Active swimming of terrestrial caterpillars on the water surface (#50831)

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Active swimming of terrestrial caterpillars on the water surface

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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 swimming on the surface of a pond in Japan until it successfully reached the shore. To further investigate this behaviourin 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 species swam on the water surface, whereas those of six species did not. Two types of swimming behaviour 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 swimming); in contrast, larvae of *Acosmetia biguttula* (Noctuidae) rapidly moved the abdomen (posterior segments) up and down for propulsion along the water surface (i.e., flick swimming). Although thoracic legs were not used for undulatory and flick swimming, rapid movements of the abdomen were used to propel caterpillars on the water surface. We also observed that undulatory and flick swimming on the water surface aided caterpillars in escaping aquatic predators under field conditions. In addition, we investigated the relationship between body size and undulatory swimming on the water surface in the erebid *S. retorta* under laboratory conditions. The frequency and speed of swimming 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 behaviour that may have led to the acquisition of swimming behaviour in terrestrial caterpillars.

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Running title (40 characters): Swimming in terrestrial caterpillars

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 swimming 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 species swam on the water surface, whereas those of six species did not. Two types of swimming behaviour 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 swimming); in contrast, larvae of *Acosmetia biguttula* (Noctuidae) rapidly moved the abdomen (posterior segments) up and down for propulsion along the water surface (i.e., flick swimming). Although thoracic legs were not used for undulatory and flick swimming, rapid movements of the abdomen were used to propel caterpillars on the water surface. We also observed that undulatory and flick swimming on the water surface aided caterpillars in escaping aquatic predators under field conditions. In addition, we investigated the relationship between body size and undulatory swimming on the water surface in the erebid *S. retorta* under laboratory conditions. The frequency and speed of swimming 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 behaviour that may have led to the acquisition of swimming behaviour in

terrestrial caterpillars.

Keywords: anguilliform, aquatic behaviour, 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 swim 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*). Swimming behaviour has been reported for the adult stages of terrestrial insects, but rarely for the immature stages.

The larvae of butterflies and moths (Lepidoptera) are predominantly terrestrial; however, approximately 0.5% of 157,000 known species are aquatic at the larval stage (*van Nieukerken et al. 2011; 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* Walker (Lepidoptera: Erebidae) moving forward on the water surface of a pond in Unnan, Shimane, Japan. The caterpillar undulated from side to side, propelling 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* Durazz. (Fabaceae), which commonly grows 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 ‘swimming’ behaviour on the water surface appeared to avoid drowning and

aquatic predators (e.g., water striders; Fig. 1b; Video S1).

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

MATERIALS AND METHODS

To test whether terrestrial caterpillars can swim on the water surface, we experimentally placed the larvae of 13 moth species (from four families) on a water surface and observed their behaviour 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) 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* (Fabricius) (Erebidae), *Acosmetia biguttula* (Motschulsky) (Noctuidae), and *Theretra oldenlandiae* (Fabricius) (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 (i.e., swam) on the water surface. To examine the possible 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 caterpillar based on their morphological characteristics (*Sugi, 1987; Yasuda, 2010, 2012, 2014; Suzuki et al., 2018*), and raised some larvae to the adult stage to confirm their identity (*Kishida, 2011*).

In caterpillars, various types of behaviour 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 swimming behaviour in the erebid *Spirama retorta* (Clerck) (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 individually on the water surface in a plastic vessel (390 × 265 × 65 mm) with 2 L of water (20 mm depth) under well-lit conditions at 25°C. We filmed the behaviour of the larvae (n = 70) using video cameras (V2; Nikon, Tokyo, Japan). We played back the footage of the recorded behaviour 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 (i.e., swam) 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 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 (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 (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 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) swam on the water surface (Table 1). Two types of swimming behaviour were observed (Table 1): larvae of *D. deponens*, *H. vespertilio*, *S. retorta*, *Laelia coenosa* (Hübner), *Lymantria dispar* (Linnaeus) (all Erebidae), and *Naranga aenescens* Moore (Noctuidae) swung their bodies side to side quickly to propel themselves on the water surface (i.e., undulatory swimming; Figs. 1c–e, 2a; Video S2); in contrast, larvae of *A. biguttula* (Noctuidae) moved the end of the abdomen (posterior segments) up and down quickly to propel themselves on the water surface (i.e., flick swimming; Figs. 1f, 2b; Video S3). Thoracic legs were not used for undulatory and flick swimming (Videos S2, S3). One larva of *A. biguttula* was observed escaping from an aquatic predator (*Notonecta triguttata* Motschulsky) in a pond (Video S3).

