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Animal–robot interaction induces local enhancement in the Mediterranean fruit fly *Ceratitis capitata* Wiedemann

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Abstract

Animal–robot interaction (ARI) is an emerging field that uses biomimetic robots to replicate biological cues, enabling controlled studies of animal behavior. This study investigates the potential for ARI systems to induce local enhancement (e.g. where animals are attracted to areas based on the presence or actions of conspecifics) in the Mediterranean fruit fly, *Ceratitis capitata* (*C. capitata*), a major agricultural pest. We developed biomimetic agents that mimic *C. capitata* in morphology and color, to explore their ability to trigger local enhancement. The study employed three categories of artificial agents: full biomimetic agent (FBA), partial biomimetic agent (PBA) and non-biomimetic agent (NBA) in both motionless and moving states. Flies exposed to motionless FBAs showed a significant preference for areas containing these agents compared to areas with no agents. Similarly, moving FBAs also attracted more flies than stationary agents. Time spent in the release section before making a choice and the overall experiment duration were significantly shorter when conspecifics or moving FBAs were present, indicating that *C. capitata* is highly responsive to biomimetic cues, particularly motion. These results suggest that ARI systems can be effective tools for understanding and manipulating local enhancement in *C. capitata*, offering new opportunities for sustainable pest control in agricultural contexts. Overall, this research demonstrates the potential of ARI as an innovative, sustainable approach to insect population control, with broad applications in both fundamental behavioral research and integrated pest management.

1. Introduction

Animal–robot interaction (ARI) is an interdisciplinary field within bioinspiration and biomimetics that investigates how robotic agents designed to replicate biological cues or behaviors can engage with animal populations (Krause *et al* 2011, Romano *et al* 2019, Schmickl and Romano 2024). By simulating specific stimuli, ARI studies allow researchers to examine animal cognition, decision-making, and social behaviors in ways that would otherwise be challenging to achieve in natural settings (Halloy *et al* 2007, Macrì *et al* 2020, Barmak *et al* 2023, Maxeiner *et al* 2023, Romano and Stefanini 2024). These biohybrid systems can provide controlled, repeatable interactions that help scientists manipulate environmental variables, offering insights into the mechanisms underlying animal behavior. Recent advances

in ARI have enabled researchers to explore species-specific behaviors in novel ways, paving the way for applications in behavioral science, pest management, and environmental sustainability (Polverino *et al* 2022, Romano and Stefanini 2022a, Ulrich *et al* 2024).

Robots can mimic conspecific signals or environmental cues to trigger specific behaviors in target animals, enabling researchers to study how animals perceive and respond to their surroundings (Bierbach *et al* 2020, Romano *et al* 2021, Barmak *et al* 2023). These techniques have proven useful across different species, including studies on fish schooling (Polverino *et al* 2019, Landgraf *et al* 2021, Romano and Stefanini 2022b), birds (de Margerie *et al* 2011, Araguas *et al* 2022), mammals (Shi *et al* 2015, Chen *et al* 2021), insects (Landgraf *et al* 2011, Romano *et al* 2020, Rekabi-Bana *et al* 2023), and more. In

applied contexts, ARI has great potential for developing non-invasive methods to influence animal populations, such as controlling pest species without relying on chemical pesticides. ARI systems can be engineered to attract or repel specific species, offering sustainable, behavior-based solutions that align with eco-friendly environmental management practices (Foster and Harris 1997, Serra and Ogando 2013).

In agricultural pest control, ARI can offer particularly promising strategies for managing insect populations, which is crucial for minimizing crop damage and reducing chemical interventions (Romano *et al* 2023). Robotics-based strategies could play a key role in controlling populations of economically important pests. Among these, the Mediterranean fruit fly or Medfly, *Ceratitis capitata* Wiedemann (Diptera: Tephritidae) is a major agricultural pest that infests a wide variety of fruit crops, causing significant economic losses worldwide (Malacrida *et al* 2007, Giunti *et al* 2023, Papadopoulos *et al* 2024). Although *C. capitata* is a primarily solitary species, high population densities in fruit crops can lead to emergent interactions with conspecifics (Diamantidis *et al* 2011, Benelli and Romano 2018, Lux 2018), such as lek formations (Field *et al* 2002) and aggregating in areas where resources are abundant (Rull *et al* 2003).

One behavior of particular interest is local enhancement (Heyes *et al* 2000, Avarguès-Weber and Chittka 2014), a phenomenon where individuals are drawn to a specific location attracted by the presence or actions of other individuals. While local enhancement is often observed in social species, it can also occur in solitary species that aggregate under specific conditions, such as high population density or shared resource availability (Pérez-Cembranos and Pérez-Mellado 2015). Local enhancement plays an essential role in influencing the movement and distribution of animals, and its underlying mechanisms are highly relevant to fields such as behavioral ecology and applied pest management. By understanding and manipulating local enhancement behaviors, researchers can effectively attract or deter certain species to manage populations or protect specific areas.

In tephritid flies, including *C. capitata*, local enhancement has been documented (Prokopy *et al* 2000, Piñero and Prokopy 2004), where individuals are attracted to locations where conspecifics are found, particularly around food sources or oviposition sites. Although *C. capitata* is generally solitary, situations with high population densities can induce behaviors that resemble those of social species (e.g. aggregating in shared resource zones, trophallaxis, etc) (Prokopy *et al* 2000, Benelli and Romano 2018). This behavior is relevant for developing ARI systems, as it suggests that *C. capitata* populations might be guided towards designated areas by introducing specific cues that elicit aggregation, thereby

increasing the effectiveness of trapping or other control measures. By simulating the presence of conspecifics or other attraction cues, biomimetic robotic agents may trigger these behaviors.

The purpose of this study is to investigate local enhancement behaviors in *C. capitata* by developing biomimetic agents that can replicate conspecific cues and attract flies to specific locations. The ARI paradigm will enable us to explore how *C. capitata* responds to artificial cues under controlled conditions. Through this work, we aim to understand whether robotic agents can effectively induce local enhancement in this species, thereby facilitating aggregation in a way that could be used to add new knowledge on the behavioral ecology of this key agricultural species, improving its sustainable control.

2. Materials and methods

2.1. Ethic statement

This research complies with the ethical guidelines set forth for the treatment of animals in behavioral research and teaching (ASAB/ABS 2014), adheres to Italian regulations (D.M. 116192), and aligns with European Union standards (European Commission 2007). All experiments were limited to behavioral observations. No specific permits were required from the Italian government for tests involving *C. capitata*.

2.2. Insect rearing and general information

The *C. capitata* strain used in this study originated from the University of Pisa, which has maintained a continuous culture of the species since 1994. The initial population was established with approximately 4000 wild individuals collected from fruit orchards in Sicily, Italy. To sustain genetic diversity, the strain was periodically supplemented with wild flies in 1997, 2003, 2007, 2012, and 2016, with around 2000 flies introduced during each refresh (maintaining a 1:1 sex ratio). Flies were reared in cylindrical PVC cages, each holding approximately 2000 individuals with equal numbers of males and females. Adult flies were fed a dry diet composed of yeast extract and sucrose in a 1:10 weight ratio. Water was supplied separately through a cotton wick.

Eggs were collected every two days and placed in shallow plastic trays (50 cm × 15 cm with a 2 cm depth) containing 500 g of an artificial larval diet. The pupae, held under carefully controlled conditions (21 ± 1 °C, $55 \pm 5\%$ relative humidity, with a 16:8 h light cycle), were transferred to the BioRobotics Institute of Scuola Superiore Sant'Anna in Pisa for experimental procedures.

