Arthropod Structure & Development xxx (2017) 1–5

Contents lists available at ScienceDirect

Arthropod Structure & Development

journal homepage: www.elsevier.com/locate/asd

Jumping and the aerial behavior of aquatic mayfly larvae (*Myobaetis ellenae,* Baetidae)[☆]

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A R T I C L E I N F O

Article history:
Received 8 March 2017
Accepted 30 June 2017
Available online xxx

Keywords:
Archaeognatha
Costa Rica
Ephemeroptera
Flight
Gills

A B S T R A C T

Mayfly larvae generally are aquatic, but some madicolous taxa (i.e., living in thin water films) crawl over rocks within streams and waterfalls. When startled, these larvae can break the water film, jump, and enter an aerial phase of locomotion. Because mayfly larvae have been suggested as potential exemplars for the origin of insect wings as tracheal gills, and furthermore represent the most basal extant lineage of pterygotes, we analyzed jumping behavior and free-fall trajectories for one such species of mayfly (*Myobaetis ellenae*, Baetidae) in Costa Rica. Jumping was commonplace in this taxon, but was undirected and was characterized by body spinning at high angular velocities. No aerodynamic role for the tracheal gills was evident. By contrast, jumping by a sympatric species of bristletail (*Meinertellus* sp., Archaeognatha) consistently resulted in head-first and stable body postures during aerial translation. Although capable of intermittently jumping into the air, the mayfly larvae could neither control nor target their aerial behavior. By contrast, a stable body posture during jumps in adult bristletails, together with the demonstrated capacity for directed aerial descent in arboreal representatives of this order, support ancestrally terrestrial origins for insect flight within the behavioral context of either jumping or falling from heights.

1. Introduction

Current understanding of the origins of winged flight in insects is limited due to a lack of fossil intermediates. Various hypotheses have suggested that insect wings evolved either in a terrestrial ancestor for which wings served to effect controlled aerial behavior in falls and when gliding, or in aquatic ancestors for which winglike structures were initially used in underwater flapping (reviewed by Dudley, 2000; Grimaldi and Engel, 2005). Hexapods are a monophyletic group derived from a lineage of terrestrialized crustaceans (Grimaldi, 2010); all extant apterygotes are terrestrial with the exception of some secondarily derived aquatic collembolans (D'Haese, 2002). Developmental studies also suggest that the insect wing derives from a complex integration of lateral thoracic outgrowths and possibly limb exites, but does not incorporate gills *per se* (Clark-Hachtel et al., 2013; Engel et al., 2013; Ohde et al., 2013; Prokop et al., 2017). Moreover, an insect fossil from the Late Devonian (Garrouste et al., 2012) exhibits no obvious morphological adaptations for aquatic life, a finding also consistent with ancestral terrestriality in pterygotes. Absent relevant paleontological information, we can alternatively look to extant taxa and behaviors to try to infer the feasibility of different scenarios for flight origins.

Recent studies have suggested that, for both volant vertebrates and pterygote insects, controlled aerial behaviors may have preceded the origin of wings proper (Dudley et al., 2007; Dudley and Yanoviak, 2011). For example, many wingless arboreal arthropods can control their trajectories whilst falling via the steep form of gliding termed directed aerial descent (Yanoviak et al., 2005, 2009; Dudley and Yanoviak, 2011). Similarly, a dorsoventral aerial righting reflex characterizes certain squamate taxa as well as some larval hemimetabolous insects (Jusufi et al., 2011), and jumping via a startle reflex is widespread in terrestrial animals (Eaton, 1984). The origin of wings is not, therefore, necessarily congruent with the origin of flight if we construe the latter phenomenon to indicate a broader spectrum of controlled aerial behaviors, including jumping

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[☆] This is a contribution to the ASD Special Issue “Wings and powered flight: morphological core novelties in insect evolution” organized by Dr. Günther Pass, University of Vienna.

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http://dx.doi.org/10.1016/j.asd.2017.06.005

Please cite this article in press as: Yanoviak, S.P., Dudley, R., Jumping and the aerial behavior of aquatic mayfly larvae (*Myobaetis ellenae*, Baetidae), Arthropod Structure & Development (2017), http://dx.doi.org/10.1016/j.asd.2017.06.005

from heights (Dudley and Yanoviak, 2011). Suggestively, a recently proposed fossil sister group to the pterygote insects (Order Carbotriplurida) shows no obvious adaptations for aquatic life, and moreover exhibits pronounced lateral lobes consistent with controlled gliding and maneuvering (Staniczek et al., 2014).

Such behaviors tend not to be found, however, among the diverse fauna of aquatic and semiaquatic arthropods. Presumably because of physical constraints imposed by surface tension on such small-bodied animals, rapid transitions across the air/water interface are rare. However, larvae of the mayfly *Mayobaetis ellenae* (Ephemeroptera: Baetidae) voluntarily jump from wet surfaces when disturbed, a behavior otherwise not documented in this order. These mid-elevation, Neotropical insects are madicolous, inhabiting millimeter-thick water films over rock faces in seeps and waterfall spray zones (Waltz and McCafferty, 1985; Lugo-Ortiz and McCafferty, 1996). The larvae also intermittently crawl from rock surfaces into surrounding bryophyte mats, where they presumably forage in a wet but effectively terrestrial environment (Fig. 1). Given the fairly basal placement of Baetidae within the Ephemeroptera (Sun et al., 2006), along with the potential evolutionary relevance of movable tracheal gills in this group, we hypothesized that examination of jumping in *M. ellenae* could clarify the origins of aerial behavior in pterygotes. Specifically, if wings evolved from gills in mayfly precursors or similarly basal (and putatively aquatic) hexapods, then *M. ellenae* might be expected to exhibit stable body postures and possibly directed trajectories when airborne. Contrariwise, if pterygotes are ancestrally terrestrial, then today's aquatic larvae of the basal winged lineages (i.e., the Ephemeroptera and Odonata) are secondarily derived (see Grimaldi and Engel, 2005), and would be expected to have no capacity for targeting or aerial control.

