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Parasitoid wasp affects metabolism of cockroach host to favor food preservation for its offspring

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Abstract Unlike predators, which immediately consume their prey, parasitoid wasps incapacitate their prey to provide a food supply for their offspring. We have examined the effects of the venom of the parasitoid wasp *Ampulex compressa* on the metabolism of its cockroach prey. This wasp stings into the brain of the cockroach causing hypokinesia. We first established that larval development, from egg laying to pupation, lasts about 8 days. During this period, the metabolism of the stung cockroach slows down, as measured by a decrease in oxygen consumption. Similar decreases in oxygen consumption occurred after pharmacologically induced paralysis or after removing descending input from the head ganglia by severing the neck connectives. However, neither of these two groups of cockroaches survived more than six days, while 90% of stung cockroaches survived at least this long. In addition, cockroaches with severed neck connectives lost significantly more body mass, mainly due to dehydration. Hence, the sting of *A. compressa* not only renders the cockroach prey helplessly submissive, but also changes its metabolism to sustain more nutrients for the developing larva. This metabolic manipulation is subtler than the complete removal of descending input from the head ganglia, since it leaves some physiological processes, such as water retention, intact.

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Abbreviations SEG: Subesophageal ganglion · TTX: Tetrodotoxin

Introduction

Most predators kill their prey and consume them immediately, and most venomous predators are no exception to this rule. In contrast, parasitic animals do not necessarily kill their host/prey. They often alter the behavior of their hosts in many ways, including phototaxis, locomotion, behavioral fevers, foraging behavior, reproduction and a variety of social interactions, to name a few (see Moore 2002, for review). Although the alteration of host behavior by parasites is a widespread phenomenon, underlying mechanisms are only beginning to be deciphered (Moore 2002; Beckage 2002). The most fascinating examples of behavioral manipulation are seen in arthropods parasitized by various species of parasitoid wasps. For instance, the aculeate wasp *Ampulex compressa* (Sphecidae) uses an unusual strategy to incapacitate its prey, the cockroach *Periplaneta americana*, which serves as a food supply for its larvae (Williams 1942). Unlike most other venomous hunters, the wasp stings and injects its venom directly into specific head and thoracic ganglia of its prey (Haspel et al. 2003). This venom injection induces a transient paralysis of the front legs (Haspel and Libersat 2003) followed by grooming behavior and then by a long-term hypokinesia of its cockroach prey (Weisel-Eichler et al. 1999; Weisel-Eichler and Libersat 2002; Libersat 2003). In this state, the cockroach remains alive but immobile and unresponsive, and serves to nourish the wasp larva (Williams 1942). The long lasting lethargic state occurs when the venom is injected into the head but not when it is injected only into the thorax (Piek et al. 1989; Fouad et al. 1994). Under laboratory conditions, and if not parasit-

ized by the wasp larva, cockroaches gradually recover from this lethargic state within about 3 weeks (Fouad et al. 1996; Weisel-Eichler and Libersat 2002). In nature, cockroaches probably rarely reach recovery as the *A. compressa* larva consumes them before the end of this convalescent time.

Besides behavior, parasitoids may also affect the metabolism of the prey in ways that are beneficial to their offspring (Moore 2002; Beckage 2002; Rivers et al. 1999). Parasitoid animals, and in particular wasps, incapacitate their prey to provide a food supply for their offspring (Quicke 1997; O'Neill 2001; Libersat 2003). It has been found that for several different species of wasps, successful development depends on the wasp's ability to regulate the host's physiology following oviposition (for review, see: Vinson and Iwantsch 1980; Quicke 1997; Rivers et al. 1999; Gnatzy 2001; Beckage and Gelman 2004). In many cases, the behavioral changes induced in the host by the parasitic wasp are geared to the nutritional needs of the developing larva (Rivers et al. 1998). The larva of aculeate wasps hatches soon after oviposition, and start feeding on the host. This feeding may last for a few days before the host dies and the larva pupates. To this end, these wasps have evolved venom cocktails tailored to the wasp hunting and larva feeding strategies. Furthermore, for wasps laying one egg per host, the larva may need to consume the entire host in order to complete development successfully (Vinson and Iwantsch 1980). While some hosts of parasitoid wasps continue to move and feed after being parasitized, the cockroach hosts of *A. compressa* are led to and buried alive in a small burrow and do not eat or drink. In order to maximize the nutritional quality of the food supply for its offspring, it might be beneficial for the wasp to affect the prey's metabolic rate and morbidity.