All experiments took place in a controlled environment at 21 ± 1 °C and $55 \pm 5\%$ relative humidity. To provide consistent lighting, fluorescent daylight tubes were set to a 16:8 light schedule, turning

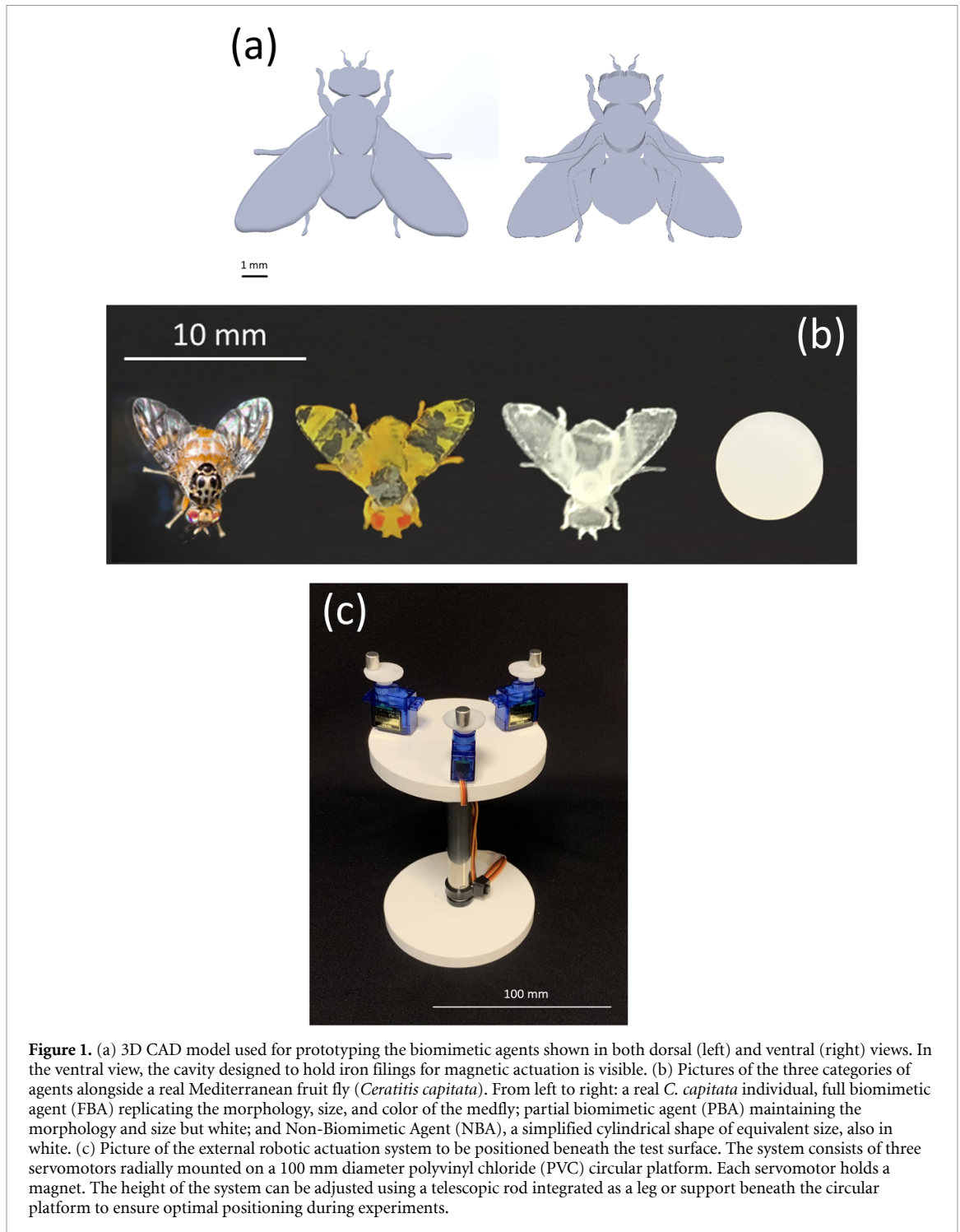


Figure 1. (a) 3D CAD model used for prototyping the biomimetic agents shown in both dorsal (left) and ventral (right) views. In the ventral view, the cavity designed to hold iron filings for magnetic actuation is visible. (b) Pictures of the three categories of agents alongside a real Mediterranean fruit fly (*Ceratitidis capitata*). From left to right: a real *C. capitata* individual, full biomimetic agent (FBA) replicating the morphology, size, and color of the medfly; partial biomimetic agent (PBA) maintaining the morphology and size but white; and Non-Biomimetic Agent (NBA), a simplified cylindrical shape of equivalent size, also in white. (c) Picture of the external robotic actuation system to be positioned beneath the test surface. The system consists of three servomotors radially mounted on a 100 mm diameter polyvinyl chloride (PVC) circular platform. Each servomotor holds a magnet. The height of the system can be adjusted using a telescopic rod integrated as a leg or support beneath the circular platform to ensure optimal positioning during experiments.

on at 06:00 am. Illumination within the test arena was measured at approximately 1000 lx using an LI-1800 spectroradiometer (LI-COR Inc., Lincoln, NE, U.S.A.) equipped with a remote cosine receptor, capturing a light range from 300 to 1100 nm. Ambient lighting was diffused to reduce reflections and directional light that might influence fly behavior through phototaxis. In each experimental replicate, new flies of the same age were used to maintain consistency across trials.

2.3. Artificial agents and robotic apparatus

Artificial agents with varying degrees of biomimicry were developed to evaluate the role of biomimetic traits in interactions with *C. capitata* adults.

All agents were designed using three-dimensional (3D) computer-aided design (CAD) software (SolidWorks, Dassault Systèmes, France) and manufactured with biocompatible resin (VisiJet® M3 Crystal, 3D Systems) via additive manufacturing. In figure 1(a) is presented the 3D CAD model, shown

