

Factors influencing the capture of Japanese beetles: wind speed and direction, trap deployment protocol, lure type and trap efficiency

Quentin Guignard^{1,2,3,*}, Joel Goodwin^{1,4}, Troy Kimoto⁵, Kenneth F. Haynes⁶, Jeremy D. Allison^{1,2,3,4}

¹Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen Street E, Sault Ste. Marie, Ontario, P6A 2E5, Canada

²African Centre of Chemical Ecology, Innovation Africa @UP, University of Pretoria, South Africa

³Department of Zoology and Entomology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria 0002, South Africa

⁴University of Toronto, Institute of Forestry & Conservation, 33 Willcocks Street, Toronto, Ontario M5S 3B3, Canada

⁵Canadian Food Inspection Agency, 4321 Still Creek Dr, Burnaby, BC, V5C 6S7, Canada

⁶Department of Entomology, University of Kentucky, S-225 Agricultural Science Center North, Lexington, KY.

*Corresponding author email: Quentin.guignard@nrcan-rncan.gc.ca

Keywords

Coleoptera, insect pest, upwind flight, kairomone, pheromone

Abstract

In this study, factors affecting Japanese beetle (JB) trap captures (e.g., wind direction and speed, lure type, trap deployment and efficiency) were investigated in the field using semiochemical baited traps. Fifty-two percent of 667 JB observed flew directly upwind toward a trap with a dual lure (sex pheromone + floral kairomone), especially when wind speed exceeded 1.5 m/s. Within thirty seconds after approaching 2-m of a trap baited with a dual lure, 43%, 35% and 22% of 138 observed beetles were captured, flew away or landed on the trap, respectively. Of 265 884 beetles captured, 48% were captured by a cluster of three traps each with a single dual lure, 30% by a single trap baited with three dual lures, and 22% by a single trap baited with one dual lure. Traps baited with the floral lure (i.e., kairomone) and the floral lure and the sex pheromone (i.e., dual lure) captured similar numbers (39% and 41%, respectively) of JB and both captured more beetles than traps baited with the pheromone alone (12% and 8% for the sex-pheromone from the dual lure and sex-pheromone standard, respectively). Traps baited with the floral kairomone alone or with sex pheromone captured a 1:1 sex ratio (M:F) while pheromone-only traps captured a 3:1 (M:F) ratio of JB. No additive or synergistic effects of the pheromone and floral kairomone were observed. To our knowledge, this study is the first to quantify in real time the flight behaviour of a beetle toward traps in the field.

Introduction

Since its introduction to New Jersey (USA) from Japan in 1916 the Japanese beetle (JB), *Popillia japonica* (Coleoptera: Scarabaeidae), has spread to 28 states in the USA and five Canadian provinces (Potter and Held 2002; Shanovich et al. 2019; Althoff and Rice 2022). Subsequently, JB from North America were the suspected origin of populations in Portugal (Azores), Italy and Switzerland (Potter and Held 2002; EPPO 2017). In the early 2000s the cost associated with JB control and land restoration on turf and ornamentals alone was estimated at \$460 million in the USA (USDA/APHIS 2015). The total current costs associated with JB are likely to be much higher due to the continued increase in distribution and associated access to new host plants. The cost will likely increase if the beetle colonizes additional habitats where it has not yet been detected (e.g., Africa, Oceania) (Della Rocca and Milanesi 2022).

The biology of JB makes it a challenge to manage. The larvae feed belowground on grass roots making it difficult to monitor and target this stage. It is possible to manage larvae with insecticide application, however, adults can fly long distances (Lessio et al. 2022). After emergence, adults disperse to feed and mate and often aggregate on host plants (Potter and Held 2002). This cycle can occur multiple times during the 4 to 6 week lifespan of the insect. Adults are polyphagous, attacking a wide variety of hosts including some crop, orchard, small fruit and ornamental plants (Flemming 1972). A highly effective dual lure that combines floral volatiles (kairomones) with synthetic sex pheromone was developed and is used for monitoring JB adults. The floral attractant is a combination of phenethyl propionate + eugenol + geraniol (Ladd et al. 1981). The sex pheromone released by females was identified as (*R,Z*)-5-(1-decenyl)dihydro-2(3H)-furanone, and is called Japonilure (Tumlinson et al. 1977).

Trap performance in operational surveillance and detection programs is affected by numerous factors (Allison et al. 2014, Allison and Redak 2017, Staton et al. 2023). Trap protocol (e.g., how many traps are deployed, trap placement relative to landscape features or gradients and other traps) and abiotic factors (e.g., wind speed, direction) are important considerations for the optimization of capture efficiency and to minimize deployment costs. Although considerable research effort has been invested on the development of survey and detection tools for JB, the primary focus has been the development of attractants. Comparatively less is known about how deployment protocol and abiotic factors influence the capture of JB. A few studies have observed that trap height, repellency from decaying beetles, lure types, trap placement relative to infested plants and trap collection container design are factors that impact capture of JB (Gordon and Potter 1985; Gordon and Potter 1986; Alm et al. 1996; Piñero and Dudenhoefter 2018).

An eradication program in the lower mainland of British Columbia (Canada) for JB was initiated in 2018 by many stakeholders including the Canadian Food Inspection Agency (CFIA) which is responsible for regulations and surveillance in the eradication program (Allison et al. 2021). In support of this JB eradication program, this study aimed to examine trap deployment protocols to provide guidance on effective implementation of traps to detect and delimit JB infestations (e.g., detecting JB infestations to inform decisions on pesticide application by stakeholders). Specifically, field trapping and direct observation experiments were used to assess: i) the impact of wind speed and direction on the approach of JB to green Trécé Pherocon traps baited with the Trécé dual lure; ii) the impact of using trap clusters versus single traps on the number of JB captured; iii) comparison of the number and sex-ratio of JB captured by the floral lure, pheromone lure and floral and pheromone lure together, and iv) the capture efficiency of baited traps.

