produced by histrionicotoxin (*1*), and suggest that amantadine's action is voltage-dependent.

This conclusion receives additional support from observations that amantadine alters the relation between the EPC half-decay time and membrane potential. The half-decay time of the control EPC varied exponentially and became shorter as the membrane potential was driven from −150 to +60 mV (Fig. 1). In the presence of amantadine ($2 \times 10^{-4} M$) the slope of the relation between half-decay time and membrane potential underwent a very striking reversal such that the EPC's now became faster with hyperpolarization. Although small shifts in the slope for half-decay time versus membrane potential have been reported before (*13*) they have never been as complete as with amantadine. Thus, during exposure to amantadine the slope of the logarithm of the half-decay time was $+1.344\ V^{-1}$ and under control condition was $-3.05\ V^{-1}$. Consequently, amantadine appears to be a useful pharmacological probe for examining the coupling of the end-plate channel kinetics with the membrane electrical field.

These findings raise several questions relating to the other effects of amantadine. How does amantadine block virus entry into host cells? Is amantadine selective for the peripheral nicotinic cholinergic ICM or does it also affect central cholinergic ICM or possibly ICM's associated with other receptors? Does the beneficial effect of amantadine in Parkinsonism depend on the capacity of this drug to inhibit ionic conductance in certain neuronal circuits involved in the central control of muscular movement? Answers to these and similar questions will undoubtedly improve our understanding of basic biological mechanisms and the mode of action of the drug.

EDSON X. ALBUQUERQUE
AMIRA T. ELDEFRAWI
MOHYEE E. ELDEFRAWI
NABIL A. MANSOUR
MING-CHENG TSAI

*Department of Pharmacology and Experimental Therapeutics, University of Maryland School of Medicine, Baltimore 21201*

### References and Notes

1. E. X. Albuquerque, E. A. Barnard, T. H. Chin, A. J. Lapa, J. O. Dolly, S. E. Jansson, J. Daly, B. Witkop, *Proc. Natl. Acad. Sci. U.S.A.* **70**, 949 (1973); A. J. Lapa, E. X. Albuquerque, J. Daly, B. Witkop, *Pharmacologist* **15**, 171 (1973); A. T. Eldefrawi, M. E. Eldefrawi, E. X. Albuquerque, A. C. Oliveira, N. A. Mansour, M. Adler, J. Daly, G. B. Brown, W. Burgermeister, B. Witkop, *Proc. Natl. Acad. Sci. U.S.A.* **74**, 2172 (1977).
2. G. Kato and J.-P. Changeux, *Mol. Pharmacol.* **12**, 92 (1976); J. O. Dolly, E. X. Albuquerque, J. M. Sarvey, B. Mallick, E. A. Barnard, *ibid.* **13**, 1 (1977); A. J. Lapa, E. X. Albuquerque, J. M. Sarvey, J. Daly, B. Witkop, *Exp. Neurol.* **47**, 558 (1975).
3. M. Adler and E. X. Albuquerque, *J. Pharmacol. Exp. Ther.* **196**, 360 (1976).
4. W. L. Davies, R. R. Grunert, R. F. Haff, J. W. McGahen, E. M. Neumayer, M. Paulshock, J. C. Watts, T. R. Wood, E. C. Hermann, C. E. Hoffmann, *Science* **144**, 862 (1964); V. G. Vernier, J. B. Harman, J. M. Stump, T. E. Lynes, J. P. Marvel, D. H. Smith, *Toxicol. Appl. Pharmacol.* **15**, 642 (1969).
5. C. E. Hoffmann, E. M. Neumayer, R. F. Haff, R. A. Goldsby, *J. Bacteriol.* **90**, 623 (1965).
6. R. S. Schwab, A. C. England, Jr., D. C. Poskanzer, R. R. Young, *J. Am. Med. Assoc.* **208**, 1168 (1969); J. D. Parkes, D. M. Calver, K. T. Zilkha, R. P. Knill-Jones, *Lancet* **1970-I**, 259 (1970); R. P. Grelak, R. Clark, J. M. Stump, V. G. Vernier, *Science* **169**, 203 (1970).
7. W. L. Nastuk, P. C. Su, P. Doubilet, *Nature (London)* **264**, 76 (1976).
8. M. E. Eldefrawi and A. T. Eldefrawi, in *Receptors and Recognition*, P. Cuatrecasas and M. F. Greaves, Eds. (Chapman & Hall, London, 1977), p. 197.
9. E. X. Albuquerque and R. J. McIsaac, *Exp. Neurol.* **26**, 183 (1970).
10. The technique used for voltage clamp was similar to that described by A. Takeuchi and N. Takeuchi [*J. Neurophysiol.* **22**, 3951 (1959)], and modified by E. X. Albuquerque and K. Kuba (unpublished data). Essentially one of the vertical amplifiers of the Tektronix 502A oscilloscope (gain = ×4000 to ×10,000) was used as a feedback amplifier. The second vertical amplifier of the same oscilloscope served as an operational amplifier to convert the membrane current to voltage. The resistance of the recording and current microelectrodes ranged from 3 to 7 megohms. The end-plate regions of surface fibers were inserted with two microelectrodes, one to record and the other to inject current. For further details see K. Kuba, E. X. Albuquerque, J. Daly, E. A. Barnard, *J. Pharmacol. Exp. Ther.* **189**, 499 (1974).
11. R. S. Eisenberg and P. W. Gage, *Science* **158**, 1700 (1967).
12. T. Deguchi and T. Narahashi, *J. Pharmacol. Exp. Ther.* **176**, 423 (1971); R. L. Ruff, *J. Physiol. (London)* **264**, 89 (1977); K. G. Beam, *ibid.* **258**, 279 (1976).
13. V. E. Dionne and C. F. Stevens, *J. Physiol. (London)* **251**, 270 (1976); M. Kordas, *ibid.* **204**, 493 (1969); K. L. Magleby and C. F. Stevens, *ibid.* **223**, 151 (1972).
14. We thank B. Witkop and J. Daly of the National Institutes of Health for providing us with $[^3H]H_{12}$-HTX and $H_8$-HTX, and V. G. Vernier and G. Shotzberger of E. I. Du Pont de Nemours for donating amantadine. We are indebted to W. Beachey and S. Shumaker for photographic work and to M. Kappelman for making available the illustrative facilities of his department. This work was supported in part by PHS grant NS-12063, by a grant from the Muscular Dystrophy Association of America (E.X.A.), and by NSF grant BNS76-21683 (M.E.E.).

