nature portfolio

Peer Review File

Passive wing deployment and retraction in beetles and flapping microrobots

Corresponding Author: Dr Hoang-Vu Phan

Figures originally included in the author's rebuttal have been redacted from this file.

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)
In this work, the authors investigate the wing deployment and retraction mechanisms of Coleoptera beetles. Through analyzing high speed videos and constructing robotic models, they hypothesize that the wing deployment process is purely passive. The retraction process is aided by the elytra closing motion. Based on this finding, they designed a passive mechanism for a flapping-wing robot and demonstrated passive wing deployment and retraction. Overall, this work is very interesting and relevant to multiple research areas. The design and implementation are very effective in folding the wings of flapping-wing robots without adding new actuators. In my opinion, this paper is of broad interest to biologists and roboticists. I think this paper could be accepted after addressing my major and minor comments below.

Major comments:
The authors describe the hindwing elevation as mostly contributed by the centrifugal force, while the aerodynamic drag and the inertial forces are negligible (line 94-97). I hope the authors can offer a more detailed analysis about this process. As the wing starts to rotate, it also generates lift and drag forces. Does the lift force play a role in elevating the hindwing? Can the authors compare the effects of centrifugal force and lift force quantitatively? For example, if the same experiments can be repeated in vacuum, can we observe similar kinematics? Alternatively, can the authors describe this motion using a dynamical/ quasi-steady model?
Following up on this question, I also find the wing unfolding fascinating. Can the authors explain this process as well? Video 2 seems to suggest that before flapping, the wing collapses. During the flapping process, it extends. After the flapping motion stops, the wing seems to remain extended. Is it possible to replicate this mechanism on the robot wing too? If the robot wing can both elevate at the wing root and also extend the wing around a collapsible joint, I feel the analogy between biology and robotics could be further strengthened.
When the authors perform experiments with the beetle's wing, I'm curious about the wing's state during flapping. Specifically, I have tried similar experiments but have difficulties with insect wings drying out quickly under illumination. Do the flapping-wing experiments need to be done immediately after the wings are extracted from the beetle? And how long can this wing be used before it dries out (i.e., inertial properties start to change)?
I am curious about scaling. In this work, the size of the beetle is a lot smaller than that of the robotic model. When the wing size is scaled down, will centripedal force still dominate over aerodynamic forces? Will a similar design also work if the robot size (and wing size) is scaled down to that of a Coleoptera beetle? I am not asking for new experiments. I think adding a discussion on the effects of scaling can strengthen paper.
Does Fig. 4c-e correspond to the same flight as Fig. 4f-i? It seems the flight in c-d is 6.8s, but the flight in f-i is 30+ seconds. I think it is better to present data from the same experiment.
I feel the collision test (Fig. 4j and Video 10) does not add a lot to the paper. It is already clear from Fig. 4e that the wing retracts within 100 ms. In the collision test, how was the collision detected? Is it detected through an onboard sensor or by the operator? If there is mechanical intelligence in detecting the collision and retracting the wings, I feel the paper could be further strengthened.
I am curious about the mechanism's endurance. How frequently does this passive wing deployment mechanism needs to be tuned or changed? Can the authors report some data on robot reliability?

Minor comments:
• Scale bars should be added to some of the videos (like 9 and 10) and figures (like Extended Data Fig. 5).
• The authors used a Nano 17 force sensor and collected the data at 3200 Hz. Is the data filtered and if so, what is the cutoff

frequency?
• Can the robot land upright repeatedly? Is it possible for the robot to fly, land, and then fly again?

Overall, this is a very interesting paper on mechanism design for flapping-wing robots. The design takes inspiration from biology and develops a very effective mechanism. This robot is used to evaluate hypothesis about the beetle's passive wing deployment process. This paper reports original and high-quality results, and it is of broad interest to the flapping-wing flight community. After adding more flight data and analysis, I think it merits publication in Nature.

Referee #2

(Remarks to the Author)
This manuscript present detailed hindwing kinematics for initial extension, flapping, and retraction in one beetle species. The core hypothesis is that extension as well as retraction do not involve activity of thoracic muscles, but this possibility is not tested empirically. To eliminate the possibility of muscular contributions, it would be necessary to either knock out putatively involved muscles (via ablation or anesthetic injection), or to monitor their activity during extension and retraction. The kinematic extension data of Fig. 1d and 1e are certainly consistent with underdamped dynamics of an elastic system, but initial involvement of thoracic muscles (of which there are many, including some bifunctional muscles inserting on leg segments as well as on thoracic cuticle) cannot be excluded. The initial triggering of extension (i.e., during ~10 ms prior to actual wing motion) and the onset of impulsive extension (e.g., the first 50 ms) may well involve muscular contraction along with pre-loading and associated cuticular deformation, but no data currently address this issue. The point is certainly well taken (l. 49) that there are no experimental data showing such muscle activity, but neither is there any electromyographic evidence excluding such activation. The behavioral inability to retract the hindwing following ipsilateral elytral removal may simply derive from a neural program whereby sequential displacement of first the elytron initiates physical contact with the hindwing, which then sensorily initiates contraction of relevant metathoracic musculature to close the wing; given that simple leg contact also can result in hindwing retraction, this possibility cannot be excluded (but could be easily tested experimentally). Also, one general test of passive extension/retraction mechanisms would be to elicit equivalent wing motions in anesthetized beetles, but this approach was not utilized. Use of a robotic flapper to activate a beetle hindwing (Extended Data, Fig. 2) suggests that sufficiently high torque can result in passive wing extension, but this demonstration does not necessarily replicate the activational mechanics at the wing base as experienced by the wing in vivo. Experimentally, it is also important to note that experimental beetles were suspended vertically with no apparent leg contact, which is an unnatural configuration that may have altered activity of bifunctional leg muscles known in other insects to contribute to wing motions. Finally, the analysis is restricted to one (of numerous, i.e., ~10^6) beetle species, and the text throughout overgeneralizes to "beetles", whereas there are likely to be numerous mechanisms of wing extension/retraction among the Coleoptera. A strength of the manuscript is the implementation of passive wing deployment into a robotic flapping model, with ensuing strong flight performance and advantages in particular aerial contexts. This is an important contribution to robotics independent of the conceptually motivating biology, and should be received with interest in the microair vehicle community.

l. 11. Orthoptera similarly have modified forewings (tegmina) with complex hindwing deployment.
l. 47. basalar sclerite, not basilar
l. 94. Wing added mass, i.e., the mass of air around the wing accelerated in each half-stroke, may also contributed to the effective mass of the system.

