





COMPLIMENTARY/POSTER SESSION PAPER

Limb Loss and Specialized Leg Dynamics in Tiny Water-Walking Insects

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Synopsis The air–water interface of the planet’s water bodies, such as ponds, lakes, and streams, presents an uncertain ecological niche with predatory threats from above and below. As *Microvelia americana* move across the water surface in small ponds, they face potential injury from attacks by birds, fish, and underwater invertebrates. Thus, our study investigates the effects of losing individual or pairs of tarsi on *M. americana*’s ability to walk on water. Removal of both hind tarsi causes *M. americana* to rock their bodies (yaw) while running across the water surface at $\pm 19^\circ$, compared to $\pm 7^\circ$ in nonablated specimens. This increase in yaw, resulting from the removal of hind tarsi, indicates that *M. americana* use their hind legs as “rudders” to regulate yaw, originating from the contralateral middle legs’ strokes on the water’s surface through an alternating tripod gait. Ablation of the ipsilateral middle and hind tarsi disrupts directionality, making *M. americana* turn in the direction of their intact limbs. This loss of directionality does not occur with the removal of contralateral middle and hind tarsi. However, *M. americana* lose their ability to use the alternating tripod gait to walk on water on the day of contralateral ablation. Remarkably, by the next day, *M. americana* adapt and regain the ability to walk on water using the alternating tripod gait. Our findings elucidate the specialized leg dynamics within the alternating tripod gait of *M. americana*, and their adaptability to tarsal loss. This research could guide the development and design strategies of small, adaptive, and resilient micro-robots that can adapt to controller malfunction or actuator damage for walking on water and terrestrial surfaces.

Introduction

For tiny water-walking insects, venturing across the water’s surface involves more than balancing on surface tension. These tiny organisms encounter competition and predation from above, below, and on the water itself. Locomotion—an organism’s method of moving through its environment—serves as a significant evolutionary pressure shaping morphological traits (Dickinson et al. 2000). In aquatic environments, the manner in which an insect moves across water often determines its vulnerability to predators, making the ability to quickly adapt to changing conditions essential for epineuston organisms living on the water surface. *Microvelia americana* is a water-walking insect that, unlike other water striders, possesses the ability to move on land (Bush and Hu 2006; Crumière et al. 2016; O’Neil et al. 2024), allowing it to navigate obstacles on the wa-

ter’s surface, such as floating plants like duckweed, or even to flee to land to escape aquatic predators. Beyond maneuvering on the surface of water without sinking (Hu and Bush 2010), water striders must contend with multiple predators in and out of the water (Krupa and Sih 1998), compete for resources and mates (Wilson et al. 1978; Crumière et al. 2019; Toubiana et al. 2021), and navigate the aftermath of conflicts that result in bodily damage. Should an *M. americana* escape with its life but lose a limb, it faces the challenge of continuing to move on water.

Key evolutionary drivers for the ability to walk on water include predator avoidance, as seen in the basilisk lizard, mate displays or “rushing” in birds like Western and Clark’s grebes, and a combination of these factors for organisms that spend significant time at or near the water’s surface, such as fishing spiders (*Dolomedes*)

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or water striders (*Gerridae*) (Hsieh 2003; Suter 2003; Clifton et al. 2015). For these smaller epineuston insects and spiders (Bush and Hu 2006; Hu and Bush 2010), surface tension plays a crucial role in water locomotion. Their bodies, covered in hydrophobic hairs, enable them to propel across the water without sinking (Andersen 1976; Suter et al. 1997; Bush et al. 2007; Crumière et al. 2016). Although researchers have extensively studied the morphological adaptations that allow insects like *M. americana* to walk on water (Gao and Jiang 2004; Suter 2013; Koh et al. 2015; Steinmann et al. 2021), and the unique use of the alternating tripod gait, similar to ants and cockroaches (Kram et al. 1997; Bohn et al. 2012; Humeau et al. 2019), the impact of limb loss on *M. americana* and how it affects their locomotion remain unexplored. During our observations of *M. americana* in the wild, we have found some organisms missing parts of limbs, which inspired our investigation into locomotive performance after natural ablation. In our laboratory observations, since *Microvelia* cannot regenerate their limbs after their final molt (Frick 1949), the loss of a limb can lead to them becoming easy prey to predators both above and below the water's surface. While insects commonly lose body parts (Arbas and Weidner 1991; Maginnis 2008), and some may even shed limbs intentionally through autotomy (Joseph et al. 2018; Emberts et al. 2020; Steinmann et al. 2021), it becomes an additional challenge when each tarsus helps to leverage surface tension to float and walk on the water (Bush and Hu 2006; Hu and Bush 2010).

