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The Cocoon of the Developing Emerald Jewel Wasp (*Ampulex compressa*) Resists Cannibalistic Predation of the Zombified Host

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Keywords

Evolution · Parasitoid · Development · Predator · Defense · Adaptation · Behavior

Abstract

Introduction: To reproduce, the parasitoid emerald jewel wasp (*Ampulex compressa*) envenomates an American cockroach (*Periplaneta americana*) and barricades it in a hole with an egg on the host's leg. The larval wasp feeds externally before entering the host and consuming internal organs before forming a cocoon inside the host carcass. ***Methods:*** The vulnerability of jewel wasp larvae to predation by juvenile cockroaches was investigated, and data were recorded with time-lapse videography. ***Results:*** Cockroaches were found to be predators of parasitized hosts. When parasitized cockroaches were exposed to hungry cockroaches on days 0–8 of development, the developing larva was killed. Eggs were dislodged or consumed, larvae on the leg were eaten, and larvae inside the host were eaten along with the host. On day 9, 80% of the wasp larvae were killed and eaten along with the host. Conversely, on day 10, 90% of the larvae survived. On developmental day 11 or later, the wasp larva always survived, although the host carcass was consumed. Survival depended entirely on whether the cocoon had been completed. ***Conclusion:*** The results highlight the vulnerability of larvae to predation and suggest the cocoon defends from insect mandibles. This may explain the unusual feeding behavior of the jewel wasp larvae, which eat the host with remarkable speed, tapping into the host respiratory system in the process, and consuming vital organs early, in contrast to many other parasitoids. Results are discussed in relation to larval wasp behavior, evolution, and development, and potential predators are considered.

Introduction

The genesis of this research project was the surprising discovery, in the laboratory, of a pristine cocoon of the emerald jewel wasp (*Ampulex compressa*) in the absence of the typical host body that inevitably surrounds this developing parasitoid. To appreciate the significance of this anomalous observation, the life cycle of the emerald jewel wasp (hereafter referred to as the jewel wasp) must be briefly reviewed. The jewel wasp targets only the American cockroach, *Periplaneta americana* [1–8]. When a hunting female encounters a cockroach, she pacifies the host with a sting to the brain, pulls it to a hole, and lays a single egg on the coxa of the mesothoracic (middle) leg. She then barricades the entrance thus entombing the cockroach with the egg.

After about 3 days, the egg hatches, and the larva develops as outlined in Figure 1. First, the small larva feeds on hemolymph externally; next, the grub enters the cockroach and ravenously eats the internal organs (stage

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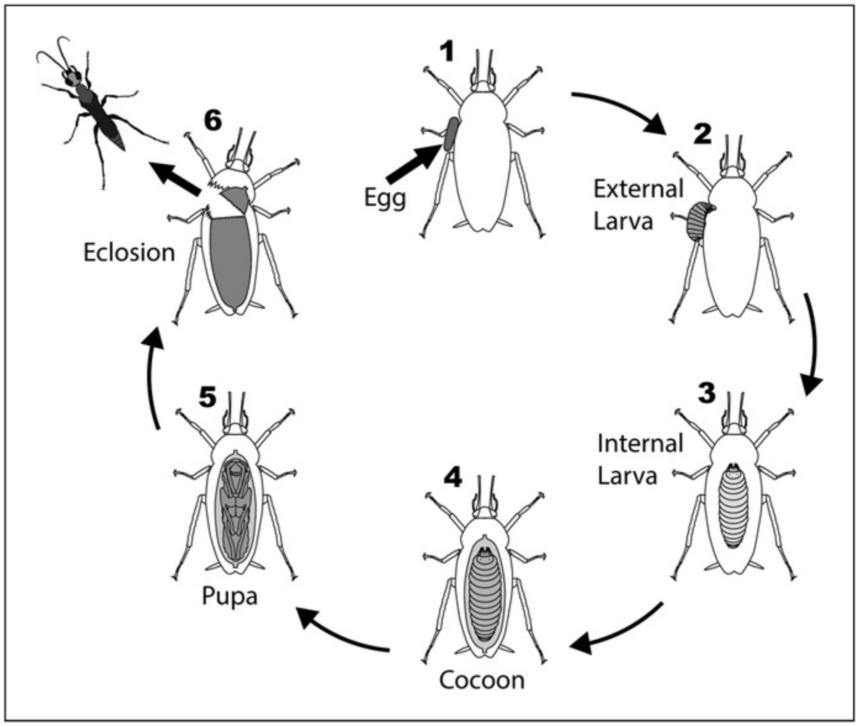

Fig. 1. Life cycle of the parasitoid emerald jewel wasp, *Ampulex compressa*. After subduing an American cockroach (*Periplaneta americana*) with several stings to the nervous system, the female wasp pulls the pacified but ambulatory host to a preexisting hole and lays a single egg on the host's right or left second leg (1). After several days, the egg hatches and the larva bites a small hole in a soft membrane at the base of the coxa. It then feeds externally on hemolymph for several more days (2). Next, the larva enlarges the hole in the host cuticle, crawls inside, and rapidly consumes the host's internal organs (3). After hollowing out most of the cockroach, the larva forms a cocoon inside of the dead cockroach (4). After a week or more, depending on the temperature, the larva pupates within the cocoon (5). After a total of approximately 40–60 days, depending on the temperature and sex of the wasp, an adult wasp emerges from the cocoon and carcass of the cockroach (6).