There were three aims for the present study: (1) To determine the developmental time table of the wasp from egg to pupation, (2) to assess the effect of the sting of *A. compressa* on the life expectancy of its specific host, *P. americana*, (3) to evaluate possible changes in the metabolic rate of stung cockroaches.

Methods

Animals

The wasps, *A. compressa* (*Hymenoptera*: *Sphecidae*), were raised at 30°C on a 12L:12D cycle in Perspex cages and provided with abundant water and honey. Adult cockroaches (*P. americana*) were raised at 26°C on a 12L:12D cycle in plastic cages and provided with abundant water and cat food pellets.

There were five experimental groups of cockroaches-control, stung, neck-connectives-cut, sham-operated and injected with TTX (the minimal paralyzing dose, 10 µl of 10^{-4} M TTX/cockroach; tetrodotoxin, Sigma).

Nervous system lesions

To disconnect both brain and subesophageal ganglion (SEG) of the cockroach from the thoracic ganglia, a longitudinal incision was made in the ventral cuticle of the neck and the neck connectives were cut with fine scissors. Sham operations were conducted in a similar manner without cutting nerves. The wound sealed by hemolymph coagulation immediately after the operation. All animals were allowed to recover for one day before testing.

Larva life cycle

The development of *A. compressa* larvae was followed visually from egg to pupa on parasitized cockroaches. Morphological or positional changes were recorded daily and imaged with a digital camera (Camedia C-5050, Olympus). The parasitized cockroaches were kept at 26°C in an incubator.

Body mass loss and mortality rate

In an attempt to determine whether the lower metabolic rate in stung cockroaches was correlated with changes in body mass, we followed changes in the body mass of the cockroaches. Cockroaches from each of the five experimental groups were weighed, confined in 20-ml-glass vials (similar in size to the burrows used by *A. compressa*) and kept at 26°C for 10 days without food or water. The cockroaches were weighed daily, and mass loss was calculated as a fraction of the cockroach's initial mass. The number of dead cockroaches in each group was recorded daily.

Additional samples of control, stung, cut-neck-connectives and sham-operated animals were used in order to determine whether possible changes in body mass resulted from changes in body dry mass or water content. TTX-injected animals were not used because they did not survive more than 2 days following injection. In this experiment, animals were weighed at 0, 3 and 6 days and then desiccated in an incubator for 24 h at 47°C (Heraeus B15l, Kendro laboratory products) and weighed again. The water fraction was calculated by subtracting the dry mass from the total mass and dividing by the total mass ((TM-DM)/TM).

Oxygen consumption rate

Cockroaches from all five experimental groups were individually weighed (±0.1 mg) and then each cockroach was placed in a 100-ml-plastic syringe that was previously flushed with dry air. We withdrew the syringe plunger to the 100 ml mark and sealed the needle hub holder. Preweighed silica gel (3–8 g) in cloth bags was used to keep the syringe atmosphere dry. The syringes

were then kept in a temperature-controlled cabinet, at 26°C in light (during the cockroach's light cycle), for 2–3.5 h. The TTX group was kept in the syringes for about 5 h in order to achieve a sufficient decrease in oxygen concentration, as their O_2 consumption rate ($\dot{M}O_2$) was expected to be lower. Following this period, 60 ml of the syringe gas was injected at a rate of 20 ml min^{-1} into a precalibrated Servomex (OA 272) O_2 analyzer through ascarite and drierite columns in series, made of 1-ml-plastic syringes, in order to absorb any CO_2 and water vapor, and the oxygen concentration was determined ($\pm 0.01\%$). Dry-air filled syringes were used for reference values throughout the measurements. The mass-specific O_2 consumption rate ($sp\dot{M}O_2$) was calculated from the difference in O_2 concentration between experimental and dry-air syringes, and the initial syringe gas volumes (V_I). The initial syringe gas volume was calculated assuming a density of 1.0 g ml^{-1} for the cockroaches, and 1.6 g ml^{-1} for the silica gel. Mass-specific O_2 consumption rates were calculated using the following equation:

$$sp\dot{M}O_2 = \frac{V_I \cdot (F_IO_2 - F_FO_2)}{(1 - F_FO_2) \cdot T \cdot W}$$

where sp $\dot{M}O_2$ is in $\mu l_{[STPD]}\ g^{-1}\ h^{-1}$; V_I is in $ml_{[STPD]}$; F_IO_2 is the oxygen fraction in dry air (0.2095); F_FO_2 is the final oxygen fraction in the syringe; T = time (hours) and W = body mass (g).

