, sex ratio

Japanese beetles, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), were introduced to the United States in the early 1900s and quickly became significant pests of turfgrass as larvae and of horticultural and agricultural plants as adults (Fleming 1972). Efforts to control or manage Japanese beetles have included chemical pesticides, pathogens and parasites, mass-trapping, release of sterile individuals, identification of resistant plants and cultivars, and feeding deterrents (reviewed by Potter and Held 2002). Traps have traditionally been one of the primary methods for monitoring and nonchemical control trapping (USDA-APHIS 2000, Potter and Held 2002, Hamilton et al. 2007). Many studies have attempted to identify the most effective ways to design and implement traps to maximize their ability to capture Japanese beetles (Ladd and Jurimas 1972, Ladd et al. 1983, Ladd and Klein 1986, Alm et al. 1994; see Fleming 1969 for a review of the early literature). Originally, traps contained lures of food-related volatile oils, but once the existence of the volatile sex pheromone was determined (Ladd 1970), studies experimented with using

pheromone-producing, virgin females in traps (e.g., Klein et al. 1973). Inclusion of sex pheromone with traps became more practical once the pheromone compound was synthesized (Tumlinson et al. 1977, Klein et al. 1981, Ladd 1986, Ladd and Klein 1986). Current, commercially available traps tend to use a combination of floral compounds (3:7:3 mixture of phenethyl propionate:eugenol:geraniol) and synthetic pheromone (japonilure) as a lure.

The effectiveness of lure-based traps for pest insects will be influenced by the ability of the trap to attract individuals to the vicinity of the trap and by the ability of the trap to capture individuals once they have arrived at the trap. These two factors, in turn, may be affected by the location of the trap (Judd and Borden 1991, Vernon et al. 1994), climatic conditions (e.g., Sappington 2002), intrinsic properties of the trap design and lure (e.g., bait formulation, color, collection method; Webb et al. 1985, Vernon et al. 1994, Petrice et al. 2004, de Graaf et al. 2005), and the characteristics of the individual pest insects. Individual characteristics may include their state (e.g., sex, mating status, or migration status; Judd and Borden 1992, Duelli et al. 1997, Borgemeister et al. 1999, Rieske 2000, Jackson et

¹ Corresponding author, e-mail: pvschwitzer@eiu.edu.

al. 2005, Knight and Light 2005) and their behavior upon arrival (Elkinton and Childs 1983, Phillips and Wyatt 1992, Sutcliffe et al. 1995, Reynolds et al. 1996).

Although typical Japanese beetle traps can capture thousands of individuals (e.g., Klein et al. 1981), some evidence exists that that trap design and/or characteristics of individuals may lead to ineffectiveness of traps to manage beetles on a local scale. Gordon and Potter (1985, 1986) documented that Japanese beetle traps actually increase the damage caused on plants in the vicinity of the trap because of the trap attracting, but not capturing, beetles. Thus, even though the traps are capturing large numbers of beetles, the spillover onto surrounding host plants leads to traps being counterproductive. Instructions for commercially available traps take this 'trap spillover' phenomenon into account and recommend that traps are placed some distance from the plants needing protection (e.g., USDA-APHIS 2000).

We designed the current study to examine whether trap design, individual characteristics, or a combination explain the trap spillover in Japanese beetles by asking two major questions. First, do individuals approaching the trap only perch on the surrounding plants after failing first to get caught? Or, do beetles instead perch on surrounding plants before contacting the trap itself? Our second major question examines potential differences in the beetles that are captured. Specifically, do beetles caught in the trap differ from those individuals around the trap or individuals that were not attracted to the trap?

Materials and Methods

This study was conducted in a 26-ha soybean field in Coles County, IL, from 30 July to 2 August 2006. Soybean, *Glycine max* (L.) Merr., was used to provide a relatively homogenous, suitable habitat around traps. The weather during this time was consistent, with daytime highs of $\approx 34^{\circ}\text{C}$, night time lows of $\approx 24^{\circ}\text{C}$, and winds from 8 to 16 km/h from the south. Traps used in these studies were Trécé style (The Tanglefoot Company, Grand Rapids, MI) with a collection device consisting of yellow vanes, a funnel, and a detachable green plastic jar for holding captured beetles (see Klein and Edwards 1989 for a more detailed description). Lures were the standard floral lure (eugenol, geraniol, and 1-phenyl ethyl propionate) and sex lure [(R,Z)-5-(1-decenyl) dihydro-2-(^3H) furanone] combination supplied with the trap. Traps were placed on metal poles that were set in the ground so that the lure was 1 m above the ground. This height placed the lure slightly above the level of the soybean plants.