3, Fig. 1). After approximately 2 more days (roughly 8 days total since the egg was laid), the larva begins to form a cocoon within the hollowed-out husk of the now-dead cockroach (stage 4, Fig. 1). After a total time of approximately 1–2 months, depending on sex and temperature (see Arvidson and colleagues [9] for details at 26°C), the adult wasp breaks out of the cocoon and surrounding husk of the cockroach (stage 6, Fig. 1).

Considering these aspects of the jewel wasp's life cycle, it was surprising to find a solitary and pristine jewel wasp cocoon, as seen in Figure 2, in the enclosure of a female jewel wasp that had died some days earlier. Where was the cockroach that must have provided all the nutrients for this now late-stage developing wasp inside the cocoon? A search of the small enclosure for a possible dead husk of the host cockroach was fruitless. However, a healthy adult cockroach (that had evaded the wasp) with intact antennae was discovered under the water bowl in the enclosure. It is not possible for the cocooned wasp larva to have used this living cockroach as a host because wasp larvae destroy the dorsal vessel and respiratory system of their host when feeding [10], consume the majority of the cockroach internal organs to develop [9], and the female wasp cuts short the cockroach antennae of the host before depositing an egg [11].

There seemed to be only one possible solution to this enigma. The wasp had parasitized a cockroach and entombed it under the water dish. Later, another adult cockroach was introduced but managed to evade the wasp. After the wasp died, the unparasitized cockroach unearthed and fed on the parasitized cockroach, eating every available scrap, but was unable to penetrate the cocoon housing the larval wasp.

This interpretation, if correct, provides several new insights into the biology of the emerald jewel wasp. For example, to date, the wasp's unusually hard, oblique cocoon has been interpreted as primarily an antimicrobial defense [12, 13]. Moreover, the significance of host entombment is not entirely clear for this parasitoid, but host (and therefore larval) susceptibility to predation could be the main pressure that selected entombing behavior. Finally, a recent study suggests larval jewel wasp development is an outlier; the larva feeds with extraordinary speed and shows a surprising disregard for the preservation of host vital organs [9], in contrast to many parasitoids that feed more slowly [14]. Selection for rapid cocoon formation, as a defense against opportunistic predators, could explain the unusually rapid feeding sequence of jewel wasp larvae and concomitant early destruction of host vital organs.

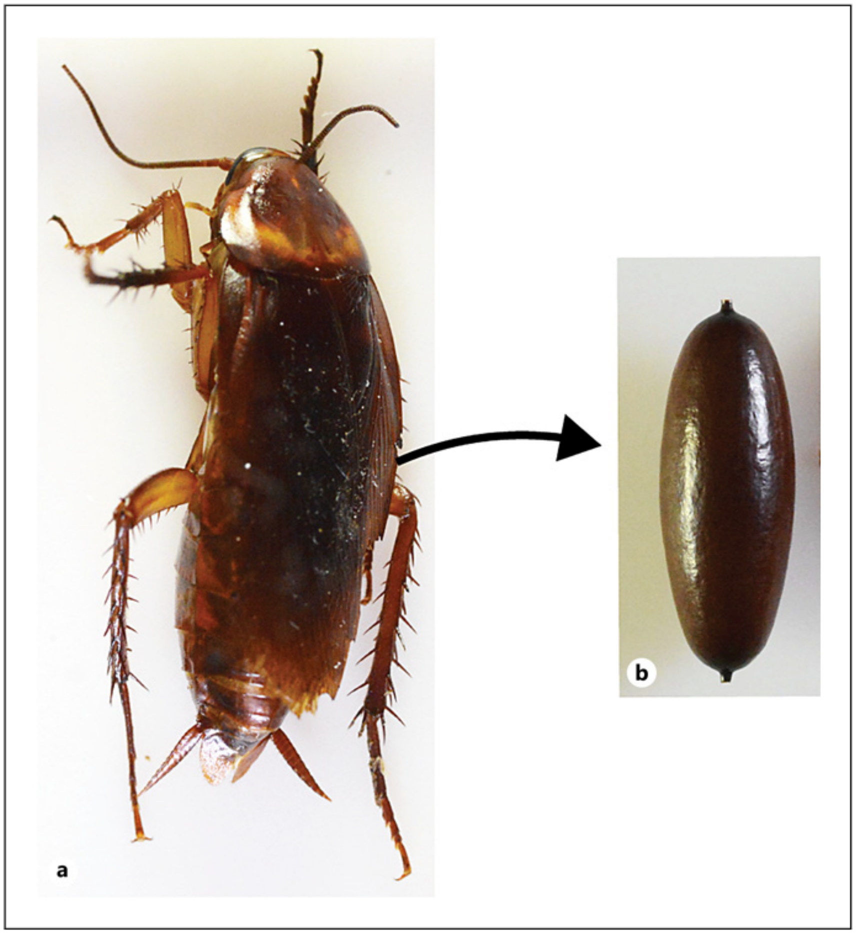

Fig. 2. A parasitized cockroach and pupa with carcass and silk removed. **a** A dead cockroach with a swollen abdomen showing the typical appearance of a successfully parasitized host containing a wasp cocoon. **b** The smooth hard cocoon surrounding the larva as shown with the cockroach carcass and outer silk layers removed.

Because maintaining a colony of jewel wasps also requires maintaining a colony of American cockroaches, the hypothesis that jewel wasp larvae are susceptible to opportunistic predation and that jewel wasp cocoons defend against powerful insect jaws was easily investigated by presenting hungry cockroaches with their parasitized compatriots. The results support the hypothesis that parasitized cockroaches are vulnerable and that the cocoon is resistant to insect mandibles.

