Active behaviour of terrestrial caterpillars on the water surface

Masakazu Hayashi Equal first author, [1], **Shinji Sugiura** Equal first author, [2]

[1] Hoshizaki Green Foundation, Izumo, Shimane, Japan
[2] Graduate School of Agricultural Science, Kobe University, Kobe, Hyogo, Japan

Corresponding Author: Masakazu Hayashi
Email address: hgf-haya@green-f.or.jp

Most butterfly and moth larvae (Lepidoptera) are terrestrial. When terrestrial caterpillars accidentally fall into water, they may drown or be preyed upon by aquatic predators before they can safely reach land. However, how terrestrial caterpillars escape aquatic environments and predators remains unclear. In July 2018, we observed a terrestrial caterpillar actively moving forward on the surface of a pond in Japan until it successfully reached the shore. To further investigate this behaviour in terrestrial caterpillars, we experimentally placed larvae of 13 moth species (four families) on a water surface under laboratory and field conditions. All caterpillars floated. Larvae of seven ~~caterpillar~~ species moved forward on the water surface, whereas those of six species did not. Two types of behaviours were observed; in *Dinumma deponens*, *Hypopyra vespertilio*, *Spirama retorta*, *Laelia coenosa*, *Lymantria dispar* (all Erebidae), and *Naranga aenescens* (Noctuidae), larvae swung their bodies rapidly from side to side to propel themselves along the water surface (i.e., undulatory behaviour); in contrast, larvae of *Acosmetia biguttula* (Noctuidae) rapidly moved the end of the abdomen up and down for propulsion along the water surface (i.e., kicking behaviour). Although thoracic legs were not used for undulatory and kicking behaviour, rapid movements of the anal prolegs were used to propel caterpillars on the water surface. We also observed that undulatory and kicking behaviour on the water surface aided caterpillars in escaping aquatic predators under field conditions. In addition, we investigated the relationship between body size and undulatory behaviour on the water surface in the erebid *S. retorta* under laboratory conditions. The frequency and speed of forward movement on the water surface increased with increasing body length. Together, these results show that the rapid movement of elongated bodies results in forward propulsion on the water surface, allowing some terrestrial caterpillars to avoid drowning or aquatic

Commented [WD1]: This is swimming according to my English dictionary Text reads better if called swimming. And other workers will be able to find the work, if it is called swimming.

predators. We further suggested potential factors related to morphology, host plant habitat, and defensive behaviours that may have led to the acquisition of water surface behaviour in terrestrial caterpillars.

Active behaviour of terrestrial caterpillars on the water surface

Masakazu Hayashi[1] and Shinji Sugiura[2]

[1]Hoshizaki Green Foundation, Sono, Izumo, Shimane, 691-0076 Japan.

[2]Graduate School of Agricultural Science, Kobe University, 1-1 Rokkodai, Nada-ku, Kobe, 657-8501 Japan.

Equal first author:

Masakazu Hayashi, hgf-haya@green-f.or.jp

Shinji Sugiura, ssugiura@people.kobe-u.ac.jp

Running title (40 characters): Caterpillar behaviour on water

ABSTRACT (word limit: 500)

Most butterfly and moth larvae (Lepidoptera) are terrestrial. When terrestrial caterpillars accidentally fall into water, they may drown or be preyed upon by aquatic predators before they can safely reach land. However, how terrestrial caterpillars escape aquatic environments and predators remains unclear. In July 2018, we observed a terrestrial caterpillar actively moving forward on the surface of a pond in Japan until it successfully reached the shore. To further investigate this behaviour in terrestrial caterpillars, we experimentally placed larvae of 13 moth species (four families) on a water surface under laboratory and field conditions. All caterpillars floated. Larvae of seven caterpillar species moved forward on the water surface, whereas those of six species did not. Two types of behaviours were observed; in *Dinumma deponens*, *Hypopyra vespertilio*, *Spirama retorta*, *Laelia coenosa*, *Lymantria dispar* (Erebidae), and *Naranga aenescens* (Noctuidae), larvae swung their bodies rapidly from side to side to propel themselves along the water surface (i.e., undulatory behaviour); in contrast, larvae of *Acosmetia biguttula* (Noctuidae) rapidly moved the end of the abdomen up and down for propulsion along the water surface (i.e., kicking behaviour). Although thoracic legs were not used for undulatory and kicking behaviour, rapid movements of the anal prolegs were used to propel caterpillars on the water surface. We also observed that undulatory and kicking behaviour on the water surface aided caterpillars in escaping aquatic predators under field conditions. In addition, we investigated the relationship between body size and undulatory behaviour on the water surface in the erebid *S. retorta* under laboratory conditions. The frequency and speed of forward movement on the water surface increased with increasing body length. Together, these results show that the rapid movement of elongated bodies results in forward propulsion on the water surface, allowing some terrestrial caterpillars to avoid drowning or aquatic predators. We further suggested potential factors related to morphology, host plant habitat, and defensive behaviours that may

have led to the acquisition of water surface behaviour in terrestrial caterpillars.