Trap Capture and Spillover. The trap collection portion of the study consisted of three treatments: trap, lure-only (placed on a 12-cm-diameter plastic weighing pan and hung vertically from a pole), and control (1.5-m green pole with no lure or trap; it simply marked a location).

Experimental stations were arranged to take advantage of prevailing winds and allow replication within

the soybean field. Because the wind was primarily from the south during the study, we minimized overlap of the odors from each particular station by establishing stations in a line that went from east to west across the soybean field, with ≈ 35 m between each station. This distance is ≈ 3 times the distance often used to test Japanese beetle traps and lures (Ladd and Klein 1986). Soybean rows ran from north to south in the areas of the field we used. The order of the treatments was established in blocks of three, with the order on the first trap day randomized within the first block of three and then the same order repeated within each block for that day. On days 2, 3, and 4 of the experiment, the traps were moved to the south (upwind) by 50 m and the order of the traps within each the block of three was changed such that each site had different treatments to the left or right of them across the east-west line but was still consistent among blocks. For example, if the trap treatment had a control treatment to the left of it on day 1 (even if it was in the next block of three), it would have the lure-only treatment on the left on day 2. Stations were established between 1000 and 1100 hours.

We collected beetles at two different times. First, we wanted to ensure that any patterns we observed were not caused by the traps being full and therefore unable to capture more beetles. Accordingly, at 1400 hours we removed all beetles already caught by the traps (traps were not full of beetles at this point). Second, the next morning (between 0700 and 0900), we made collections at each station. At each trap station, we collected 1) all beetles within a 2-m radius of the trap, keeping pairs and single beetles separate; 2) all beetles that were within the trap, and 3) all beetles that were downwind (north) of the trap in a rectangular area 25 m in length and 10 soybean rows (≈ 5 m) in width. At each lure-only station, we collected ≈ 100 beetles that were within a radius of 2 m from the lure. These beetles were collected systematically (i.e., moving from plant to plant, collecting all beetles), and pairs and singles were kept separate. This procedure allowed us to determine the frequency of pairs and the sex ratio of beetles at the site, but not beetle density. At the control stations, we collected all beetles within a 2-m radius of the control pole, again keeping pairs and singles separate. All collected beetles were frozen for later analysis; beetles were sexed using foreleg morphology (Smith and Hadley 1926).

From these collected beetles, we determined beetle density (for trap and control treatments), sex of the individuals, pair frequency (number of paired individuals per total number of beetles), size (using maximum body width; Van Timmeren et al. 2000), and egg load (number of mature eggs carried by a female; Saeki et al. 2005). Because of the large number of beetles, for sex ratio (number of males/total number of individuals) of the trapped beetles we used a random subsample of ≈ 200 beetles. Similarly, for size and egg load determination we used random subsamples of ≈ 20 males and 20 females from each collection. Sample size differs among treatments because of occasional damage to the treatment site (e.g., trap falling

to the ground during the course of the trial) or damage to the collected beetles during storage.

Behavior of Approaching Beetles. To determine the fate of beetles arriving at a trap, we conducted two studies. In the first, we made focal observations on beetles approaching a station from 1400 to 1630 hours at traps that had been established 3–4 h before observations. A focal observation consisted of locating a beetle that was directly approaching the trap but was still at least 2 m from the trap. We then recorded its behavior until it was captured in the trap, remained on a plant for at least 1 min., or was lost from view (e.g., because it was not possible to be sure we were observing the same individual). Behaviors recorded included landing on a plant, landing on the trap, hitting the trap but not being captured, crawling, and falling into the soybean plants either from flight or from crawling. For those beetles that were lost from view, we analyzed their initial behavior upon approaching the trap but no subsequent behavior. When possible, beetles that remained on the plants for at least 1 min were captured for later analysis. All collected beetles were sexed for comparison.

