

UC Berkeley

UC Berkeley Previously Published Works

Title

Moving like a model: mimicry of hymenopteran flight trajectories by clearwing moths of Southeast Asian rainforests

Permalink

<https://escholarship.org/uc/item/7w43j7c4>

Journal

Biology Letters, 14(5)

ISSN

1744-9561

Authors

Volponi, Marta A Skowron
McLean, Donald James
Volponi, Paolo
et al.

Publication Date

2018-05-01

DOI

10.1098/rsbl.2018.0152

Peer reviewed

Research



Cite this article: Skowron Volponi MA, McLean DJ, Volponi P, Dudley R. 2018 Moving like a model: mimicry of hymenopteran flight trajectories by clearwing moths of Southeast Asian rainforests. *Biol. Lett.* **14**: 20180152. <http://dx.doi.org/10.1098/rsbl.2018.0152>

Received: 5 March 2018
Accepted: 13 April 2018

Subject Areas:
behaviour, ecology

Keywords:
Batesian mimicry, Sesiidae, locomotor mimicry

Author for correspondence:
Marta A. Skowron Volponi
e-mail: marta.a.skowron@gmail.com

Animal behaviour

Moving like a model: mimicry of hymenopteran flight trajectories by clearwing moths of Southeast Asian rainforests

Marta A. Skowron Volponi^{1,2}, Donald James McLean³, Paolo Volponi² and Robert Dudley⁴

¹Department of Molecular Biology, Faculty of Biology, University of Gdansk, 80-308 Gdansk, Poland

²ClearWing Foundation for Biodiversity, 01-866 Warsaw, Poland

³Department of Biological Sciences, Macquarie University, Sydney, NSW, 2109, Australia

⁴Department of Integrative Biology, University of California, Berkeley, CA 94720, USA

MASV, 0000-0001-5525-0566; DJM, 0000-0001-6229-7063; RD, 0000-0003-3707-5682

Clearwing moths are known for their physical resemblance to hymenopterans, but the extent of their behavioural mimicry is unknown. We describe zigzag flights of sesiid bee mimics that are nearly indistinguishable from those of sympatric bees, whereas sesiid wasp mimics display faster, straighter flights more akin to those of wasps. In particular, the flight of the sesiids *Heterosphacia pahangensis*, *Aschistophleps argentifasciata* and *Pyrophleps cruentata* resembles both *Tetragonilla collina* and *T. atripes* stingless bees and, to a lesser extent, dwarf honeybees *Apis andreniformis*, whereas the sesiid *Pyrophleps* sp. resembles *Tachysphex* sp. wasps. These findings represent the first experimental evidence for behavioural mimicry in clearwing moths.

1. Introduction

Clearwing moths (Lepidoptera: Sesiidae) are a textbook example of Batesian mimicry, being non-toxic insects that imitate various bees and wasps to gain protection from predators. Their morphological resemblance to hymenopterans is widely known, but the evidence for behavioural mimicry in Sesiidae has thus far only been anecdotal [1–6]. Webster [3, p.67] suggested as early as 1897 that:

(...) *Podosesia syringae* Harris, somewhat resembles *Polistes annularis* Linnaeus, in form, while its movements are almost an exact reproduction of those of the latter species, which is an armed wasp, while the former is a helpless moth. (...) There are a number of insects that, prepared and placed in our cabinets, have comparatively little resemblance to each other, while in the midst of life and activity, are distinguishable from each other only with extreme difficulty.

More generally, locomotor mimicry has been characterized under laboratory or enclosure conditions for tracks of ant-mimicking spiders [7,8], and for the flight of *Heliconius* [9] and *Papilio polytes* [10] butterflies. Golding *et al.* [11] recorded hoverflies and their hymenopteran models under conditions similar to natural environments. During our fieldwork in Malaysia, which led to the description of a new species of sesiid, *Heterosphacia pahangensis* Skowron [4], we observed that it flies in a zigzag trajectory nearly indistinguishable from that of similarly sized bees occurring in the same area. *Tachysphex* wasps, on the other hand, flew faster and with straighter trajectories, and were easily distinguished from both bees and bee mimics.