We specifically investigate the mechanics of *M. americana* with missing tarsi. The focus of this paper is on which tarsus removal affects direction and propulsion and how *M. americana* moves in spite of limb loss. Previous studies have identified the middle legs as primary “propulsers” due to their large stroke amplitudes compared to the front and hind legs (Andersen 1976), but the roles of other legs remain less understood. We explore the effects of tarsus loss on *M. americana* locomotion by examining body velocity and directionality on water. Through high-speed imaging, pose estimation software (DeepLabCut) (Nath et al. 2019), and *in situ* ablation, we observe how *M. americana*, despite these challenges, adapts and continues to navigate water surfaces.

Materials and methods

Rearing and experimental setup

We collected *M. americana* from ponds and creeks in Kennesaw, GA, USA. The insects were housed in a 17.5 × 14.0 × 6.5 inch³ plastic container, filled with water maintained at a lab temperature of 20°C, and supplemented with duckweed from their original habi-

tats. We exposed the *M. americana* to circadian lighting from 8 a.m. to 8 p.m. Additionally, from Monday through Friday, we fed the specimens daily with fruit flies procured from Carolina Biological Supply Company, Burlington, NC, USA. In total, we analyzed the locomotion of 20 specimens in response to the following ablations ($N = 3$ specimens for each case): nonablated (control), single front tarsus, single middle tarsus, single hind tarsus, both front tarsi, both middle tarsi, both hind tarsi, ipsilateral middle and hind tarsi, and contralateral middle and hind tarsi (Fig. 1C). We observed only one specimen for both middle tarsi and single front tarsus ablations. Single front tarsus ablation was not statistically different from the nonablated specimen (Supplementary Table S6), and both middle tarsi ablated *M. americana* were unable to walk on water and did not survive beyond 48 h post-ablation. Given these outcomes and the limited availability of specimens, we prioritized the preservation of specimens.

Microvelia americana tarsus ablation

Before a particular *M. americana* was ablated, it was anesthetized by placing it into a freezer for ~2 min. This led to the insect's temporary incapacitation, which allowed for easier and more accurate ablation to be done. After being taken out of the freezer, we placed the *M. americana* under a magnifying glass, and the corresponding segment(s) (Fig. 1C) of the leg(s) were removed with a Fine Science Tools (Fine Science Tools (USA), Inc, 4000 East 3rd Avenue, Suite 100 Foster City, CA 94404-4824) dissecting knife. An example of an *M. americana* with its middle tarsi ablated is shown in Fig. 1A. After being cut, the specimen would regain consciousness and be placed into a small container of water from its natural habitat for recovery. After 1 h of being in the container, the *M. americana* was removed, its locomotion was recorded, and it was then placed back into containment. Additionally, after having 24 h to recuperate from the initial ablation, the insect's locomotion was once again recorded.

Recording

To record the response of the *M. americana* to their ablations, a Photron FASTCAM Mini AX2000 (Photron USA Inc, 9520 Padgett Street Suite 110 San Diego, CA 92126) was used with a frame rate of 1000–2000 frames per second at a resolution of 1024 × 1024 pixels. A Nikon 70–200 mm f/2.8G ED VR II AF-S NIKKOR Zoom lens, purchased from B&H Photo (420 9th Avenue, New York, NY USA 10001), was mounted on the camera for enhanced documentation. The camera was mounted vertically on a Thorlabs Optical Rail for a top view of *M. americana* locomotion on water. The