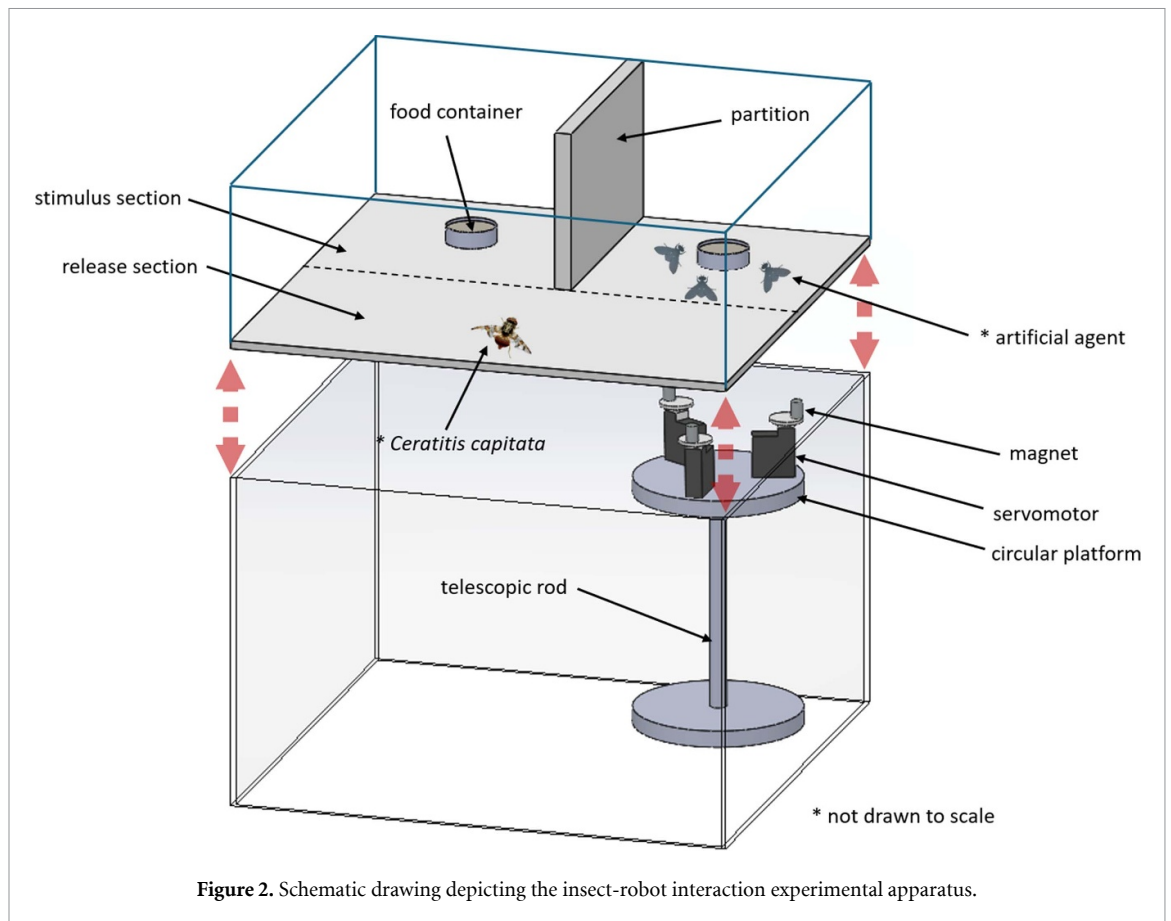


Figure 2. Schematic drawing depicting the insect-robot interaction experimental apparatus.

in both dorsal and ventral views, reproducing the structural details designed to replicate *C. capitata* morphology and size accurately.

Three categories of agents were fabricated (figure 1(b)): (i) full biomimetic agent (FBA): designed to replicate the morphology, size, and color of *C. capitata*, the FBA included a head (with compound eyes and antennae), thorax (with three pairs of legs and a single pair of wings), and abdomen. The body length (head-to-abdomen) was 5 mm, and the wingspan was 9 mm. (ii) Partial biomimetic agent (PBA): maintained the morphology and size of *C. capitata* but was uniformly white. (iii) Non-biomimetic agent (NBA): simplified into a cylindrical shape of equivalent size to *C. capitata*, also white in color.

To accurately reproduce the FBA's coloration, non-toxic pigments were applied. Iron filings (medium particle size ~ 0.420 mm) were embedded in a cavity on the ventral side of each agent (figure 1(a) right), enabling magnetic actuation.

Movement within the experimental arena was achieved through magnetic coupling with an external robotic actuation system beneath the test surface. This system comprised three servomotors radially mounted on a polyvinyl chloride circular platform (\varnothing 100 mm), each controlling a magnet moving along a 180° arc with a radius of 10 mm

(figure 1(c)). The servomotors were independently controlled by Arduino Mega 2560 microcontroller, which activated them asynchronously to emulate the individual movements of artificial flies. The microcontrollers were connected with an external computer (Dell XPS, Intel® Core™ i7) to handle control signal generation and coordination of multi-agent motion.

2.4. Experiment

The testing arena (300×300 mm; length \times width) was divided into three sections: a release section and two stimulus sections (figure 2). The entire arena was enclosed within a transparent box ($300 \times 300 \times 100$ mm; length \times width \times depth). The two stimulus sections were separated by a partition, while the release section was connected to both stimulus sections, forming a two-choice arena. To minimize external cues, the testing arena was covered by an opaque cubic Plexiglas enclosure ($500 \times 500 \times 500$ mm; length \times width \times depth) with a top and a lateral surface transparent, and removable to allow for inspection and access.

Each stimulus section contained a food container positioned at its center. In one stimulus section, the food container was surrounded by three agents of a specific category, while the food container in the other section was devoid of any agents. The stimulus section

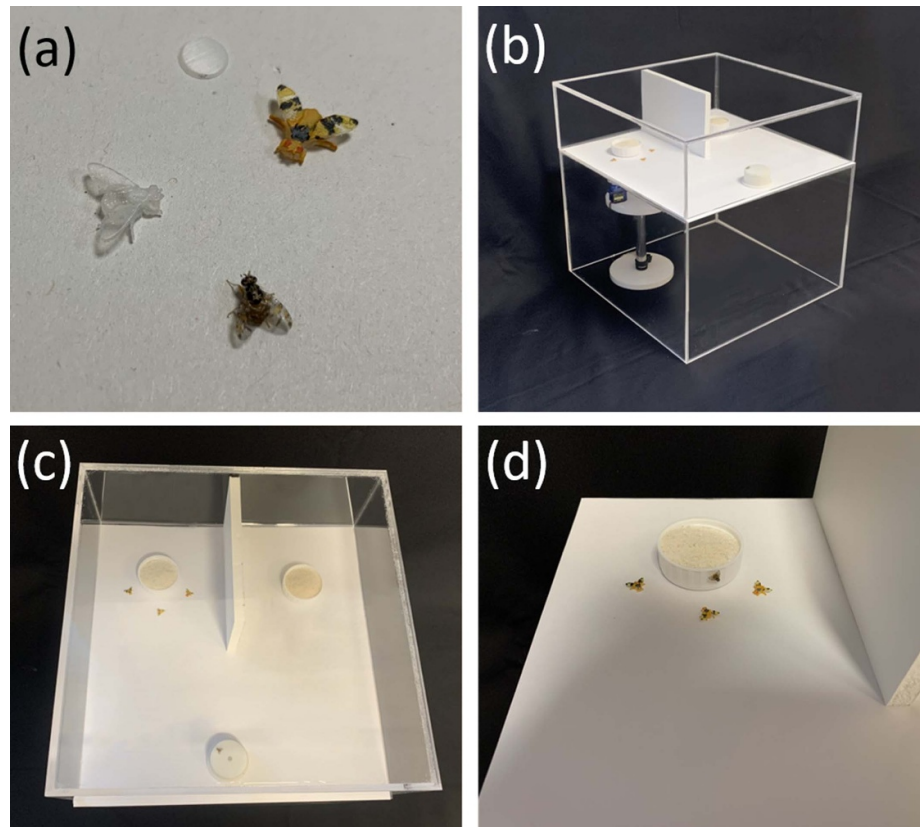


Figure 3. Overview of the experimental setup and key components. (a) A real *Ceratitis capitata* alongside the three artificial agents: (FBA), (PBA), and (NBA). (b) The experimental apparatus, including the external robotic actuation system beneath the testing arena. (c) Top view of the testing arena showing the layout with food containers, distinct sections, artificial agents, and a *C. capitata* on the cylindrical container in the release section. (d) Close-up of FBAs surrounding the food container in a stimulus section, with a *C. capitata* that moved on the food container.

containing agents was alternated between replicates to avoid positional bias.

Medflies were individually introduced into the testing arena using a cylindrical container (base: \varnothing 30 mm; height: 15 mm) with an apical opening (\varnothing 4 mm), which was placed in the center of the release section. The test started when a fly exited the cylindrical container entirely, enabling it to perceive the experimental environment. The test finished when a fly entered a stimulus section, and began palpatting the food with their mouthparts, and started feeding.

We investigated the effects of motionless FBAs, PBAs, and NBAs. In addition, we tested the effects of moving FBAs, PBAs, and NBAs. As a control, we included food containers surrounded by three adult medflies, each confined in a small transparent cylinder to prevent escape.

