



Jumping of flea beetles onto inclined platforms

Le Zong^{1,2} · Jianing Wu^{1,3} · Pingping Yang^{1,4} · Jing Ren¹ · Guanya Shi⁵ · Siqin Ge¹ · David L. Hu⁶

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Abstract

The flea beetle, *Altica cirsiicola*, escapes predators by jumping and landing in a dense maze of leaves. How do they land on such varied surfaces? In this experimental study, we filmed the take-off, flight, and landing of flea beetles on a configurable angled platform. We report three in-flight behaviors: winged, wingless, and an intermediate winged mode. These modes significantly affected take-off speed, acceleration, and the duration that wings were deployed. When wings were closed, flea beetles rolled or pitched up to five times in the air. This work may help to understand how insects can jump and right themselves onto variable surfaces.

Keywords Self-righting · Flea beetle · Landing · Jumping

Introduction

Rapid escape from predators has long driven the evolution of jumping (Gronenberg 1996). As a result, jumping is present across a range of insect sizes, including fleas (Krasnov et al. 2004; Sutton and Burrows 2011), locusts (Sutton and

Burrows 2008; Cofer et al. 2010), flies (Card and Dickinson 2008; Burrows 2013), moths (Burrows and Dorosenko 2015a), caddis flies (Burrows and Dorosenko 2015b), and many others (Brackenbury and Wang 1995; Burrows and Sutton 2013; Truong et al. 2014). For small insects to jump adequate distances, they recruit biological springs to store and release energy explosively. Due to their explosive jump, small insects are considered to have less control over their direction and landing.

In our work, we focused on the flea beetle *Altica cirsiicola*, a small insect of body length 4 mm and width 2 mm. A lack of control would make it difficult for flea beetles to land successfully in cluttered environments such as its host plant, the flowering *Cirsium setosum*. In this study, we investigated the behaviors that flea beetles use to land on various inclinations of a landing platform.

Given that flea beetles jump explosively, we expect them to perform mid-air corrections as they approach a target. Reorientation in mid-air is called adaptive behavioral righting, and consists of both passive and active strategies. For example, pea aphids (*Acyrtosiphon pisum*) passively right themselves by dropping off a plant and assuming aerodynamically stable postures (Ribak et al. 2013). In contrast, active aerial righting involves movements of the torso, leg, or tail (Jusufi et al. 2011). Geckos and anoles right themselves using the inertial torques generated by whipping their tails. Even wingless stick insect nymphs right themselves in midair by using their bodies as an airfoil (Zeng et al. 2017). How flea beetles accomplish aerial righting is not well understood as they often spin many times in mid-air (Brackenbury and Wang 1995).

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Le Zong and Jianing Wu contributed equally to this study.

✉ Siqin Ge
gesq@ioz.ac.cn

✉ David L. Hu
hu@me.gatech.edu

¹ Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, People's Republic of China

² College of Life Science, University of Chinese Academy of Sciences, Beijing 100049, People's Republic of China

³ School of Aeronautics and Astronautics, Sun Yat-Sen University, Shenzhen 518107, People's Republic of China

⁴ The Key Laboratory of Zoological Systematics and Application, School of Life Science, Institute of Life Science and Green Development, Hebei University, Baoding 071002, People's Republic of China

⁵ Department of Computing and Mathematical Sciences, California Institute of Technology, Pasadena 91125, USA

⁶ George W. Woodruff School of Mechanical Engineering and School of Biology, Georgia Institute of Technology, Atlanta, GA 30332, USA

Brackenbury and Wang (1995) investigated the ballistics and visual targeting in seven species of flea beetles Alticinae. To test their visual targeting, they provided black stripes or illuminated cross-shapes. Several species targeted these patterns when they jumped, demonstrating control their jumping direction. They classified the jumps into two modes: with or without the use of their wings. If the beetle's wings were closed, they spun repeatedly in mid-air, and rarely landed on their legs. If their wings were open, body rotation was halted, facilitating a leg-first landing (Brackenbury and Wang 1995). Because of the technology of the day, strobe photography, Brackenbury did not provide videos of the flight or details of the spinning process. In our work, we used high-speed digital videography to gather enough trials to be amenable to statistics. Our work will help characterize landing success and whether take-off behavior depends on the inclination angle of the landing platform.

maintained at a temperature of 25 °C and humidity of 50% in a tank with leaves of their host plant, *Cirsium setosum* (Fig. 1a). No permissions were needed for insect collection at our chosen locations, and no endangered or protected species were collected. We conducted specimens annually from 2015 to 2019, collecting 5–22 beetles on each trip. The videos varied in quality, and the identity of individual beetles could only be confirmed from a subset of these videos. Thus, the number of beetle n and the number of jumps N varied across the tests reported. For all trials conducted, we recorded if the landing was successful as well as the mode used. Using this data, we reported the success rate of flight modes and platform angles. Kinematics were only analyzed for successful trials since we only systematically kept videos for successful trials. The precise number of jumps used for each statistical test is listed in the tables in the Supplementary material (Table S1, S2).

