## SYMPOSIUM

# Scaling of Jumping Performance in Click Beetles (Coleoptera: Elateridae)

Ophelia Bolmin [*], Thomas C. McElrath[†], Aimy Wissa[‡] and Marianne Alleyne[*,§,l]

*Mechanical Science and Engineering, University of Illinois at Urbana-Champaign, Urbana, IL 61820, USA; †Illinois Natural History Survey, University of Illinois at Urbana-Champaign,  Urbana, IL 61820, USA; ‡Mechanical and Aerospace Engineering, Princeton University, Princeton, NJ 08540, USA; §Entomology, University of Illinois at Urbana-Champaign, Urbana, IL 61820, USA

[1]E-mail: vanlaarh@illinois.edu

**Synopsis**    Click beetles (Coleoptera: Elateridae) are known for their unique clicking mechanism that generates a powerful legless jump. From an inverted position, click beetles jump by rapidly accelerating their center of mass (COM) upwards. Prior studies on the click beetle jump have focused on relatively small species (body length ranging from 7 to 24 mm) and have assumed that the COM follows a ballistics trajectory during the airborne phase. In this study, we record the jump and the morphology of 38 specimens from diverse click beetle genera (body length varying from 7 to 37 mm) to investigate how body length and jumping performance scale across the mass range. The experimental results are used to test the ballistics motion assumption. We derive the first morphometric scaling laws for click beetles and provide evidence that the click beetle body scales isometrically with increasing body mass. Linear and nonlinear statistical models are developed to study the jumping kinematics. Modeling results show that mass is not a predictor of jump height, take-off angle, velocity at take-off, and maximum acceleration. The ballistics motion assumption is strongly supported. This work provides a modeling framework to reconstruct complete morphological data sets and predict the jumping performance of click beetles from various shapes and sizes.

## Introduction

Many organisms use jumping as a mode of locomotion to overcome obstacles, reach elevated surfaces, and cover longitudinal distances. Numerous arthropods have evolved jumping mechanisms where the extension of leg limbs generates the motion (Evans 1972; Bennet-Clark, 1975; Burrows 2006; Bolmin et al. 2021). Fleas and froghoppers, for example, may reach heights of more than 100 times their body length using legs (Burrows 2006; Sutton et al. 2011), Animals that rely on legs to jump face the challenge of not being able to perform the jumping motion if one of their limbs is injured. Click beetles, springtails, and fruit fly larvae have evolved jumping mechanisms that do not rely on legs. Springtails use a springing organ (the manubrium) at the extremity of the abdomen. The eversion and extension of this jumping adaptation in a snapping manner launches the animal into the air (Brackenbury and Hunt 1993). Fruit fly larvae use their entire body to jump. From an initial folded body position, mouth hooked onto the tail, fruit flies store elastic energy by bulging body segments. The animal is launched into the air through the elastic recoil of the entire body structure (Maitland 1992). Click beetles (Coleoptera: Elateridae) have also evolved a body folding mechanism that enables them to be airborne. From a supine position and when the body is unconstrained (Fig. 1B), a unique morphological adaptation, the thoracic hinge, enables the jumping motion. The thoracic hinge links the beetle's two major body units, the head and prothorax,

**Fig. 1** A. Four click beetle species used in this study. From left to right: *Alaus oculatus,* one of the largest species studied, *Parallelosthetus attenuatus, Ampedus nigricollis,* and *Aeolus melillus.* The body can be divided into two major units, the head and prothorax and the meso-, metathorax, and abdomen. (B) Jump of a *P. attenuatus* specimen recorded as part of this study. From a supine position, click beetles can generate a jump that does not involve legs.

and meso-, metathorax, and abdomen (Fig. 1A) and allows for rapid body folding and unfolding movements (Evans 1972).