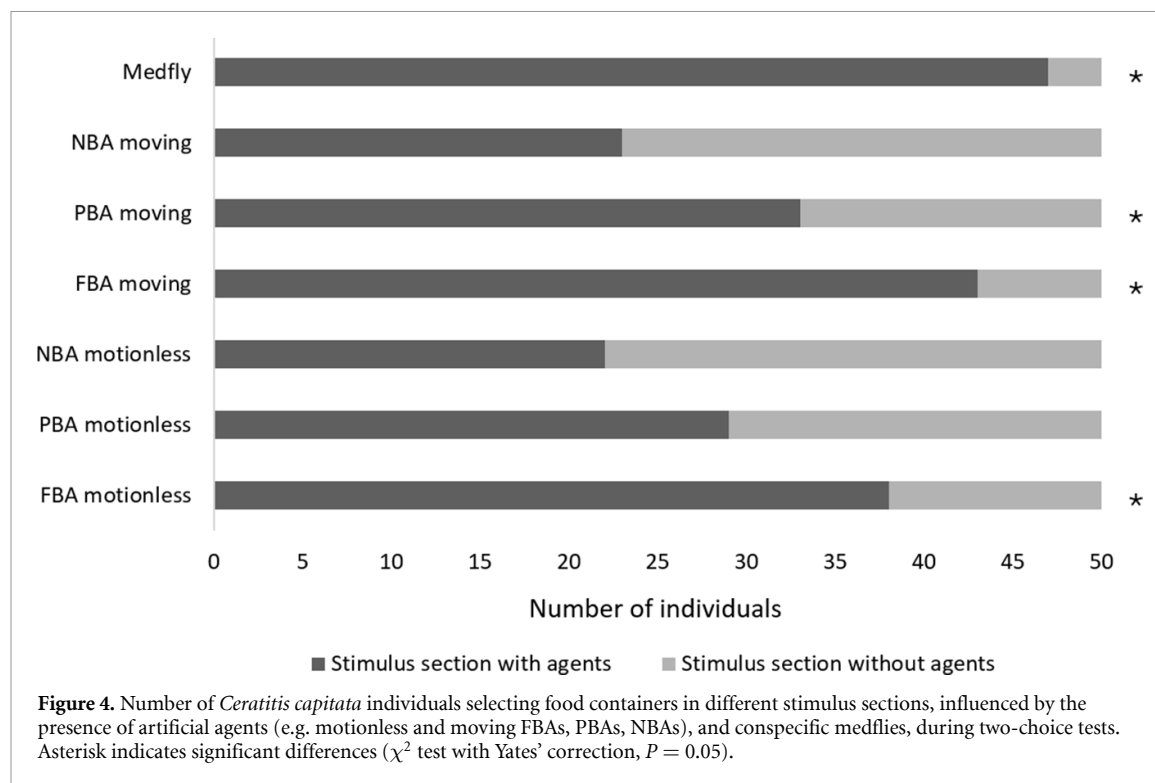
For each fly, we recorded the following metrics: (1) the number of flies that selected the food containers located in the two stimulus sections, (2) the time spent in the release section before making the first choice, and (3) the whole duration of the experiment defined as the time from when a fly completely exited the cylindrical container to when it entered a stimulus section and began feeding for the first time during the

observation. Each two-choice test involved the individual analysis of 50 flies. Figures 3(a)–(d) provides a visual overview of the experimental setup, including the real Medflies and the artificial agents, as well as details of the testing arena and apparatus used in the study.

2.5. Statistical analysis

The differences in the number of medflies feeding on the food containers located in one or the other stimulus chamber were analyzed using a χ^2 test with Yates' correction ($P < 0.05$).

For the data on the effect of different artificial agents on the time spent in the release section before making the first choice and the whole duration of the experiment, we used non-parametric tests. Preliminary assessments indicated non-normality and heteroscedasticity, as determined by the Shapiro–Wilk test ($P < 0.05$) and Levene's test ($P < 0.05$). Consequently, the Wilcoxon test was used for pairwise comparisons. When multiple groups were involved, post-hoc analyses were performed using the Steel–Dwass test to account for multiple comparisons while maintaining the non-parametric framework. Statistical significance was set at $P < 0.05$.



All analyses were performed using R software v4.2.0.

2.6. Results

The results indicated that *C. capitata* individuals exhibited a preference for the food container located in the stimulus section containing the biomimetic agents, as well as the presence of other conspecific medflies, as shown in figure 4.

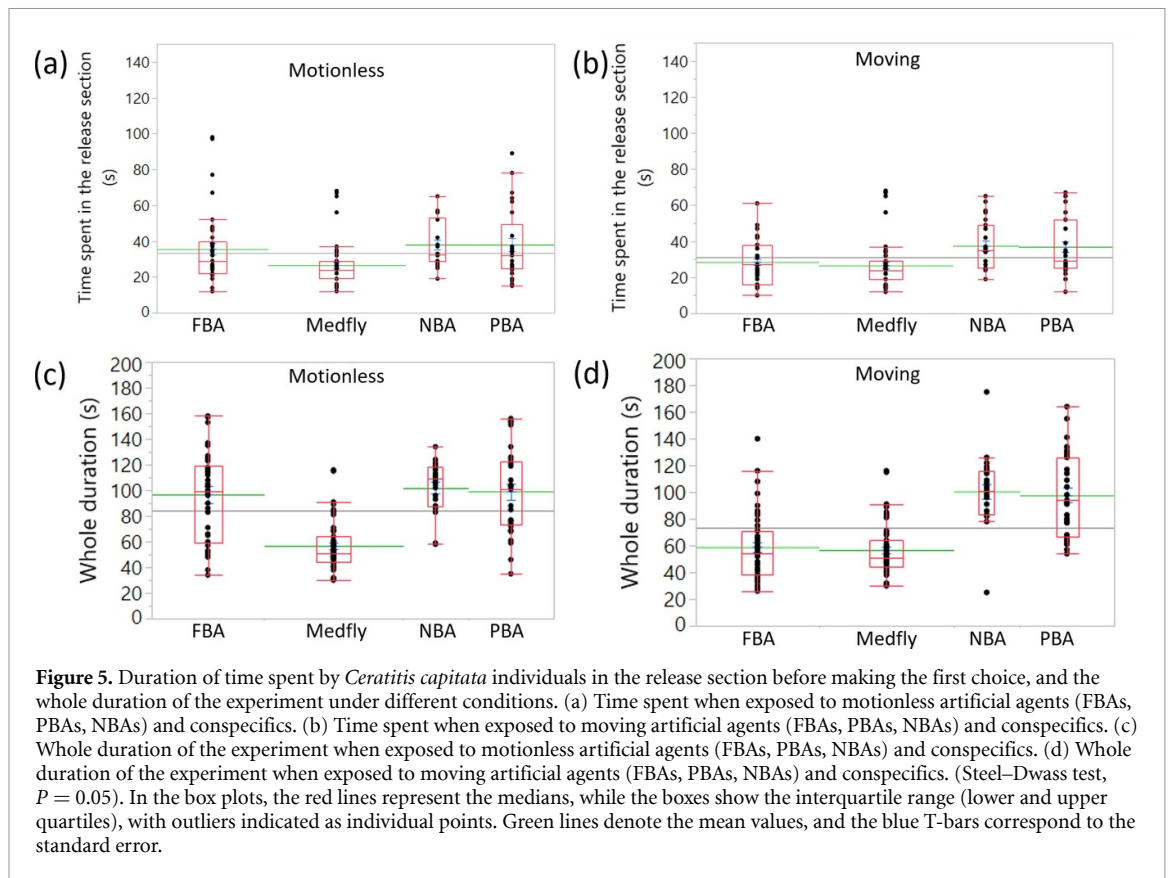
Significantly more *C. capitata* individuals chose the stimulus section containing the food container surrounded by motionless FBAs compared to the stimulus chamber with the food container lacking agents (39 versus 12; $\chi^2_1 = 12.25$; $P < 0.0004$). The number of *C. capitata* individuals that selected the stimulus section with the food container surrounded by motionless PBAs was not significantly different from those that chose the stimulus chamber containing the food container without agents. (29 versus 21; $\chi^2_1 = 0.98$; $P = 0.3222$). The number of *C. capitata* individuals choosing the stimulus section with the food container surrounded by motionless NBAs did not differ significantly from those selecting the stimulus chamber with the food container lacking agents (22 versus 28; $\chi^2_1 = 0.99$; $P = 0.3197$). A significantly greater number of *C. capitata* individuals selected the stimulus section with the food container surrounded by moving FBAs, compared to the stimulus chamber containing the food container without agents (43 versus 7; $\chi^2_1 = 24.5$; $P < 0.0001$).