Statistics

Statistical tests and analysis were carried out using STATISTICA for Windows 5.0 and SigmaStat 2.03. Comparisons of $sp\dot{M}O_2$ between groups were carried out using ANCOVA and Tukey HSD test for post-hoc comparisons of adjusted means. Comparisons of body mass loss and water fraction, expressed as % of initial values were carried out using ANOVA of arcsine-transformed percentages. Fisher exact test was used to compare mean mortality rates of the five experimental groups as a function of time. Results are given as mean ± SD.

Results

Larva life cycle

The development of *A. compressa* from egg to pupa in our experimental conditions lasted between seven to nine days. The wasp lays an egg and affixes it on the cuticle of the coxal segment of the middle cockroach leg (Fig. 1a, b). A larva hatched from the egg within two days (2.3 ± 0.5, $n = 14$) (Fig. 1c) and perforated the cuticle of the cockroach coxa to feed from the hemolymph for the next few days (Fig. 1d, e). About five days (5.5 ± 0.5, $n = 14$) after the egg was laid (Fig 1f), the larva moved to the thoraco-coxal junction of the metathoracic leg and bit a large hole along the soft cuticular joint until it penetrated the cockroach. Most of the feeding was done within two days, since it can be observed through the transparent ventral abdominal cuticle that the wasp larva occupied the entire abdominal cavity two days after entering the host. Pupation occurred roughly eight days (8.1 ± 0.4, $n = 14$) after oviposition (Fig. 1g, h).

Body mass loss and mortality rate

Since the wasp larva feeds on the cockroach from day two until day eight after oviposition, we wished to determine whether the wasp sting affects the host metabolism within the time frame of the wasp's larva feeding for development. Because the wasp stings the cockroach into the head ganglia, we wished to evaluate the role of these ganglia in controlling the survival rate

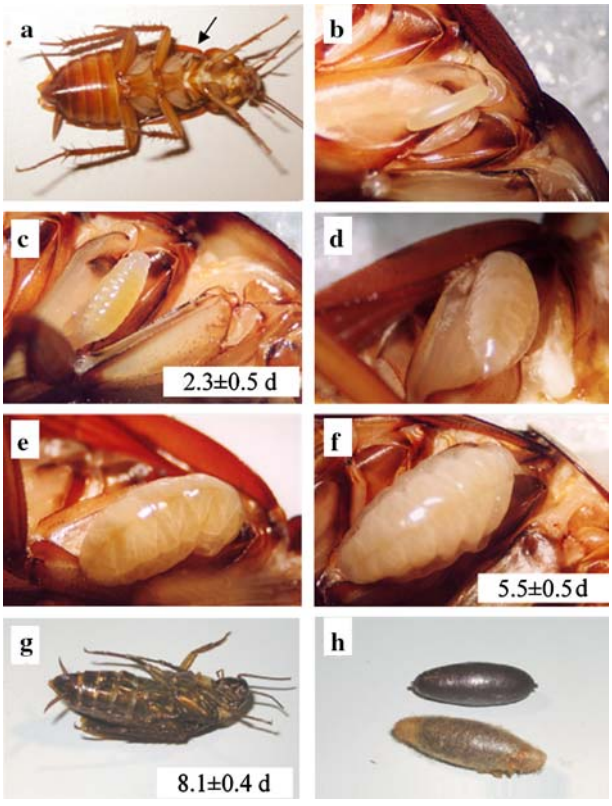

Fig. 1 Development of *Ampulex compressa* larva. **a** A single egg (*arrow*) is laid by *A. compressa* on each stung cockroach. **b** The egg is glued to the middle coxa of a cockroach (higher magnification of **a**). This exact spot is unreachable by the cockroach. **c** A larva, as big as the egg, hatches within about 2 days. **d**, **e** The larva bites a hole in the cockroach coxa and feeds on hemolymph. **f** About 5 days after the egg was laid, the larva is ready to penetrate the cockroach. **g** The larva consumes the organs of the cockroach and pupates inside the cockroach, which dies at this stage. The pupa fills most of the cockroach's abdomen. **h** The cocoon is a hard, brown, spindle-like case (*top*) covered with a silk-like weave (*bottom*)

