

Jumping Performance in Flightless Hawaiian Grasshopper Moths (Xyloryctidae: *Thyrocopa* spp.)

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Abstract. Saltatorial locomotion has evolved multiple times in flightless Lepidoptera, particularly on oceanic islands and in habitats with high winds. The kinematics of this behavior are unknown but are clearly relevant to escape performance in the absence of wings. We investigated jumping in two non-sister species of brachypterous Hawaiian moths (genus *Thyrocopa*). Moths were collected from the islands of Maui and Hawaii. Lateral views of jumps were recorded on video and then digitized. Jump distances of both species averaged about ten body lengths. In males of *Thyrocopa apatela*, jump distance was significantly correlated with the maximum horizontal component of jump velocity. Jumping ability may become enhanced as a means of evading predators when selection for flight performance is relaxed under high-wind regimes.

Key words: Brachyptery, kinematics, Lepidoptera, locomotion, morphology, predation

Jumping is a specialized locomotor behavior that has evolved numerous times in insects. Within the Lepidoptera, secondary flightlessness and concomitantly enhanced jumping abilities are particularly noted on islands, in habitats with scattered vegetation, and under high-wind regimes (Carlquist 1965; Medeiros 2008; Powell 1976; Sattler 1988, 1991). The jumping “grasshopper moths” of the Hawaiian islands (Xyloryctidae: *Thyrocopa* spp.) are of particular interest given that their jumping motions are similar to those of Orthoptera and likely serve a similar role in escaping from terrestrial predators. The kinematics of jumping in grasshopper moths have never been investigated but are relevant to understanding possible tradeoffs between flight and escape per-

formance in brachypterous insects more generally (see Dudley 2000).

Here, we evaluate jumping in two rare species of flightless grasshopper moths in Hawaii, *Thyrocopa apatela* (Walsingham) and *T. kikaelekea* Medeiros. These species are unusual in that both sexes, although partially winged, are flightless. Brachyptery in Lepidoptera is typically restricted to females (Roff 1990), and selection for flightlessness in *Thyrocopa* might accordingly have been particularly strong. *T. apatela* occurs on Haleakala Volcano (Maui) at high elevations, historically above 2200 m (although two specimens were collected in 1976 at 1524 m; Medeiros 2009). The species is now restricted to elevations above ~2900 m (M. Medeiros, pers. obs.), probably due to predation by introduced

ants (Krushelnycky et al. 2005). *T. kikaelekea* typically occurs at elevations of 2800–3000 m but is occasionally found as low as 2100 m. The high-elevation habitats of both species are characterized by high winds, low air temperatures, only scattered vegetation, an absence of native vertebrate predators, and low relative humidity. The larvae are detritivores on dead leaves under rocks (Howarth 1979, Medeiros 2008), and adults probably do not feed, though they have a normal proboscis and may drink water droplets. Locomotor behavior of adults in the field is restricted to walking and intermittent jumping (M. Medeiros, pers. obs.). Here, we quantify jumping performance, infer important jump kinematics, and investigate morphological correlates of jumping in *Thyrocopa*.

Materials and Methods

Individual *Thyrocopa apatela* were collected in 2006 from the Sliding Sands area (~2925 m) of Haleakala National Park, Maui. *T. kikaelekea* were collected from above the Hale Pohaku area (~2900 m) of the Mauna Kea Forest Reserve, island of Hawaii. The inability to fly was confirmed for both species using a “drop test” identical to that used for cave-dwelling *Schrankia* (Noctuidae) moths (Medeiros et al. 2009). Individuals were collected by hand, kept within plastic vials, and were brought indoors within two hours of capture for filming and morphological measurements. For *T. apatela*, filming took place at an elevation of ~975 m, whereas filming of *T. kikaelekea* occurred near sea level; both filming locations were at room temperature (approx. 20°C). At both locations, weight of individual moths was first measured on a portable balance (Acculab PP2060D), and the body length was then measured from the anterior tip of the head to the tip of the abdomen (excluding the ovipositor length in females). Individual

moths were then placed into a clear acrylic chamber (27 x 13.5 x 10.5 cm) with a sheet of graph paper attached to the rear wall for scale. A Sony DCR–HC26 Handycam digital video camera was positioned ~1 m in front of the jumping chamber such that its optical axis was perpendicular to the front wall of the chamber. The camera was used to film at 30 frames/s both a lateral view of the chamber and a vertical perspective, as reflected from a mirror set up at a 45° angle above the chamber. Jumping was induced by gently touching moths with a probe. Because no features of jumps have been described for any moth taxon, we sought to provide a preliminary description of jumping performance using a filming rate of 30 frames/s, including distances and angles for which such a filming rate is sufficient. Jump trajectories and velocities are, by contrast, undersampled in time but are still informative relative to the absence of any information on such behaviors.

