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## Report

# Petal-shaped femoral lobes facilitate gliding in orchid mantises

Xin Zhao<sup>1,2</sup>, Jing-Xin Liu<sup>1</sup>, Tristan Charles-Dominique<sup>3,4</sup>, Ahimsa Campos-Arceiz<sup>5,6</sup>, Bing Dong<sup>7</sup>, Lin Yan<sup>8</sup>, James C. O’Hanlon<sup>9</sup>, Yu Zeng<sup>10,11,\*</sup>, Zhanqi Chen<sup>1,11,12,\*\*</sup>

<sup>1</sup>Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan 666303, China

<sup>2</sup>University of Chinese Academy of Sciences, Beijing 100049, China

<sup>3</sup>CNRS UMR5120, UMR AMAP, University Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier 34980, France

<sup>4</sup>CNRS UMR7618, Sorbonne University, Institute of Ecology and Environmental Sciences, 4 Place Jussieu, Paris 75005, France

<sup>5</sup>Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan 666303, China

<sup>6</sup>Southeast Asia Biodiversity Research Institute, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan 666303, China

<sup>7</sup>School of Biology, University of St Andrews, Dyers Brae, St Andrews KY16 9TH, UK

<sup>8</sup>Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA 94720-3114, USA

<sup>9</sup>Freelancer, Armidale, New South Wales, 2350, Australian

<sup>10</sup> Department of Integrative Biology, University of South Florida, Tampa, FL 33620, USA