With the second behavioral study, we looked for patterns in the initial “settlers” near a trap by conducting a set of trap collections at newly established trap stations. We collected beetles arriving and landing on plants (as opposed to being caught in traps) from 1400 to 1600 hours. These collections took place from 1400 to 1600 hours in a portion of the field not being used for the collection experiment. We then collected the first 20 beetles to arrive and remain for 1 min on a soybean plant within 2 m of the trap. Because some of these first 20 beetles had actually formed a mating pair with each other, we also recorded the number of mating pairs included within the 20 beetle group. After 20 individuals were collected (which typically took between 20 and 30 min), for comparison we collected all of the beetles that had been caught in the trap during that time. This procedure was then repeated by moving the trap to a location at least 20 m perpendicular to the direction of the wind from the previous station. All collected beetles were sexed for comparison.

Analysis. Parametric tests were used for all data except female egg loads, for which nonparametric comparisons were used. Tests were conducted using JMP software version 5.1.2 (SAS Institute, Cary, NC) and all means are presented \pm SE.

Results

Trap Capture and Spillover. After just 1 d of trap establishment, aggregations of beetles formed on the soybean within a few meters of the trap, resulting in substantial, visible damage to the leaves of these plants. The difference in beetle number is evident whether analyzed without respect to day or block (outside trap, 163 ± 28.7 beetles, $N = 18$; control, 9.1 ± 3.2 beetles, $N = 18$; $t = 5.32$, $df = 17$, $P < 0.0001$) or when each trap site was compared with the control site within its block for that day (mean difference

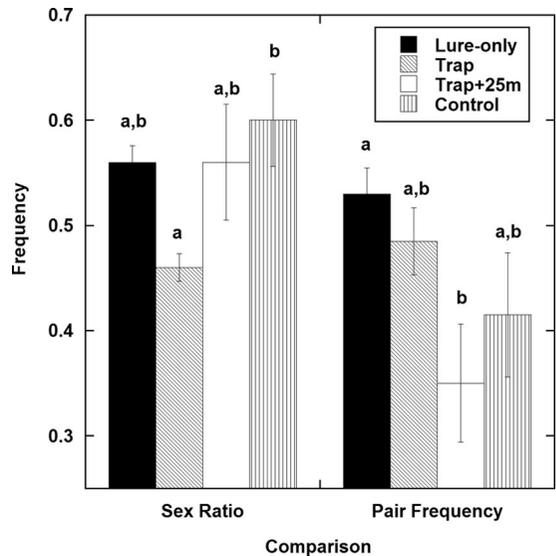


Fig. 1. Mean sex ratio (number of males/total number of beetles) and pair frequency (number of paired individuals/total number of beetles) \pm SE for lure-only ($N = 16$), trap ($N = 18$), 25 m upwind of trap ($N = 15$), and control ($N = 13$) collection sites. For sex ratio, the trap value contains beetles collected both within and around the traps. Within either sex ratio or pair frequency, bars not connected with the same letter are significantly different using Tukey-Kramer post hoc tests.

[trap – control], 153.9 ± 27.6 beetles, paired $t = 5.58$, $df = 17$, $P < 0.0001$).

Beetles removed from the traps in the morning were less male-biased than beetles removed from the same traps the previous afternoon (a.m. sex ratio, 43.3% male; previous p.m. sex ratio, 50.6% male, mean difference (a.m.–p.m.), $-7.3 \pm 1.9\%$, paired $t = 3.82$, $df = 17$, $P = 0.001$). Neither the size of males (a.m. body width, 6.14 ± 0.02 , $N = 285$; p.m. body width, 6.18 ± 0.02 mm, $N = 300$; $t = 1.48$, $P = 0.14$) nor female egg load (a.m. egg load, 1.67 ± 0.2 eggs, $N = 278$; p.m. egg load, 1.52 ± 0.2 eggs, $N = 301$; Wilcoxon two-sample test, $S = 81486$, $z = 0.48$, $P = 0.63$) differed among the afternoon and morning trap captures. Female size, however, did differ with capture time, with females caught the previous afternoon being significantly larger than females caught inside the trap in the morning (a.m. females, 6.74 ± 0.03 mm, $N = 278$; previous p.m. females, 6.83 ± 0.03 mm, $N = 301$; $t = 2.34$, $P = 0.02$).