Materials and Methods

Emerald jewel wasps (*Ampulex compressa*) were maintained in a USDA approved facility under permit number P526P-17-01368. Lights were cycled on a 14-10 light-dark regimen and room temperature was maintained at approximately 24–26°C. Male wasps were housed 2 to 5 specimens to a cage in 1452 Bioquip Bug Dorms (Bioquip Inc., Rancho Dominguez, CA, USA) and provided with a water supply by means of a Little Giant screw-on poultry watering jar (Miller Manufacturing Company, Glencoe, MN, USA) with a section of sponge place into the exposed, circular water compartment, along with sucrose on separate wet filter paper in a petri dish. Newly emerged female wasps were placed in an enclosure with males and given 48 h to mate. After mating, each female was removed and housed individually in a 1452 Bioquip Bug Dorm (Bioquip Inc., Rancho Dominguez, CA, USA) and provided with sucrose and water as described above. Up to 20 female wasps were maintained at a time.

To maintain the wasp colony, cockroaches (*P. americana*) were obtained from either an in-laboratory colony or ordered as adults from Carolina Biological (Carolina Biological Supply Company Burlington, NC, USA). Cockroaches were housed in plastic cages with a screened top and supplied with egg carton sections for refuge and fed Fluker's 70008 High Calcium Cricket Feed. Cages were misted daily to supply water and supplementary

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fluid and nutrients were provided with Nature Zone Total Bites.

Female wasps were frequently supplied with adult or late-stage cockroaches to parasitize. To provide a place for female wasps to entomb parasitized cockroaches, each enclosure was supplied with a series of custom-made, rectangular, open-ended boxes made of plexiglass (approximately 8 cm long, and 2 cm × 2 cm length and height). Sides of the entombment chambers were clear, but the top was black plexiglass to enhance the wasp's perception of the chamber as an enclosed space. Small colored aquarium gravel provided the enclosure substrate as well as the material that female wasps used to barricade the box opening after egg deposition on the host.

Parasitized cockroaches were transferred (inside the entombment chamber) to a separate plexiglass incubation chamber. Supplementary radiant heat lamps were thermostatically regulated to maintain the temperature between approximately 30–31°C. A passive, open water jar kept the humidity above 40% in the incubation chamber.

Cockroaches were food-deprived for several days prior to the experiments. Parasitized cockroaches at various stages were placed into the cockroach enclosure inside of a white-bottomed plexiglass chamber with clear walls and a clear, removable lid. An adjustable gap (kept at roughly 4 mm height) at the base of the container allowed the small (predatory) cockroaches to enter, but prevented the larger parasitized cockroach, or cocoon if it had been constructed, from being removed from the container.

Time-lapse video of was made with either a Nikon D5 SLR, or a Nikon D4 SLR (Nikon Inc., Melville, NY, USA) at high ISO settings to reduce lighting requirements. Lighting was provided by two CN-216 Neewer LEDs. The camera was attached to a JJC model MC-30 intervalometer set to 1 s or 2 s intervals. Images were collected as a series of jpegs, transferred to a Macintosh computer (Mac Studio), and imported into Premier Pro Version 22.5.0 (Build 62). Time-lapse movies were annotated and exported as mp4s.

Results

To test the susceptibility of parasitized cockroaches and the jewel wasp larva to opportunistic predation, 74 parasitized cockroaches, at a range of larval developmental stages, were presented to colonies of cockroaches. For time-lapse videography, many of the parasitized cockroaches were placed into a small custom plexiglass chamber that had a narrow opening at the bottom, too small to allow the parasitized cockroach (or cocoon) to be removed, but wide enough to allow the smaller cockroaches of the colony to enter (see Fig. 3 and online suppl. Movie S1; for all online suppl. material, see https://doi.org/10.1159/000540971).

Parasitized cockroaches containing wasp larvae were ravenously consumed, and the results revealed the critical dependence of larval wasp survival on cocoon formation. Between day 0 and 8 of development, all eggs or larvae were killed (n = 22). Conversely, on day 11, or later, all wasp larvae survived (n = 32). On day 9, 80% of the larvae were killed (8 of 10), whereas on day 10, 90% (9 of 10) of larvae survived (Fig. 4). As shown in Figure 3, the obvious, key variable determining either death or survival of the wasp larva was the completion of the hard, smooth cocoon that surrounds the larva within the cockroach body (stage 4, Fig. 1). Larvae within a host that had not completed a cocoon were often killed and eaten in less than 2 h – in 4 cases observed in real time (2 for day 7 and 2 for day 8), the cockroach cuticle was breached and the larva removed and eaten in less than 10 min. Figure 3 shows frames from time-lapse video, illustrating the side-by-side results typical for before and after a cocoon has been completed – in this case showing examples from day 9 and day 10 larvae (located within the host body) attacked by cockroaches. Online supplementary Movie S1 illustrates the details of these events. Note that although early stages of larva development are represented by only one trial each in Figure 4, this small sample size was considered inconsequential to the conclusions, in part because the disposition of egg or larva is similar until the larva enters the host on day 6. But more importantly, early-stage larvae exposed to predators would necessarily have to pass through the later developmental time points to survive, and this never happened unless the cocoon had been completed.

