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A new galloping gait in an insect

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An estimated three million species of insects all walk using variations of the alternating tripod gait [1]. At any one time, these animals hold a stable triangle of legs steady while swinging the opposite triangle forwards. Here, we report the discovery that three species of flightless desert dung beetles use an additional gallop-like gait, which has never been described in any insect before. Like a bounding hare, the beetles propel their body forward by synchronously stepping with both middle legs and then both front legs. Surprisingly, this peculiar galloping gait delivers lower speeds than the alternating tripod gait. Why these beetles have shifted so radically away from what is the most widely used walking style on our planet is as yet unknown. Future research into this novel gait will further our understanding of insect locomotory biomechanics, evolution and navigation.

Like all insects described so far, four of seven observed species of *Pachysoma*, a dung beetle genus endemic to the coastal deserts of South Africa and Namibia, typically walk with an alternating tripod gait (Suppl. Video 1). In this gait, the first and third leg on one side of the body move in unison with the contralateral middle leg [2] (Figure 1A,C), forming a moving tripod. This tripod alternates with the static, stable tripod made up of the remaining three legs. In many insects, this pattern of leg coordination changes with speed, creating a continuum of stepping patterns ranging from the tripod gait to a “tetrapod gait”, where only two legs (diagonally opposed, one on either side) swing at any one time [3-5]. All of these seemingly diverse patterns, however, follow a small set of simple rules [2], including the principal one that each leg moves out of phase with its contralateral pair, i.e. legs of a pair move alternately. In almost all insect species, synchronous (in-phase) stepping of a leg pair is only observed in exceptional circumstances, e. g. when crossing an obstacle [6], when swimming [7], or for a few steps when the animal begins to walk [4].

Three other species of *Pachysoma* – *P. endroedyi* (Figure 1, bottom right), *P. hippocrates* and *P. glentoni* – are the exception to this rule. Living on the sands of Namaqualand (South Africa), these flightless desert dung beetles forage on dry vertebrate dung and plant detritus, which they drag with their hind legs while walking forwards to their burrow [8-9]. Although they can walk in the normal tripod gait, these beetles usually employ a unique galloping gait, in which they move each pair of legs synchronously, stepping alternately with the front and the middle legs (Figure 1B,D; Suppl. Video 1). The hind legs are dragged behind, even if the beetle carries no load, and seem to contribute little to propulsion. Although no aerial phase occurs, as in the case of galloping mammals, the leg coordination is that of a gallop, specifically a full bound as found in hares and rabbits [10].

There should be significant reasons underlying the evolution of this additional gait, which supplements the most common walking gait in the animal kingdom. In this light it is useful to consider the only other insect species walking with a similar,

synchronous gait: the primitive “jumping bristletail” *Petrobius brevistylis* [11]. The bristletail’s “jumping gait” differs from the *Pachysoma* gallop in that all three leg pairs alternate in metachronal order – back, middle, front – and that the abdomen and tail are dragged on the ground for stability. Furthermore, a galloping *Pachysoma* can maintain this gait for at least 100 m, whereas on a rocky beach, the jumping gait of *Petrobius* will be restricted to a displacement of decimetres at most. Mechanically, the jumping gait is enabled by the bristletails’ leg morphology in which the first and second joints (pleurites-coxa and coxa-trochanter, respectively) are unique among the arthropods, allowing extensive leg movements. *Petrobius* also has unusual thoracic and abdominal musculature, which is highly specialised for another type of locomotion: fast escape jump reactions [11]. This musculature enables the animals to cover up to twenty body lengths per second with their jumping gait, which is twice as fast as other, similarly small insects. We found no such speed advantage for the *Pachysoma* galloping gait. On the contrary, when observing beetles on sandpaper or fabric surfaces (to provide grip), we measured running speeds in the tripod-walking *P. striatum* that were slightly but significantly faster than those for the sympatric, similarly-sized galloping *P. endroedyi* (Figure 1F,G). This is true both in absolute terms (9.1 ± 1.5 cm/s vs. 7.6 ± 1.6 cm/s, mean \pm s.d.; two-sample t-test, $t = -2.1$, $d.f. = 18$, $p = 0.0498$) and in relation to body size (4.2 ± 0.9 body-lengths/s vs. 3.1 ± 0.6 body-lengths/s, mean \pm s.d.; two-sample t-test, $t = -3.2$, $d.f. = 18$, $p = 0.003$).