Referee #3

(Remarks to the Author)
This is nice work, and with some amendments should be worth publishing. The research is well-conducted and informative, and certainly contributes to the understanding of the operation of hindwing folding and unfolding.
However, I am not entirely convinced by all the conclusions. The statement (lines 48-9) that there is no evidence that muscle activity is involved in deployment in no way proves that is not. The conclusion seems to be based on supplementary video 1, which indeed shows the extension of the proximal part of the hindwings to be virtually simultaneous with the elevation of the elytra; and on the pattern of oscillation, which they claim indicates that stage 1 of the extension is driven by stored elasticity. I am not qualified to judge the significance of the oscillation pattern, but I should wish for stronger evidence that the promotor muscles are not causing or at least assisting the process, as is assumed to be the case in all other insects. The use of the elytron in folding is nicely demonstrated, though the distal part of the wing is still extended when the videoclip ends – probably abdominal movements help here.
It would be useful to know to what extent the authors have examined, manipulated and tested the wings themselves. Some years ago I carried out preliminary mechanical experiments on the deployment and folding hindwings of freshly killed Pachnoda variegata, a scarabaeoid with nearly identical hindwings to Allomyrina. The work wasn't rigorous enough for publication, but if I remember correctly the wings were stable in three positions: folded, fully unfolded and in the intermediate condition with the distal area flexed relative to the proximal. To move between each of these pairs of positions would need an energy hump to be overcome, and the default assumption was that the first stage was achieved by action of the promotor muscle, the second by leverage - in the strict sense – within the wing, achieved by the mutually antagonistic flexor and promotor muscles contracting simultaneously and stretching the base. This latter may not be the case, and I am quite happy to accept that centrifugal force contributes to the extension of the outer part of the wing, though there is no reason why the two processes should not act together. However many beetles do fully extend the wing before taking flight, so that centrifugal force would not be available to them.

This brings me to a serious, though easily corrected, fault: the tendency to generalise from one species to beetles as a whole, particularly in the abstract, lines 21, 27; and the conclusion. Beetles are hugely diverse and their wing-folding patterns vary from the very simple, where the tip merely unfolds by a basic four-fold mechanism, to the hugely complex folded packages of staphylinids and the concertina-like folding and unfolding of the slender wings of scydmaenids , resembling three strips of a Miura-ori; and to the hinged feather-like wings of the tiny Ptiliidae. At the least, the word 'some' should precede 'beetles', or else Allomyrina should be specified.
The robot is a delight, and the effectiveness of centrifugal force and a simple elastic ligament in driving wing deployment and folding, and the advantages of the folding wings in avoiding collision damage are nicely demonstrated by the video clips. The robot does not particularly simulate the beetle: the wing is not extended elastically and doesn't fold transversely.

Other points. I dislike the use of the word 'leverage' as a verb, and suggest 'employ' would be better (lines 21, 86, 116, 128, 213, 220). 'Leverage' is confusing in this context because previous work on hindwing folding/unfolding implicates actual leverage within the wing as the driving mechanism (Haas F. & Wootton R.J. (1996). Two basic mechanisms in insect wing folding Proceedings of The Royal Society of London Series B 263 (1377), 1651-1658) which should certainly be in the references).
Line 106 is not a sentence.

Robin Wootton

Author Rebuttal letter:

Authorsâ Response to the Comments from Reviewers

Journal: Nature
Manuscript ID: 2024-02-04220
Title of Paper: Passive wing deployment and retraction in beetles and flapping microrobots
Authors: Hoang-Vu Phan, Hoon Cheol Park, Dario Floreano

We appreciate the editor and reviewersâ time and effort to review our manuscript. We found the comments helpful for improving the quality of the manuscript. This document describes how we addressed the reviewerâs comments: text in blue denotes our reply, text in red describes modifications made to the revised manuscript, and text in black is the original text.

Reviewer #1
In this work, the authors investigate the wing deployment and retraction mechanisms of Coleoptera beetles. Through analyzing high speed videos and constructing robotic models, they hypothesize that the wing deployment process is purely passive. The retraction process is aided by the elytra closing motion. Based on this finding, they designed a passive mechanism for a flapping-wing robot and demonstrated passive wing deployment and retraction. Overall, this work is very interesting and relevant to multiple research areas. The design and implementation are very effective in folding the wings of flapping-wing robots without adding new actuators. In my opinion, this paper is of broad interest to biologists and roboticists. I think this paper could be accepted after addressing my major and minor comments below.
ï We thank the reviewer for the positive comments.

Major comments:
The authors describe the hindwing elevation as mostly contributed by the centrifugal force, while the aerodynamic drag and the inertial forces are negligible (line 94-97). I hope the authors can offer a more detailed analysis about this process. As the wing starts to rotate, it also generates lift and drag forces. Does the lift force play a role in elevating the hindwing? Can the authors compare the effects of centrifugal force and lift force quantitatively? For example, if the same experiments can be repeated in vacuum, can we observe similar kinematics? Alternatively, can the authors describe this motion using a dynamical/ quasi-steady model?

ï We agree with the reviewer that lift force may also contribute to the elevation of the hindwing. However, we observed that in the first flapping cycle, while the hindwing elevated at the root, the wing surface was still almost perpendicular to the direction of flapping motion, resulting in very high angles of attack (70Â° - 90Â°) (Extended Data Fig. 2d of the revised manuscript). Additionally, the tip of the hindwing still remained in a folded configuration. Therefore, we presumed that lift force is very small during this period, and its contribution to the hindwing elevation is negligible compared to the centrifugal force. This is why we did not consider the effect of lift in the hindwing elevation motion. To understand better contributions of force components on the elevation, we have also described force components acting on the hindwing

during flapping and elevation in the first flapping cycle, as reported in Extended Data Fig. 2c of the revised manuscript (and below). With a vertical body orientation, gravitational force (W) and aerodynamic drag

(D) always hinder the hindwing elevation motion. In addition, inertial force (FI) hinders the elevation during acceleration at the beginning of stroke but facilitates the elevation during deceleration at the end of stroke. However, from Extended Data Fig. 2d, we can see that the hindwing is fully elevated before the start of deceleration period at the end of the upstroke motion (shaded area in Extended Data Fig. 2d), and thus the net inertial force does not contribute significantly to the elevation motion. Therefore, we expected that the elevation of the hindwing is caused mostly by centrifugal force (Fc). We have better explained the contributions of force components in the revised manuscript, as follows:
Page 4, lines 100-109:
âWhen flapping, the hindwing experiences aerodynamic lift and drag, inertial force arising from the acceleration and deceleration of the hindwing, gravitational force due to the hindwingâs mass, and centrifugal force due to the flapping motion (Extended Data Fig. 2c). During the first cycle, the wing surface moves approximately perpendicular to the direction of flapping motion, whilst the wingtip remains folded (Extended Data Fig. 2d). Consequently, lift force is marginal and does not contribute significantly to the elevation of the hindwing. With a vertical body orientation, gravitational force and aerodynamic drag always hinder the hindwing elevation motion. Meanwhile, the inertial force hinders hindwing elevation during the acceleration phase at the beginning of the stroke but facilitates it during the deceleration phase at the end of the stroke. However, its net effect on the elevation motion is negligible.â

Extended Data Fig. 2. c, Forces acting on the hindwing during flapping-and-elevation motion with a velocity V in the first cycle. With a vertical body orientation, gravitational force (W) and aerodynamic drag (D) hinder the hindwing elevation motion. Inertial force (FI) hinders the elevation during acceleration at the beginning of stroke but facilitates the elevation during deceleration at the end of stroke. In contrast, centrifugal force (Fc) and aerodynamic lift (L) drive the elevation motion. d, Hindwing kinematics in the first flapping cycle. The hindwing was fully elevated at the base (Î´h,base) during the first half of the upstroke motion while flapping at a high angle of attack (Î±h) with a folded wingtip (Î´h,tip). The angle of attack is defined as the angle between the wing surface and the direction of flapping motion. The shaded area corresponds to upstroke motion. The small magnitude of lift, due to high angles of attack and folded wingtip, does not contribute significantly to hindwing elevation.