For trials conducted on day 10 or later (with one exception for which the larva had not fully completed the cocoon), the cockroaches usually consumed every accessible part of the remaining host cockroach, leaving behind a pristine cocoon as described in the introduction and shown in online supplementary Movie S1 (arrow, Fig. 3). There was no suggestion from cockroach behavior that the cocoon itself was repellant. For example, the cockroaches continued to chew at the cocoon ends, explored and touched the cocoon with the antennae, and had usually eaten away all of the closely adhered outer silk sheath from the larval cocoon.

Three cocoons were left in an enclosure with three large adult cockroaches for over a month as the wasp larvae developed to adulthood and eventually eclosed. All survived with no evident damage to the cocoons during the long cohabitation with cockroaches.

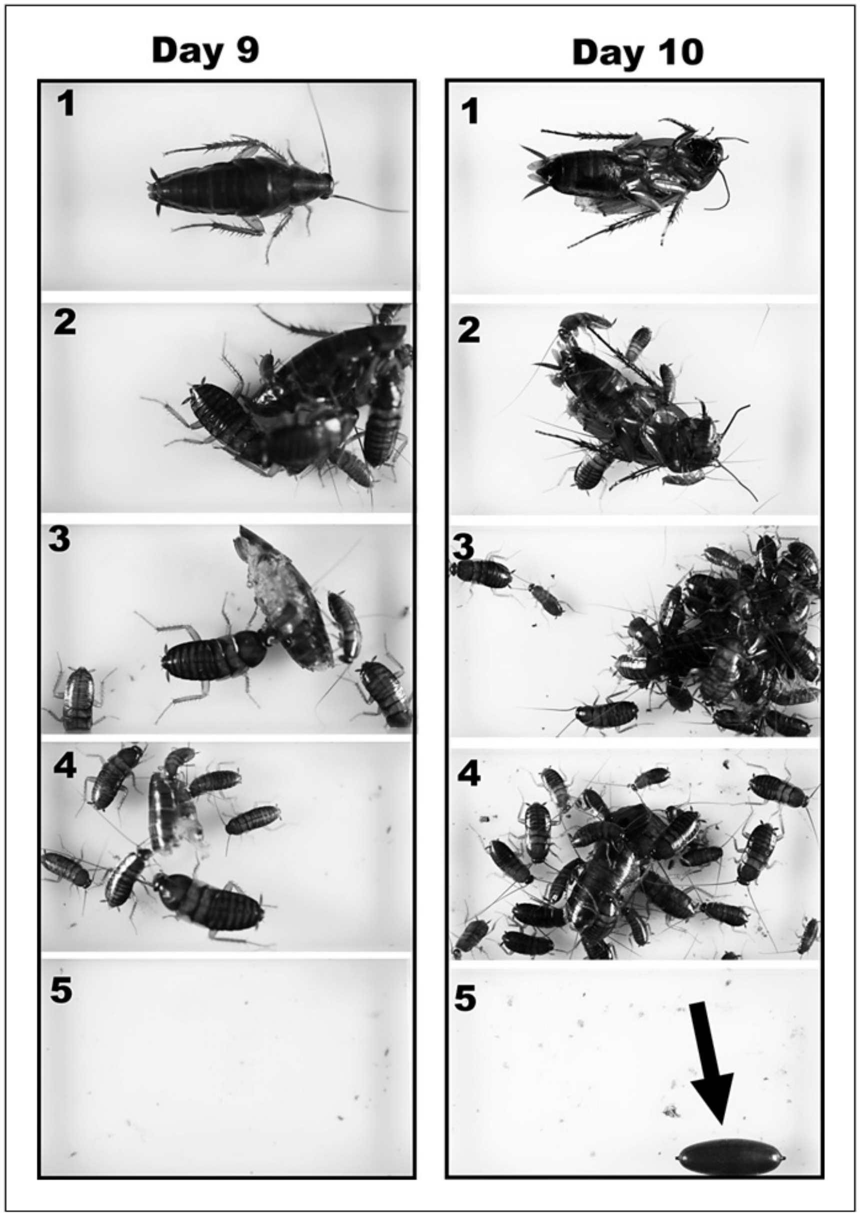

Fig. 3. Example results of cockroach predation on parasitized hosts on either day 9 or day 10. For the day 9 case, the larval jewel wasp inside the host had not yet completed its cocoon; hence, it was exposed, removed, and eaten in 89 min. On day 10, the larva had completed the cocoon, and hence, it survived (arrow) while all the remaining unprotected organic material (cockroach carcass and outer layers of cocoon silk) was eaten.

In the trials for wasp larvae on day 9 of development, the larvae were typically in the process of energetically constructing the cocoon when they were removed and eaten. Often portions of the partially formed cocoon were left as a remnant (Fig. 5; online suppl. Movie S1). On days 3–6, when the small wasp larva was still feeding on the exterior of the cockroach, the larva was detected, apparently with the antennae, by investigating cockroaches and eaten. Interestingly, in some cases, the wound on the host cockroach, from which the larva had been feeding, subsequently became a focal point of the cockroach colony and the wounded (zombified) roach was then overwhelmed and eaten, starting from the wound (online suppl. Movie S2). Figure 4 illustrates the clear dependence of larval survival on the formation of the cocoon.

