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A wind-oriented sticky trap for evaluating the behavioural response of the leaf-beetle *Diabrotica speciosa* to cucurbit extracts

G. Cabrera Walsh[a]*, Federico Mattioli[a,#] and Donald C. Weber[b]

[a]FuEDEI (Invasive Species Research Foundation) Bolívar 1559, -B1686EFA- Hurlingham, Buenos Aires, Argentina; [b]USDA Agricultural Research Service, Invasive Insect Biocontrol and Behavior Laboratory, Beltsville, MD 20705, USA

Cucurbitacins are plant defensive chemicals that attract many species of adapted insect herbivores such as luperine leaf beetles, and they have been employed in traps and toxic baits. Male and female beetles feed avidly on baits containing these compounds, but field trials have revealed that males find them far more attractive than females. A wind-oriented baited sticky trap was designed to evaluate the response of *Diabrotica speciosa* to cucurbit extracts, by means of a mark–release–recapture experiment. The spatial range of attraction was less than 20 m, and captures were almost exclusively of males (99.91%). Distance attraction for *D. speciosa* to a point-source of bitter cucurbit juices is probably exclusive to males. These conclusions probably apply to most *Diabrotica* species, of which many are crop pests.

Keywords: attraction range; cucurbitacins; pest Chrysomelidae; vane trap

1. Introduction

The tribe Luperini (Coleoptera: Chrysomelidae: Galerucinae) is a group of leaf-beetles that includes several pest species, notably those belonging to the subtribe Diabroticina. Regardless of the hosts and geographical distribution of these beetles, most of them feed readily on plant tissues containing cucurbitacins – which to humans are very bitter-tasting, and to non-adapted insect herbivores are repellent and toxic, as they function – and probably evolved – as plant defences (Metcalf et al. 1980; Agrawal et al. 2002) To the adapted beetles, the cucurbitacins are phagostimulants (Contardi 1939; Howe et al. 1976).

Several pest management tactics have been implemented based on the phagostimulatory effect of cucurbitacins on diabroticine beetles. These include lacing bitter cucurbit roots or fruit with an insecticide (Lorenzato 1984; Hamerschmidt 1985), using the roots or fruits in traps for monitoring and collecting Luperini (Shaw et al. 1984; Ventura et al. 1996; Cabrera Walsh and Cabrera 2004; Cabrera Walsh et al. 2008), bitter cucurbit juice formulations combined with fungal pathogens (Daoust and Pereira 1986), and in toxic baits (Metcalf et al. 1987; Lance and Sutter 1990; Barbercheck at al. 1995; Schroder et al. 2001; Pedersen and Godfrey 2011). Cucurbitacins have also been included as baits in traps for monitoring purposes (Shaw et al. 1984, Tallamy and Halaweish 1993; Cabrera Walsh and Cabrera 2004; Ventura et al. 2005; Cabrera Walsh et al. 2008).

Although is it clear that cucurbitacins are phagostimulants, they are considered volatile kairomones by some authors, and merely as arrestants by others (Cabrera Walsh et al. 2008, for a full discussion on the subject). The difference is that volatile kairomones have the power to attract the recipient from a distance, whereas arrestants cause the recipient to remain after the individual has made contact with the compound, there being no distance attraction. The usefulness of an arrestant versus an attractant differs significantly. In the first case, the bait/trap would act only if the insect happened to encounter or contact it randomly. In the second, the bait/trap could attract the target from a distance, and thus potentially capture more insects.

In addition, previous studies have reported sex differences in the response to cucurbitacins and cucurbit extracts (Tallamy and Halaweish 1993; Tallamy et al. 1997; Smyth et al. 2002). For most *Diabrotica* species studied, males show a stronger response than females (Cabrera Walsh et al. 2008). However, the distance from which bitter cucurbit extracts can be detected, and under what conditions attraction can occur, remains unknown. There are several ways to define the reach of a chemical signal. The sampling range (R_S) of a trap is defined as the maximum distance from which the trap recruits insects in a given time period. The range of attraction (R_A) is the maximum distance over which the insects can be observed to direct their movement towards the source (Wall and Perry 1987; Schlyter 1992). The value of R_S is normally calculated by means of a regression model, in which recapture data $P(r)$ are regressed on release distance r. R_S is then calculated by solving for $P(r) = 0$ (Sufyan et al. 2011). R_A, however, is a more observational measurement, and normally entails observing the take-off behaviour of the subject insects, and timing their arrival at traps placed at different distances (Wall and Perry 1987; Östrand et al. 2000).