Material and methods

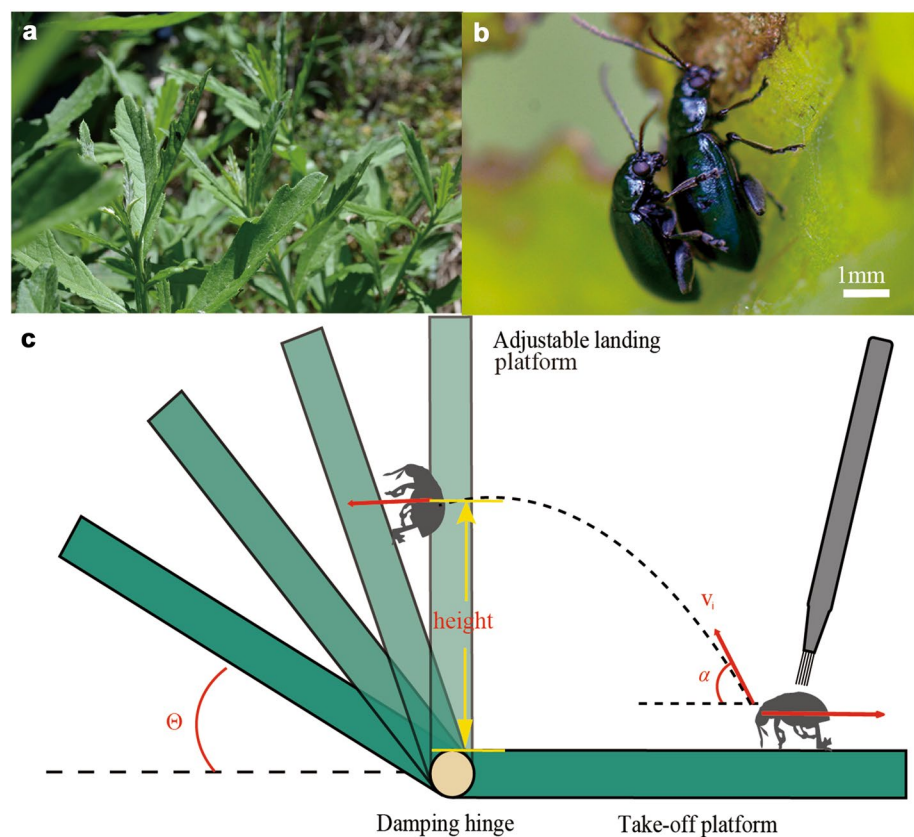
Beetle collection

Altica cirsiicola specimens were collected from Olympic Forest Park (40.00°N, 116.33°E) and Beijing Botanical Garden (39.60°N, 116.12°E) in Beijing, China. They were

Experimental setup and video processing

The experimental setup comprised an inclined plane made using a pair of rectangular acrylic panels, which includes the take-off platform (165 mm × 50 mm) and the landing platform (140 mm × 50 mm). The hinge connecting the platform was rotated to form inclination angles θ of 30°, 50°, 70°,

Fig. 1 The flea beetle *Altica cirsiicola*. **a** The flea beetle is monophagous and lives in a maze of host plants, *Cirsium setosum*. **b** A pair of mating flea beetles. **c** Schematic of the experimental setup where the beetle jumps with take-off angle α and initial speed v_i . The setup includes an adjustable landing platform with an inclination angle θ ranging from 0° to 90° to mimic the orientations of leaves in nature



and 90° to mimic the orientations of leaves on which the flea beetle lands in nature (Fig. 1c). We recorded as many jumps as possible with one flea beetle before moving onto another beetle. Between each jump, the beetle was placed on the take-off platform to rest for five min. We alternated platform angle with each subsequent trial, recording an average of four jumps per beetle. We used GraphPad Prism 5 (GraphPad Inc., California, USA) for drawing box plots.

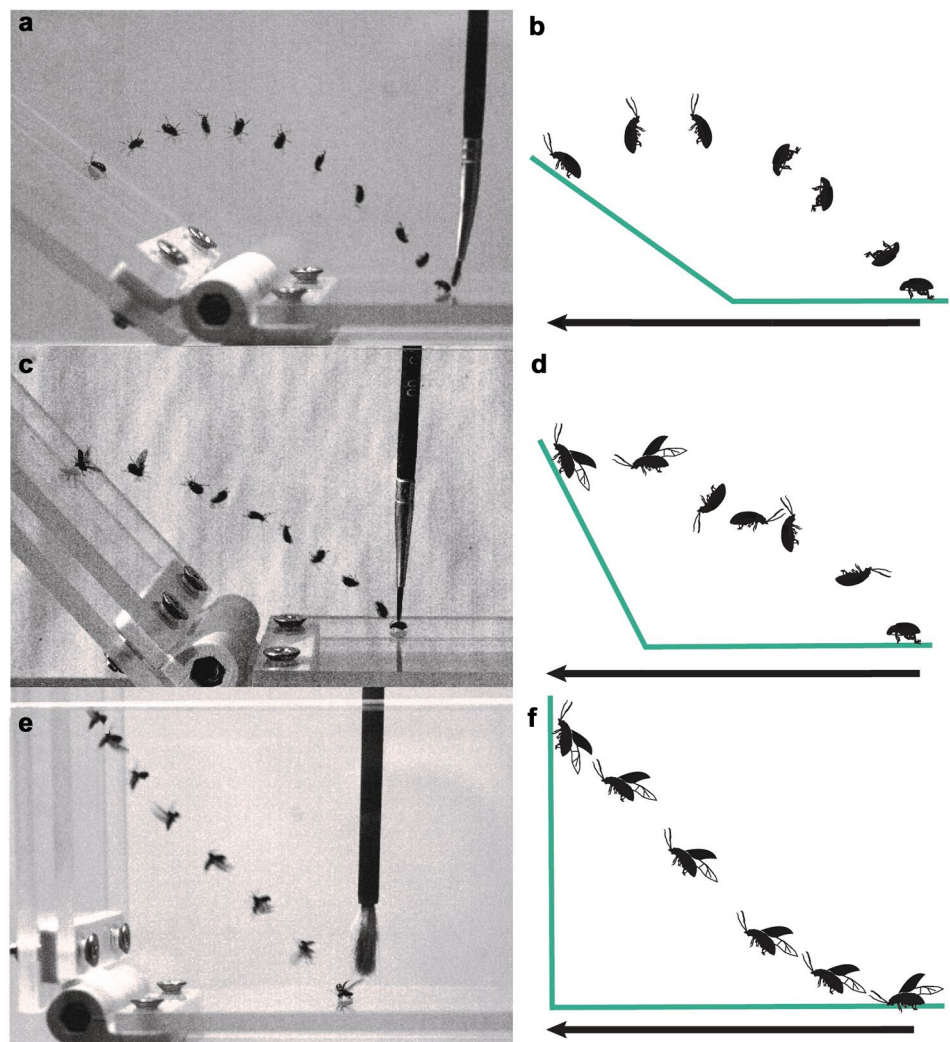
A trial began using a straw (10 mm in radius) to place a live flea beetle on the horizontal platform. A brush, with a soft hairy tip with a diameter of 5–10 mm, provoked the beetle to jump. We completed the jumping experiments within 10 h of capturing the flea beetle in the wild. The whole jumping process, including take-off, flight, and landing, was recorded by a high-speed camera (Phantom M110, VL0910, and LC311, USA) set at frame rates of $f=700$ fps, 3200 fps, and 3500 fps, and retrofitted with a microlens (WWL08-110CN, China). The camera was equipped with a 3-DOF

positioner with accuracy of 0.01 mm. The video captured by the high-speed camera was processed via the software PCC 3.1 (Phantom, USA). We tracked the trajectories of the flea beetle by calculating its centroid using an algorithm in Adobe Photoshop CS5 and Illustrator CS 6 (Adobe Inc., California, USA) (Fig. 2). We graphed Fig. 5, using Origin 2019b (OriginLab Corporation, USA), but we could not generate statistics of beetle rotations because the resolution of the videos required them to be tracked by hand.