The relationship between body size and undulatory swimming in *S. retorta* was investigated under laboratory conditions. All larvae floated (Table 2). The frequency of swimming 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 seventh instars swam on the water surface, respectively (Table 2). Furthermore, the swimming speed (mm/s) increased with body

141 length (Fig. 3b; Table 4).

142

143 **DISCUSSION**

144 Aquatic behaviour on/under the water surface have been reported in some aquatic and semi-
145 aquatic caterpillars (*Welch, 1914; Mey & Speidel, 2008; Meneses et al., 2013; Coates & Abel,*
146 *2019; De-Freitas, De Agostini & Stefani, 2019*). The aquatic larvae of *Paracles klagesi*
147 (Rothschild) (Erebidae: Arctiinae) and *Neoschoenobia testacealis* Hampson (Crambidae) move
148 and feed under the water surface (*Nagasaki, 1992; Meneses et al., 2013*), and semi-aquatic larvae
149 of moths such as *Bellura vulnifica* (Grote) (Noctuidae) and *Ostrinia penitalis* (Grote)
150 (Crambidae) can swim on the water surface (*Welch, 1914; Coates & Abel, 2019*). However,
151 whether typically terrestrial caterpillars can swim on or under the water surface has received
152 little attention. In the present study, we observed the behaviour on water surfaces of 13 terrestrial
153 caterpillar species from four families under laboratory and field conditions. Among these, seven
154 species were observed to swim on the water surface (Figs. 1 and 2; Table 1), none broke through
155 the surface tension. We also observed two types of swimming behaviour on the water surface
156 (undulatory and flick swimming) in the caterpillars (Figs. 1 and 2; Table 1). The undulatory
157 swimming observed in this study was similar to anguilliform movement, which has been
158 reported in slender-bodied animals such as eels, snakes, and centipedes (*Graham et al., 1987;*
159 *Sfakiotakis, Lane & Davies, 1999; Yasui et al., 2019*). The frequency and speed of undulatory
160 swimming increased with body length in *S. retorta* larvae (Fig. 3; Tables 3 and 4). Directed
161 movements on the water surface can help caterpillars to avoid aquatic predators (Video S1).
162 All of the terrestrial caterpillars used in the present study floated due to water surface tension.
163 Some, but not all, of these floating caterpillars swam on the water surface (Table 1). Three
164 factors may influence the acquisition of swimming behaviour in terrestrial caterpillars: (1)

morphology, (2) host plant habitat, and (3) locomotive and defensive behaviour.

Caterpillars that swam had distinct morphological traits such as relatively elongated bodies. In this study, long-bodied caterpillars were more capable of swimming than those with short bodies (Fig. 3a; Table 3). This relationship has been suggested to explain the swimming behaviour of the semi-aquatic caterpillar species *E. vulnifica*, although its morphological traits were not quantified (*Welch, 1914*). In addition, 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 swimming behaviour, because long bodies, prolegs, and body hairs have other important functions in their terrestrial habitats, e.g., they may be involved in natural enemy defence, maintaining their perch, and still others (Fig. 4; *Skelhorn et al., 2010; van Griethuijsen & Trimmer, 2014; Sugiura & Yamazaki, 2014*).

Caterpillars use silk threads emitted from their spinnerets to disperse aerially (*Bell et al., 2005*) or 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 descend into open water. Six of the seven caterpillar species observed swimming in this study were collected from waterside plants such as *A. julibrissin* (Table 1).

Terrestrial behaviour may also provide insight into the origins of swimming behaviour in terrestrial caterpillars. Caterpillars that exhibit undulatory swimming 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 swimming may have originated from this defensive behaviour, rather than walking behaviour. Caterpillars that exhibit flick swimming typically move their abdomen up and down

to move on land (i.e., crawling; *van Griethuijsen & Trimmer, 2014*; Table 1); the similarity of the flick-swimming and crawling motions suggests that flick swimming originated from crawling motion.

CONCLUSIONS

Our results showed that some terrestrial caterpillars could swim 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 swimming behaviour observed in terrestrial caterpillars in this study will probably be found in other lepidopteran families. However, future studies will likely find that many species of terrestrial caterpillars are unable to swim. Differences in swimming ability among species should be investigated. Kinematic and anatomical studies may help elucidate the mechanism of swimming behaviour in lepidopteran larvae.