These results suggest that *Pachysoma*, in contrast to *Petrobius*, have not evolved their galloping gait to provide higher speeds. The reason why this strange and rare gait has evolved is thus still unknown. Does it provide an advantage in terms of energy consumption or mechanical stress? Does it make it easier to move straight or stabilize head and eyes while transporting large loads across shifting sands? If true, this would suggest an advantage for navigation between the nest and a foraging site. Testing these hypotheses will bring us one step closer to understanding the ecological and evolutionary significance of *Pachysoma*’s unusual gait.

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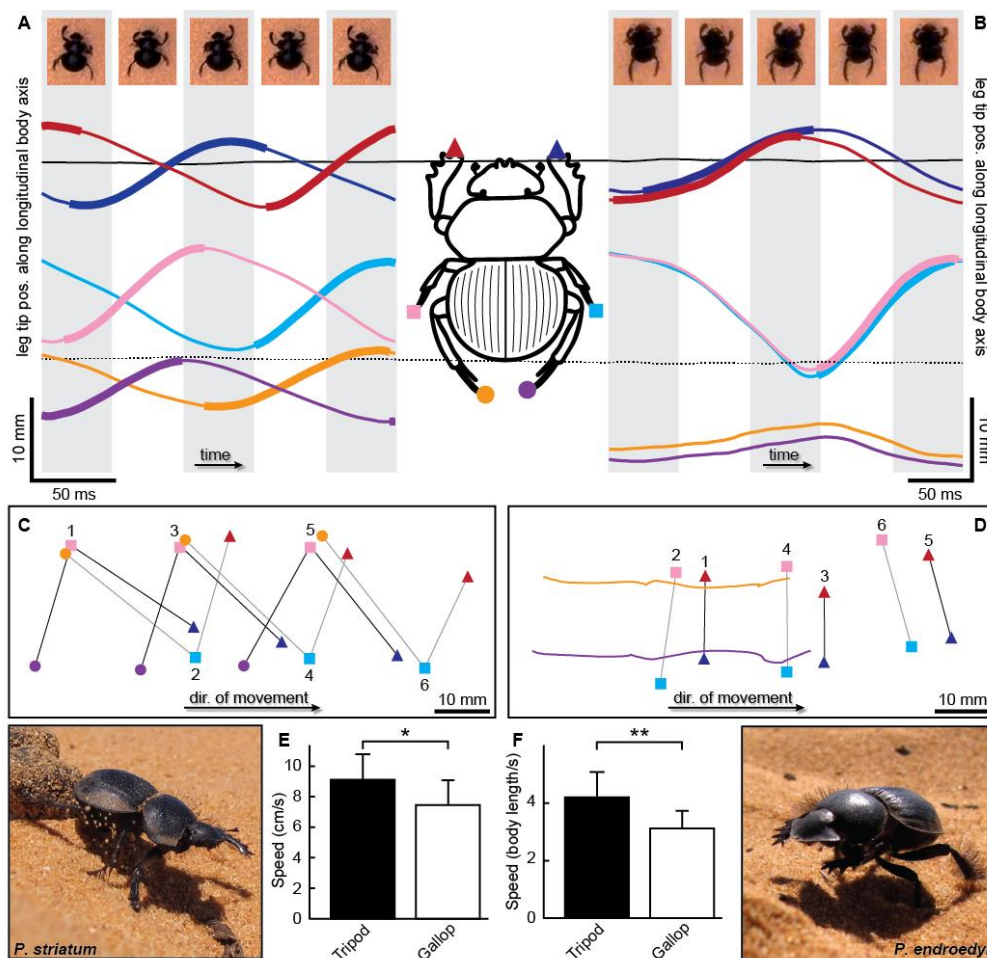


Figure 1. Comparison of tripod gait and gallop.