*Corresponding author: Email: gcabrera@fuedei.org
#Current address: Syngenta Agro S.A. Corrientes 2050, Bella Vista. CP 1661, Buenos Aires, Argentina

In this work we describe a series of experiments using a simple wind-oriented trap (vane trap) baited with bitter cucurbit extracts. The experiments were designed to assess the distance attraction and sexual differences in the response of *Diabrotica speciosa* (Germar), the main pest species in that genus in the Neotropics, to point sources of cucurbitacin-rich extracts, and test the role of random interceptions on the trap yields. These experiments could help explain how cucurbit-containing formulations can be used as a management tool for pest *Diabrotica* species, and why they have failed in some cases.

2. Material and methods

2.1. Trap design and use

The vane traps consisted of three aluminium double frames, each one measuring $45 \times 30 \times 4$ cm. Each double frame, fitted and adjusted with butterfly nuts, and thus resembling a rectangular embroidery "hoop", was attached in tandem with screws onto a 55-cm aluminium arm, forming one triple frame 12 cm deep. A triangular clear polycarbonate vane was riveted to the end of the arm. The entire assembly was suspended from a curved steel rod, 20 cm above the ground, in such a way that the traps could spin freely with the wind (Figure 1). The trap was designed so that the same side always faced the wind, the other side of the trap being downwind. This design ensured that we could always determine which trapped beetles had travelled from upwind, and those that did not. The outer frames held in place a piece of plastic mosquito netting with a light coat of "tangle-trap" (Tanglefoot, Grand Rapids, Michigan). The middle frame held a polyester fabric dipped in the bitter extracts of *Cucumis myriocarpus* Naudin as a Diabroticina lure (Cabrera Walsh et al. 2008). These lure fabrics have been shown to make cucurbitacin-rich extracts much more detectable to leaf beetles than previous kairomone release objects such as vials, cups, or bait formulations (Cabrera Walsh et al. 2008).

The triple-frame design allowed for the sticky nets and/or lure fabrics to be changed easily. Preliminary experiments showed that if lure fabrics were coated directly with insect adhesive they lost their attractive properties (G. Cabrera Walsh and F. Mattioli, unpublished work).

2.2. Mark–release–recapture experiment

A mark–release–recapture experiment was devised in order to test the range of attraction (R_A) and sampling range (R_S) of the trap using *D. speciosa* adults fed for 6 d on a standard corn rootworm adult diet mixed with fluorescent pigments; this foodstuff acted as a marker (Day-Glo, Cleveland, Ohio; 0.016% w/w). A previous study revealed that the marker was very reliable for around 5 d, and it did not affect beetle survival and mobility (Mattioli and Cabrera Walsh 2008). *Diabrotica speciosa* was chosen as an experimental subject because it is the most common *Diabrotica* species in the study area, and it is the main pest species in South America (Cabrera Walsh and Cabrera 2004).

The experiments were carried out within a 4-year-old alfalfa (*Medicago sativa* L.) field of 5 ha located in Mercedes, Buenos Aires province (34°34′19″S; 59°21′1″W), Argentina. Alfalfa was chosen because it is one of the preferred hosts of adult *D. speciosa*, and the only known crop that hosts this species year-round (Cabrera Walsh 2003). The marked beetles were released at 10, 20 and 30 m, in 8 different releases, at 10 a.m. The beetles released at 10 m were dyed pink, at 20 m blue, and at 30 m green. A mean of 721 adults of *D. speciosa* was released on each of the release dates (mean = 240 beetles per release station). The exact number depended on the mortality observed during the dyeing period, and the availability of beetles in our colonies (Table 1). The marked beetles were transported in 2-L clear plastic jars with ventilated lids. Release consisted simply of placing the jar on the ground at the release point, uncapping it, and allowing the insects to leave the container by their own means. A sample of 40 beetles was sexed before release by observing the last
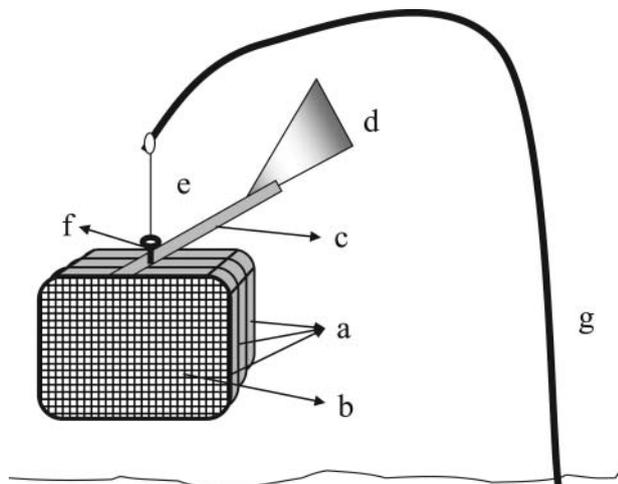

