Active swimming in terrestrial caterpillars: Implications for preadaptation to aquatic environment (#50831)

First submission

Guidance from your Editor

Please submit by **1 Aug 2020** for the benefit of the authors (and your $200 publishing discount) .

✓ **Structure and Criteria**
Please read the 'Structure and Criteria' page for general guidance.

▦ **Raw data check**
Review the raw data.

🖼 **Image check**
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files Download and review all files from the materials page.	4 Figure file(s) 4 Table file(s) 3 Video file(s)

Structure and Criteria

2

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

🗋 You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- ✓ Original primary research within Scope of the journal.
- ✓ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- ℹ Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ All underlying data have been provided; they are robust, statistically sound, & controlled.
- ✓ Speculation is welcome, but should be identified as such.
- ✓ Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Active swimming in terrestrial caterpillars: Implications for preadaptation to aquatic environment

Masakazu Hayashi Corresp., 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

Similar behaviours, including swimming, are exhibited by animals of markedly different lineages due to convergent evolution. Elucidation of the role selective pressures play in convergent evolution of behaviours is a fundamental goal in ecology and evolutionary biology. Although swimming behaviour has been reported in many animals, the evolutionary and behavioural origins of this behaviour remain unclear. Most butterfly and moth larvae are terrestrial; however, the larvae of several groups are aquatic. When terrestrial caterpillars fall into water, they may drown or be preyed upon by aquatic predators. In July 2018, we observed a terrestrial caterpillar actively swimming on the surface of a pond in Japan. To further investigate swimming in terrestrial caterpillars, we experimentally placed the larvae of 13 moth species (four families) on a water surface under laboratory and field conditions. We documented two types of swimming behaviours (undulatory and kick swimming) in seven species from two moth families (Noctuidae and Erebidae). Because some aquatic caterpillar species belong to these moth families, we posit that the active swimming observed in these terrestrial caterpillars represents preadaptation to an aquatic environment. Furthermore, we suggest potential factors related to specific morphologies, host plant habitats, and defensive behaviours that could lead to the acquisition of swimming behaviour in lepidopterans.

Active swimming in terrestrial caterpillars: implications for preadaptation to an aquatic environment

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.

[*] e-mail: hgf-haya@green-f.or.jp; sugiura.shinji@gmail.com

Corresponding author:
Masakazu Hayashi

ABSTRACT

Similar behaviours, including swimming, are exhibited by animals of markedly different lineages due to convergent evolution. Elucidation of the role selective pressures play in convergent evolution of behaviours is a fundamental goal in ecology and evolutionary biology. Although swimming behaviour has been reported in many animals, the evolutionary and behavioural origins of this behaviour remain unclear. Most butterfly and moth larvae are terrestrial; however, the larvae of several groups are aquatic. When terrestrial caterpillars fall into water, they may drown or be preyed upon by aquatic predators. In July 2018, we observed a terrestrial caterpillar actively swimming on the surface of a pond in Japan. To further investigate swimming in terrestrial caterpillars, we experimentally placed the larvae of 13 moth species (four families) on a water surface under laboratory and field conditions. We documented two types of swimming behaviours (undulatory and kick swimming) in seven species from two moth families (Noctuidae and Erebidae). Because some aquatic caterpillar species belong to these moth families, we posit that the active swimming observed in these terrestrial caterpillars represents preadaptation to an aquatic environment. Furthermore, we suggest potential factors related to specific morphologies, host plant habitats, and defensive behaviours that could lead to the acquisition of swimming behaviour in lepidopterans.