Materials and methods

Field Site

Field trials were conducted at the Southeastern Turfgrass Research Center in Kentucky (USA) (<http://setrc.com/experiment-station.html>) (Figure 1). This facility has 20 acres of highly maintained turf and 230 acres of sod production and crops and forages used for research. Field trials were run between 12-15 July, 2022. Each experiment was run at different times of the day and on different days between 0900 and 1700 (Table 1 supplementary material). Green Trécé Pherocon® JB traps were hung from metallic poles ca. 1.3-m above ground. At collection, trap catches were placed in re-sealable bags on ice in a cooler and transported daily to a freezer and subsequently transported on ice in a cooler to the laboratory (16th of July 2022), at which time they were placed at -20°C until they could be processed.

Experiment 1: JB direction of approach to a baited trap

A single trap baited with a dual lure from Trécé was placed in the middle of a 2-m diameter circle. The circle was divided into six equal sections of 60 degrees, with the first section starting from magnetic north. Three observers were placed on the outside of the circle 120 degrees apart with each observer positioned at the border of two adjacent sections. When a beetle was observed to enter the circle, the time and section it entered were recorded. Simultaneously, date, time and wind direction and speed were recorded with a 3D sonic anemometer (CSAT3B, Campbell Scientific, Logan, Utah, United states) deployed ~1-m above the trap. All wind speeds observed fell within the range of measurement of the sonic anemometer (0 to 4.74 m/sec). Each of the four replicates in this experiment was conducted once and separately (i.e., one at a time), each at a different location at the field site (red flags, Figure 1).

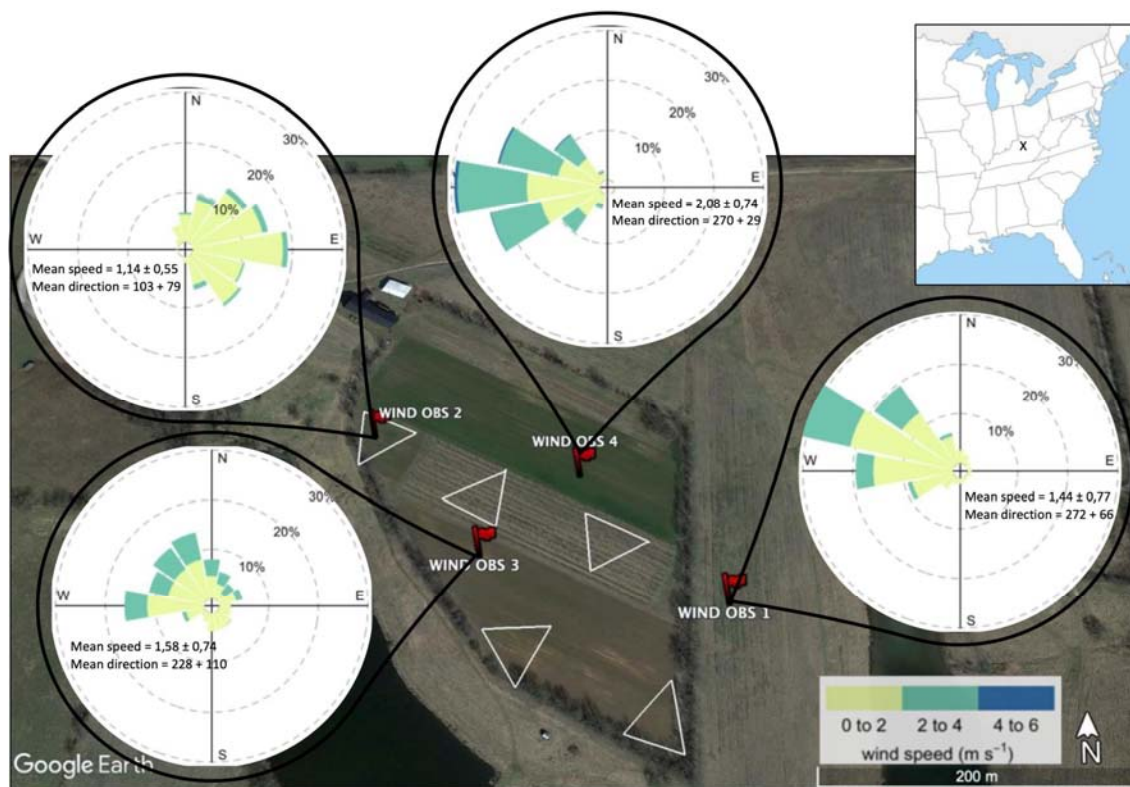


Figure 1: Top view of the field site. For experiment 2, the location of the five replicates of the three treatments (1L, 3L and 3T) are shown by the white triangles. The red flags indicate the locations where experiments 1 and 3 were conducted. The concentric circles in the rose plots represent the frequencies of wind direction and speed (mean ± STD) measured for experiment 1. The wind speed categories and a spatial scale are showing in on the bottom right. The top right panel shows the location of the field site in Kentucky (USA).

Experiment 2: Single vs. cluster trap trial

The National Plant Protection Organization for Canada, the CFIA, was interested in the relationship between trap sensitivity or the number of beetles captured and the number of traps and lures deployed per location. To explore this relationship, a total of five replicate blocks were simultaneously deployed and each replicate block consisted of the following treatments: i) a single trap baited with a single dual lure (1L), ii) a single trap baited with three dual lures (3L), and iii) a cluster of three traps each baited with a single dual lure (3T) (white triangles,

Figure 1). The three treatments in each replicate block were deployed one per vertex of an equilateral triangle with 50-m sides. Replicate blocks were placed at least 50-m from each other. Three replicate blocks were deployed on turf, and two in an old hop field with few remaining living plants surrounded by turf. For the 3T treatment, the first trap was placed 50-m away from the other two treatments. The two other traps of treatment 3T were placed in a 2-m equilateral triangle in the opposite direction of the 1L and 3L to avoid interference among treatments. Replicates of field trapping trials were run for less than 1.5 hours to avoid trap saturation. After each collection, traps were emptied, and treatments were rotated clockwise for a total of 9 collections over 3 days for a total of 45 (9 temporal x 5 spatial) replicate blocks, each comparing the three treatments.

