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First case of endothermy in semisessile animals

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Abstract

Endothermy is generally believed to have coevolved with highly active lifestyle in animals, and to be permanent (combined with homeothermy) only in some vertebrates, due in part to size restrictions on endothermic animals. All invertebrates are known to possess endothermy and exhibit it only when engaged in physically intensive behaviors. I report the discovery of permanent endothermy during one part of the life cycle in two species of semisessile lanternflies (Fulgoridae), proving the established assumptions about physiological and morphological prerequisites for permanent endothermy to be wrong: apparently, permanent endothermy can evolve even in very small, semisessile animals as long as they have access to sufficient energy supply.

KEYWORDS

Fulgoridae, Hemiptera, *Lycorma*, *Penthicodes*, spotted lanternfly

1 | INTRODUCTION

Endothermy (the ability to maintain elevated body temperature by generating heat) and homeothermy (the ability to keep body temperature constant) are relatively uncommon in nature. Permanent endothermy (endothermy combined with homeothermy) is virtually universal in birds and mammals, which usually maintain near-constant body temperature permanently or when not hibernating. A few species of fish and reptiles become endothermic when swimming or incubating eggs (McNab, 2009), and many reptiles maintain homeothermy by clever use of temperature gradients in their environment (see overview in Doody et al., 2021). Many insects become endothermic when flying or otherwise exercising thoracic muscles, and some species of cicadas also while producing sound (see overview in Heinrich, 2013), but no invertebrates are currently known to maintain permanent endothermy. Endothermy is energetically costly: permanent endothermy can increase the animal's energy requirements by more than an order of magnitude (Clarke & Pörtner, 2010; Huey, 1982), and is particularly demanding for small-bodied animals. The smallest known permanently endothermic animal is the Etruscan shrew (*Suncus etruscus*) with an adult weight of 1.3–2 g; the smallest bat and bird are nearly as small, so that size has been suggested to be the lowest possible size for a permanently endothermic animal; notably, all these species enter torpor in adverse conditions (Mcnab, 2009; Taylor, 1998). Paleontologists consider evidence of endothermy in extinct taxa such as nonavian dinosaurs to be a sign of active lifestyle, high speed and endurance, and vice versa (Pontzer et al., 2009; Ruben, 1995).

Lanternflies (Fulgoridae) are large insects (Figure 1) that feed on tree sap and expel extra water and sugar in the form of copious amounts of honeydew (Kim et al., 2011). Adults are capable of flight but are semisessile, often spending the first few weeks of their adult lives attached to the same spot, and conducting only short dispersal flights afterward (Myrick & Baker, 2019). Here, I report discovering endothermy combined with homeothermy in two species of lanternflies, *Lycorma delicatula*, and *Penthicodes atomaria*.

2 | METHODS AND STUDY SITES

Studies on *P. atomaria* were carried out in a park-like area around the headquarters of Pu Mat National Park, Vietnam, in February 2018; on *L. delicatula*—in a suburban area in West Orange, New Jersey, USA, in August–September 2020 and in a primary broadleaf forest in Hutcheson Memorial Forest, New Jersey, USA, in August–September 2021. Observations were conducted opportunistically using Pulsar

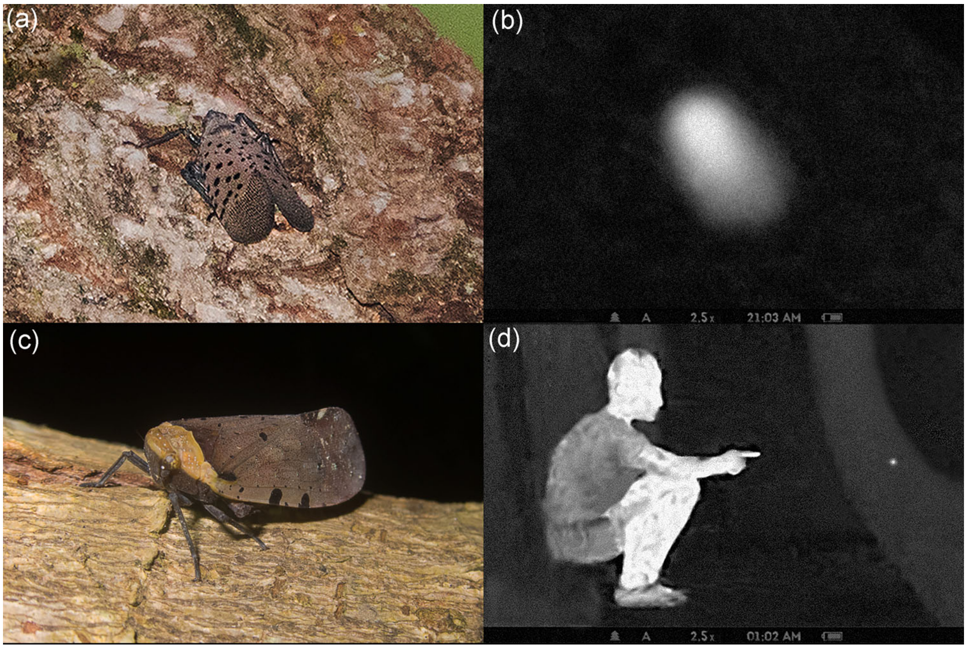

FIGURE 1 Endothermic lanternflies: (a) *Lycorma delicatula* in visible light; (b) the same insect as seen through Pulsar Quantum Lite XQ30V thermal imager; (c) *Penthicodes atomaria* in visible light; (d) the same insect as seen through a thermal imager from ~25 m away