23 August 1977; revised 8 November 1977

## "Wolf-in-Sheep's-Clothing" Strategy of a Predaceous Insect Larva

Abstract. *The larva of the green lacewing* Chrysopa slossonae *lives in colonies of the wooly alder aphid* Prociphilus tesselatus *upon which it feeds. It disguises itself as its prey by plucking some of the waxy "wool" from the bodies of the aphids and applying this material to its own back. The investiture protects it from assault by the ants that ordinarily "shepherd" the aphids. Larvae artifically denuded are seized by the ants and removed from the aphid colonies. A larva requires on the average less than 20 minutes to coat itself with wax. A hungry denuded larva gives the coating procedure about the same behavioral priority as feeding.*

Aphids, except when dispersing by flight, are relatively immobile and need little carbohydrate. But they are extraordinarily prolific and hence require nitrogenous materials in disproportionately large amounts. They feed by pumping large quantities of plant juices through their bodies, thereby meeting the nitrogenous demands but also inevitably imbibing excess carbohydrate. They void this excess as part of their excreta, a sweet fluid appropriately called honeydew. As is well known, aphids do not necessarily waste this honeydew, but may present it as an offering to ants, which drink the fluid and in exchange shepherd the aphids and provide them with protection. Predators intent on feeding on aphids must contend with such ants, which are provenly aggressive when guarding their aphid flock (*1*). We now describe the extraordinary behavior of a predaceous insect larva that feeds on aphids and copes with ants by masquerading as an aphid.

The larva, a member of the aphidophagous family Chrysopidae (order Neuroptera), lives in colonies of the wooly alder aphid *Prociphilus tesselatus*. Previously undescribed as a larva (*2*), it was identified as *Chrysopa slossonae* after being raised to adulthood. Its association with *P. tesselatus* appears to be obligatory; we found it with no other aphids. At the various sites in Tompkins and Albany counties, New York, where we made our observations, it is relatively plentiful. From August to October, hardly a colony of *P. tesselatus* can be found that does not harbor at least several of these chrysopid larvae.

*Prociphilus tesselatus* derives its wooly appearance from the fluffy investiture of brilliantly white wax that covers its body (Fig. 1B). This material, recently identified as a long-chain ketoester (*3*), is secreted in the form of dense tufts of thin filaments from patches of integumental glandular cells. It renders the aphids extremely conspicuous against the dark branches of the alder bushes (*Alnus rugosa*) on which they typically occur (Fig. 1A). Three species of ants, all of the subfamily Formicinae, were


0036-8075/78/0217-0790$00.50/0 

commonly seen to guard the aphids: *Camponotus pennsylvanicus*, *C. noveboracensis*, and *Formica* sp. (*fusca* group). Moving about over the surface of the aphids and contrasting sharply against the white "wool" of the "flock," such ants were always instantly detectable. Large colonies of hundreds of aphids were guarded by dozens of ants, while smaller colonies were guarded by few ants only. The ants associated with any one aphid colony were always of a single species and could usually be traced by their trails to a nest on the ground nearby.