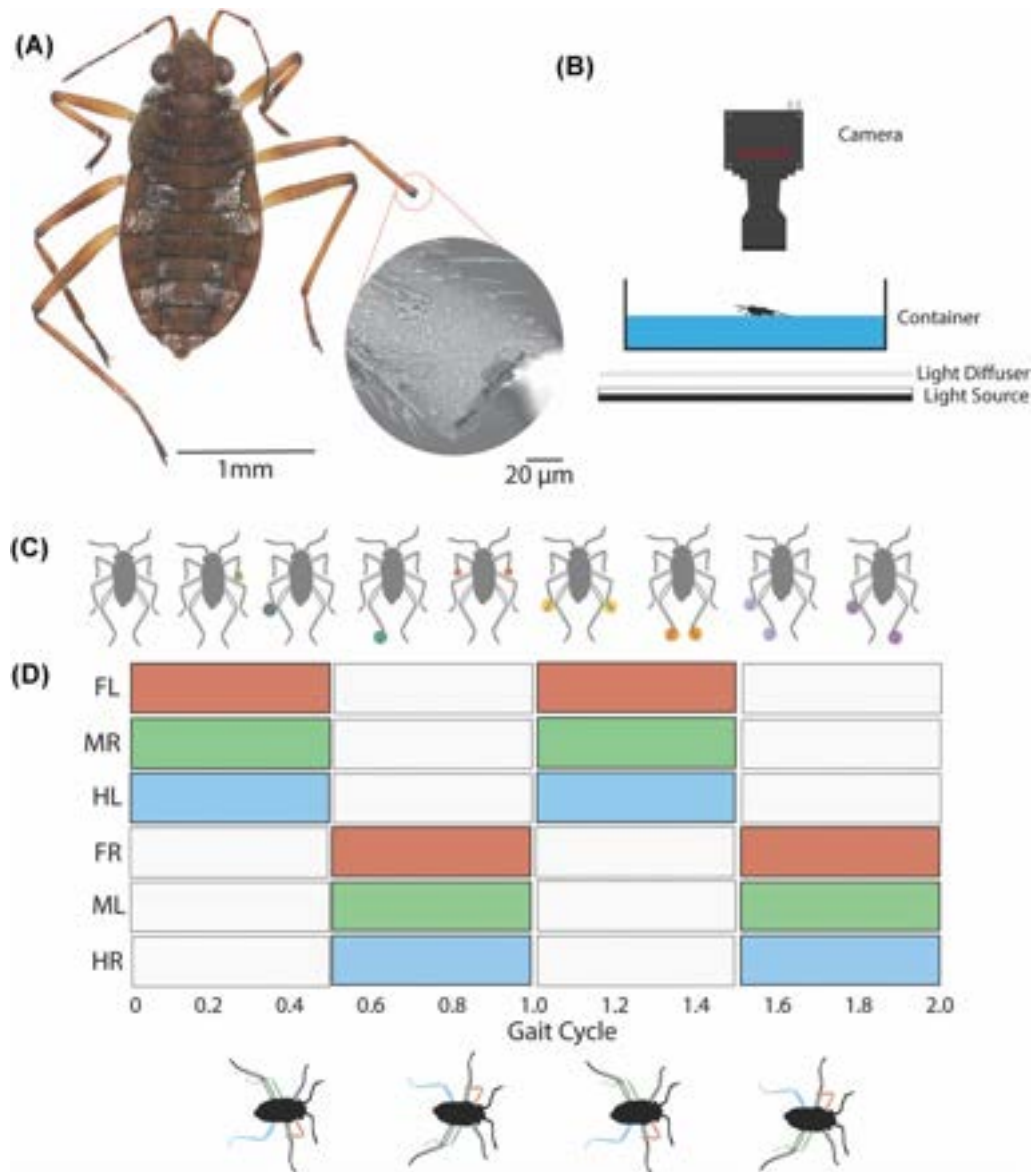


Fig. 1 (A) High-resolution z-stack image and scanning electron microscopy image of a *M. americana* with an ablated middle right tarsus. (B) Schematic of experimental setup. A high-speed camera is mounted above a container of water, which rests on a diffuser. A light source is set at a short distance below the diffuser to provide even lighting when recording. *Microvelia americana* are recorded individually running on the water. (C) Illustration showing tested *M. americana* ablations. Circled parts of legs indicate the different locations of ablations. Eight ablation conditions are investigated in this paper. (D) Gait cycle indicating the power stroke (filled rectangles) and recovery phase (blank rectangles) of the alternating tripod gait. Colored legs corresponding to the gait cycle showcase the alternating movement.

M. americana were placed in a $10.0 \times 10.0 \times 1.5 \text{ cm}^3$ Petri dish (Thermo Fisher Scientific, 168 Third Avenue Waltham, MA USA 02451) that was filled halfway with water and rested on top of a white diffuser (Fig. 1B). An LED light was also lit underneath the Petri dish for better lighting. The ablated insects were then prodded for movement, which was recorded and analyzed one video at a time.

Tracking, postprocessing, and analysis

After recording, DeepLabCut (Mathis et al. 2018; Nath et al. 2019) pose estimation machine learning software was utilized to track the head and abdominal tip of the *M. americana* in each video. A custom Matlab (The MathWorks Inc. 2022) script was used to calculate the displacement, velocity, and yaw angle from the DeepLabCut tracking data.

Statistical analysis

For statistical analysis, we used a linear mixed-effects model (Bates et al. 2015) to find whether the set of treatment effects yielded differences among the means of each group with post-hoc Tukey's difference criterion to find which pairs of treatment effects were statistically different (all of the pairwise comparisons are given in Supplementary Information). We used a linear mixed-effects model since ablation types vary in the number of trials per specimen and to account for any possible random effects from individual specimens. We compared different models with and without repeated trials as a treatment effect and found no statistical difference between models. Therefore, we used the model with only ablation type as a treatment effect. In all models, specimen number is treated as a random effect. A custom R script (R version 4.4.0) (Hothorn et al. 2008; Genz and Bretz 2009; Bates et al. 2015; RStudio Team 2020; R Core Team 2024) was used for statistical analysis. We defined statistical significance as * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