As already noted by Webster, Sesiidae are not necessarily perfect morphological mimics. The evolution of imperfect mimicry has been evaluated from

Table 1. Comparison of natural logarithm of mean speed (m s^{-1}) by species. ANOVA, $F_{7,64} = 13.62$, $p = 1.23 \times 10^{-10}$. Tukey–Kramer test showed significant differences (indicated by an asterisk) between pairs of species. The per cent ratio between sample means indicates the magnitude and direction of differences between each pair of species. Upper value: p , lower: relative sample means (untransformed) as per cent (column/row), e.g. *H. pahangensis* was more than two times slower than *Tachysphex* sp. (ratio 42%). (Online version in colour.)

| | <i>H. pahangensis</i> | <i>A. argentifasciata</i> | <i>P. cruentata</i> | <i>T. collina</i> | <i>T. atripes</i> | <i>A. andreniformis</i> | <i>Pyrophleps</i> sp. |
|---------------------------|-----------------------|---------------------------|----------------------|----------------------|----------------------|-------------------------|-----------------------|
| <i>A. argentifasciata</i> | $p = 0.806$ 136% | | | | | | |
| <i>P. cruentata</i> | $p = 0.006^*$ 214% | $p = 0.736$ 157% | | | | | |
| <i>T. collina</i> | $p = 0.934$ 122% | $p = 0.998$ 89% | $p = 0.098$ 57% | | | | |
| <i>T. atripes</i> | $p = 1.000$ 103% | $p = 0.924$ 76% | $p = 0.020^*$ 48% | $p = 0.994$ 84% | | | |
| <i>A. andreniformis</i> | $p = 0.101$ 64% | $p = 0.024^*$ 47% | $p = 0.000^*$ 30% | $p = 0.005^*$ 52% | $p = 0.067$ 62% | | |
| <i>Pyrophleps</i> sp. | $p = 0.009^*$ 36% | $p = 0.002^*$ 27% | $p = 0.000^*$ 17% | $p = 0.001^*$ 30% | $p = 0.006^*$ 35% | $p = 0.479$ 57% | |
| <i>Tachysphex</i> sp. | $p = 0.000^*$ 42% | $p = 0.000^*$ 31% | $p = 0.000^*$ 20% | $p = 0.000^*$ 34% | $p = 0.000^*$ 41% | $p = 0.290$ 66% | $p = 1.000$ 116% |

■ – bee mimics, ■ – bees, ■ – wasp mimics, ■ – wasps. ■ – unexpected p values

diverse perspectives. We consider three possible scenarios underpinning this phenomenon in our studied clearwing moths: (i) selection pressure imposed by predators led to developing accurate behavioural mimicry that compensates for morphological imperfections; (ii) different predators exerted opposing selective forces leading to the development of an optimal mimetic phenotype (multiple predator hypothesis [12]); and (iii) by frequenting diverse habitats, they have evolved to resemble multiple models [13]. We here present detailed documentation of unperturbed flight trajectories for clearwing moths in their natural habitat, and assess the extent of their locomotor mimicry relative to flight of sympatric hymenopterans.

2. Material and methods

Flight videos were obtained in Southeast Asian rainforests along banks of rivers. Only natural flight behaviours were filmed, without use of attractants or of captured insects. A Sony DSC-RX10 camera was mounted on a tripod at 90° to the ground to obtain a vertical view (approx. 100 cm from the ground). A measuring tape was placed on the ground for calibration. Videos are either 1000 or 500 frames per second. All of the studied insects flew in a relatively horizontal plane right above the ground (approx. 1–10 cm). Filming was triggered only when there was no discernible wind.

Flight trajectories for the following insects were obtained: bee-mimicking sesiids *H. pahangensis* ($n = 14$), *Aschistophleps argentifasciata* Skowron Volponi ($n = 4$) and *Pyrophleps cruentata* Swinhoe ($n = 6$); wasp-mimicking sesiid *Pyrophleps* sp. ($n = 4$); stingless bees, *Tetragonilla collina* Smith ($n = 12$) and *T. atripes* Smith 1857 ($n = 11$); dwarf honeybee *Apis andreniformis* Smith ($n = 13$) and wasps, *Tachysphex* sp. ($n = 9$) (figure 1). One of the *Pyrophleps* sp. flights was excluded from analysis because the insect landed mid-way through the filmed trajectory. The bee and wasp species were selected because they occurred in the same area as the sesiids, displayed similar mud-puddling behaviour, were all of similar size (body length: bees, 5–10 mm; bee mimics, 5–11 mm; wasps, approx. 8 mm; wasp mimics, approx. 9 mm), and when in flight, were often confused with sesiids (M.A.S.V. & P.V. 2014–2018, personal observations).