Only those jumps for which the projected planar trajectory was <15° from the vertical image plane of the camera were used for analysis; this restriction was necessary to ensure accurate two-dimensional reconstruction of the jump (i.e., an angular displacement of the trajectory by 15° from the plane of view will maximally underestimate projected values of the x coordinate by $(1 - \cos 15^\circ)$, or 3.4%). The average trajectory angle relative to the image plane was 6° for all analyzed sequences, corresponding to a reconstruction error of only 1%. Following a recording bout, specimens were pinned and later accessioned to the National Park Service (Maui) and the Bishop Museum.

Video sequences of interest were uploaded into a Macintosh computer, and individual movie files containing one jump each were made using QuickTime. ImageJ software was used to digitize for each frame the (x, y) coordinates of the

centroid of the moth's image, with the absolute length scale determined from the graph paper in the immediate background. The distance traveled during a jump was defined as the horizontal difference between the frame immediately preceding and that following a jump. Takeoff angle relative to horizontal was measured from the first aerial point of a jump and the immediately preceding frame using the coordinates of the moth's centroid. Horizontal and vertical velocity components were determined from a three-point rolling average of frame-to-frame displacements in x and y , respectively. These two orthogonal components were summed vectorially to calculate the magnitude of the two-dimensional velocity vector; the maximum magnitude was determined for each jump. One-way ANOVA was used for jump data for *T. apatata* males (the only sex-by-species class with more than ten jumps); see Table 1 to assess effects of individual identity on kinematic variables.

For an additional set of dried and pinned specimens of *T. apatata* and *T. kikaelekea*, measurements were made with digital calipers of the interocular distance (the transverse distance between the two compound eyes, as a proxy for overall size), and of both the femur and the tibia lengths for the right hindlimb. To determine if leg morphology between volant and flightless species is different, the same morphological data were also taken from dried and pinned specimens of *T. abusa* Walsingham, a typical non-jumping and flighted *Thyrocopa* species of comparable body length (~ 10 mm). None of the three aforementioned *Thyrocopa* species are sister taxa to each other (Medeiros and Gillespie 2010). Two separate (by sex) one-way ANOVA tests were applied to morphological data for the three species to assess potential differences in the ratio of the interocular distance to femur length and to tibia length.

Results

A range of 1–3 individuals per sex per species was captured in the field, and 1–5 jumps were filmed for each individual (Table 1). The extreme rarity of these two species precluded larger sample sizes, with the field collecting effort for the samples obtained here exceeding twenty hours. Moths always jumped forwards relative to their anteroposterior axis via hindleg extension, and also extended their wings laterally when in the air. No abdominal contact with the ground was noted during jumps.

Jumps by individuals were highly variable, but averaged about 10 body lengths (Table 1; Fig. 1). Application of one-way ANOVA to kinematic data for jumps of *T. apatata* males showed no effect of individual identity on either takeoff angle, maximum velocity, horizontal and vertical components of velocity, or jump length (d.f.=2,10; $F>0.5$ and $P>0.25$ in all cases). Data for these individuals were accordingly pooled. Jump distance in *T. apatata* males was significantly correlated with maximum velocity ($r^2=0.53$, $P<0.005$), and this correlation derived from variation in the maximum horizontal component of velocity (see Fig. 2). Jump distance was, not surprisingly, independent of the maximum vertical component of velocity ($r^2=0.05$, $P<0.40$).

Relative hindlimb size was substantially different among females of different species but not males (Table 2). For females, the three species differed significantly in the ratio of the interocular distance to femur length (d.f.=2, 10, $F=5.9$, $P<0.02$; *T. abusa* vs. *T. apatata*, post-hoc $P<0.03$; *T. abusa* vs. *T. kikaelekea*, post-hoc $P<0.01$). Similarly, the ratio of interocular distance to tibia length was significantly different among females of the three species (d.f.=2, 11, $F=6.2$, $P<0.02$; *T. abusa* vs. *T. kikaelekea*, post-hoc $P<0.01$). No significant differences were found for male

Table 1. Morphological and mean kinematic data for jumping in two *Thyrocopa* species. See text for details.