Results

Widened yaw angle

First, we track each specimen as it walks across the water surface (Fig. 2B). In comparing nonablated *M. americana* to those *M. americana* with both hind tarsi removed, we observe an increase in yaw along the body as it walks on water. We then measure the maximum body velocity of each specimen, based on the tarsi removed, and compare these velocities to that of the nonablated specimens (Fig. 2C). *Microvelia americana* with no tarsi removed achieve as maximum velocity ($v_{max} = 14$ cm/s, $N = 3$ specimens, and $n = 21$ trials). Despite removing either both front or both hind tarsi, *M. americana*'s maximum body velocity remains at 12 cm/s ($N = 3$, $n = 21$, and $P > 0.05$). This aligns with previous researchers' predictions that the middle legs are the main propulsors generating forward thrust (Andersen 1976). Consequently, removing both middle tarsi renders a *M. americana* incapable of moving across the water (see Supplementary Movie S1), reducing its velocity to 2 cm/s. Next, we calculate the yaw angle over time for each tested specimen (Fig. 2A). We find that, post-ablation, *M. americana* exhibits an increase in yaw in both directions as they move on the water surface. Analyzing the yaw angle versus time data, we identify the change in yaw angle ($\Delta\theta = \theta_f - \theta_i$) for each cycle, where the absolute value of the yaw angle is shown in Fig. 2D. For both nonablated specimens and those with front tarsi ablated, the yaw angle reaches $\Delta\theta = \pm 7^\circ$ as they run across the water surface (Fig. 2D). Specimens with both hind tarsi ablated exhibit a yaw an-

gle more than double ($\Delta\theta = \pm 19^\circ$) that of the nonablated and frontablated specimens ($P < 0.001$). This result underscores the role of the hind tarsi as "rudders" that serve to minimize side-to-side rocking during water walking (see Supplementary Movie S2). We did not measure the yaw angle for specimens with both middle tarsi ablated as they could not walk across the water surface.

Deviated directionality

To assess the impact of tarsal loss on *M. americana* directionality, we calculated the ratio of the final displacement (D_2) to the total distance traveled (D_1) for both nonablated and ablated *M. americana* (Fig. 3A). For a straight path, the ratio $D_2/D_1 \sim 1$. For nonablated specimens and most types of ablations, *M. americana* typically travel in a straight line, with $D_2/D_1 > 0.90$, and showed no statistical difference between groups ($P > 0.05$). However, *M. americana* missing ipsilateral middle and hind tarsi are notable exceptions, exhibiting $D_2/D_1 \approx 0.86$, indicating a significant deviation from a straight line ($P < 0.001$). Fig. 3A illustrates this deviation with an example of an ipsilaterally ablated specimen traveling in a circular path and ending up facing the opposite direction from where it started (see Supplementary Movie S3). D_2/D_1 was found to vary significantly from 0.5 to 0.99 (Fig. 3B).

Adaptation to tarsus loss

Microvelia americana adapts to the loss of key body locomotive parts (tarsi, leg) after ablation. We observed changes in the body velocities of *M. americana* immediately following ablation (within an hour) compared to 24 h later. Before ablation, *M. americana* achieved a mean maximum body velocity (v_{max}) of ~ 14 cm/s. Those missing their contralateral middle and hind tarsi initially struggled with a lower maximum velocity of 2 cm/s on the day of their ablation ($N = 3$, $n = 15$). However, by the next day, their v_{max} increased to ~ 8 cm/s ($N = 3$, $n = 21$, $P < 0.001$, see Supplementary Movie S4). For *M. americana* undergoing ipsilateral middle and hind ablation, despite also missing two tarsi, the difference in v_{max} between the day of ablation and the following day was not statistically significant ($N = 3$, $n = 15$, Fig. 4A, $P > 0.05$). The type of ablation also significantly affected their gait cycle. *Microvelia americana* with ipsilateral ablations continued to use the alternating tripod gait. In contrast, those with ablations on opposite sides displayed no discernible periodicity in their gait on the day of their ablation (Fig. 4B), yet managed to return to the alternating tripod gait within 24 h (Fig. 4C).