Figure 1. Design of the baited sticky vane traps: a, aluminium frames; b, sticky mosquito mesh (windward side shown); c, vane arm and frame holder; d, clear polycarbonate vane; e, steel cable; f, swivel; g, supporting steel rod.

Table 1. Results of the vane trap mark recapture tests: total captures for each release date are pooled.

		No. beetles recaptured			
Release date	No. released	10 m	20 m	30 m	No. wild beetles
07 Dec 2005[a]	690	3	0	0	24
20-Dec 2005[a]	1029	9	0	0	5
14 Feb 2006[a]	580	0	0	0	0
01 Mar 2006[a]	595	2	0	0	138
28 Dec 2006[b]	686	80	6	1	184
14 Feb 2007[b]	699	96	54	2	875[c]
02 Mar 2007[b]	775	36	0	0	97
09 Mar 2007[b]	720	222	2	0	434
Total	5774	448	62	3	1757

[a]Laboratory-reared beetles.
[b]Wild-collected beetles marked in the laboratory.
[c]Includes 2 wild females captured.

two segments of the ventral view of the abdomen under a dissecting microscope (Smith and Allen 1931); the proportion of each sex in the released sample was recorded. The vane traps were inspected at 1, 2, 24, and 48 h, and at 1 week, unless a rain event occurred within this period, in which case the trap yield was considered only up to the last inspection before the rain. The beetles captured on the traps were, sexed, crushed on brown paper, and scanned in a dark room with a 352/370 nm UV lamp (Sylvania 8Watt F8T5/ BLB) in order to identify the marked beetles present in the sample.

The release points were situated within the alfalfa field, placed along a northeast–southwest line. This direction was chosen because the dominant winds in the area for the summer season are from the northeast. Releases were made in December, February, and March, encompassing the period of peak abundance of *D. speciosa* (Table 1). The wind direction at the time of the releases was always from the traps to the release points, roughly within 45° of the northeast direction. Every time we visited the trap line a sample of *D. speciosa* was collected in the same alfalfa field at a distance greater than 150 metres away from the traps with 500 sweeps of a heavy duty, canvass sweepnet with a 30-cm mouth. These samples were counted and sexed in order to obtain a measure of relative *D. speciosa* density in the field, and the expected sex ratio on any given inspection date.

The trapping line consisted of three traps placed in a line perpendicular to the release line, with a 3-m separation between adjacent traps. A control trap was placed between two baited traps; it consisted of a vane trap assembled as described above, but with an untreated polyester cloth, in order to account for accidental beetle interceptions. Placing a control trap on the same line in between two baited traps was intended to ensure that captures on baited traps were not due to casual interceptions (for instance, by insects flying in the direction of the traps for reasons unrelated to the traps themselves, such as dominant winds or attraction to nearby crops), and that insects could fine-tune to the location of the trap instead of simply orienting in their general direction. In other words, placement was chosen to test fine directional tuning in the beetles within close distances, ensuring there was no element of randomness in the captures. The main set of control traps consisted of four yellow sticky traps (Trécé Pherocon® AM trap) deployed 10 m away from the vane traps, positioned 20 cm above ground, facing each cardinal point. These traps were meant to assess the proportion of random interceptions of any given, unbaited, sticky trap; they are commonly used to monitor *Diabrotica* spp. in North America and Europe (Chandler 2003). All the traps were placed 5–10 m from the edge of the alfalfa plot, and roughly equidistant from the release points.