Keywords: aquatic behaviour, anguilliform, Erebidae, Lepidoptera, Noctuidae

INTRODUCTION

Most terrestrial insects have not adapted to aquatic environments; for example, many terrestrial insect species only rarely escape from a water surface. However, terrestrial insects such as locusts, cockroaches, praying mantises, and ants can successfully move forward on a water surface using their legs (*Miller, 1972; Franklin, Jander & Ele, 1977; Pflüger & Burrows, 1978; Graham et al., 1987; Bohn, Thornham & Federle, 2012; Yanoviak & Frederick, 2014; Gripshover, Yanoviak & Gora, 2018*). Forward movement on a water surface has been reported ~~during~~ for the adult stages of terrestrial insects, but rarely ~~during~~ for the immature stages.

The larvae of butterflies and moths (Lepidoptera) are predominantly terrestrial; however, approximately 0.5% of 165,000 known species are aquatic at the larval stage (*Pabis, 2018*). When terrestrial caterpillars accidentally fall into water, they can drown or be preyed upon by aquatic predators such as fish before they can safely reach land (*Gustafsson, Greenberg & Bergman, 2014; Iguchi et al., 2004*). Some caterpillars (i.e. aquatic species) exhibit behavioural adaptations to aquatic environments and predators to avoid these risks (*Pabis, 2018*), but the behavioural responses of terrestrial caterpillars to aquatic environments remain unclear.

On July 20, 2018, we observed a terrestrial caterpillar of *Dinumma deponens* (Lepidoptera: Erebidae) moving forward on the water surface of a pond in Unnan, Shimane, Japan. The caterpillar undulated from side to side, ~~to~~ propeling itself forward on the water surface; it was able to successfully reach the shore (Fig. 1a). The caterpillar may have accidentally fallen into the pond because *D. deponens* larvae feed on leaves of the tree species *Albizia julibrissin* (Fabaceae), which commonly grows ~~in riparian forests~~ along the edges of wetlands (*Kishida, 2011*). We placed the same caterpillar on the water surface again and observed the same behaviour (Fig. 1b; Video S1). This active behaviour on the water surface appeared to aid the caterpillar in evading aquatic predators (e.g., water striders; Fig. 1b; Video S1). On the basis of this observation, we hypothesised that some

Commented [WD2]: Maybe provide a references. Many workers use 157,000 species of Lepidoptera have been described (Nieukerken et al. 2011, Mitter et al. 2017).

Commented [WD3]: To implies intent

Commented [WD4]: The behavior could be multifunctional. Beyond helping to avoid predation, the behavior is necessary to reunite the caterpillar with its hostplant, it also prevent drowning, and may return the larva to substrate upon which it could/would settle…to rest until it would time to feed again. If they placed the caterpillar on glass over white paper, many erebids would move to a new site of safety where its coloration was more cryptic.

We know the animal swims. We don't know the motivation.

Commented [WD5]: What's to hypothesize? You watched it happen. This hypothesis feels forced.

Formatted: Left: 0.46", Top: 0.46", Bottom: 0.5"

terrestrial caterpillars can exhibit forward movement on the water surface.

To test this hypothesis, we experimentally placed the larvae of 13 moth species (belonging to four families), including *D. deponens*, onto a water surface and observed their behaviours under laboratory and field conditions. In addition, we experimentally investigated the relationship between a caterpillar's body size and behaviour on the water surface ~~in a moth species~~ to clarify how body size can influence propulsive power in water.

MATERIALS AND METHODS

To test whether terrestrial caterpillars can exhibit forward movement on the water surface, we experimentally placed the larvae of 13 moth species (from four families) on a water surface and observed their behaviours under laboratory and field conditions (Table 1). We collected 52 larvae from eight plant species from June 2019 to July 2019 in Shimane Prefecture and in June 2020 in Hyogo Prefecture, Japan. We carefully placed each caterpillar (*n* = 49) on the water surface in a plastic vessel (390 × 265 × 65 mm^3~~, length × width × height~~) containing 2 L of water (20 mm depth, 25°C) under well-lit conditions, with an air temperature of 25°C. We also placed the larvae of three species, *Hypopyra vespertilio* (Erebidae), *Acosmetia biguttula* (Noctuidae), and *Theretra oldenlandiae* (Sphingidae), on the surfaces of ponds in Shimane Prefecture. During each 2-min observation period, we investigated whether the larvae (1) remained at the water surface (supported by water tension) and (2) moved forward on the water surface. To examine the possible origins of this movement behaviour, we also observed how caterpillars of each species walk on twigs or leaves (i.e., inching or looping; *van Griethuijsen & Trimmer, 2014*; Table 1). We identified each ~~lepidopteran species~~caterpillar based on their morphological characteristics of ~~the larvae~~ (*Sugi, 1987; Yasuda, 2010, 2012, 2014; Suzuki et al., 2018*~~).~~), and or ~~We also reared~~ raised some larvae ~~under laboratory conditions (25°C)~~ to the adult stage to confirm their identify ~~the species based on the morphological~~

~~characteristics of the emerged adults~~ (*Kishida, 2011*).