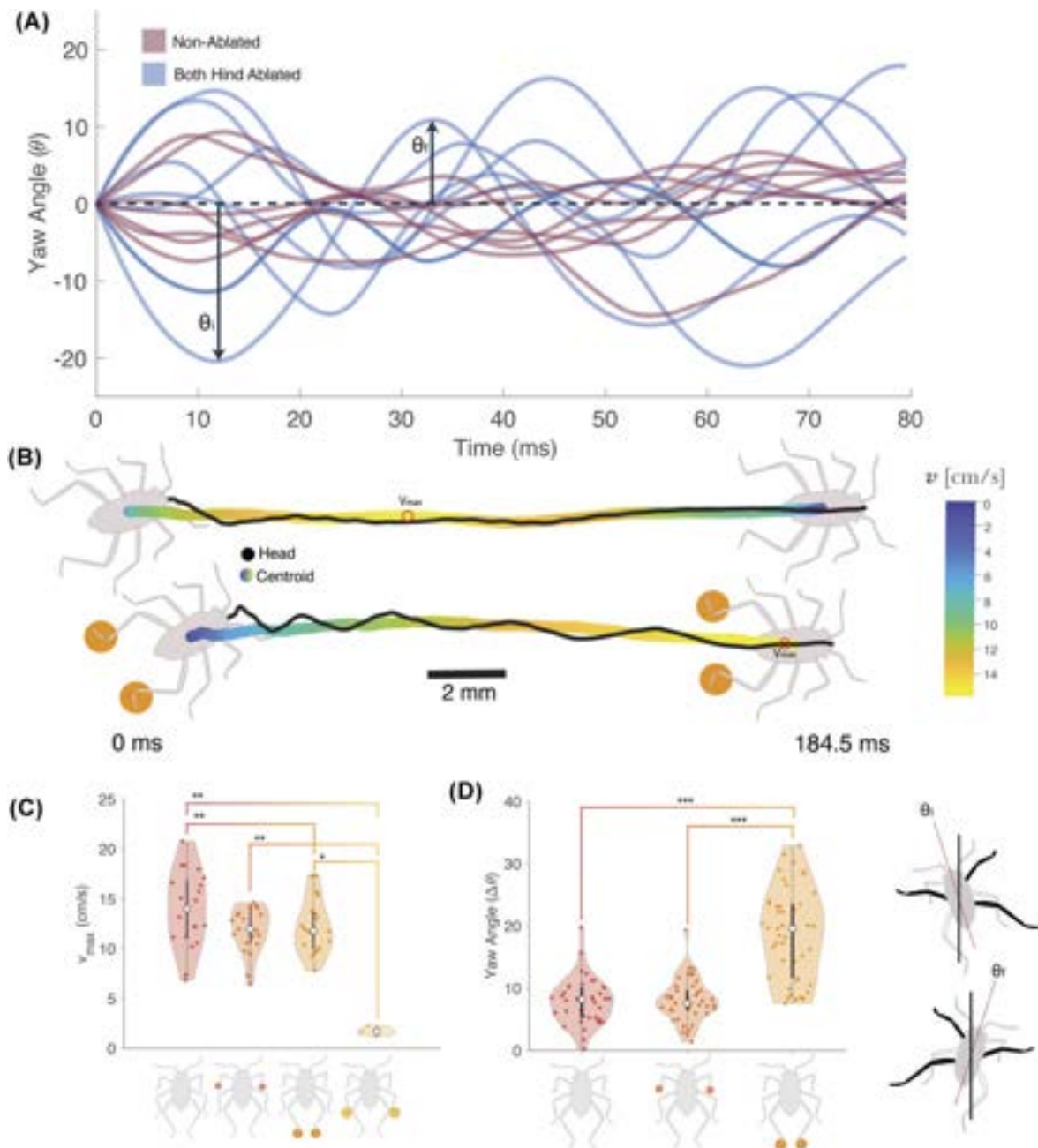


Fig. 2 Yaw angle, trajectory, and maximum velocity for nonablated and ablated *M. americana*. **(A)** Yaw angle over time of an *M. americana* before ablation (nonablated) and after ablation (both hind ablated conditions), with a visual difference in the size of yaw angles. **(B)** Trajectories of a nonablated and both-hind ablated *M. americana*. The increase in yaw of a both-hind ablated *M. americana* is visibly greater. The labeled circles indicate the point of maximum velocity along the path. **(C)** Violin and box plot of maximum velocities (v_{max}) of four *M. americana*, representing the distribution of v_{max} for every trial in each condition. Pairs without bars had no statistical difference. From left to right: control (nonablated) *M. americana* ($N = 3$ specimens, $n = 21$ trials), both front tarsi ablated ($N = 3$, $n = 21$), both hind tarsi ablated ($N = 3$, $n = 21$), and both middle tarsi ablated ($N = 1$, $n = 4$). *Microvelia americana*, missing their middle tarsi lose the ability to propel themselves. Only one middle ablated specimen was tested to preserve the population since the specimen did not survive within 48 h of ablation. The white circle represents the median. Other points represent experimental values from each trial. The box represents the second and third quartiles, with the extended lines representing the first and fourth quartiles. **(D)** Violin and box plot of yaw angles ($\Delta\theta$) of three *M. americana* conditions. Pairs without bars had no statistical difference. From left to right: control (nonablated), both front tarsi ablated, and both hind tarsi ablated. When missing its hind tarsi, the *M. americana*'s yaw angle increases. The yaw angle for both the left and right directions is plotted. Statistical analysis shown are pairwise comparisons of treatment groups. We defined statistical significance as * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