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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 areas 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/

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Figure legends

Figure 1 Swimming behaviour in terrestrial caterpillars. (a) *Dinumma deponens* (Erebidae). (b) *Dinumma deponens* swimming on a pond surface. (c) Undulatory swimming in *Spirama retorta* (Erebidae). (d) Undulatory swimming in *Hypopyra vespertilio* (Erebidae). (e) Undulatory swimming in *Laelia coenosa* (Erebidae). (f) Flick swimming in *Acosmetia biguttula* (Noctuidae). Arrows indicate anal prolegs. Photo credit: (a–d, f) M. Hayashi, (e) S. Sugiura.

Figure 2 Two types of swimming behaviour in terrestrial caterpillars. (a) Temporal sequence of undulatory swimming in *Hypopyra vespertilio*. (b) Temporal sequence of flick swimming in *Acosmetia biguttula*. Arrows indicate anal prolegs. Photo credit: (a) S. Sugiura, (b) M. Hayashi.

Figure 3 Relationship between body size and swimming behaviour in *Spirama retorta.* (a) Relationship between body length and frequency of undulatory swimming (n = 70). (b) Relationship between body length and swimming speed (mm/s) (n = 70). Lines and blue areas represent logistic regression lines and 95% confidence intervals derived from generalised linear models, respectively (Tables 3 and 4). Photo credit: 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). Photo credit: S. Sugiura.

Supplementary videos

Video S1. Undulatory swimming by a *Dinumma deponens* larva on a pond water surface. Active swimming aided the larva in evading water striders [*Aquarius paludum* (Fabricius)]. Video credit: M. Hayashi.

Video S2. Undulatory swimming by *Hypopyra vespertilio* larvae under laboratory and field conditions. Video credit: S. Sugiura and M. Hayashi.

Video S3. Flick swimming by *Acosmetia biguttula* larvae under laboratory and field conditions. Active swimming aided the larva in evading predation by a backswimmer (*Notonecta triguttata*) in the pond. Video credit: M. Hayashi.

Table 1(on next page)

Table 1 Swimming behaviour of the caterpillars placed on water surfaces.

Table 1 Swimming ~~Behaviours~~ behaviour of the caterpillars placed on water surfaces.

Family	Species	Instar[a]	Length (mm)	Host plant range	Plant species (sampling)	Habitat (sampling)	Walking locomotion	Swimming ~~Behavior~~behaviour ~~on water~~[b]	~~Forward movement on water~~ Frequency of swimming % (*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~~Flick	100 (6/6)[c]
	Naranga aenescens							Undulatory	100 (4/4)
		M–L	13–24	Poaceae	*Pseudoraphis sordida*	Paddy field	Inching		
	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~~ Swimming behaviour on the water surface: Undulatory, forward movement by undulating; ~~Kicking~~Flick, forward movement by ~~kicking~~flicking; –, 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.

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Table 2(on next page)

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

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

Instar	Body weight (mg)[a]	Body length (mm)[a]	Head width (mm)[a]	Floating (%)	~~Forward movement~~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

[a]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 ~~forward movement on the water surfaces~~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
~~Forward distance on water~~Swimming behaviour[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)

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). Photo credit: S. Sugiura.

Table 4 Relationship between body size and ~~forward~~ swimming 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~~Swimming distance[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 Swimming behaviour in terrestrial caterpillars.

(a) *Dinumma deponens* (Erebidae). (b) *Dinumma deponens* swimming on a pond surface. (c) Undulatory swimming in *Spirama retorta* (Erebidae). (d) Undulatory swimming in *Hypopyra vespertilio* (Erebidae). (e) Undulatory swimming in*Laelia coenosa* (Erebidae). (f) Flick swimming in *Acosmetia biguttula* (Noctuidae). Arrows indicate anal prolegs. Photo credit: (a–d, f) M. Hayashi, (e) S. Sugiura.


a
b
c
d
e
f

Figure 2

Figure 2 Two types of swimming behaviour in terrestrial caterpillars.

(a) Temporal sequence of undulatory swimming in *Hypopyra vespertilio*. (b) Temporal sequence of flick swimming in *Acosmetia biguttula*. Arrows indicate anal prolegs. Photo credit: (a) S. Sugiura, (b) M. Hayashi.

