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HIGH-SPEED VIDEO OF A FLYING GHOST MOTH, *PHASSUS N-SIGNATUS* (HEPIALIDAE) REVEALS SLIGHT FOREWING-HINDWING OUT-OF-PHASE FLAPPING

Additional key words: Behavior, Costa Rica, flight, Swift moth, wing-beat

Ghost moths (Hepialidae) include 701 species in 82 genera, occurring worldwide except for Antarctica (Nielsen et al. 2010, Grehan et al. 2023). Hepialids are among the few families of non-heteroneuran Glossata and have a flap-like jugum at the base of the forewing that help wing coupling (Philpott 1925). They are unusual among the lower "microlepidoptera" in often having large wingspans that are greater than 10 cm (Kristensen 1998). Hepialids often lay eggs in mass numbers—in some species a single female may lay more than 30,000 eggs, and in others, eggs can be broadcast while in flight (Kristensen 1998). Larvae of Hepialidae are phytophagous on live angiosperms, gymnosperms, pteridophytes and mosses, and often feed internally on stem, branch or root tissue (Grehan 1989). Many Hepialidae are thought to be crepuscular (Kristensen 1998), although some are solely nocturnal (Nielsen et al. 2010, Wagner & Rosovsky 1991).

Phassus n-signatus Weymer, 1907 (Fig. 1) is known to reside in forests and mixed urban habitats, from southern Mexico to Central America, and one of its known hosts is *Ligustrum lucidum* (Oleaceae)(Grehan et al. 2021, 2023). The life history of *P. n-signatus* was outlined in Grehan et al. (2021), and its morphology described by Grehan (2018). Although many natural history observations have been made of Hepialidae in general, including their flight time and lekking behaviour (Rydell 1998, Turner 2013), very little is known about how they fly. Here we present a 3D high-speed flight video of *Phassus n-signatus*, which, to our knowledge represents the first a non-heteroneuran Lepidoptera filmed in flight.

We made field recordings at CIEE, Monteverde Field station, Costa Rica, under permit numbers M-P-SINAC-0000 issued by SINAC (National System of Conservation Areas). Data were collected for three moths on the evenings (19:30–21:30) of 4–6 May 2024. Recordings were taken by releasing a moth near a 9W 19A LED blacklight bulb in a large, dark room on 4 May. The moth flew around the light which was mounted approximately 10 ft above the ground.

On 5th and 6th May, we filmed moths in the dark taking off from a 3 ft high table and we also filmed some flights with UV actinic 18 W Philips Tube 21 ft. away. We used a pair of monochrome shutter-synchronized Fastec TS5 high-speed cameras mounted on a single tripod cross-arm with two infrared (IR) illumination lights (Larsen wide angle IR Illuminators; 850 nm) from below. Videos were taken at 500 fps, giving a good temporal resolution for flight behavior. We centered the light source in the field of view of both cameras, following the methods of Fabian et al. (2024). To provide stereo calibration, we waved a known-sized checkerboard through the overlapping views of both cameras. We used the inbuilt OpenCV camera calibration tools to both detect the checkerboards in views of both cameras and estimate the intrinsic (optical center, focal length, and radial distortion) and extrinsic camera parameters (relative camera orientation and translation).

FIG. 1. Adult male of *P. n-signatus*. This specimen was filmed for this study. Photo by Akito Y. Kawahara.