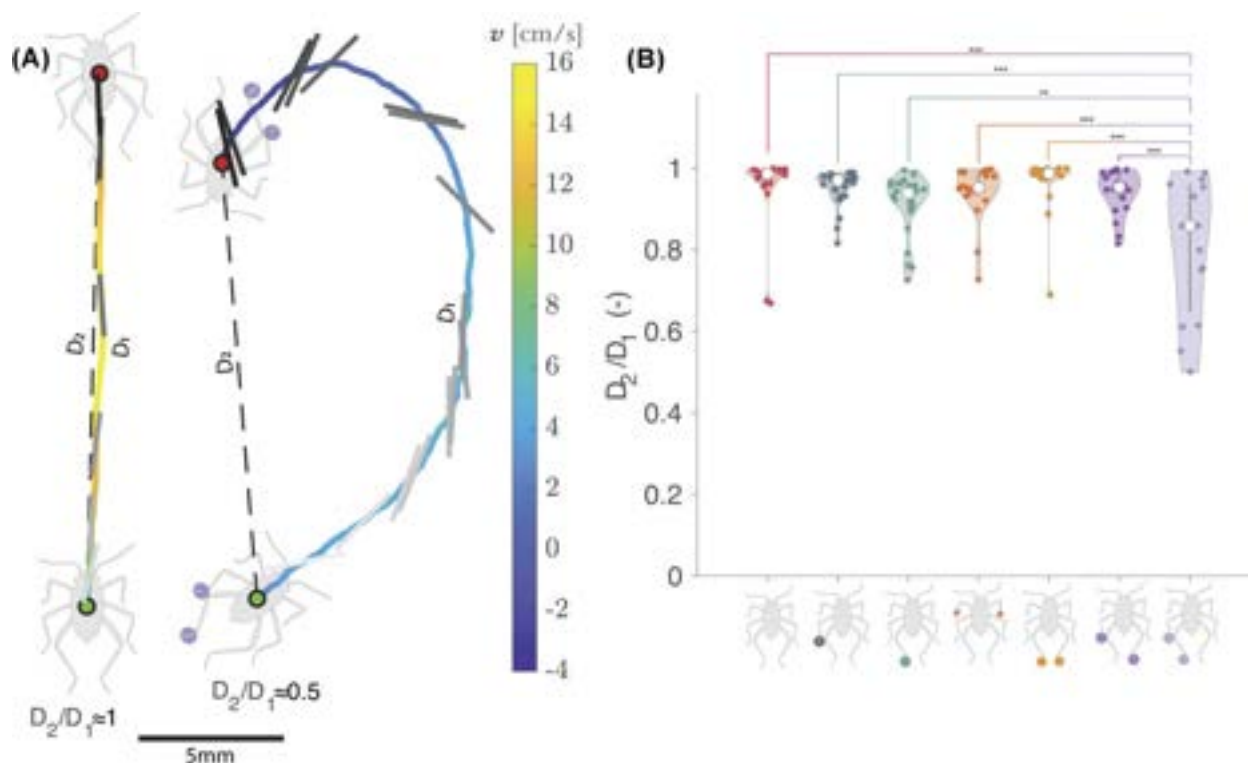


Fig. 3 Displacement compared to actual distance traveled. **(A)** Displacement (D_2) of *M. americana* compared to distance traveled (D_1), showcasing circular path for the ipsilateral ablated *M. americana* versus a nonablated *M. americana*, which moves in a straight line. The trajectory of the *Microvelia* is from bottom to top. **(B)** Violin and box plot showing the comparison of a set of *M. americana* ablation conditions and their displacement–distance ratio traveled in each trial ($N = 3$ for each ablation condition). White circle represents the median. Other points represent experimental values from each trial. Statistical analysis shown are pairwise comparisons of treatment groups. Pairs without bars had no statistical difference. Ipsilateral ablated *M. americana* were the only treatment group to have hindered directionality shown by its lower displacement–distance ratio ($N = 3$, $n = 16$). We defined statistical significance as $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

Discussion

For locomotion on the water surface, it is a well-documented strategy among water striders to rely on their middle legs as the primary propulsors of interfacial movement (Andersen 1976). Water striders such as *Gerridae* (Hu and Bush 2010; Crumière et al. 2016), *Rhagovelia* (Santos et al. 2017; Ortega-Jimenez and Bhamla 2021), and *Velia* (Andersen 1976) use a rowing gait in which only the middle legs row against the water surface to propel themselves forward. The remaining legs are used for support to float on the water's surface. This research affirms that *M. americana*, despite using an alternating tripod gait, prioritize their middle legs for propulsion, a finding consistent with previous studies (Andersen 1976). The critical role of these legs becomes evident upon their ablation, which results in a significant decrease in velocity from 14 to 2 cm/s, underscoring their indispensability for water traversal (Fig. 2C).

Contrasting the alternating tripod gait of *M. americana* with other hexapods that occasionally (or accidentally) enter aquatic environments reveals a unique adaptation in its locomotion strategy. For instance, *Cam-*

ponotus schmitzi ants swimming in pitcher plant digestive fluids or ants that accidentally fall into water use both their front and middle legs for propulsion (Bohn et al. 2012). Their front legs kinematically mimic terrestrial movement, their middle legs serve as rudders, and their hind legs act as roll stabilizers (Yanoviak and Frederick 2014). Despite these ants employing an alternating tripod gait, their “swimming” episodes are brief and rare, lasting under 45 s in pitcher plant fluids or longer when they fall from a tree canopy into water. In contrast, *M. americana* spends most of its time on water surfaces (Andersen 1976; Crumière et al. 2016). The removal of *M. americana*'s front tarsi does not impact velocity or directionality, suggesting that the front tarsi do not play a large role in powering water walking but may still exist to support the balance of the alternating tripod gait. Ablation studies reveal that *M. americana*'s hind legs function as rudders, facilitating directional movement and reducing yaw on water's slippery surface.

