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Arachnid aloft: directed aerial descent in neotropical canopy spiders

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The behaviour of directed aerial descent has been described for numerous taxa of wingless hexapods as they fall from the tropical rainforest canopy, but is not known in other terrestrial arthropods. Here, we describe similar controlled aerial behaviours for large arboreal spiders in the genus *Selenops* (Selenopidae). We dropped 59 such spiders from either canopy platforms or tree crowns in Panama and Peru; the majority (93%) directed their aerial trajectories towards and then landed upon nearby tree trunks. Following initial dorsoventral righting when necessary, falling spiders oriented themselves and then translated head-first towards targets; directional changes were correlated with bilaterally asymmetric motions of the anterolaterally extended forelegs. Aerial performance (i.e. the glide index) decreased with increasing body mass and wing loading, but not with projected surface area of the spider. Along with the occurrence of directed aerial descent in ants, jumping bristletails, and other wingless hexapods, this discovery of targeted gliding in selenopid spiders further indicates strong selective pressures against uncontrolled falls into the understory for arboreal taxa.

1. Introduction

The tropical rainforest canopy supports tremendous macroarthropod abundance and diversity [1]. Volant inhabitants of the canopy can readily fly to escape predators or to pursue dispersed resources despite living 30 m or more above the ground. By contrast, wingless arthropods dwelling within tree crowns face significant hazards if they fall to the forest floor. Landing within the understory presents both unfamiliar terrain and a suite of ground-dwelling predators which, in some cases, may rapidly and lethally attack such intruders from the canopy [2,3]. To avoid these problems, workers of many ant species, and many other wingless hexapods, orient their falls towards tree trunks upon which they land [4–6]. Using visual cues [7] and either appendages or axial structures to manoeuvre [5,8], these taxa generate both lift and drag on the body to glide at steep angles in the behaviour we have termed directed aerial descent [4]. The capacity of wingless species or morphs to control their glide trajectory, along with an initial aerial righting reflex, have important implications for our understanding of the origins of animal flight [9].

Here, we provide the first description of similar locomotor behaviour in arachnids, and specifically for neotropical arboreal spiders in the genus *Selenops* (Araneae: Selenopidae). Arachnids opportunistically tested in prior studies [4,5] included opilionids, pseudo scorpions, scorpions, amblypygids and various spider taxa, of which only *Selenops* spp. exhibited directed aerial descent. These are relatively large and common spiders that are found in lowland rain forests and that are nocturnal hunters, often hiding in crevices or under bark during the day [10]. Some arboreal species are well camouflaged, with coloration and patterning closely resembling the lichen-covered tree trunks upon which they remain motionless and exposed during daylight hours (figure 1). *Selenops* spp. are characterized by strong dorsoventral flattening, earning them the common name of 'flatties' [10,11] (figure 2). The principal goal of this study was to document the occurrence of directed aerial descent in tropical *Selenops* species. As with gliding ants [4], we hypothesized that glide performance would decline

Figure 1. *Selenops banksi* on Barro Colorado Island, Republic of Panama, as typically encountered on a tree trunk during daylight hours. Scale bar equals 1 cm. (Online version in colour.)

with increased body size. Specifically, we tested whether the glide index (i.e. the ratio of horizontal to vertical displacement in a successful glide) declined with increasing body mass, and with the ratio of body weight to their effective aerodynamic surface area. We also compare glide performance of these spiders with that of other arthropod taxa known to engage in directed aerial descent.

2. Material and methods

Fieldwork was conducted on Barro Colorado Island, Panama (BCI; 9.16° N, 79.85° W), and at the Amazon Conservatory for Tropical Studies field station located 67 km northeast of Iquitos, Peru (ACTS; 3.25° S, 72.90° W) on various dates between March 2006 and December 2012 (see [12–14] for additional site information). We collected *Selenops* spp. spiders by hand from tree trunks during the day on BCI ($n = 12$), and at night from the ACTS canopy walkway ($n = 51$), and transported them to the laboratory in plastic containers. The following day, each spider was weighed to the nearest 1 mg on a portable electronic balance. Digital photographs of a haphazardly chosen subset of experimental subjects resting on a horizontal substrate ($n = 25$) were taken from a vertical perspective, and were then analysed (using NIH's IMAGEJ, v. 1.46r) to estimate the horizontally projected areas of different segments and appendages, including contributions from each leg, the pedipalps, the cephalothorax (including the chelicerae) and the abdomen. An effective wing loading was calculated as the ratio of the body weight to the sum of these individual component areas. Most study individuals were either juveniles or subadults and could not be identified below the genus level given available keys [11,15,16]. However, *S. banksi* was the most common species found in the forest canopy on BCI. Vouchers were deposited at the Fairchild Museum (University of Panama) and at the United States National Museum of Natural History in Washington, DC.