The number of *C. capitata* individuals that chose the stimulus section with the food container

surrounded by moving PBAs was significantly higher compared to those individuals that chose the stimulus chamber with the food container without agents (33 versus 17; $\chi^2_1 = 4.5$; $P = 0.0338$).

The number of *C. capitata* individuals choosing the stimulus section with the food container surrounded by moving NBAs did not differ significantly from those selecting the stimulus chamber with the food container lacking agents (23 versus 27; $\chi^2_1 = 0.5$; $P = 0.4795$). The number of *C. capitata* individuals that chose the stimulus section with the food container surrounded by conspecific individuals was significantly higher compared to those individuals that chose the stimulus chamber with the food container without agents (47 versus 3; $\chi^2_1 = 36.98$; $P < 0.0001$).

C. capitata individuals exposed to different motionless artificial agents and to other conspecifics exhibited significantly different duration of time spent in the release section before making the first choice ($\chi^2 = 19.65$; $d.f. = 3$; $P = 0.0002$) (figure 5(a)). The time spent in the release section before making the first choice was significantly shorter when other conspecifics were present in the stimulus chamber, compared to when motionless FBAs ($Z = 2.74$; $P = 0.031$), PBAs ($Z = 3.05$; $P = 0.0121$), and NBAs ($Z = 4.05$; $P = 0.0003$), were presented. *C. capitata* individuals exposed to different moving artificial agents and to other conspecifics exhibited significantly different duration of time spent in the release section before making the first choice ($\chi^2 = 18.95$; $d.f. = 3$; $P < 0.0003$) (figure 5(b)). The time spent in



the release section before making the first choice was significantly shorter when other conspecifics were present in the stimulus chamber, compared to when moving PBAs ($Z = 3.34$; $P = 0.0046$), and NBAs ($Z = 3.73$; $P = 0.0011$), were presented. Interestingly, the time spent in the release section when conspecifics were present was not significantly different from the time spent when moving FBAs were present ($Z = 1.02$; $P = 0.7326$).

The whole duration of the experiment varied significantly among *C. capitata* individuals exposed to different motionless artificial agents and to other conspecifics ($\chi^2 = 47.60$; $d.f. = 3$; $P < 0.0001$) (figure 5(c)). The whole duration of the experiment was significantly shorter when conspecifics were present in the stimulus chamber, compared to when motionless FBAs ($Z = 4.84$; $P < 0.0001$), PBAs ($Z = 5.36$; $P < 0.0001$), and NBAs ($Z = 5.63$; $P < 0.0001$), were presented. The whole duration of the experiment varied significantly among *C. capitata* individuals exposed to different moving artificial agents and to other conspecifics ($\chi^2 = 58.82$; $d.f. = 3$; $P < 0.0001$) (figure 5(d)). The whole duration of the experiment was significantly shorter when conspecifics were present in the stimulus chamber, compared to when moving PBAs ($Z = 5.86$; $P < 0.0001$), and NBAs ($Z = 5.47$; $P < 0.0001$), were presented. However, the whole duration of the experiment was not significantly different when conspecifics were

present compared to when moving FBAs were present ($Z = 0.09$; $P = 0.9997$). In addition, the whole duration of the experiment was significantly shorter when moving FBAs were present in the stimulus chamber, compared to when moving PBAs ($Z = 5.18$; $P < 0.0001$), and NBAs ($Z = 4.94$; $P < 0.0001$), were presented.

In addition, to further evaluate the effect of movement on the visual perception and ecology of Medflies, we compared each class of artificial agents in the two kinematic states: moving and motionless. In particular, we noted no significant differences in the time spent in the release section before making the first choice between motionless and moving FBAs ($\chi^2 = 1.84$; $d.f. = 1$; $P = 0.1738$) (figure 6(a)), motionless and moving PBAs ($\chi^2 = 0.0002$; $d.f. = 1$; $P = 0.9887$) (figure 6(b)), as well as between motionless and moving NBAs ($\chi^2 = 0.14$; $d.f. = 1$; $P = 0.6987$) (figure 6(c)).

Concerning the whole duration of the experiment, we noted significant shorter duration in the presence of the moving FBA compared to the motionless the FBA ($\chi^2 = 19.29$; $d.f. < 1$; $P = 0.0001$) (figure 6(d)). No significant differences in the whole duration of the experiment were recorded between motionless and moving PBAs ($\chi^2 = 0.03$; $d.f. = 1$; $P = 0.8489$) (figure 6(e)), and between motionless and moving NBAs ($\chi^2 = 0.51$; $d.f. = 1$; $P = 0.4743$) (figure 6(f)).