Ants that guarded aphids responded characteristically by fighting back when disturbed. When either they or the aphids beside them were prodded by hand or with an inert probe, they promptly turned upon the offending agent and attempted to bite it. If they secured a hold, they maintained it tenaciously (Fig. 1D). Ants not directly on guard, which were merely trailing along alder branches on their way to and from an aphid colony, usually offered no such opposition but simply fled or dropped to the ground. Ants on guard were repeatedly observed to consume honeydew, which they drank as it emerged as droplets from the anus of the aphids (Fig. 1E). In the manner typical for such ants (*1*), they usually obtained the fluid by "solicitation," inducing its delivery from individual aphids by stroking them with their antennae.

In their basic habits, the *C. slossonae* larvae proved to be in no way unusual. They fed on aphids as chrysopid larvae

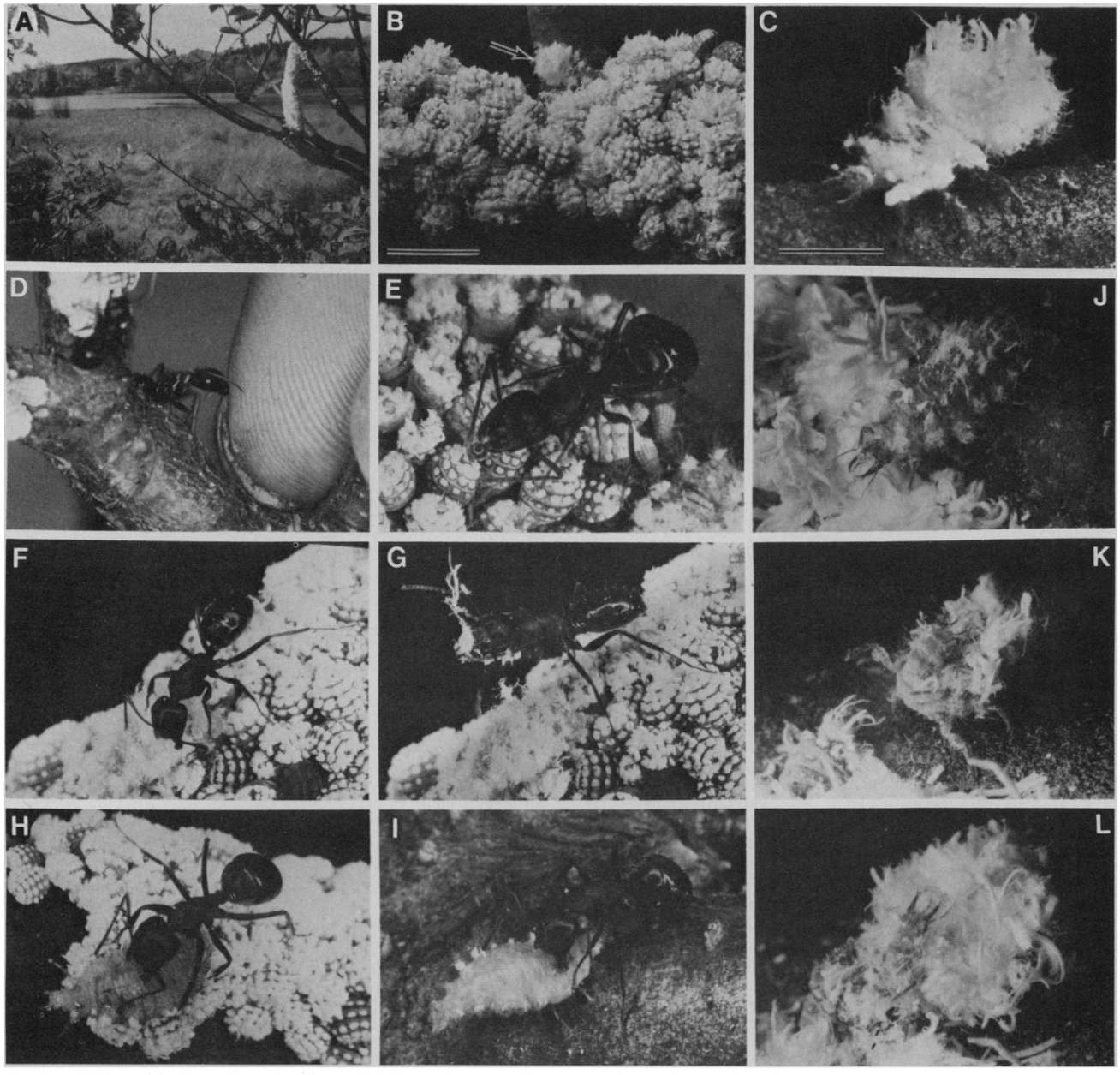


Fig. 1. (A) Typical habitat of wooly alder aphid (*Prociphilus tesselatus*). A colony of the aphid, distinguishable by its white color, is seen on branch of alder bush in foreground. (B) Closeup of portion of an aphid colony with a larva of *Chrysopa slossonae* (arrow) (bar, 1 cm). (C) Larva of *Chrysopa* in its normal, wax-covered (shielded) condition. The larva was set up by itself for photographic purposes (bar = 3 mm). (D) Ant protecting aphids by biting an "attacking" finger. (E) Ant imbibing a droplet of honeydew delivered by an aphid. (F) Ant biting a shielded *Chrysopa* larva that was released in its vicinity. (G) Same ant, shown as it releases its hold, with its mouthparts conspicuously contaminated with wax. (H) Ant biting a denuded larva that it has just detected. (I) Ant in process of transporting a denuded larva away from the aphid colony that it was guarding. (J) Denuded larva, shown just before onset of reloading procedure. (K) Same larva applying plucked wax to its rump with the head. (L) Same larva, doing same, but at a later stage when its shield is nearly complete. All ants shown are *Formica noveboracensis*.