Click beetles initiate the jump from a supine position by folding their bodies around the hinge. They maintain a braced position and store elastic energy in a distributed spring system, partially contained in the hinge (Bolmin et al. 2021). After a couple of milliseconds, the energy is suddenly released and the body unfolds through a quick rotation of the head and prothorax around the hinge. This fast rotation accelerates the animal's center of mass (COM) upwards, and the beetle is launched into the air (Fig. 1B) (Evans 1972; Bolmin et al. 2019). While airborne, the beetle somersaults (Fig. 1B) before landing on its ventral or dorsal side. In all prior work, authors have assumed that click beetles follow an airborne ballistic trajectory to describe and model the jump (Evans 1972; Ribak and Weihs 2011; Ribak et al. 2012; Ribak et al. 2013). However, this assumption has not yet been tested. Testing this assumption is critical to identify the forces that govern the airborne phase of the click beetle jump. Ballistic motion relies on the assumption that only gravity acts on the body. Other forces, such as drag, are neglected. In a bio-inspired design framework, understanding the core physics of the jump is essential to create accurate analogies and guide the design of click beetle-inspired robots (Hashemi Farzaneh 2020).

Prior studies focused on relatively small species. Evans studied species of body length varying from 4 to 12 mm, and Ribak considered species that were about 20 mm (Evans 1972; Ribak and Weihs 2011; Ribak et al. 2012). Kaschek's 1984 study encompassed a larger number of species, with a body length ranging from 7 to 24 mm (Hashemi Farzaneh 2020). In this paper, we augment the range of species considered, with the body length varying from 7 to 37 mm. This large size range enables us to investigate how jumping performance scales with increasing mass. Statistical models

are developed to quantify how the major body units (head and prothorax and meso-, metathorax, and abdomen) scale across the mass range and test the ballistics motion assumption.

## Materials & methods

### Collection and identification

Thirty-eight click beetle specimens were collected in Champaign, Piatt, and Vermillion Counties in Illinois; Barry County in Michigan; and Allen County in Ohio from private property with the permission of the property owners or from permanent research sites owned by the University of Illinois at Urbana-Champaign with permission from the University's Committee of Natural Areas. Two sets of live beetles were collected during the summers of 2017 and 2018. The first set was collected from April to July 2017, and the second from May to August 2018. The specimens were manually collected by excavating wood debris, on live trees at fluorescent lights, or by using modified black cross-vane panel traps (AlphaScents, Portland, OR, USA), coated with the fluoropolymer dispersion Fluon® PTFE (AGC Chemicals Americas, Inc., Exton, PA, USA) to improve trapping efficiency (Kaschek 1984). Polyethylene sachets (press-seal bags, Bagette model 14772, 10 × 15 cm, 0.05 mm thick, Cousin Corp., Largo, FL, USA) loaded with 100 mL of 90% ethanol lures were used to collect the specimens in 2017. In 2018, an experimental lure provided by Dr. Jocelyn G. Millar (Dept. of Entomology, University of California at Riverside) was used (Graham 2010).