The first four releases (summer of 2005–2006) consisted of marked laboratory-reared *D. speciosa* beetles from our colonies. These beetles were under one week old (mean longevity in the laboratory = 55.7 d), reared on maize roots as larvae, and artificial adult diet after emergence (Cabrera Walsh 2001). The experiment was repeated the following summer but using wild beetles collected in the field, and also fed for 6 d on an adult diet mixed with fluorescent pigments. The use of laboratory-reared beetles was considered preferable initially because they were guaranteed to have never fed on cucurbitacins, which was expected to provide a more consistent response to the feeding stimulant by standardizing the exposure history of the subject insects. However, due to the relatively low number of captures, we turned to field-collected beetles during the second season because we suspected the laboratory beetles had shown low vigour in the field.

2.3.   Data analyses

The numbers of beetles captured after each release date were pooled for the duration of each trapping period. Both trapping seasons were treated as separate experiments, although they were compared statistically for discussion purposes. Given the non-normal distribution of the data obtained, Mann–Whitney U-tests were used to compare beetle captures. The number of recaptured marked laboratory beetles was compared to the number of marked wild beetles from the following season. The number of unmarked wild beetles captured was also compared among seasons.

The relative density of beetles in the field was compared among seasons, and the sex ratio on the traps was compared to the expected frequency according to the ratio in the field samples with a Pearson's χ^2 goodness-of-fit test. The number of wild beetles stuck to the traps was correlated to the relative density of *D. speciosa* in the field for each inspection date with Pearson's correlations to evaluate the relationship between trap catches and insect density (SYSTAT 2004).

The number of marked beetles recaptured from the different release distances was used to estimate the R_S of the trap. In our tests, marked beetles recaptured in under 1 h were considered to have directed their flight to the traps by responding immediately to their attraction. Under this assumption, the R_A was estimated as the maximum distance from which any beetles were recaptured in under 1 h.

3.   Results

Of the total number of beetles captured on the sticky traps, 99.8% were collected on the downwind side of the traps, indicating that the beetles approached the traps upwind. All 513 beetles captured from releases were male, compared to an estimated 56% of males in those releases. All but two of the 1757 wild beetles captured were males (99.9%), whereas the proportion of females in the field samples collected by sweeping during the trapping period ranged from 21.9% to 64.8% (mean = 39.7%).

In the mark–release–recapture experiment, between 0 and 2.5% of the male beetles released were recaptured in the first trapping series (laboratory-reared beetles), and between 10% and 61.7% of the males were recaptured during the following summer (marked wild beetles) (Table 1). The number of recaptured wild marked beetles

was significantly larger ($\approx$ 30 times) than the number of laboratory-reared marked beetles ($U = 0.000$, $P = 0.021$) (Table 1). Captures of wild beetles were also significantly higher ($\approx$ 9 times) during the second trapping period than during the previous summer ($U = 0.021$, $P < 0.001$) (Table 1), but do not account for the difference between seasons for the marked beetles. Estimated relative density in the field, however, was not significantly different between the first and second trapping periods ($U = 47.0$; $P = 0.483$). Also, catches of wild beetles were not correlated with relative density ($r = -0.128$; $k_{0.05} = 0.433$). No marked females were recaptured during either test, although the mean proportion of females among the laboratory-reared beetles was 0.51, and 0.37 among the field collected beetles. Only 2 wild females were captured, against 2268 males in total. The probability of obtaining this result by sampling error is $< 1/10,000$ ($\chi^2 = 1216.77$, $df = 1$, $P < 0.0001$).

Of the marked beetles recaptured after each of the release dates, 448 (87.3%) beetles were recovered from the 10-m release station; 62 beetles from the 20-m release station; and 3 from the 30-m release station (Table 1). Also, the beetles released from 30 m were recaptured between 48 and 170 h after release. A total of 65 beetles was recaptured in under an hour from 10 m, and 10 beetles from 20 m. The data obtained were not suitable to apply a regression model to calculate R_S.

A total of 4 beetles was captured on the control trap, and none on the yellow cards, compared to the 2,270 beetles captured on the two baited traps. This indicates that random interception plays no part in the captures on the baited sticky traps. It also indicates that, unlike some of the North American *Diabrotica* species, *D. speciosa* is not readily attracted to unbaited yellow sticky traps.