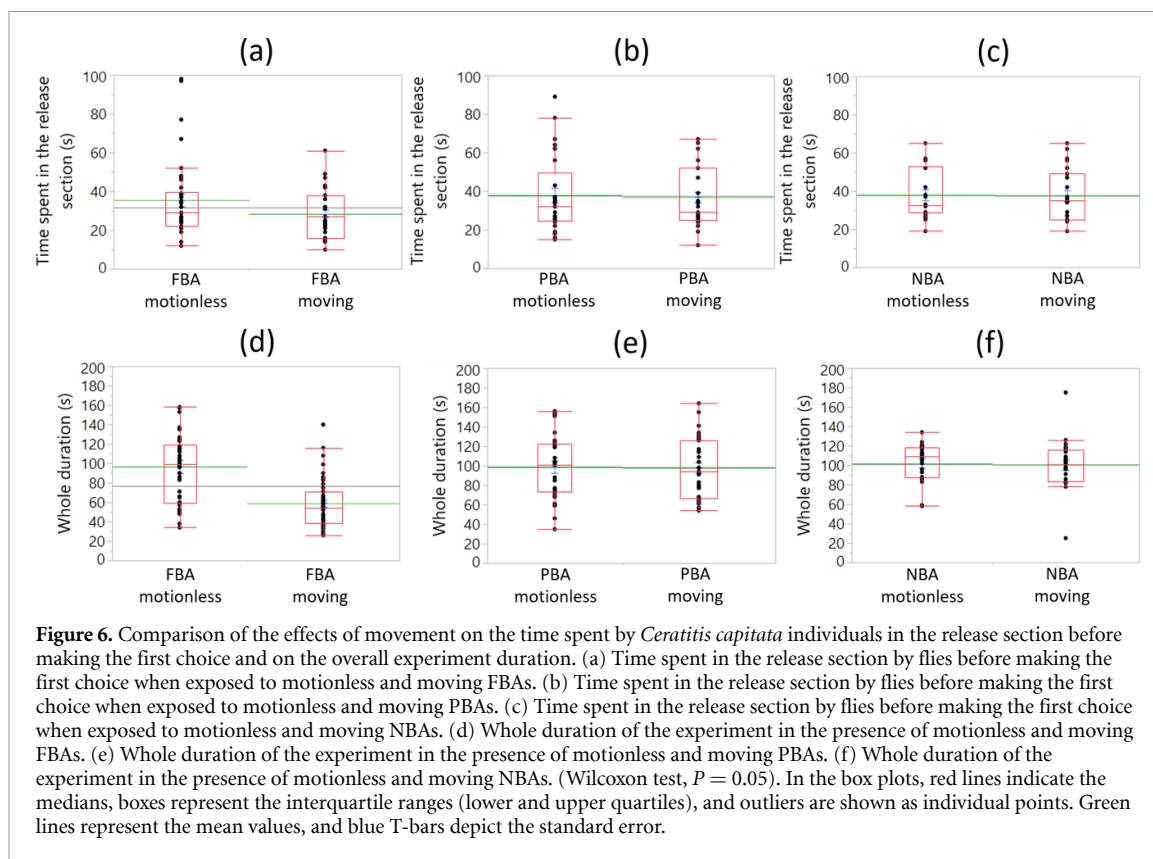


Figure 6. Comparison of the effects of movement on the time spent by *Ceratitis capitata* individuals in the release section before making the first choice and on the overall experiment duration. (a) Time spent in the release section by flies before making the first choice when exposed to motionless and moving FBAs. (b) Time spent in the release section by flies before making the first choice when exposed to motionless and moving PBAs. (c) Time spent in the release section by flies before making the first choice when exposed to motionless and moving NBAs. (d) Whole duration of the experiment in the presence of motionless and moving FBAs. (e) Whole duration of the experiment in the presence of motionless and moving PBAs. (f) Whole duration of the experiment in the presence of motionless and moving NBAs. (Wilcoxon test, $P = 0.05$). In the box plots, red lines indicate the medians, boxes represent the interquartile ranges (lower and upper quartiles), and outliers are shown as individual points. Green lines represent the mean values, and blue T-bars depict the standard error.

3. Discussion

The field of ARI has made significant progress in bridging the gap between animal-animal and ARI, with two-dimensional and 3D robotic systems with varying levels of spatial and behavioral complexity. These approaches have been applied primarily to more extensively studied species, such as cockroaches (Caprari *et al* 2005), honeybees (Landgraf *et al* 2008, Barmak *et al* 2023), zebrafish (Porfiri 2018), rats (Jia *et al* 2024), and more. Our study demonstrates the potential of ARI as a strategy for influencing *C. capitata* behavior through the phenomenon of local enhancement (Heyes 1994) and aligns with broader efforts in the field by showing that biomimetic agents can effectively induce this effect. By relying on biomimetic artificial agents that replicate key conspecific cues, we observed that Medflies were drawn to specific stimulus locations, especially in the presence of moving FBAs. These findings have crucial implications for understanding the behavioral ecology of Medflies, establishing biohybrid systems, and developing sustainable pest management strategies.

Our results highlight the role of biomimicry and motion in mediating Medfly attraction. Among the tested agents, FBAs (designed to closely replicate the morphology, size, and coloration of *C. capitata* adults) elicited the strongest local enhancement responses, particularly when in motion. Moving FBAs were as effective as live conspecifics in attracting Medflies, evidenced by comparable reduction in

decision latency (time spent in the release section) and the whole experiment duration. This suggests that biomimetic agents capable of simulating dynamic conspecific cues can reliably trigger aggregation behaviors in Medflies, providing a compelling case for their use in applied contexts.

On the other hand, PBAs and NBAs exhibited a markedly reduced ability to attract Medflies, even when in motion. While PBAs demonstrated some efficacy, particularly when moving, the absence of species-specific visual and morphological traits reduced their impact. NBAs, with their simplified, non-biomimetic design, were largely ineffective regardless of motion. These findings underscore the importance of selecting biologically relevant features into ARI systems to maximize their effectiveness in eliciting target behaviors.

The role of motion emerged as a key determinant in enhancing the efficacy of artificial agents. Moving FBAs outperformed their motionless counterparts, significantly reducing experiment duration and increasing Medfly attraction. In contrast, motion did not significantly enhance the performance of PBAs or NBAs, suggesting that motion alone is insufficient to elicit local enhancement in the absence of specific biomimetic traits. This aligns with previous research indicating that the combination of species-specific cues and dynamic stimuli is critical for effective ARI-based interventions in various species (Bierbach *et al* 2020), including *C. capitata* (Romano *et al* 2023).

The observed differences in Medfly responses to FBAs, PBAs, and NBAs provide insights into the mechanisms underlying local enhancement in this species. Although *C. capitata* is primarily solitary, our findings confirm that local enhancement behaviors can be induced under specific conditions, such as high-density environments or the presence of conspecific cues. These behaviors likely serve an adaptive function, enabling individuals to exploit shared resources or optimize oviposition sites (Pöysä 1992, Raitanen *et al* 2014, Rouviere and Ruxton 2022). The behavior of fruit flies, particularly in their social interactions and resource selection, reflects complex mechanisms of local enhancement and social facilitation. Female Medflies for instance, are highly responsive to the presence of conspecifics on resources. Prokopy *et al* (2000) showed that females were more likely to be attracted to fruit mimics occupied by other females, even when these were motionless or dead, underlining the importance of visual stimuli. This form of local enhancement suggests that the mere presence of conspecifics can signal a resource's value, potentially reducing search time or indicating a safe oviposition site. In natural contexts, as Hendrichs and Hendrichs (1990) observed, Medflies' resource-use patterns align closely with environmental cues and predator avoidance strategies. Females primarily interact with fruiting host trees, particularly during morning and late afternoon peaks, when they oviposit on fruits like guava and citrus. Such patterns, coupled with males' lekking behaviors in canopy-protected areas, highlight how spatial and temporal organization minimizes risks and maximizes reproductive success. This behavior could be interpreted as a further extension of social facilitation, where group dynamics provide survival advantages. Further supporting these observations, Piñero and Prokopy (2004) examined local enhancement in *Bactrocera cucurbitae* (Coquillett). They found that female melon flies were more likely to alight on host fruits or fruit mimics occupied by conspecifics, a behavior consistent across varied environmental settings and stimuli types. Importantly, even the presence of dead females stimulated this response, reinforcing the idea that visual presence alone can be a sufficient trigger for aggregation. These findings have implications for understanding resource selection in other tephritid species. Golden and Dukas (2014) extend these insights into the adaptive significance of copying behaviors in resource selection. Female fruit flies were found to trade off nutritional quality for social cues, choosing lower-quality patches with conspecific larvae over higher-quality solitary patches. While the precise benefits of this behavior remain unclear, it likely aligns with dynamic microbial interactions that affect both food quality and larval survival in natural settings. Together, these studies emphasize the role of social cues in resource

evaluation among fruit flies. By exploiting the presence of conspecifics, females optimize oviposition choices and exploit ecological niches more effectively. These behaviors, rooted in visual and social stimuli, underscore the evolutionary advantages of local enhancement and social facilitation in highly competitive and variable environments.

By synthetically reproducing these natural cues in biomimetic agents, ARI systems can effectively manipulate animal behavior, offering a scalable and environmentally friendly alternative to traditional pest control methods (Schmickl and Romano 2024). In applied contexts, our results pave the way for the development of robotics-based pest management strategies (Balaska *et al* 2023). For instance, biomimetic cues could be deployed in agricultural settings to aggregate Medflies in designated areas, enhancing the efficiency of trapping systems or bait application. Such approaches would reduce reliance on chemical pesticides, aligning with the principles of sustainable agriculture and integrated pest management (Muhie 2022). Furthermore, the versatility of ARI systems allows for fine-tuned adjustments to target specific behavioral traits or environmental conditions, ensuring compatibility with diverse agricultural ecosystems.