The live beetles were kept until filmed in plastic containers with bark and soil. The animals were fed sugar and water *ad libitum* using a 1.5 mL microcentrifuge tube (Denville Scientific, Holliston, MA, USA) filled with 10% sucrose solution capped with a cotton ball. The animals were identified to genus and species when possible following (Roache 1960; Ramberg 1979; Lin
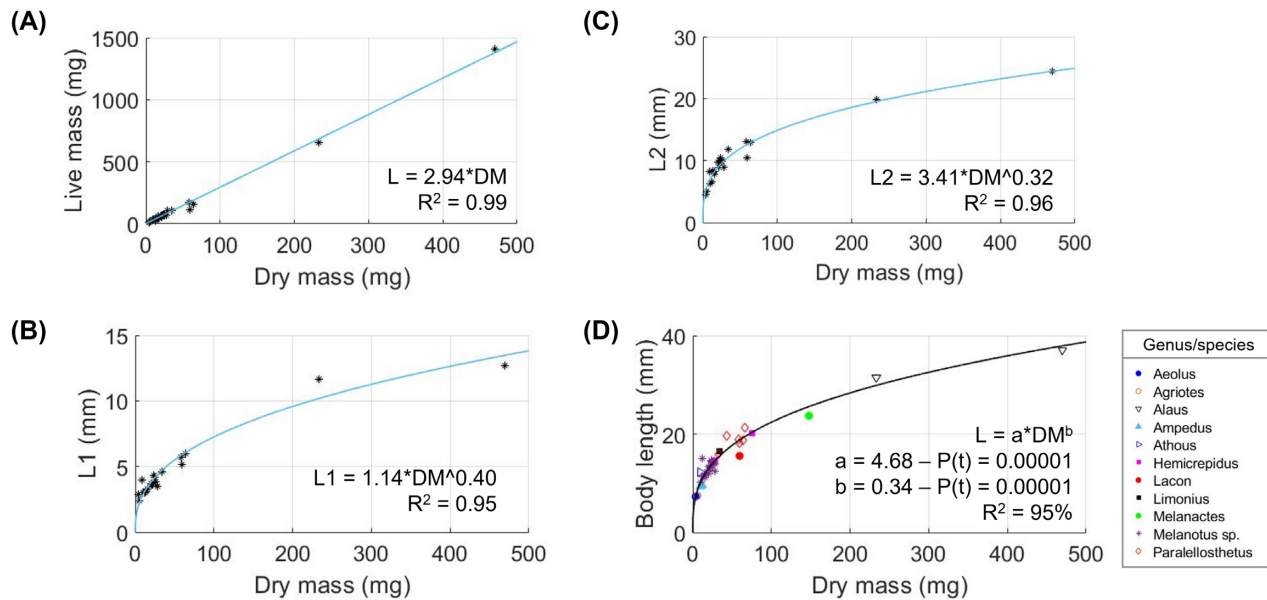
**Fig. 2** Variation of the live mass (LM) and body lengths with the dry mass. (A) The LM for all specimens is about three times the dry mass. B–D. Allometric growth models describing the variation of the three body lengths of interest, L1, L2, and L, show that the body scales isometrically with increasing mass. All parameters are statistically significant, and the models explain well the variance in the data ($R^2$ = 95% and 96%).

1997; Johnson 2003; and Evans 2014). Voucher specimens were deposited in the Illinois Natural History Survey Insects Collection, Prairie Research Institute, the University of Illinois at Urbana-Champaign, Champaign, IL, USA (Dmitriev 2015).

## Morphological measurements

The live mass (LM) of the live animals collected in 2018 was measured after filming using a Fisher Scientific Scale (Waltham, MA, USA) scale, with a sensitivity of 1mg. The dry mass (DM) of all specimens (2017 and 2018) was measured by desiccation using an oven (Chicago Surgical & Electrical Co. 300, formerly at Chicago, IL, USA) at 28C for approximately 10 days. The DM was measured every 2 days until stabilization. The LM of the specimens collected in 2017 was not recorded.

For most specimens, the body length (L) was determined by adding the length of the head and prothorax (L1) to the length of the meso-, metathorax, and abdomen (L2) (Fig. 1A). L1 and L2 were measured from the base to the apex using Mitutoyo Absolute calipers (Kawasaki, Japan). The body length could not be measured for 3 specimens out of 38 due to damage to part of the body. Regression models (see Fig. 2), were used to estimate the body length for these three specimens. For one specimen, the DM was not measured and was estimated based on the LM of the individual (specimen #31 in Supplementary Appendix A). Supplementary Appendix A shows all measurements and reconstructed morphological data set.

## Motion capture and kinematics

The jumping motion of each individual was filmed at 20,000 fps using a Photron FASTCAM SA-Z camera (San Diego, CA, USA) at the Beckman Institute (UIUC). The animals jumped from a delrin plate in a custom white box. The set-up was illuminated using two LED Lights (SugarCUBE™ LED Illuminators, Edmunds Optics Inc., Barrington, NJ). The exposure time was 1/20,664 s and the resolution 1024 × 1024. Each animal was filmed 2–4 days within a 7-day period. A minimum of five jumps per individual per day were recorded. The exact number of jumps collected for each individual is detailed in Supplementary Appendix A. Most animals jumped with no external stimuli when placed in the supine position. However, some animals tended to "play dead" when manipulated and placed in the supine position. These specimens were stimulated to jump by lightly touching their abdomen with tweezers. We made sure that the tweezers did not contact the body not to interfere with the jump at all times. Video recordings were analyzed using ProAnalyst (Xcitex, Woburn, MA, USA). The animals were placed perpendicular to the camera providing a side view during most of the jump. The origin of the reference frame was placed at the initial position of the center of mass (COM, braced position before take-off). The COM position was deter-