Statistics

Statistics were performed using SPSSAU (Version 21.0). Hierarchical Linear Model (HLM) are models used to determine the effect of various factors on beetle kinematics (Man et al. 2022). We applied HLM to study the effect of platform angle, jump mode, and individual variance on kinematic performance. We fixed the effects of jump mode and platform

Fig. 2 Mid-air maneuvering during the leap. Three cases of successful landing for wingless, intermediate, and winged jumping modes. **a, c, e** show superimposed photos of the jump. **b, d, e** are redrawn trajectories. **a, b** Wingless jumping onto a 30° incline. The flea beetle jumps with wings folded, pitches and rolls in midair, and orients to stick a perfect landing. The take-off velocity is 1.02 m/s. **c, d** Intermediate jumping to a 50° incline. The flea beetle achieved a wingless take-off ($v_i=1.26$ m/s), spins and flings elytra and hind wings in mid-air, and finally lands on the platform. **e, f** Winged jumping to a 90° incline. The flea beetle takes off with wings, travels with little body rotation and attaches to the target successfully



angle, and considered beetle identity as the random effect based on the restricted maximum likelihood (REML). The Shapiro–Wilk test was used to test for normality and chi-squared test was used to test for independence. We also performed chi-squared tests to determine if platform angle and jump mode affected jumping success rate.

Definition of successful and unsuccessful landings

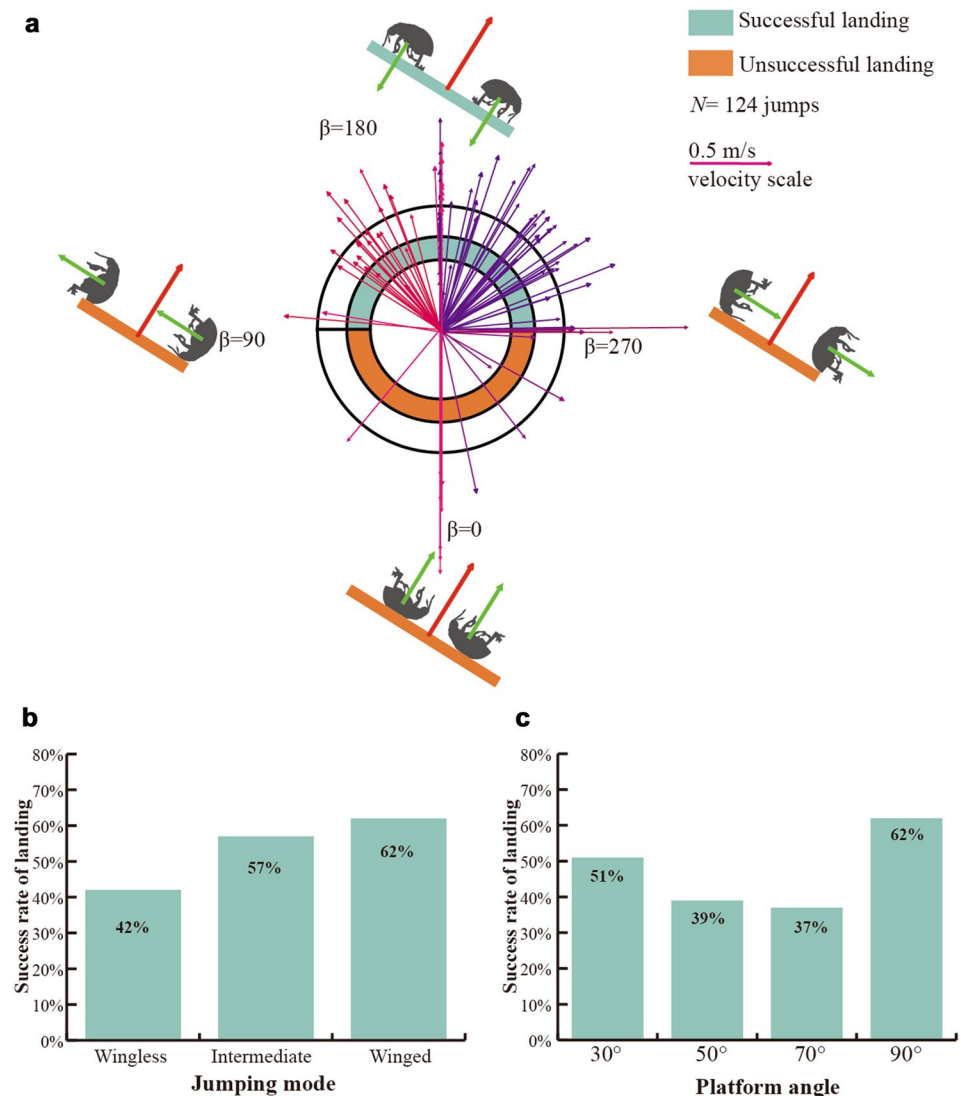
We defined a successful landing as one where the beetle attached its legs to the landing platform, and a failed landing as one where the beetle bounced or landed on its back. To understand the range of successful landings, we analyzed jumps in terms of the relative angle β between the ground and beetle vector at impact. We defined the ground vector as normal and upwards from the landing platform. The beetle vector was normal to the ventral surface of the flea beetle. Vectors in Fig. 3a show the range of possible landing

orientations of the beetle ($n = 33$ beetles, $N = 124$ jumps). Traveling clockwise from $\beta = 0^\circ$ on the diagram denotes clockwise rotations of the beetle. A successful landing occurred if $90^\circ < \beta < 270^\circ$. A perfect landing is denoted by $\beta = 180^\circ$, as shown by the top image in Fig. 3a. An unsuccessful landing is defined as an under-rotation, $\beta < 90^\circ$, or over-rotation, $\beta > 270^\circ$. The worst possible landing occurs if it lands completely on its back, $\beta = 0^\circ$.