In caterpillars, various behaviours such as anti-predator defences are closely related to body size (*Sugiura & Yamazaki, 2014; Hossie et al., 2015; Sugiura et al., 2020; Sugiura, 2020*). To clarify how caterpillar size can influence propulsive power in water, we experimentally investigated the relationship between body size and behaviour on the water surface in the erebid *Spirama retorta* (Erebidae). We reared *S. retorta* larvae from the eggs of two females on *A. julibrissin* leaves under laboratory conditions (26–29°C). *Spirama retorta* passes through seven larval instars before pupation (Table 2). We measured the body weight of each larva to the nearest 1 mg using an electronic balance (CJ-620S; Shinko Denshi, Co., Ltd., Tokyo, Japan); we measured the body length and head capsule width to the nearest 0.01 mm using slide callipers or an ocular micrometre. We placed 10 larvae per instar stage individually on the water surface in a plastic container (390 × 265 × 65 mm^3) with 2 L of water (20 mm depth) under well-lit conditions at 25°C. We filmed the behaviours of the larvae (*n* = 70) using video cameras (V2; Nikon, Tokyo, Japan). We played back the footage of the recorded behaviours using iMovie version 10.0.6 (Apple, Inc., Cupertino, CA, USA). During each 2-min observation period, we recorded (1) whether the larva remained at the water surface (supported by water tension), (2) whether the larva moved forward on the water surface, and (3) the distance (mm) travelled by the larva in 2 s.

To investigate the relationship between larval body length and behaviour on the water surface in *S. retorta*, we ran a generalised linear model with a binomial error distribution and logit link function (i.e., logistic regression). We used 10 individuals per instar stage (*n* = 70) for the analysis. We used forward movement (1) or non-forward movement (0) as the binary response variable; we regarded body length as a fixed factor. We also ran a generalised linear model with a Poisson error distribution and log link function (i.e., Poisson regression) to investigate the relationship between body size and movement distance in *S. retorta*, analysing 10 individuals per instar stage (*n* = 70). We used forward speed (mm/s) as the response variable; we regarded body length as a fixed factor. When the residual deviance was smaller (underdispersion) or larger (overdispersion) than the residual degrees of freedom, we used a quasi-binomial or quasi-Poisson error distribution, respectively, rather than a binomial or Poisson error distribution (*Sugiura & Sato, 2018*). We performed all analyses using R software version 3.5.2 (*R Core Team, 2019*).

RESULTS

All caterpillars examined in this study floated (i.e., remained at the water surface). Larvae from six of the 13 caterpillar species did not move forward on the water surface, whereas larvae from seven species (two families: Erebidae and Noctuidae) exhibited forward movement on the water surface (Table 1). Two types of behaviours were observed (Table 1): larvae of *D. deponens*, *H. vespertilio*, *S. retorta*, *Laelia coenosa*, *Lymantria dispar* (all Erebidae), and *Naranga aenescens* (Noctuidae) swung their bodies side to side quickly to propel themselves on the water surface (i.e., undulatory behaviour; Figs. 1c–d, 2a; Video S2); in contrast, larvae of *A. biguttula* (Noctuidae) moved the end of the abdomen up and down quickly to propel themselves on the water surface (i.e., kicking behaviour; Fig. 2b; Video S3). Although thoracic legs were not used for undulatory and kicking behaviour, quick movements of the anal prolegs were used to propel the caterpillars on the water surface (Videos S2, S3). One larva of *A. biguttula* was observed escaping from an aquatic predator in a pond (Video S3).

The relationship between body size and behaviour on the water surface in *S. retorta* was investigated under laboratory conditions. All larvae floated (Table 2). The frequency of forward movement on the water surface increased with increasing body length (Fig. 3a; Tables 2 and 3): 0%, 0%, 40%, 70%, 100%, 100%, and 100% of the first, second, third, fourth, fifth, sixth, and

Commented [WD6]: No. These movement include the entire terminus of the abdomen and not just the prolegs. This is an abdominal flick involving the last ?4 segments o the abdomen. The terminal segments are slowly bent ventrally, and then kicked upward/backward propelling the larva forward.

seventh instars exhibited forward movement on the water surface, respectively (Table 2). Furthermore, the forward speed (mm/s) increased with body length (Fig. 3b; Table 4).