mined by tracing and tracking the contour of the body for each frame. Assuming an equal distribution of mass, the COM was approximated as the geometrical center of the contour of the body. The position of the COM data was filtered using a median filter and a fourth-order low-pass Butterworth filter in Matlab R2019a (Mathworks, Natick, MA). From the COM position data, four kinematics parameters were calculated: (1) the velocity at take-off $V_{TO}$ through numerical differentiation of the position data; (2) the angle at take-off $\alpha$ from the COM position data; (3) the maximal acceleration Acc through numerical differentiation of the calculated velocity data; and (4) the maximal jump height h from the position data. Take-off was defined as the instant when the peak velocity was reached, which happened about 0.1–0.2 ms after the animal was observed to leave the ground in the video recordings. The maximum jump height h was defined as the maximum elevation of the COM. The values reported in the Results section are the mean maximum jump height for each individual. The take-off angle was measured at take-off as $\alpha = \arctan(\frac{y_{TO}}{x_{TO}})$ , where ($x_{TO}$, $y_{TO}$) is the position of the COM at take-off. The maximal acceleration Acc was reached in about 0.1–0.3 ms before take-off. The relative jump height was defined as $h/L$ and calculated for each individual from the mean of the jump height and the reconstructed body length data.

## Mathematical models and statistics

### Statistics and regression models

The mean and standard deviation of all kinematic parameters ($h$, $V_{TO}$, $\alpha$, Acc) were calculated using Matlab. In this study, we assumed that the clicking mechanism was very similar for all species, per (Bolmin et al. 2019). The mean values of all the jumps for each specimen were used to run regression models using NLREG (Version 6.5,1998, P.H. Sherrod, Nashville, TN, USA). For all regression models, the reconstructed data of the DM and the length were used (see Supplementary Appendix A). An allometric growth model was used to model the increase of length (L, L1, and L2) as a function of mass. Linear regressions were used to model $h$, $V_{TO}$, $\alpha$, and Acc as a function of increasing mass. Two nonlinear decay models were considered to model the decrease of the relative jump height with increasing mass: (1) a power decay model, and (2) an exponential power decay. The power decay model was developed based on allometric scaling results and the assumption that the airborne trajectory followed ballistics motion. The exponential decay model was developed to describe the abrupt "drop" of the relative jump height for small masses.

For each model fit, the proportion of variance explained ($R^2$), and the probability of obtaining the estimated parameter value if the actual parameter is zero, "Prob(t)," parameter in NLReg) were reported. High values of Prob(t) indicate that the parameter has a high probability of being zero. The adjusted $R^2$ value was not considered in this study because of the small number of parameters of each model fit (one, two, or three; the values reported in NLReg for $R^2$ and adjusted $R^2$ were very similar). For each model, the residuals were plotted in NLReg (plots not shown) to verify that the residuals were relatively small and did not follow a clear distribution pattern.

### Ballistics motion equation

Assuming that only gravity acts on the beetle body during the jump, then the ballistics motion equation (Equation 1) allows for the prediction of the maximum jump height from the velocity at take-off and the take-off angle only. We considered the gravitational constant $g$ to be 9.81 m/s$^2$.

$$h = \frac{V_{TO}^2 \sin(\alpha)}{2g}. \tag{1}$$

From Equation (1), assuming that the velocity at take-off $V_{TO}$ and the take-off angle $\alpha$ are known, the maximum jump height $h$ can be predicted. The predicted maximum jump height was compared to the measured maximum jump height to estimate the ballistics motion assumption error.

## Results

### Morphometric scaling

For all specimens, the body length L varied from 7.3 to 37.1 mm, the head and prothorax length L1 from 2.4 to 4.4 mm, and meso-, metathorax, and abdomen L2 from 4.4 to 24.4 mm. The DM varied from 3.7 to 469.8 mg, and the LM from 9.5 to 1406.8 mg. The LM varied linearly with the DM (see Fig. 2A), with a slope of 2.94 [$R^2 = 99\%$, $P(t) = 0.00001$].