Keywords: anguilliform, Erebidae, Noctuidae, preadaptive behaviour

INTRODUCTION

Similar behaviours, including flying and swimming, are exhibited by animals of markedly different lineages due to convergent evolution (*Gleiss et al., 2011*). Elucidation of the role selective pressures play in the convergent evolution of behaviours is a fundamental goal in ecology and evolutionary biology (*Gleiss et al., 2011*). Some terrestrial animals exhibit swimming behaviour (*Miller, 1972; Franklin, Jander & Ele, 1977; Pflüger & Burrows, 1978; Graham et al., 1987; Bohn, Thornham & Federle, 2012; Yanoviak & Frederick, 2014; Gripshover, Yanoviak & Gora, 2018; Yasui et al., 2019*). Terrestrial insects such as locusts, cockroaches, praying mantises, and ants use their legs to swim (*Miller, 1972; Franklin, Jander & Ele, 1977; Pflüger & Burrows, 1978; Bohn, Thornham & Federle, 2012; Yanoviak & Frederick, 2014; Gripshover, Yanoviak & Gora, 2018*), whereas terrestrial snakes and centipedes swim by undulating their bodies to propel themselves forward (*Graham et al., 1987; Yasui et al., 2019*). The behavioural origins of these behaviours, however, have not fully been elucidated.

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 fall into water, they can drown or be preyed upon by aquatic predators such as fish (*Gustafsson, Greenberg & Bergman, 2014; Iguchi et al., 2004*). Some caterpillars (i.e., aquatic species) may have evolved behavioural responses to aquatic environments and predators to avoid these risks (*Pabis, 2018*), but the evolutionary processes underlying these aquatic behaviours remain unclear.

On July 20, 2018, we observed a terrestrial caterpillar of *Dinumma deponens* (Lepidoptera: Erebidae) swimming on the surface of a pond in Unnan, Shimane, Japan. The caterpillar undulated from side to side to propel 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 the leaves of *Albizia julibrissin* (Fabaceae) (*Kishida, 2011*). We placed the same caterpillar on the water surface again and confirmed its swimming behaviour (Fig. 1b; Video S1). This active swimming behaviour could aid in evading aquatic predators (i.e., water striders; Fig. 1b; Video S1). On the basis of this observation, we hypothesised that terrestrial caterpillars can swim 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 body size and swimming behaviour in a moth species to clarify how body size can influence propulsive power in water.

MATERIALS AND METHODS

To test the swimming capacity of terrestrial caterpillars, 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 (Table 1). 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 two larvae (*Hypopyra vespertilio* and *Acosmetia biguttula*) and one larva (*Theretra oldenlandiae*) on the surfaces of ponds in Shimane Prefecture, respectively. During each 2-min observation period, we investigated (1) whether the larva floated on the water surface and (2) whether the larva moved forward on the water surface (i.e., swam). To examine the possible behavioural origins of swimming 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 based on the morphological characteristics of the larvae (*Sugi, 1987; Yasuda, 2010, 2012, 2014; Suzuki et al., 2018*). We also reared some larvae under laboratory conditions (25°C) to identify the species based on the morphological characteristics of the emerged adults (*Kishida, 2011*).

To clarify how caterpillar size can influence propulsive power in water, we experimentally investigated the relationship between body size and swimming behaviour in the erebid species *Spirama retorta*. We reared *S. retorta* larvae from the eggs of two females that were collected in Shimane, Japan, in August 2019. We reared the larvae 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 swimming behaviours using iMovie version 10.0.6 (Apple, Inc., Cupertino, CA, USA). During each 2-min observation period, we recorded (1) whether the larva floated on the water surface, (2) whether the larva moved forward on the water surface (i.e., swam), and (3) the distance (mm) the larva had swum in 2 s.

To investigate the relationship between larval body size and swimming behaviour 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 swimming (1) or non-swimming (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 swimming distance in *S. retorta,* analysing 10 individuals per instar stage (*n* = 70). We used swimming 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 floated in this study. 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) could swim on the water surface (Table 1). Two types of swimming behaviours were observed (Table 1): larvae of *D. deponens*, *H. vespertilio*, *S. retorta*, *Laelia coenosa*, *Lymantria dispar* (Erebidae), and *Naranga aenescens* (Noctuidae) swung their bodies side to side quickly to propel themselves on the water surface (i.e., undulatory swimming; 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., kick swimming; Fig. 2b; Video S3). Although thoracic legs were not used for undulatory and kick swimming, quick movements of the anal prolegs were used to propel the caterpillars on the water surface (Videos S2 and S3). One larva of *A. biguttula* was observed kick swimming to escape from an aquatic predator in a pond (Video S3).

