Spiders wheel to escape

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Spiders wheel to escape

Use of the wheel by animals has not been reported in scientific literature.[1] Beating cilia of Rotifera only appear to be wheels, and stories of looping snakes, rolling pangolins and cartwheeling baboons remain unconfirmed. Dune spiders, *Carparachne aureoflava* (Heteropodidae), however, commonly transform themselves into wheels and roll down smooth sand dunes at speeds of 0.5–1.5 m s^{-1} and rotation rates of 10–44 s^{-1}. Wheeling blurs spiders' outlines, enabling them to escape predatory wasps. These spiders are endemic to the central Namib Desert dunes, and common on upper plinths, slipfaces and crests of ridges (448 ± s.d. 562 ha^{-1} range: 11–1776 ha^{-1}; n=9). Nesting behaviour and habitat selection tend to minimize predation: long trapdoor burrows in steeply sloping (>15°), unvegetated, smooth unconsolidated sand decrease the wasp's ability to excavate spiders, and increase a spider's ability to flee when excavated.

To determine spider posture in the wheel, I observed and photographed them during wheeling or when toppled after wheeling. A spider initiated wheeling after a short run, flipping its body sideways and rotating. The legs curled into semicircles with only the tibio-metatarsal joints touching the ground (Fig.1).

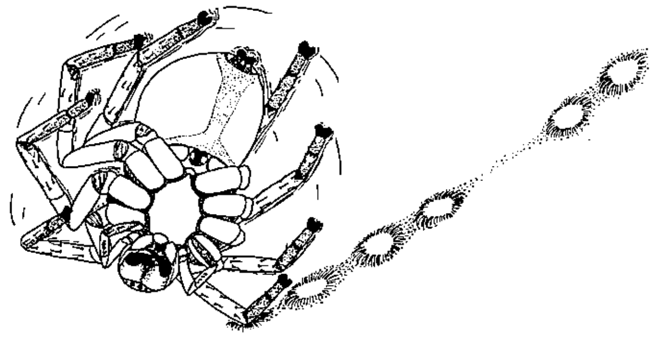

Fig. 1. Ventral view of the posture of *Carparachne aureoflava* wheeling downhill from right to left. The tibia-metatarsus leg joints contact the ground, leaving impact marks on the sand.

Wheeling occurred only downhill on slopes >15°. I estimated rotational speed from slow-motion film and from ground speed divided by wheel circumference, measured from tracks left by wheeling spiders. Average speed was 1.0 ± s.d. 0.3 m s^{-1} (n=54) and rotation rate 20.6 ± s.d. 8.4 s^{-1} (n=54). Speed of the wheel varied with surface slope and spider size (Table 1). Maximum speed increased with surface slope, whereas maximum rotation rate decreased with larger size. Wheeling ceased after 1–100 m, either by toppling when the slope became <15°, or by the spider straightening its legs. Potential energy that is lost by wheeling downhill is recovered by ascending slopes minutes to days later.

Spiders wheeled when predators or I excavated them from their burrows or disturbed them on the surface. This suggests that wheeling is used for flight. Their most important predators are 60-mg female pompilid wasps (n=6), specialist spider hunters that feed their progeny on immobilized spiders.[2] Less important predators are spiders *Palpimanus stridulator*, which capture *C. aureoflava* inside their burrows (n=3).

Table 1. Relationship of rotation rate (RR; r s^{-1}) and ground speed (GS; m s^{-1}) to spider body length (BL; 7–17 mm) and sand surface slope (SS; 15–33°)·(n=54)

	RR = 31.58 – 2.14 × BL + 0.51 × SS (r^2=0.61)
Maximum	RR = 72.74 – 3.66 × BL
Maximum	GS = –0.36 + 0.07 × SS

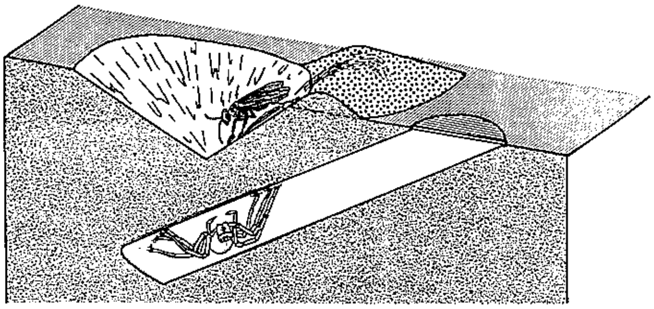

Fig. 2. Schematic representation of a pompilid wasp digging a *Carparachne aureoflava* from its burrow. Excavating spiders is more difficult in steeply sloping loose sand (°) because depth (cm) of a hole of given volume (l) decreases as follows:

$$\text{Depth} = \left(\frac{\text{Volume} \times \sin(33 - \text{Slope})^2 \times 6000}{\pi \times [1 + \cos\{2 \times (33 - \text{Slope})\}]}\right)^{1/3}.$$