Fig. 2D shows that L grows allometrically with increasing body mass. The parameters of the allometric equation used to describe the length increase with increasing body mass are statistically significant [$P(t) = 0.00001$], and the model explains the variance well ($R^2 = 95\%$). The growth constant (power exponent) is estimated to be 0.34. This supports that the body mass scales with the length cubed. Allometric models also describe the increase of L1 and L2 with increasing body mass, as shown in Figs. 2B and C.

### Jumping kinematics

Fig. 3 shows the mean values of the jump height (A), take-off angle (B), the velocity at take-off (C), and max
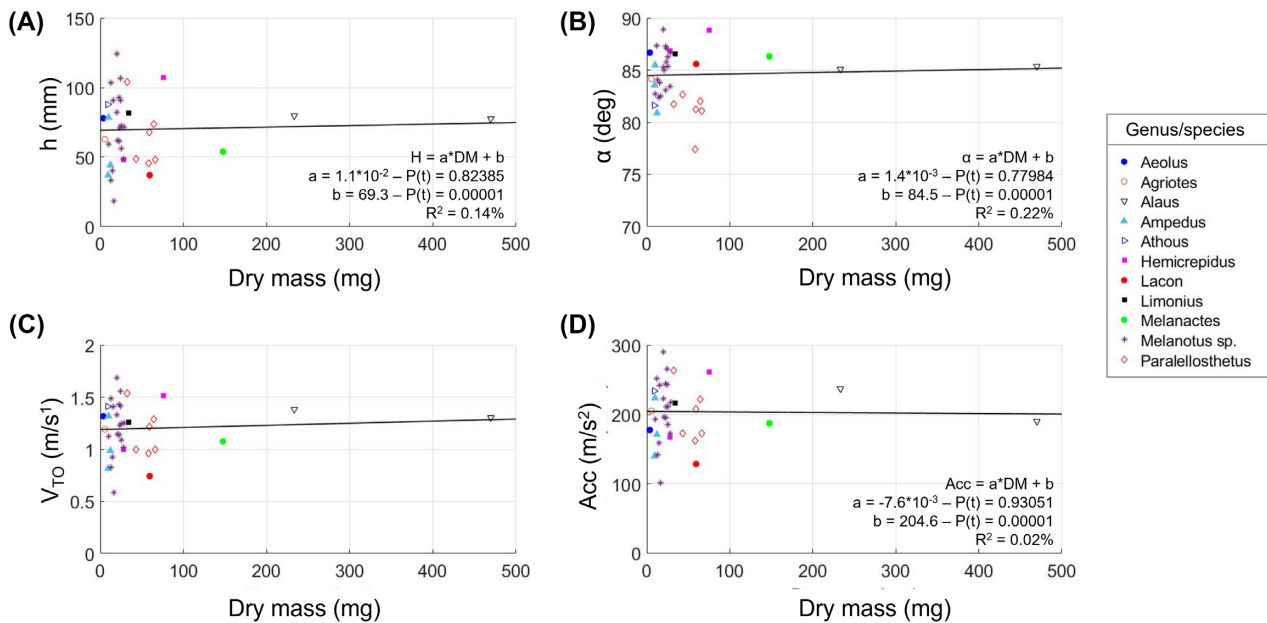
**Fig. 3** Linear model fits for the (A) jump height, (B) take-off angle, (C) the velocity at take-off, and (D) max acceleration with increasing body mass. The kinematic parameters can be considered constant across the mass range, indicating that mass is not a predictor of these parameters for the specimen considered.
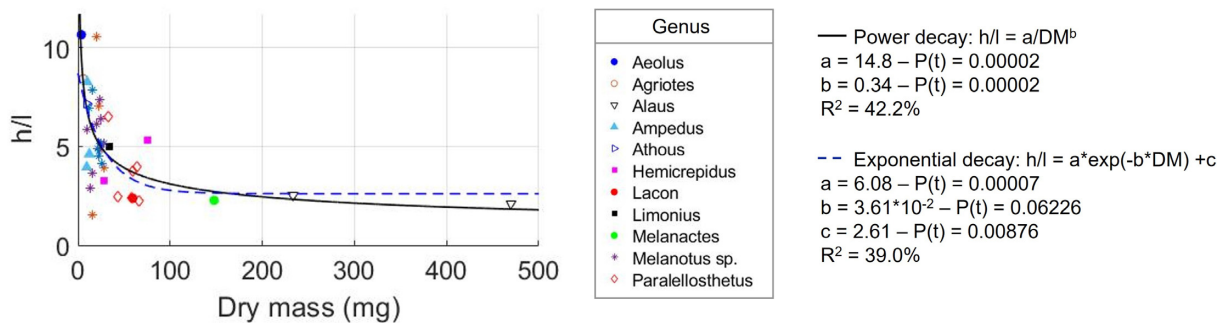