The relationship between body size and swimming behaviour in *S. retorta* was investigated under laboratory conditions. All larvae floated (Table 2). The frequency of swimming increased with increasing body size: 0%, 0%, 40%, 70%, 100%, 100%, and 100% of the first, second, third, fourth, fifth, sixth, and seventh instars could swim, respectively (Table 2). Consequently, swimming frequency increased with body length (Fig. 3a; Tables 2 and 3). Furthermore, the swimming speed (mm/s) increased with body length (Fig. 3b; Table 4).

Discussion

Swimming on the water surface has been observed in some aquatic and semi-aquatic caterpillars, such as those of *Bellura vulnifica* (Noctuidae) (*Welch, 1914*), *Paracles klagesi* (Erebidae) (*Meneses et al., 2013*), and *Ostrinia penitalis* (Crambidae) (*Coates & Abel, 2019*). However, terrestrial caterpillars are not considered good swimmers (*Pabis, 2018*). In the present study, we observed two types of active swimming (undulatory and kick swimming) in terrestrial caterpillars (Figs. 1, 2; Table 1). Undulatory swimming (anguilliform) 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 undulatory swimming in larvae increased with body length (Fig. 3; Tables 3 and 4). High-speed swimming can help caterpillars to avoid aquatic predators (Video S1). The kick swimming observed in *A. biguttula* was similar to the kick action of a human swimming stroke (i.e., 'dolphin kick' of the 'butterfly stroke'). However, not all caterpillar species can swim (Table 1). We propose three factors that may influence the acquisition of swimming behaviour in lepidopterans: (1) specific morphology, (2) host plant habitats, and (3) locomotive and defensive behaviours in terrestrial caterpillars.

Swimming caterpillars exhibit distinct morphological traits, such as relatively elongated bodies. In this study, long-bodied caterpillars were more capable of swimming, compared with short-bodied caterpillars (Fig. 3a; Table 3). The same pattern has been suggested to explain swimming behaviour in the aquatic caterpillar species *B. vulnifica*, although morphological traits were not quantified (*Welch, 1914*). In addition, anal prolegs could be used in a manner similar to that of tail fins. Quick movements of elongated bodies and anal prolegs could therefore result in forward propulsive power on a water surface (Fig. 1). Furthermore, long body hairs can assist in floating on the water surface in hairy caterpillars, such as those of *La. coenosa* and *Ly. dispar* (*Meyer-Rochow, 2016*). However, these morphological characters may have evolved for reasons other than swimming because long bodies, prolegs, and body hairs have other important functions—mimicking plant twigs, gripping stems, and defending against predators, respectively (Fig. 4; *Skelhorn et al., 2010; van Griethuijsen & Trimmer, 2014; Sugiura & Yamazaki, 2014*).

Caterpillars use silk threads produced from head spinnerets as lifelines to drop from host plants (*Sugiura & Yamazaki, 2006*). However, caterpillars inhabiting host plants growing by the waterside may accidentally fall into water. Six of the seven caterpillar species observed swimming in this study were collected from waterside plants, such as *A. julibrissin* (Table 1). Therefore, active swimming behaviour could help these caterpillars survive in a waterside environment.

Terrestrial behaviours may also provide insight into the behavioural origins of swimming in terrestrial caterpillars. Undulatory swimmers 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. Undulatory swimming may therefore have originated from this defensive behaviour, rather than walking behaviour. Caterpillars that exhibited kick-swimming behaviour typically move their abdomen up and down to move on land (i.e., crawling; *van Griethuijsen & Trimmer, 2014*; Table 1); the similarity of the kick-swimming and crawling motions suggests that kick swimming originated from the crawling motion.

Swimming behaviour was observed in two lepidopteran families—Erebidae and Noctuidae

(Table 1). These moth families also include some aquatic caterpillar species (*Welch, 1914*; *Meneses et al., 2013*). Therefore, we posit that active swimming in terrestrial caterpillars represents preadaptation to an aquatic environment. Although the insect order Lepidoptera contains 133 recognised families (*Mitter, Davis & Cummings, 2017*), our investigation was limited to four families. Active swimming will likely be found in other lepidopteran families (e.g., Crambidae) that include aquatic caterpillar species.