Pompilid wasps were common on the surface by day (18 ± s.d. 14 ha^{-1}; n=8). Female pompilids spent 75% of their active time (21 h focal observations of 18 individuals over 10 days) searching for *C. aureoflava* burrows by walking over bare dune plinths, stopping frequently to test the substratum or to dig. Such searching for spiders was distinct from foraging for the nectar, honeydew or sap of plants on dune bases.

Upon encountering spider burrows, wasps explored the surroundings and sometimes entered the burrows. Spiders physically evicted intruders by striking with their legs or collapsing the burrows. To reach spiders, wasps excavated up to 300 times their own mass, digging 5–10-litre holes to depths of 8–15 cm in 1–2 h on slopes <15°, to intercept the spiders' burrows from above (Fig.2).

Spider burrows were usually long (47.8 ± s.d. 22.2 cm; range 7–125 cm; n=114), extending at shallow angles (–18.9 ± s.d. 4.8°) into loose sand of steep surface slopes (24.6 ± s.d. 11.0°). These conditions made most spiders difficult to excavate (Fig.2). Instability of sand, however, caused some burrows to collapse, necessitating construction of short new burrows. Thus, at any time, 5% of the spiders (n=114) were vulnerable to wasp predation because they could be captured by the latter excavating less than 10 litres of sand.

When I extracted *C. aureoflava* from their burrows (n>200), they showed several responses. Wheeling, including an initial run, was usually performed first, followed by running, temporary burial, or threat displays. Concealment on bare sand was only possible in windy conditions when spiders scraped and entered ditches, allowing themselves to be covered by drifting sand. When evasion was impossible, spiders adopted threatening postures by raising body and legs and opening fangs, or attacked by embracing and biting.

Wheeling was faster than running and probably required less energy. Although spiders could run at speeds of 0.9 to 1.4 m s^{-1}, progress was slow because they rested for more than 10 s after running less than 2 m. Rapid energy depletion during vigorous exercise in spiders apparently necessitates recovery.[3] *C. aureoflava* covered 10 m in more than 60 s when running compared to about 10 s when wheeling. Furthermore, wasps could follow running spider trails. Other advantages of wheeling were: blurring of the spider's outline, and the leaving of only a faint trail. These characteristics appeared to disrupt the wasp's search image. A limitation of wheeling was that direction and flight distance depended on topography.

Wheeling was evidently effective for flight. In three natural confrontations, spiders escaped from wasps by wheeling, but were captured in three further incidents when they failed to wheel ($\chi^2=6.0$; d.f.$=1$; $P<0.05$).

Wheeling behaviour is not unique to *C. aureoflava*. The congener *Carparachne alba* wheels under similar conditions ($n=15$). Other endemic heteropodids (*Leucorchestris* and *Orchestrella*) seldom lived on steep slopes[4] and could not be induced to wheel ($n=30$). Another dune spider that is capable of wheeling ($n=8$) is an unidentified salticid. When disturbed during winds greater than 5 m s^{-1}, this spider raised itself vertically to wheel, propelled by wind over level sand.

Use of the wheel by animals living in habitats with obstacle-deficient surfaces, such as Namib dunes, may be more common than is currently appreciated.

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Detection of prostaglandin $F_{2\alpha}$ by radio-immunoassay in three South African bryophytes and its relation to the occurrence of polyunsaturated fatty acids

We have demonstrated the presence of prostaglandin $F_{2\alpha}$, and some of its fatty acid precursors, in two mosses and a liverwort. This evidence points further to the possibility that prostaglandins are common to all living organisms.