and metabolism of the cockroach host. To abolish all neuronal control arising from the head ganglia, we severed the neck connectives. Complete paralysis is a strategy used by numerous venomous predators of insects that consume their prey immediately. Given this fact, to compare the effect of the sting to the effect of complete paralysis on survival rate and metabolism, we injected cockroaches with the neurotoxin TTX, which blocks voltage sensitive sodium channels (Rappuoli and Montecucco 1997). As a result, we induced a general paralysis similar to that induced by, for example, a scorpion sting (Pelhate et al. 1998; Possani et al. 1999). Such a complete paralysis is due to a cessation of both central and peripheral electrical activity. We used the minimal dose needed to achieve total paralysis (10 µl of 10^{-4} M per cockroach). When kept in conditions similar to the wasp's burrow, without food or water, TTX-paralyzed cockroaches did not survive more than 2 days ($n=10$), while 20% of the cut-connective group ($n=10$), 80% of the sham-operated ($n=10$), 89% of stung ($n=9$) and 90% of control ($n=10$) survived more than 6 days (Fig. 2). Nine days after the treatment, none of the cut-connective cockroaches survived while 30% of the sham-operated, 40% of the control and 67% of the stung cockroaches did (with no significant difference between these groups). Cockroaches paralyzed by TTX were incapable of maintaining posture and seemed to have no hemolymph circulation, probably due to paralysis of the heart muscles. By contrast, stung cockroaches sustained their normal upright posture and their hearts kept beating.

Under the same conditions, the rate of body mass loss over time differed among the groups (Fig. 3). Cockroaches of both operated groups, connective-cut and sham-operated, lost significantly more body mass in comparison with the other groups during the initial 24 h post operation ($P<0.05$). Specimens of these two groups ($n=10$ each) lost $9\pm2\%$ and $7\pm1\%$ of initial body mass, respectively. Cockroaches paralyzed with TTX lost $9\pm1\%$ ($n=10$) of their body mass in 2 days, after which they all died. However, the body mass loss of TTX-injected specimens was not significantly different from that of control and stung cockroaches at 2 days. Stung, control and sham-operated cockroaches lost comparable fractions of their body mass in 10 days (stung: $20\pm4\%$, $n=9$; control $17\pm3\%$, $n=10$; sham-operated: $24\pm4\%$, $n=10$). Only the cockroaches with cut neck connectives lost significantly ($P<0.001$) more body mass until they all died after 6 days ($32\pm1\%$, $n=10$).

To evaluate the amount of water loss in the different groups of cockroaches over a period of 6 days, cockroaches were desiccated and the water fraction was calculated by subtracting the dry mass from the total mass and dividing by the total mass (see Methods). The body water fraction of cockroaches decreased with time to a different extent in all experimental groups (Fig. 4). However, all groups except the stung group showed a significant decrease in water after 6 days. TTX-paralyzed cockroaches died within 2 days of TTX injection, preventing comparison of water loss rates with other groups. Cockroaches with cut neck connectives showed the highest degree of water loss.

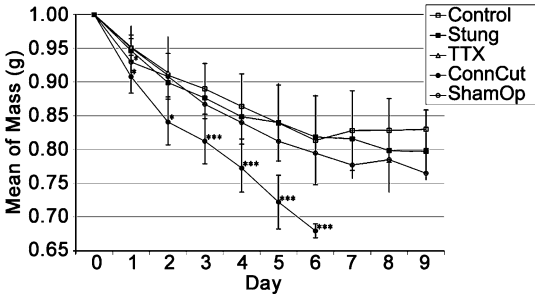

Fig. 3 Loss of body mass. Changes in the relative body mass of confined cockroaches from the five experimental groups, measured for 10 days following treatment. Cockroaches with cut neck connectives lost significantly more body mass than cockroaches of all other groups (*$P<0.05$, ***$P<0.001$)