ACKNOWLEDGEMENTS

We thank K. Sakagami for aiding in moth identification. We also thank 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 assigned to protected species ~~in~~ the study sites. ~~In~~ addition, 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.

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.

Gleiss AC, Jorgensen SJ, Liebsch N, Sala JE, Norman B, Hays GC, Quintana F, Grundy E, Campagna C, Trites AW, Block BA, Wilson RP. 2011. Convergent evolution in locomotory patterns of flying and swimming animals. *Nature Communications* **2**: 352 DOI 10.1038/ncomms1351.

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

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.

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.

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.

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

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.

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.

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.

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

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.

Yasuda M. 2012. *The Handbook of Japanese caterpillar I*. Tokyo: Bun-ichi Sogo Shuppan.

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

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 Swimming behaviour in terrestrial caterpillars. (a) *Dinumma deponens*. (b) *Dinumma deponens* swimming on the surface of a pond. (c) Undulatory swimming in *Spirama retorta*. (d) Undulatory swimming in *Hypopyra vespertilio*. (e) Kick swimming in *Acosmetia biguttula*. (f) Undulatory swimming in *Laelia coenosa*. Arrows indicate anal prolegs, which may function in a manner similar to that of tail fins.

Figure 2 Active swimming in terrestrial caterpillars. (a) Temporal sequence of undulatory swimming in *Hypopyra vespertilio*. (b) Temporal sequence of kick swimming in *Acosmetia biguttula*.

Figure 3 Relationship between body size and swimming behaviour in *Spirama retorta.* (a) Relationship between body length and swimming behaviour (n = 70). (b) Relationship between body length and swimming speed (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).

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).

Supplementary videos

Video S1 Undulatory swimming by a *Dinumma deponens* larva on the water surface of a pond.

Active swimming could aid in evading water striders (*Aquarius paludum*).

Video S2 Undulatory swimming by *Hypopyra vespertilio* larvae under laboratory and field conditions.

Video S3. Kick swimming by *Acosmetia biguttula* larvae under laboratory and field conditions.

Active swimming could aid in evading predation by backswimmers (*Notonecta triguttata*) in the pond.

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/b1ud93

Table 1(on next page)

Table 1 Swimming and other behaviours of the caterpillars placed on the water surface.

Table 1 Swimming and other behaviours of the caterpillars placed on the water surface.

Family	Subfamily	Species	Instar	Body length (mm)	Host plant range	Plant species (sampling)	Habitat (sampling)	Walking	Behavior on the water surface	Swimming % (*n*)
Erebidae	Erebinae	*Hypopyra vespertilio*	Middle-late	23–70	Fabaceae	*Albizia julibrissin*	Lake bank	locomotion	Undulatory swimming	100 (7/7) †
		Spirama retorta	Middle-late	8–42	Fabaceae	*Albizia julibrissin*	Lake bank	Inching	Undulatory swimming	100 (3/3)
	Scoliopteryginae	*Dinumma deponens*	Middle-late	20–32	*Albizia julibrissin*	*Albizia julibrissin*	Lake bank	Inching	Undulatory swimming / floating	33 (1/3)
	Lymantriinae	*Laelia coenosa*	Late	22–34	Poaceae, Cyperaceae, Typhaceae	*Typha latifolia* L.	Pondside	Inching	Undulatory swimming	100 (6/6)
		Lymantria dispar	Late	33–54	Many families	*Cerasus* × *yedoensis*	Urban area	Crawling	Undulatory swimming / floating	30 (3/10)
Noctuidae	Bagisarinae	*Xanthodes transversa*	Middle-late	25–42	Malvaceae	*Hibiscus mutabilis*	Garden	Crawling	Floating	0 (0/2)
	Condicinae	*Acosmetia biguttula*	Middle-late	20–38	*Bidens*	*Bidens frondosa*	Pondside	Inching	Kick swimming	100 (6/6) †
	Eustrotiinae	*Naranga aenescens*	Middle-late	13–24	Poaceae	*Pseudoraphis sordida*	Abandoned paddy field	Crawling	Undulatory swimming	100 (4/4)
	Hadeninae	*Sarcopolia illoba*	Early-middle	19–34	Many families	*Albizia julibrissin*	Lake bank	Inching	Floating	0 (0/3)
	Phytometrinae	*Britha inambitiosa*	Middle-late	13–20	*Pterostyrax hispidus*	*Pterostyrax hispidus*	Streamside	Crawling	Floating	0 (0/3)
Geometridae	Ennominae	*Chiasmia defixaria*	Middle-late	20–30	*Albizia julibrissin*	*Albizia julibrissin*	Lake bank	Inching	Floating	0 (0/3)
		Ectropis excellens	Late	30	Many families	*Pterostyrax hispidus*	Streamside	Inching	Floating	0 (0/1)
Sphingidae	Macroglossinae	*Theretra oldenlandiae*	Early	20	Many families	*Causonis japonica*	Garden	Inching	Floating	0 (0/1) †