Out of the studied sesiids, only *H. pahangensis* is relatively abundant in one puddling hotspot (fewer than 10 individuals were observed per day, and this was the highest count for all Sesiidae). *Aschistophleps argentifasciata* was an undescribed species at the time of fieldwork, and a total of only seven individuals were observed over two expeditions to Thailand, along with nine sightings of *P. cruentata* and five of *Pyrophleps* sp. The small sample sizes reported here are thus due to difficulty in locating and rarity of these insects.

Fieldwork permission was obtained in Malaysia from the Economic Planning Unit; permission was not required in Thailand outside protected areas.

The DLTdv5 digitizing package [14] in MATLAB (v. R2016b) was used to digitize flight trajectories from videos. Because of variable and irregular backgrounds, each trajectory was manually digitized frame-by-frame to obtain (x and y) coordinates of the head through time.

These data were smoothed using a Savitzky–Golay filter (window size of 101 samples, polynomial order of 3). We calculated and compared the following parameters for flight trajectories among species: flight speed (mean, minimum, maximum and standard deviation); maximum time of a single hovering event; straightness; sinuosity; E_{\max} , another measure of path straightness [15]; direction autocorrelation, which captures the wavelength (Δs) and amplitude ($C(\Delta s)$) of periodicity in a trajectory [8]; and the mean and standard deviation of directional change [10]. When necessary, variables were log or square root transformed to obtain normal distributions. Multivariate analysis of variance (MANOVA) was used for data analysis, followed by ANOVA tests for each variable and *post hoc* Tukey–Kramer tests (when $p < 0.05$ in ANOVA) correcting for type I errors. Significant differences in the Tukey–Kramer test are reported with a 95% confidence level ($\alpha = 0.05$; e.g. table 1).

Additionally, we performed a principal component (PC) analysis, followed by ANOVA and Tukey–Kramer test on the first principal component (PC1) results, table 2). Hovering, defined here as flight at a speed of less than 0.1 m s^{-1} (determined from speed–density plot analyses), was excluded from statistical analyses as it was not normally distributed. However, we present the longest hovering time in a box plot (figure 2b), as during the observed puddling behaviour, bees and bee mimics tended to hover, whereas wasps and wasp mimics never did. All calculations, plots and statistical tests were performed in

Table 2. Principal component analysis. (a) ANOVA of PC1 results yielded significant differences among species, $F_{7,64} = 10.01$, $p = 2.22 \times 10^{-8}$. *Post hoc* Tukey–Kramer test showed significant differences (indicated by an asterisk) between pairs of species. (b) Correlation loadings of first three PCs. (c) Eigenvalues and the percentage of variation explained by first three components. (Online version in colour.)

| (a) | <i>H. pahangensis</i> | <i>A. argentifasciata</i> | <i>P. cruentata</i> | <i>T. collina</i> | <i>T. atripes</i> | <i>A. andreniformis</i> | <i>Pyrophleps</i> sp. |
|---------------------------|-----------------------|---------------------------|---------------------|-------------------|-------------------|-------------------------|-----------------------|
| <i>A. argentifasciata</i> | $p = 0.999$ | | | | | | |
| <i>P. cruentata</i> | $p = 0.995$ | $p = 1.000$ | | | | | |
| <i>T. collina</i> | $p = 0.988$ | $p = 0.930$ | $p = 0.846$ | | | | |
| <i>T. atripes</i> | $p = 0.698$ | $p = 0.649$ | $p = 0.452$ | $p = 0.992$ | | | |
| <i>A. andreniformis</i> | $p = 0.086$ | $p = 0.184$ | $p = 0.067$ | $p = 0.521$ | $p = 0.957$ | | |
| <i>Pyrophleps</i> sp. | $p = 0.001^*$ | $p = 0.002^*$ | $p = 0.001^*$ | $p = 0.007^*$ | $p = 0.034^*$ | $p = 0.161$ | |
| <i>Tachysphex</i> sp. | $p = 0.000^*$ | $p = 0.000^*$ | $p = 0.000^*$ | $p = 0.000^*$ | $p = 0.002^*$ | $p = 0.025^*$ | $p = 1.000$ |