**Fig. 4** Relative jump height as a function of increasing mass for all 38 specimens studied. A power decay model (solid line) and an exponential decay model (dashed line) are fitted to describe the decrease of the relative jump height with increasing mass. Both models can be used to describe the overall decay but do not account for the variation in the data.

acceleration (D) measured across the mass range for all 38 specimens. While variations across jumps for each specimen were observed, no pattern was identified during one filming session or across days to explain each individual's variation in the jump behavior (see Supplementary Appendix B).

Across individuals, the mean jump height $h$ varies between 18.5 and 124.2 mm, the velocity at take-off $V_{TO}$ varies between 0.6 and 1.7 m/s, the take-off angle $\alpha$ between 77.4 and 88.9 degrees, and the maximum acceleration Acc between 101.6 and 289.9 m/s$^2$. Linear regressions show that $h$, $V_{TO}$, $\alpha$, and Acc are constant across the mass range, that is, mass is not a predictor of the

kinematic parameters considered (Fig. 3). For each linear regression, the slope is negligible (order of magnitude: $10^{-2}$–$10^{-5}$), and the probability of the slope to be zero is very high (82, 78, 68, and 70%, respectively). The proportion of variance explained $R^2$ is close to 0, which indicates that these linear models do not capture the variation in the data. Thus, linear regression models only capture the overall trend.

The relative jump height $h/L$ decays from 10.6 to 1.5 as a function of increasing mass per Fig. 4. The two nonlinear decay models (power decay in black and exponential decay in dashed blue in Fig. 4) describe the overall decay well as the model parameters are statis-

tically significant. However, the variation in the data is well captured by either model, as $R^2 = 40.6$ and $39.0\%$, respectively.

## Discussion

It is commonly assumed in biomechanics that mass scales with body length cubed. The allometric growth models developed for L, L1, and L2 (see Fig. 2) show that the body lengths increase with increasing mass following a power function with an exponent of approximately one-third (0.34, 0.40, and 0.32, respectively). Thus, for the specimens considered in this study, this assumption holds. The goodness of fit of each model can be used as a metric to define which length measurement is the best indicator of body mass. Based on the data used for this study, the allometric models fit for L, L1, and L2 explain the variation in the data in similar ways. Both of these metrics can estimate body mass from length measurements for click beetles. Morphometric scaling laws can also help evaluate the mass of specimens that have been partially damaged during an experimental campaign or in storage. When collecting experimental data, conserving dried specimens can be challenging. Care needs to be put into cleaning the specimens to avoid mold and other insects from degrading the beetles, and cautious handling is required not to break the very brittle dried bodies. When samples are damaged, having models to estimate morphological parameters is essential to reconstruct complete data sets. The parameters evaluated in Fig. 2 can be used to estimate the LM of specimens from collections or that were partially damaged. The linear correlation between LM and DM across the click beetle species indicates that the DM is about one-third of the live (wet) mass. The morphological scaling laws in Fig. 2 are also critical to infer how organs and muscles scale with increasing body length. Muscle scaling is of particular interest when studying the jump of click beetles and other insects. From a small data set relating muscle volume to body length (e.g. from CT-scans), the force generated to initiate the jump can be estimated for broad range of species. Such estimates may help inform the design of click beetle-inspired prototypes by providing initial actuation requirements for muscle-like motors.