ï We cannot test the hindwing in a vacuum chamber because it is not available at our facilities. It is also challenging to accurately model the aerodynamic forces due to the complex motion and time-varying geometry of the hindwing (unfolding of the wingtip during elevation at the wing root). From the description of force components in Extended Data Fig. 2c, projection of aerodynamic forces on the elevation plane Faero,elevation = LsinÎ¸ â DcosÎ¸, where Î¸ is the angle between the velocity vector (V) and the vertical elevation plane. Thus, aerodynamic forces either hinder or facilitate the elevation of the hindwing depending on how projected lift and drag on the elevation plane interact with each other, which is a function of hindwing flapping kinematics. As the hindwing flaps at extremely high angles of attack, the drag may dominate the lift to hinder the elevation motion. However, the net effect of the aerodynamic forces should be very small compared to the centrifugal force, which is proportional to the square of the angular velocity (ðÌ).
ï Alternatively, we can understand the effect of aerodynamic forces on the elevation of the robotic wing by carrying out a control experiment without the wing membrane where only inertial and centrifugal forces exist (Extended Data Fig. 4,c-e). We can see that the wing without the membrane (orange in Extended Data Fig. 4,c) reaches the elevation threshold (red dashed line) faster than that with the membrane (light blue), demonstrating that aerodynamic forces from the membrane hinder rather than facilitate elevation. Nevertheless, their contribution is very small compared to the centrifugal force, as in both cases the wing elevates within a flapping cycle.

Extended Data Fig. 4. c,d, Elevation angle (Î´) (c) and rate (ð¿Ì) (d) of the wings with (light blue) and without (orange) the membrane during the first flapping cycle. In the inertia-only case (orange), we added more mass to the leading-edge spar to compensate for the mass of the wing membrane. e, Stroke angle (Ï) and angle of attack (Î±) at 50% wingspan. Shaded area denotes the upstroke motion. With the membrane, the wing operated at extremely high angles of attack during the upstroke but very small angles of attack during the downstroke in the first flapping cycle (Supplementary Video 7). Therefore, aerodynamic forces from the membrane hinder rather than facilitate elevation. As a result,

they cause the wing to reach the elevation threshold slightly later than in the inertia-only case. Nevertheless, both cases enable the wing to elevate within a flapping cycle.

Following up on this question, I also find the wing unfolding fascinating. Can the authors explain this process as well? Video 2 seems to suggest that before flapping, the wing collapses. During the flapping process, it extends. After the flapping motion stops, the wing seems to remain extended. Is it possible to replicate this mechanism on the robot wing too? If the robot wing can both elevate at the wing root and also extend the wing around a collapsible joint, I feel the

analogy between biology and robotics could be further strengthened.

ï The origami-like unfolding of the wingtip was actually described in our previous work [Phan and Park, Science 370, 1214â1219 (2020)]. Therefore, here we do not describe this procedure because the main focus of this paper is the deployment and retraction of the hindwing's root. The wingtip unfolding can be triggered by flapping forces to tighten the bi-stable four-fold mechanism at the marginal joint. After flight, the four-fold mechanism (and thus the hindwing) is stable in the extended configuration, which requires the assistance of the abdominal movement [Movie S3 in Phan and Park, Science 370, 1214â1219 (2020)], to fold it back.
ï We agree that beetle-like foldable wings will bring the robot closer to its biological counterpart. However, building a small-scale and lightweight robotic wing that replicates the shape and bi-stable origami-like folding mechanism of the beetle hindwing brings many challenges. The first challenge is that adding the bi-stable foldable mechanism comes at the cost of increased mechanical complexity (sophisticated design and fabrication) and mass of the wing, which increases inertial power and thus reduces power efficiency. Second, discrete veins for folding functions (as opposed to the simple vein arrangement of our current robot) may cause changes in the distribution of angles of attack along the wingspan during flapping motion, thus also affecting power efficiency. Third, activating the bi-stable structure may require an external driving force to bring the wing back to the folding stage, similar to how beetles use the abdomen to push back the hindwing tip. Finally, undesired deflection of the foldable wing during regular flapping motion may affect the flight performance in terms of both aerodynamics and stability. Overall, these challenges may make flight of the robot impossible with the beetle-inspired foldable wings, requiring novel design and materials. Therefore, we think that it is better to leave this interesting topic for future research and keep the focus of this paper on the deployment and retraction of the wing at the root.

When the authors perform experiments with the beetleâs wing, Iâm curious about the wingâs state during flapping. Specifically, I have tried similar experiments but have difficulties with insect wings drying out quickly under illumination. Do the flapping-wing experiments need to be done immediately after the wings are extracted from the beetle? And how long can this wing be used before it dries out (i.e., inertial properties start to change)?

ï After carefully removing the beetle's hindwing at the base, we immediately attached it to the flapping mechanism using instant glue (please see text lines 95-96 of the revised manuscript and the Methods section, lines 373-376). As the reviewer noted, the hindwing of our beetle started to dry out quickly after detachment and, from our experience, it could be used for the experiment only within 20-25

minutes. Therefore, we conducted up to five experimental trials on each hindwing within 15 minutes after the hindwing was detached from the beetle. We compared data from different trials and found no significant difference.

I am curious about scaling. In this work, the size of the beetle is a lot smaller than that of the robotic model. When the wing size is scaled down, will centripedal force still dominate over aerodynamic forces? Will a similar design also work if the robot size (and wing size) is scaled down to that of a Coleoptera beetle? I am not asking for new experiments. I think adding a discussion on the effects of scaling can strengthen paper.
ï The robotic wing (90 mm) is only approximately 1.5 times longer than the beetle hindwing (55-60 mm) of our experiments. We think that if the robot and wing dimensions are scaled down to the size of beetles, the centrifugal force will still dominate aerodynamic forces in elevating the wing. As explained above, the elevations of the beetle's hindwing and the robotic wing were mainly caused by the centrifugal force. Therefore, this should be able to play the same role in elevating a robotic wing with the same size of the beetle hindwing or even smaller because the centrifugal force is linearly proportional to the wing mass but is proportional to the square of the angular velocity. Since smaller-scale robots typically operate at higher flapping frequencies (For example, 110 Hz in 80 mg Robobee) than larger-scale robots to generate effective lift for flight, the resulting centrifugal forces should remain the dominant factor in elevating the hindwing.
Although angular velocity strongly affects the centrifugal force, our experiments (Extended Data Fig. 2) showed that the hindwing was still able to elevate even when flapping at much lower frequency (26 Hz) than that used by the beetle (38 Hz). We also showed in Extended Data Fig. 4a that the leading edge bar of the robotic wing without the membrane and elastic tendon at the armpit elevated to 90Â° when flapping at only 10 Hz. These results reinforce the hypothesis that centrifugal forces are responsible for wing elevation at various scales. We have added short discussions in the revised manuscript as follows:
Page 7, lines 170-177:
âWithout the elastic tendon, the wing can fully elevate within a flapping cycle even at a lower flapping frequency (10 Hz in Extended Data Fig. 4). These results indicate that the centrifugal force is sufficient to elevate the wing, consistently with previous findings16,33. Since the centrifugal force is proportional to the square of the flapping angular velocity, smaller-scale wings could elevate too if they flap at a sufficiently high frequency.
When adding the membrane, aerodynamic forces cause the wing to reach the elevation threshold a little

later than without the membrane when only inertial and centrifugal forces are at play, but still reach full elevation within a single flapping cycle (Extended Data Fig. 4cïe).â
Page 10, lines 247-252:
âMoreover, we showed that the flapping-induced centrifugal force enables effortless elevation of both robotic wings and smaller-scale beetleâs hindwings, thereby suggesting the applicability of this passive elevation principle to flapping-wing robots across scales. Overall, our findings not only help

understanding of locomotion strategies in insects, but also have implications for flapping-wing robots, particularly for those at small-scales with limited takeoff weights37,38, enabling them to deploy and retract their wings similarly to their biological counterparts.â

Does Fig. 4c-e correspond to the same flight as Fig. 4f-i? It seems the flight in c-d is 6.8s, but the flight in f-i is 30+ seconds. I think it is better to present data from the same experiment.