| (b) | correlation loadings | | | (c) | PC1 | PC2 | PC3 |
|----------------------------|----------------------|--------|--------|-----------------------------------|--------|--------|--------|
| variable | PC1 | PC2 | PC3 | eigenvalue | 6.381 | 1.686 | 1.352 |
| sinuosity | -0.989 | 0.072 | 0.064 | percentage of variance | 58.014 | 15.325 | 12.293 |
| E_{\max} | 0.955 | -0.149 | -0.035 | cumulative percentage of variance | 58.014 | 73.339 | 85.632 |
| SD of directional change | -0.930 | 0.268 | 0.164 | | | | |
| minimum speed | 0.920 | -0.102 | -0.083 | | | | |
| mean speed | 0.911 | 0.315 | 0.086 | | | | |
| mean of directional change | -0.887 | 0.278 | 0.185 | | | | |
| maximum speed | 0.722 | 0.624 | 0.204 | | | | |
| first minimum Δs | 0.521 | 0.100 | -0.509 | | | | |
| straightness | 0.501 | -0.305 | 0.614 | | | | |
| SD of speed | 0.263 | 0.899 | 0.225 | | | | |
| first minimum C | 0.223 | -0.315 | 0.737 | | | | |

■ – bee mimics ■ – bees ■ – wasp mimics ■ – wasps ■ – unexpected p values

RStudio. The *trajr* package [16] for R was used for calculating trajectory parameters.

3. Results

When searching for a puddling spot, both bee-mimicking clearwing moths and bees flew in a rapidly meandering trajectory (figure 1), with occasional hovering. Wasps and their sesiid mimics, by contrast, flew faster and straighter, tracing out larger curves instead of tight zigzags (figure 1). Stingless bees and all bee mimics tended to hover for prolonged periods, whereas dwarf honeybees hovered for only a very short time, and wasps and wasp mimics never hovered during mud-puddling (figure 2b).

Use of MANOVA showed overall highly significant multivariate effects ($p = 3.715 \times 10^{-16}$). Univariate ANOVA tests on each variable showed further significant differences. Tukey–Kramer tests on variables for which ANOVA yielded $p < 0.05$ indicated pairwise differences:

- (i) Mean, minimum and maximum flight speeds
- Wasps were significantly faster than stingless bees and bee mimics, but not faster than wasp mimics.
 - Stingless bees and bee mimics did not differ significantly in flight speeds (electronic supplementary material, tables S1, S3, S4 and S5).
 - Dwarf honeybees differed in mean and maximum speed from both stingless bees and bee mimics

(except for *H. pahangensis*), but not from wasps (electronic supplementary material, tables S1 and S3).

- On average, wasps and wasp mimics were the fastest and *P. cruentata* and *A. argentifasciata* bee mimics, as well as *T. collina* bees, were the slowest fliers (figure 2c).
- (ii) Straightness (i.e. the ratio between straight line distance and total distance flown)
- Significant differences occurred between wasps and all bees and bee mimics (except *A. argentifasciata*).
 - There was no significant difference between wasps and wasp mimics or between bees and bee mimics.
 - Wasp mimics differed only from bees *T. atripes* and *A. andreniformis* (electronic supplementary material, table S6).
- (iii) Sinuosity
- Wasps showed significant differences from bees and bee mimics, but not from wasp mimics.
 - Bee mimics did not differ from any bees.
 - Wasp mimics did not differ from wasps or two species of bees, but differed from all bee mimics and *T. collina* (electronic supplementary material, table S7).
- (iv) E_{\max} (figure 2d)
- Results were similar to those for sinuosity, except wasp mimics did not differ from one bee mimic or any bees (electronic supplementary material, table S8).
- (v) Mean directional change and its standard deviation
- Bees and bee mimics, which flew irregularly and often changed heading, were highly similar, as were