\*Corresponding author

\*\*Corresponding author

<sup>11</sup>These authors contributed equally

<sup>12</sup>Lead contact

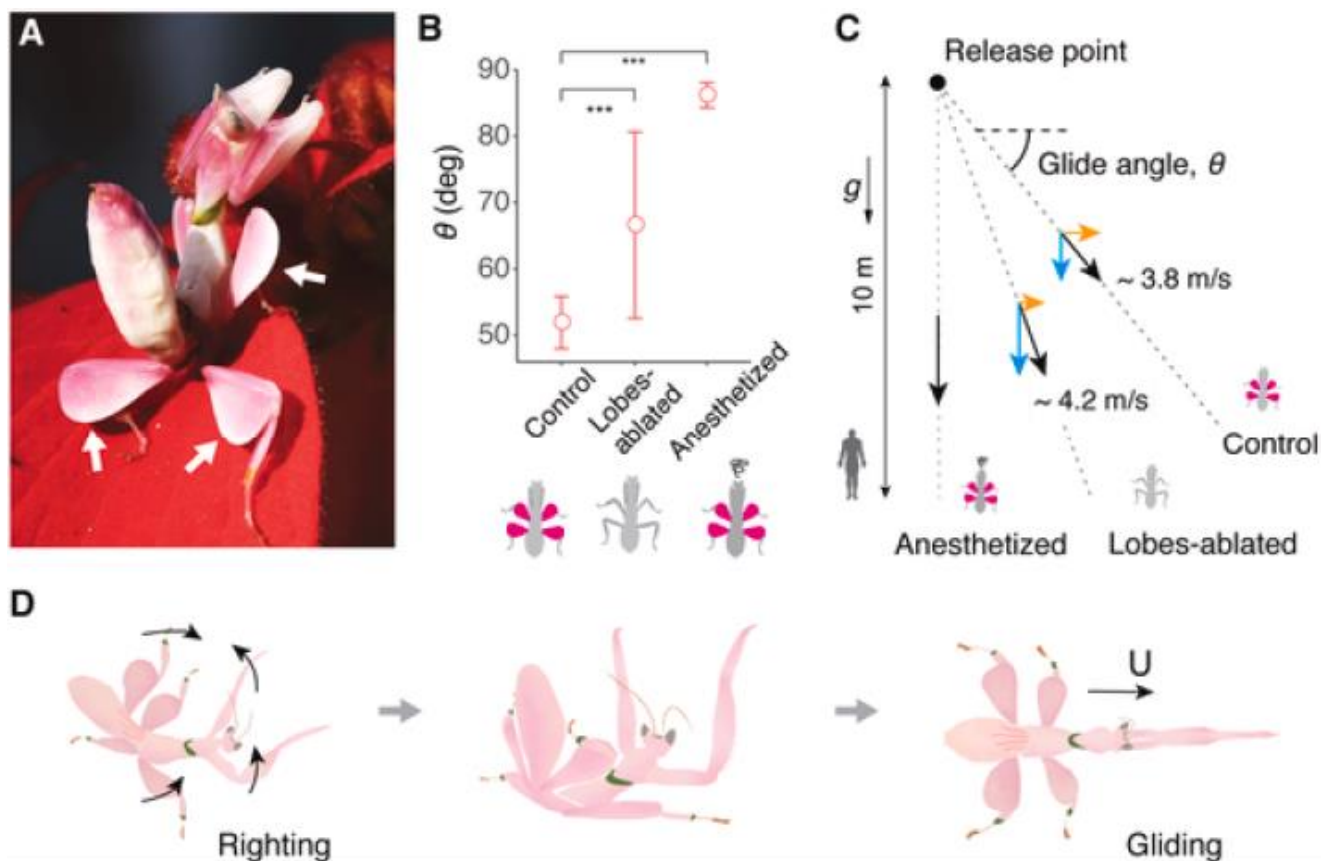
## Summary

To glide in forest canopies, arboreal vertebrates evolved various skin-derived aerodynamic structures, such as patagial membranes or webbing, but no comparable structure has been reported from wingless arboreal arthropods.<sup>1–3</sup> Orchid mantises (*Hymenopus coronatus*) have been traditionally considered a textbook example of flower mimicry for ~200 years due to their highly expanded, petal-shaped femoral lobes. However, the empirical evidence substantiating the petal-mimicry function of the femoral lobes has not been entirely conclusive.<sup>4–6</sup> Observational and experimental evidence suggests that these lobes do not contribute to flower mimicry for luring pollinators<sup>6,7</sup> and likely serve other functions.<sup>7,8</sup> After observing their aerial escape initiated with active jumping, we hypothesized that orchid mantises can glide and that their femoral lobes are used for gliding. Through behavioral investigations and morphological analyses, we show that orchid mantis nymphs are excellent gliders, exhibiting the shallowest gliding trajectories observed in terrestrial invertebrates.<sup>9–13</sup> The lobe extensions on their femoral segments are cambered airfoils, which increase the mantis projected area by ~36% and play a vital role in the aerodynamic underpinning of the observed gliding. Despite a 165-fold increase in body mass throughout ontogeny, older female mantis nymphs maintained a persistent gliding capability. We further showed a notable 40%–56% reduction in wing loading attributed to the positive size allometry of these lobes, indicating a clear promotion of gliding throughout ontogeny. This is the first documentation of gliding-adapted “leg wings” in a wingless arthropod. The evolution of such structures is potentially common among arboreal arthropods and demands a systematic re-examination.

## Results and discussion

### Orchid mantis nymphs are excellent gliders

We first tested whether orchid mantis nymphs (Figure 1A) could glide. We dropped 6th instar nymphs ( $n = 9$  for each sex; STAR Methods) from a crane, 10 m above an open lawn (Figures S1 A–S1E). After release, the nymphs adopted a right-side-up body posture and glided over  $6.09 \pm 2.25$  m (mean  $\pm$  SD; maximum = 9.57 m) horizontally within  $3.24 \pm 0.26$  s prior to landing (VIDEOS S1 and S2). The mean glide speed was  $3.08 \pm 0.25$  m/s in the vertical and  $1.88 \pm 0.15$  m/s in the horizontal (Figure 1B), with the effect of wind excluded (STAR Methods). The 6th instar female nymphs glided better than other wingless arthropods with an average glide angle of  $52^\circ$  (Figure 1C; STAR Methods), compared with a typical  $\sim 75^\circ$  in gliding ants.<sup>10</sup>



**Figure 1 Orchid mantis nymphs exhibit controlled gliding** (A) An orchid mantis nymph (6th instar). (B and C) With femoral lobes, a 6th instar nymph achieves an average glide angle ( $\theta$ ) of  $\sim 52^\circ$  with the horizontal and glide speed ( $U$ ) of  $\sim 3.8$  m/s. Lobe ablation led to reduced  $\theta$  and increased  $U$ , whereas anesthesia led to complete loss of the gliding capability. Values are means  $\pm$  SD. (D) Sequence of postures exhibited by a mantis nymph after release, from aerial righting (left) to gliding (right; in dorsal view). Black arrows denote dorsiflexion of legs. See also Figures S1 and S2; Videos S1, S2, S3, and S4; and the STAR Methods.

We expected the gliding behavior to be influenced by visual cues. After preliminary experiments (STAR Methods), we tested whether gliding was directed toward or away from black surfaces in a large glide arena (Figures S1F–S1H). We found a distinct landing bias, with a significant majority of individuals (79.8%; 154 in 193 drops) landing near the black background ( $G = 74.677$ ,  $p < 0.001$ ; G test) (Video S3). This confirmed visually influenced steering and a potential preference for landing on dark surfaces, a potential anti-predator strategy in rainforests.

### **Postural control in gliding**

Intentional control of body and leg postures is required for both steering and forward gliding.<sup>1</sup> With the same experimental setup, we dropped anesthetized individuals and found a complete loss of gliding (Figures 1B, 1C, and S2; Video S4). From video recordings of normal orchid mantises, we identified three body-leg postures adopted during initial descent and subsequent gliding (Figure 1D): (1) immediately after release, the mantis rapidly adopted a stereotypic posture, elevating abdomen and legs dorsally, presumably inducing aerodynamic instability to correct dorsoventral orientation.<sup>14</sup> (2) Subsequently, during the initiation of gliding, the mantis unfolded its abdomen and extended its mid and hind legs laterally, imposing the petal-shaped femoral lobes to the vertically upward incidental flow. (3) Last, the mantis extended its fore-legs in alignment with the abdomen and maintained this posture during gliding.

