

Correspondence

Early destruction of cockroach respiratory system and heart by emerald jewel wasp larvae

Kenneth C. Catania

In the 1880s, Henri Fabre was captivated by the “special art of eating”, whereby a parasitoid wasp larva fed selectively on host internal organs, avoiding the heart (dorsal vessel) and tracheal system (respiratory system) to preserve life. In Fabre’s words: “*The ruling feature in this scientific method of eating, which proceeds from parts less to the parts more necessary to preserve a remnant of life, is none the less obvious*”¹. Subsequent investigators have reported the same for many parasitoid wasps^{2,3}, including for the emerald jewel wasp (*Ampulex compressa*)⁴. Here it is reported that larval jewel wasps destroy the dorsal vessel and tracheae (respiratory system) in the thorax of their cockroach host (*Periplaneta americana*) at their earliest opportunity. Moreover, the broken tracheae release air into the host, which the larval jewel wasp inspires. An increase in larval chewing rate, cotemporaneous with the sudden release of air from the host’s broken tracheae, suggests the larva taps into the host respiratory system to support its metabolism while rapidly consuming the host.

To put the relative timing of these events into context, it helps to first consider the stages of wasp larval development^{5,6}. The wasp egg hatches three days after oviposition on the cockroach middle leg and the larva feeds on hemolymph through a hole chewed through the proximal coxa (upper leg). On day six after hatching, the larva begins entry into the cockroach mesothorax (middle thorax) by enlarging the hole and squeezing through. When the larva reaches the midline of

the mesothorax, it consumes the mesothoracic dorsal vessel and corresponding thoracic chamber of the heart (Figure 1A–C; Video S1, Clip 1). Shortly thereafter, it enters the metathorax and consumes the metathoracic section of the dorsal vessel and metathoracic chamber of the heart (Figure S1A in the Supplemental information). The mean time between first appearance of the head and mandibles at the dorsal margin of the mesothorax and the destruction of the dorsal vessel and heart chamber in the mesothorax was 156 minutes for 10 cases. Although the caudal (abdominal) heart chambers continue to pump after these more rostral chambers are

destroyed, the heart can no longer pump hemolymph to the head or first thoracic segment. Given that the larva does not pupate for roughly another two weeks⁷, the destruction of the heart segments in the thorax occurs early in the sequence of larval development.

In each of 24 cases observed, the larva also chewed through large respiratory tracheae as it entered, often resulting in the release of air (Figure 1D,E; Video S1, Clip 1). The larva always entered the cockroach such that its rostral spiracles on one side were oriented dorsally (with respect to the host) where pockets of air were often located. As a result, there was often prolonged