4. Discussion

The absence of a numerical relationship between the relative field density of *D. speciosa* and the trap catches of wild beetles suggests a large influence of environmental and/or physiological factors. Some of the weather factors affecting trap catches of diabroticine beetles have been explained at least partially; the explanations range from temperature-related daily activity patterns (Lance 1990), to temperature intervals and atmospheric pressure thresholds (Cabrera Walsh et al. 2008). In spite of such variability, there are at least four relevant outcomes from this experiment:

(1) From the beetles captured on the vane traps, 99.8% were collected on the downwind face of the traps, indicating that the beetles orient from a distance toward the extracts, and do not randomly encounter them, as was previously supposed (Metcalf and Lampman 1989; Nishida and Fukami 1990). The notion that they could fall on the leeward face simply because they fly upwind as part of their typical foraging behaviour is also not supported. If that were the case we would have obtained significant catches on the control vane trap and the yellow cards.

(2) Under some conditions, recaptures were quite high: up to 62% of the male beetles within 10 m of the trap were recaptured. Most beetles were recaptured in the traps within 48 hours of release, suggesting that after that period, the beetles had dispersed beyond the point of detection.

(3) Only males were captured on the traps, except for two wild females, regardless of the time the traps remained in the field. This does not support the hypothesis, advanced for North American *Diabrotica*, that females take longer to approach cucurbitacin sources due to lower dispersion capabilities (Branson and Guss 1983; Fielding and Ruesink 1985; Tallamy and Halaweish 1993). Instead, female *D. speciosa* beetles simply do not approach the traps at all. The fact that cucurbitacins are known to be contact phagostimulants for the females of several species of *Diabrotica* (Tallamy and Halaweish 1993; Cabrera Walsh and Cabrera 2004) suggests they are incapable of detecting them from a distance. This was observed both for the laboratory-reared beetles (previously unexposed to cucurbitacins), as well as the wild marked field beetles, suggesting this phenomenon does not vary significantly in relation to a previous history of exposure to cucurbitacins. In general, there is a marked male predominance on cucurbit plants, and an even higher male proportion on traps baited with cucurbitacins in any of its forms (Cabrera Walsh and Cabrera 2004). Previous experimental evidence suggests this sex difference in behaviour is a common trait of all Diabroticina (Cabrera Walsh et al. 2008).

(4) The wide variations in recapture percentage and low numbers recaptured from the farthest release stations precluded the use of a regression model to calculate a proper sampling range (R_S). This radius, defined as the maximum distance from which the trap recruits insects in a given time period (Wall and Perry 1987), would appear to be under 30 m, since only 3 marked beetles were recovered from this distance, and all of them after 48 h. Yet, the range of attraction (R_A), the maximum distance over which the insects could be shown to direct their movement to the source, seems to be more than 20 m, but clearly less than 30 m. We conclude this from the fact that 10 out of the 62 beetles recaptured from 20 m were recaptured in under 1 h. In any case, the good concordance between estimated values of $R_S < 30$ m and 20 m $< R_A < 30$ m does not seem to justify more precise determination of these variables.

The experiment revealed a relatively short detection radius as compared to the R_A of pheromone or plant volatile traps of 19–90 m reported for other Coleoptera (Schlyter 1992; Wamsley et al. 2006), but similar to that

calculated for pheromone traps for the elaterid beetles *Agriotes* spp. (Suffian et al. 2011), and probably similar to the sampling area calculated in 0.1 ha for the weevil *Dendroctonus frontalis* Zimmermann (Turchin and Odendaal 1996). Cucurbitacins are large, essentially non-volatile molecules (Tallamy et al. 2005), so it is not surprising that they do not disperse as widely as insect pheromones, most of which are highly volatile.

Although this study evaluated the behaviour of only one Neotropical pest species, namely *D. speciosa*, we have firm evidence to believe that the results can be extrapolated to most pest *Diabrotica* species. Sex differences in the response to bitter cucurbit extracts has been observed for at least 14 species of Diabroticina, including most of the pest species (Fielding and Ruesink 1985, Tallamy et al. 2002; Cabrera Walsh et al. 2008). Distance attraction, for males at least, has also been demonstrated (Cabrera Walsh et al. 2008). Thus the results suggest that point sources of cucurbitacins can be expected to attract only males for all, or most, species of *Diabrotica*. This fact, added to the wide variations in the yield of the traps in relation to the relative density of *D. speciosa*, would limit the utility of bitter cucurbit extracts in traps, at least for monitoring and control purposes.

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