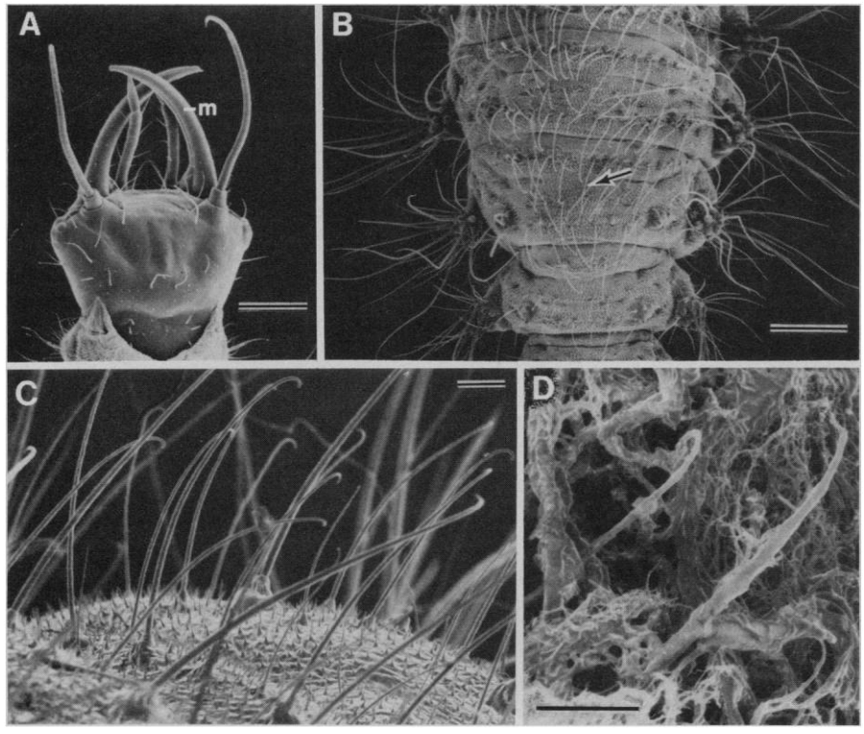


Fig. 2. Scanning electronmicrographs of *Chrysopa slossonae*. (A) Dorsal view of larval head, showing various cephalic appendages, including the sickle-shaped mandibles (*m*). (B) Portion of a denuded larval abdomen in dorsal view, showing the long bristles that jut out from the lateral tubercles, and the shorter bristles (arrow) that project upward from the back itself. (C) Enlarged lateral view of the bristles denoted by arrow in (B), showing their recurved tips. (D) Comparable to preceding, but of a shielded larva, showing two hairs projecting through the wax cover (reference bars: A, B, 300 $\mu$m; C, D, 50 $\mu$m).

generally do, by piercing them with their hollow sickle-shaped mandibles (Fig. 2A), sucking out their contents, and discarding the shriveled remains (*4, 5*). In laboratory tests, the larvae showed preference for the youngest aphids. Older larvae drained these in a few minutes (*6*) and usually took them in numbers and in quick succession if starved beforehand for several hours. What was found to be most remarkable about the larvae, and probably responsible for their having remained unknown for so long, was that they were so difficult to detect among the aphids. This is because they are also covered with wax and hence tend to blend in almost perfectly with the "wool" of the aphids (Fig. 1, B and C). They also match the aphids in overall shape, exceeding them in size only at maturity, and they typically maintain themselves tightly appressed against the aphids, moving about little even while not feeding. The mimicry is astonishing, and only after experience and at close range can the human eye come to discern them.