† 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 swimming behaviour of *Spirama retorta*larvae.

Table 2 **Body size and swimming behaviour of *Spirama retorta* larvae.**

Instar	Body weight (mg) †	Body length (mm) †	Head width (mm) †	Floating (%)	Swimming (%)	*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

† Values are mean ± SE.

Table 3(on next page)

Table 3 Relationship between body size and swimming behaviour in *Spirama retorta*larvae obtained using a generalised linear model.

Table 3 Relationship between body size and swimming behaviour in *Spirama retorta* larvae obtained using a generalised linear model.

Response variable	Explanatory variable (fixed effect)	Coefficient estimate	SE	*t* value	*P* value
Swimming behavior †	Intercept	−7.21997	1.33807	−5.396	<0.0001
	Caterpillar body length	0.28593	0.05312	5.383	<0.0001

† 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 swimming distance (mm/s) in *Spirama retorta* larvae obtained using a generalised linear model.

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

Response variable	Explanatory variable (fixed effect)	Coefficient estimate	SE	*t* value	*P* value
Swimming distance †	Intercept	0.995874	0.233774	4.26	<0.0001
	Caterpillar body length	0.056937	0.004376	13.01	<0.0001

† 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 Swimming behaviour in terrestrial caterpillars.

(a) *Dinumma deponens*.(b) *Dinumma deponens* swimming on the surface of a pond. (c) Undulatory swimming in *Spirama retorta*. (d) Undulatory swimming in *Hypopyra vespertilio*. (e) Kick swimming in *Acosmetia biguttula*. (f) Undulatory swimming in *Laeliacoenosa*. Arrows indicate anal prolegs,which may function in a manner similar to that of tail fins.


a
b
c
d
90
100
110
120
130
e
f

Figure 2

Figure 2 Active swimming in terrestrial caterpillars.

(a) Temporal sequence of undulatory swimmingin *Hypopyra vespertilio*. (b) Temporal sequence of kick swimming in *Acosmetia biguttula*.

