Extraordinary flight performance of the smallest beetles

Sergey E. Farisenkov (Сергей Фарисенков)a,b,1, Nadejda A. Lapina (Надежда Лапина)a, Ryotr N. Petrov (Рюо́т Петров)a, and Alexey A. Polilov (Алексей Полилов)a,b,1

aDepartment of Entomology, Faculty of Biology, Lomonosov Moscow State University, Moscow 119234, Russia; and bSouthern Branch, Joint Russian-Vietnamese Tropical Research and Technological Center, Ho Chi Minh 70000, Vietnam

Edited by David A. Weitz, Harvard University, Cambridge, MA, and approved September 1, 2020 (received for review June 16, 2020)

Size is a key to locomotion. In insects, miniaturization leads to fundamental changes in wing structure and kinematics, making the study of flight in the smallest species important for basic biology and physics, and, potentially, for applied disciplines. However, the flight efficiency of miniature insects has never been studied, and their speed and maneuverability have remained unknown. We report a comparative study of speeds and accelerations in the smallest free-living insects, featherwing beetles (Coleoptera: Ptiliidae), and in larger representatives of related groups of Staphylinoidea. Our results show that the average and maximum flight speeds of larger ptiliids are extraordinarily high and comparable to those of staphylinids that have bodies 3 times as long. This is one of the few known exceptions to the “Great Flight Diagram,” according to which the flight speed of smaller organisms is generally lower than that of larger ones. The horizontal acceleration values recorded in Ptiliidae are almost twice as high as even in Silphidae, which are more than an order of magnitude higher. High absolute and record-breaking relative flight characteristics suggest that the unique morphology and kinematics of the ptiliid wings are effective adaptations to flight at low Reynolds numbers. These results are important for understanding the evolution of body size and flight in insects and pose a challenge to designers of miniature biomorphic aircraft.

Allometric analysis shows that the slopes of the median speed (Vmed) and median horizontal speed (Vmed.h) do not differ between the two groups (Fig. 1 A and B), while the elevation is significantly higher in Ptiliidae (−0.52 in Ptiliidae and −1.02 in other staphylinoids; Huber’s M estimation P < 0.001 for Vmed: −0.48 in Ptiliidae and −1.05 in other staphylinoids, P = 0.003 for Vmed.h), which shows that the speeds in ptiliids are higher than in other staphylinoids of comparable body sizes. The maximum speed (Vmax) and maximum horizontal speed (Vmax.h) correlate with the body size in both groups (Fig. 1 A and B). Pairwise comparison of the horizontal flight speeds of the ptiliid Acrotrichis sericans (which displays the highest speeds among Ptiliidae; Vmax.h = 0.89 m/s) and four staphylinid species (Dinaraea sp., Atheta sp., Gyrophaena sp. 1, Gyrophaena sp. 2) shows that A. sericans has a higher median speed than staphylinids with bodies three times as long (Mann–Whitney U test, P < 0.001).

The maximum acceleration in Ptiliidae during horizontal flight (ah), reaching 14.05 m/s², is significantly higher than in miniature Staphylinidae and almost twice as high as in the larger Silphidae, in which it does not exceed 8.44 m/s² (Fig. 1C); the elevations of regression are significantly different.

The median speed of horizontal flight relative to BL (Vmed.h.rel) in Ptiliidae is 146 BL per s to 437 BL per s, higher than in the other staphylinoids (28 BL per s to 123 BL per s). The maximum horizontal flight speed (Vmax.h.rel) relative to BL is also mostly higher in Ptiliidae species (Table 1).

Discussion

The average and maximum absolute speeds and maximum accelerations of Ptiliidae are comparable with those of much longer staphylinoids. Ptiliids are also comparable in flight characteristics with the much larger Drosophila, a model organism for studying insect flight (7). Relative values are even more extraordinary: A. sericans in horizontal flight cover up to 975 BL per s, which is the highest recorded relative horizontal speed of locomotion among animals.