DISCUSSION

Aquatic behaviours have been reported in some aquatic and semi-aquatic caterpillars (*Welch, 1914; Mey & Speidel, 2008; Meneses et al., 2013; Coates & Abel, 2019; De-Freitas, De Agostini & Stefani, 2019*). ~~For example, a~~The aquatic larvae of ~~woolly bear moths such as~~of *Paracles laboulbeni* and *P. klagesi* (Erebidae: Arctiinae) ~~can submerge and move~~feed under the water surface (*Mey & Speidel, 2008; Meneses et al., 2013*), and semi-aquatic larvae of moths such as *Bellura vulnifica* (Noctuidae) and *Ostrinia penitalis* (Crambidae) can move forward on the water surface (*Welch, 1914; Coates & Abel, 2019*). However, whether typically terrestrial caterpillars can move forward on or under the water surface has ~~remained unclear~~received little attention. In the present study, we observed the behaviour on water surfaces of 13 terrestrial caterpillar species from four families under laboratory and field conditions. Among these, seven species were observed to move forward on the water surface (Figs. 1 and 2; Table 1), ~~although~~ none ~~of the larvae were submerged~~broke through the surface tension. We also observed two types of forward movement on the water surface (undulatory and ~~kicking~~ flicking behaviour) in the ~~terrestrial~~ caterpillars (Figs. 1 and 2; Table 1). The undulatory behaviour observed in this study was similar to anguilliform movement, which has been reported in slender-bodied animals such as eels, snakes, and centipedes (*Graham et al., 1987; Yasui et al., 2019; Sfakiotakis, Lane & Davies, 1999*). The frequency and speed of forward movement on the water surface increased with body length in *S. retorta* larvae (Fig. 3; Tables 3 and 4). ~~High-speed~~Directed movements on the water surface can help caterpillars to avoid aquatic predators (Video S1). The ~~kicking~~ flicking behaviour observed in *A. biguttula* was similar ~~to the kicking action of a human swimming stroke (i.e., ‘dolphin kick’ of the ‘butterfly stroke’).~~

Commented [WD7]: Not so. The caterpillar curls the terminal segments under the body then rapidly flicks the segments rearward driving the animal forward

Formatted: Indent: Left: 0.1", Space Before: 0 pt

All of the terrestrial caterpillars used in the present study floated due to water surface tension. Some, but not all, of these floating caterpillars exhibited forward movement on the water surface (Table 1). Three factors may influence forward movement on the water surface in terrestrial caterpillars: (1) morphology, (2) host plant habitat, and (3) locomotive and defensive behaviours.

Caterpillars that exhibited forward movement on the water surface had distinct morphological traits such as relatively elongated bodies. In this study, long-bodied caterpillars were more capable of forward movement on the water surface than those with short bodies (Fig. 3a; Table 3). This relationship has been suggested to explain the behaviour of the semi-aquatic caterpillar species *Bellura*. *vulnifica* at the water surface, although its morphological traits were not quantified (*Welch, 1914*). In addition, anal prolegs could be used in a manner similar to that of tail fins (Figs. 1 and 2). Quick movements of elongated bodies and anal prolegs could result in forward propulsive power on a water surface (Figs. 1 and 2). Furthermore, long body setae may assist in floating on the water surface in hairy caterpillars, such as those of *La. coenosa* and *Ly. dispar* (*Meyer-Rochow, 2016*). However, these features certainly evolved for reasons other than aquatic behavior, because long bodies, prolegs, and body hairs have other important functions in their terrestrial habitats, e.g., they may be involved in background matching, natural enemy defense, maintaining their perch, and still others~~However, these setae likely evolved for reasons other than aquatic behaviour because long bodies, prolegs, and body hairs have other important functions such as mimicking plant twigs, gripping stems, and defending against predators~~ (Fig. 4; *Skelhorn et al., 2010; van Griethuijsen & Trimmer, 2014; Sugiura & Yamazaki, 2014*).

Caterpillars use silk threads produced from their spinneret~~s~~ as a lifeline~~s~~ to prevent falls from the host plant to the ground (*Sugiura & Yamazaki, 2006*). However, some mature caterpillars have also been observed to descend from the host plant to the ground for pupation (*Sugi, 1987*). Caterpillars inhabiting host plants growing by the waterside may accidentally ~~fall~~ descend into open water. Six of the seven caterpillar species that exhibited forward movement on the water surface

Commented [WD8]: It's not just the anal prolegs. Geesh. The anal prolegs are tiny. This is the whole of the abdominal terminus that's curled under!