Kinematic variables

The jump, which starts at take-off and ends at landing, has a duration T . We define the centroid coordinates as $P(t) = (x(t), y(t))$, the velocity as $v(t)$, and angular velocity as $\omega(t)$. The initial velocity v_i is the speed when the flea beetle detaches from the substrate, which may be written $v_i = \sqrt{(x(\Delta t) - x(0))^2 + (y(\Delta t) - y(0))^2} / \Delta t$ where Δt is the

Fig. 3 Landing orientation and performance of beetles. **a** Histogram of the landing orientation with respect to all platforms ($n = 33$ with 124 jumps). Each arrow represents one trial, with arrow length indicating the velocity with respect to the scale bar. In the insets, the red arrow shows the orientation of the platform, and the green arrow the orientation of the beetle's ventral surface. **b** Landing success rate of the jumping modes. **c** Landing success rate of the platform angles



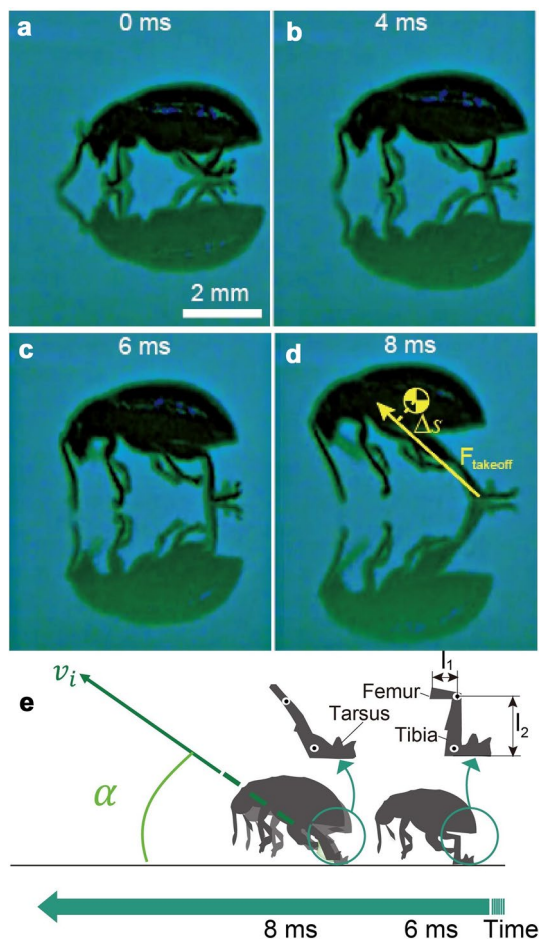


Fig. 4 Takeoff kinematics. **a–d** The flea beetle takes off by extension of its hindleg. **a** The tarsus sits on the ground, and the femur–tibia joint is flexed. **b–d** The femur and tibia joint extends, while the tarsus remains in contact. **e** Definition of the initial velocity and take-off angle

duration between camera frames. The take-off angle, namely the direction of the initial velocity, is defined as the acute angle between the take-off direction and the platform, $\alpha = \arctan[(y(\Delta t) - y(0)) / (x(0) - x(\Delta t))]$ (Fig. 4). The take-off duration t is defined as the time that encapsulates the period that the flea beetle began extending its hindleg but maintained contact with the ground. The take-off acceleration is $a = v_i / t$. The wing opening duration is the time that elapses when the wings are opened.

Results

We filmed the jumping of flea beetles ($N=246$ jumps across $n=53$ beetles) and categorized the jumps into three modes: wingless, intermediate, and winged. Figure 2 shows beetle trajectories for all three modes. In the wingless mode, the flea beetle jumped toward the landing platform with its

wings still closed (Fig. 2a, b). In the intermediate mode, the flea beetle deployed its wings in mid-air, conceivably to eliminate spinning (Fig. 2c, d). In the winged mode, the flea beetle opened and flapped its wings to take off (Fig. 2e, f). During this mode, the flea beetle performed flapping flight rather than gliding. We could not determine whether legs were used for takeoff in the winged mode.

We next investigated whether individual beetles had a preferred jumping mode. Figure 5 ($n=24$ beetles, $N=101$ jumps) shows a histogram of mode preferences for both successful and failed jumps from 24 individual beetles. We conducted tests with the same beetle until it refused to jump. Some beetles were willing to jump more than others, with some beetles jumping up to ten times. More than half the flea beetles tested (13 flea beetles) relied on just a single mode, and three of those flea beetles performed the same mode six to ten times in a row. Flea beetles that relied exclusively on one mode generally used either the wingless or the intermediate mode. Idiosyncratic mode preferences are not unique to flea beetles. In previous work, we found that Mexican jumping beans, *Laspeyresia saltitans*, which consist of a moth larva living inside a hollow seed, had individual-specific preferred temperatures, which affected the distances that they rolled in a temperature gradient (West et al. 2012). In insects, we generally expect high numbers of progeny and high variability.

We used the hierarchical linear model (HLM) to fix the effects of jump mode and platform angle without consideration of beetle identity. We then considered beetle identity as a random effect that influences kinematics. We used the intraclass correlation coefficient (ICC) value to indicate the range of variation of the dependent variables at the group level.