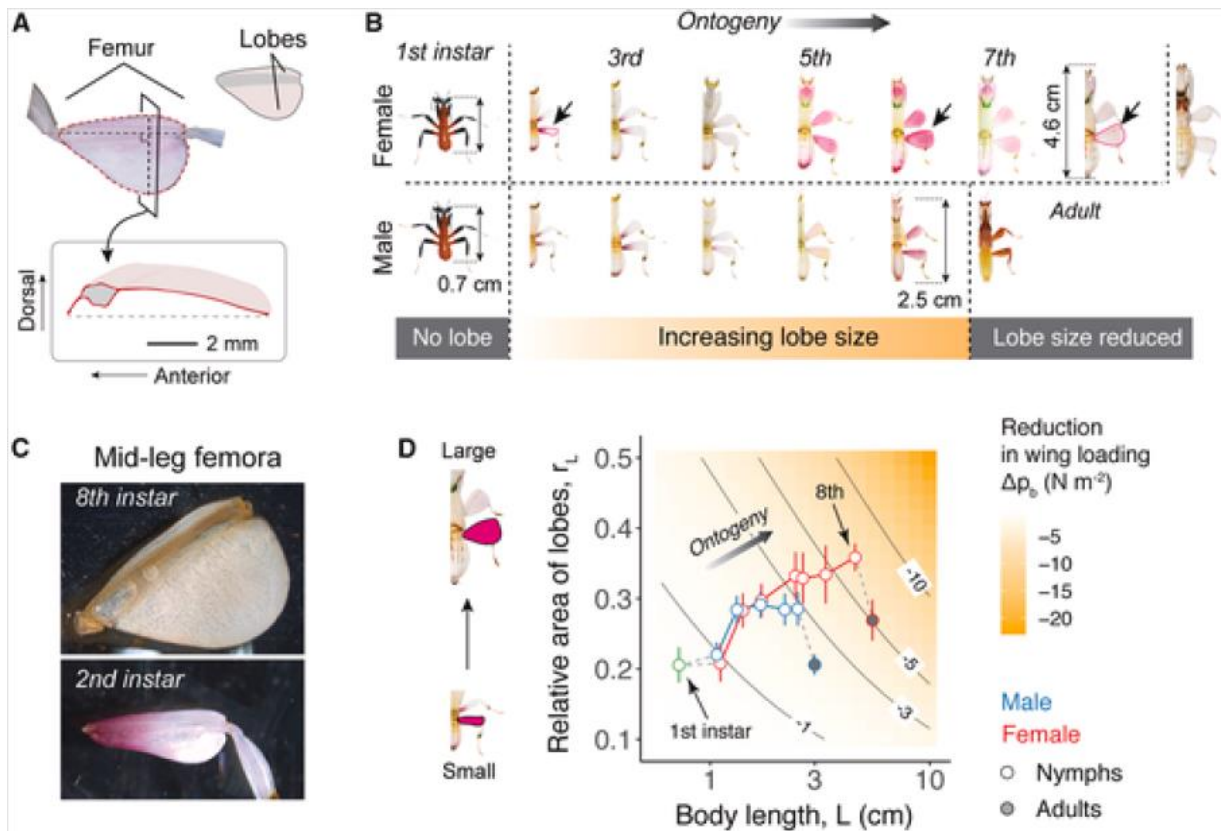
### **Femoral lobes enhance gliding**

To determine the importance of femoral lobes to gliding, we tested gliding in 6th instar nymphs ( $N = 11$ ) with their femoral lobes ablated (Figures S2 A–S2D). Lobe ablation led to a reduced gliding capability. The horizontal distances traveled reduced to  $4.08 \pm 2.39$  m,  $\sim 33\%$  shorter than in the control group ( $6.09 \pm 2.25$  m;  $t = -2.28$ ,  $p = 0.015$ ). Also, the glide angle averaged  $67^\circ$ , compared with  $52^\circ$  in intact individuals. The femoral lobes thus contribute to lift generation during descent and play a key role in orchid mantis nymphs gliding ability.

### **Morphology of femoral lobes**

The morphological examination of orchid mantis' femora revealed they are ventrally cambered. Cross sections showed that the camber structure was anteroposteriorly asymmetric, and the thickness of exoskeletal lobes ranged from

0.03 to 0.10 mm, extending in anterior and posterior directions with a greater posterior size (Figures 2A and S3).



**Figure 2 Femoral morphology and wing loading reduction by femoral lobes during ontogeny** (A) Femur segments are ventrally cambered and anteroposteriorly asymmetric, with a posterior lobe larger than the anterior one. Inset shows the cross-section sampled at 75% femur length from the basal end in 8th instar female (Data S1 at <https://doi.org/10.17632/ggsxps2v6f.1>). (B) Ontogenetic sequences in both sexes (wings ablated in adults for clarity), showing the disproportionate increase of femoral lobe size (body sizes along ontogeny not in the same scale). (C) Older nymphs have rounder femoral lobes. (D) Ontogenetic increases in femoral area effectively reduce the mantises' wing loading. Values are means  $\pm$  SD. See Data S2 (<https://doi.org/10.17632/ggsxps2v6f.1>) for detail. See also figure S3 and the STAR Methods.

The camber ratio ranged from 8% to 12%, with the maximum deviation from chord line located at  $\sim 38\%$  of the chordwise position. This camber ratio falls within the range of many airfoils found in flying and gliding vertebrates (e.g., bird wings, 10%–20%; flying lizard membrane,  $\sim 9\%$ ; flying squirrel patagium,  $\sim 14\%$ ).<sup>15–17</sup> Notably, these mantis' femur segments have a corrugated profile on both dorsal and ventral surfaces, with the leg hemocoel forming a thickened section at  $\sim 20\%$  chord length from the leading edge. Such configuration is distinct from other biological airfoils with relatively uniform thickness (e.g., insect wings) or smooth profile (e.g., bird wings).