The larvae bear wax on the dorsal surface only. The material forms a thick fluffy shield, wide enough when viewed from above to conceal the larvae in their virtual entirety. Only the head and the tops of the legs tend to protrude from beneath the shield. Casual prodding showed the wax to be loosely borne by long bristles (setae) on the animal's back and sides and not to be attached to the integument itself. The wax could be readily teased away with forceps or wiped off with a brush. Laid bare, the larvae appeared uniformly gray and, relative to the aphids, distinctly uncamouflaged (Fig. 1J).

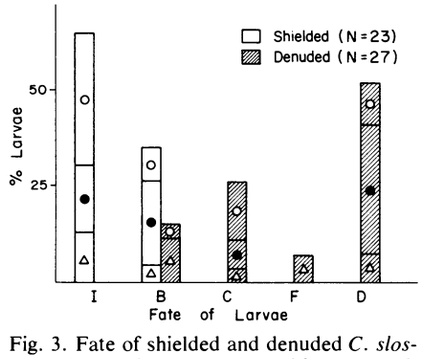


Fig. 3. Fate of shielded and denuded *C. slossonae* larvae that were released in ant-guarded aphid colonies. I, inspected and released by ants, without being bitten; B, bitten by ants and released; C, grasped by ants and carried to the ground; F, grasped by ants, which fell to the ground with the larvae; D, grasped by ants and dropped to the ground. Symbols within vertical bars denote species of ants that guarded the various aphid colonies tested: ○, *Camponotus noveboracensis*; ●, *C. pennsylvanicus*; △, *Formica* sp. (*fusca* group).

Left to themselves, denuded larvae did not produce new shields. This fact, plus the observation that under the microscope the waxy material from aphids and larvae had identical filamentous substructure, suggested that the larvae actually appropriated their covering from the aphids. This was confirmed by observing the behavior of freshly denuded larvae that were given access to aphid colonies in the laboratory. Within minutes or even immediately after being released among the aphids, the larvae commenced tearing away wax from the aphids and loading the material upon their backs. They did this with their mandibles. On contacting an aphid, a larva first shoved its head into the aphid's wool until it was deeply buried therein. With its mandibles serving as a two-pronged fork, it then plucked away some of the waxy tufts by jerking its head upward, and applied the plucking to its body hairs by flexing the head sharply over its back (Fig. 1, K and L). It then repeated the procedure, sometimes at an ongoing rate of one pluck every few seconds (*7*), shifting from aphid to aphid at intervals as it went along. It sometimes paused for varying periods, but even with interruptions it usually completed the rebuilding of its shield in less than 20 minutes (*8*). The aphids offered no resistance to being plucked and showed only an occasional twitching of their bodies.

In the application of pluckings to its back, the larva appeared to follow a preset plan. The first pluckings were always applied to the posterior third of the body. To gain access to the site, the larvae arched this region upward and forward every time the head reached backward to meet it. Later pluckings, delivered to the more accessible anterior regions of the back, were applied without simultaneous postural adjustments of the body. The bristles that receive the wax project upward in transverse rows from the dorsal surface of the animal and outward in clusters from a series of lateral tubercles (Fig. 2B). By virtue of their arrangement, and because the dorsal ones are for the most part terminally recurved (Fig. 2, C and D), they are ideally suited for the uptake and retention of the tufts of wax when these are pressed upon them by the larva's head.