ï Flights in Fig. 4c-e and Fig. 4f-i are from different tests. We separated the two experiments because the flight in Fig. 4c-e was recorded by a high-speed camera, which has a limited recording time and requires high-power lamps to illuminate the focal region. Conversely, the flight data in Fig. 4f-i was recorded by a motion capture system that tracked the reflective markers located on the robot. Initially, we attempted to set up synchronous recording of the experiments on the robot with the reflective markers. However, we found that the reflective light on the markers from the lamps impaired the tracking performance of the motion tracking cameras. The background setting for clear high-speed camera images also hindered visibility of some motion tracking cameras. On the other hand, reflective markers under strong lighting decreased the quality of the high-speed camera images. Therefore, we recorded these flights separately. Nevertheless, we believe that these flights should be very similar as they were obtained from the same robot (reflective markers added only 0.2 g to the 18 gram robot).
We have added more explanations to the method section 'Flight experiments' in the revised manuscript to make it clearer, as reported below.
Pages 15-16, lines 434-439 and 444-447:
âWe used a high-speed camera (Chronos, frame rate of 500 fps, resolution of 1,024 Ã 1,024 pixels) to film the wing deploying-retracting motion, takeoff, hovering, and landing flights of the flapping-wing robot shown in Fig. 4b-e, and collision flight shown in Fig. 4j. We used two 1 kW lamps to illuminate the focal flight area. For the experiment of wing deployment and retraction (Fig. 4b), we fixed the base of the robot to the ground so that the flapping of the wings did not generate flight. In the collision test, we remotely piloted the robot to fly sideways toward a wall. When the wings collided with the wall, we deactivated their flapping motion with a switch on the remote controller, thereby allowing the wings to passively retract along the body before hitting the ground.
To obtain the flight trajectory and body attitudes of the robot, we placed lightweight reflective markers (0.2 gram) on the robot (Extended data Fig. 5). The robot was then remotely piloted in a 10 m Ã 10 m Ã 8 m indoor flight arena equipped with a motion tracking system (26 Optitrack cameras, 120 Hz) to track these markers and convert to the three-dimensional trajectory and body attitude angles of the robot following the rollâpitchâyaw rotation sequence. The sequential images in Fig. 4b-e,j and flight attitude data in Fig. 4f-i and Extended data Fig. 6 were obtained from different flight tests because the reflective light on the markers from the lamps decreased both the tracking performance of the motion tracking cameras and the quality of the high-speed camera images.â

I feel the collision test (Fig. 4j and Video 10) does not add a lot to the paper. It is already clear from Fig. 4e that the wing retracts within 100 ms. In the collision test, how was the collision

detected? Is it detected through an onboard sensor or by the operator? If there is mechanical intelligence in detecting the collision and retracting the wings, I feel the paper could be further strengthened.

ï The collision test is actually to show potential use of the passive wing retraction to protect the membranous wings during a crash landing. We therefore think that it still contributes to strengthen the paper.
ï The collision was detected by the operator without onboard collision detection sensor. We agree with the reviewer that mechanical intelligence may help the robot to detect collisions automatically and thus, stop flapping to retract the wings. However, adding such mechanism may increase mechanical complexity and mass of the robot, which has a limited takeoff weight, thus making flight inefficient or even impossible.
As we attempted to demonstrate how simple beetle-inspired passive mechanism enables flapping robots to deploy and retract their wings reducing mechanical complexity, we therefore have not considered collision detection mechanism in this work as it is not our focus. We think that it is a potential research topic for our near future work to improve flight ability of the robot in dense and unstructured environments.
We have added more texts to the method section 'Flight experiments' of the revised manuscript to explain the experimental procedure, as reported below.
Page 15, lines 436-439:

âIn the collision test, we remotely piloted the robot to fly sideways toward a wall. When the wings collided with the wall, we deactivated their flapping motion using a switch on the remote control transmitter, thereby allowing the wings to passively retract along the body before hitting the ground.â

I am curious about the mechanismâs endurance. How frequently does this passive wing deployment mechanism needs to be tuned or changed? Can the authors report some data on robot reliability?

ï Our simple passive-wing mechanisms is made of carbon frames and high-quality elastic tendons, and could undergo all the flapping experiments reported in this manuscript without any damage. In case of any failure, we could replace the passive mechanism with ease. Additionally, both the robot and the passive mechanism are quite resilient to collisions and crashes, whether intentional or accidental (such as those resulting from power failure in mid-flight). To address possible concerns of robot reliability, we added more flight trials in the supplementary video 9 of the revised manuscript.

Minor comments:
â¢ Scale bars should be added to some of the videos (like 9 and 10) and figures (like Extended Data Fig. 5).
ï We added scale bars to videos 9 and 10, and to Extended Data Fig. 5 in the revised manuscript.

â¢ The authors used a Nano 17 force sensor and collected the data at 3200 Hz. Is the data filtered and if so, what is the cutoff frequency?

ï We did not apply any filter to the force measurement data as we obtained only the cycle-average force values, which were not significantly affected by flapping noise.

â¢ Can the robot land upright repeatedly? Is it possible for the robot to fly, land, and then fly again?

ï Yes, the robot can repeatedly land upright (please see Video 9 of the revised manuscript). Honestly, the landing success depends mostly on the pilot's skill. Once the robot lands upright, it can resume flight without any issue by simply activating again the flapping motion. We have added repeated takeoff-and-landing tests in the supplementary video 9 of the revised manuscript.

Overall, this is a very interesting paper on mechanism design for flapping-wing robots. The design takes inspiration from biology and develops a very effective mechanism. This robot is used to evaluate hypothesis about the beetleâs passive wing deployment process. This paper reports original and high-quality results, and it is of broad interest to the flapping-wing flight community. After adding more flight data and analysis, I think it merits publication in Nature.

ï We thank the reviewer again for positive feedback and critical comments, which were very helpful to improve the quality of our paper. We hope that our replies and additional flight data and analysis addressed all the reviewerâs concerns.

Reviewer #2
This manuscript present detailed hindwing kinematics for initial extension, flapping, and retraction in one beetle species. The core hypothesis is that extension as well as retraction do not involve activity of thoracic muscles, but this possibility is not tested empirically. To eliminate the possibility of muscular contributions, it would be necessary to either knock out putatively involved muscles (via ablation or anesthetic injection), or to monitor their activity during extension and retraction. The kinematic extension data of Fig. 1d and 1e are certainly consistent with underdamped dynamics of an elastic system, but initial involvement of thoracic muscles (of which there are many, including some bifunctional muscles inserting on leg segments as well as on thoracic cuticle) cannot be excluded. The initial triggering of extension (i.e., during ~10 ms prior to actual wing motion) and the onset of impulsive extension (e.g., the first 50 ms) may well involve muscular contraction along with pre-loading and associated cuticular deformation, but no data currently address this issue.