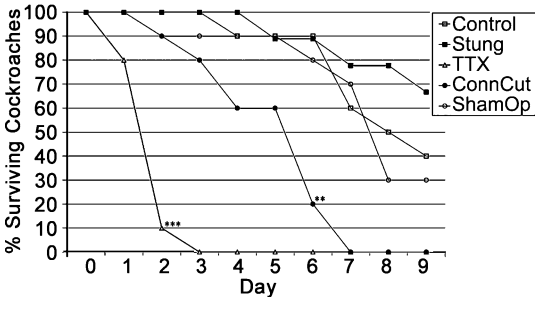

Fig. 2 Life expectancy of stung and treated cockroaches. Significantly fewer TTX-paralyzed ($n=10$) cockroaches survived the second day following treatment than stung ($n=9$), control ($n=10$) or sham-operated animals ($n=10$) (***$P<0.001$, Fisher Exact Test). Significantly fewer cockroaches with cut neck connectives ($n=10$) survived the sixth day than stung, control or sham-operated cockroaches (**$P<0.005$)

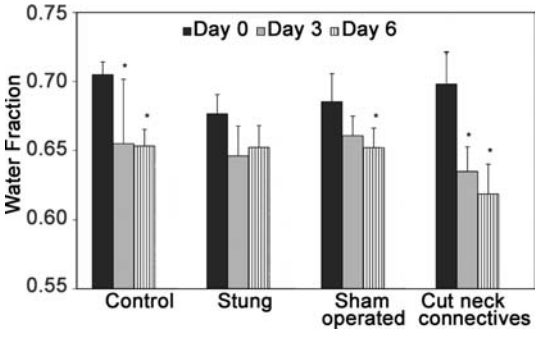

Fig. 4 Loss of body water. Change over time in the body water fraction in confined cockroaches from the five experimental groups. Connective-cut cockroaches lose water faster than any other group. All other groups except for the stung group lost a significant amount of water at 6 days. Data presented as mean ± SD ($n=6$ for each group). *$P<0.05$, significant difference from initial values

Metabolic rate of the cockroach prey

We measured the mass-specific oxygen consumption rate ($sp\dot{M}O_2$), which reflects the overall energy metabolic rate per unit of body mass. This oxygen consumption rate was affected in stung, connective-cut, and TTX paralyzed cockroaches (Fig. 5). Stung cockroaches consumed significantly less ($P < 0.005$) oxygen than controls (stung: 371.5 ± 67.5 µl g^{-1} h^{-1}, $n = 9$; control: 530.0 ± 74.0 µl g^{-1} h^{-1}, $n = 9$). Cockroaches with neck connectives cut consumed oxygen at a rate very similar to stung cockroaches and significantly less ($P < 0.005$) than sham-operated cockroaches (cut-neck-connectives: 378.0 ± 97.0 µl g^{-1} h^{-1}, $n = 9$; sham-operated: 512.0 ± 34.5 µl g^{-1} h^{-1}, $n = 9$). There was no significant difference between the control and sham operated groups. The $sp\dot{M}O_2$ of cockroaches paralyzed by an injection of TTX (292.7 ± 97.4 µl g^{-1} h^{-1}) was also significantly lower than controls ($P < 0.0001$, $n = 9$) and not significantly different from that of stung cockroaches.

Discussion

In the present study, we show that, in addition to behavioral manipulation, the wasp *A. compressa* manipulates the physiological state of the cockroach in ways that are most likely beneficial to the development of its feeding larvae.

Prey metabolism and the developing larva

Unlike many other venomous predators that consume prey immediately, the developmental timetable of *A. compressa* offspring requires that the host be preserved for about eight days after envenomization (Fig. 1). *A. compressa* uses a strategy of behavioral modulation, including venom-induced lethargy, which differs from that of other venomous predators that induce muscular paralysis in their prey. There might be adaptive significance to the induction of this unique lethargy, as opposed to paralysis or death as the host organs are maintained as fresh nutrients for the developing larva. Cockroaches paralyzed with TTX did not survive more than three days, while 90% of stung cockroaches survived more than 6 days (Fig. 2). Moreover, by day nine, only 40% of the control cockroaches but nearly 70% of the stung cockroaches survived, increasing almost twofold the larva's chances of successful development. A similar manipulation by a parasitoid wasp has been demonstrated for the tobacco hornworm (*Manduca sexta*) that carries the eggs and pupae of the braconid wasp *Cotesia congregata* (Adamo et al. 1997; Beckage and Gelman 2004). The caterpillar stops feeding and becomes lethargic towards the end of wasp development so it does not hurt the emerging wasps but does not die and decay.