Aerial behaviour was quantified via drop tests conducted during the day (generally between 09.00 and 15.00 in fair weather) either from within tree crowns on BCI, or from a platform on the ACTS canopy walkway. Drop tests were similar to those used in other studies of gliding arthropods [2,4,5]. Each spider was released from a plastic container held a known

distance (average: 1.67 m; range: 0.5–4.6 m) from the surface of a nominally vertical tree trunk. A small amount of fluorescent orange fingerprint powder was added to the container to prevent the spider from clinging to the walls, and to make its legs and body more visually apparent during descent. The spider was released by inverting and then tapping the container, upon which the spider fell at an initially arbitrary body orientation. Drops were filmed at 60 frames s^{-1} using a vertically mounted video camera (Flip MinoHD). Descents were tracked visually and, for successful glides to a tree trunk, the distance from the point of release to the point of first contact was measured immediately upon impact using a laser distance meter (Leica Disto D5). Aerial performance of such glides was quantified using the glide index (i.e. the ratio of initial horizontal distance from the trunk to total vertical distance travelled). Glide performance was also qualitatively characterized as either direct (following a visually rectilinear glide to a tree trunk), indirect (following an apparently helical or otherwise irregular trajectory towards a tree trunk), or as failed (i.e. landing on the ground or otherwise missing a tree trunk). All glide tests were conducted under windless conditions, as indicated by an apparent lack of leaf motion in the surrounding vegetation. Each spider was tested only once, as it was not possible to recover individuals post-descent.

Initial inspection of drop videos suggested that the spiders were using bilaterally asymmetric motions of the forelegs to manoeuvre. For three videos of dropped spiders, we accordingly digitized body heading angles and the right and left foreleg angles relative to the body heading through time for turns in yaw (using the connected segments of the tarsus and tibia to indicate foreleg orientation). The rate of change in body heading angle was calculated as the derivative of the angular data through time (using the numerical gradient function from NumPy), and was then smoothed using a fourth-order Butterworth filter with a cut-off frequency of 15 Hz. Data for the simultaneous difference between the left and right leg angles over the same time interval were similarly smoothed. The same analysis was also applied to an additional four video sequences obtained for spiders turning within the jet of a custom-built vertical wind tunnel operated at a wind speed of 3 m s^{-1}. Three orthogonal and synchronized video sequences were taken at 60 frames s^{-1} for these spiders, but only the camera view from above was analysed so as to permit comparison with films taken of drops from the canopy walkway. The rates of change in body heading were then correlated with values for the simultaneous left/right differences in foreleg angle for each individual sequence, and then for all pooled data. Although these estimates only represent projected body and appendage angles within the horizontal plane, and do not necessarily correspond to similar dynamic states among individual spiders, they can nonetheless identify, in part, those control mechanisms underlying changes in body orientation [8].

We used principal component analysis (PCA) to evaluate morphometric differences among individuals based on 16 variables: the areas of 12 different body regions, their total summed area, the two axial dimensions of the cephalothorax and the area of an ellipse delimited by the leg apices. We used linear regression to determine how the glide index varied with body mass, the best representative measure of area as indicated by the PCA, and a measure of wing loading (see below). Sample sizes differed among analyses because some individuals for which morphometric data were obtained subsequently escaped during attempted experimental trials. All data were tested for normality and were transformed as necessary to meet statistical assumptions.