Experiment 3: Lure type & sex ratio

We wanted to test the interaction between pheromone and kairomone as some uncertainty exists in the literature about whether synergy between the pheromone and kairomone occurs. A single replicate block with one trap with each of the following treatments was established: i) a pure pheromone standard, ii) Trécé dual lure, iii) Trécé floral lure from the dual lure and iv) Trécé pheromone septum from the dual lure. The pure standard pheromone treatment was made of a septum impregnated with 10 μ l of 3 ppm pheromone (donated by Trécé) diluted in *n*-hexane. The four treatments were deployed one per corner of a 2-m square. Treatments were rotated clockwise after every collection for a total of 7 collections all on the same day (i.e., seven temporal replicates). Each temporal replicate was run between 20-60 minutes. The sex-ratio was determined in the lab by sexing a haphazard selection of 100 individuals from each trap based on front leg morphology (Fleming 1969). When fewer than 100 individuals were present in a single trap capture, all the beetles were sexed.

Experiment 4: Trap efficiency upon first approach

The experiment was conducted for 1 hour at the same four different locations as the direction of approach experiment (red flags, Figure 1), but not at the same time. For this experiment, when a beetle entered the 2-m circle a 30-second timer was started. A pilot study indicated that we could confidently track beetles from this distance to the trap. That assay length was arbitrarily chosen to assess if the trap was efficient at rapidly capturing flying beetles. During that time, three observers standing 120 degrees apart around a 2-m diameter circle with the trap at its center recorded the first of the three outcomes: the insect was captured, landed on the trap or flew away. If any of these three outcomes occurred before 30 seconds, the observation was terminated. An event was only recorded if all three observers reported the same outcome.

Statistical analyses

For Experiment 1 the 3D sonic anemometer collected measurements at 20 Hz continuously during the time of the experiment and these data were averaged for every second. Time of recording and wind speed and direction were computed, and magnetic north was corrected to true north in subsequent analyses. Wind speed and direction were extracted to match the exact time a beetle entered the circle. The direction the beetle approached the trap (i.e., which of the six sections the beetle entered) was analyzed relative to the wind direction. Beetles were scored as “upwind flight” if the vector that described wind direction exited the circle from the section the beetle entered the circle. If the beetle and vector that described wind direction entered the same section, the beetle was scored as “downwind flight” (Figure 2A). Cross upwind and cross downwind referred to beetles entering the circle from the sections sharing a side with the current upwind or downwind section, respectively. A multinomial logistic regression and a 2 tailed Z-test on the regression coefficients were used to determine the effect of wind speed and direction on the direction of beetle approach to the trap. The direction of approach relative to

wind direction was also tested against theoretical frequencies (1/3 for cross downwind and cross upwind, 1/6 for downwind and upwind) with a χ^2 test.

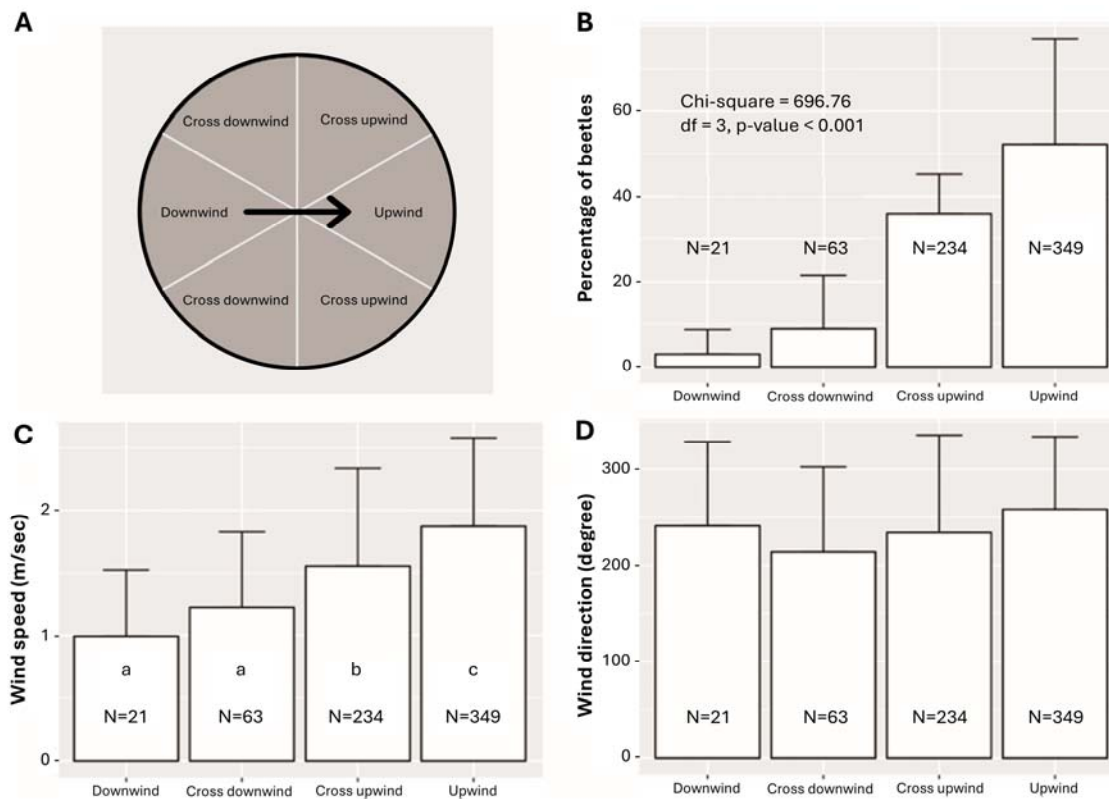


Figure 2: Direction of JB approach to baited traps. Panel A: Section labelling relative to the wind direction during real time measurement. When the wind was blowing from left to right (black arrow) the section situated directly downwind relative to the trap placed at the center was labelled “upwind” (for upwind flight). Panel B: Percentages of JB captured (mean \pm STD) approaching the trap from different directions relative to the wind direction. All four treatments differed significantly from each other. Panel C: Wind speed (mean \pm STD) for each of the different directions of flight approach. Different letters indicate significant differences. Panel D: The influence of wind direction (mean \pm STD) on how beetles approach a trap. No effect of wind direction was observed.