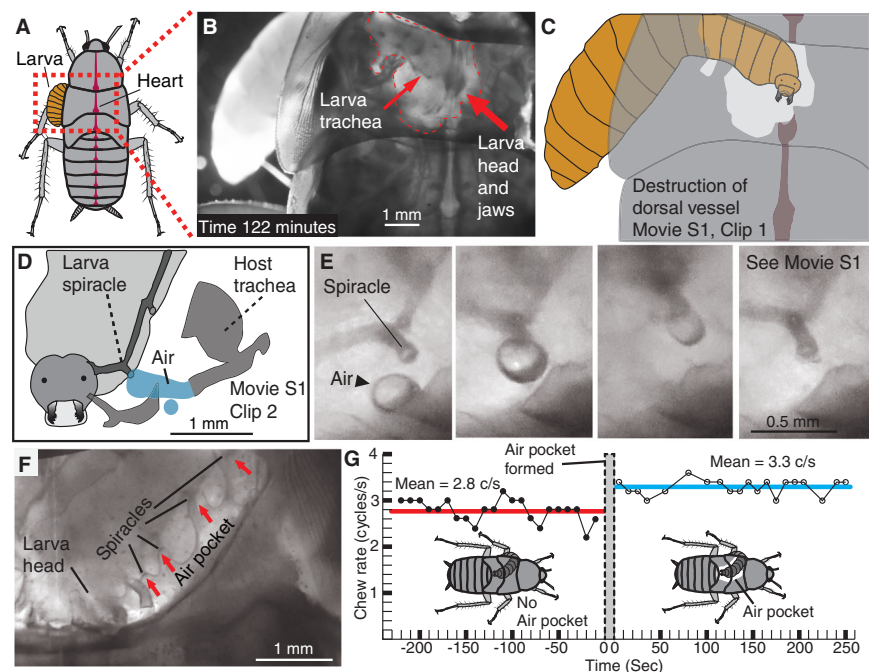


Figure 1. Key early events as the larval jewel wasp enters the body of its cockroach host. (A) The approximate position of the caudal half of larva as shown in (B) and (C). (B) A transilluminated cockroach with the head and mandibles of the larva indicated. Red dotted line indicates area consumed by larva. (C) Schematic showing the portion of the mesothoracic heart destroyed in (B). Notice that the caudal half of the larva (and associated spiracles) remain outside the cockroach at this point. (D) Association of the larva's left, rostral-most spiracle with an air pocket emanating from a severed host trachea. Video S1, Clip 2 shows this long-term association as the air pocket expands and contracts, suggesting the larva has tapped into the host's respiratory system. (E) Plates captured from video show an air bubble inspired through a larval spiracle within the host mesothorax, as captured in real-time (see Video S1). (F) The larva's body distorts an air pocket, bringing portions of the air pocket into contact with spiracles. (G) Change in the larva's cyclical chewing rate after the formation of an air pocket in the metathorax of the host. The left side shows a plot of chew rate (five second samples) verses time for a case in which no air pocket had formed until the larva's head had reached the metathorax. The gray bar in the center indicates the time at which an air pocket suddenly formed as the larva chewed through tracheae. After the air pocket formed, chew rate increased from a mean of 2.8 cycles per second (red line) to 3.3 cycles per second (blue line). A t-test shows a significant difference ($t(11.9) = 6.4$; $P < 0.0001$).



contact between larval spiracles and air pockets. These air pockets, in turn, were often still attached to the host's severed tracheae, expanding and contracting in apparent coordination with host respiration (Figure 1D; Video S1, Clips 2 and 3). This provided a link between the respiratory system of the host and the parasitoid. Moreover, air from the host's broken tracheae created isolated bubbles. When one of the larva's first or second spiracles encountered a bubble, the bubble was usually inspired. This remarkable and consistent behavior (Figure 1E; Video S1, Clips 4 and 5) clearly shows the larva's spiracles are active within the host.

At the earliest stages of host consumption described here, the larva's caudal spiracles have yet to be drawn inside the host. But as the larva moves progressively further into the host, the remaining spiracles are necessarily drawn progressively into the host's body. Hence the distance from the active mandibles to the dwindling free spiracles increases with each increment of larva ingress, until finally the larva's entire body is inside the host (Video S1).

To investigate the possibility that air derived from severed host tracheae serves the larva's metabolic needs, cases were identified in which air did not leak into the mesothorax to create an air pocket despite severed tracheae. In these cases, subsequent movement of the larva into the metathorax, while severing additional tracheae, eventually caused leakage of air into the host body cavity. In four such cases, it was possible to sample the cyclical chewing rate for repeated, five second intervals when the larva mandibles were periodically visible, both before and after an air pocket had suddenly formed around the head and rostral segments of the larva. For each case, there was a statistically significant increase in chewing rate after the air pocket formed. Figure 1G shows a case in which the larva mandibles were visible almost continuously before and after the formation of the air pocket, allowing for a clear graphical representation of chewing rate verses time, relative to air pocket formation (see Figure S1 for more cases). Note

that as the larva continues to feed, moving into the abdomen while breaking additional tracheae, the air pocket usually expands to eventually surround the entire larva at later stages.