Sex ratio and pair frequency differed among beetles collected at the different locations. For sex ratio, beetles captured at control sites were the most male-biased and the beetles captured 25 m downwind of Trap sites being the least male-biased (Fig. 1; $F_{3, 58} = 3.29$, $P = 0.027$). Beetles caught in a trap were significantly less male-biased than the beetles on the plants surrounding the same trap (mean difference $7.8 \pm 1.8\%$ more males outside than inside the trap, paired $t = 4.30$, $df = 17$, $P = 0.0005$). For pair frequency, lure-only sites had the highest pair frequency and

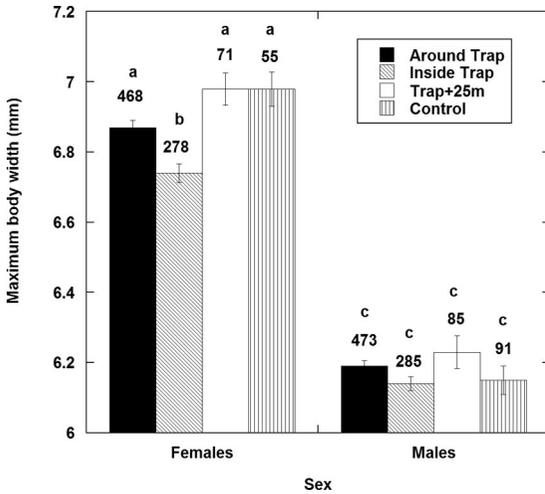


Fig. 2. Mean size (\pm SE) for female and male Japanese beetles captured at different locations. The number above bars refers to sample size. Within a sex, bars not connected with the same letter are significantly different using Tukey-Kramer post hoc tests.

beetles 25 m upwind of traps had the lowest pair frequency (Fig. 1; $F_{3,58} = 3.63, P = 0.018$).

Characteristics of females, but not males, differed among capture locations. In terms of size, females downwind of the traps were the largest and females in the trap being the smallest (Fig. 2; $F_{3,868} = 9.67, P < 0.0001$); interestingly, the females caught in a trap were smaller than females surrounding traps (Fig. 2). No significant difference existed for male size (Fig. 2; $F_{3,930} = 2.01, P = 0.11$). With respect to egg load, an overall difference existed among locations (Fig. 3; Kruskal-Wallis, $\chi^2 = 18.8, df = 3, P = 0.0003$). Females

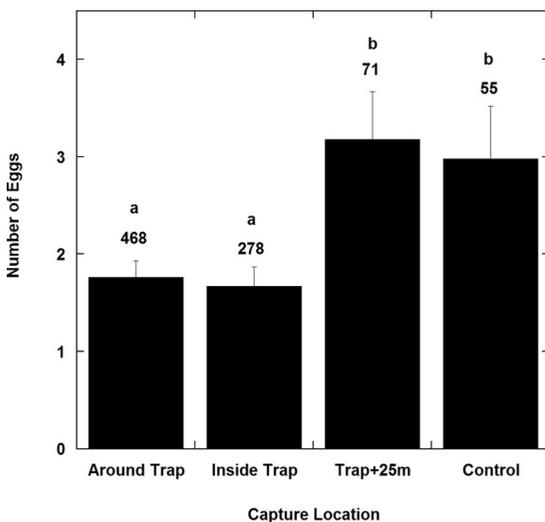


Fig. 3. Mean egg load (\pm SE) for females captured at different locations. The number above bars refers to sample size. Bars not connected with the same letter are significantly different using post hoc Mann-Whitney pairwise tests.

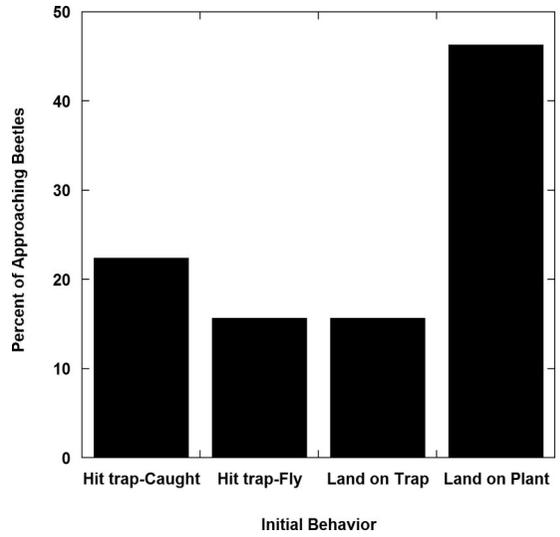


Fig. 4. Behavior of individual Japanese beetles ($N = 134$) upon initial approach to a trap that had been established for several hours. Hit-caught are individuals that made contact with the trap during flight and were immediately caught. Hit-fly are individuals that made contact with the trap and then flew away. Land on Trap are those beetles who initially flew to the trap and landed on it, without being caught inside the collection area of the trap. Land on Plant are those individuals who initially landed on a nearby plant.

collected at control sites and downwind of trap sites tended to have more eggs than females collected in or around traps.