Evidence was obtained that the waxy shield effectively protects the larvae against the ants that guard the aphids. Twenty-seven nearly mature larvae, freshly denuded by wiping the wax from their backs with a brush, were individ-

ually released among aphids of several colonies. Twenty-three shielded larvae were similarly released. The aphid colonies were selected to include tending ants of all three species. The results (Fig. 3) were clear-cut. All denuded larvae were quickly encountered by ants, and were usually bitten by the first ones that contacted them (Fig. 1H). Only four of these escaped such assaults and made their way to an unguarded region of the colony where they proceeded to rebuild their shields. The other denuded larvae were effectively dealt with by the ants. Most (14 larvae) were grasped in the mandibles of individual ants and persistently pulled until they lost their foothold, and then lifted over the margin of the branch and released so that they fell to the ground. Another two that were similarly grasped fell to the ground with the ants. The remaining seven were carried off the plant by individual ants that held them tenaciously in their mandibles as they descended along the branches to the ground (Fig. 1I), pausing only occasionally to pull the larvae loose when these regained a purchase. Two of these larvae were actually pierced by the ants' bites, and they died as the ants stopped during their descent to feed on the fluids that oozed from the wounds of the larvae. Other larvae that we retrieved as the ants dropped them to the ground or carried them along the ground showed no visible signs of injury. The body of the larva is rubbery and resilient and evidently not easily torn open by the ants.

In sharp contrast were the results with the 23 larvae that were released among aphids with their shields intact. These larvae were also encountered by ants, but only eight were bitten and the bites were only momentary. No sooner had an ant clamped down on the back of a larva than it released its hold and, with its mouthparts visibly contaminated with wax, backed away (Fig. 1, F and G). It then proceeded to engage in protracted cleansing activities, without resuming the assault. A second and third ant sometimes bit the larva, but always with identical results. Undeterred, and deprived of only a small portion of its shield, the larva simply moved on among the aphids, settling eventually when it located a site where it fit inconspicuously into the colony. The remaining 15 larvae were merely "inspected" by the ants and then ignored. The ants contacted them (in response to which the larvae always halted abruptly) but they then quickly broke away without overtly responding to the larvae in any fashion. The larvae, it seemed, had "passed" as aphids. Like "wolves in sheep's clothing" they appeared to have fooled the guardians of their prey. Although these observations suggest that the deception operates on contact only, this need not be strictly true. Ants have eyes and are said to be visually responsive when guarding aphids (*1*), and they might therefore also be deceived visually by the larvae. Moreover, the aphidlike appearance might also prove adaptive to the larvae in other contexts. Birds, for example, appear to ignore wooly aphids, and they might similarly discriminate against mimics of the aphids.

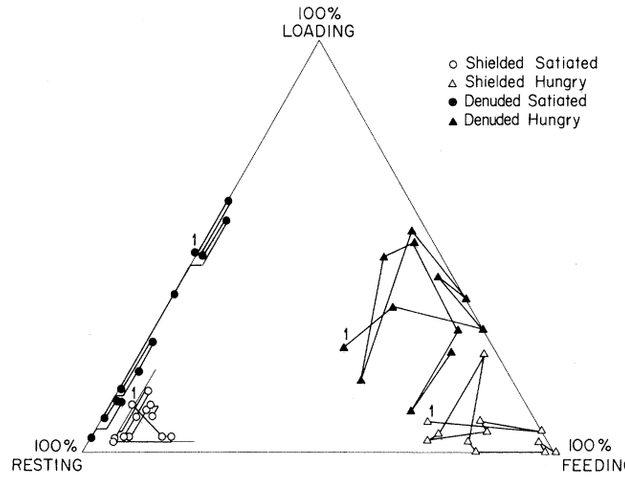


Fig. 4. Activity traces showing successive time allocations by four different groups of larvae ($N = 6$ per group) to feeding, loading with wax, and resting. Initial allocations are denoted by the numeral 1. A barycentric coordinate system is used (*9*). Each point gives the mean for the six larvae of the group. For purposes of clarity, one trace in lower left corner is shown in an inwardly displaced position.

Shield construction is essentially a defensive activity and a principal alternative to feeding in the behavioral repertoire of the larva. An effort was made to obtain some measure of the relative priority that the larva gives to these two activities. Larvae were prepared so that they were either hungry or satiated, and in turn either shielded or deprived of their shield, and they were then observed as they were released in laboratory colonies of the aphids. Twenty-four larvae, six to each group, were studied in this fashion. Starvation was effected by isolating the larvae from aphids for 24 hours. Shields were removed with a brush. Observations were carried out on each larva for 1 hour, and the data were recorded as the percentage of the time that the larva allocated to feeding, or to loading with wax, or to resting, during each 5-minute period of the hour. The lumped data for each group of six larvae thus consist of 12 consecutive activity allocations, each having three coordinates which sum to 100 percent. A segmental trajectory connecting these successive points on the simplex (*9*) in Fig. 4 traces these activity allocations through the hour of observation of each treatment group. As was expected, the larvae that were pressed for neither wax nor food (shielded, satiated) spent virtually all their time resting. Also as was expected, the larvae that were satiated but denuded devoted time primarily to loading (*10*), while those that were shielded but hungry did little but eat. It was the larvae in the fourth category, which had the double need and hence the potential conflict (denuded, hungry), that showed the interesting result: they neither devoted themselves exclusively to feeding nor to loading, but divided their time between both activities.