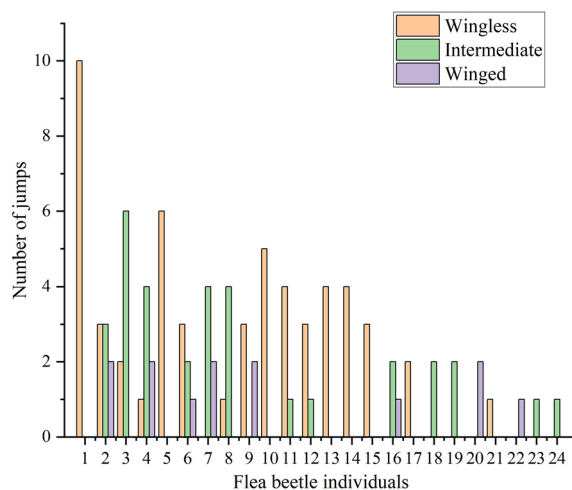


Fig. 5 Histogram of the mode selection for individual flea beetles ($n=24$ beetles, $N=101$ jumps)

First, we calculated the ICC by fixing the effects of jump mode and platform angle without considering beetle identity, finding ICC values for take-off velocity (ICC = 0.084), take-off acceleration (ICC = 0.147), take-off angle (ICC < 0.001), jump height (ICC < 0.001) and wing deploy duration (ICC = 0.366). If the ICC values were less than 0.1, we conclude the varying strength of the dependent variable was low, and data aggregation was weak. Thus, for most of these variables, we directly abandoned the HLM model, and instead, use a common regression model. If the ICC values were greater than 0.1, the variation brought by beetle identity as a random effect was explored.

In another analysis, using the beetle identity as a random effect, we found the ICC for take-off acceleration (ICC = 0.091) and wing deploy duration (ICC = 0.580) (Supplementary material Table S13–S26). To compare, the take-off acceleration ICC value without beetle identity as a random effect was 0.147, and the ICC value obtained with beetle identity random effects was 0.091. The difference in the ICC, 0.046, indicated that the addition of beetle identity produced 4.6% of the explanatory power of variation. Since the explanatory power of variation was small, we concluded that we did not need to consider the effects of individuals for take-off acceleration. However, for the wing deploy duration, there was a substantial increase of 21.4% explanatory power due to beetle identity. Thus, we concluded that individual differences between beetles indeed affected wing deploy duration.

We proceed by considering success rate as a function of platform angle and jumping mode (Fig. 3b, c, $N = 122$ jumps, datasets from 2018 and 2019). Note that these success rates do not add up to 100 percent. They simply relate the chance of landing successfully if beetles were given a certain platform angle or chose a certain mode. There were 122 jumps on all four platform angles. Across all the jumps observed, the success rates were 51% (21 out of 41 jumps) for the 30° platform angle, 39% (11 out of 28 jumps) for the 50° platform angle, 37% (10 out of 27 jumps) for the 70° platform angle, and 62% (16 out of 26 jumps) for the 90° platform angle (Fig. 3c). The fraction of successful landings for the wingless mode was 42% (33 out of 79 jumps), for the intermediate mode 57% (17 out of 30 jumps), and for the winged mode 62% (8 out of 13 jumps) (Fig. 3b). We used a chi-squared test to estimate whether the modes and platform angle significantly affected success rate. The result showed that there was no statistically significant difference among the three jump modes ($\chi^2 = 4.2247$, $p = 0.2382 > 0.05$) and four platform angles modes ($\chi^2 = 2.0987$, $p = 0.3502 > 0.05$). We concluded that the observed differences in success rate were due to sampling.

We proceed by combining successful jumps into a single dataset, without distinguishing how many jumps per individual (Fig. 6, $N = 58$ jumps, datasets from 2018 and

2019). We calculated the take-off time, take-off velocity, take-off acceleration, take-off angle, and jumping height on the different platforms (Supplementary material Table S4). Since the number of beetles in this set was less than 50, the Shapiro–Wilk test was used to test for normality (Shapiro and Wilk 1965). The null hypothesis is that these samples come from a normal distribution: if the p -value < 0.05, the null hypothesis is rejected. Supplementary material Table S5 shows that take-off velocity, take-off acceleration, and wing deploy duration all have p -value > 0.05 and are thus normally distributed. However, the null hypothesis was rejected for take-off times, take-off angle and jump height. We proceed by considering the kurtosis and skewness: if the absolute value of kurtosis was less than 10 (the values were 0.883, 0.635 and 0.713) and the absolute value of skewness was less than 3 (the values were 1.136, -0.044 and 0.033), then these variables could all be considered to be normally distributed.

To test the independence between platform angle and jumping mode, we performed a chi-squared test on a 4 × 3 table (Clegg 1988, Supplementary material Table S6). The $\chi^2 = 5.818$ and $p = 0.444 > 0.05$ showed that jumping modes and platform angle were independent.

After confirming normality and independence, we determined if kinematic parameters were affected by platform angle and jump mode. A two-way ANOVA test (Mishra 2019) showed no effect of platform angle on kinematics, including take-off velocity ($F = 0.141$, $p = 0.935 > 0.05$), take-off acceleration ($F = 0.252$, $p = 0.859 > 0.05$), take-off time ($F = 2.344$, $p = 0.089 > 0.05$), take-off angle ($F = 0.594$, $p = 0.623 > 0.05$), and jump height ($F = 0.113$, $p = 0.952 > 0.05$) (Fig. 6b–e). Thus, while previous work showed that certain species of flea beetles aimed their bodies toward visual targets, our species showed no evidence of changing behavior based on platform angle (Supplementary material Table S9–S14).

Jump mode, however, did influence a portion of the kinematics: take-off times ($F = 4.785$, $p = 0.013 < 0.05$), take-off velocity ($F = 6.976$, $p = 0.003 < 0.05$) and take-off acceleration ($F = 7.220$, $p = 0.002 < 0.05$). Take-off angle ($F = 0.683$, $p = 0.511 > 0.05$) and jump height ($F = 1.519$, $p = 0.232 > 0.05$) were not affected by jump mode (supplementary material Tables S9–S14), and there was no second-order effect between platform angle and jumping mode.

To test how the kinematics were affected by each of the three jumping modes, we conducted a one-way ANOVA (Table 1). The table shows how the jump modes had significant effects on take-off times ($F = 4.785$, $p = 0.013 < 0.05$, winged > intermediate > wingless), take-off velocity ($F = 7.422$, $p = 0.002$, intermediate > wingless > winged) and take-off acceleration ($F = 7.484$, $p = 0.002$, intermediate > wingless > winged).