3. Results

Fifty-nine individual spiders were successfully drop-tested, and most of these (55, or 93%) exhibited directed aerial descent
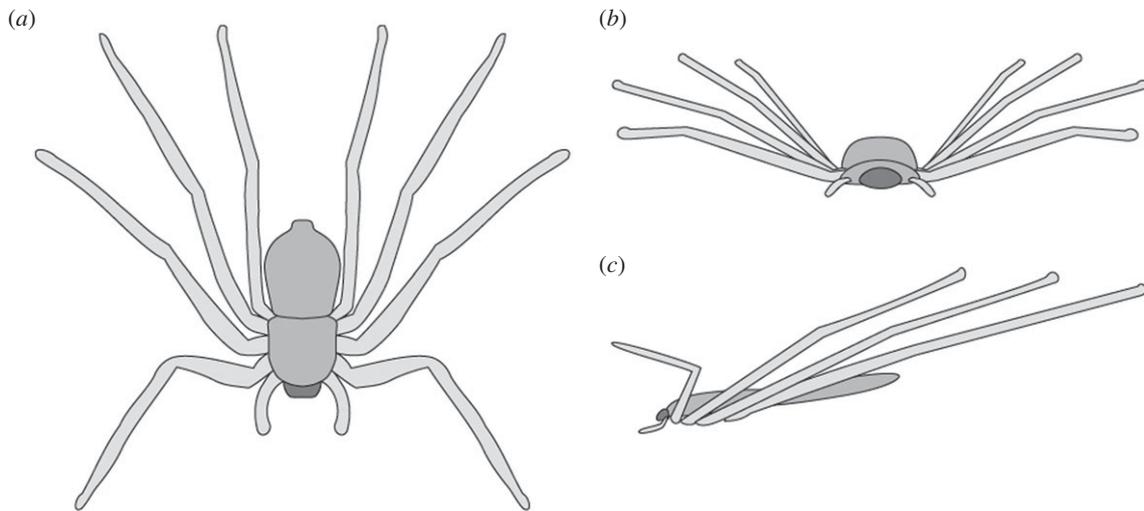
Figure 2. Representative gliding posture for *Selenops* spp. spiders in dorsal (*a*), frontal (*b*) and lateral (*c*) perspectives, as determined from glides in the jet of a vertical wind tunnel (see electronic supplementary material, video S4).

towards a tree trunk, followed by a successful landing (electronic supplementary material, videos S1–S3). The remaining 7% of study spiders either landed on the ground or on understory vegetation following apparently undirected parachuting. By contrast, opportunistically tested representatives of other common arboreal and ground-dwelling spiders (e.g. hersiliids, ctenids, mygalomorphs, lycosids) fell with legs extended and exhibited dorsoventral righting, but showed no obvious directional control when dropped. *Selenops* spp. adopted stereotypical body postures when dropped and during subsequent gliding. Shortly after initiation of a fall, spiders oriented their bodies dorsoventrally (via an aerial righting reflex, when necessary), and then descended head first. The forelegs generally were held laterally and slightly anteriorly, whereas other leg pairs tended to splay posterolaterally (figure 2). Spiders never attached draglines to the specimen vial during the initial drop, nor was silk ever seen during descent. Repeated twitching of the legs while airborne was sometimes evident, especially during protracted falls.

Most (86%) gliding *Selenops* spp. that successfully landed also exhibited trajectories qualitatively classified as direct (e.g. electronic supplementary material, video S2), and about half of these (51%) were characterized by glide indices of 0.30 or higher. Average (± 1 s.e.m.) glide indices were marginally higher for direct gliders (0.32 ± 0.019) than for indirect gliders (0.20 ± 0.050; Welch's test, $p = 0.047$), although there was no difference in body mass between the two groups (Welch's test, $p = 0.46$). The average body mass of tested spiders was 95 mg (range: 2–556 mg). Glide indices for direct trajectories to tree trunks decreased with increasing mass ($F_{1,44} = 20.8$, $p < 0.0001$, $R^2 = 0.32$; figure 3). All 16 morphometric variables were highly correlated with each other ($r > 0.90$) and had similar loadings on the first principal component (i.e. all eigenvectors ≈ 0.25), which accounted for 95.2% of the total variance. The second principal component accounted for only 1.4% of the variance and mainly reflected variation in abdominal area. We accordingly used the horizontally projected area as the best proxy of total area; this parameter increased with increasing mass ($F_{1,22} = 402.6$, $p < 0.0001$, $R^2 = 0.95$), but showed no relationship with glide index ($F_{1,17} = 1.19$, $p = 0.29$). However, glide index and wing loading were inversely correlated ($F_{1,12} = 6.0$, $p < 0.03$,
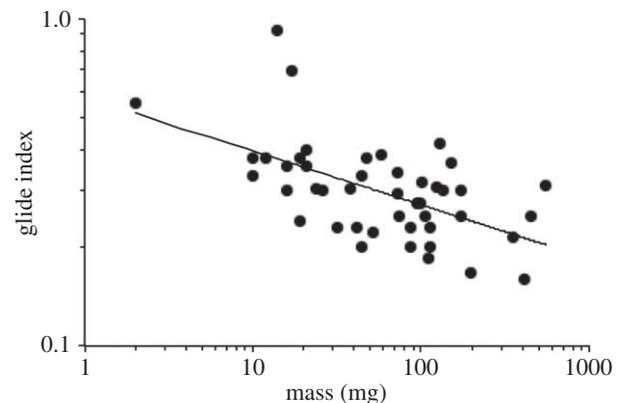

Figure 3. Glide index versus body mass for *Selenops* spp. spiders ($n = 46$) exhibiting direct and successful glides to tree trunks. The corresponding power function is given by: glide index $= 0.58(\text{mass})^{-0.164}$; see text for statistical results.