Species	Accession no. (# of jumps)	Sex	Mass (g)	Length (mm)	Takeoff angle (°)	Maximum velocity (m/s)	Jump distance (cm)	Jump range (cm)
<i>T. apatela</i>	06A29 (5)	male	0.020	10.1	36.2	0.87	13.0	11.1–14.0
<i>T. apatela</i>	06A32 (5)	male	0.020	10.5	31.8	0.80	14.5	8.4–19.2
<i>T. apatela</i>	06A33 (3)	male	0.017	10.4	27.2	0.94	15.7	12.8–19.1
<i>T. apatela</i>	06A30 (5)	female	0.077	13.4	39.1	0.75	11.7	10.2–13.7
<i>T. kikaelekea</i>	06A64 (3)	male	0.021	10.9	23.9	0.68	10.3	9.7–25.7
<i>T. kikaelekea</i>	06A65 (3)	male	0.029	11.5	36.7	0.81	9.6	9.6–14.7
<i>T. kikaelekea</i>	06A62 (5)	female	0.030	11.1	41.1	0.72	11.4	8.7–14.7
<i>T. kikaelekea</i>	06A66 (1)	female	0.053	12.3	32.4	0.71	8.1	8.1

morphological parameters of the three species (post-hoc $P > 0.25$ in all comparisons).

Discussion

Jumping performance in *Thyrocopa* is impressive, with jumps typically on the order of ten body lengths. Little data is available to compare this with other Lepidoptera, although jumping has evolved ~20 times independently in this order (Sattler 1991). Jumps of “5 cm or more” have been reported (Sattler 1991); Powell (1976) reports that *Areniscythis brachyptervis* Powell (Scythrididae) “jumped into the air an estimated 10–15 cm” when disturbed (this species also has hindlimb femurs longer than in closely related volant species). These distances are however relatively modest compared to more dedicated jumping taxa such as flea beetles and leafhoppers (e.g., Brackenbury and Wang 1995, Burrows 2007). The low takeoff angles characterizing most jumps (i.e., $<45^\circ$; see Table 1) suggest that distance maximization *per se* may not be the immediate goal of jumping, as opposed to a startle-induced escape response from the immediate vicinity of a potential predator. However, jump distance was variable among and within individuals, and was correlated with the horizontal component of translational jump velocity (Figure 2). We consider horizontal jump velocities to contribute primarily to jump distance, although potential effects of lift and drag once airborne (along with the low sample sizes) may also contribute to this result. The possibility of

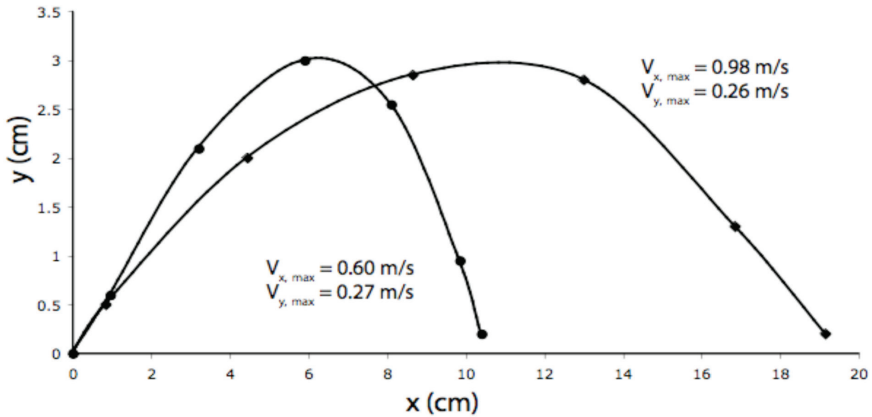


Figure 1. Representative jump trajectories for shortest and longest jumps of one individual *Thyrocopa apatela* (accession no. 06A32). The maximum vertical ($V_{y,max}$) and horizontal ($V_{x,max}$) velocity components are indicated for each jump. The points here represent intervals of 1/30 sec.

Table 2. The average ratio of interocular distance (*IOD*) to either hindlimb femur length or hindlimb tibia length to for three *Thyrocopa* species (sample size *N*). Standard deviations for the two ratios are given in parentheses.