ï We agree with the reviewer that eliminating involved muscles or monitoring muscle activity could provide stronger evidence of muscle contributions to the hindwing deployment and retraction. We actually cold-anesthetized and tried to remove the cuticles and muscles at the hindwing base of our beetle Allomyrina but the beetle did not initiate voluntary flight. During the surgery, we noticed a lot of

liquid coming out from the hindwing base of the Allomyrina, and therefore, we assumed that the surgery damaged the beetle and affected its ability to fly (the insect is not very active even in normal conditions). Unfortunately, we do not have the facilities for monitoring muscle activity; however, we think that it is challenging to monitor muscle activity of beetles during the hindwing deployment and retraction due to the presence of the elytra and front legs impairing visibility.
We actually observed that at rest, the hindwings could still be stowed over the abdomen when the elytra are removed (Fig. 1a (inset) of the revised manuscript). We therefore agree with the reviewer that it is still possible that muscles may also be involved in releasing the preloaded energy to partly elevate the proximal part of the hindwing. In this case, the beetle may use the same muscle that controls the opening of the elytron to also trigger the initial release of the hindwing because the two wings are released virtually simultaneously in most tests. However, we think that the muscle does not directly drive the elevation of the hindwing because of the underdamped response of the hindwing, as explained above, and also because the beetle cannot proactively retract its hindwing without the pushing force from the elytron. We note here that the hindwing retraction was triggered by pushing force of the elytron but not by simple contact, as we explain in the response to the next comment (the hindwing springs back after releasing the leg in the Response Fig. R1 below). Although further studies are necessary to validate our hypothesis by recording or monitoring muscle activity during the deployment and retraction of the hindwing, we think that the two pieces of evidence mentioned above are sufficient to suggest that the beetle can recruit pre-existing mechanisms instead of distinct muscles.
We have added more discussion in the revised manuscript to make it clearer, as follows:
Page 3, lines 65-73:
âWe thus suggest that the first phase of the hindwing elevation is triggered by the release of preloaded energy rather than by active muscular control. Unlike beetles such as ladybirds4, which employ intrinsic

elasticity to fully deploy their hindwings upon the opening of the elytra, the hindwings of Allomyrina dichotoma can remain folded over the abdomen even when the elytra are removed (Fig. 1a (inset)). It is possible that when the beetle takes flight, the muscles responsible for the opening of the elytra may also be involved in releasing the preloaded energy to partly elevate the hindwings. However, we think that these muscles do not directly drive the elevation of the hindwing because it displays an underdamped response and also because the beetle cannot proactively retract its hindwing without assistance of the elytron as described later.â
Page 9, lines 237-238:
âNevertheless, further experimental studies to record or monitor muscular activity35,36 during hindwing deployment and retraction would be needed to definitely test the conclusions of our study.â
Added references:
[35] Melis, J. M., Siwanowicz, I. & Dickinson, M. H. Machine learning reveals the control mechanics of an insect wing hinge. Nature 1â9 (2024).
[36] Vo-Doan, T. T., Dung, V. T. & Sato, H. A Cyborg Insect Reveals a Function of a Muscle in Free Flight. Cyborg Bionic Syst. 2022, (2022).

The point is certainly well taken (l. 49) that there are no experimental data showing such muscle activity, but neither is there any electromyographic evidence excluding such activation.

ï A study on beetles Mecynorrhina torquata [see Sato et al., Current Biology, 25, 798-803, 2015 (cited)] using electromyography (EMG) measured response (150 out of 216 tests) of the third axillary muscle (responsible for the wing deploying and folding in beetles) during wing retraction, but also showed that the muscle was inactivated in 66 out of 216 tests. However, how the beetles retracted their hindwings in those 66 inactivated cases was not explained. In addition, when the third axillary muscle was removed, the beetles could still deploy and retract their hindwings, demonstrating that the third axillary muscle did not play a primary role. Although the study did not explain how the hindwing deployment and retraction were done without the muscle, these results strengthen our hypothesis that elytra are used to retract the hindwings, possibly also in the beetles Mecynorrhina torquata.
We have added more explanation on page 2, lines 49-51 of the revised manuscript, as follows:
âHowever, there is no experimental evidence showing muscle activity during hindwing deployment and retraction. A previous study showed that beetles Mecynorrhina torquata deploy and retract their hindwings even when the third axillary muscle was inactivated or removed15, but how these movements were initiated was not explained.â
Added reference:
[15] Sato, H. et al. Deciphering the Role of a Coleopteran Steering Muscle via Free Flight Stimulation. Curr. Biol. 25, 798â803 (2015).

The behavioral inability to retract the hindwing following ipsilateral elytral removal may simply derive from a neural program whereby sequential displacement of first the elytron initiates physical contact with the hindwing, which then sensorily initiates contraction of relevant metathoracic musculature to close the wing; given that simple leg contact also can result in hindwing retraction, this possibility cannot be excluded (but could be easily tested

experimentally).

ï The explanation by the reviewer on the retraction of the hindwing is possibly an option but we think that such process of the hindwing retraction may be too complicated for the beetle. If the hindwing is controlled by an active muscle, it can retract actively by itself rather than waiting for the elytron to contact. As shown in Fig. 2d in the manuscript and also in the Supplementary Video 3, we can see that after physical contact, the hindwing retracts together with the elytron rather than immediately at the time of contact. There are cases that the elytron touches the hindwing and then both wings stay there for a while before retracting together (Supplementary Video 3). We also showed that without the elytron, the beetle tried to use its leg to depress the hindwing (Supplementary Video 5). However, the hindwing could bounce back to the elevated state after releasing contact from the leg (Fig. R1 below). These data suggest that the beetle uses its elytra to physically retract the hindwings rather than using dedicated hindwing muscles triggered by physical contact.

Fig. 2d. The hindwing retracts together with the elytron but not always immediately upon contact. The time instant is set to 0 s when the elytron touches the hindwing while closing.

Fig. R1. The beetle can use its foreleg to depress the hindwing. However, the hindwing can bounce back after releasing leg contact (time sequence 0.13s - 0.3s).

Also, one general test of passive extension/retraction mechanisms would be to elicit equivalent wing motions in anesthetized beetles, but this approach was not utilized. Use of a robotic flapper to activate a beetle hindwing (Extended Data, Fig. 2) suggests that sufficiently high torque can result in passive wing extension, but this demonstration does not necessarily replicate the activational mechanics at the wing base as experienced by the wing in vivo.

ï We utilized the flapping mechanism to replicate the activation of the hindwing because we do not have a method to induce a flapping motion in anesthetized beetles through electrical stimulation, although we think that this may be very challenging. Our work is not aimed at replicating the muscular and mechanical structure of the beetle hindwing, but rather at showing the possibility of passive deployment. We believe that if only flapping forces enable passive elevation of the hindwing in our flapper, these forces should also allow the beetle to elevate the hindwing without the need of additional muscular activity.