$R^2 = 0.33$); values of wing loading for this sample of individuals averaged 7.44 N m^{-2} (range: 3.8–15.1 N m^{-2}).

Close-up views of spiders gliding within the jet of a vertical wind tunnel revealed rapid changes in leg orientation and considerable variation in body pitch and yaw (electronic supplementary material, video S4). Of seven analysed turning sequences (with a mean turn duration of 410 ms), four yielded significant regressions between the rate of change in body heading in the horizontal plane and the asymmetry in foreleg position, such that posterior flexion of either foreleg resulted in ipsilateral rotation of the body. For the seven aforementioned sequences, we combined their individual regression probabilities using Fisher's combination of significance test (assuming each individual spider to represent an independent test of this correlational hypothesis), and obtained an overall significant result ($\chi^2 = 47.9$, d.f. $= 14$, $p < 0.0001$). Pooling data points from all sequences, rate of change in body heading was also significantly correlated with foreleg asymmetry ($F_{1,172} = 47.6$, $p < 0.0001$, $R^2 = 0.22$; figure 4). Qualitatively, body steering initiated by leg motions also typically seemed to overshoot any desired orientation, and then to require further corrections in yaw
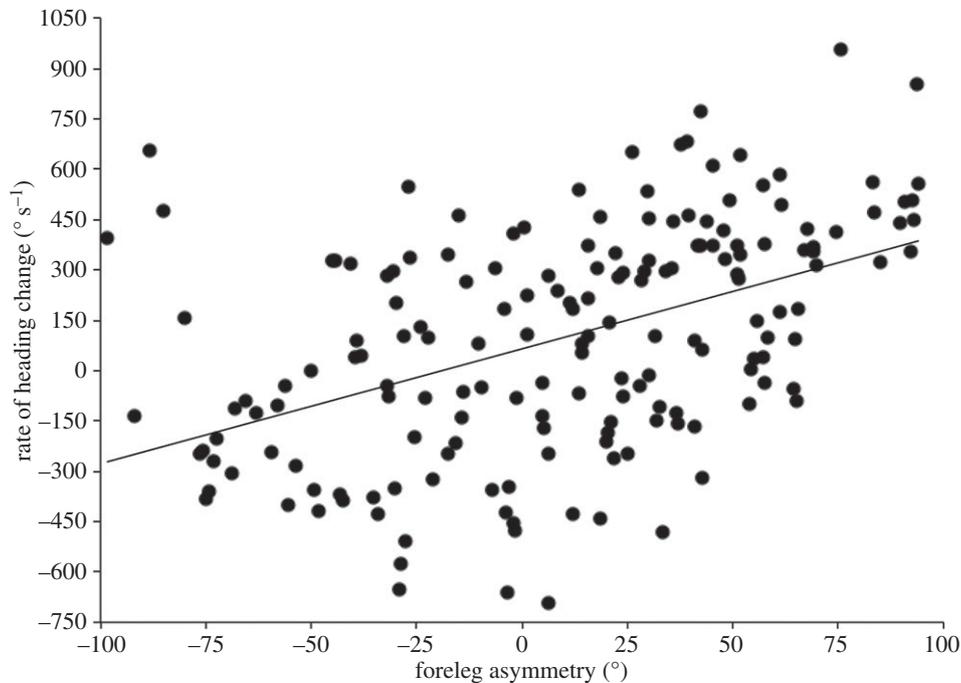
Figure 4. Rate of change in body heading versus the simultaneous difference in left and right foreleg angular orientation relative to the longitudinal body axis. Data points are pooled for seven separate yaw turns from different spiders (see text). The regression line is given by: rate of heading change = 3.4 (foreleg asymmetry) + 64.9; see text for statistical results.

to target the tree trunk (e.g. electronic supplementary material, S3).

4. Discussion

Here, we provide the first documentation of directed aerial descent in arboreal spiders. The existence of such behaviour in any spider taxon is unexpected, in part, given our negative results for similar drop tests with representatives of other arachnid lineages (e.g. scorpions, amblypygids, and opilionids). Also, the use of draglines during jumping or in volitional drops is widespread among spiders [17–19], and free falls over distances of metres may simply not be characteristic of most spider taxa. Upwards ballooning on silk threads is well documented in spiders and some other arthropods, but does not involve directional control. However, arboreal arthropods more generally may be confronted with a diversity of behavioural challenges (e.g. predatory attack, high winds) that elicit falls or intentional jumps at initially arbitrary body orientations [6,9]. Under most circumstances, selenopid spiders avoid an approaching disturbance by moving rapidly to the other side of the tree trunk or branch. However, we observed that *Selenops* spp. will jump from tree surfaces to escape attacking ants (e.g. *Azteca* spp.). In all such cases, the spiders fell several metres and then successfully glided back to the trunk. Given the utility of this behaviour, we accordingly might expect to observe directed aerial descent in additional taxa of arboreal spiders.