Commented [WD9]: Redundant. Repetitive.

in this study were collected from waterside plants such as *A. julibrissin* (Table 1). For example, a *D. deponens* larva successfully reached the pond shore by moving forward on the water surface

(Fig. 1a); thus, active movement at the water surface could help terrestrial caterpillars to escape from aquatic environments.

Commented [WD10]: Redundant. Been said 3 or 4 times already.

Terrestrial behaviours may also provide insight into the origins of aquatic behaviours in terrestrial caterpillars. Caterpillar species that undulate on the water surface typically locomote in a characteristic looping manner on leaves or stems (i.e., inching; *van Griethuijsen & Trimmer, 2014*; Table 1). When disturbed, these caterpillars violently bend their bodies from side to side (i.e., jerking, twisting, or thrashing behaviour; *Gross 1993; Greeney, Dyer & Smilanich, 2012*). Undulating behaviour on the water surface may have originated from this defensive behaviour, rather than walking behaviour. Caterpillars that exhibited kicking behaviour at the water surface typically move their abdomen up and down to move on land (i.e., crawling; *van Griethuijsen & Trimmer, 2014*; Table 1); the similarity of the kicking and crawling motions suggests that kicking behaviour on the water surface originated from crawling motion.

CONCLUSIONS

Our results showed that some terrestrial caterpillars exhibited forward movement on the water surface to avoid drowning and aquatic predators (Table 1; Videos S1, S3). However, this behaviour was observed in only two of the four lepidopteran families tested: Erebidae and Noctuidae (Table 1).

Our investigation was limited to four families, although the insect order Lepidoptera contains 133 recognised families (*Mitter, Davis & Cummings, 2017*). Thus, the aquatic behaviour observed in terrestrial caterpillars in this study will likely be found in other lepidopteran families. Further kinematic and anatomical studies are required to understand the mechanism of aquatic behaviours in lepidopteran larvae.

ACKNOWLEDGEMENTS

We thank the editor and reviewers for their helpful comments on an earlier version of the manuscript. We also thank K. Sakagami for aiding in moth identification and K. Okai for assistance with caterpillar sampling.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

Masakazu Hayashi conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Shinji Sugiura conceived and designed the experiments, performed the experiments, analysed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

The experiments were undertaken in accordance with the Kobe University Animal Experimentation Regulations (Kobe University’s Animal Care and Use Committee, 30–01). Ours study was not conducted in any national parks or protected areas. Study insects were not protected species; no specific permissions are required to collect non-protected insects in non-protected area in Japan.

Data Availability

Data available from the Figshare Digital Repository:
https://figshare.com/s/b1bcd137726734746076

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/

REFERENCES

Bohn HF, Thornham DG, Federle W. 2012. Ants swimming in pitcher plants: kinematics of aquatic and terrestrial locomotion in *Camponotus schmitzi*. *Journal of Comparative Physiology A* **198**: 465–76 DOI 10.1007/s00359-012-0723-4.

Coates BS, Abel CA. 2019. Differentiation of European corn borer (Lepidoptera: Crambidae) and American lotus borer (Lepidoptera: Crambidae), *Ostrinia penitalis*, from north American field collections. *Journal of Economic Entomology* **112**: 2007–2011 DOI 10.1093/jee/toz078.

De-Freitas I, De Agostini J, Stefani V. 2019. The aquatic Lepidopterans: A mysterious and unknown fauna. In: Del-Claro K, Guillermo R, eds. Aquatic insects. Cham: Springer, 341–347. https://doi.org/10.1007/978-3-030-16327-3_13

Franklin R, Jander R, Ele K. 1977. The coordination, mechanics and evolution of swimming by a grasshopper, *Melanoplus differentialis* (Orthoptera: Acrididae). *Journal of the Kansas Entomological Society* **50**: 189–199.

Graham JB, Lowell WR, Rubinoff I, Motta J. 1987. Surface and subsurface swimming of the sea snake *Pelamis platurus*. *Journal of Experimental Biology* **127**: 27–44

Greeney HF, Dyer LA, Smilanich AM. 2012. Feeding by lepidopteran larvae is dangerous: A review of caterpillars' chemical, physiological, morphological, and behavioral defenses against natural enemies. *Invertebrate Survival Journal* **9**: 7–34.

Gripshover ND, Yanoviak SP, Gora EM. 2018. A functional comparison of swimming behavior in two temperate forest ants (*Camponotus pennsylvanicus* and *Formica subsericea*) (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* **111**: 319–325 DOI 10.1093/aesa/say026.

Gross P. 1993. Insect behavioural and morphological defenses against parasitoids. *Annual Review of Entomology* **38**: 251–273.