Discussion

The results of this study touch on many different aspects of emerald jewel wasp biology, including development, evolution, and behavior. There are also implications for the

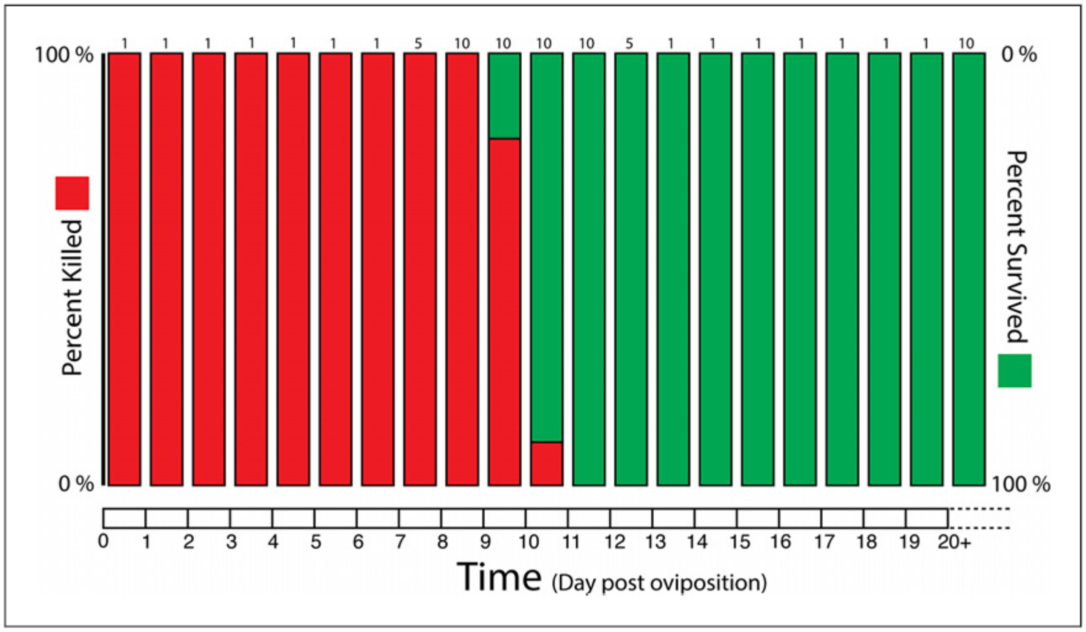

Fig. 4. The relationship between time after oviposition and survival of jewel wasp larvae exposed to cockroach predation. All larvae or eggs were killed on day 8 or earlier. All larvae survived on day 11 or later. On day 9, 80 percent (8 of 10) of larvae were killed. On day 9, 90 percent (9 of 10) of larvae survived. Survival depended on completion of the cocoon. Numbers above bars represent the number of cases tested. Ten cases past 20 days (arrow) were tested without tracking specific days; all survived.

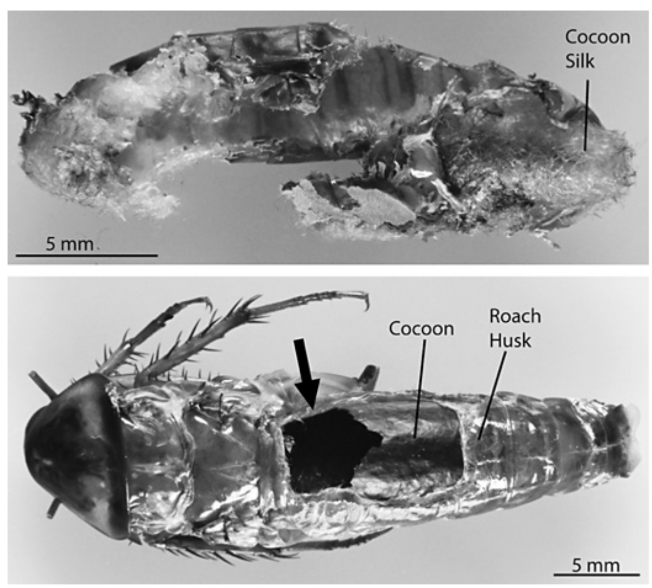

Fig. 5. Examples of partially or mostly completed cocoons from which the larva had been removed and eaten.

wider field of insect development, as the functional role of cocoons and the relative vulnerability of parasitized hosts to predation are areas of substantial interest and investigation.

But how relevant are the laboratory experiments presented here to emerald jewel wasps in their natural habitat? American cockroaches are not the first species that comes to mind when considering insect predators. Ants are perhaps highest on the list, and it is reasonable to consider ants as a prime selective force for the evolution of a mechanically defensive cocoon [15]. In fact, Veltman and Wilhelm [3] report ants targeting jewel wasp larvae at the Artis zoo in the Netherlands, though no details were provided. Nevertheless, the case for cockroaches also posing a threat is stronger than might at first be imagined.

The American cockroach is a gregarious species that often congregates in large numbers [16], and there is an aggregation pheromone that helps facilitate this behavior [17, 18]. Moreover, they have powerful jaws [19] and are known to feed on virtually all organic matter – human food of course, but they also feed on cloths, boots, hair, bark, canvas, paper, and even reptile eggs [20, 21]. They are opportunistically predatory, and have been recorded eating termites, bedbugs, mites and other insects [22] and are cannibalistic when food is short with juvenile or wounded cockroaches being most vulnerable [22, 23]. Considering these characteristics, it is perhaps not surprising that when given the chance cockroaches readily consumed the weakened cockroach host or dead cockroach carcass that surrounds the later stages of larval jewel wasps. You might say that cockroaches have the motive for predation on larval jewel wasps, but do they have the opportunity?