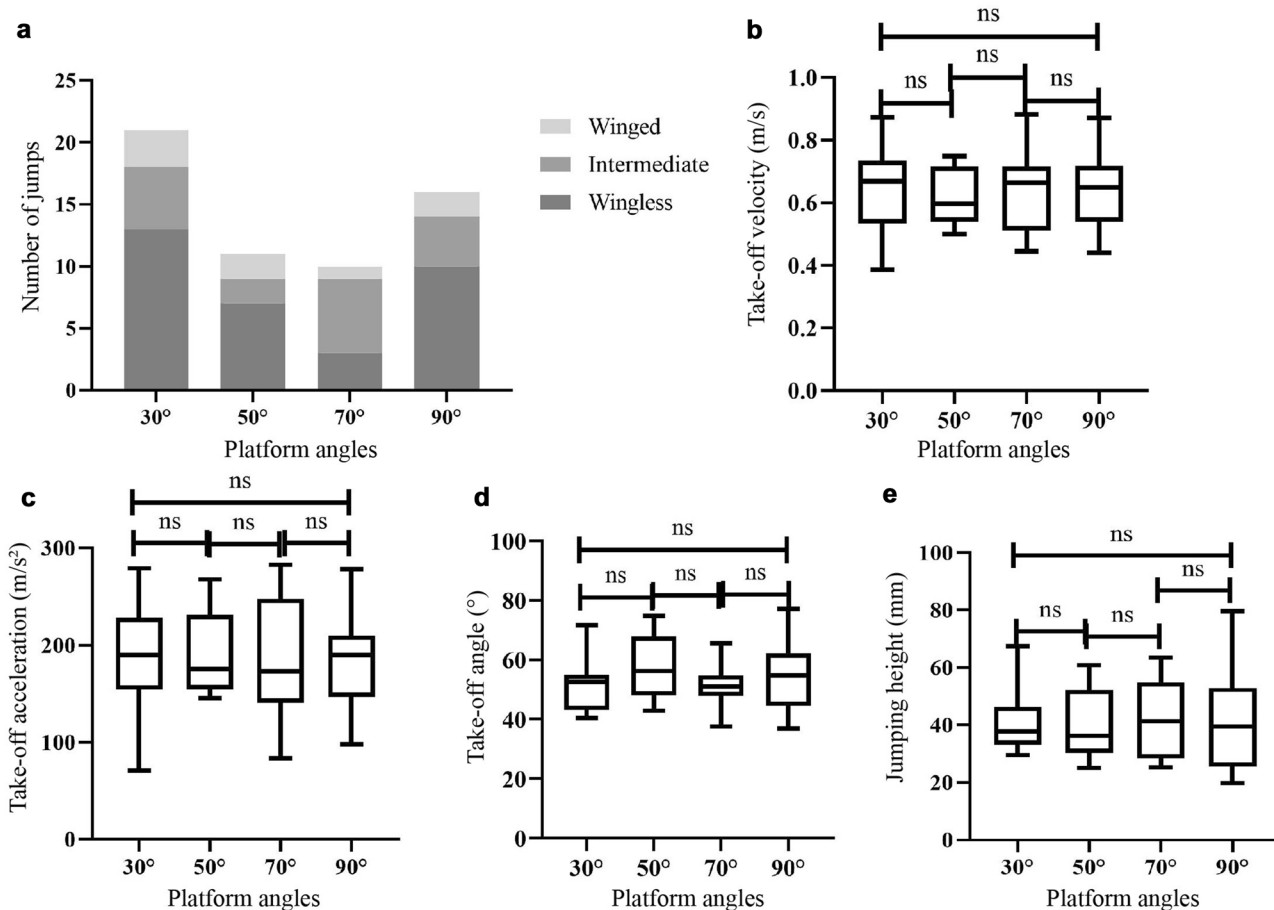


Fig. 6 **a** Jumping mode selection for flea beetles as a function of platform angle ($N=58$ jumps). **b–e** Take-off velocity, take-off acceleration, take-off angle, jumping height as a function of platform angle ($N=50$ jumps). *ns* means not significant

Table 1 Analysis of variance for kinematic parameters

	Jump modes (mean \pm std. deviation)			<i>F</i>	<i>p</i>
	Wingless ($n=30$)	Intermediate ($n=15$)	Winged ($n=5$)		
Take-off velocity (m/s)	0.65 \pm 0.10	0.68 \pm 0.11	0.46 \pm 0.03	7.422	0.002**
Take-off time (ms)	3.60 \pm 0.70	3.35 \pm 0.41	4.45 \pm 0.78	4.785	0.013*
Take-off acceleration (m/s ²)	188.28 \pm 47.64	206.08 \pm 44.23	107.15 \pm 26.56	7.484	0.002**
Wing deploy duration (s)	–	0.017 \pm 0.006	0.025 \pm 0.004	6.358	0.023*

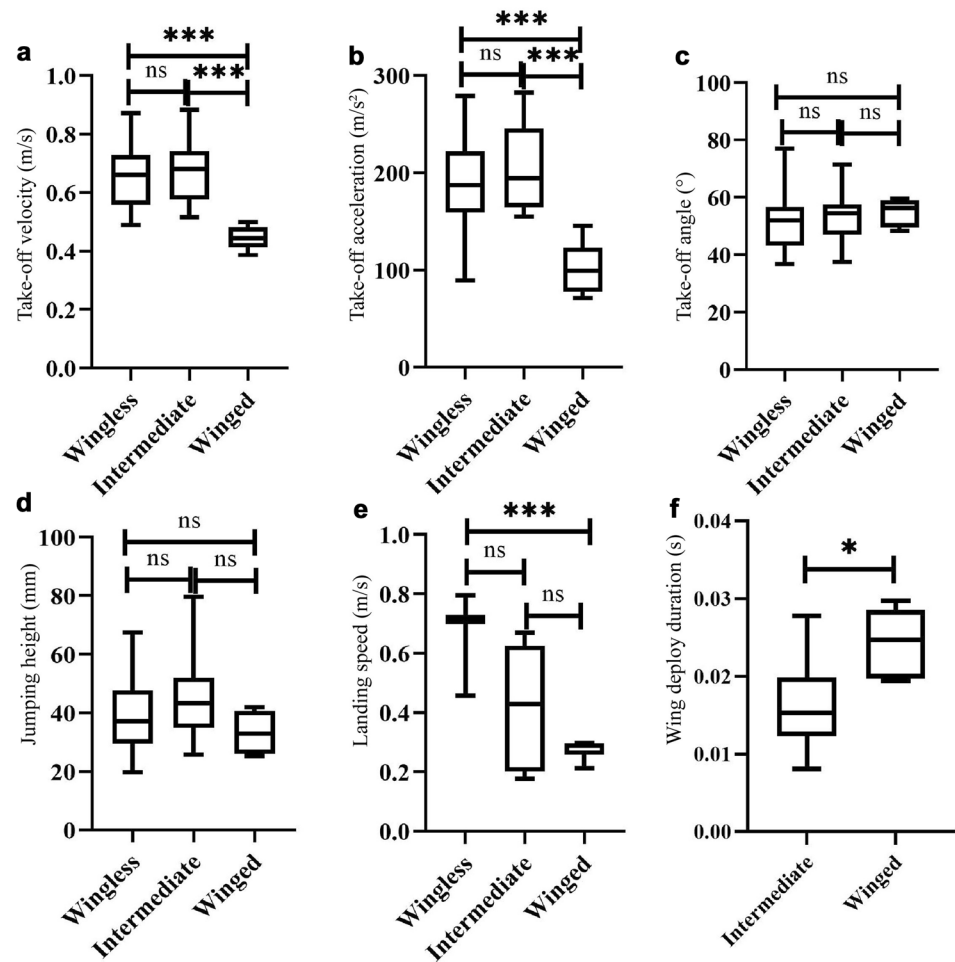
* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

