Caterpillar kinematics

The design of a caterpillar's body forces it to walk slowly — but even though it cannot run away from danger, it can roll up quickly into a protective coil. Here, I show that the mother-of-pearl moth, *Pleurotya ruralis*, uses this reflex coiling as the basis for a method of high-speed escape. By anchoring the end of its body to the ground and recoiling against it, the larva converts itself into a backwardly rolling wheel. In doing this, it shows that the limitations of a soft, segmented body can be overcome, using the basic assemblage of segmental muscles, by temporarily sacrificing the need for stability.

During forwards locomotion a wave of contraction followed by relaxation runs along the body from tail to head, producing the characteristic travelling 'hump'[1–3] on a caterpillar's back. As the wave passes, each segment is raised from the ground, is telescoped forwards into its neighbour in front, then is lowered back to the ground (Fig. 1a). The legs attached to terminal segment 13 (claspers) and segments 6–9 are retracted, borne forwards with their segment, then put down again one 'step' ahead. Hence for the whole body to progress forwards one step, each segment needs to take its own step forwards. Each foot is airborne for only 35% of the cycle: although this maximizes stability it prevents the body from building up significant momentum. Caterpillar crawling is thus slow and uneconomical compared with terrestrial locomotion in animals with muscles harnessed to a rigid skeleton. Caterpillars walk at only 10% of the maximum speeds seen in adult running insects of the same weight[4–7].

Like other moth larvae that seek protection inside rolled-up nettle leaves, the larva of *Pleurotya ruralis* lacks most of the normal caterpillar defences against birds and ichneumon wasps, such as cryptic coloration, irritant hairs or unpalatability[8]. But if an individual is isolated on a flat surface and provoked by mechanical shock, it displays a range of withdrawal responses of increasing speed and intensity, all based on locomotion in reverse.

Mild shock to the head or thorax elicits backwards walking, the exact kinematic inverse of walking forwards in that the peristaltic wave now begins at the head and moves tailwards. Stronger stimulation provokes a much faster wave, which arches up the whole body, wrenching all the legs free of the ground except the terminal claspers (Fig. 1b). The latter now serve as an anchor to which the body can be jerked during its 'airborne' phase, until the intervention of the relaxation phase of the wave lowers the legs to the ground. As the relaxation wave reaches the claspers they detach, then reattach further back, thereby completing the step. Technically, this fast running retreat can be considered a 'reverse gallop' because the entire body (except the claspers) is airborne for a significant part of the locomotory cycle.

The third and most dramatic escape response begins like a reverse gallop but this time the relaxation wave fails to appear. The body continues to move under its own momentum, coils up into a wheel, and begins to roll backwards releasing the claspers as it goes (Figs 1c and 2). Depending on initial conditions, such as the flatness and texture of the surface, and any slight imbalances in the body during arch formation, the momentum is sufficient to produce up to five complete revolutions, and a withdrawal speed of 39±3.6 cm s^{-1} (n= 31), nearly 40 times normal walking speed.

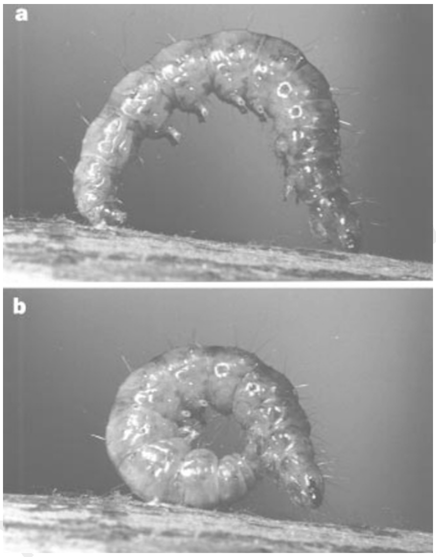

Figure 2 Still photographs of two stages in the recoil-and-roll manoeuvre of *Pleurotya* caterpillar. **a**, Recoil; **b**, beginning of roll, with claspers detached from ground. Flash exposures at 1/8000 s.

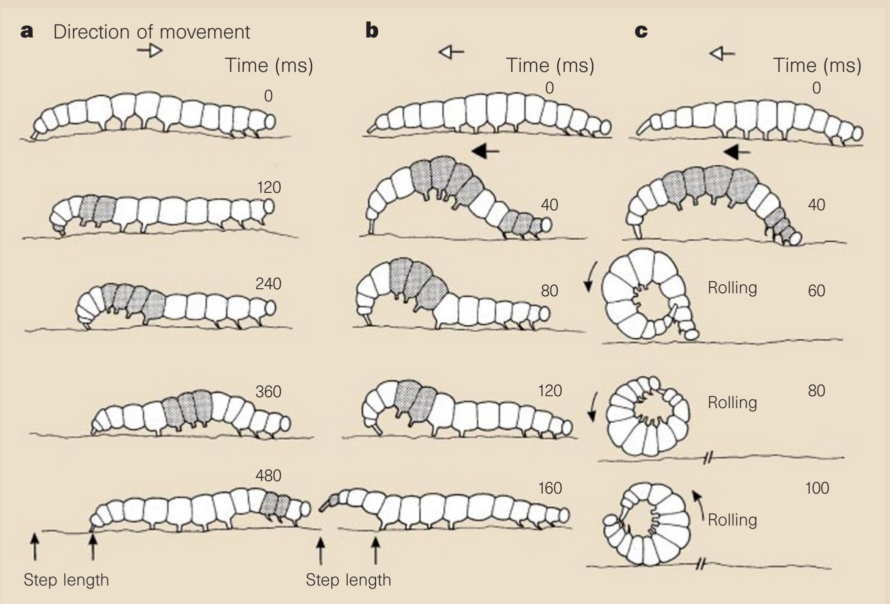

Figure 1 Main locomotory gaits in *Pleurotya* caterpillar. In **a** the insect is walking from left to right; in **b** and **c** it is retreating from right to left. Stippling indicates when leg-bearing segments (6–9, 13) are off the ground. The black arrow in **b** and **c** signifies the rapid recoil stage of locomotion. Speed, stride frequency and stride length during normal forward walking were 1.0±0.2 cm s^{-1}, 1.7±0.2 Hz and 0.6 cm, respectively. Measurements were made from video images (Panasonic, 50 frames per second, shutter speed 0.001 s, and NAC200, 200 frames per second with strobe synchronization).

Recoil-and-roll uses the same set of segmental muscles as ordinary locomotion, but more quickly, dispensing with the need for serial contraction. The manoeuvre is derived from the basic coiling response of caterpillars under attack from their natural enemies. By harnessing the output of the flexural muscles involved in spiralling to a fixed point provided by the claspers, the caterpillar converts the coil into a rolling wheel. I have found no evidence for the involvement of an elastic spring in this mechanism, such as the pre-tensioning of the skin that allows maggots to leap up to 8 cm into the air[9]; on the contrary, recoil-and-roll makes maximum use of the power available from real-time muscle contraction.

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