### Ontogenetic augmentation of femoral lobes

As the mantis nymphs grew in size, the femoral lobes also became rounder and disproportionately increased in area (Figures 2B and 2C). The lobe area increased continuously throughout the whole nymphal stage, until an abrupt reduction occurred when the mantis reached adulthood. In the last nymphal stage (6th for males and 8th for females), the combined area of all femora covered a remarkable ~30% and ~36% of the whole-mantis projected planform area ( $A_{tot}$ ) in males and females, respectively.

We evaluated the functional importance of femoral size allometry by calculating wing loading ( $P_b$ , with  $b$  representing “body”), which indicates the aerodynamic pressure experienced by the mantis during equilibrium gliding. This calculation relies on the projected area of the entire mantis ( $A_{tot}$ ) and is expressed as  $P_b = mg/A_{tot}$ , with  $m$  representing mass and  $g$  denoting gravitational acceleration (STAR Methods). An increase in the lobes’ relative area should reduce wing loading. Integrating the allometric scaling of body mass and planform area throughout nymphal stages (Figures S4), we developed a power-law scaling model and showed that the reduction of wing loading ( $\Delta p_b$ ) increased with the relative area of lobed femur segments ( $rL$ ) and body size ( $L$ ) (Figure 2D). Overlaying the ontogenetic trajectories of  $rL$  onto a landscape of  $\Delta p_b$ , an increasing effect of wing loading reduction was evident in both sexes, reaching 28%–36% reduction in late instars.

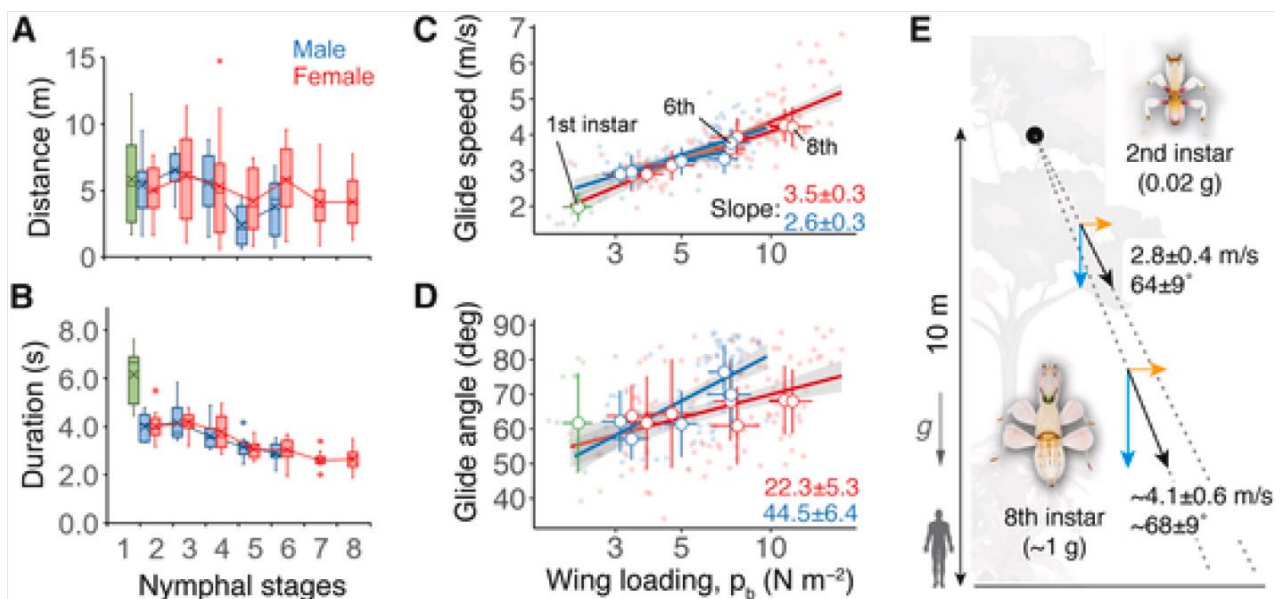
For each nymph, the total area of their four lobed femora contributed a remarkable 21%–36% of the total planform area, contrasting with the lack of extensions in other gliding arthropods (e.g., gliding ants and spiders). In a gliding related morpho-space defined by body size and relative area of gliding-adapted flat extensions, the orchid mantis nymphs characterize unique positions by laying between other wingless gliding arthropods,<sup>10,13</sup> gliding salamanders,<sup>18</sup> and gliding vertebrates with large areas of membranes or webbing (Figure 4A).