(A,B) Movement of legs relative to the beetle's body during an average step cycle. *P. striatum* (bottom left) walks in the insect-typical tripod gait; legs of each pair step alternately (A). *P. endroedyi* (bottom right) employs a galloping gait; legs of a pair move in unison (B). Images at the top are video frames at the respective times during the stride. Individual legs are colour-coded as indicated on the schematic beetle. Thin lines indicate periods of ground contact, thick lines striding periods. In the galloping gait, hind legs are dragged behind (thin lines). Position of front of head and rear of abdomen are indicated by solid and dotted black lines, respectively. Note the different time scales. (C,D) Bird's-eye view of footsteps created by three typical step cycles in *P. striatum* (C) and *P. endroedyi* (D). Legs are colour-coded as above, thin lines connect legs that move together (black/grey lines represent first/second half of step cycle, respectively). Numbers indicate the order of footfalls. (E,F) Average walking speed measured in tripod-walking *P. striatum* (black bars) and galloping *P. endroedyi* (white bars), shown as absolute values (E) and relative to body length (F). All bars show mean \pm s.d. of ten beetles per species. Statistics were performed using independent-sample two-sided t-tests. * $p < 0.05$; ** $p < 0.01$.

Supplemental Videos

One supplemental video can be found at <http://youtu.be/IHPNNhal13s>.

Supplemental Video S1: Comparison of tripod gait and gallop

Compilation of high-speed videos illustrating the dynamics of the two gaits. *Pachysoma striatum* walks in the insect-typical tripod gait, stepping legs of each pair alternately. *Pachysoma endroedyi* employs a galloping gait, where legs of a pair move in unison.

Supplemental Experimental Procedures

Animals and field sites

Beetles of seven of the thirteen species in the genus *Pachysoma* were observed and collected during September 2010, October 2011 and November 2012 at four field sites in South Africa and Namibia: *P. glentoni* at Hoekdam Farm, Namaqualand, South Africa (32°13'S, 18°26'E); *P. striatum*, *P. endroedyi* and *P. hippocrates* at Kommandokral Farm (31°30'S, 18°12'E), Namaqualand, South Africa (GPS); *P. hippocrates* at West Coast National Park (33°11'S, 18°08'E); *P. denticolle*, *P. rotundigena* and *P. rodriguesi* in NamibRand Nature Reserve, Namibia (24°53'S, 15°54'E). After collection, beetles were kept at the field station in sand-filled plastic boxes and provided with sheep dung and flowers collected from their natural habitat.

Gait description

To characterise the different gaits, beetles were filmed at 300 frames per second using high-speed video cameras (Casio Exilim EX-F1) as they were walking on rough sandpaper or fabric, which provided them with sufficient grip to walk without slipping. An average step cycle was calculated for *P. striatum* (tripod) and *P. endroedyi* (gallop) in the following way: i) Five full step cycles (starting and ending when the right front leg begins to move forwards) were selected for a straight run for one beetle of each species filmed from above; ii) the position of the tip of each leg, of the front of the head, and of the rear of the abdomen were tracked and calibrated using custom-made tracking software [S1] in Matlab (2013b); iii) leg positions were projected onto the animal's longitudinal body axis, i.e. only movements *along* this body axis were considered; iv) the average step period was determined from the maxima and minima of these projected tracks (i.e. the point in time when each leg is furthest forward or backward) and the tracks were averaged over this period to create a mean step cycle (Fig. 2a,b). Foot prints were obtained from the same sequences by averaging tracked leg positions over each period during which a given leg was touching the ground.

Speed calculation

Ten beetles of each of the two species were filmed at least five times as described above. To calculate walking speeds, the total distance traversed by the front of the head was divided by the time taken to cover this distance. For each beetle, we chose the two straightest runs, analysed a run of at least six full step cycles, and then averaged the speed measurements from both runs. To calculate the speed relative to size, body length was measured from the videos between the front of the head and the rear of the abdomen. Half the beetles were tested on sand paper and half on fabric; no speed difference was observed between these two substrates.

Statistics

All statistical tests were performed in Matlab (version 2013b). All speed distributions were tested for normality (Anderson-Darling test) and for equal variance (two-sample F test) before t-tests were

performed, and no significant deviations from normality or equal variance were found. Neither the experimenter nor the analyser were blinded to experimental group allocation (since the different gaits were immediately obvious from observations and videos).

Supplemental References

- S1. Smolka, J., Baird, E., Byrne, M. J., el Jundi, B., Warrant, E. J., and Dacke, M. (2012). Dung beetles use their dung ball as a mobile thermal refuge. *Curr. Biol.* 22, R863–4.