Here too, the case is stronger than might at first be imagined. Many wasps paralyze hosts for their developing offspring and then fly a great distance to barricade them in often deep or remote chambers constructed by the wasp (see [24]). In contrast, the emerald jewel wasp is somewhat famous for using a simpler strategy [11, 25–27]. After pacifying (zombifying) the cockroach with a sting directly into the brain, the jewel wasp pulls the still-ambulatory host to a nearby, preexisting hole or crevice. After the wasp's egg is laid on the mesothoracic (middle) leg of the cockroach, the jewel wasp then barricades the entrance with nearby debris. The result is likely more variable than the stereotyped fortress custom-made by wasps that can travel far to choose the best location and construction materials for engineering efficient entombment [28]. Presumably, the jewel wasp entombment is less secure, at least on some occasions when construction materials are not ideal. Moreover, as may be expected, the jewel wasp hunts for cockroaches where they are abundant [1]. It is a veritable truism that where you find one American cockroach, you are likely to find many [16]. It therefore seems a reasonable conclusion that many jewel wasp hosts are secured in proximity to other cockroaches, which are denizens of the kinds of holes and crevices used to entomb hosts.

Finally, a second accidental example of predation in the laboratory further attests to the potential for cockroach predation in nature. In the laboratory, not all cockroaches offered to wasps are attacked and parasitized. These cockroaches are routinely removed from wasp enclosures and later freeze-killed. This is done to assure that, in the event that a cockroach was parasitized but misdiagnosed, no wasp would later hatch out and be untracked in the facility. During this process at least one parasitized cockroach was indeed misdiagnosed, and the result was telling. The jar holding several cockroaches was being brought to the freezer, when a chewed open, near complete cocoon was observed (Fig. 5). This recently formed cocoon must have contained a jewel wasp larva that was eaten by the other cockroaches, and it appears to represent a very close call with the larva having almost completed its defense.

Whichever potential predators may threaten the developing jewel wasp, the present results suggest that at least one role of the cocoon is defense from insect mandibles. But this is certainly not the only role for the cocoon. Previous investigations have demonstrated that the cocoon is infused with antimicrobials [12], thus forming a key chemical barrier to pathogenic microorganisms that threaten the developing larva during its many weeks of subsequent development, which occurs inside the remaining carcass of the cockroach. In fact, the threat from microbes, including fungi, is sufficient that even the cockroach carcass is infused with antimicrobials by the larva [13]. Finally, it seems likely the cocoon serves to prevent desiccation of the larva during its development, though conversely it could also protect the larva from periodic flooding [29].

Nevertheless, investigators have also pointed out physical properties of the cocoon that seem admirably suited to withstand insect mandibles. Williams [1] comments that the cocoon is "smooth, strong, tight, and varnished" [1], Buys notes the brittle nature [30] of the protective hard capsule, and Arvidson et al. [10] model the smooth fusiform shape as a parabola. These characteristics would likely make it difficult for insect mandibles to get purchase on the cocoon's surface. Though the most compelling argument for the defensive nature of the cocoon are the present results – showing the mature cocoon's unfailing resistance to an onslaught of

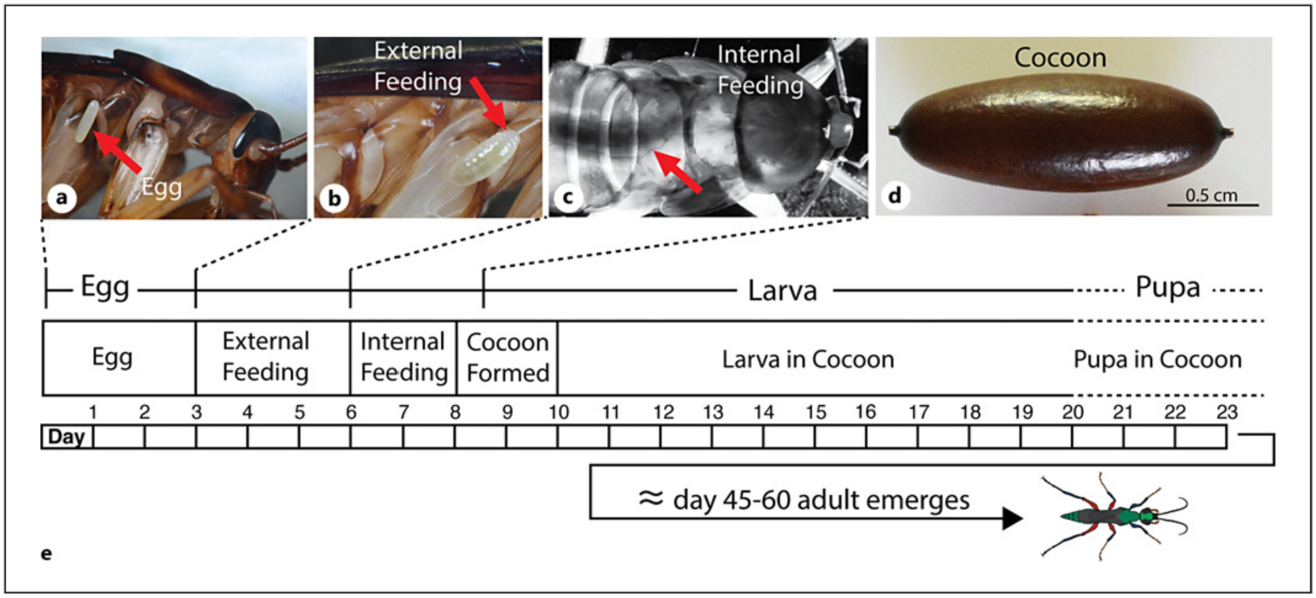

Fig. 6. The approximate timing of developmental events for jewel wasp larvae maintained in the laboratory at 30–31°C. Plates **a–d** illustrate the appearance for each stage on the timeline shown in **e**.

comparatively large, determined predators that usually eat every bit of surrounding organic material but never reach the prize within (Fig. 3; online suppl. Movie S1).