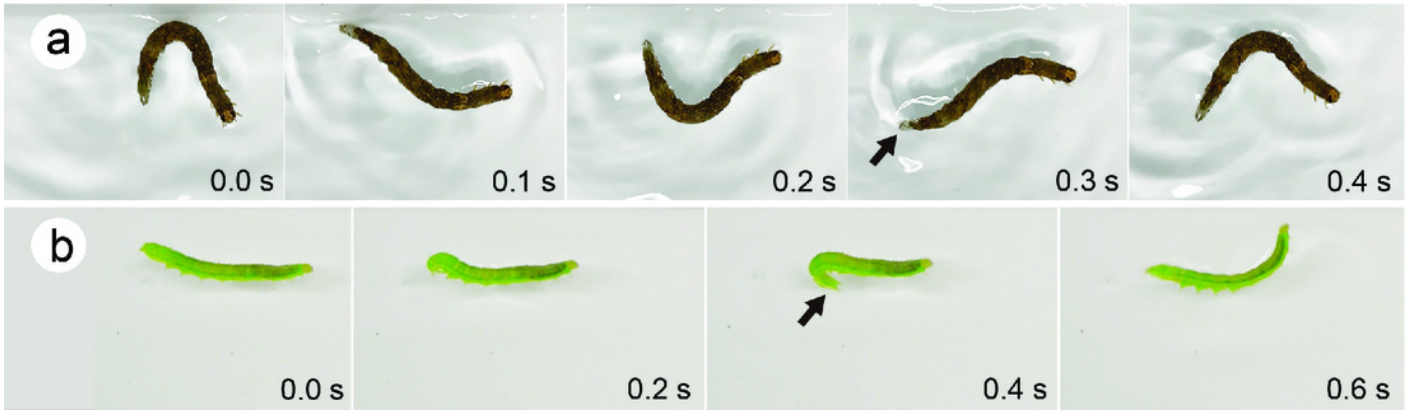

Figure 3

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

(a) Relationship between body length and frequency of undulatory swimming (*n* = 70). (b) Relationship between body length and swimming speed (mm/s) (*n* = 70). Lines and blue areas represent logistic regression lines and 95% confidence intervals derived from generalised linear models, respectively (Tables 3 and 4). Photo credit: M. Hayashi.

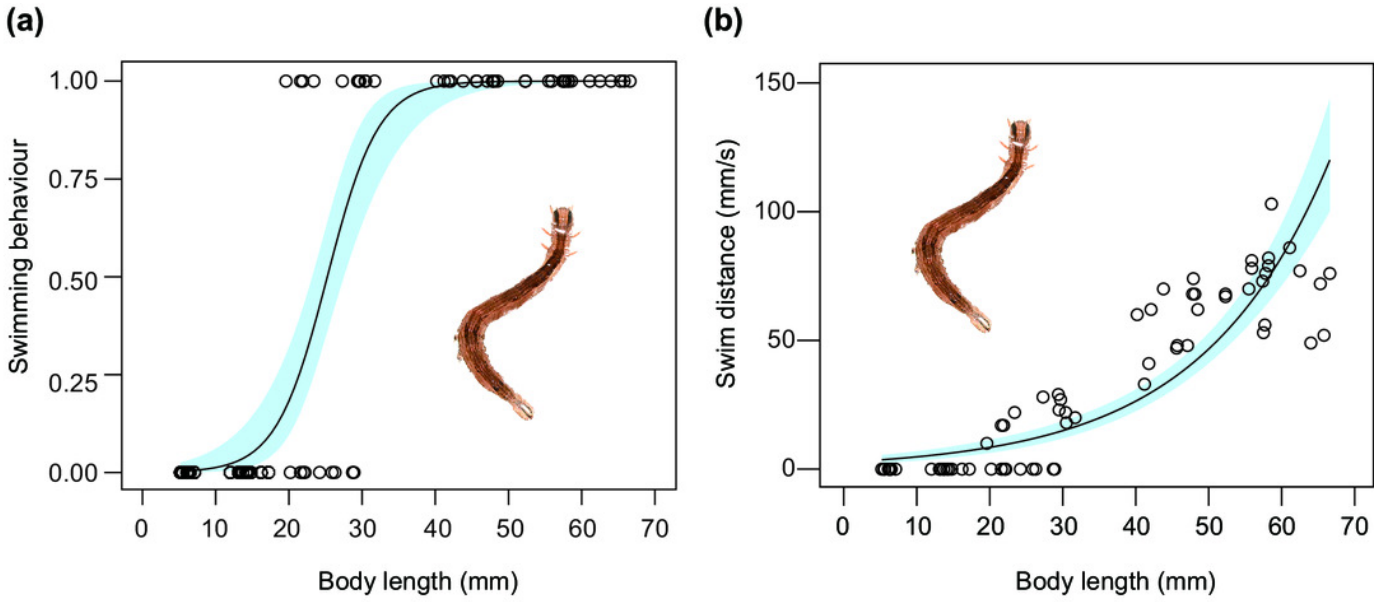

Figure 3

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). Photos: S. Sugiura.