The predator–prey dynamic underlines the importance of adaptation for survival, not just in evading predators but in recovering from attacks. While many

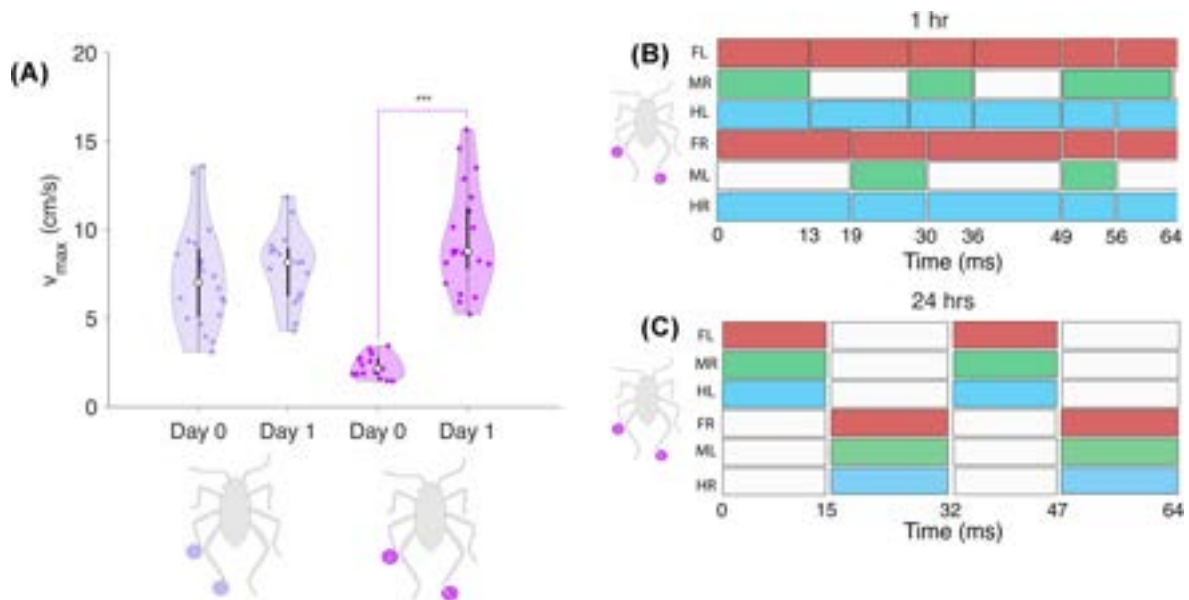


Fig. 4 Velocity of *M. americana* and how they adapt their gait. **(A)** Violin and box plot of maximum velocity (v_{max}) comparison of two ablated conditions, a contralateral middle and hind tarsus ablation and an ipsilateral middle and hind tarsus ablation, on the day they are ablated ($N = 3, n = 21$ for ipsilateral and $N = 3, n = 15$ for contralateral) and one day after ($N = 3, n = 16$ for ipsilateral and $N = 3, n = 21$ for contralateral). Pairs without bars had no statistical difference. For the contralateral ablation, *M. americana* are unable to walk on water on the day of ablation, but can walk the next day. White circle represents the median. Lines represent the first and fourth quartiles. Other points represent experimental values from each trial. The box represents the second and third quartiles. **(B)** Gait plot of an *M. americana* with a contralateral ablation within 1 h of its ablation. **(C)** Gait plot of an *M. americana* with an opposite side ablation >24 h after its ablation, which matches with the alternating tripod gait of nonablated *M. americana*. We defined statistical significance as $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

insects can regenerate limbs during larval stages after molting (Michaud et al. 2020; Zhong et al. 2023), many do not, especially after autotomy (Joseph et al. 2018), muscle degeneration (Personius and Chapman 2002), or reaching final molting stages (Sustar and Tuthill 2022). *Microvelia americana* undergoes five instars, after molting ceases (Frick 1949; Nakasuji and Dyck 1984), making any postmolt damage, such as tarsus or limb loss from an aerial bird or underwater fish, permanently affect their mobility and directionality.

Microvelia americana uses its middle legs as primary propulsors, causing a side-to-side rocking motion in the direction of the active leg (due to alternating leg strides). Without hind tarsi, this rocking motion intensifies, indicating their role as rudders (see Supplementary Movie S2). However, the removal of front tarsi does not alter the yaw angle. For a nonablated specimen, this is at a range of $\pm 7^\circ$ (Fig. 2D). Upon removal of both hind tarsi, *M. americana* rocks (yaws) at $\pm 19^\circ$.