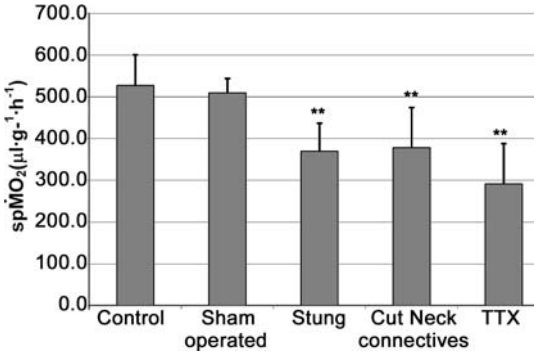

Fig. 5 Oxygen consumption rates. The mass specific oxygen consumption rates ($sp\dot{M}O_2$, µl g^{-1} h^{-1}) were significantly lower in TTX-paralyzed, stung, and neck-connectives-cut cockroaches in comparison with control and sham-operated cockroaches (**$P < 0.01$). Data presented as mean ± SD ($n = 9$ for each group)

Cockroach metabolism is decreased by the sting

Stung cockroaches were found to consume 30% less oxygen than control or sham-operated cockroaches. Any observed differences in mass specific oxygen consumption rate are unlikely to have resulted from a decrease in activity during the lethargic state because cockroaches from all groups showed little activity, even immediately following handling. The differences between groups in mass specific oxygen consumption were not correlated with the rates of body mass loss-stung cockroaches did not lose body mass slower than controls, while cut-connective cockroaches lost body mass at a significantly higher rate than sham operated cockroaches (Fig. 3). The lost body mass was probably composed of catabolized fat tissue and water lost to dehydration. It is possible to estimate the consumption of fat tissue, assuming lipid catabolism and given that 0.5 g of lipid is consumed per 1 ml O_2. This calculation gives 3.8 mg/day of lipids catabolized for control cockroaches, 2.7 mg/day of lipids for stung, and 2.1 mg/day of lipids for TTX-paralyzed cockroaches. However, since cockroaches weigh approximately 600 mg, and they lost approximately 12 mg/day of body mass, the catabolization of lipids can account for, at most, about 30% of the lost body mass and about 8% of the difference between the groups. Furthermore, for every mg of catabolized lipids 1.07 mg metabolic water is produced. Hence, most of the lost body mass was probably not due to lipid catabolism. Cut-connective, sham-operated, and control cockroaches lost water faster than stung within 6 days following treatment (Fig. 4). This implies that *Ampulex's* venom, which affects head ganglia centers controlling metabolic rate, also affects centers controlling water balance. In addition, we have shown previously that the heart rate of resting stung cockroaches is higher than the heart rate of resting control animals (Libersat et al. 1999). Similarly, crickets paralyzed by the parasitoid wasp *Liris niger* were also found to have lower metabolic and mortality rates

(Roces and Gnatzy 1997). These stung crickets produced less CO_2 than the control groups (fed, starved and starved-dehydrated) and also breathed more slowly and regularly. In that study, the stung crickets lost as much body mass as the starved and dehydrated group (the only group that was confined in small vials and deprived of both food and water like the stung crickets) and lost more body mass than the control and starved groups.

In summary, stung cockroaches survive longer, lose less water and consume less oxygen. The metabolic changes induced by the sting into the head ganglia are subtler than those induced either by removal of descending modulation from head ganglia or by non-specific muscular paralysis. The head ganglia of insects contain various neuromodulatory neurons some of which have been directly or indirectly implicated in the control of heartbeat and water balance (Davis and Hildebrand 1992; Veenstra and Davis 1993; Nichols et al. 1999; Zornik et al. 1999; Nassel 2002). We hypothesize that the sting manipulates these neuromodulatory systems in the head ganglia to modify the host's metabolism and increase the survival of the host, which remains fresh while the larva feeds on until it is ready to pupate. Hence, with a single but precise sting into the brain, the wasp not only converts the cockroach into a submissive prey but also alters its metabolism, apparently to the larva's benefit. The results of the present study lay the foundation for more experiments aimed at identifying the neuromodulatory systems manipulated by the wasp to control host's metabolism. Thus, the wasp and cockroach relationship is a fruitful model for examining not only the neuronal basis of parasite-induced alterations of host behavior but also of the alterations in its physiology.

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