For Experiment 2: “single trap vs. cluster design”, Kruskal-Wallis tests showed no significant differences among spatial replicates ($H(4) = 8.86$, p-value = 0.06) or trap positions within each

block ($H(14) = 9.79$, $p\text{-value} = 0.77$) on the number of beetles collected per hour, but differences between days ($H(2) = 43.31$, $p\text{-value} < 0.0001$) and time of day when the collection occurred ($H(8) = 84.78$, $p\text{-value} < 0.0001$) were observed. Similarly, Kruskal-Wallis tests showed a significant effect of time of collection ($H(6) = 14.54$, $p\text{-value} = 0.02$) in Experiment 3: “lure type & sex ratio”. For these reasons, data collected in experiment 2 and 3 were first normalized into number of beetles captured per hour by i) adjusting the absolute number of beetles based on the time elapsed between baiting the trap and collecting the beetles to account for time variation, and ii) transformed to percentages of beetles captured per hour for each treatment of each replicate to account for spatial variation. Kruskal-Wallis tests were subsequently used for each experiment to determine if at least one treatment was different from the others. For each experiment when differences were shown, a Dunn’s test with an “Holm” correction was performed (Holm 1979). All statistical analyses were performed in R V4.3.1 (R core team, 2017) using Rstudio (Posit team, 2025).

Results

A total of 293 916 JB were captured in the direction of trap approach, single versus cluster trap and lure type trials.

Experiment 1: JB direction of approach to baited traps

A total of 667 beetles were observed (Figure 2 and Table 2 supplementary material). The pattern of direction of beetles approaching the trap differed significantly from the expected random pattern ($\chi^2 = 696.76$, $df = 3$, $p\text{-value} < 0.0001$). Beetles predominantly flew upwind ($52 \pm 25\%$, mean \pm STD), followed by cross upwind ($36 \pm 9\%$, mean \pm STD), cross downwind ($9 \pm 13\%$, mean \pm STD) and finally downwind ($3 \pm 6\%$, mean \pm STD) (Figure 2B). The multinomial logistic regression showed a significant effect of wind speed on the flight pattern

but no effect of wind direction (relative to the cardinal points) (Figure 2C, D). Posthoc analyses showed that the mean wind speed for downwind and cross downwind approach were similar (0.99 ± 0.53 and 1.22 ± 0.60 m/s respectively, mean \pm STD) (p-values > 0.05) and was significantly lower than the mean wind speed for upwind and cross-upwind approaches (1.56 ± 0.78 and 1.87 ± 0.71 m/s, respectively, mean \pm STD) (p-values < 0.05).

Experiment 2: Single trap vs. cluster design

A total of 265 884 beetles were captured in the traps deployed over 9 hours and 18 min of sampling (Table 3 supplementary material). An average of $2\ 001 \pm 1\ 535$ (mean \pm STD) beetles were captured per hour, ranging from 134 to 7 400 beetles captured per hour. Kruskal-Wallis tests showed that at least one treatment captured a different percentage of beetles than the other treatments ($H(2) = 22.58$, p-value < 0.0001). Posthoc analyses showed that all treatments captured significantly different percentages of beetles (p-value < 0.05). Treatment 3T followed by 3L and 1L captured $48 \pm 8\%$, $30 \pm 7\%$ and $22 \pm 7\%$ (mean \pm STD) of the beetles per hour, respectively (Figure 3). Each individual trap of the 3T treatment captured significantly fewer beetles than the 1L treatment with an average of $16 \pm 3\%$ per individual trap.