Such outstanding values can be linked to two factors: structural features and kinematics of the wings, and size and efficiency of muscles. Physical characteristics of the musculature of Ptiliidae have not been studied, but it is known that miniaturization does not considerably increase relative volumes of muscles in beetles, in contrast to dipters, where miniature species have membranous anterior volume.

Author contributions: A.A.P. designed research; S.E.F. and A.A.P. performed research; S.E.F. and N.A.L. analyzed data; and S.E.F., P.N.P., and A.A.P. wrote the paper.

The authors declare no competing interest.

This open access article is distributed under Creative Commons Attribution License 4.0 (CC BY).

1To whom correspondence may be addressed. Email: farisenkov@mail.bio.msu.ru or polilov@gmail.com.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2012404117/-/DCSupplemental.

www.pnas.org/cgi/doi/10.1073/pnas.2012404117

PNAS Latest Articles | 1 of 3
The wings and very large flight muscles (8). The power of flight muscles depends on both volume and some structural features (9), but this aspect has not yet been studied in any ptilopterous insects, and the contribution of muscles to the flight efficiency of microinsects requires further study. The other productive way to increase flight efficiency is to optimize the structure and kinematics of the wings.

If the Reynolds numbers are low, the lift-to-drag ratio is very small both for membranous and for bristled wings of a similar shape (10) over the entire range of angles of attack; therefore, at low Reynolds numbers, it is more advantageous, in terms of energy, to use rowing flight, in which translational movements occur at a great angle of attack and create drag-based lift. Ptiliidae have bristled wings with peripheral setae covered with secondary outgrowths (11). This structure can reduce wing mass compared to that of a membranous wing of the same size, thus reducing inertial losses; at the same time, the permeability of bristled wings at low Reynolds numbers is very low, creating aerodynamic forces similar to those of membranous wings of the same size (10, 12). Bristled (compared to membranous) wings make use of the clap and fling mechanism more efficiently: smaller forces are required to draw such wings apart (13, 14); this is especially important, as the flight cycle of Ptiliidae includes not only the upper clap above the body but also the lower clap under the body (8). Features of this wing cycle may strongly increase aerodynamic efficiency: The wing moves back at a high angle of attack relative to the body and to the direction of movement during both upstroke and downstroke, while, in other miniature insects, the downstroke is directed forward and mostly creates drag-based lift (5).

Thus, the peculiar wing structure of Ptiliidae and peculiar features of their flight kinematics result in high flight efficiency despite minute size. Further study of the kinematics and aerodynamics of Ptiliidae can reveal new drag-based aerodynamic mechanisms. The ongoing miniaturization of artificial flying devices in electronics and robotics can make the knowledge of principles of flight aerodynamics of these and other microinsects useful for developing swimming and flying biomimetic devices.

**Materials and Methods**

The method developed by us for studying flight characteristics of beetles is similar to earlier ones (15) but modified for studying miniature insects. We analyzed 17 species of staphylinoid beetles: eight Ptiliidae, six Staphylinidae, and three Silphidae (Table 1). Free flight was recorded using two Evercam 4000 synchronized high-speed cameras (Evercam) with a frequency of 60 frames per second (fps) to 300 fps. Between 5 and 30 individuals were placed in a closed transparent flight chamber illuminated from two sides and from above by 850-nm infrared LED. Additional visible light sources provided a natural level of illumination. The temperature in the chambers was 24 °C to 26 °C. The linear dimensions of the chambers exceeded the BLs of the beetles by a factor of at least 70, allowing the beetles to move freely and fly for up to several minutes. We have analyzed, on average, 9.76 tracks with an average duration of 561 frames (Dataset S1). We analyzed at least three records for each species, including a total of at least 492 track points. The flight trajectories were captured in two projections using Tracker (Open Source Physics). Three-dimensional reconstructions of trajectories, adjusted for scale and perspective, were made using visual markers on chamber walls inside chambers. The distances between adjacent points of tracks did not exceed 15 BLs and were, on average, 1.36 BLs.