Much remains to be learned about *C. slossonae*. We know that the adult females oviposit on alder leaves close to the aphid colonies since their characteristically stalked eggs are often found at such locations, but we do not know how the emergent young locate the aphids or about the risks that they run before acquiring their first protective load of wax. Nor do we know where they eventually pupate.

The larvae of *C. slossonae* are not the only chrysopid larvae that place exogenous materials upon their backs. Other species load themselves with vegetable matter, arthropod remains, or general debris (or all) (*4, 11, 12*). The bristles on such larvae are arranged essentially as they are in *C. slossonae* and are sometimes also terminally hooked (*11, 13*). Existing evidence suggests that this "trash-carrying behavior" serves for defense against insect predators (*14*). What is anomalous about *C. slossonae* is that it loads itself with an integumental outgrowth of its prey and as a result becomes a mimic of the prey itself.

THOMAS EISNER
KAREN HICKS, MARIA EISNER
*Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853*
DOUGLAS S. ROBSON
*Department of Plant Breeding and Biometry, Cornell University*

**References and Notes**

1. M. J. Way, *Annu. Rev. Entomol.* **8**, 307 (1963).
2. A chrysopid larva has been listed as an enemy of *Prociphilus tesselatus* [T. Pergande, *U.S. Dept. Agric. Technol. Ser. No. 24* (1912), pp. 1–28] but no details are given about its morphology or behavior. Its given identification (*Chrysopa quadripunctata*) remains open to question.
3. J. Meinwald, J. Smolanoff, A. C. Chibnall, T. Eisner, *J. Chem. Ecol.* **2**, 269 (1975).
4. F. J. Killington, *A Monograph of the British Neuroptera* (Ray Society, London, 1936–1937), vols. 1 and 2; R. C. Smith, *Mem. Cornell Agric. Exp. Stat.* **58**, 1287 (1922).
5. T. R. New, *Trans. R. Entomol. Soc. London* **127**, 115 (1975).
6. Consumption time of individual newborn aphids averaged 4.72 ± 0.75 minutes for six 2nd and 3rd instar larvae (25 aphids).
7. Duration of the plucking procedure (from insertion of larval head into aphid's wool to application of plucking to rump of larva), determined from motion picture analyses, averaged 4.30 ± 0.51 seconds per plucking for seven 2nd and 3rd instar larvae (64 pluckings).
8. Shield rebuilding time was 18.50 ± 2.63 minutes (seven shields made by seven 2nd and 3rd instar larvae).
9. Coordinates of each point are measured by perpendicular distances to the three sides of an equilateral triangle as described, for example, in C. C. Li, *Population Genetics* (Univ. of Chicago Press, Chicago, 1955).
10. Since these larvae rebuilt their shield in less than an hour (*8*), they loaded intensively only during the first portion of the experimental period.
11. H. Dewitz, *Biol. Zentralbl.* **4**, 722 (1885).
12. R. D. Slocum and J. D. Lawrey, *Can. J. Bot.* **54**, 1827 (1976).
13. C. A. Tauber, *Ann. Entomol. Soc. Am.* **68**, 695 (1975).
14. Ants that were offered unidentified trash-carrying chrysopid larvae in the laboratory often discontinued their attacks if upon attempting to bite the larvae they secured only parts of the trash packets. Reduviid bugs also rejected trash-carrying larvae if they failed to reach the bodies of the larvae when probing through the trash packets with their beaks (T. Eisner, unpublished). Trash-carrying larvae were shown to be better protected against anthocorid bugs than naked counterparts [T. R. New, *Entomol. Gaz.* **20**, 119 (1969)].


15. Supported in part by NSF grant PCM 74-15084. We thank Dr. P. A. Adams and Dr. W. L. Brown, Jr., for identifying *C. slossonae* and the ants respectively, and Drs. C. A. and M. J. Tauber for advice and comments on the manuscript. Most of the work was done at the Huyck Preserve, Rensselaerville, N.Y. R. E. Silberglied and T.E. discovered the larvae. Paper No. 58 of the series Defense Mechanisms of Arthropods.