While this study provides new insights into the role of biomimetic cues in eliciting local enhancement in Medflies, several alternative experiments can be done. First, the experimental setup constrained the movement of artificial agents to a limited area, preventing a full exploration of spatial dynamics in Medfly interactions. Although our results demonstrate that motion enhances attraction, further works should investigate whether agents with greater spatial freedom (e.g. movement along an expanded x - y plane [Romano *et al* 2023]), further amplify local enhancement effects. Additionally, our study primarily focused on visual and tactile stimuli, leaving open the question of how other sensory modalities, such as olfactory or auditory cues, may contribute to Medfly attraction. Given that many tephritid species rely on multimodal communication in foraging and mating contexts (Ekanayake *et al* 2019, Li *et al* 2024), a broader sensory approach could yield deeper biological insights. Future research should build on these findings by exploring the influence of additional sensory modalities, such as olfactory and auditory cues, in shaping Medfly responses to artificial agents. While this study focused primarily on visual mimicry, incorporating multi-sensory stimuli could significantly enhance the effectiveness of ARI systems (Pouw *et al* 2021). For example, Lihoreau and Rivault (2011) found that the gregarious cockroach *Blattella germanica* Linnaeus, preferentially aggregate at feeding sites where conspecifics are present, a behavior predominantly driven by olfactory cues from feeding conspecifics. This reliance on olfactory

signals for local enhancement contrasts with studies on fruit flies, where visual stimuli often play a more prominent role. Such differences underscore the diversity of sensory modalities underlying social facilitation across insect species. These insights suggest that local enhancement may represent a broadly conserved mechanism that promotes efficient resource use and social cohesion in varied ecological settings.

Overall, this study underscores the potential of ARI as an innovative and sustainable approach for understanding and managing insects populations of economic importance. By combining biomimetic design and motion, artificial agents can effectively induce local enhancement, providing an advanced technology for both fundamental behavioral research and applied pest management. Future research should expand on these findings by increasing movement pattern complexity in artificial agents, allowing them to navigate more dynamically within experimental arenas. Investigating whether fully mobile agents (e.g. robotic flies capable of free locomotion) modulate attraction behaviors differently than stationary or semi-mobile agents would provide deeper insights into spatial aspects of local enhancement. Another promising avenue is the translation of these experimental insights into field applications. Optimizing their design for real-world conditions such as crop environments could validate their feasibility for pest control. By bridging laboratory findings with applied strategies, ARI could become a scalable and environmentally sustainable tool for managing pest populations.

Our findings represent a step forward in bridging the gap between animal behavior and robotics, showing the promising potential of interdisciplinary approaches in addressing ethological, ecological, and agricultural challenges.

4. Conclusions

This study demonstrates the potential of ARI to induce local enhancement in insect species of economic interest such as the Mediterranean fruit fly, a major agricultural pest. FBAs effectively mimicked conspecific cues, with moving FBAs eliciting responses comparable to live medflies. These findings highlight the importance of motion and biomimetic morphological traits in manipulating fly behavior. PBAs were less effective, emphasizing the importance of species-specific traits, including pigmentations. ARI systems may offer a sustainable, behavior-based approach to pest management, reducing reliance on chemical pesticides. Additionally, this research broadens understanding of local enhancement in *C. capitata* and showcases the integration of robotics and ethology. Future efforts should incorporate multi-sensory cues and field testing to optimize ARI applications for pest control and ecological research.

Data availability statement

The data generated and/or analyzed during the current study are available from the corresponding author on request.

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References

- Araguas A, Guellaï B, Gauthier P, Richer F, Montone G, Chopin A and Derégnaucourt S 2022 Design of a robotic zebra finch for experimental studies on developmental song learning *J. Exp. Biol.* **225** jeb242949
- ASAB/ABS 2014 Guidelines for the treatment of animals in behavioural research and teaching *Anim. Behav.* **99** 1–9
- Avarguès-Weber A and Chittka L 2014 Local enhancement or stimulus enhancement? Bumblebee social learning results in a specific pattern of flower preference *Anim. Behav.* **97** 185–91
- Balaska V, Adamidou Z, Vryzas Z and Gasteratos A 2023 Sustainable crop protection via robotics and artificial intelligence solutions *Machines* **11** 774
- Barmak R, Stefanec M, Hofstadler D N, Piotet L, Schönwetter-Fuchs-Schistek S, Mondada F and Mills R 2023 A robotic honeycomb for interaction with a honeybee colony *Sci. Robot.* **8** eadd7385
- Benelli G and Romano D 2018 Does indirect mating trophallaxis boost male mating success and female egg load in Mediterranean fruit flies? *J. Pest Sci.* **91** 181–8
- Bierbach D, Mönck H J, Lukas J, Habedank M, Romanczuk P, Landgraf T and Krause J 2020 Guppies prefer to follow large (robot) leaders irrespective of own size *Front. Bioeng. Biotechnol.* **8** 441
- Caprari G, Colot A, Siegwart R, Halloy J and Deneubourg J L 2005 Animal and robot mixed societies: building cooperation between microrobots and cockroaches *IEEE Robot. Autom. Mag.* **12** 58–65
- Chen C, Jia G, Gao Z, Guo X, Huang Q, Fukuda T and Shi Q 2021 A real-time motion detection and object tracking framework for future robot-rat interaction 2021 *IEEE/RSJ Int. Conf. on Intelligent Robots and Systems (IROS)* (IEEE) pp 7404–9
- de Margerie E, Lumineau S, Houdelier C and Yris M R 2011 Influence of a mobile robot on the spatial behaviour of quail chicks *Bioinspir. Biomim.* **6** 034001
- Diamantidis A D, Carey J R, Nakas C T and Papadopoulos N T 2011 Population-specific demography and invasion potential in medfly *Ecol. Evol.* **1** 479–88