To remove tracking errors, the Cartesian coordinates of the tracks were smoothed after triangulation using local polynomial regression fitting, and calculated speeds were smoothed using moving average. The speeds and accelerations in horizontal sections of the trajectory (±30° relative to the horizon) were analyzed separately. The average value of each flight characteristic was calculated as the median for all values obtained for each species in each frame. Maximum speeds and accelerations were calculated as the 99th percentiles for all tracks for each species. Smoothing (stats package), descriptive statistics, and allometric analysis (smatr package) were performed in R. The scheme of the experimental setup and procedure of trajectory reconstruction are shown in Movie S1.

**Data Availability.** All study data are included in the article, Dataset S1, and Movie S1.

---

**Fig. 1.** Flight parameters and body sizes of beetles: (A) median and maximum speed, beetles in flight (left to right): Ptiliidae, Staphylinidae, Silphidae; (B) median and maximum horizontal speed, color key as in A; (C) maximum horizontal acceleration.
Table 1. Flight parameters of studied beetles

| Family | Species                          | BL, mm | $V_{\text{med}}$, m/s | $V_{\text{med,sp}}$, m/s | $V_{\text{med,h,rel}}$, BL/s | $V_{\text{max}}$, m/s | $V_{\text{max,sp}}$, m/s | $V_{\text{max,h,rel}}$, BL/s | $a_0$, m/s² |
|--------|---------------------------------|--------|-----------------------|--------------------------|-------------------------------|----------------------|--------------------------|-------------------------------|------------|
| **Ptiliidae** | *Acrotrichis grandicollis* Mannerheim, 1844 | 1.03   | 0.29                  | 0.30                     | 293                           | 0.73                 | 0.66                     | 645                           | 13.97      |
|        | *A. sericans* Heer, 1841       | 0.90   | 0.37                  | 0.39                     | 437                           | 0.88                 | 0.88                     | 975                           | 14.05      |
|        | *Limulosa waspucensis* Hall, 1999 | 0.40   | 0.08                  | 0.08                     | 204                           | 0.30                 | 0.19                     | 476                           | 6.47       |
|        | *Mikado* sp.                  | 0.46   | 0.08                  | 0.07                     | 146                           | 0.36                 | 0.26                     | 556                           | 4.92       |
|        | *Nanosella* sp.               | 0.37   | 0.07                  | 0.07                     | 202                           | 0.30                 | 0.16                     | 421                           | 3.97       |
|        | *Nephes titan* Newman, 1834    | 0.60   | 0.15                  | 0.16                     | 267                           | 0.52                 | 0.52                     | 870                           | 7.33       |
|        | *Paratupa placenta* Deane, 1931 | 0.38   | 0.13                  | 0.13                     | 351                           | 0.31                 | 0.21                     | 540                           | 7.25       |
|        | *Ptenidium pusillum* Gyllenhal, 1808 | 1.00   | 0.16                  | 0.18                     | 183                           | 0.49                 | 0.49                     | 495                           | 10.65      |
| **Staphylinae** | *Atheta* sp.              | 2.06   | 0.16                  | 0.16                     | 79                            | 0.77                 | 0.50                     | 242                           | 4.77       |
|        | *Dinareaa* sp.                | 3.11   | 0.22                  | 0.24                     | 78                            | 0.77                 | 0.71                     | 229                           | 6.58       |
|        | *Gyrophaena* sp. 1            | 1.43   | 0.10                  | 0.08                     | 58                            | 0.93                 | 0.94                     | 658                           | 4.28       |
|        | *Gyrophaena* sp. 2            | 2.92   | 0.32                  | 0.36                     | 123                           | 0.71                 | 0.63                     | 214                           | 4.80       |
|        | *Lorithon lunulatus* Linnaeus, 1760 | 6.16   | 0.61                  | 0.70                     | 114                           | 1.87                 | 1.91                     | 311                           | 6.72       |
|        | *Philonthus* sp.              | 11.97  | 0.69                  | 0.71                     | 60                            | 1.46                 | 1.36                     | 114                           | 7.93       |
| **Silphidae** | *Nicrophorus investigator* Zetterstedt, 1824 | 21.07  | 1.21                  | 1.26                     | 60                            | 2.34                 | 2.33                     | 111                           | 6.61       |
|        | *Nicrophorus vespillo* Linnaeus, 1758 | 21.04  | 0.73                  | 0.58                     | 28                            | 2.06                 | 1.66                     | 79                            | 8.44       |
|        | *Oiceoptoma thoracicum* Linnaeus, 1758 | 15.39  | 0.93                  | 1.01                     | 66                            | 2.07                 | 1.89                     | 123                           | 8.00       |