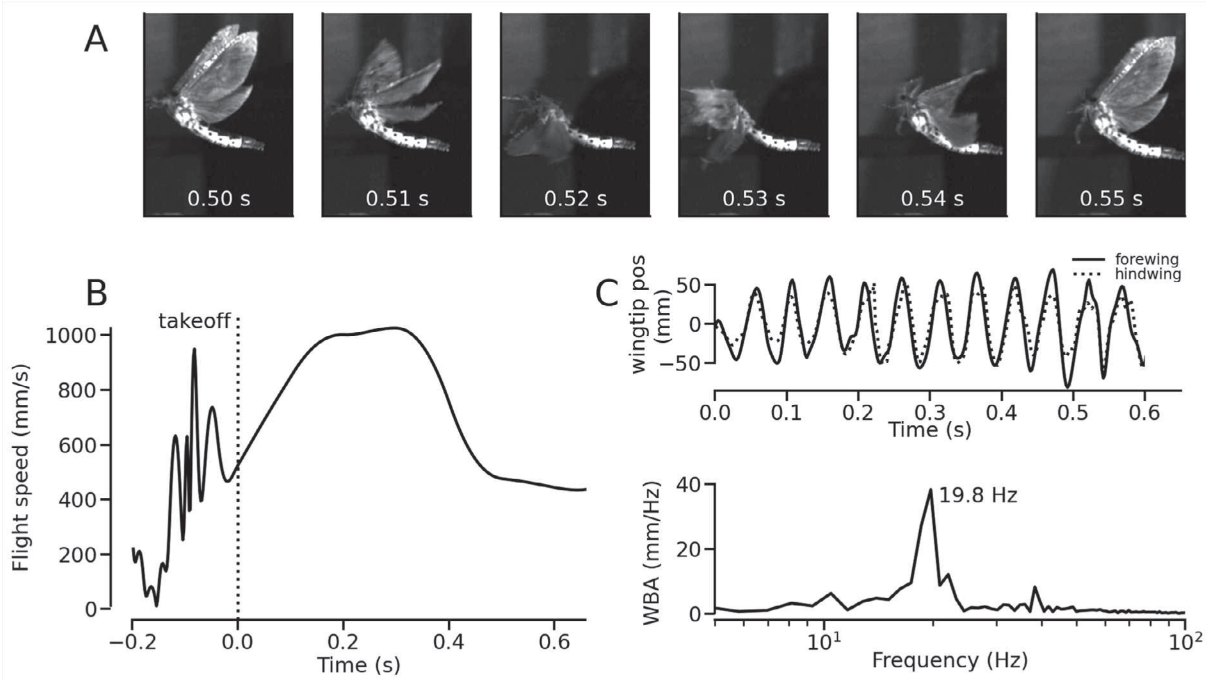

FIG. 2. Flight pattern of *P. n-signatus.* **A**) A time-sequence at 500 frames per second of *P. n-signatus* flapping shortly after takeoff. **B**) Flight speed at takeoff (before to after takeoff), with jitters in body motion that precede lifting off the ground. **C**) The amplitude spectrum of wing stroke relative to the body plane identifies the wing beat frequency. The most prominent amplitude is wing beat frequency (~20 beats/second).

We digitized flights from all three moths, capturing full wing strokes during takeoffs and flight (selected frames in Fig. 2a, Supplementary Videos 1–3). Three dimensional trajectories showed slow, jerky takeoffs, followed by smooth flight that rapidly accelerated to over 1 m/s (Fig. 2b). In flight, wings frequently clapped at the apex of the wing stroke above the animal, and spectral analysis of wing tip trajectories showed an approximately 20 Hz wing beat frequency (Fig. 2c). We noted we could direct moth flight with a red light, suggesting that this moth has a long-wavelength visual gene duplication (Sondhi et al. 2021).

Our observation represents what we believe is the first recorded high-speed footage of a non-heteroneuran Lepidoptera, showcasing how its forewings and hindwings create out-of-phase flapping, a phenomenon absent in higher Lepidoptera, although common in other insects like dragonflies (Rüppell 1989). Flight speed and wing beat frequencies have been measured in Sphingidae and Saturniidae, with Sphingidae recording wing beat frequencies around 30 Hz, and Saturniidae approximately 14 Hz (Aiello et al. 2021), the latter which is comparable to that of *P. n-signatus*. While the wing shape of hepialids resemble sphingids more than saturniids, the flight strategy seems to be more akin to wild silkmoths based on flight kinematics. Given their large body mass, wing coupling mechanism, and phylogenetic position among the lower Lepidoptera (Kawahara et al. 2019), hepialids serve as an important taxon for future research on the flight kinematics of insects.

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SUPPLEMENTARY FILES

High speed videos are available at the following online links:

Video 1: gm1.avi: Take-off video at 500 fps. http://www.lepsoc.org/journal/Kawahara_78-4_1.avi
Video 2: gm2.avi: Take-off video from at 500 fps. http://www.lepsoc.org/journal/Kawahara_78-4_2.avi
Video 3: gm3.avi: Clip showing moth released from hand at 500 fps.
http://www.lepsoc.org/journal/Kawahara_78-4_3.avi