Current Biology

Dispatches

Orb weavers: Patterns in the movement sequences of spider web construction

Julie H. Simpson[1] **and Benjamin L. de Bivort**[2]
[1]Department of Molecular, Cellular, and Developmental Biology and Neuroscience Research Institute, University of California, Santa Barbara, Santa Barbara, CA 93106, USA
[2]Department of Organismic and Evolutionary Biology and Center for Brain Science, Harvard University, Cambridge, MA 02138, USA
Correspondence: jhsimpson@ucsb.edu (J.H.S.), debivort@oeb.harvard.edu (B.L.d.B.)

https://doi.org/10.1016/j.cub.2021.09.066

Quantitative behavior analyses of spider movements — large and small — reveal repeated action sequences that define stages of web building.

Anyone who has seen a web outlined in dew and sunlight has probably wondered “how did a spider build that?!” Web-construction is surely one of the most mysterious and appealing innate behaviors out there to capture the naturalist mind (Figure 1). Because different species have characteristic web shapes and young spiders make them without training, the capacity to build webs must be genetically encoded, hard-wired in their nervous systems. But the geometrically diverse substrates on which a spider can build its web — branches, blades of grass, stones — suggest impressive adaptive ability. How exactly do they assemble the finished product? Do they have a pattern in mind from the start or do they string strands in reflexive response to sensory cues?

As they report in this issue of *Current Biology*, using new experimental methods to film spiders spinning webs over many hours and automatically classify their motion sequence, Corver *et al.*[1] have discovered numerous connections between repeated patterns of leg and abdomen motion and web structure. Prior arachnological understanding divides web construction into five stages. First, an exploratory proto-web is assembled from straight but haphazard lines. Then, spoke-like radii connect the web center to its rim, to form a frame of skinny triangles. Next, an auxiliary spiral is built from the center outward, connecting the radii. This temporary scaffold is removed as the spider switches to a rim-to-center trajectory, embellishing the web with tight fringes and loops to produce the ominous space-filling capture spiral. And lastly, some spiders add a compact downy structure of variable morphology and enigmatic function at the center, called the stabilimentum. Corver *et al.*[1]’s computational approach recapitulates these classical divisions, discovers new subtleties, and relates these stages to detailed leg kinematics representing the atomic units of web-building behavior.

These stages describe the appearance of the web at different time-points, but they also reflect the movement of the spider as a whole. During construction of the radii, for example, the spider follows straight paths, but while assembling the spirals, she orbits around the web center. The connection between the spider’s overall trajectory and the physical shape of the web makes sense — the spider is literally leaving lines of silk behind as it moves, so the web is a direct record of her movements, subject to equilibrated tension in the silk strands.

These whole-body movements may be apparent to any human observer willing to stay up late — orb weavers build their webs in complete darkness — but the detailed movements of the spider’s eight dexterous legs and its abdominal bending only become apparent by combining the modern techniques of high resolution video, deep learning neural networks for image analysis[2,3], and multidimensional statistical classification. The computational ethology approach[4] of Corver *et al.*[1] reveals that spider web building can be decomposed into a finite list of stereotyped, brief action patterns (atomic elements or micro-behaviors) that are strung together in stage-specific sequences.

Spiders use distinct limb and body movements for tactile exploration of the web, walking on it, and pulling and attaching silk. These repeated movements were discovered using new, automated deep-learning body-part trackers (DeepLabCut[2] and LEAP[3]). These software systems allow visible features of organisms — such as leg joints — to be identified and followed over time through numerous video frames, to produce trajectories describing movements. Corver *et al.*[1] used statistical algorithms to cluster these trajectories, producing a catalog of repeated micro-behaviors. They discovered that while a few movements are specific to certain stages of construction, most stages contain the same repertoire of movements in different proportions. Just as you can use eggs, milk, and flour to make either cake or quiche, and the same 26 letters to compose Hamlet or the Gettysburg Address, spiders can make radii or spirals using common leg movements in different combinations.