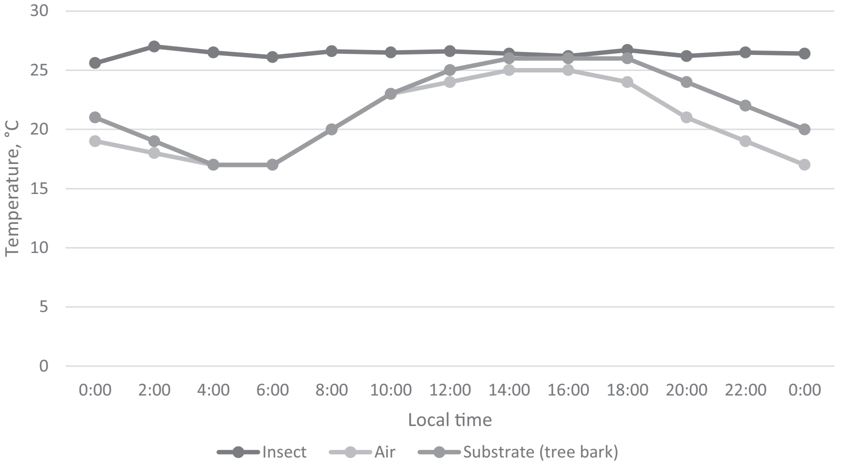

FIGURE 2 Body temperature of a lanternfly *Lycorma delicatula* (measured every 2 h with TP30 laser thermometer, ThermoPro), air temperature, and substrate temperature during a 24-h period, September 2, 2020, New Jersey, USA. This and eight other individuals were also observed at least four times a day for 5–8 days and always maintained body temperature within 24–27°C range, while the ambient temperature changed within 14–27°C range (see text)

Quantum Lite XQ30V thermal imager (Yukon Advanced Optics Worldwide, Ltd.) and TP30 laser thermometer (ThermoPro). The thermal imager is capable of showing temperature differences as little as 0.2°C when used at ambient temperatures between +10°C and +30°C, according to product specifications. Thermometer readings were taken at approximately a right angle to the tree surface from 30 to 40 cm away, with the temperature of tree bark 5–10 cm from the animal used as control. Multiple tests (performed by comparing measurement results with those obtained with a mercury thermometer) showed the accuracy of the laser thermometer to be ±2°C when measured temperatures were within 13–36.6°C range. Individual *L. delicatula* is easy to follow, thanks to unique patterns of black spots on their front wings; wing patterns in *P. atomaria* are also individual but the differences are usually less obvious.

3 | RESULTS

The discovery that *P. atomaria* are consistently warmer than their environment was made accidentally: at any time of day they could be easily located with a thermal imager from as far as 100 m away (Figure 1). The same individuals ($N = 4$) were observed at exactly the same locations on tree trunks day and night for more than 6 days, although they would rapidly fly away if approached too closely.

Subsequent observations on *L. delicatula* in West Orange ($N = 9$, of which four were observed at least four times a day for 5 days, and one was observed every 2 h for 24 h; Figure 2) showed that the insects maintained constant body temperature of 24–27°C, with changes within the accuracy range of the thermometer, while the ambient temperature changed within 14–27°C range. Although four of the insects changed their location between branches of the same tree once or twice during the 5-day observation period, five others did not move at all. One animal was able to fly away when approached to within 2 m at an air temperature as low as 15°C. To make sure the insects produce heat rather than feed on warm tree sap, I measured the temperature of sap seeping from 1 to 3 cm deep cuts in the branches and found it to be warmer than the air temperature by up to 3°C at night and not warmer at all during the day.

Observations of very large numbers (thousands) of *L. delicatula* in Hutcheson Memorial Forest showed that the insects became homeothermic within 24 h after metamorphosis into adults and maintained homeothermy for 2–3 weeks, at which point their temperature decreased and was no longer measurably different from the ambient. As a result, trees covered with adult lanternflies could at first be seen through the thermal imager from over 100 m away, but later in the season were not distinguishable from lanternfly-free trees even when covered with hundreds of insects. During the observation period, postmetamorphosis insects kept covering new trees, and the number of lanternfly-covered trees along a 1-km trail increased from one on August 6 to five (four of them with homeothermic lanternflies) on August 25 to 17 (11 of them with homeothermic lanternflies) on September 14. Homeothermic lanternflies were removed from trees and kept in a glass jar ($N = 5$) maintained homeothermy for 26–30 h and then gradually cooled down to the ambient temperature (22°C) within approximately an hour; they died after 44–50 h without food.