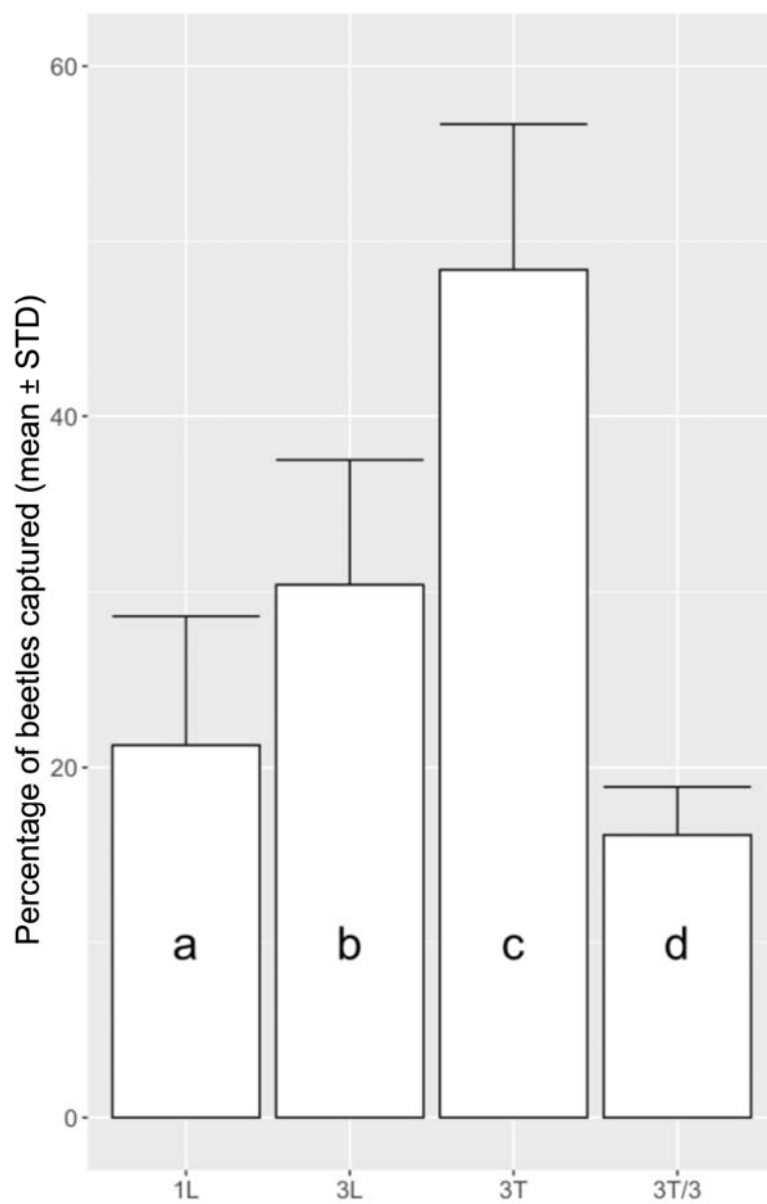


Figure 3: Percentage of beetles captured (mean \pm STD) in the single trap with one lure (1L), single trap with three lures (3L), cluster of three traps (3T) and the average percentage of beetles captured per hour per trap of the 3T treatment (3T/3). Different letters indicate significant differences.

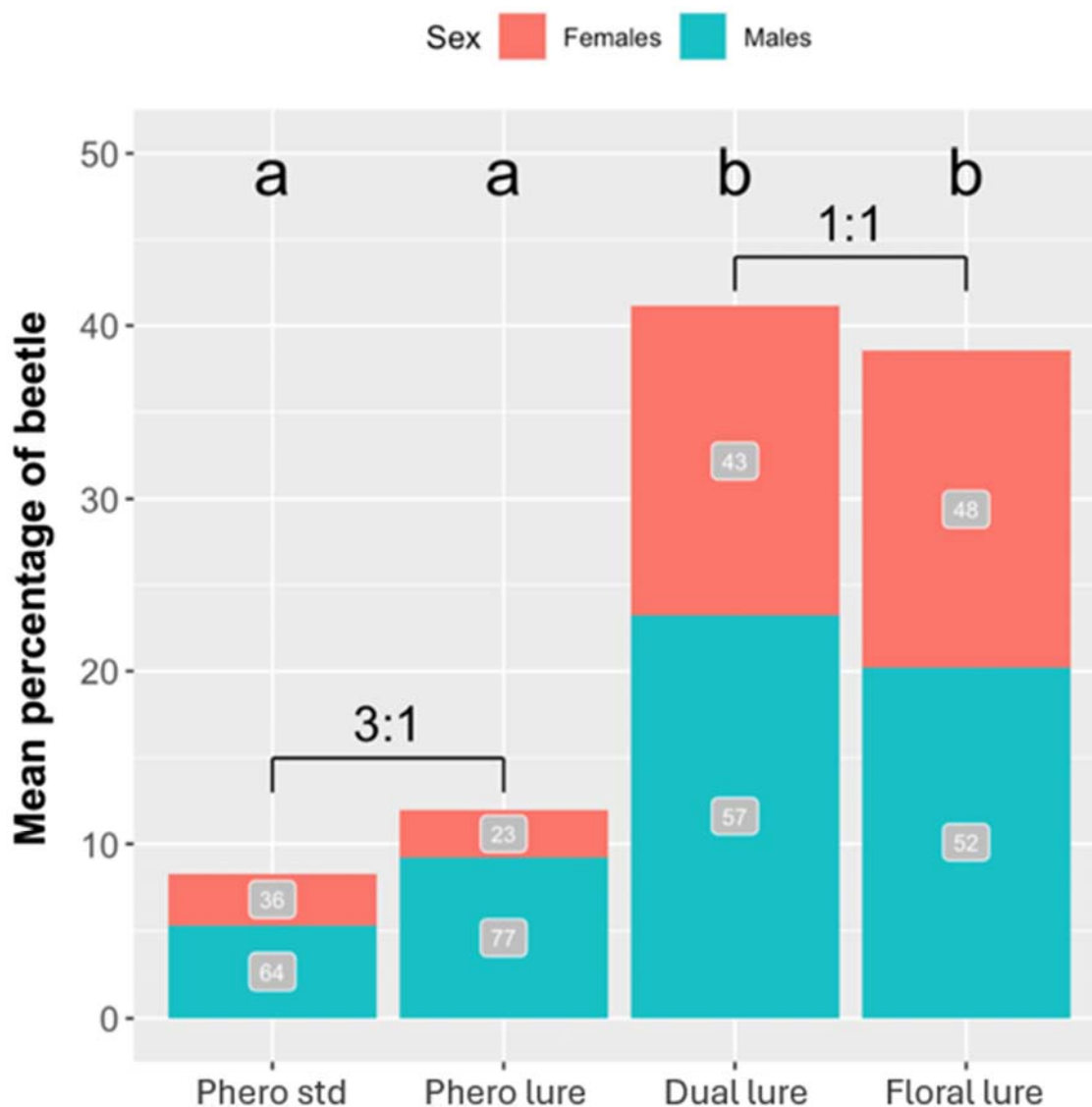


Figure 4: Mean percentage of beetles captured in traps baited with the pheromone standard (Phero std), the pheromone from the Trécé dual lure (Phero lure) alone, the Trécé dual lure (Dual lure) and the Trécé floral lure (Floral lure) from the DL alone. A total of 2 710 beetles were individually sexed. Different letters indicate significant differences. Sex ratio for the pheromone standard and Trécé septa was approximately 3:1 (M:F) and 1:1 for the Trécé lure and Trécé patch. Numbers in grey indicate the average percentage of males (blue) or females (red) captured for each treatment.