The results show that the larva destroys portions of the dorsal vessel and tracheae of its host at a comparatively early stage relative to many other parasitoids^{8,9}. Whether the heart is simply in the path of the feeding larva, or alternatively its early destruction has been selected, for example to facilitate consumption of hemolymph, is not clear. As first described by Williams⁷ in 1942, the larva "ravenously" consumes most of the internal organs of its large host with remarkable speed. The cockroach usually dies within 48 hours. Perhaps by consuming host tissues rapidly, the larva dispenses with the need to preserve otherwise vital tissues. However, this strategy necessarily comes with a higher metabolic rate than typical of many parasitoids, for which the challenge of respiration within the host may usually be mitigated by low muscular activity¹⁰. The apparent solution for the active jewel wasp larva is to tap into the host's respiratory system by breaking tracheae and positioning its spiracles favorably for accessing air. When considering these observations, it is astonishing that Clausen, in 1950, made the following prescient statement¹⁰: "*Though it has been assumed that the spiracles of free-floating endophagous hymenopterous larvae are not functional, yet this may not be altogether true. It is possible that laceration of tracheae by the mandibles of the parasite may set free a bubble of air, or provide access to the air in the tracheae, and thus permit the functioning of spiracles, if they are open and applied to the wound*". In the case of the jewel wasp, this ability seems to include adaptations of the larva's body surface to channel air toward the spiracles, as often observed (Figure 1F; Video S1). Finally, these observations raise the question of what selective pressures might have led to the jewel wasp larva's comparatively rapid consumption of its host.

SUPPLEMENTAL INFORMATION

Supplemental information includes experimental procedures, one figure, and one video and can be found with this article online at <https://doi.org/10.1016/j.cub.2023.06.005>.

A video abstract is available at <https://doi.org/10.1016/j.cub.2023.06.005#mmc3>.

ACKNOWLEDGEMENTS

This research was supported by National Science Foundation grant number 2114264 to Kenneth Catania. Special thanks to Anita Manning and Steven Montgomery for collecting wasps for this research.

DECLARATION OF INTERESTS

The author declares no competing interests.

INCLUSION AND DIVERSITY

The author supports inclusive, diverse, and equitable conduct of research.

REFERENCES

1. Fabre, J.H. (1921). *More Hunting Wasps* (UK: Dodo Press).
2. Punzo, F. (2005). Studies on the natural history, ecology, and behavior of *Pepsis cerberus* and *P. mexicana* (Hymenoptera: Pompilidae) from Big Bend National Park, Texas. *J. N.Y. Entomol. Soc.* 113, 84–95.
3. Chudek, J.A., Crook, A.M., Hubbard, S.F., and Hunter, G. (1996). Nuclear magnetic resonance microscopy of the development of the parasitoid wasp *Venturia canescens* within its host moth *Plodia interpunctella*. *Magn. Reson. Imaging* 14, 679–686.
4. Arvidson, R., Landa, V., Frankenberg, S., and Adams, M.E. (2018). Life history of the emerald jewel wasp *Ampulex compressa*. *J. Hymenopt. Res.* 63, 1–13.
5. Catania, K.C. (2020). Getting the most out of your zombie: Abdominal sensors and neural manipulations help jewel wasps find the roach's weak spot. *Brain Behav. Evol.* 95, 181–202.
6. Haspel, G., Gefen, E., Ar, A., Glusman, J.G., and Libersat, F. (2005). Parasitoid wasp affects metabolism of cockroach host to favor food preservation for its offspring. *J. Comp. Physiol. A.* 191, 529–534.
7. Williams, F.X. (1942). *Ampulex compressa* (Fabr.) A cockroach-hunting wasp introduced from New Caledonia into Hawaii. *Proc. Haw. Ent. Soc.* 11, 221–233.
8. Godfray, H.C.J. (1994). *Parasitoids: Behavioral and Evolutionary Ecology* (Princeton: Princeton University Press).
9. Strand, M.R. (2002). The interactions between larval stage parasitoids and their hosts. In *The Behavioural Ecology of Parasites*, E.E. Lewis, J.F. Campbell, M.V.K. Sukhdeo, eds. (Wallingford, UK: CAB International), pp. 129–152.
10. Clausen, C.P. (1950). Respiratory adaptations in the immature stages of parasitic insects. *Arthropoda* 1, 197–224.

Department of Biological Sciences,
Vanderbilt University, Nashville, TN 37232,
USA.
E-mail: ken.catania@vanderbilt.edu