Gustafsson P, Greenberg LA, Bergman E. 2014. Woody debris and terrestrial invertebrates — effects on prey resources for brown trout (*Salmo trutta*) in a boreal stream. *Environmental Biology of Fishes* **97**: 529–542 DOI 10.1007/s10641-014-0250-y.

Hossie TJ, Skelhorn J, Breinholt JW, Kawahara AY, Sherratt TN. 2015. Body size affects the evolution of eyespots. *Proceedings of the National Academy of Sciences USA* **112**: 6664–6669 DOI 10.1073/pnas.1415121112

Iguchi K, Matsubara N, Yodo T, Maekawa K. 2004. Individual food niche specialization in stream-dwelling charr. *Ichthyological Research* **51**: 321–326 DOI 10.1007/s10228-004-0237-3.

Kishida Y. 2011. *The standard of moths in Japan 2*. Tokyo: Gakken Education Publishing (in Japanese).

Meneses AR, Bevilaqua MVC, Hamada N, Querino RB. 2013. The aquatic habit and host plants of *Paracles klagesi* (Rothschild) (Lepidoptera, Erebidae, Arctiinae) in Brazil. *Revista Brasileira de Entomologia* 57:350–352. DOI 10.1590/S0085-56262013005000025

Mey W, Speidel W. 2008. Global diversity of butterflies (Lepidoptera) in freshwater . *Hydrobiologia* **595**: 521–528. DOI 10.1007/s10750-007-9038-9

Meyer-Rochow B. 2016. Depilation increases while hairiness decreases the risk of drowning: A hitherto unappreciated survival role of setae in woolly bear caterpillars of the moth *Lemyra imparilis* (Lepidoptera: Noctuoidea: Erebidae). *European Journal of Entomology* **113**: 130–134 DOI 10.14411/eje.2016.016

Miller PL. 1972. Swimming in mantids. *Journal of Entomology A* **46**: 91–97 DOI 10.1111/j.1365-3032.1972.tb00113.x.

Mitter C, Davis DR, Cummings MP. 2017. Phylogeny and evolution of Lepidoptera. *Annual Review of Entomology* **62**: 265–283. DOI 10.1146/annurev-ento-031616-035125

Pabis K. 2018. What is a moth doing under water? Ecology of aquatic and semi-aquatic Lepidoptera. *Knowledge & Management of Aquatic Ecosystems* **419**: 42 DOI 10.1051/kmae/2018030

Pflüger HJ, Burrows M. 1978. Locusts use the same basic motor pattern in swimming as in jumping and kicking. *Journal of Experimental Biology* **75**: 81–93.

R Core Team. 2019. R, a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Sfakiotakis M, Lane DM, Davies JBC. 1999. Review of fish swimming modes for aquatic locomotion. *IEEE Journal of Oceanic Engineering* **24**: 237–252 DOI 10.1109/48.757275.

Skelhorn J, Rowland HM, Speed MP, Ruxton GD. 2010. Masquerade: camouflage without crypsis. *Science* **327**: 51 DOI 10.1126/science.1181931

Sugi, T. 1987. *Larvae of larger moths in Japan.* Tokyo: Kodansha (in Japanese).

Sugiura S. 2020. Predators as drivers of insect defenses. *Entomological Science* **23**: 316–337 DOI 10.1111/ens.12423

Sugiura S, Sato T. 2018. Successful escape of bombardier beetles from predator digestive systems. *Biology Letters* **14**: 20170647 DOI 10.1098/rsbl.2017.0647

Sugiura S, Yamazaki K. 2006. The role of silk threads as lifelines for caterpillars: pattern and significance of lifeline-climbing behaviour. *Ecological Entomology* **31**: 52–57 DOI 10.1111/j.0307-6946.2006.00755.x.

Sugiura S, Yamazaki K. 2014. Caterpillar hair as a physical barrier against invertebrate predators. *Behavioral Ecology* **24**: 975–983 DOI 10.1093/beheco/aru080.

Sugiura S, Takanashi T, Kojima W, Kajiura Z. 2020. Squeaking caterpillars: independent evolution of sonic defense in wild silkmoths. *Ecology* **10**: e03112 DOI 10.1002/ecy.3112

Suzuki T, Yokota M, Tsutsui M, Sugimoto M, Hirowatari T, Yago K. 2018. *Caterpillars: butterfly and moth larvae*. Tokyo: Shogakukan (in Japanese).

van Griethuijsen LI, Trimmer BA. 2014. Locomotion in caterpillars. *Biological Reviews* **89**: 656–670 DOI 10.1111/brv.12073.

Welch PS. 1914. Habits of the larva of *Bellura melanopyga* Grote (Lepidoptera). *Biological Bulletin* **27**: 97–114 DOI 10.2307/1535952.