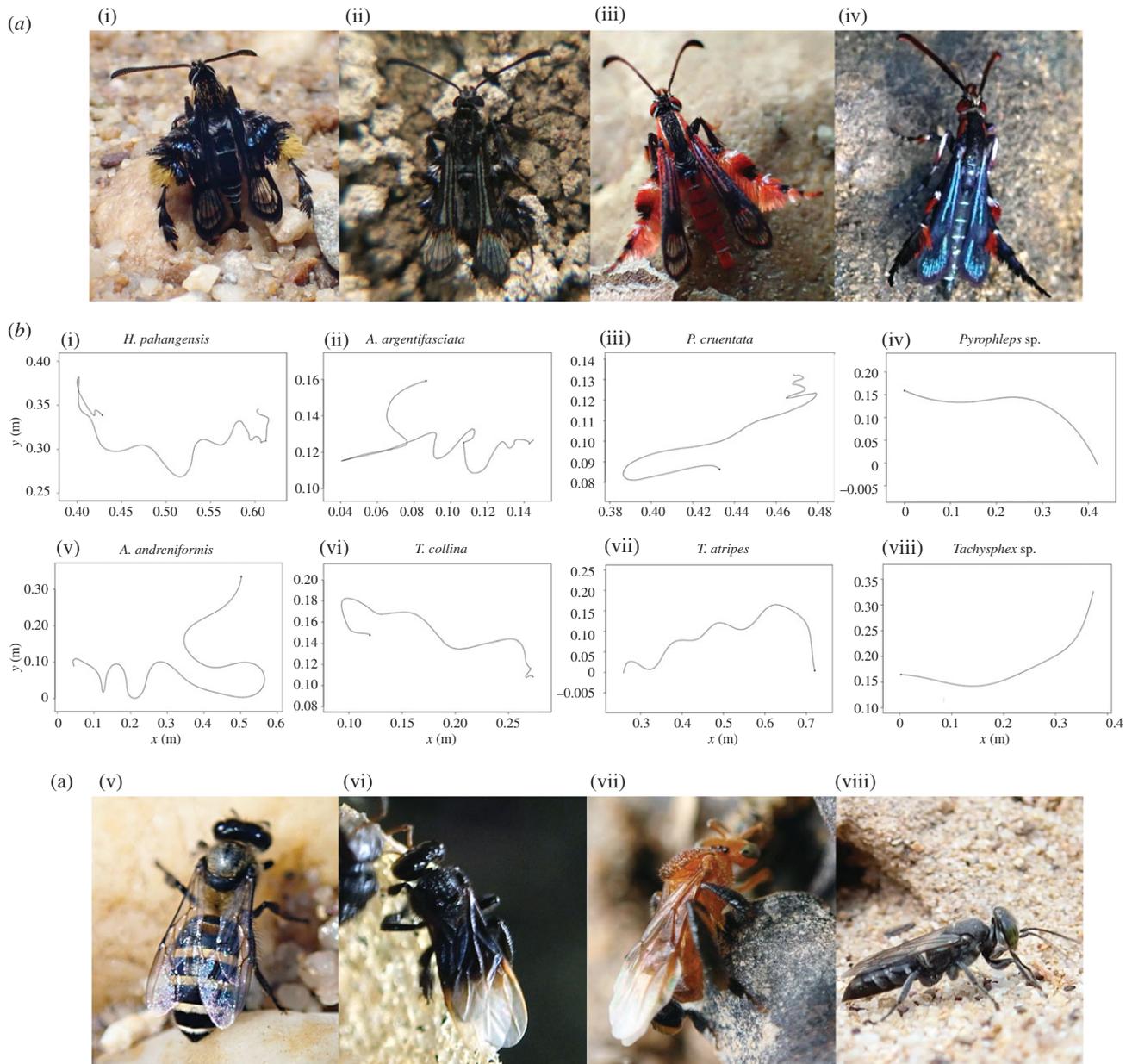


Figure 1. (i–viii) Filmed insects and corresponding example flight trajectories. (i) *Heterosphecia pahangensis*, (ii) *Aschistopheps argentifasciata*, (iii) *Pyrophleps cruentata*, (iv) *Pyrophleps* sp., (v) *Apis andreniformis*, (vi) *Tetragonilla collina*, (vii) *Tetragonilla atripes* and (viii) *Tachysphex* sp. Photo credits: Skowron Volponi & Volponi.

wasps and wasp mimics, which flew in a more regular manner.

- Wasps and wasp mimics were significantly different from bees and bee mimics (electronic supplementary material, tables S9 and S10).

(vi) Direction autocorrelation $C(\Delta s)$ and Δs

- No significant differences among groups (ANOVA $p = 0.721$).
- Only one significant difference in Δs (between *A. andreniformis* and *H. pahangensis*; electronic supplementary material, table S11), indicating similar amplitudes of periodicity and wavelengths of trajectory curves for all groups.

Wasps (except for one), wasp mimics and some bee mimics exhibited no local minima in direction autocorrelations ('NA' values in electronic supplementary material, File III), indicating a lack of periodicity in their trajectories.

Use of PC analysis showed bees and bee mimics clustered away from wasps and wasp mimics. A high value of variance in the analysed data was explained by PC1 (58%), and over 85% by the first three components (table 2). PC1 (figure 2a) was most heavily weighted positively by E_{\max} minimum speed and mean speed, and was negatively weighted by sinuosity and directional change.