- Ekanayake W M, Clarke A R and Schutze M K 2019 Close-distance courtship of laboratory reared *Bactrocera tryoni* (Diptera: tephritidae) *Aust. Entomol.* **58** 578–88
- European Commission 2007 Commission recommendations of 18 June 2007 on guidelines for the accommodation and care of animals used for experimental and other scientific purposes *Annex II to European Council Directive 86/609 See 2007/526/EC* (available at: <http://eurex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2007:197:0001:0089:EN:PDF>)
- Field S A, Kaspi R and Yuval B 2002 Why do calling medflies (Diptera: tephritidae) cluster? Assessing the empirical evidence for models of medfly lek evolution *Florida Entomol.* **85** 63–72
- Foster A and S P and Harris M O 1997 Behavioral manipulation methods for insect pest-management *Annu. Rev. Entomol.* **42** 123–46
- Giunti G, Benelli G, Campolo O, Canale A, Kapranas A, Liedo P and Papadopoulos N T 2023 Biology, ecology and invasiveness of the Mediterranean fruit fly, *Ceratitidis capitata*: a review *Entomol. Gen.* **43** 1221–39
- Golden S and Dukas R 2014 The value of patch-choice copying in fruit flies *PLoS One* **9** e112381
- Halloy J, Sempo G, Caprari G, Rivault C, Asadpour M, Tâche F and Deneubourg J L 2007 Social integration of robots into groups of cockroaches to control self-organized choices *Science* **318** 1155–8
- Hendrichs J and Hendrichs M A 1990 Mediterranean fruit fly (Diptera: tephritidae) in nature: location and diel pattern of feeding and other activities on fruiting and nonfruiting hosts and nonhosts *Ann. Entomol. Soc. Am.* **83** 632–41
- Heyes C M 1994 Social learning in animals: categories and mechanisms *Biol. Rev.* **69** 207–31
- Heyes C M, Ray E D, Mitchell C J and Nokes T 2000 Stimulus enhancement: controls for social facilitation and local enhancement *Learn. Motiv.* **31** 83–98
- Jia G, Chen Z, Zhang Y, Bing Z, Quan Z, Chen X and Shi Q 2024 Modulating emotional states of rats through a rat-like robot with learned interaction patterns *Nat. Mach. Intell.* **6** 1580–93
- Krause J, Winfield A F and Deneubourg J L 2011 Interactive robots in experimental biology *Trends Ecol. Evol.* **26** 369–75
- Landgraf T, Gebhardt G H, Bierbach D, Romanczuk P, Musiolek L, Hafner V V and Krause J 2021 Animal-in-the-loop: using interactive robotic conspecifics to study social behavior in animal groups *Annu. Rev. Control Robot. Auton. Syst.* **4** 487–507
- Landgraf T, Moballegh H and Rojas R 2008 Design and development of a robotic bee for the analysis of honeybee dance communication *Appl. Bionics Biomech.* **5** 157–64
- Landgraf T, Rojas R, Nguyen H, Kriegel F and Stettin K 2011 Analysis of the waggle dance motion of honeybees for the design of a biomimetic honeybee robot *PLoS One* **6** e21354
- Li X L, Li D D, Cai X Y, Cheng D F and Lu Y Y 2024 Reproductive behavior of fruit flies: courtship, mating, and oviposition *Pest Manage. Sci.* **80** 935–52
- Lihoreau M and Rivault C 2011 Local enhancement promotes cockroach feeding aggregations *PLoS One* **6** e22048
- Lux S A 2018 Individual-based modeling approach to assessment of the impacts of landscape complexity and climate on dispersion, detectability and fate of incipient Medfly populations *Front. Physiol.* **8** 1121
- Macri S, Karakaya M, Spinello C and Porfiri M 2020 Zebrafish exhibit associative learning for an aversive robotic stimulus *Lab. Anim.* **49** 259–64
- Malacrida A R, Gomulski L M, Bonizzoni M, Bertin S, Gasperi G and Guglielmino C A 2007 Globalization and fruitfly invasion and expansion: the medfly paradigm *Genetica* **131** 1–9
- Maxeiner M, Hocke M, Moenck H J, Gebhardt G H, Weimar N, Musiolek L and Landgraf T 2023 Social competence improves the performance of biomimetic robots leading live fish *Bioinspir. Biomim.* **18** 045001
- Muhie S H 2022 Novel approaches and practices to sustainable agriculture *J. Agric. Food Res.* **10** 100446
- Papadopoulos N T, De Meyer M, Terblanche J S and Kriticos D J 2024 Fruit flies: challenges and opportunities to stem the tide of global invasions *Annu. Rev. Entomol.* **69** 355–73
- Pérez-Cembranos A and Pérez-Mellado V 2015 Local enhancement and social foraging in a non-social insular lizard *Anim. Cogn.* **18** 629–37
- Piñero J C and Prokopy R J 2004 Local enhancement of alighting in the melon fly, *Bactrocera cucurbitae*: effect of olfactory, visual, and acoustical stimuli *J. Insect Behav.* **17** 493–510
- Polverino G, Karakaya M, Spinello C, Soman V R and Porfiri M 2019 Behavioural and life-history responses of mosquitofish to biologically inspired and interactive robotic predators *J. R. Soc. Interface* **16** 20190359
- Polverino G, Soman V R, Karakaya M, Gasparini C, Evans J P and Porfiri M 2022 Ecology of fear in highly invasive fish revealed by robots *iScience* **25** 103529
- Porfiri M 2018 Inferring causal relationships in zebrafish-robot interactions through transfer entropy: a small lure to catch a big fish *Anim. Behav. Cogn.* **5** 341–67
- Pouw W, Proksch S, Drijvers L, Gamba M, Holler J, Kello C and Wiggins G A 2021 Multilevel rhythms in multimodal communication *Phil. Trans. R. Soc. B* **376** 20200334
- Pöysä H 1992 Group foraging in patchy environments: the importance of coarse-level local enhancement *Ornis Scand.* **23** 159–66
- Prokopy R J, Miller N W, Duan J J and Vargas R I 2000 Local enhancement of arrivals of *Ceratitidis capitata* females on fruit mimics *Entomol. Exp. Appl.* **97** 211–7
- Raitanen J, Forsman J T, Kivelä S M, Mäenpää M I and Välimäki P 2014 Attraction to conspecific eggs may guide oviposition site selection in a solitary insect *Behav. Ecol.* **25** 110–6
- Rekabi-Bana F, Stefanec M, Ulrich J, Keyvan E E, Rouček T, Broughton G and Arvin F 2023 Mechatronic design for multi robots-insect swarms interactions *2023 IEEE Int. Conf. on Mechatronics (ICM)* (IEEE) pp 1–6
- Romano D, Benelli G and Stefanini C 2021 Opposite valence social information provided by bio-robotic demonstrators shapes selection processes in the green bottle fly *J. R. Soc. Interface* **18** 20210056
- Romano D, Benelli G and Stefanini C 2023 How aggressive interactions with biomimetic agents optimize reproductive performances in mass-reared males of the Mediterranean fruit fly *Biol. Cybern.* **117** 249–58
- Romano D, Bloembergen J, Tannous M and Stefanini C 2020 Impact of aging and cognitive mechanisms on high-speed motor activation patterns: evidence from an orthoptera-robot interaction *IEEE Trans. Med. Robot. Bionics* **2** 292–6
- Romano D, Donati E, Benelli G and Stefanini C 2019 A review on animal-robot interaction: from bio-hybrid organisms to mixed societies *Biol. Cybern.* **113** 201–25
- Romano D and Stefanini C 2022a Robot-fish interaction helps to trigger social buffering in neon tetras: the potential role of social robotics in treating anxiety *Int. J. Soc. Robot.* **14** 963–72
- Romano D and Stefanini C 2022b Any colour you like: fish interacting with bioinspired robots unravel mechanisms promoting mixed phenotype aggregations *Bioinspir. Biomim.* **17** 045004
- Romano D and Stefanini C 2024 Robot-locust social information transfer occurs in predator avoidance contexts *Int. J. Soc. Robot.* **16** 489–500
- Rouviere A and Ruxton G D 2022 The effects of local enhancement on mean food uptake rate *Am. Nat.* **199** 21–33
- Rull J, Prokopy R J and Vargas R I 2003 Effects of conspecific presence on arrival and use of hosts in *Ceratitidis capitata* flies *J. Insect Behav.* **16** 329–46

- Schmickl T and Romano D 2024 Robots and animals teaming up in the wild to tackle ecosystem challenges *Sci. Robot.* **9** eado5566
- Serra C A and Ogando F 2013 Improvement of ethological methods for integrated management of fruit flies, *Anastrepha* spp.(Diptera: tephritidae) in fruit orchards in the Dominican Republic *10th Int. Mango Symp.* 1075 pp 193–206
- Shi Q, Ishii H, Tanaka K, Sugahara Y, Takanishi A, Okabayashi S and Fukuda T 2015 Behavior modulation of rats to a robotic rat in multi-rat interaction *Bioinspir. Biomim.* **10** 056011
- Ulrich J, Stefanec M, Rekabi-Bana F, Fedotoff L A, Rouček T, Gündeğer B Y and Krajník T 2024 Autonomous tracking of honey bee behaviors over long-term periods with cooperating robots *Sci. Robot.* **9** eadn6848