Yanoviak SP, Frederick DN. 2014. Water surface locomotion in tropical canopy ants. *Journal of Experimental Biology* **217**: 2163–2170 DOI 10.1242/jeb.101600.

Yasuda M. 2010. *The Handbook of Japanese caterpillar*. Tokyo: Bun-ichi Sogo Shuppan (in Japanese).

Yasuda M. 2012. *The Handbook of Japanese caterpillar II*. Tokyo: Bun-ichi Sogo Shuppan (in Japanese).

Yasuda M. 2014. *The Handbook of Japanese caterpillar III*. Tokyo: Bun-ichi Sogo Shuppan (in Japanese).

Yasui K, Kano T, Standen EM, Aonuma H, Ijspeert AJ, Ishiguro A. 2019. Decoding the essential interplay between central and peripheral control in adaptive locomotion of amphibious centipedes. *Scientific Reports* **9**: 18288 DOI 10.1038/s41598-019-53258-3

Figure legends

Figure 1 Behaviours of terrestrial caterpillars on the water surface. (a) *Dinumma deponens* (Erebidae). (b) *Dinumma deponens* moving forward on a pond surface. (c) Undulatory behaviour in *Spirama retorta* (Erebidae). (d) Undulatory behaviour in *Hypopyra vespertilio* (Erebidae). (e) Kicking behaviour in *Acosmetia biguttula* (Noctuidae). (f) Undulatory behaviour in *Laelia coenosa* (Erebidae). Arrows indicate anal prolegs~~, which may function in a manner similar to that of tail fins.~~ Photos: (a)–(e) M. Hayashi, (f) S. Sugiura.

Figure 2 Two types of caterpillar behaviours on the water surface. (a) Temporal sequence of undulatory behaviour in *Hypopyra vespertilio*. (b) Temporal sequence of kicking behaviour in *Acosmetia biguttula*. Arrows indicate anal prolegs~~, which may function in a manner similar to that of tail fins~~. Photos: M. Hayashi.

Figure 3 Relationship between body size and behaviour on the water surface in *Spirama retorta.* (a) Relationship between body length and frequency of forward movement on the water surface (n = 70). (b) Relationship between body length and forward distance (mm/s) (n = 70). Lines and blue areas represent regression lines and 95% confidence intervals derived from generalised linear models, respectively (Tables 3 and 4). Photos: M. Hayashi.

Figure 4 Larval morphology of *Hypopyra vespertilio*. (a) A larva on a host plant leaf. (b) A larva on the water surface. *Hypopyra vespertilio* larvae have three pairs of thoracic legs (T1–T3) and five pairs of abdominal prolegs (A3–A6 and A10). Photos: S. Sugiura.

Supplementary videos

Video S1. Undulatory behaviour by a *Dinumma deponens* larva on a pond water surface. Active movement aided the larva in evading water striders (*Aquarius paludum*). Movie: M. Hayashi.

Video S2. Undulatory behaviour by *Hypopyra vespertilio* larvae on water surfaces under laboratory and field conditions. Movie: M. Hayashi.

Video S3. Kicking behaviour by *Acosmetia biguttula* larvae on water surfaces under laboratory and field conditions. Active movement aided the larva in evading predation by a backswimmer (*Notonecta triguttata*) in the pond. Movie: M. Hayashi.

The English in this document has been checked by at least two professional editors, both native speakers of English. For a certificate, please see: http://www.textcheck.com/certificate/KfI7Vo

Table 1(on next page)

Table 1 Behaviours of the caterpillars placed on water surfaces.

Table 1 Behaviours of the caterpillars placed on water surfaces.