4. Discussion

Based on flight speed, hovering behaviour and path straightness, bee-mimicking clearwing moths tend to fly like bees, whereas wasp mimics (as determined by anatomical resemblance) fly more similarly to wasps. Bee mimics have slower, more zigzaggy and irregular flight paths, whereas wasp mimics fly faster, less erratically and in a straighter trajectory, as do wasps. These modes of flight were displayed during mud-puddling behaviour on river banks, where the

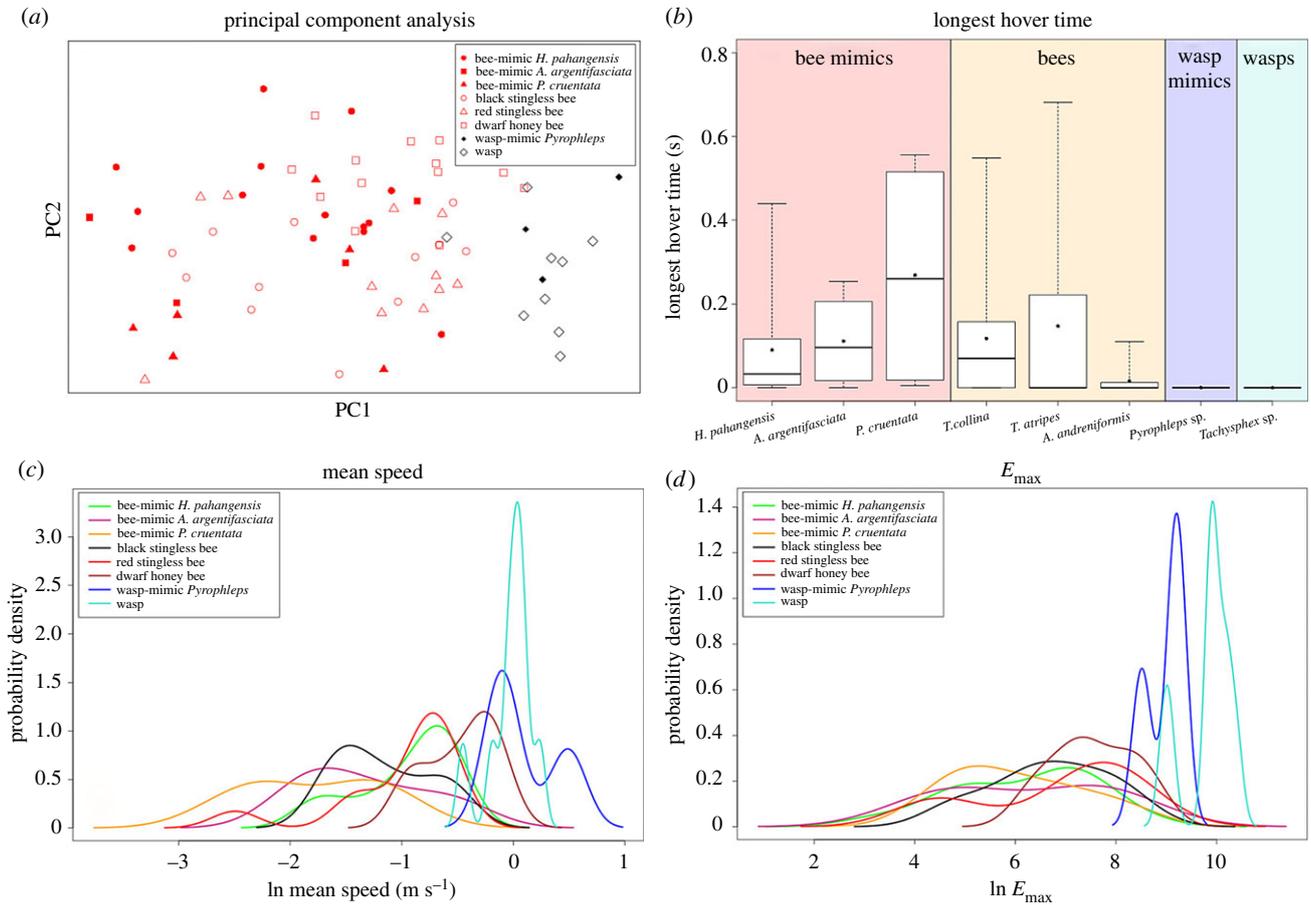


Figure 2. (a) Plot of first two principal components from PC analysis; (b) box plot of maximum hovering time (dots indicate means); (c) density plots of natural logarithm of mean speed; and (d) E_{\max} .

insects were highly exposed and possibly vulnerable to predation, especially by volant insectivores. Display of bee- or wasp-like flight trajectories by sesiids may confer greater resemblance than morphological similarity relative to potential predators observing at distances too great to resolve detailed colour or other anatomical features.