It is well known that prostaglandins (PGs) are formed in mammals and that they occur widely in the rest of the animal kingdom. Prostaglandins were discovered in plants in 1973,[1] and their presence subsequently confirmed by more exact tests.[2] Since then, these compounds have been found in other plants.[4–8] Furthermore, PGE_2 and $PGF_{2\alpha}$ were detected in the red alga, *Gracilaria lichenoides*.[3] Prostaglandin-like compounds also occur in a number of different plants.[9–13] An enzyme (lipoxygenase-2) was extracted from soybeans, which catalysed the oxygenation of arachidonic acid to form $PGF_{2\alpha}$.[14]

The occurrence of fatty acid precursors (bishomo-γ-linolenic acid, arachidonic acid and eicosapentaenoic acid) of prostaglandins has been reported in certain algae and mosses.[15] The lipid classes from four species of mosses, namely *Mnium cuspidatum* and *Mnium medium* from Minnesota and *Hylocomium splendens* and *Pleurozium schreberi* from Alaska, have been analysed.[16] The total lipids of all species contained 30 – 40% arachidonic and eicosapentaenoic acids. The high content of arachidonic acid, which was also pointed out by Huneck,[17] is noteworthy. In their expectation of finding new physiologically active compounds in mosses, Ichikawa *et al.*[18] isolated from Japanese mosses novel fatty acids having a cyclopentenone ring similar to prostanoids and jasmonoids. A prostaglandin-like fatty acid was isolated from the freshwater sedge, *Eleocharis microcarpa*.[11] This compound appeared to act as an allelopathogen.

Moreover, PGs are known to be physiologically active in plants. For instance, Freimanis (personal communication, 1985) found with *Nitella flexilis* that prostaglandin increased membrane permeability to potassium ions. The effect was observed only in the presence of calcium ions. Prostaglandins may also play a role in the flowering of *Pharbitis nil*.[19,20,8] It was found[21] with *Cassia fasciculata* that certain PGs speeded up the dark-induced (scotonastic) and light-induced (photonastic) leaflet movements of the plant. In this case the PGs affected the permeability of membranes. Furthermore, it has been reported that the application of prostaglandins induced enzyme (acid phosphatase) activity in embryoless barley half seeds.[22]

The relatively large amounts of arachidonic acid found in certain mosses[15,16] encouraged us to investigate the possibility of the occurrence of $PGF_{2\alpha}$ in two South African mosses and a liverwort. $PGF_{2\alpha}$ appears also to be the most abundant PG found thus far in other plants.[3,7,8,11] In addition, the presence of certain polyunsaturated indirect and direct precursors of PG was investigated.

The liverwort *Marchantia parviloba* Steph. and the mosses *Brachythecium implicatum* (Hornsch.) Jaeg. and *Amblystechium serpens* (Hedw.) B.S.G. were collected in the Ladybrand district of the Orange Free State. The plant material was washed with distilled water and freeze-dried.

The extraction and preparation of the fatty acid methyl esters were carried out according to Gunasekaran and Hughes.[23] The methyl esters (in *n*-hexane) were analysed on a Hewlett-Packard Model 5830A gas chromatograph with a glass column (2.5 mm i.d. × 1.5 m) filled with 3% SP2310/2% SP 2300 adsorbed on chromosorb W (80 – 100 mesh) as stationary phase. The nitrogen flow rate was 40 ml min^{-1} and the column temperature programmed to increase linearly from 160°C to 230°C at 30°C min^{-1}. The esters were identified by comparison with authentic standards.

Prostaglandin was extracted from freeze-dried material (*M. parviloba* 140.7 g, *B. implicatum* 114.9 g and *A. serpens* 192.6 g) and purified by the method of Lee *et al.*[24] $PGF_{2\alpha}$ was isolated from this extract by thin-layer chromatography (silica gel) using authentic $PGF_{2\alpha}$ as standard and the organic phase of ethyl acetate:MeOH:H_2O (160:3:100 v/v) as solvent. The standard $PGF_{2\alpha}$ was revealed with the aid of iodine vapour, after which the corresponding layer of silica gel of the test sample was removed and extracted with methanol. After evaporating the methanol, the residue was radio-immunoassayed for prostaglandin $F_{2\alpha}$ using the kit, and according to instructions, provided by Clinical Assays specifically for $PGF_{2\alpha}$. The assay procedure includes the preparation of a standard curve in which known amounts of PG (radioactive and non-radioactive) are used to compete for a fixed amount of prostaglandin antibody. This standard curve is then used to determine the prostaglandin content