Experiment 3: Lure type & sex ratio

A total of 2 710 JB were sexed from 27 227 beetles captured (Figure 4 and Table 4 supplementary material). Kruskal-Wallis tests showed a significant treatment effect on sex ratio ($H(3) = 17.31$, $p\text{-value} < 0.001$) and percentage of beetles captured ($H(3) = 20.98$, $p\text{-value} < 0.001$), but there was not a significant effect of the time of collection ($H(6) = 2.14$, $p\text{-value} = 0.91$). Posthoc analyses showed no differences between the floral lure (Trécé patch, 1:1 sex ratio, $39 \pm 9\%$ of beetles captured) and Trécé dual lure (1:1 sex ratio, $41 \pm 11\%$ of beetles captured) in sex-ratio ($Z = 0.75$, $p\text{-value} = 0.91$) or percentage of beetles captured ($Z = 0.16$, $p\text{-value} = 0.09$). Similarly, no differences were shown between the Trécé pheromone septa (3:1 sex ratio, $12 \pm 5\%$ of beetles captured) and pheromone standard septa (3:1 sex ratio, $8 \pm 4\%$ of beetles captured) on sex-ratio ($Z = -0.33$, $p\text{-value} = 0.74$) or percentage of beetles captured ($Z = -0.81$, $p\text{-value} = 0.83$).

Experiment 4: Trap efficiency upon first approach

A total of 138 beetles were observed for 30 seconds (or until one of the three outcomes was observed) after entering a 2-m radius around the trap. For these beetles, 43% were captured, 22% landed on the trap and 35% exited the circle without being captured (Figure 5).

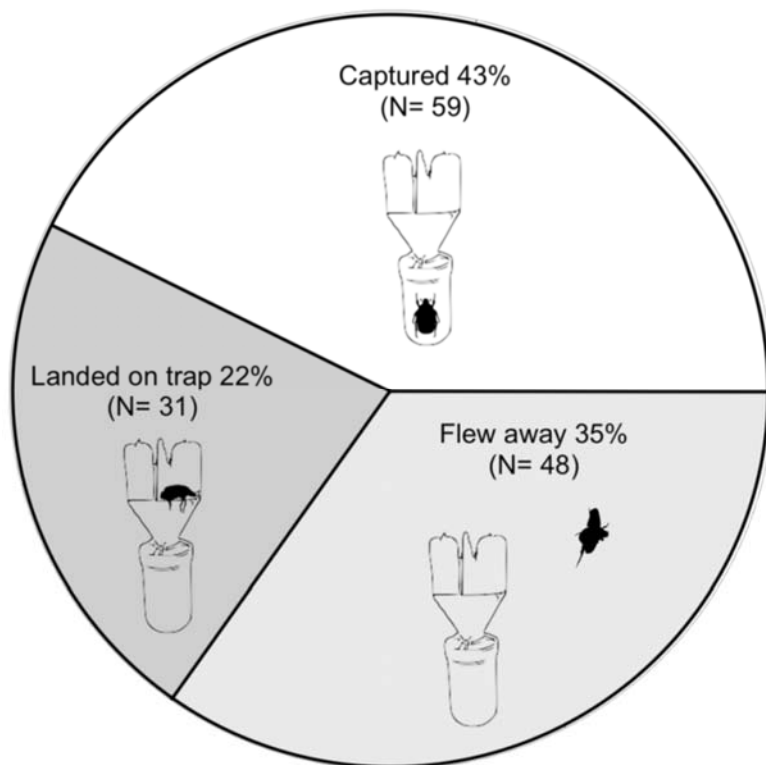


Figure 5: Percentage of beetles that were captured, flew away or landed on a baited trap within thirty seconds of approaching within 2m of a trap baited with a DL. Observations were conducted at four different locations (red flags, Figure 1).

Discussion

The direction of JB flight is strongly linked to wind direction and speed in the field. Over half of JB observed to approach a baited trap did so from the downwind direction (i.e., flew upwind to the trap). This result is consistent with previous reports that male JB fly upwind to females but no data were presented to support this observation (Fleming 1969). Upwind flight to odorants in the field has only been observed in a few species of Coleoptera [i.e., *Ips typographus* (Schlyter et al. 1987), *Dendroctonus brevicomis* (Byers 1988), *Meligethes aeneus* (Williams et al. 2007), *Dendroctonus frontalis* (Sullivan and Brownie 2022), and *Agriotes obscurus* (van Herk and Vernon 2023)]. Wind speed also affects the number of JB captured, with trap catches significantly higher at wind speeds above 1.5 m/s. Wind direction (relative to

the cardinal points) did not affect the direction of approach suggesting that the flight behavior of the beetle was not an artifact of external factors (i.e., obstruction, position of the sun, magnetic field, visual background). This is the first study we are aware of to characterize in real-time the effect of wind direction and speed on the flight behaviour of a beetle in the field.

The highest number of beetles was captured by placing a cluster of three traps together. However, placing one trap baited with three dual lures captured the highest number of beetles relative to the cost per trap. The difference in beetle catch is likely caused by inter-trap competition, as individual traps within the cluster on average captured fewer beetles than the one trap with one lure treatment. The material cost of deploying a cluster of three traps is about 2.5 times greater than one trap baited with three dual lures but only captures 1.5 times more JB. However, utilizing the trap configuration that captures the most JB may be beneficial and a more accurate indicator of treatment success (e.g., insecticide application) within an eradication program. The importance of optimizing the total number of beetles captured versus number captured relative to the cost per trap will vary with program objectives. While eradication programs are likely to emphasize optimizing the total number of beetles captured, monitoring programs may focus on optimizing the number captured relative to the cost. Future research on inter-trap distance and number of dual lures per trap in support of eradication and monitoring efforts could consider these differences in program priorities.