An unpaired *t* test showed that the use of wings had significant effects on take-off velocity and take-off acceleration (Fig. 7a–e). We conducted three pairwise tests to determine the significance of pairs of flight modes on take-off velocity and take-off acceleration. The six pairwise *p* values were: $P_{v(\text{winged-intermediate})} = 0.0003$, $P_{v(\text{wingless-winged})} = 0.0001$, $P_{a(\text{winged-intermediate})} < 0.0001$, $P_{v(\text{wingless-winged})} = 0.0003$, $P_{t(\text{winged-intermediate})} = 0.0002$, and $P_{v(\text{winged-wingless})} = 0.0045$. Using the 0.05 significance level, the take-off time, take-off velocity and acceleration of the wingless and intermediate modes were all significantly different from those of the

winged mode. Bonferroni correction was used to counteract the multiple comparisons problem, finding that the *p*-value for significance should be less than $0.05/3 = 0.0167$; thus, the six tests were statistically significant.

The take-off time was longest for the winged mode: it took 4.45 ± 0.78 ms for the flea beetle to take off with wings and 3.35 ± 0.41 ms and 3.60 ± 0.70 ms for intermediate and wingless modes. The average take-off angle across all modes was $53^\circ \pm 10^\circ$, as expected for maximizing the distance of travel. The intermediate mode had the highest speed of 0.68 ± 0.11 m/s, followed by the wingless mode

Fig. 7 a–d Take-off velocity, take-off acceleration, take-off angle, and jumping height as a function of mode ($N=50$ jumps). **e** Landing speed as a function of mode ($N=16$ jumps). **f** Wing deployment duration as a function of intermediate and winged mode ($N=19$ jumps). *ns* means not significant ($p > 0.05$). * ($p \leq 0.05$) and *** ($p \leq 0.001$) means very significant



(0.65 ± 0.10 m/s), and winged mode (0.46 ± 0.03 m/s). Surprisingly, wing deployment did not have a significant effect on maximum height, indicating that any lift generated was somehow canceled by the increased drag. To verify the difference between the intermediate and winged modes, we measured the duration that the wings were open (Fig. 7f, Table S11). A two-way ANOVA test showed that wing deploy duration was not affected by platform angle ($F=2.360$, $p=0.127 > 0.05$), but was affected by jumping mode ($F=5.978$, $p=0.033 < 0.05$). The one-way ANOVA (Table 1) showed that wing deploy duration was affected by jump mode at a 0.05 level of significance ($F=6.358$, $p=0.023$), with winged jumpers having longer wing deploy duration than intermediate-winged, as expected. The wing deploy duration for the intermediate mode (0.017 ± 0.006 s, $N=15$ jumps) was significantly shorter than the winged mode (0.025 ± 0.004 s, $N=5$ jumps).

Successful landings were characterized in terms of the body angle when landing ($n=33$ beetles, $N=124$ jumps). The colored arrows in Fig. 3a show the landing orientations and velocities. Each arrow represents a recorded trial. The arrow lines were more densely distributed in the region of

a successful landing, corresponding to a net body rotation of 90° or less.

We now go into further detail about the body posture and behaviors during each of the three modes. From viewing the videos, we assert that the examples shown here are representative of other instances of the same mode.

For the wingless mode in Fig. 2a, the flea beetle took off from the horizontal platform at time $t=0$. Nearly instantaneous with take-off ($t=7$ ms), the flea beetle pitched backward. To investigate the dual-axial rotation, we mapped the pitch and roll angles with respect to duration (Fig. 8). The total-accumulated pitch angle was -1494° , which meant that the beetle pitched 4.15 cycles before landing. We next considered the intermediate jump in Fig. 2b. The flea beetle began with a wingless take-off. It pitched and rolled from $t=0$ to 42 ms. At 42 ms, the flea beetle oriented its body almost horizontally. The beetle pitched 2.14 cycles and rolled 360° from 42 to 70 ms, which helped it maneuver to the correct orientation before landing. The wings were deployed at 70 ms, which instantly stopped body rolling. The flea beetle flapped its wings and stuck a winged landing at 93 ms, where “stuck” indicated that the beetle was motionless once it hit