### **Ontogeny of gliding capability**

Orchid mantis nymphs’ body mass underwent a dramatic 165-fold increase in females (from  $6.2 \pm 0.8$  mg in the 1<sup>st</sup> instar to  $0.99 \pm 0.20$  g in 8th instar) and 24-fold in males ( $0.18 \pm 0.04$  g in 6th instar) (Figure S4). With isometric scaling, larger gliding animals experience a proportionally higher aerodynamic loading compared with smaller animals and demand a greater equilibrium glide speed; they likely fall

over a greater distance before reaching equilibrium speed and thus exhibit reduced glide index (i.e., increased average glide angle). A positive allometry of body mass leads to a reduction in average glide angle, as shown in flying lizards,<sup>19</sup> gliding ants,<sup>10</sup> and spiders.<sup>13</sup> For wingless arthropod nymphs, ontogenetic increases in body size and mass should also lead to a positive allometry of wing loading and a glide angle reduction. This can be overcome by developing more aerodynamic surfaces. Is the ontogenetic augmentation of orchid mantis' femoral lobes an adaptation for gliding with larger size? If the femoral lobes were ineffective in helping glide, we would at least expect an ontogenetic reduction in glide angle.

We tested this hypothesis by dropping different-aged nymphs from the 10-m crane. In female nymphs, we found relatively persistent glide distances (4–6 m) across age groups (Figure 3A), whereas mean glide speed increased from ~2 m/s in 1st instar nymphs to ~4 m/s in 8th instar females (Figures 3B, 3C, and 3E). The increases in glide speed correspond with an increase in aerodynamic force to offset body weight.<sup>3</sup> With increasing wing loading, the average glide angle remained between 60° and 70° in females but increased more steeply in males (Figures 3D and 3E). This shows sex-specific allometries in gliding reduction, with a persistent gliding capability in female nymphs despite a two-order of magnitude increase in wing loading.

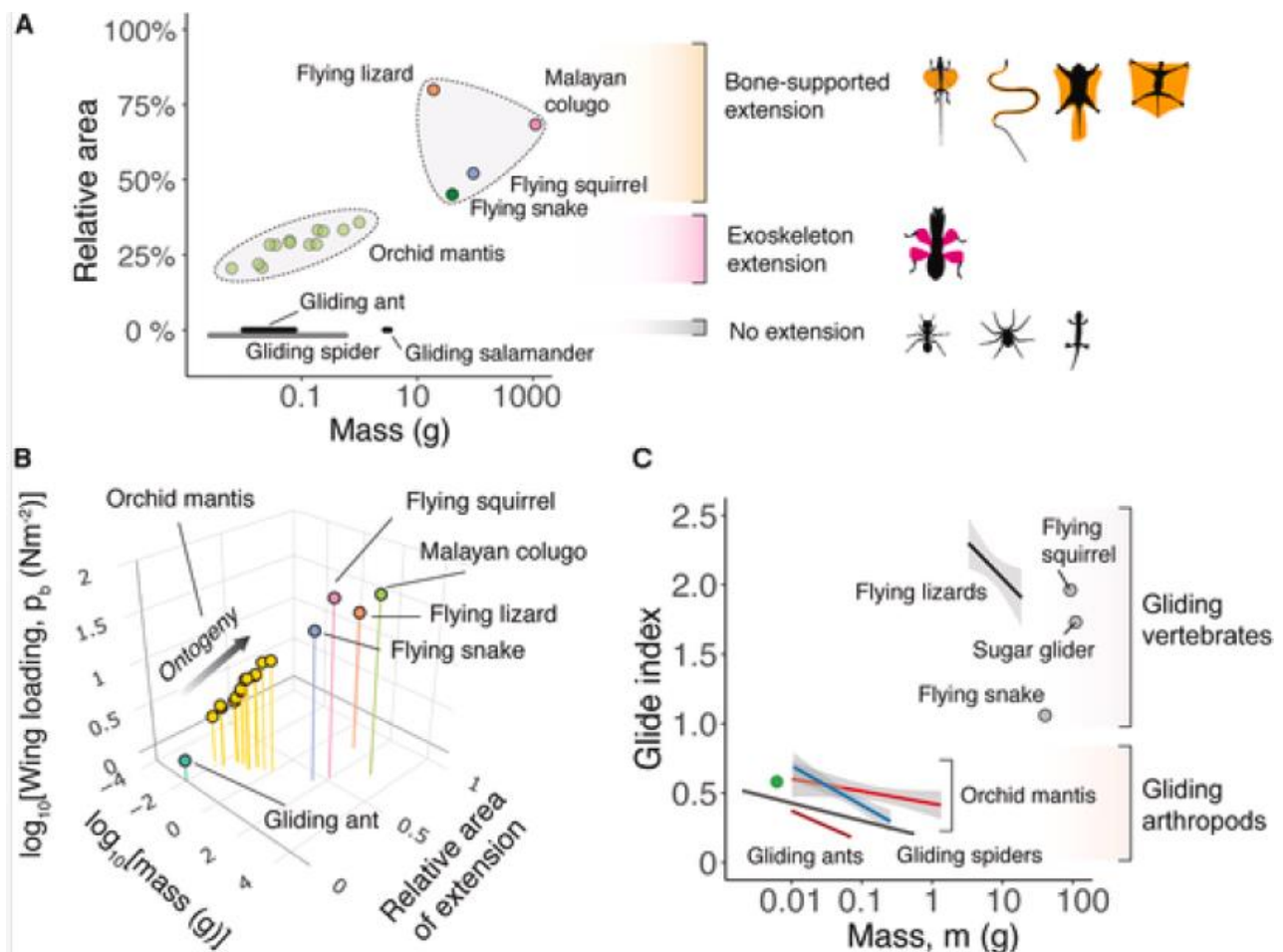


**Figure 3 Ontogeny of gliding in orchid mantis nymphs** (A and B) Despite increases in body size and mass, the horizontal distance traveled (A) did not decrease, whereas duration (B) declined. Boxplots show 25th to 75th percentiles, median (lines),