4 | DISCUSSION

Insects currently known to be capable of endothermy maintain it by intense muscular activity such as flight or wing shivering (Heinrich, 2013), but lanternflies were observed to maintain elevated body temperature without any visible movement. It is likely that lanternflies could evolve energy-costly endothermy thanks to having constant access to a virtually unlimited supply of energy in the form of sugar-rich sap, which would make possible a high metabolic rate required for endothermy (McNab, 2009). But why do these semisessile animals need endothermy and homeothermy in the first place? It has been suggested that constantly high body temperature provides protection from fungal infections (Robert & Casadevall, 2009). It might improve their ability to rapidly flee when threatened, which is their common antipredatory response (Kang et al., 2017), or shorten egg development times, like in some reptiles (Huey, 1982). The latter explanation seems least likely because for unknown reasons the lanternflies stop being endothermic a few weeks before egg-laying, which in North America takes place in late September–October (Liu, 2019). It is actually possible that lowering body temperature is required for successful egg development as the eggs are in the overwintering stage and thus presumably the most cold-adapted one.

In any case, the presence of endothermy and homeothermy in these semisessile animals shows that neither trait is a reliable indicator of active lifestyle in extinct or little-known animals; conversely, inactive or even semisessile lifestyle cannot be considered certain evidence of ectothermy.

Adult *L. delicatula* weighs 250 mg on average (Frantsevich et al., 2008) and *P. atomaria* are similar in size. That makes them at least four times smaller than the smallest known fully endothermic animals, showing that full endothermy can evolve in much smaller animals than previously known. This is also the first known case of full endothermy in invertebrates; all animals previously known to be fully endothermic were either mammals or birds (there is also some evidence of full endothermy in extinct archosaurs, see Pontzer et al., 2009).

Both *L. delicatula* and *P. atomaria* belong to Aphaeninae subfamily of lanternflies. It remains to be found how widespread is endothermy among lanternflies.

L. delicatula is an invasive pest in North America, where it is known as the spotted lanternfly (Urban, 2020). Discovering that it is easy to detect with a thermal imager provides an efficient method of finding these insects, which are cryptic and sometimes difficult to locate in tree canopies.

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CONFLICT OF INTERESTS

The author declares that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

All data obtained during the study are included in the manuscript. Original field notes can be provided upon request.

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REFERENCES

Clarke, A., & Pörtner, H. O. (2010). Temperature, metabolic power and the evolution of endothermy. *Biological Reviews*, *85*, 703–727.

Doody, J. S., Dinets, V., & Burghardt, G. M. (2021). *The secret social lives of reptiles*. Johns Hopkins.

Frantsevich, L., Ji, A., Dai, Z., Wang, J., & Gorb, S. N. (2008). Adhesive properties of the arolium of a lantern-fly, *Lycorma delicatula* (Auchenorrhyncha, Fulgoridae). *Journal of Insect Physiology*, *54*, 818–827.

Heinrich, B. (2013). *The hot-blooded insects: strategies and mechanisms of thermoregulation*. Springer Verlag.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In C. Gans, & F. H. Pough (Eds.), *Biology of the Reptilia* (Vol. 12, pp. 25–91). Academic Press.

Kang, C., Moon, H., Sherratt, T. N., Lee, S. I., & Jablonski, P. G. (2017). Multiple lines of anti-predator defence in the spotted lanternfly, *Lycorma delicatula* (Hemiptera: Fulgoridae). *Biological Journal of the Linnean Society*, *120*, 115–124.

Kim, J. G., Lee, E. H., Seo, Y. M., & Kim, N. Y. (2011). Cyclic behavior of *Lycorma delicatula* (Insecta: Hemiptera: Fulgoridae) on host plants. *Journal of Insect Behavior*, *24*, 423–435.

Liu, H. (2019). Oviposition substrate selection, egg mass characteristics, host preference, and life history of the spotted lanternfly (Hemiptera: Fulgoridae) in North America. *Environmental Entomology*, *48*, 1452–1468.

McNab, B. K. (2009). Energetics, body size, and the limits to endothermy. *Journal of Zoology*, *199*, 1–29.

Myrick, A. J., & Baker, T. C. (2019). Analysis of anemotactic flight tendencies of the spotted lanternfly (*Lycorma delicatula*) during the 2017 mass dispersal flights in Pennsylvania. *Journal of Insect Behavior*, *32*, 11–23.

Pontzer, H., Allen, V., & Hutchinson, J. R. (2009). Biomechanics of running indicates endothermy in bipedal dinosaurs. *PLOS One*, *4*, e7783.

Robert, V. A., & Casadevall, A. (2009). Vertebrate endothermy restricts most fungi as potential pathogens. *Journal of Infectious Diseases*, *200*, 1623–1626.

Ruben, J. (1995). The evolution of endothermy in mammals and birds: From physiology to fossils. *Annual Review of Physiology*, *57*, 69–95.

Taylor, J. R. E. (1998). Evolution of energetic strategies in shrews. In J. M. Wojcik, & M. Wolsan (Eds.), *Evolution of shrews* (pp. 309–346). Mammal Research Institute, Polish Academy of Sciences.

Urban, J. M. (2020). Perspective: Shedding light on spotted lanternfly impacts in the USA. *Pest Management Science*, *76*, 10–17.

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