16 September 1977


# Thermoregulation Is Impaired in an Environment Without Circadian Time Cues


Abstract. *Squirrel monkeys synchronized to a 24-hour light-dark cycle show a prominent circadian rhythm in body temperature which is regulated against mild environmental cold exposures throughout the 24-hour day. However, cold exposures produce significant decreases in core body temperature when the circadian rhythms of the animal are free-running in the absence of environmental time cues. Effective thermoregulation appears to require the precise internal synchronization of the circadian timekeeping system.*


Body temperature in homeotherms is not regulated at a constant level over the day, but rather oscillates with a prominent circadian (about 24 hours) rhythm (*1*). Circadian rhythms, which have been observed in many physiological variables, are generated by an endogenous system of oscillators within the organism which is normally synchronized by 24-hour cues in nature (*2*). When animals are placed in an environment free of time cues, circadian rhythms persist with a period usually significantly different from 24 hours. We report here that in such constant conditions the capability of squirrel monkeys to maintain body temperature during mild cold exposures is significantly impaired. Regulation against cold is more effective when animals are synchronized by periodic inputs from the environment.

Thirteen adult male squirrel monkeys (*Saimiri sciureus*), weighing 800 to 1200 g were conditioned to sit in a special metabolism chair (*3*) for two or more weeks. Studies were conducted on the chair-restrained animals within an isolation chamber in which the environmental lighting and ambient temperature ($T_a$) were controlled. The animals were allowed free access to food and water. Colonic temperature ($T_{co}$) was measured with a thermistor probe (YSI, model 401) inserted 6 cm beyond the anus. The probe was connected to a bridge circuit (YSI Telethermometer, model 43TD) and the bridge output was continuously amplified and recorded (Grass polygraph, model 7).

The monkeys were subjected to mild 6-hour cold exposures at all circadian phases of the 24-hour day. Each animal was studied for at least three consecutive days at 28°C before being exposed to 20°C for 6 hours (*4*). Eight experiments were conducted with animals entrained to a 24-hour light-dark cycle with 12 hours of light (600 lux) and 12 hours of dark (<1 lux) (LD 12 : 12). The results of these experiments were compared with those of nine other experiments in which the animals were maintained in constant light (LL) of 600 lux.

In animals entrained to the LD cycle, the $T_{co}$ had a 24-hour mean of 37.5° ± 0.1°C (mean ± S.E.M.) and an average daily range of 1.9° ± 0.1°C. The $T_{co}$ was maintained above the mean when lights were on, and then fell progressively throughout the night until it began to rise again about 2 hours before the lights were scheduled to come on (*5*). In LL where there were no environmental time cues to synchronize the circadian system, the rhythm in $T_{co}$ persisted with an average free-running period of 25.2 hours (*6*). The mean $T_{co}$ in these conditions (37.7° ± 0.2°C) was not significantly different from that observed in LD. However, the circadian range of the rhythm was reduced to 1.0° ± 0.2°C, and the waveform was also altered so that a greater fraction of the cycle was elevated above the mean than in LD.

Cold exposure had little effect on $T_{co}$ in an animal entrained to an LD cycle when $T_{co}$ was compared to the mean ± the standard deviation (S.D.) of the three control days (Fig. 1a). The $T_{co}$ was defended when the animals were exposed to cold at any time of day or night with a mean maximum decline in $T_{co}$ of −0.1° ± 0.2°C (Fig. 2). However, most animals in LL showed an impaired ability to maintain a stable $T_{co}$ during similar cold exposures. Figure 1b shows an example in which a major fall in $T_{co}$ occurred. The maximum fall in $T_{co}$ in the LL experiments averaged −1.0° ± 0.2°C below the control mean (Fig. 2). The decrease in $T_{co}$ of animals free-running in constant light was significantly greater ($P < .01$) than that of animals entrained to the LD cycle.

These results are the first demonstration of a failure of homeostasis caused by the removal of LD cues from the environment. There are three reasonable ways in which this impaired defense of $T_{co}$ in constant light might be explained.

1) The stress of chair restraint or the isolation conditions (or both) could result in impaired thermoregulation in the animals. However, when animals were studied for similar lengths of time in the chair in LD and LL, only the monkeys in LD could consistently defend $T_{co}$. Therefore, it appears unlikely that these results are anomalies of restraint or isolation (or both) per se.

2) Constant bright light could detrimentally affect the thermoregulatory system. Yet, this does not seem to be the case either. We have shown previously that squirrel monkeys in LL (600 lux) are capable of being entrained to 24-hour cycles of food availability (*7*). When these animals were provided with this form of external synchronization in LL, they were able to defend $T_{co}$ effectively against similar cold exposures at various circadian phases. Because these monkeys were also chair-restrained, a combination of chair restraint and bright light together cannot account for the observed response. A further possible test would



0036-8075/78/0217-0794$00.50/0