We did not observe any evidence of synergism or additive effects of the floral attractant and pheromone lure on JB captures. In fact, the dual lure was the most attractive treatment and the number of JB captured was not affected by the removal of the pheromone lure. Potter and Held (2002) report that Ladd et al. (1981) observed synergism of JB captures when traps were baited with the floral attractant and pheromone, but examination of the original experimental design

of Ladd et al. (1981) suggests that they could not have observed synergism as the pheromone was not tested on its own. In another study, synergism between a pheromone and floral attractant lure was reported but that study used a different floral blend without geraniol (Ladd and Klein 1982). A later study tested the floral lure and the pheromone separately, but not the combination of both in the same year (Ladd and Klein 1986). It is possible that the high density of JB or differences in release rates of the floral lure and pheromone septum contributed to the absence of an effect of the pheromone on the capture of JB by traps baited with the floral lure in this study.

Traps baited with the floral lure captured a 1:1 sex ratio of JB with or without the presence of the pheromone lure. However, the sex ratio shifted to 3:1 (M:F) and the number of beetles captured decreased significantly when traps were only baited with the pheromone. These results agree with the results of previous studies. Traps baited with the dual lure and placed in soybeans captured a 1:1 sex-ratio (Switzer et al. 2009). Allsopp et al. (1992) reported no differences in the sex-ratio or number captured by traps baited with the floral lure + pheromone or floral lure alone. These authors also reported fewer beetles were captured by traps baited with pheromone alone and the sex ratio was biased toward males and varied with beetle density. However, only the lowest and highest mean number of catches were reported and the variation in sex-ratio and in catch number between lures from that study are not clear.

Of the 138 JB observed to approach within 2-m of a baited trap, more were captured than landed on the trap or flew away. However, individual beetles that made multiple approaches without being captured within the 30 second observation period may have been counted more than once, introducing a possible bias. Similar results were reported by Switzer et al. (2009) where more JB were also captured than landed on the trap or flew away. Although not

quantified, we observed that when more than one beetle landed on the trap, they could form an aggregation that blocked the trap entrance. These blockages likely reduce trap performance. A larger entrance hole or coating the traps with a lubricant (Graham and Poland 2012; Allison et al. 2014) could mitigate this problem and increase trap efficiency. For heavily infested areas, an adapted design with trash bins as a receptacle has been shown to be more efficient at mass trapping beetles than traditional traps (Piñero and Dudenhoefler 2018).

In summary, this study demonstrated that the majority of JB that were captured had approached traps from downwind and that a cluster of three traps captured the most JB. Our study was limited to a single site and a one-week time window. However, large numbers of JB were captured, suggesting that at least for this population and given environmental conditions, our results have good statistical power. It is possible that given the broad distribution of this insect that geographical variation exists. The very high numbers of JB at this site in Kentucky might have influenced the outcome of the single trap vs. cluster design and lure type and sex ratio experiments compared to if they were conducted in lower density populations such as those in British Columbia. Further studies on the influence of JB density on the effect of trap deployment protocol should be conducted to facilitate present and future implementation of eradication programs.

Acknowledgments

We thank Dr. Daniel Potter from University of Kentucky and Dr. Mike Harrell at the Southeastern Turfgrass Research Center for advice and permission to conduct experiments on this site, respectively. The University of Kentucky Agricultural Experiment Station provided access to laboratory facilities. We also thank Hannah Dunlop, Amy Carlson, Samara Mendes, Isabelle Ochoa and Josephine Queffelec for their help in processing and counting beetles. This

research was funded by SERG International, the Canadian Food Inspection Agency (CFIA), Natural Resources Canada (NRCan), the Tree Protection Cooperative Program (TPCP) and the DSI NRF Centre of Excellence in Plant Health Biotechnology (CPHB) in South Africa. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. In addition, we would like to acknowledge the efforts of the BC Ministry of Agriculture and Food, BC Landscape and Nursery Association, the Invasive Species Council of BC and the cities of Vancouver and Burnaby for their role in the JB eradication program.

Author's contribution

QG contributed to the conceptualisation, method, data curation, formal analyses, visualisation, wrote the original draft and reviewed and edited the manuscript; JG participated in the investigation, data curation, formal analyses; TK was involved in the conceptualisation, resources and funding acquisition; KH took part in the conceptualisation, methodology, project administration and resources, JA contributed to the conceptualisation, funding acquisition, supervision of QG and JG, reviewed and edited the manuscript.

Conflict of interest

The authors declare no conflicts of interest.

References

- Allison JD, Bhandari BD, McKenney JL, Millar JG. 2014. Design factors that influence the performance of flight intercept traps for the capture of longhorned beetles (Coleoptera: Cerambycidae) from the subfamilies Lamiinae and Cerambycinae. *PLoS One*. 9(3). <https://doi.org/10.1371/journal.pone.0093203>
- Allison JD, Marcotte M, Noseworthy M, Ramsfield T. 2021. Forest biosecurity in Canada – an integrated multi-agency approach. *Front. For. Glob. Change*. 4.
- Allison JD, Redak RA. 2017. The impact of trap type and design features on survey and detection of bark and woodboring beetles and their associates: a review and meta-analysis. *Annu. Rev. Entomol.* 62(1):127–146. <https://doi.org/10.1146/annurev-ento-010715-023516>
- Allsopp PG, Ladd TL, Klein MG. 1992. Sample sizes and distributions of Japanese beetles (Coleoptera: Scarabaeidae) captured in lure traps. *J. Econ. Entomol.* 85:1797–1801. <https://doi.org/10.1093/jee/85.5.1797>
- Alm SR, Yeh T, Dawson CG, Klein MG. 1996. Evaluation of trapped beetle repellency, trap height, and string pheromone dispensers on Japanese beetle captures (Coleoptera: Scarabaeidae). *Environ. Entomol.* 25:1274–1278. <https://doi.org/10.1093/ee/25.6.1274>
- Althoff ER, Rice KB. 2022. Japanese beetle (Coleoptera: Scarabaeidae) invasion of North America: history, ecology, and management. *J. Integr. Pest Manag.* 13(2). <https://doi.org/10.1093/jipm/pmab043>
- Byers JA. 1988. Upwind flight orientation to pheromone in western pine beetle tested with rotating wind vane traps. *J. Chem. Ecol.* 14:189–198. <https://doi.org/10.1007/BF01022541>
- Della Rocca F, Milanesi P. 2022. The new dominator of the world: modeling the global distribution of the Japanese beetle under land use and climate change scenarios. *Land*. 11:567. <https://doi.org/10.3390/land11040567>