For gliding ants, detailed three-dimensional trajectory reconstructions indicate an initial fall and capture of a dorsoventral posture, followed by increasing lift production and a reduction in trajectory incline coupled with active steering towards a target [20]. In aggregate, these behaviours yield a strong inverse dependence of the glide index upon body mass, both within and among species of ants [4]. The

relationships here between glide index and spider mass (figure 3), and between glide index and wing loading, are similarly negative. These results presumably reflect, in part, the absolute time required for larger animals to accelerate under gravity to airspeeds at which aerodynamic lift becomes significant relative to body weight. Additional size-dependent effects may, however, characterize the aerial righting reflex and the ability to change body heading. Because it is not possible using available two-dimensional video data for gliding spiders to quantify the temporal contributions of these different behaviours, we cannot at this stage characterize their relative duration or aerodynamic contributions. Nonetheless, the overall glide index identified here for spiders (typically 0.2–0.6; figure 3) is broadly comparable to those found in both gliding ants (0.2–0.5, with an interspecific mass range of 0.5–30 mg; [4]) and in archaeognathan bristletails (approx. 0.4, with an interspecific mass range of 2–30 mg; [5]). Given the morphological differences and presumably variable aerial capacities among these three groups of gliding arthropods, the overall similarity of their glide indices is striking. The spiders studied here, however, did qualitatively seem to reach equilibrium glide velocities more quickly than the other taxa, perhaps as a consequence of their flattened bodies and relatively low wing loadings.

Because these spiders glide headfirst and appear to steer with the forelegs, their associated control mechanisms must differ substantially from those identified in ants and bristletails. Most gliding ants studied to date typically glide backwards and steer with the leading hind legs [8], whereas bristletails use head-first gliding and have been inferred to use lateral and dorsoventral flexion of the abdomen to effect steering [5]. Success rates for glides among the three arthropod groups are however comparably high under similar experimental protocols (85–90%), suggesting different functional solutions to a common behavioural problem. *Selenops* spp. have moderately large, anteriorly directed posterior median

eyes [15], and appear to use visual cues to locate tree trunks during a fall, as do gliding ants [4]. For gliding ants, experimental placement in either the understory or in local waters substantially increases mortality at the figurative hands of either arthropod predators or fish, respectively [2,3]. The behavioural consistency of directed aerial descent, both within and among those arthropod lineages studied to date, suggests substantial advantages to remaining within the canopy once airborne.

Gliding spiders represent an unlikely if not truly ungainly aerodynamic platform. Nonetheless, the rapidity with which *Selenops* spp. achieve an aerially effective posture when falling (e.g. the aerial righting evident at the start of electronic supplementary material, video S3), and then subsequently control their glide trajectory, suggests novel mechanisms of body righting and manoeuvring, and may be relevant to robotic design. The initial aerial righting reflex is impressive, given the enhanced rotational moments of inertia that must ensue from such a flattened body design (figures 1–2). Inferred control motions of the forelegs in gliding would benefit from detailed kinematic studies of leg and body orientations during manoeuvres. Similarly, three-dimensional trajectory reconstruction under field conditions would enable descent velocities and manoeuvres to be quantified for comparison with existing data on gliding ants [20]. The relatively high body moment of inertia for these spiders in yaw, and relatively small forces associated with their small legs, may yield somewhat imprecise control. Landing manoeuvres are similarly unknown; the majority of spiders successfully landed on the first try, but we observed several instances (as with gliding ants) of a failed first attempt at landing, followed by further gliding and a successful second attempt (see electronic supplementary material, video S3).

Overall, these spiders represent a remarkable evolutionary adventure in the animal conquest of the air. The discovery of gliding behaviour in *Selenops* spp. raises multiple avenues for further investigation that were beyond the scope of this study. For example, the variety of habitat associations within *Selenops*, the influence of a laterigrade locomotor style, and taxonomic diversity in Selenopidae more generally [11], provide opportunities to explore variation in this behaviour in both functional and phylogenetic contexts. Additional experiments are also needed to determine the importance of visual cues, leg positioning and spines and setae to aerodynamic performance. As with gliding arthropods generally, we suggest that there are many other as yet undescribed examples of controlled aerial behaviour in non-winged taxa.

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