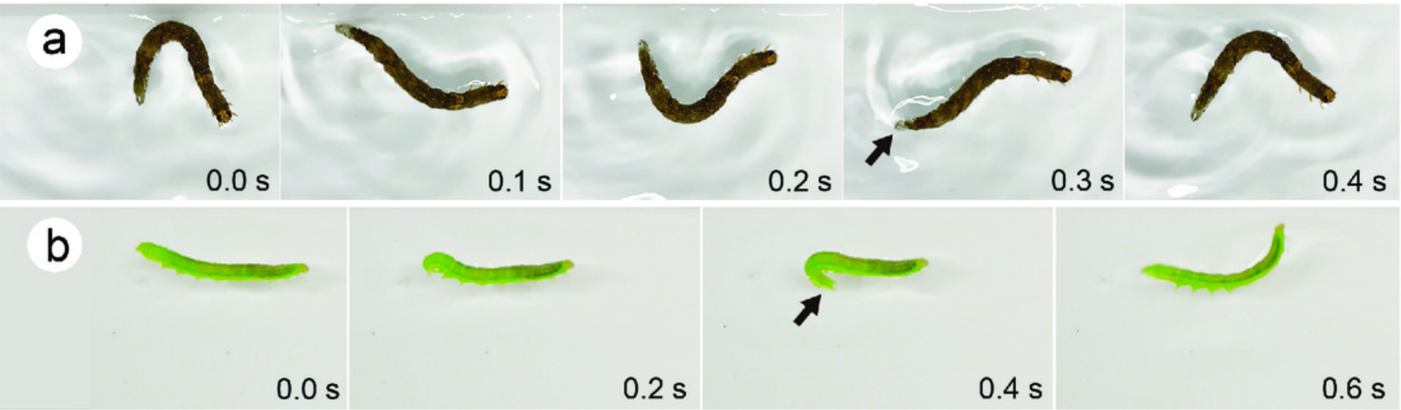

Figure 3

Figure 3 Relationship between body size and swimming behaviour in *Spirama retorta.*

(a) Relationship between body length and swimming behaviour (*n*= 70[illegible]b) Relationship between body length and swimming speed (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).

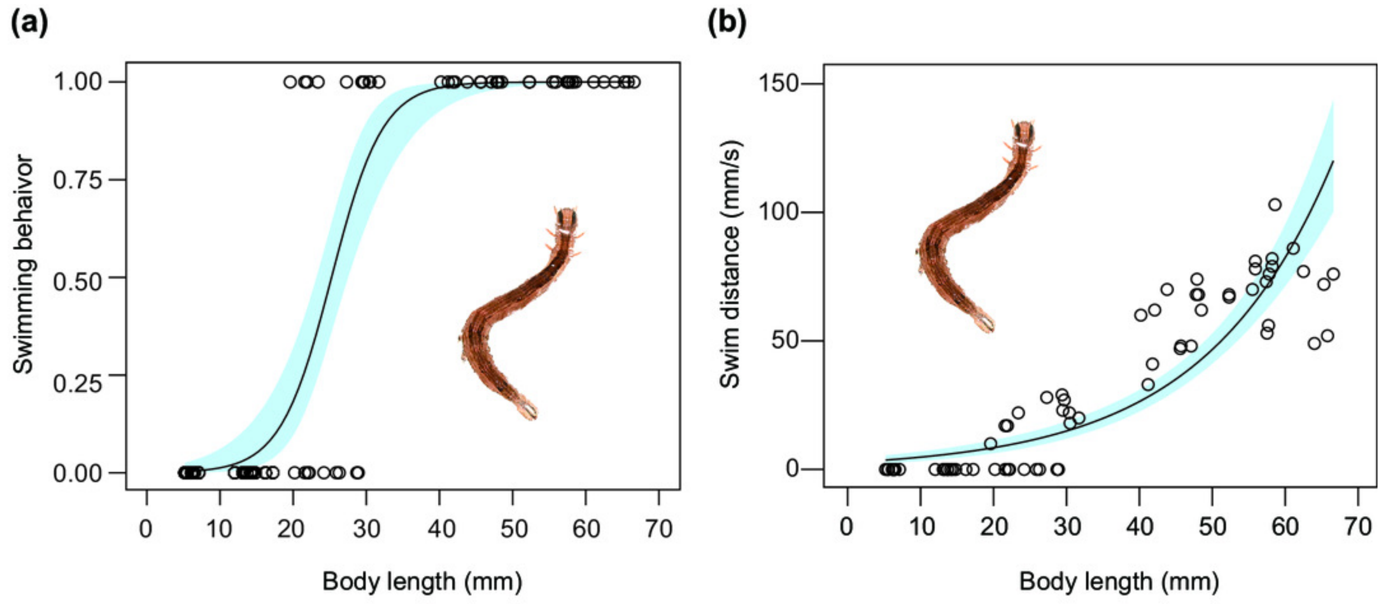

Figure 3

Figure 4

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).