- EPPO. 2017. First report of *Popillia japonica* in Switzerland.
- Fleming WE. 1969. Attractants for the Japanese Beetle. Agricultural Research Service.
- Fleming WE. 1972. Biology of the Japanese beetle, technical bulletin No. 1449, USDA.
- Gordon CF, Potter DA. 1986. Japanese beetle (Coleoptera: Scarabaeidae) traps: evaluation of single and multiple arrangements for reducing defoliation in urban landscape. J. Econ. Entomol. 79:1381–1384. <https://doi.org/10.1093/jee/79.5.1381>
- Gordon F, Potter DA. 1985. Efficiency of Japanese beetle (Coleoptera: Scarabaeidae) traps in reducing defoliation of plants in the urban landscape and effect on larval density in turf. J. Econ. Entomol. 78:774–778. <https://doi.org/10.1093/jee/78.4.774>
- Graham EE, Poland TM. 2012. Efficacy of fluon conditioning for capturing cerambycid beetles in different trap designs and persistence on panel traps over time. J. Econ. Entomol. 105:395–401. <https://doi.org/10.1603/EC11432>
- Holm S. 1979. A simple sequentially rejective multiple test procedure. Scand. J. Stat. 6(2):65–70.
- Ladd TL, Klein MG. 1986. Japanese beetle (Coleoptera: Scarabaeidae) response to color traps baited with phenethyl propionate + eugenol + geraniol (3:7:3) and japonilure. J. Econ. Entomol. 79:84–86. <https://doi.org/10.1093/jee/79.1.84>
- Ladd TL, Klein MG. 1982. Trapping Japanese beetles with synthetic female sex pheromone and food-type lures [*Popillia japonica*]. Insect Suppression with Controlled Release Pheromone Systems II.
- Ladd TL, Klein MG, Tumlinson JH. 1981. Phenethyl propionate + eugenol + geraniol (3:7:3) and japonilure: a highly effective joint lure for Japanese beetles. J. Econ. Entomol. 74:665–667. <https://doi.org/10.1093/jee/74.6.665>

- Lessio F, Pisa CG, Picciau L, Ciampitti M, Cavagna B, Alma A. 2022. An immunomarking method to investigate the flight distance of the Japanese beetle. *Entomol. Gen.* 45–56. <https://doi.org/10.1127/entomologia/2021/1117>
- Piñero JC, Dudenhoefter AP. 2018. Mass trapping designs for organic control of the Japanese beetle, [*Popillia japonica*] (Coleoptera: Scarabaeidae). *Pest Manag. Sci.* 74:1687–1693. <https://doi.org/10.1002/ps.4862>
- Posit team. 2025. RStudio: Integrated Development Environment for R. Available from <http://www.posit.co/>
- Potter DA, Held DW. 2002. Biology and management of the Japanese beetle. *Annu. Rev. Entomol.* 47:175–205. <https://doi.org/10.1146/annurev.ento.47.091201.145153>
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Schlyter F, Löfqvist J, Byers JA. 1987. Behavioural sequence in the attraction of the bark beetle *Ips typographus* to pheromone sources. *Physiol. Entomol.* 12:185–196. <https://doi.org/10.1111/j.1365-3032.1987.tb00741.x>
- Shanovich HN, Dean AN, Koch RL, Hodgson EW. 2019. Biology and management of Japanese beetle (Coleoptera: Scarabaeidae) in corn and soybean. *J. Integr. Pest Manag.* 10:9. <https://doi.org/10.1093/jipm/pmz009>
- Staton T, Girling RD, Redak RA, Smith SM, Allison JD. 2023. Can morphological traits explain species-specific differences in meta-analyses? A case study of forest beetles. *Ecol. Appl.* 33(4). <https://doi.org/10.1002/eap.2838>
- Sullivan BT, Brownie C. 2022. The role of wind and semiochemicals in mediating switching behavior in the southern pine beetle (Coleoptera: Curculionidae: Scolytinae). *Environ. Entomol.* 51:340–350. <https://doi.org/10.1093/ee/nvac006>

- Switzer PV, Enstrom PC, Schoenick CA. 2009. Behavioral explanations underlying the lack of trap effectiveness for small-scale management of Japanese beetles (Coleoptera: Scarabaeidae). *J. Econ. Entomol.* 102:934–940. <https://doi.org/10.1603/029.102.0311>
- Tumlinson JH, Klein MG, Doolittle RE, Ladd TL, Proveaux AT. 1977. Identification of the female Japanese beetle sex pheromone: inhibition of male response by an enantiomer. *Science.* 197:789–792.
- USDA/APHIS. 2015. Managing the Japanese beetle: a homeowner's handbook. US Department of Agriculture. <https://www.aphis.usda.gov/aphis/ourfocus/planthealth/plant-pest-and-disease-programs/pests-and-diseases/japanese-beetle/japanese-beetle>
- van Herk WG, Vernon RS. 2023. Capture of wild and marked *Agriotes obscurus* in pheromone traps according to distance, wind direction and date of trapping. *Arthropod-Plant Interact.* <https://doi.org/10.1007/s11829-023-09961-0>
- Williams IH, Frearson D, Barari H, McCartney A. 2007. Migration to and dispersal from oilseed rape by the pollen beetle, *Meligethes aeneus*, in relation to wind direction. *Agric. For. Entomol.* 9:279–286. <https://doi.org/10.1111/j.1461-9563.2007.00343.x>