Experimentally, it is also important to note that experimental beetles were suspended vertically with no apparent leg contact, which is an unnatural configuration that may have altered activity of bifunctional leg muscles known in other insects to contribute to wing motions.
ï We actually could not make the beetle fly voluntarily if it was on the ground. Therefore, we suspended the beetle with the body orientation simulating its flight configuration. In addition, experiments with suspended insects have been done in many previous studies. We also found that the beetle had no difficulty in deploying and retracting its wings in this configuration. Therefore, we think that this method is applicable to our study.
ï We agree with the reviewer that bifunctional leg muscles may supposedly contribute to wing motions. However, if the suspension altered or prevented the leg muscle contribution but the beetle was still able to deploy and retract its wing, it then strengthens our result of passive strategies and also shows insignificant role of the leg muscles in the hindwing deployment and retraction.

Finally, the analysis is restricted to one (of numerous, i.e., ~10^6) beetle species, and the text throughout overgeneralizes to "beetles", whereas there are likely to be numerous mechanisms of wing extension/retraction among the Coleoptera.
ï We agree with the reviewer that our study is limited to one beetle species, but we think that other species of beetles with the same unfolding/retracting patterns as the Allomyrina dichotoma may also use similar passive strategies. We have changed the word âbeetlesâ to the more specifically rhinoceros beetles Allomyrina dichotoma throughout the revised manuscript. We have also added a short discussion in the Conclusions section as follows:
Pages 9-10, lines 239-242:
âAlthough the study focuses on one beetle species and there exist many other species of beetles, such as ladybird beetles4 that fully deploy their hindwings before flapping, we hypothesize that beetles with patterns of hindwing deployment and retraction similar to Allomyrina dichotoma may resort to passive

strategies too. More broadly, the findings open the door for additional studies to investigate to what extent other small-scale flying insects may use similar strategies.â

A strength of the manuscript is the implementation of passive wing deployment into a robotic flapping model, with ensuing strong flight performance and advantages in particular aerial contexts. This is an important contribution to robotics independent of the conceptually motivating biology, and should be received with interest in the microair vehicle community.

ï We thank the reviewer for the appreciation of our robotic model.

l. 11. Orthoptera similarly have modified forewings (tegmina) with complex hindwing deployment.
ï We agree that there are insect species that have complex hindwing deployment. Therefore, we stated in the text (line 11) that beetles are just one of them.

l. 47. basalar sclerite, not basilar
ï Thank you for spotting this typo. We have corrected it to âbasalar scleriteâ in the revised manuscript.

l. 94. Wing added mass, i.e., the mass of air around the wing accelerated in each half-stroke, may also contributed to the effective mass of the system.
ï We consider added mass as an unsteady aerodynamic term because it depends on the acceleration of the surrounding air, whose volume is determined by the wing membrane surface. We therefore think that it may not contribute to the mass of the system, and thus to the centrifugal force.

Reviewer #3
This is nice work, and with some amendments should be worth publishing. The research is well-conducted and informative, and certainly contributes to the understanding of the operation of hindwing folding and unfolding.

ï We greatly thank the reviewer for the overall appreciation of our work.

However, I am not entirely convinced by all the conclusions. The statement (lines 48-9) that there is no evidence that muscle activity is involved in deployment in no way proves that is not. The conclusion seems to be based on supplementary video 1, which indeed shows the extension of the proximal part of the hindwings to be virtually simultaneous with the elevation of the elytra; and on the pattern of oscillation, which they claim indicates that stage 1 of the extension is driven by stored elasticity. I am not qualified to judge the significance of the oscillation pattern, but I should wish for stronger evidence that the promotor muscles are not causing or at least assisting the process, as is assumed to be the case in all other insects.

ï What we mean by this statement is that to date there are no experimental data that explicitly show muscle activity in the hindwing deployment and retraction. We propose that the first-phase elevation of the proximal part of the hindwing does not require active muscular control based on our observation of the hindwing releasing response (similar to an underdamped spring-mass system) and behavior (unable to retract without an external force). Actually, the hindwing (blue color in Extended Data Fig. 1d below) is not always simultaneously released with the opening of the elytra (orange in Extended Data Fig. 1d below). We observed that since the tips of the left and right hindwings overlap when stowed against the abdomen, a hindwing (the left hindwing in Fig. R2 below) may not be instantaneously released upon the opening of the ipsilateral elytron if the contralateral elytron and hindwing remain folded. It is possible that friction force between the two hindwings due to compression of the contralateral elytron hinders the elevation. Therefore, if friction is high enough, the hindwing remains folded and starts to elevate only when the right hindwing and elytron elevate (Fig. R2 below and Supplementary Video 1). This also explains the difference in elevating speed of the hindwing irrelevant to the release of the ipsilateral elytron (Extended Data Fig. 1b,d). Additionally, during elevation, the hindwing oscillates similarly to an underdamped spring-mass system, in which amplitude of the oscillation is linearly proportional to the speed of elevation (Extended Data Fig. 1a-c below). We therefore suggest that the first-phase elevation of the hindwing results from release of preloaded energy rather than from active muscular control. We also observed that the hindwings could still be stowed neatly over the abdomen when the elytra are removed (Fig. 1a (inset) of the revised manuscript). Therefore, we think that the term âstored elastic energyâ in our original manuscript may not precisely describe the system. It is still possible that the muscles controlling the opening of the elytra may also be involved in releasing the preloaded energy to elevate the hindwings. However, they should not directly drive the elevation of the hindwing because of the underdamped response, as explained above, and also because the beetle cannot proactively retract its hindwing without a pushing force from the elytron. Further experimental studies are necessary to validate our hypothesis by monitoring muscular activity during the deployment and retraction of the hindwing. However, conducting such experiments in a living beetle may be challenging. We therefore think that the two pieces of evidence mentioned above are sufficient to suggest that the beetle can recruit

pre-existing mechanisms instead of distinct muscles. We have added more discussion to the revised manuscript to make these points clearer, as follows:
Page 3, lines 65-73:
âWe thus suggest that the first phase of the hindwing elevation is triggered by the release of preloaded energy rather than by active muscular control. Unlike beetles such as ladybirds4, which employ intrinsic elasticity to fully deploy their hindwings upon the opening of the elytra, the hindwings of Allomyrina dichotoma can remain folded over the abdomen even when the elytra are removed (Fig. 1a (inset)). It is possible that when the beetle takes flight, the muscles responsible for the opening of the elytra may also be involved in releasing the preloaded energy to partly elevate the hindwings. However, we think that these muscles do not directly drive the elevation of the hindwing because it displays an underdamped response and also because the beetle cannot proactively retract its hindwing without assistance of the elytron as described later.
Page 9, lines 237-239:
âNevertheless, further experimental studies to record or monitor muscular activity35,36 during hindwing deployment and retraction would be needed to definitely test the conclusions of our study.â

Extended Data Fig. 1| Wing deployment kinematics of beetles. a,b, At the end of the partial release (phase I of the deployment), the hindwing experiences decreasing oscillations around the equilibrium position, Î´h,base = 48.5 Â± 0.7Âº: (a) elevation angle (b) and angular rate. c, Amplitude of the first oscillation (shown in a) is proportional to the releasing rate of the hindwing in b. Red line denotes the linear fit. d, Elevation angles of the elytron (orange) and the hindwing (dark blue). The time instant is set to 0 s when the elytron starts to elevate.