Our findings indicate that the extent and location of limb loss critically influence *M. americana*'s ability to maintain direction while moving on water. Loss of both the middle tarsi is fatal as the organism cannot propel itself and eventually dies of fatigue. However, in most other cases of tarsus damage, *M. americana* is still able to move on water after tarsus loss. Particularly, *M. amer-*

icana with ipsilateral middle and hind tarsi removed show compromised straight-line movement, often veering off course (Fig. 3A) (see Supplementary Movie S3). This impairment suggests challenges in predator evasion or prey capture due to reduced directional control.

Contrastingly, *M. americana* with contralateral middle and hind tarsi ablated initially lose the alternating tripod gait (Fig. 4A) and show a significant drop in body velocity (2.17 cm/s), but within 24 h, they regain the tripod gait (Fig. 4B) (see Supplementary Movie S4) and approximate the speed (v_{max}) of those with ipsilateral ablations, favoring straighter paths. These observations underscore the hind tarsi's role in moderating yaw caused by contralateral middle leg movement, aiding in directional stability. This insight contrasts with the rowing gait, where any immobilization increases yaw (Meshkani et al. 2023), highlighting the alternating tripod gait's biomechanical advantage in maintaining directionality despite limb loss. Thus, *M. americana*, despite lacking the ability to regenerate limbs post-final molt, demonstrates remarkable resilience and adaptability in the face of physical impairments, adding another compelling narrative of survival and adaptation within the natural world.

Adaptable multisurface gaits, such as the alternating tripod gait utilized by *M. americana*'s specialized leg dy-

namics, can be mimicked in future designs of small amphibious robots as much interest is gathering in robotics at the air–water interface and increasingly complex terrains (Li et al. 2009; Song et al. 2024). A robust robot will be able to traverse a variety of surfaces without having to enact more complex motion than an alternating tripod gait.

Limitations and future outlook

Our study only focuses on the removal of tarsi, as the removal of the femur or the entire leg would have a greater impact on the overall balance, directionality, and velocity of *M. americana*, which would conflate the roles that each leg has in locomotion. Furthermore, different numbers of trials were done for different specimens due to fatigue of some specimens during experiments. Yet, our experimental setup was able to provide us consistent results. Future work can increase the sample size and also explore juvenile instars to further study the specialized dynamics of *M. americana*'s legs and effect of organism size when walking on water. Future studies can also determine whether other water-walking insects that use the alternating tripod gait also have these specialized leg dynamics. Moreover, our studies only focus on changes in yaw angle. We did not record videos from side view or measure forces to see how missing tarsi may impact changes in pitch, balance, weight distribution, or body height. Future research can record ablated *Microvelia* from the side view and measure the forces (Zheng et al. 2016; Wildeman 2018) produced by each leg before and after ablation to further understand other changes in locomotion from tarsus loss.

Microvelia has another means of propulsion on the water surface, namely Marangoni propulsion (Andersen 1976), in which it spits a fluid from its proboscis to lower the surface tension within a limited area. This reduction in surface tension allows the *Microvelia* to propel itself forward, and is used as an escape mechanism. Due to the reduced velocity caused by certain ablations, Marangoni propulsion can be a more preferred way to move in certain conditions such as predation. Future studies could study whether the use of Marangoni propulsion is more likely when *Microvelia* is missing a tarsus or limb.

Conclusion

Through ablation, we investigate the specialized leg dynamics within *M. americana*'s alternating tripod gait. Through high-speed imaging and pose estimation deep learning software, we measure the velocity, yaw angle, and directionality of the *M. americana* with different missing tarsi. Our results show that *M. ameri-*

cana uses its hind legs as rudders to stabilize the direction of movement, while the middle legs are the main propulsors for locomotion on water. When the front tarsi were ablated, we observed no impact in overall body velocity or yaw angle, suggesting that the front legs help in balancing when *M. americana* walk on water.

When removing the contralateral middle and hind legs, *M. americana* was initially unable to traverse the water surface. Yet, the same specimen adapted to their missing tarsi and performed the alternating tripod gait the next day. This contrasted with the removal of the ipsilateral middle and hind tarsi, where *M. americana* were able to use the alternating tripod gait immediately after removal. However, *M. americana* with the ipsilateral ablation had reduced directionality and sometimes traveled in curved paths rather than straight paths. These results suggest that the removal of middle and hind tarsi poses a threat to *M. americana* in the wild as *M. americana* would have higher difficulty avoiding predators or catching prey from their reduced body velocity and inhibited directionality. Ultimately, this study can influence the design of future robotics that may implement their own specialized leg dynamics for locomotion on the surface of water.

Author contributions

J.N.O. designed the experiments. J.N.O., K.L.Y., and G.D. carried out the experiments and acquired the data. J.N.O. analyzed the data and interpreted the results. P.R. assisted with data analysis and manuscript review. M.S.B. reviewed the design and execution of experiments, data analysis, interpretations, and manuscript. All authors contributed to writing the manuscript.

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Supplementary data

Supplementary data available at *ICB* online.

Conflict of interest

No conflict of interest is declared.

Data availability

The data underlying this article are available in the article and in its online supplementary material.

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