Species	Sex	IOD/femur length	IOD/tibia length
<i>T. apatela</i>	male (<i>N</i> =4)	0.44 (0.065)	0.28 (0.026)
<i>T. apatela</i>	female (<i>N</i> =3)	0.41 (0.036)	0.29 (0.020)
<i>T. kikaelekea</i>	male (<i>N</i> =5)	0.43 (0.039)	0.29 (0.004)
<i>T. kikaelekea</i>	female (<i>N</i> =4)	0.39 (0.057)	0.26 (0.023)
<i>T. abusa</i>	male (<i>N</i> =5)	0.43 (0.027)	0.30 (0.025)
<i>T. abusa</i>	female (<i>N</i> =5)	0.46 (0.012)	0.31 (0.019)

active modulation of aerial performance in response to variable stimuli also cannot be excluded, for which more time-resolved biomechanical studies of jumping would be appropriate.

The morphological underpinnings to jumping performance in *Thyrocopa* are not clear, as their relative scarcity precluded anatomical investigations on study specimens. However, femur and tibia lengths in female *T. apatela* and *T. kikaelekea* are significantly greater than

those of a typical flying, non-jumping *Thyrocopa* species (see Table 2), though these differences are not immediately obvious upon visual inspection (Sattler 1991). No such differences were evident in analogous comparison of males among the aforementioned species. Females may need relatively longer legs in order to enhance jumping, as they are typically much heavier than males (see Table 1). In one other flightless but saltatorial lepidopteran (*A. brachypteris*), the hindleg tarsi and

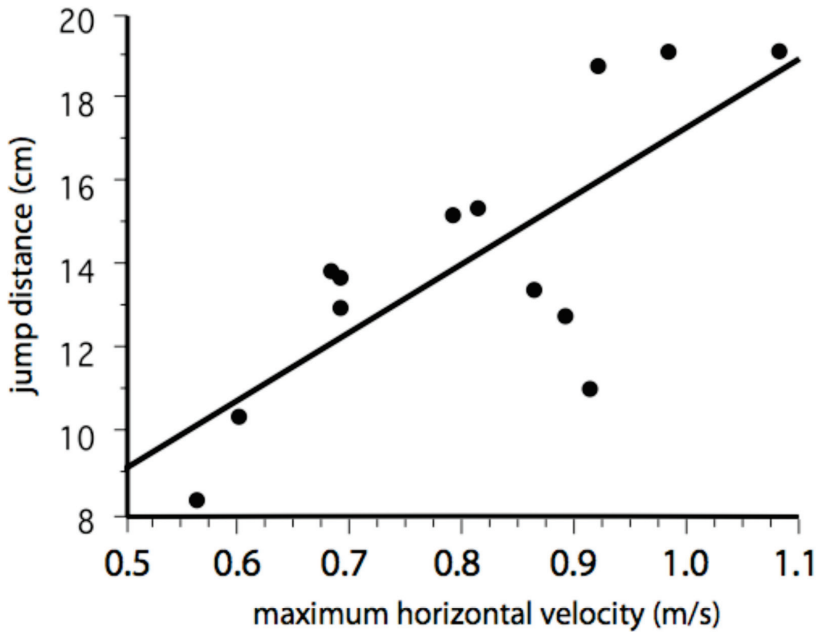


Figure 2. Jump distance versus the maximum horizontal velocity component for 13 total jumps of male *T. apatela*. The regression is given by: $y = 1.01x + 16.39$, $r^2 = 0.57$, $P < 0.004$.

femur lengths are only slightly longer than those of closely related species of similar size (Powell 1976, Sattler 1991).

T. apatela and *T. kikaiekea* have evolved flightlessness and associated jumping behavior independently, and apparently in less than 0.5 million years for the latter species (Medeiros and Gillespie 2010). The ecological associations of dedicated jumping behavior, as distinct from volant escape, are not known for *Thyrocopa*. Evolution of brachyptery in both sexes of the Lepidoptera may derive from cold daily temperatures, a lack of avian predators, and/or due to persistently high winds that prevent males from tracking female pheromones over long distances (Powell 1976, Sattler 1991). However, jumping as a means of locomotion may be retained in such contexts, perhaps to evade predation from arachnids. Jumping has

probably evolved from normal take-off mechanisms, though many brachypterous Lepidoptera exhibit no capacity for jumping whatsoever (Sattler 1991), and the ecological contexts for multiple origins of this behavior in *Thyrocopa* merit further investigation. The restriction of these jumping species to alpine environments in Hawaii with a much-reduced suite of vertebrate predators suggests that presence of arachnids may underlie the origins of this behavior.

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