mean (crosses), maximum and minimum values (whiskers), and outliers (dots). (C) Mean glide speed increased with increasing wing loading. (D and E) Mean glide angle increased in male nymphs but was relatively consistent in females. Values are means  $\pm$  SD in (C) and (D); trend lines represent linear regressions with log<sub>10</sub>-transformed ( ); shades representing SEM. (E) Increase in glide speed without reduction of glide angle in female nymphs, comparing 2nd and 8th instars. Arrow size represents the relative magnitude of velocity components based on mean values. See Data S2 (<https://doi.org/10.17632/ggsxps2v6f.1>) for details. See also Figure S4.

Orchid mantis nymphs exhibited an intermediate wing loading (2.2–11.9 N m<sup>-2</sup>) between those of wingless gliding arthropods and vertebrates (Figure 4B). Compared with gliding ants and spiders, orchid mantis nymphs also showed negative allometries of glide index (with sex-specific slopes), but they glided better at equivalent body masses (Figure 4 C). In particular, female mantis nymphs (glide index 0.4–0.6) traveled 20%–50% farther than gliding spiders and 50%–200% farther than gliding ants of similar masses. Despite their gliding abilities, wingless gliding arthropods are limited to a glide index < 1 (with average glide angle > 45°).



**Figure 4 Comparisons of gliding morphology and gliding capability between gliding animals** (A) Relative areas of extended surfaces (relative to the animal's projected planform area) against whole-animal mass. Orchid mantis' femoral lobes provide a

smaller surface area compared with vertebrate gliders' membranes or webs (orange highlight), but they stand out compared with gliding animals without obvious extensions. (B) Comparison of wing loading ( ) between orchid mantis nymphs, gliding ants, and gliding vertebrates within a morpho-space defined by mass and the relative area of extensions. For orchid mantis, points represent instar-specific means of both sexes. Morphology data of other taxa were aggregated based on availability (Data S3 at <https://doi.org/10.17632/xzx5srxf8k.1>). (C) Glide index versus mass in different gliding animals. Glide index allometries in wingless arthropods (lower left) and vertebrates (upper right). Slopes in orchid mantis (female,  $-0.09 \pm 0.05$ ,  $p < 0.0001$ ; males,  $-0.28 \pm 0.06$ ,  $p < 0.001$ ) are comparable to those of gliding ants ( $-0.097$ )<sup>10</sup> and spiders ( $-0.164$ ).<sup>12,13</sup> Orchid mantis nymphs traveled farther per unit descent than the other two arthropods of similar mass. Lines represent linear regressions for all nymphal stages, excluding the first; shades represent SEM. Vertebrate data were obtained from the literature.<sup>3,19</sup>

## Leg wings and gliding in orchid mantises

We showed that wingless orchid mantis nymphs are remarkable gliders owing to their femoral lobes acting as wing-like structures. Why do orchid mantises glide in the first place? They are presumably subject to the same selective pressure for aerial escape and dispersal as other arboreal invertebrates,<sup>2,20</sup> and they may also rely on gliding to access hunting territories.

Lobe-ablation experiments and preliminary characterization of femoral lobe morphology revealed a new type of biological airfoil—non-flapping “leg wings” derived from exoskeleton and used in gliding. The ventrally cambered shape likely facilitates lift generation during gliding,<sup>21</sup> but its aerodynamic properties require more detailed examination, especially concerning the contributions of the corrugated camber profile, body kinematics, and leg postures. The aerodynamic mechanism of these lobed femora may vary with their size, shape, and gliding performance at different air speeds. For example, as female mantises progressed from the 1st to the 8th instar, the Reynolds number increased by over 300 times (from  $\sim 70$  to  $2.2 \times 10^3$ ), whereas the increase in body length was just  $\sim 14$  times (from  $\sim 9 \times 10^2$  to  $1.3 \times 10^4$ ). The lobe-ablated mantises also performed well in gliding compared with other wingless gliding arthropods, suggesting substantial aerodynamic capability conferred by the body and legs, especially a flat, broad abdomen. The expanded femoral lobes may be particularly important to reducing wing loading in larger nymphs. This hypothesis may be partially supported by the gliding capability of the 1st instar orchid mantis nymphs and gliding ants,<sup>10</sup> which have similar body mass and lack extensions on body and legs.

We further showed that the expansion of femoral lobes along ontogeny reduced wing loading and improved gliding. This likely corresponds with a sustained selective pressure for gliding throughout the nymphal stage. Compared with males, the persistent gliding capability in females may help compensate for the

relatively higher energetic cost of dispersal and higher predation risk associated with larger body sizes.<sup>22</sup> The decrease in relative lobe size from the last nymphal stage to adulthood (Figure 2) could be indicative of a reduced need for gliding because adults possess fully developed wings and are capable of powered flight.