How do other features of jewel wasp behavior fit the interpretation that the cocoon protects from insect predators? In his seminal early paper describing the jewel wasp, Williams [1] describes the larva as feeding "ravenously" once inside the host. More recently, my own investigation suggested that larval feeding on the host is exceptionally fast, explaining why vital organs are not preserved for last [10]. The larva destroys the thoracic section of the dorsal vessel and breaks into the tracheae at the earliest stages of host feeding. In other words, the larva feeds so quickly that preservation of the host is presumably not a concern. Moreover, the larva inspires air from broken tracheae within the host while feeding, and this appears to be a means to support the unusually high metabolic rate of the larva [31] as it feeds rapidly [10].

It has been suggested that idiobiont parasitoids (those that do not allow the host to continue growing) develop at their physiological maximum, presumably because there is no benefit to delaying development [32] – i.e., the host will not accrue more caloric value over time, so why wait? Thus, it could be argued that the fast-eating jewel wasp larva is simply behaving as expected. Except feeding is not development. Cocoon formation commences as soon as feeding is complete. But as pointed out by Williams [1], pupation (a distinct developmental stage characterized the morphological transition from larval grub to exarate pupa as illustrated in Fig. 2, stage 5) does not co-occur with cocoon formation. Rather pupation occurs within the cocoon more than a week later, and sometimes many weeks later [1].

Figure 6 helps clarify the relative time points of various stages of larval behavior and development, as approximated from our laboratory colony kept at 30–31°C. Notice the internal feeding stage, which obviously cannot begin until the larva has entered the host. This stage lasts only about 2 days. This seems a surprisingly short time for a small grub to eat virtually the entire contents of its large host – the larva expands dramatically in the process (the larva spares the gut and underlying ventral nerve cord [10]). Hence, the suggestion that the larva need not preserve the vital host heart and tracheal system.

One interpretation of these previous and current results is that the larva is often under pressure from opportunistic predation by other insects. Hence, it has been selected to win a cocoon-forming race for survival by rapidly filling itself with the valuable contents of the host body, then forming the defensive cocoon where it can process the nutrients and develop in relative safety. Further study of potential predators of the larva and the efficacy of the cocoon as a defense may shed further light on this possibility (no hyperparasitoids of the jewel wasp, which the cocoon might defend against, have been reported). Finally, if there has been strong selective pressure to rapidly form a defensive cocoon, then there has presumably been similar selective pressure on the adult female wasp to hold back predators by constructing an efficient barrier when entombing the host with its offspring. The jewel wasp could provide a potential avenue for exploring how insects build efficient barriers from variable building materials.

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Statement of Ethics

Animal experiments conform to internationally accepted standards. The ethics statement is not applicable as there are no review boards for work on insects.

Conflict of Interest Statement

The author has no conflict of interest to declare.

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Author Contributions

K. Catania was responsible for all aspects of this study and wrote the paper.

Data Availability Statement

Data for this paper are included in the results. Further inquiries can be directed to the corresponding author.

References

1 Williams FX. Ampulex compressa (Fabr.), 1942 a cockroach-hunting wasp introduced from New Caledonia into Hawaii. Proc Haw Ent Soc. 1942;11:221–33.

2 Piek T, Visser JH, Veenendaal RL. Change in behaviour of the cockroach, Periplaneta Americana, after being stung by the sphecid wasp Ampulex Compressa. Entomol Exp Appl. 1984;35(2):195–203. https://doi.org/10.1111/j.1570-7458.1984.tb03379.x

3 Veltman J, Wilhelm W. Husbandry and display of the Jewel wasp: Ampulex compressa and its potential value in destroying cockroaches. Int Zoo Yearb. 1990;30(1):118–26. https://doi.org/10.1111/j.1748-1090.1990.tb01150.x

4 Richardson BA, Paul RK. Quantitative aspects of behaviour and reproduction in the Jewel wasp Ampulex compressa. Int Zoo Yearb. 1992;32(1):177–83. https://doi.org/10.1111/j.1748-1090.1992.tb02497.x

5 Fouad K, Rathmayer W, Libersat F. Neuromodulation of the escape behavior of the cockroach Periplaneta Americana by the venom of the parasitic wasp Ampulex compressa. J Comp Physiol. 1996;178(1):91–100. https://doi.org/10.1007/bf00189593

6 Weisel-Eichler AV, Haspel G, Libersat FR. Venom of a parasitoid wasp induces prolonged grooming in the cockroach. J Exp Biol. 1999;202(8):957–64. https://doi.org/10.1242/jeb.202.8.957

7 Weisel-Eichler A, Libersat F. Are monoaminergic systems involved in the lethargy induced by a parasitoid wasp in the cockroach prey? J Comp Physiol. 2002;188(4):315–24. https://doi.org/10.1007/s00359-002-0305-y

8 Haspel G, Libersat F. Wasp venom blocks central cholinergic synapses to induce transient paralysis in cockroach prey. J Neurobiol. 2003;54(4):628–37. https://doi.org/10.1002/neu.10195