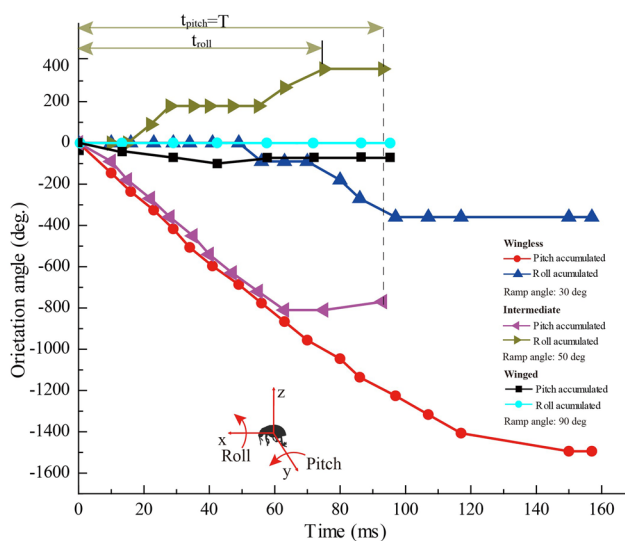


Fig. 8 Accumulated pitch and roll angle for **a** wingless case, **b** intermediate case, and **c** winged case

the ground. Last, we considered a winged jump. The flea beetle took off with the wings deployed and flew directly to the vertical wall. The body achieved a soft landing at 93 ms without rotation. Observing Fig. 8c, we observed that the body overpitched to -114° at $t=43$ ms, and then corrected itself to the correct orientation of 90° to land on the vertical wall. The beetle flapped its wings multiple times before landing.

High-speed film shows that take-off forces were generated by straightening the back leg (Fig. 4a–d), whose extension was actuated by the meta-femoral spring (Ruan et al. 2020). To understand this process, we tracked the linear and angular velocities of a beetle's wingless jump onto a 30-degree platform. We found that the hindleg was almost fully extended at take-off, but the tarsus remained in contact with the ground throughout its length. We concluded that the displacement was made by straightening the femur–tibia joint (Fig. 4e). The high-speed images indicated that the body displacement during take-off was approximately 1 mm. After take-off, the kinetic energy of the body could be written as $E_{kT} = Mv_i^2/2$ and the rotational energy as $E_{kR} = I\omega^2/2$. Using the initial velocity $v_i=1.49$ m/s and angular velocity $\omega = 710$ rad/s, the average body mass $M=4.16$ mg, and moment of inertia $I = \frac{1}{2}Mr^2 = 9.13 \times 10^{-13}$ kg m², where r is half the body length, we arrived at a rotational energy of $E_{kR} = 160$ μ J, occupying only 1.7% of the kinetic energy $E_{kT} = 9.5 \times 10^3$ μ J. As found by Brackenbury and Wang (1995), our beetle's rotational energy was negligible compared to the kinetic energy. By the law of energy conservation, the work done by the leg was equal to the kinetic energy $Fl = E_{kT}$, where $l=1$ mm was the displacement of the leg during jumping. Thus, we inferred that the force applied by all the beetle

legs was $F=9.5$ mN, which was 233 times the beetle's body weight.

Discussion

Brackenbury and Wang (1995) performed experiments in which a high-contrast target was placed to lure the beetles. While we did not include such a target, we found that our species of beetle readily landed on a transparent plexiglass platform. Future workers may vary the intensity and orientation of the light to verify the role of the flea beetle's vision during the jump. Wingless stick insect nymphs find landing targets by their luminance and chromatic contrast (Zeng et al. 2015).

Brackenbury and Wang (1995) found take-off angles ranging from 14° to 72° , which encapsulated the range found here. Brackenbury and Wang only described two jumping modes, winged and wingless. Perhaps those were the only two modes that could be seen with the stroboscopic photography of the day. We here introduced a third jumping mode, the intermediate mode where wings opened in mid-air. Brackenbury and Wang stated that wingless landings had only a 10% chance of success, whereas our wingless success rate was much higher at 42%. This difference may be due to the landing target surface: we used a 10 cm scale platform whereas Brackenbury and Wang used a 1 cm long illuminated cross shape. Brackenbury and Wang presented average kinematics across multiple trials, but here we show that individual beetles have preferred modes. Wingless jumping was the most common mode. It would be useful in the future to see if flea beetles in the wild have damaged wings that may prevent them from using them in the jump.

The flea beetle's jumping modes showed similarity to those of moths (Burrows and Dorosenko, 2015a, b). Moth jumping modes involved a wingless jump in which the wings flapp either right before or right after takeoff. They did not have an intermediate winged jump like the beetles. Moreover, moth jumps are powered by both mid- and hindlegs, whereas the flea beetle was powered only by its hindlegs. Since the power of the moth was mainly provided by direct contraction of leg muscles, the power output (1.1–62.1 μ J) was lower than the flea beetle (9.5×10^3 μ J) which was powered by the meta-femoral spring. Unlike the flea beetle, for which wings slowed down take-off, the use of wings did not affect the take-off velocity of the moth, suggesting that the moth had coordinated its wings and legs. Nadein and Betz (2016) studied the jumping of five species of flea beetles finding comparable take-off velocities (1.25–3.60 m s⁻¹) and take-off durations (1.35–2.25 ms).

One of the contributions of this work was resolving the beetle's 2–4 rotations in both pitching and rolling. It remains unknown whether these rotations have any utility. When cats

land on their feet, they perform a single rotation. It's possible the beetle's rotations help the beetle orient its feet or visually track targets, which may also give the beetle more opportunities to observe the landing environment. Brackenbury and Wang stated that rotation was an inevitable part of the explosive jumping of small jumpers. Indeed, we showed here that these rotations result from just a small 2% transfer of rotational energy from kinetic energy.

It's possible that the flea beetle's rotation may be influenced by antenna motion. During the locomotion of the fire ant *Solenopsis invicta* in subterranean tunnels, the ant's antenna was used as an appendage to prevent falls (Gravish et al. 2013). Our high-speed video showed the antenna in both erect and retracted states, but our frame rate could not resolve the antenna's position. Future workers should employ three-dimensional reconstructions using several cameras.

Conclusion

We filmed the flea beetle jumping onto inclines of 30–90°, finding that the flea beetle could jump in wingless, intermediate, or winged mode. Mode choice was highly individual-specific, with some beetles using the same mode for all inclines. Modes involving wings showed lower initial velocities and accelerations, which reduced the impact of landing. However, wings did not significantly affect the height of the jump. Wingless and intermediate jumping involved a number of pitching and rolling rotations, but winged jumping generally avoided these rotations.

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Author contributions DLH and SG planned the study. JW, PY, and GS conducted the experiments. PY, JR, and LZ drafted the manuscript. All authors reviewed the manuscript.

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Declarations

Conflict of interest The authors declare no competing interests.

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