The kinematic data set measured in this study enables us to test whether the click beetle jump follows ballistics motion, that is, to test the assumption that gravity is the only force acting on the insect during the jump. The kinematic parameters measured in Fig. 3 are coherent with the jumping data reported in the literature for small click beetles ($L = 4$–$20$ mm) (Evans 1972; Ribak and Weihs 2011; Ribak et al. 2012; Hashemi Farzaneh 2020). As the maximum jump height h can be consid-

ered constant across the mass range (Fig. 3), a first necessary condition for the ballistics equation to hold is for the right-hand side of Equation (1) to also be constant. The analysis of the kinematics parameters showed that the velocity at take-off $V_{TO}$ and the take-off angle $\alpha$ are indeed constant with increasing mass. Ballistics motion may thus be assumed. We can test the ballistics motion assumption using two methods. First, assuming that Equation (1) holds, the relative jump height should decrease following a power decay model with increasing mass. As $h$ is constant and $L \sim m^{0.3}$, then we expect $h/L \sim \beta/m^{0.3}$, with $\beta$ is a constant. Fig. 4 shows that $\beta$ can be estimated at 0.34, supporting this first injunction. Second, we may calculate the maximum jump height using Equation (1), assuming that the velocity at take-off $V_{TO}$ and the take-off angle $\alpha$ are known for each specimen and compare the estimated value and the measured ("true") jump height. The error is shown in Supplementary Appendix C. For 68% of the specimens, the maximum jump is predicted by Equation (1) with less than a 15% error. For 27 out of 28 specimens, the maximum jump is predicted with less than a 20% error, supporting that the ballistics motion equation describes well the airborne trajectory of the jump. An airborne ballistic trajectory indicates that gravity is the only significant force acting on the beetle body during the airborne stage. Thus, other forces acting on the body, such as drag, can be neglected. For the one specimen studied (*Lacon marmoratus*), estimating the maximum jump height per Equation (1) yields an error of 41%. For this specific specimen, the ballistics motion equation cannot be used to predict the airborne trajectory. As it the only specimen of *L. marmoratus* studied, it is unclear if it is an outlier or if this species has different airborne physics.

While our data support the ballistics motion assumption, the variation in the data is not well explained by the first model developed in Fig. 4 (power decay model), especially when considering the abrupt decay for small individuals (DM < 80 mg). The exponential decay model describes the abrupt decay for small individuals slightly better. An exponential decay model suggests that the relative jump height reaches an asymptote as the mass increases. However, as the current data doesn't include many large individuals, the model cannot capture the behavior of large mass and is suited to test this hypothesis. To refine both models describing the relative jump height decay, a larger number of large animals (DM > 80 mg) should be considered. Other models could be developed to describe the relative jump height decay, such as biphasic models, to better describe the data variation. Biphasic models would suggest that airborne physics are mass-dependent. A larger data set would be needed to identify such mass-dependent transitions.

This study expands the available data set on the jumping performance of click beetles and includes species commonly found in the American Midwest (prior data sets focused on species found in Europe and Israel (Evans 1972; Kaschek 1984; Ribak and Weihs 2011; Ribak et al. 2012). Our findings are similar to prior work conducted by a subset of the authors (Bolmin et al. 2017), and found in the literature (Evans 1972; Kaschek 1984; Ribak and Weihs 2011; Ribak et al. 2012). These similarities speak of the quality of the data sets collected in the collected in the 1970s and the 1980s and suggest that the various data sets may be combined in future studies to include a large number of species and individuals. This augmented data set is of great interest to current and future efforts to guide the design of click-beetle inspired robotic platform.

In this study, we record and quantify the morphology and the jumping performance of a large number of click beetle species of various sizes. We investigate how the body scales with increasing mass and establish scaling laws that can be used to reconstruct data sets and estimate morphological parameters in museum specimens. The statistical models used to describe jumping performance show that the jumping parameters considered (jump height, take-off angle, velocity at take-off, and maximum acceleration) are constant across the mass range. Hence, for the specimen considered, mass is not a predictor of the kinematics. Furthermore, we show that the COM follows ballistics motion during the airborne stage. Hence gravity is the dominant force acting on the beetles while airborne, regardless of body size. The velocity at take-off and the take-off angle are the only parameters affecting jumping performance. This work tests this assumption at the core of literature modeling the click beetle jump and provides a framework for studying insect jumping performance.

## Acknowledgments

## Funding

## Supplementary data

Supplementary data available at *ICB* online.

## Conflict of interest

The authors have no conflicts to declare.