### **Evolution of gliding-adapted structures in wingless arthropods**

To our knowledge, this is the first documentation of an arthropod leg wing used for gliding. The lack of reports of such structures may be partly attributed to the long-term misinterpretation of their function. Among terrestrial arthropods, although visual mimicry is frequently interpreted as the main function of flat structures, the actual utility and underlying evolutionary motivation can only be justified through empirical experiments. For example, orchid mantis femoral lobes, although interpreted as flower mimics for ~200 years, do not contribute to luring pollinating preys<sup>6</sup> but facilitate gliding.

We speculate that a substantial diversity of flat exoskeletal structures found on body and appendages in terrestrial arthropods may contribute to gliding, especially among hemimetabolous insects, such as leaf insects, stick insects, mantids, and leaf-footed bugs.<sup>23–25</sup> Many of these insects are arboreal, undergo relatively long nymphal stages, and grow into large nymphs, thus possibly being subject to selective pressures for gliding.<sup>24</sup>

Unlike vertebrates' collapsible membranes and webbings<sup>26–29</sup> and insects' winglets,<sup>30</sup> rigid exoskeletal extensions on arthropod legs cannot change shape or size during aerial performances and have limited flexibility and mobility. Although larger lobes may be advantageous for improved gliding, they could potentially have adverse effects on survivorship due to prolonged molting, increased risk of molting failure, hindered locomotion, or increasing the mantis conspicuousness to predators.<sup>19</sup> Therefore, the evolution of flat extensions on arthropod body and legs could be subject to functional tradeoffs, which deserves further investigation.

Future work should study three-dimensional glide trajectories in orchid mantises to reveal mid-air maneuvers and forward gliding performance toward the end of trajectories. Considering the scarcity of gliding allometry data (Figure 4 C), it becomes crucial to conduct further investigations into the ontogeny of gliding and gliding kinematics, particularly in large wingless arthropods. Such research is

essential to comprehending how gliding-adapted structures evolve in different clades and body sizes.

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### **Author contributions**

Conceptualization, Z.C., X.Z., J.-X.L., and Y.Z.; methodology, X.Z., Y.Z., J.-X.L., and Z.C.; investigation, X.Z., J.-X.L., Z.C., B.D., and L.Y.; visualization, Y.Z., X.Z., Z.C., J.-X.L., and T.C.-D.; funding acquisition, Z.C.; project administration, Z.C.; supervision, Z.C. and Y.Z.; writing – original draft, X.Z., Y.Z., Z.C., and J.-X.L.; writing – review & editing, all authors.

### **Declaration of interests**

The authors declare no competing interests.

### **Supplemental information**

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2023.11.003>.

### **References**

- 1 Dudley R., Byrnes G., Yanoviak S.P., Borrell B., Brown R.M., McGuire J.A. Gliding and the functional origins of flight: biomechanical novelty or necessity? *Annu. Rev. Ecol. Evol. Syst.* 2007;38:179–201.
- 2 Dudley R., Yanoviak S.P. Animal aloft: the origins of aerial behavior and flight. *Integr. Comp. Biol.* 2011;51:926–936.

- 3 Socha J.J., Jafari F., Munk Y., Byrnes G. How animals glide: from trajectory to morphology. *Can. J. Zool.* 2015;93:901–924.
- 4 O’Hanlon J.C., Li D., Norma-Rashid Y. Coloration and morphology of the orchid mantis *Hymenopus coronatus* (Mantodea: Hymenopodidae). *J. Orthop. Res.* 2013;22:35–44.
- 5 O’Hanlon J.C. Orchid mantis. *Curr. Biol.* 2016;26:R145–R146.
- 6 O’Hanlon J.C. The roles of colour and shape in pollinator deception in the orchid mantis *Hymenopus coronatus*. *Ethology* 2014;120:652–661.
- 7 Siedlecki M. Spadochronowy lot niektórych owadów – Der Fallschirmflug einiger Insekten. *Bull. Int. Acad. Pol. Sci. Lett.* 1917;ser B:230–256.
- 8 Zhao X., Liu J.X., Chen Z.Q. The orchid mantis exhibits high ontogenetic colouration variety and intersexual life history differences. *Evol. Ecol.* 2023;37:569–582.
- 9 Yanoviak S.P., Kaspari M., Dudley R. Gliding hexapods and the origins of insect aerial behaviour. *Biol. Lett.* 2009;5:510–512.
- 10 Yanoviak S.P., Dudley R., Kaspari M. Directed aerial descent in canopy ants. *Nature* 2005;433:624–626.
- 11 Yanoviak S.P., Munk Y., Kaspari M., Dudley R. Aerial manoeuvrability in wingless gliding ants (*Cephalotes atratus*). *Proc. Biol. Sci.* 2010;277:2199–2204.
- 12 Yanoviak S.P., Munk Y., Dudley R. Evolution and ecology of directed aerial descent in arboreal ants. *Integr. Comp. Biol.* 2011;51:944–956.
- 13 Yanoviak S.P., Munk Y., Dudley R. Arachnid aloft: directed aerial descent in Neotropical canopy spiders. *J. R. Soc. Interface* 2015;12:0534.
- 14 Zeng Y., Lam K., Chen Y., Gong M., Xu Z., Dudley R. Biomechanics of aerial righting in wingless nymphal stick insects *Extatosoma tiaratum*. *Interface Focus* 2017;7:20160075.
- 15 Rader J.A., Hedrick T.L., He Y., Waldrop L.D. Functional morphology of gliding flight II. Morphology follows predictions of gliding performance. *Integr. Comp. Biol.* 2020;60:1297–1308.