Behavior of Approaching Beetles. We observed the initial approaches for 134 beetles at traps that had been established for several hours. The most common behavior was for beetles to land on the plants near the trap (Fig. 4). Only 22% of the beetles were caught in the trap upon their initial approach (Fig. 4). Of the 90 individuals whose fate was observed, 69% (62/90) were ultimately caught in the trap (either from flight or after landing on the trap and crawling). The remaining 31% (28/90) remained on the plants surrounding the trap for at least 1 min. Of those that originally landed on a nearby plant, 16/41 were caught eventually in the trap, whereas 25/41 stayed on the plant for at least one minute. Beetles settling on plants tended to be female; 16/22 beetles (76%) captured after they remained on the plants for at least 1 min were female ($\chi^2 = 5.76, df = 1, P = 0.016$).

To examine the individuals settling near traps in more detail, we used data from our study comparing individuals caught or landing near traps immediately after trap establishment. The sex ratio of the beetles settling on the plants for at least 1 min was significantly female-biased ($42.3 \pm 0.03\%$ male; one-sample t -test, $t = 2.4, df = 21, P = 0.026$), but the sex ratio of the beetles collected in the trap during the same time period did not differ from 1:1 ($49.4 \pm 0.02\%$ male; $t = 0.28, df = 1, P = 0.78$). The beetles collected in the trap tended to be more male-biased than the individuals settling on plants around the same trap (18/22 trap

collections were more male-biased than leaf settlers, mean difference $7.1 \pm 2.7\%$ more male biased; paired *t*-test, $t = 2.64$, $P = 0.01$). The sex ratio of the beetles that settled around the trap was more male-biased, with an increase in the number of pairs that had formed during the trial ($r = 0.48$, $P = 0.024$).

Discussion

Our data for trap captures indicated that the spillover effect was present in our study; soybean plants surrounding traps receiving significantly more beetles (and consequently more beetle damage) than control sites. Thus, the situation that Gordon and Potter (1985, 1986) documented was occurring during our study. Our results indicate that consistent differences exist among those beetles attracted to the trap and those not attracted to the trap (even within a sex) and also suggest that variation in behavior within and among the sexes may explain why the trap spillover phenomenon develops.

Characteristics of Captured Beetles. The sex ratio of the beetles we caught in the traps was $\approx 1:1$, which is less male-biased than some previous studies (Klein et al. 1981, Ladd and Klein 1986). This may reflect a seasonal difference (this study was conducted during the latter half of the flight season) or be a result of cumulative captures in the area (Klein et al. 1981). The sex ratio of trap captures in the morning was more female-biased than the ratio of beetles on surrounding plants, lure-only sites, or at control sites. This lower sex ratio could be caused by our emptying the traps the previous afternoon, because the afternoon removals had approximately the same sex ratio as the ratio on the surrounding plants. If this explanation is valid, it suggests that the males are attracted and/or caught more quickly than females. However, an alternative explanation is that females that are attracted to the trap area but are not captured may not stay for an extended period of time, unless, for example, they are paired with a male. Additionally, fewer males may be captured in the morning because some males are searching in areas where females are emerging (Ladd 1970); however, the current study was done later in the flight season and so fewer beetles would be emerging at this time (Van Timmeren et al. 2000).

Although the sex ratio at sites downwind from a trap was similar to lure-only sites, the pair frequency was much lower. In fact, downwind sites had the lowest pair frequency of all collection locations. Therefore, either those beetles who are motivated to mate are more attracted to the lure, or the lure itself increases the motivation to pair, or both.

In general, the beetles captured in the traps were not a random subset of the beetles present in the field. Although no patterns existed for male size, females caught in traps tended to be smaller than those around the traps. Furthermore, females in or around the traps had fewer eggs than those downwind of the traps or at control sites. The female size difference may be a result of smaller females being more likely to be caught once attracted to the traps than larger females.