## Data availability statement

The datasets generated during this study are included in the supplementary information files. The original high-speed videos are available from the corresponding author on reasonable request.

## References

Bennet-Clark HC. 1975. The energetics of the jump of the locust Schistocerca gregaria. J Exp Biol 63:53–83.

Bolmin O, Duan C, Urrutia L, Abdulla MA, Hazel AM, Alleyne M, Dunn AC, Wissa A. 2017. Pop! observing and modeling the legless self-righting jumping mechanism of click beetles. In: Mangan M, Cutkosky M, Mura A, Verschure P, Lepora N, editors. Biomimetic and biohybrid systems. Living machines. Springer, Cham. p. 35–47.

Brackenbury J, Hunt H. 1993. Jumping in springtails: mechanism and dynamics. J Zool 229:217–36.

Burrows M. 2006. Jumping performance of froghopper insects. J Exp Biol 209:4607–21.

Bolmin O, Socha JJ, Alleyne M, Dunn AC, Fezzaa K, Wissa AA. 2021. Nonlinear elasticity and damping govern ultra-fast dynamics in click beetles. Proc Natl Acad Sci USA 118:e2014569118

Bolmin O, Wei L, Hazel AMAM, Dunn ACAC, Wissa A, Alleyne M. 2019. Latching of the click beetle (Coleoptera: Elateridae) thoracic hinge enabled by the morphology and mechanics of conformal structures. J Exp Biol 222:jeb196683.

Dmitriev D. 2015. Illinois Natural History Survey Insect Collection. Occurrence data set. Accessed: Feb 15, 2022.

Evans MEG. 1972. The jump of the click beetle (Coleoptera, Elateridae)—a preliminary study. J Zool 167:319–36.

Evans AV. 2014. Click beetles, family Elateridae". In: Beetles of eastern north America. Princeton (NJ): Princeton University Press. p. 213–28.

Graham EE, Mitchell RF, Reagel PF, Barbour JD, Millar JG, Hanks LM. 2010. Treating panel traps with a fluoropolymer enhances their efficiency in capturing cerambycid beetles. J Econ Entomol 103:641–7.

Hashemi Farzaneh H. 2020. Bio-inspired design: the impact of collaboration between engineers and biologists on analogical transfer and ideation. Res Eng Des 31:299–322.

Johnson PJ. 2003. Elateridae leach 1815. In: Arnett R.H.,Thomas M. C.,Skelley P. E.,Frank J. H., editors. American beetles: Polyphaga: Scarabaeoidea through Curculionoidea. Vol. 2. Boca Raton, Florida: CRC Press. p. 160–73.

Kaschek N. 1984. Vergleichende Untersuchungen über Verlauf und Energetik des Sprunges der Schnellkäfer (Elateridae, Coleoptera). Zool Jahrb Abt Anat Physiol Tiere 88: 361–85.

Lin X. 1997. A taxonomic revision of the genus Aeolus Eschscholtz of North America, North of Mexico

(Coleoptera:Elateridae) [Master's dissertation]. Brookings(SD): South Dakota State University.

Maitland DP. 1992. Locomotion by jumping in the Mediterranean fruit-fly larva *Ceratitis capitata*. Nature 355:159–61.

Ramberg FB. 1979. A revision of the species of the genus Ampedus (Coleoptera, Elateridae) of America north of Mexico [Ph.D. dissertation]. Ithaca (NY): Cornell University.

Ribak G, Mordechay O, Weihs D. 2013. Why are there no long distance jumpers among click-beetles (Elateridae)?. Bioinspir Biomim 8. doi:10.1088/1748-3182/8/3/036004

Ribak G, Reingold S, Weihs D. 2012. The effect of natural substrates on jump height in click-beetles. Funct Ecol 26:493–9.

Ribak G, Weihs D. 2011. Jumping without using legs: the jump of the click-beetles (*Elateridae*) is morphologically constrained. PLoS One 6:1–7.

Roache LC. 1960. A revision of the north American elaterid beetles of the Tribe Elaterini (Coleoptera:Elateridae). Trans Am Entomol Soc (1890) 86:275–324.

Sutton GP, Burrows M, Rosario Mv, Edwards DH. 2011. Biomechanics of jumping in the flea. J Exp Biol 214:836–47.