**ACKNOWLEDGMENTS.** We thank all students of the Faculty of Biology, Lomonosov Moscow State University, who participated in pilot experiments. This study was supported by the Russian Foundation for Basic Research (Project 18-34-20063: design and construction of equipment, experiments with most species) and Russian Science Foundation (Project 19-14-00045: video recording of some species in Vietnam and analysis of data).

1. H. Tennekes, *The Simple Science of Flight: From Insects to Jumbo Jets*, (MIT Press, ed. 4, 2000).
2. G. A. Horridge, *The flight of very small insects.* Nature 178, 1334–1335 (1956).
3. B. B. Rohdendorf, *The evolution and classification of the flight apparatus of insects.* Trans. Paleontol. Inst. USSR Acad. Sci. 16, 1–176 (1949).
4. A. A. Polilov, Small is beautiful: Features of the smallest insects and limits to miniaturization. *Annu. Rev. Entomol.* 60, 103–121 (2015).
5. Y. Z. Lyu, H. J. Zhu, M. Sun, *Flapping-mode changes and aerodynamic mechanisms in miniature insects.* Phys. Rev. E 99, 012419 (2019).
6. S. Q. Zhang et al., Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nat. Commun.* 9, 205 (2018).
7. C. T. David, *The relationship between body angle and flight speed in free-flying Drosophila.* *Physiol. Entomol.* 3, 191–195 (1978).
8. M. I. Yavorskaya, R. G. Beutel, S. E. Farisenkov, A. A. Polilov, The locomotor apparatus of one of the smallest beetles—The thoracic skeletal musculature system of Nephanes titan (Coleoptera, Ptiliidae). *Arthropod Struct. Dev.* 48, 71–82 (2019).
9. J. H. Marden, *Variability in the size, composition, and function of insect flight muscles.* *Annu. Rev. Physiol.* 62, 157–178 (2000).
10. D. Kolomenskiy et al., *Aerodynamic performance of a bristled wing of a very small insect.* *Exp. Fluids* 61, 194 (2020).
11. A. A. Polilov, N. I. Reshetnikova, P. N. Petrov, S. E. Farisenkov, Wing morphology in featherwing beetles (Coleoptera: Ptiliidae): Features associated with miniaturization and functional scaling analysis. *Arthropod Struct. Dev.* 48, 56–70 (2019).
12. S. H. Lee, D. Kim, *Aerodynamics of a translating comb-like plate inspired by a fairyfly wing.* *Phys. Fluids* 29, 081902 (2017).
13. S. K. Jones, Y. J. J. Yun, T. L. Hedrick, B. E. Griffith, L. A. Miller, *Bristles reduce the force required to “fling” wings apart in the smallest insects.* *J. Exp. Biol.* 219, 3759–3772 (2016).
14. A. Santhanakrishnan et al., *Clap and fling mechanism with interacting porous wings in tiny insect flight.* *J. Exp. Biol.* 217, 3898–3909 (2014).
15. H. Wagner, *Flight Performance and visual control of flight of the free-flying housefly (Musca domestica L.)* I. Organization of the flight motor. *Philos. Trans. R. Soc. B* 312, 527–551 (1986).