Fig. R2. The left hindwing may not be released instantly upon the opening of the left elytron if the right elytron and hindwing remain folded (0.265s). When the right elytron and hindwing elevate, the left hindwing also starts to elevate.

The use of the elytron in folding is nicely demonstrated, though the distal part of the wing is still extended when the videoclip ends â probably abdominal movements help here.
ï We agree with the reviewer that abdominal movements help in folding the distal part of the hindwing, as we already showed in our previous study [Movie S3 in Phan and Park, Science 370, 1214â1219 (2020)] and mentioned in lines 119-120 of the revised manuscript. We therefore do not describe again this procedure here to keep the focus of the manuscript on the deployment and retraction of the hindwing's root.

It would be useful to know to what extent the authors have examined, manipulated and tested the wings themselves. Some years ago I carried out preliminary mechanical experiments on the deployment and folding hindwings of freshly killed Pachnoda variegata, a scarabaeoid with nearly identical hindwings to Allomyrina. The work wasnât rigorous enough for publication, but if I remember correctly the wings were stable in three positions: folded, fully unfolded and in the intermediate condition with the distal area flexed relative to the proximal. To move between each of these pairs of positions would need an energy hump to be overcome, and the default assumption was that the first stage was achieved by action of the promotor muscle, the second by leverage - in the strict sense â within the wing, achieved by the mutually antagonistic flexor and promotor muscles contracting simultaneously and stretching the base. This latter may not be the case, and I am quite happy to accept that centrifugal force contributes to the extension of the outer part of the wing, though there is no reason why the two processes should not act together. However many beetles do fully extend the wing before taking flight, so that centrifugal force would not be available to them.

ï We carefully investigated the hindwings not only with high-speed camera images but also with naked eyes by folding and unfolding the hindwing manually. Similar to Pachnoda, the hindwings of the Allomyrina dichotoma are also stable in three configurations: fully folded in the abdomen, partly unfolded, and fully extended.
As we explained in the response to the reviewer's first comment, we observed that unlike beetles such as ladybirds, which employ intrinsic elasticity to fully deploy their hindwings, the hindwings of Allomyrina dichotoma can remain folded over the abdomen at rest even when the elytra are removed.

Thus, elastic elements may be not enough to serve as the energy source to release the hindwing during the first and later stage of elevation. We therefore think that the term âstored elastic energyâ in our original draft may not precisely describe the system and have changed it to âpreloaded energyâ in the revised manuscript. This is because when the beetle takes flight, the muscles responsible for the opening of the elytra may also be involved in releasing the preloaded energy to deploy the hindwing. However, we suggest that these muscles may not directly drive the elevation of the hindwing due to its

underdamped response as explained above, and also because the beetle cannot proactively retract its hindwing without assistance from the elytron.
We also agree with the reviewer that centrifugal force may not be necessary for beetles such as ladybirds with intrinsic elasticity in their hindwings. However, beetles sharing the same hindwing deploying and retracting patterns as the Allomyrina dichotoma may employ passive strategies too. We have added more discussion in the revised manuscript, as follows:
Pages 9-10, lines 239-242:
âAlthough the study focuses on one beetle species and there exist many other species of beetles, such as ladybird beetles4 that fully deploy their hindwings before flapping, we hypothesize that beetles with patterns of hindwing deployment and retraction similar to Allomyrina dichotoma may resort to passive strategies too. More broadly, the findings open the door for additional studies to investigate to what extent other small-scale flying insects may use similar strategies.â

This brings me to a serious, though easily corrected, fault: the tendency to generalise from one species to beetles as a whole, particularly in the abstract, lines 21, 27; and the conclusion. Beetles are hugely diverse and their wing-folding patterns vary from the very simple, where the tip merely unfolds by a basic four-fold mechanism, to the hugely complex folded packages of staphylinids and the concertina-like folding and unfolding of the slender wings of scydmaenids , resembling three strips of a Miura-ori; and to the hinged feather-like wings of the tiny Ptiliidae. At the least, the word âsomeâ should precede âbeetlesâ, or else Allomyrina should be specified.
ï We agree with the reviewer that our study is limited to one beetle species, although we think that other species of beetles with the same unfolding/retracting patterns as the Allomyrina dichotoma may use a passive strategy too. We have changed the word âbeetlesâ to the more specifically rhinoceros beetles Allomyrina dichotoma throughout the revised manuscript.

The robot is a delight, and the effectiveness of centrifugal force and a simple elastic ligament in driving wing deployment and folding, and the advantages of the folding wings in avoiding collision damage are nicely demonstrated by the video clips. The robot does not particularly simulate the beetle: the wing is not extended elastically and doesnât fold transversely.

ï We greatly thank the reviewer for positive comment on the robot. We agree with the reviewer that the robotic wing is simpler than the beetleâs hindwing as our focus is on the deployment and retraction of the wing root rather than on the wing tip. However, building a small-scale and lightweight robotic wing that replicates the shape and bi-stable origami-like folding mechanism of the beetle hindwing brings many

challenges. The first challenge is that adding the bi-stable foldable mechanism comes at the cost of increased mechanical complexity (sophisticated design and fabrication) and mass of the wing, which increases inertial power and thus reduces power efficiency. Second, discrete veins for folding functions (as opposed to the simple vein arrangement of our current robot) may cause changes in the distribution of angles of attack along the wingspan during flapping motion, thus also affecting power efficiency. Third, activating the bi-stable structure may require an external driving force to bring the wing back to the folding stage, similar to how beetles use the abdomen to push back the hindwing tip. Finally, undesired deflection of the foldable wing during regular flapping motion may affect the flight performance in terms of both aerodynamics and stability. Overall, these challenges may make flight of the robot impossible with the beetle-inspired foldable wings, requiring novel design and materials. Therefore, we think that it is better to leave this interesting topic for future research and keep the focus of this paper on the deployment and retraction of the wing at the root.

Other points. I dislike the use of the word âleverageâ as a verb, and suggest âemployâ would be better (lines 21, 86, 116, 128, 213, 220). âLeverageâ is confusing in this context because previous work on hindwing folding/unfolding implicates actual leverage within the wing as the driving mechanism (Haas F. & Wootton R.J. (1996). Two basic mechanisms in insect wing foldingâ¨Proceedings of The Royal Society of London Series B 263 (1377), 1651-1658) which should certainly be in the references).

ï Thank you for pointing out this ambiguity. We have replaced âleverageâ with âemployâ in the revised manuscript. We have also added the suggested reference [3] in the revised manuscript as follows:
3. Haas, F. & Wootton, R. J. Two basic mechanisms in insect wing folding. Proc. R. Soc. Lond. B Biol. Sci. 263, 1651â1658 (1997).

Line 106 is not a sentence.
ï Thank you. We have corrected the sentence in the revised manuscript as follows.
Page 5, lines 118-121:

âBeetles can employ the abdomen and elytra to pull the tips of the hindwings into a fully folded configuration4,8,14, whereas active thoracic muscles have been proposed to drive the retraction of the hindwing at the base6,10,11

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)
The authors have addressed all my comments in the first round of review. I appreciate the authors' effort in adding more flight repeatability experiments. I feel the manuscript has been substantially strengthened. I have also read their response to the other reviewers' comments. In my view, this paper is suitable for publication in Nature. I congratulate the authors for designing and performing this interesting work.