The two species of stingless bees (black *T. collina* and red *T. atripes*) flew in a highly similar manner. Both black and red sesiid bee mimics flew like these two stingless bees. Similarly, the studied wasp-mimicking sesiids were not perfect morphological mimics of wasps, but were indistinguishable from them in flight. Thus, characteristics of flight trajectories may be common among different species of models and mimics, in which case the studied clearwing moths are not specialized mimics but rather imitate features of multiple models, i.e. either bees (*T. collina*, *T. atripes* and *A. andreniformis*) or wasps, which differ in coloration but that are highly similar in the way they fly. The wasp mimic resembled *Tachysphex* wasps but in the field, it was also often confused with potter wasps, including *Coleuemenes burmanicus* Bingham, which could be an additional mimicry model.

Bee-mimicking sesiids more closely resembled stingless bees than dwarf honeybees in terms of flight speed and time spent hovering (figure 1). Although they lack functional stings, the stingless *Tetragonilla* bees display aggressive behaviours such as chasing and biting [17], which may discourage potential predators. Stingless bees may gain protection simply through resemblance to stinging bees in external morphology and flight style, and also through their own aggressive behaviours, making them adequate mimicry models for clearwing moths. It is important to note that

only hymenopteran females have a sting, yet males still gain protection from predators through similarity to females [18]. However, sesiid bee mimics also behaviourally resembled dwarf honeybees, as measured by changes in heading direction, flight irregularity, path straightness and sinuosity (electronic supplementary material, tables S6–S10). In the case of wasps and wasp mimics, our small sample size inevitably results in low statistical power, and further studies with larger sample sizes would be helpful to assess variance in all the general trends identified here.

Predator confusion between model and mimic may derive from a diversity of similarities in flight kinematics and behaviour, which could furthermore interact with visual features of the flying insect to influence overall mimetic resemblance. Different predators (e.g. volant insectivores versus sit-and-wait terrestrial taxa) may also perceive the same cues of anatomy and flight behaviour very differently. We observed potential predators of sesiids: insectivorous birds and invertebrates (wolf spiders and tiger beetles) that could be exerting different selective forces on the mimics, leading to the development of an optimal, 'imperfect' phenotype.

Nonetheless, we have demonstrated the presence of flight behavioural mimicry in sesiids relative to sympatric models, along with more specific matching of broadly defined bee- and wasp-like morphologies to their corresponding flight styles. These observations confirm historical qualitative observations of locomotor mimicry by sesiids, and invite further assessment of the evolutionary interplay between behaviour and visual similarity that yields such remarkable interordinal resemblances.

Data accessibility. Data available from Dryad Digital Repository: (<http://dx.doi.org/10.5061/dryad.682dc>) [19] (i) tables S3–S11: results of ANOVA and Tukey–Kramer tests for flight parameters by species; (ii) R code; (iii) calculated parameters; (iv) minima, maxima and means of calculated variables; (v) (x, y) coordinates of digitized flight trajectories; and (vi) video showing representative flights: <https://vimeo.com/250560272>, password: mimicry.

Authors' contributions. M.A.S.V. developed the research concept, filmed and digitized trajectory videos, did calculations, interpreted results, wrote the manuscript. D.J.M. wrote the code for R and did calculations. P.V. helped develop the concept and produced videos. R.D. advised on the concept, provided research consultation, and wrote parts of the manuscript. All authors have critically revised the

manuscript, agree to be held accountable for the content herein and approve the final version.

Competing interests. We declare we have no competing interests.

Funding. M.A.S.V. received funding through a doctoral scholarship ID 2016/20/T/NZ8/00541 from National Science Centre (Poland); D.J.M. from Australian Research Council, Project ID: DP170101617. Research partially funded by task funds DS530-L140-D242-17 and DS530-8645-D691-17.

Acknowledgements. We thank Dr Victor Ortega for his priceless advice on MATLAB, Dr John Ascher for identifying *Apis andreniformis*, Dr Drew Allen for his statistical advice, Prof. Grzegorz Węgrzyn for supporting this research, and two anonymous reviewers for their valuable comments.