9 Arvidson R, Landa V, Frankenberg S, Adams ME. Life history of the emerald jewel wasp Ampulex compressa. J Hymenopt Res. 2018;63:1–13. https://doi.org/10.3897/jhr.63.21762

10 Catania KC. Early destruction of cockroach respiratory system and heart by emerald jewel wasp larvae. Curr Biol. 2023;33(15):R799–800. https://doi.org/10.1016/j.cub.2023.06.005

11 Keasar T, Sheffer N, Glusman G, Libersat F. Host-handling behavior: an innate component of foraging behavior in the parasitoid wasp Ampulex compressa. Ethology. 2006;112(7):699–706. https://doi.org/10.1111/j.1439-0310.2006.01214.x

12 Weiss K, Parzefall C, Herzner G. Multifaceted defense against antagonistic microbes in developing offspring of the parasitoid wasp Ampulex compressa (Hymenoptera, Ampulicidae). PLoS One. 2014;9(6):e98784. https://doi.org/10.1371/journal.pone.0098784

13 Herzner G, Schlecht A, Dollhofer V, Parzefall C, Harrar K, Kreuzer A, et al. Larvae of the parasitoid wasp Ampulex compressa sanitize their host, the American cockroach, with a blend of antimicrobials. Proc Natl Acad Sci U S A. 2013;110(4):1369–74. https://doi.org/10.1073/pnas.1213384110

14 Fabre J-H. More hunting wasps. Translated by Alexander Teixeire de Mattos: Dodd, Mead; 1921; p. 29.

15 Silverman J, Apple A. The pupal cocoon of the cat flea Ctenocephalides felis Bouché Siphonaptera pulicidae: a barrier to ant predation. Proc Entomol Soc Wash. 1984;86:660–3.

16 Lihoreau M, Costa JT, Rivault C. The social biology of domiciliary cockroaches: colony structure, kin recognition and collective decisions. Insectes Soc. 2012;59(4):445–52. https://doi.org/10.1007/s00040-012-0234-x

17 Burk T, Bell WJ. Cockroach aggregation pheromone: inhibition of locomotion (Orthoptera: blattidae). J Kans Entomol Soc. 1973:36–41.

18 Rust MK, Burk T, Bell WJ. Pheromone-stimulated locomotory and orientation responses in the American cockroach. Anim Behav. 1976;24(1):52–67. https://doi.org/10.1016/s0003-3472(76)80099-1

19 Weihmann T, Reinhardt L, Weißing K, Siebert T, Wipfler B. Fast and powerful: biomechanics and bite forces of the mandibles in the American cockroach Periplaneta americana. PLoS One. 2015;10(11):e0141226. https://doi.org/10.1371/journal.pone.0141226

20 Nigam LN. The life-history of the common cockroach (Periplaneta Americana Linneus). Indian J Agric Sci. 1933;3(Pt. 3).

21 Lederer G. Ein Beitrag zur Ökologie der amerikanischen Schabe Periplaneta americana (Linné 1758). Anzeiger für Schädlingskunde. 1952;25(7):102–4. https://doi.org/10.1007/bf02276514

22 Roth LM. Introduction. In: Bell WJ, Adiyodi KG, editors. The american cockroach. Springer Science & Business Media; 1981. Vol. 1982. p. 1–14.

23 Guthrie DM, Tindall AR. The biology of the cockroach. London: Edward Arnold Publishers LTD; 1968.
24 Evans HE. The behavior patterns of solitary wasps. Annu Rev Entomol. 1966;11(1):123–54. https://doi.org/10.1146/annurev.en.11.010166.001011
25 Gal R, Libersat F. On predatory wasps and zombie cockroaches: investigations of free will and spontaneous behavior in insects. Commun Integr Biol. 2010;3(5):458–61. https://doi.org/10.4161/cib.3.5.12472
26 Libersat F, Gal R. What can parasitoid wasps teach us about decision-making in insects? J Exp Biol. 2013;216(Pt 1):47–55. https://doi.org/10.1242/jeb.073999
27 Libersat F, Gal R. Wasp voodoo rituals, venom-cocktails, and the zombification of cockroach hosts. Am Zool. 2014;54(2):129–42. https://doi.org/10.1093/icb/icu006
28 Park JS, Saleh NS, Lin H, Alqrinawi H, Lord NP. Investigating physical and mechanical properties of nest soils used by mud dauber wasps from a geotechnical engineering perspective. Sci Rep. 2022;12(1):2192. https://doi.org/10.1038/s41598-022-06162-2
29 Sarzetti LC, Genise JF, Dinghi P, Molina MA. An overview of hymenopteran cocoons as a tool to interpret ichnospecies of Fictovichnus (Pallichnidae) and other fossil cocoons of wasps. Palaios. 2019;34(11):562–74. https://doi.org/10.2110/palo.2019.053
30 Buys SC. Morphological studies on the last instar larva of Ampulex compressa (Fabricius) from Brazil. Spixiana. 2007;30/1:33–7.
31 Clausen CP. Respiratory adaptations in the immature stages of parasitic insects. Arthropoda. 1950;1(2–4):197–224.
32 Harvey JA. Factors affecting the evolution of development strategies in parasitoid wasps: the importance of functional constraints and incorporating complexity. Entomol Exp Appl. 2005;117(1):1–13. https://doi.org/10.1111/j.1570-7458.2005.00348.x