Here, we examine jumping (also termed here to be takeoffs) and subsequent aerial behavior in larval mayflies to assess their capacity for gliding and directional control during a fall. Specifically, we quantify trajectories and landing patterns of *M. ellenae* larvae following their jumps from variably oriented flat surfaces, and also compare their initiation of jumps to that of a fully terrestrial adult archaeognathan, which serves as a representative apterygote that is ancestrally terrestrial. Our goals were to: 1) characterize jumping takeoffs in *M. ellenae*, 2) determine if jumping *M. ellenae* larvae exhibit targeting once airborne, and 3) compare this jumping behavior with that in a syntopic but fully terrestrial bristletail species capable of controlled jumps and gliding.

2. Material and methods

In March 2008 and December 2010, we collected *M. ellenae* larvae from rock faces above the water line and from waterfalls in the rivers Alondra and Guacimal near the University of Georgia Research Station (UGACR) in the village of San Luis, near Monteverde in Costa Rica (10.282°N, 84.799°W). Larvae were patchily distributed within streams and in boulder fields at the base of waterfalls, and were most common on larger boulders and along steeper inclines. Larvae tended to jump in response to approaching objects, and also in response to water flow induced along rock faces as we moved upstream against the current. All sizes of larvae were present and co-occurred. Subimagos were occasionally observed, and possessed flight-capable wings. Observations of lab-housed larvae suggested that the jumping tendency ceased at least 12 h prior to eclosion as a subimago.

Following collection in the field, larvae were maintained individually in plastic Petri dishes in the UGACR laboratory. The bottom of each dish was lined with a disc of filter paper saturated with tap water. Larvae kept under these conditions and covered with only a thin layer of water survived for >24 h. Larvae that were either completely immersed or that were trapped within water droplets with no underlying filter paper tended to die within 2 h. The filter paper was changed and the Petri dishes were cleaned every 6–10 h.

2.1. Takeoff performance

Jumping takeoffs were recorded for *M. ellenae* larvae in the UGACR research lab using a high-speed digital video camera (TroubleShooter TS1000CS, Fastec Imaging) operated at 1000 frames/s (Fig. 2). Artificial illumination was provided by a halogen lamp mounted on a flexible tripod (Fig. 2). Wet body mass, mean length of the two caudal cerci, and the distance between the anterior tip of the head and the base of the median filament (i.e., the effective body length) were measured immediately before recordings. Air temperature was 28 °C during experiments. All jumps were initiated from a rigid stage fitted with a scale bar (1 mm increments) and a plumb line for vertical reference. Individual larvae

Fig. 1. Larva of *Mayobaetis ellenae* on rock surface in natural habitat in Costa Rica (scale bar = 5 mm), with tracheal gills extending laterally from abdominal segments.

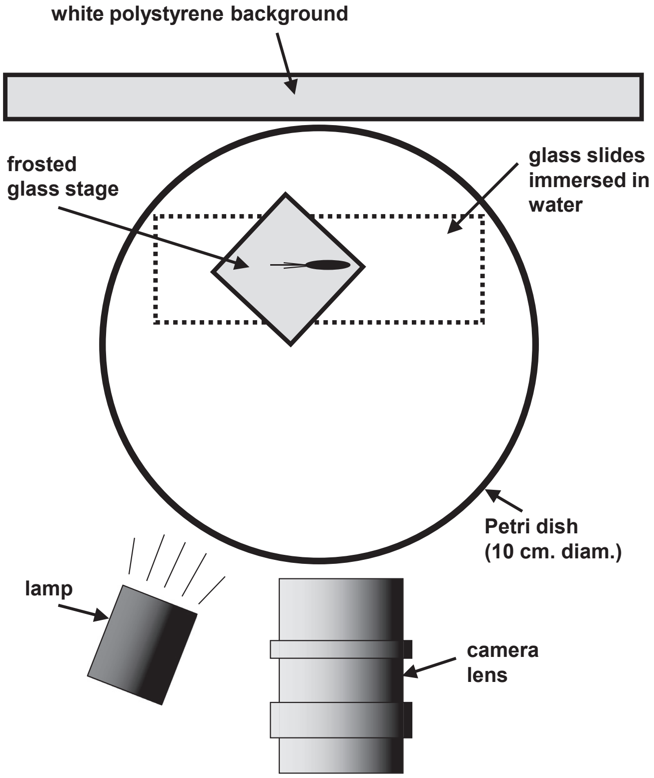

Fig. 2. Vertical schematic view of the jumping takeoff recording theater. In each case, the specimen (either a bristletail or mayfly larva, indicated by the dark ellipse) was positioned orthogonal to the camera axis.

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