References

1. Englehardt G. 1946 *The North American clearwing moths of the family Aegeriidae*. *Bulletin* 190, pp. 100,101,153. Washington, DC: U.S. National Museum.
2. Duckworth WD, Eichlin TD. 1974 Clearwing moths of Australia and New Zealand (Lepidoptera: Sesiidae). *Smithson Contrib. Zool* **180**, 1–45. (doi:10.5479/si.00810282.180)
3. Webster FM. 1897 The protective value of action, volitional or otherwise, in 'protective mimicry'. *J. N. Y. Entomol. Soc.* **5**, 67–77.
4. Skowron MA, Munisamy B, Hamid SBA, Węgrzyn G. 2015 A new species of clearwing moth (Lepidoptera: Sesiidae: Osminiini) from Peninsular Malaysia, exhibiting bee-like morphology and behaviour. *Zootaxa* **4032**, 426–434. (doi:10.11646/zootaxa.4032.4.7)
5. Skowron Volponi MA, Volponi P. 2017 A new species of wasp-mimicking clearwing moth from peninsular Malaysia with DNA barcode and behavioural notes (Lepidoptera, Sesiidae). *Zookeys* **692**, 129–139. (doi:10.3897/zookeys.692.13587)
6. Skowron Volponi MA, Volponi P. 2017 A 130-year-old specimen brought back to life: a lost species of bee-mimicking clearwing moth, *Heterosphecia tawonoides* (Lepidoptera: Sesiidae: Osminiini), rediscovered in peninsular Malaysia's primary rainforest. *Trop. Conserv. Sci.* **10**, 1–7. (doi:10.1177/1940082917739774)
7. Nelson XJ, Card A. 2016 Locomotory mimicry in ant-like spiders. *Behav. Ecol.* **27**, 700–707. (doi:10.1093/beheco/arv218)
8. Shamble PS, Hoy RR, Cohen I, Beatus T. 2017 Walking like an ant: a quantitative and experimental approach to understanding locomotor mimicry in the jumping spider *Myrmarachne formicaria*. *Proc. R. Soc. B* **284**, 20170308. (doi:10.1098/rspb.2017.0308)
9. Srygley RB. 1999 Locomotor mimicry in *Heliconius* butterflies: contrast analyses of flight morphology and kinematics. *Phil. Trans. R. Soc. Lond. B* **354**, 203–214. (doi:10.1098/rstb.1999.0372)
10. Kitamura T, Imafuku M. 2015 Behavioural mimicry in flight path of Batesian intraspecific polymorphic butterfly *Papilio polytes*. *Proc. R. Soc. B* **282**, 20150483. (doi:10.1098/rspb.2015.0483)
11. Golding YC, Ennos AR, Edmunds M. 2001 Similarity in flight behaviour between the honeybee *Apis mellifera* (Hymenoptera: Apidae) and its presumed mimic, the dronefly *Eristalis tenax* (Diptera: Syrphidae). *J. Exp. Biol.* **204**, 139–145.
12. Pekár S, Jarab M, Fromhage L, Herberstein ME. 2011 Is the evolution of inaccurate mimicry a result of selection by a suite of predators? A case study using myrmecomorphic spiders. *Am. Nat.* **178**, 124–134. (doi:10.1086/660287)
13. Kikuchi DW, Pfennig DW. 2013 Imperfect mimicry and the limits of natural selection. *Q. Rev. Biol.* **88**, 297–315. (doi:10.1086/673758)
14. Hedrick TL. 2008 Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 1–6. (doi:10.1088/1748-3182/3/3/034001)
15. Cheung A, Zhang S, Stricker C, Srinivasan MV. 2007 Animal navigation: the difficulty of moving in a straight line. *Biol. Cybern.* **97**, 47–61. (doi:10.1007/s00422-007-0158-0)
16. McLean JD, Skowron Volponi MA. 2018 Trajr: an R package for characterisation of animal trajectories. *Ethology*. (doi:10.1111/eth.12739)
17. Nagamitsu T, Inoue T. 1997 Aggressive foraging of social bees as a mechanism of floral resource partitioning in an Asian tropical rainforest. *Oecologia* **110**, 432–439. (doi:10.1007/s004420050178)
18. Quicke DLJ. 2017 *Mimicry, crypsis, masquerade and other adaptive resemblances*. Hoboken, NJ: Wiley.
19. Skowron Volponi MA, McLean JD, Volponi P, Dudley R. 2018 Data from: Moving like a model: mimicry of hymenopteran flight trajectories by clearwing moths of Southeast Asian rainforests. Dryad Digital Repository. (doi:10.5061/dryad.682dc)