Alternatively, the difference may be because larger females were attracted more quickly to the traps and were removed in the collections the previous afternoon (in which females were larger on average). The egg load difference, however, seems to be a consequence of females with fewer eggs being the ones that were attracted to the trap (whether or not they were captured), because the egg loads of females removed the previous afternoon did not differ from those collected in the morning.

At least three possible explanations exist for why attracted females had lesser egg loads than those females not attracted. First, less-gravid females may be in search of host plants, perhaps because they have recently oviposited. Female Japanese beetles feed between successive oviposition events (Fleming 1972, Van Timmeren et al. 2000), and their attraction to plant kairomones has been suggested as a way for females to quickly find suitable mates or host plants (Loughrin et al. 1995). Second, the egg loads may differ as a side-effect of beetle mating behavior. Male Japanese beetles tend to prefer to pair with relatively large females and will guard relatively large females for longer (Saeki et al. 2005a; Switzer et al. 2008). Also, paired females tend to have more eggs than single females (Saeki et al. 2005a; N. Tigreros et al., unpublished data), although this pattern may be affected by the nutritional status of the individuals involved (Tigreros and Switzer 2008). Therefore, females with fewer eggs may be less likely to be paired and therefore more able to fly and approach the lure. Third, females with higher egg loads may be less likely to fly because of increased flight costs or a decrease in ability.

Mechanisms Underlying Trap Spillover. Our observations on beetles approaching a trap provide some insight on how the trap spillover patterns may develop. Most beetles were not captured immediately upon arrival to the trap; rather, they tended to land on nearby plants (Gordon and Potter 1985). A portion of these plant-landing beetles quickly flew again and were ultimately caught in the trap. Others, however, remained on the plant for an extended period of time, and these beetles tended to be females. Some later arriving males found these females and would pair with them. We found that as more pairs formed in the vicinity of a trap, the sex ratio of the beetles on surrounding plants became relatively more male-biased. These patterns suggest that beetle behavior, rather than specific aspects of trap design, best explains the trap spillover effect in Japanese beetles. That is, even though a different trap design may more effectively capture beetles once they make contact the trap, the major cause of the spillover effect in Japanese beetles seems to be a result of the lack of precision of beetles for localizing the lure scent. We offer the following, tentative hypothesis for how Japanese beetle behavior leads to the trap spillover effect.

Trap spillover may be a direct consequence of individuals, particularly females, tending to be attracted to the general area rather than to the specific location of the lure. This lack of precision may be a limitation of their sensory abilities or may be a motivational

difference. For example, females, who are primarily attracted by the floral lure component of the trap, may only be trying to locate a general food source, not a particular location. Males, however, may be approaching the lures looking for females. This is obviously true for males attracted by the sex pheromone, and such males may be likely to contact the lure and trap. However, males also may be attracted to the floral lure to find receptive females, much like what has been suggested for why males are attracted to plant kairomones released by feeding beetle aggregations (Loughrin et al. 1995). Consequently, when males approach the trap and see females on plants near the trap, they land and attempt to pair with them, which results in the spillover. In this way, the trap-spillover phenomenon may more correctly be viewed as a "lure-spillover" phenomenon.

In conclusion, many of our explanations for our results are speculative or exist as alternatives. To help better understand the behavior of Japanese beetles, future studies in our laboratory will examine some of the possibilities brought up by the current study. For instance, we need to know the relative rate of attraction between males and females, between individuals of different sizes, and between single versus paired individuals. In addition, information on whether there is a time of day component to when different types of individuals are attracted to the traps would be very useful; the design of the current study did not provide any conclusive information on temporal patterns. Males and females leave food plants at different times (Tigreros and Switzer 2009), and many aspects of Japanese beetle behavior may differ depending on time of day (Switzer et al. 2001, 2004; Kruse and Switzer 2007) and weather conditions (Heath et al. 2001; Saeki et al. 2005b; Switzer et al. 2008). Furthermore, the specific point in the emergence season may affect trap capture (Klein et al. 1981). Studies designed to identify the effects of time of day, seasonal, and climatic conditions could go a long way to further our understanding of how beetles are responding to traps and will help us design more effective ways to use traps to manage this invasive pest. Finally, our study suggests that researchers using traps to capture beetles for laboratory experiments should consider whether potential biases in which beetles are captured would affect their intended studies.

Acknowledgments

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