Family	Species	Instar[a]	Length (mm)	Host plant range	Plant species (sampling)	Habitat (sampling)	Walking locomotion	Behavior on water[b]	Forward movement on water % (*n*)
Erebidae	*Hypopyra vespertilio*	M–L	23–70	Fabaceae	*Albizia julibrissin*	Lake bank	Inching	Undulatory	100 (7/7)[c]
	Spirama retorta	M–L	8–42	Fabaceae	*Albizia julibrissin*	Lake bank	Inching	Undulatory	100 (3/3)
	Dinumma deponens	M–L	20–32	*Albizia julibrissin*	*Albizia julibrissin*	Lake bank	Inching	Undulatory	33 (1/3)
	Laelia coenosa	L	22–34	Poaceae, Cyperaceae, Typhaceae	*Typha latifolia*	Pondside	Crawling	Undulatory	100 (6/6)
	Lymantria dispar	L	33–54	Many families	*Cerasus* × *yedoensis*	Urban area	Crawling	Undulatory	30 (3/10)
Noctuidae	*Xanthodes transversa*	M–L	25–42	Malvaceae	*Hibiscus mutabilis*	Garden	Inching	–	0 (0/2)
	Acosmetia biguttula	M–L	20–38	*Bidens*	*Bidens frondosa*	Pondside	Crawling	Kicking	100 (6/6)[c]
	Naranga aenescens	M–L	13–24	Poaceae	*Pseudoraphis sordida*	Paddy field	Inching	Undulatory	100 (4/4)
	Sarcopolia illoba	E–M	19–34	Many families	*Albizia julibrissin*	Lake bank	Crawling	–	0 (0/3)
	Britha inambitiosa	M–L	13–20	*Pterostyrax hispidus*	*Pterostyrax hispidus*	Streamside	Inching	–	0 (0/3)
Geometridae	*Chiasmia defixaria*	M–L	20–30	*Albizia julibrissin*	*Albizia julibrissin*	Lake bank	Inching	–	0 (0/3)
	Ectropis excellens	L	30	Many families	*Pterostyrax hispidus*	Streamside	Inching	–	0 (0/1)
Sphingidae	*Theretra oldenlandiae*	E	20	Many families	*Causonis japonica*	Garden	Crawling	–	0 (0/1)[c]

[a]Instar: E, early instar; M, middle instar; L, late instar.

[b]Caterpillar behaviour on the water surface: Undulatory, forward movement by undulating; Kicking, forward movement by kicking; –, non-forward movement (floating).

[c]One larva of each species was observed on the water surface of a pond, while other larvae were observed under laboratory conditions.

Table 2 (on next page)

Table 2 Body size and forward movement on the water surface in *Spirama retorta* larvae.

Table 2 Body size and forward movement on the water surface in *Spirama retorta* larvae.

Instar	Body weight (mg)[a]	Body length (mm)[a]	Head width (mm)[a]	Floating (%)	Forward movement (%)	*n*
First	0.4 ± 0.2	6.1 ± 0.2	0.4 ± 0.0	100	0	10
Second	8.4 ± 1.1	14.3 ± 0.5	0.7 ± 0.0	100	0	10
Third	27.9 ± 2.0	22.3 ± 0.6	1.3 ± 0.0	100	40	10
Fourth	79.1 ± 5.7	29.2 ± 0.5	2.0 ± 0.0	100	70	10
Fifth	281.6 ± 21.0	44.4 ± 0.9	2.7 ± 0.0	100	100	10
Sixth	587.4 ± 47.6	54.8 ± 1.4	3.5 ± 0.1	100	100	10
Seventh	884.8 ± 72.3	61.1 ± 1.3	4.1 ± 0.0	100	100	10

[a]Values are mean ± SE.

Table 3(on next page)

Table 3 Relationship between body size and forward movement on the water surface in

Spirama retorta larvae obtained using a generalised linear model.

Table 3 Relationship between body size and forward movement on the water surface in *Spirama retorta* larvae obtained using a generalised linear model.

Response variable	Explanatory variable (fixed effect)	Coefficient estimate	SE	*t* value	*P* value
Forward distance on water[a]	Intercept	−7.21997	1.33807	−5.396	<0.0001
	Caterpillar body length	0.28593	0.05312	5.383	<0.0001

[a]A quasi-binomial error distribution (rather than a binomial error distribution) was used because the residual deviance was smaller than the residual degrees of freedom (underdispersion).

Table 4(on next page)

Table 4 Relationship between body size and forward distance (mm/s) on the water surface in *Spirama retorta* larvae obtained using a generalised linear model.

Table 4 Relationship between body size and forward distance (mm/s) on the water surface in *Spirama retorta* larvae obtained using a generalised linear model.

Response variable	Explanatory variable (fixed effect)	Coefficient estimate	SE	*t* value	*P* value
Forward distance on water[a]	Intercept	0.995874	0.233774	4.26	<0.0001
	Caterpillar body length	0.056937	0.004376	13.01	<0.0001

[a]A quasi-Poisson error distribution (rather than a Poisson error distribution) was used because the residual deviance was larger than the residual degrees of freedom (overdispersion).

Figure 1

Figure 1 Behaviours of terrestrial caterpillars on the water surface.

(a) *Dinumma deponens* (Erebidae). (b) *Dinumma deponens* moving forward on a pond surface. (c) Undulatory behaviour in *Spirama retorta* (Erebidae). (d) Undulatory behaviour in *Hypopyra vespertilio* (Erebidae). (e) Kicking behaviour in *Acosmetia biguttula* (Noctuidae). (f) Undulatory behaviour in *Laelia coenosa* (Erebidae). Arrows indicate anal prolegs, which may function in a manner similar to that of tail fins. Photos: (a)–(e) M. Hayashi, (f) S. Sugiura.