16 Bishop K.L. The relationship between 3-D kinematics and gliding performance in the southern flying squirrel, *Glaucomys volans*. *J. Exp. Biol.* 2006;209:689–701.

17 Khandelwal P.C., Hedrick T.L. Combined effects of body posture and three-dimensional wing shape enable efficient gliding in flying lizards. *Sci. Rep.* 2022;12:1793.

18 Brown C.E., Sathe E.A., Dudley R., Deban S.M. Gliding and parachuting by arboreal salamanders. *Curr. Biol.* 2022;32:R453–R454.

- 19 McGuire J.A., Dudley R. The cost of living large: comparative gliding performance in flying lizards (Agamidae: Draco). *Am. Nat.* 2005;166:93–106.
- 20 Khandelwal P.C., Ross S.D., Dong H., Socha J.J. Convergence in gliding animals: morphology, behavior, and mechanics. *Convergent Evolution: Animal Form and Function*. Springer; 2023. p. 391–429.
- 21 Sunada S., Takashima H., Hattori T., Yasuda K., Kawachi K. Fluid-dynamic characteristics of a bristled wing. *J. Exp. Biol.* 2002;205:2737–2744.
- 22 Chown S.L., Gaston K.J. Body size variation in insects: a macroecological perspective. *Biol. Rev. Camb. Philos. Soc.* 2010;85:139–169.
- 23 Boisseau R.P.G.E. *The Evolution of Morphological Diversity and Sexual Dimorphism in Stick and Leaf Insects*. University of Montana; 2022.
- 24 Emberts Z., St Mary C.M., Howard C.C., Forthman M., Bateman P.W., Somjee U., Hwang W.S., Li D., Kimball R.T., Miller C.W. The evolution of autotomy in leaf-footed bugs. *Evolution* 2020;74:897–910.
- 25 Svenson G.J., Hardy N.B., Cahill Wightman H.M., Wieland F. Of flowers and twigs: phylogenetic revision of the plant-mimicking praying mantises (Mantodea: Empusidae and Hymenopodidae) with a new suprageneric classification. *Syst. Entomol.* 2015;40:789–834.
- 26 McGuire J.A., Dudley R. The biology of gliding in flying lizards (genus Draco) and their fossil and extant analogs. *Integr. Comp. Biol.* 2011;51:983–990.
- 27 Jackson S.M. Glide angle in the genus *Petaurus* and a review of gliding in mammals. *Mamm. Rev.* 2000;30:9–30.
- 28 Wu W., Gao Y.-D., Jiang D.-C., Lei J., Ren J.-L., Liao W.-B., Deng C., Wang Z., Hillis D.M., Zhang Y.-P., et al. Genomic adaptations for arboreal locomotion in Asian flying treefrogs. *Proc. Natl. Acad. Sci. USA* 2022;119:e2116342119.
- 29 Socha J.J. Gliding flight in *Chrysopelea*: turning a snake into a wing. *Integr. Comp. Biol.* 2011;51:969–982.
- 30 Zeng Y., Park S., Gonzales C., Yom S., Rahim F., Dudley R. Beyond winglets: evolutionary scaling of flight-related morphology in stick insects (Phasmatodea). *Biol. J. Linn. Soc.* 2023;140:blad050.

- 31 Roeder K.D. An experimental analysis of the sexual behavior of the praying mantis (*Mantis religiosa* L.). *Biol. Bull.* 1935;69:203–220.
- 32 Brannoch S.K., Wieland F., Rivera J., Klass K.D., Olivier B., Svenson G.J. Manual of praying mantis morphology, nomenclature, and practices (Insecta, Mantodea). *ZooKeys* 2017;696:1–100.
- 33 Abràmoff M.D., Magalhães P.J., Ram S.J. Image processing with ImageJ. *Biophotonics Int.* 2004;11:36–42.
- 34 Kandori I., Hiramatsu M., Soda M., Nakashima S., Funami S., Yokoi T., Tsuchihara K., Papaj D.R. Long horns protect *Hestina japonica* butterfly larvae from their natural enemies. *Sci. Rep.* 2022;12:2835.
- 35 Zeng Y., Lin Y., Abundo A., Dudley R. Visual ecology of directed aerial descent in first-instar nymphs of the stick insect *Extatosoma tiaratum*. *J. Exp. Biol.* 2015;218:2305–2314.
- 36 Yanoviak S.P., Dudley R. The role of visual cues in directed aerial descent of *Cephalotes atratus* workers (Hymenoptera: Formicidae). *J. Exp. Biol.* 2006;209:1777–1783.
37. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing; 2022.
- 38 RStudio Team. RStudio: integrated development for R. RStudio; 2022.
- 39 Lüdecke D., Ben-Shachar M., Patil I., Waggoner P., Makowski D. performance: an R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* 2021;6:3139.
- 40 Lüdecke D. Performance: assessment of regression models performance R package version 0.10.0. 2022.
- 41 Pinheiro J., Bates D., R Core Team. Nlme: linear and nonlinear mixed effects models R package version 3.1-158. 2022. <https://CRAN.R-project.org/package=nlme>.