Referee #2

(Remarks to the Author)
1. Muscle activation has not been empirically excluded in hindwing extension, and the arguments presented by the authors in favor of the alternative hypothesis, although strong, are not definitive. Instead of an either/or presentation, the language throughout the manuscript could better reflect the ambiguity deriving from the absence of physiological evidence. The 2015 paper by Sato, cited by authors in support of reduced (or zero) muscle activity in hindwing deployment/retraction, was done on a different beetle of undescribed phylogenetic affinity to the current study species. Given the diversity of hindwings/elytra/thoracic design among the Coleoptera, these results are certainly suggestive, but are not conclusive. The Sato 2015 paper also only examined one of a number of possibly involved muscles, and this restriction should be mentioned as well.

2. Vertical suspension of the beetles may have induced a variety of changes in muscle configuration and activation (possibly including enhancement of putative contributions to extension), so the ability in this body orientation to extend/retract wings doesn't exclusively support a passive extension.

3. Added mass is certainly a function of acceleration of the wing, and as such for oscillating wings adds an additional and potentially substantial "virtual mass" to the wing inertial response that can't necessarily be excluded from the centrifugal force estimates. Further characterization of this effect, using the existing literature in unsteady aerodynamics, is necessary here to ballpark the magnitude of the added mass (particularly given the high wing accelerations/decelerations), and to assess possible force contributions.

Referee #3

(Remarks to the Author)
All my concerns have now been met, and I am glad to support publication.

Author Rebuttal letter:

Authorsâ Response to the Comments from Reviewers

Journal: Nature
Manuscript ID: 2024-02-04220
Title of Paper: Passive wing deployment and retraction in beetles and flapping microrobots
Authors: Hoang-Vu Phan, Hoon Cheol Park, Dario Floreano

We appreciate the editor and reviewersâ time and effort to review our manuscript. This document describes how we addressed the reviewerâs comments: text in blue denotes our reply, text in red describes modifications made to the revised manuscript, and text in black is the reviewersâ comments and original text of the manuscript.

Reviewer #1
The authors have addressed all my comments in the first round of review. I appreciate the authors' effort in adding more flight repeatability experiments. I feel the manuscript has been substantially strengthened. I have also read their response to the other reviewers' comments. In my view, this paper is suitable for publication in Nature. I congratulate the authors for designing and performing this interesting work.

ï We greatly thank the reviewer for the overall appreciation of our work.

Reviewer #2

1. Muscle activation has not been empirically excluded in hindwing extension, and the arguments presented by the authors in favor of the alternative hypothesis, although strong, are not definitive. Instead of an either/or presentation, the language throughout the manuscript could better reflect the ambiguity deriving from the absence of physiological evidence. The 2015 paper by Sato, cited by authors in support of reduced (or zero) muscle activity in hindwing deployment/retraction, was done on a different beetle of undescribed phylogenetic affinity to the current study species. Given the diversity of hindwings/elytra/thoracic design among the Coleoptera, these results are certainly suggestive, but are not conclusive. The Sato 2015 paper also only examined one of a number of possibly involved muscles, and this restriction should be mentioned as well.

ï We have revised the manuscript with a more appropriate language reflecting the lack of direct evidence of muscle activation in our work. We had also discussed in the original manuscript that muscles are not completely excluded but may be involved in the first-phase deployment of the beetle's hindwing.

Page 3:

âIt is possible that when the beetle takes flight, the muscles responsible for the opening of the elytra may also be involved in releasing the preloaded energy to partly elevate the hindwings. However, we think that these muscles may not directly drive the elevation of the hindwing because it displays an underdamped response and also because the beetle cannot proactively retract its hindwing without assistance of the elytron as described later.â

Furthermore, in the original manuscript, we had included a suggestion that further studies of recording or monitoring muscular activity during the hindwing deployment and retraction are needed to confirm our results.

Page 9:

âNevertheless, further experimental studies to record or monitor muscular activity35,36 during hindwing deployment and retraction would be needed to definitely test the conclusions of our study.â

ï Our discussion on the work of Sato et al., 2015 is not meant to support the idea of reduced (or zero) muscle activity in hindwing deployment/retraction. Rather, it is meant to show that even in vivo experiments with EMG recording and physical removal of muscles cannot explain how beetles deploy and retract hindwing because no electrical trace of muscle activation was detected. We agree with the reviewer that Sato et al., 2015 examined only the third axillary muscle, which they proposed to be driving wing deployment/retraction, among a number of other potential muscles. However, we think that methods based solely on direct muscle recording/monitoring are not sufficient because it is challenging to record or monitor simultaneously all possible muscles in the thorax and to precisely determine which muscle drives wing deployment/retraction.

2. Vertical suspension of the beetles may have induced a variety of changes in muscle configuration and activation (possibly including enhancement of putative contributions to extension), so the ability in this body orientation to extend/retract wings doesn't exclusively support a passive extension.

ï Although the beetle was vertically suspended, its wings could still deploy and freely retract without constraints. In addition, wing deployment in suspended and ground beetles displays the same two-phase sequence (see Figure 1 in Phan et al., Journal of Bionic Engineering, 9, 391-401, 2012 for wing deployment and takeoff from the ground). We therefore think that vertical body orientation may not support, but rather hinder, the deployment because it requires counteracting the gravity force operating on the hindwing. Similarly, although the gravity force should facilitate hindwing retraction, our results show that the beetle cannot retract them without the elytra.

3. Added mass is certainly a function of acceleration of the wing, and as such for oscillating wings adds an additional and potentially substantial "virtual mass" to the wing inertial response that can't necessarily be excluded from the centrifugal force estimates. Further characterization of this effect, using the existing literature in unsteady aerodynamics, is necessary here to ballpark the magnitude of the added mass (particularly given the high wing accelerations/decelerations), and to assess possible force contributions.

ï We agree with the reviewer that added mass of the accelerated surrounding air induces centrifugal force. However, in unsteady aerodynamics based on three-dimensional wing kinematics, the centrifugal force induced by added mass is typically modelled as a spanwise component of added mass force, which is an unsteady aerodynamic force (see Section 2.2 Added mass force in Truong et al., Bioinspiration & Biomimetics, 6, 2011). Thus, when building a theoretical model, added mass should be modeled as an aerodynamic component rather than an inertial component. Nevertheless, in our paper, we provided only explanation of the centrifugal force, which is decoupled from other force components. By this way, all components that induce the centrifugal force can be combined and thus added mass of the surrounding air can still be included in the centrifugal force equation along with the wing mass to

contribute to the hindwing elevation. However, in the robotic wing without the wing membrane, we have shown that actual wing mass alone is sufficient to induce the wing elevation. We have corrected the centrifugal force equation to include the mass of accelerated surrounding air in the revised manuscript as follows:
Page 4:
âThus, hindwing elevation is driven mostly by the centrifugal force16, ð¹c = ðw,e ðÌ 2 ðw,CG , where mw,e is an effective mass that includes both actual wing mass and mass of the accelerated surrounding air, ðÌ denotes the angular velocity, and rw,CG is the distance between the flapping axis and the center of mass of the wing.â

Reviewer #3
All my concerns have now been met, and I am glad to support publication.

ï We greatly thank the reviewer for the overall appreciation of our work.