Such statistical methods, called ‘unsupervised classification’, have the potential to produce detailed categorizations of behavior with little subjective investigator input. But are the categories biologically meaningful? Corver *et al.*[1] addressed this question by asking if the observed sequences of micro-behaviors could be used to predict the stage of web construction. Specifically, they used a Hierarchical Hidden Markov Model to identify stages of web construction using just the spiders’ detailed leg movements. The automatically inferred stages aligned closely to the classical web construction

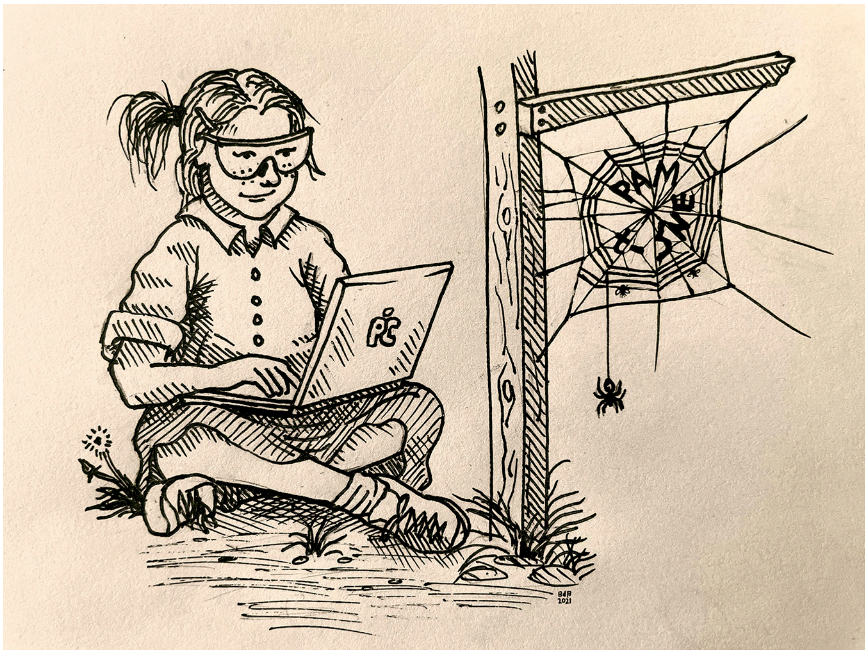

Figure 1. A modern-day biologist/computational neuroethologist admiring a spider's web, while the spider tells us how best to appreciate it.
Style and content homage to E.B. White's *Charlotte's Web* © 1952 as illustrated by Garth Williams. (Figure concept J.H.S. and B.L.d.B., illustration by B.L.d.B.)

stages. In other words, the abundance and sequence of leg movements alone are sufficient to reliably identify the stages of the web construction, even with no knowledge of where the spider is located or how the web looks.

While this automated approach largely reiterated the classical understanding, it also revealed high-level patterns that have evaded manual classification. Specifically, the proto-web and radii stages are hard to distinguish because the proto-web is actually being deconstructed while the radii are being constructed — the two stages overlap in time, with no hard boundary. Another discovery is that the path to a complete web does not always proceed deterministically from the first stage to the last. Spiders sometimes repeat stages, for example, going back to add radii after starting the spirals. Apparently do-overs are allowed. This finding suggests that the spiders have a plan, or internal model, for their web, which they can implement flexibly, perhaps in response to acute sensory feedback. One future direction could be to establish the nature of these sensory cues: perhaps spiders are measuring the distribution of tension across strands or the distance between them. If they can flexibly adjust strand placement to optimize the web's mechanical properties, it could indicate that they have evolved an internal model of web physics.

These results demonstrate the value of observation, by humans with the assistance of machines, to gain insights into the algorithms governing behavior. One product of such efforts is an 'ethome' — an exhaustive catalog of behaviors[5], in this case, those that compose web-building, at least in this laboratory context. This has parallels with other biological datasets that aim for completeness, such as nervous system connectomes and genomes, where a thorough description of the parts list provides a starting point for mechanistic, comparative, and evolutionary studies.

Ethology is replete with systems for the study of innate behavior, including courtship, aggression, grooming, song production, foraging, oviposition, etc. But fewer well-studied behaviors leave a physical artifact in the world, among them nest-building[6,7] and burrowing[8]. Corver *et al.*[1]'s experimental system is a welcome addition. Krogh's principle states that for any problem there is an ideal animal for its convenient study (for a recent perspective, see[9]). We believe spiders may be such a system for the study of behavioral algorithms underlying constructed environments.

Successful examples where experiments on non-traditional model systems uncover behavioral algorithms include elegant physical perturbations (stilts) and translocations (airlifts) to reveal the use of path integration in ants[10], or the analysis of near misses in dragon fly prey capture to demonstrate that they employ anticipatory interception strategies[11]. Corver *et al.*[1]'s characterization of spider web-building behavior establishes the opportunity to investigate what is going on in the spider's brain using controlled damage to the web or by moving spiders around on the web or even between webs. These perturbation experiments can probe specific hypotheses, such as whether spiders have a blueprint in mind or at least an internal model of web physics, or whether they respond reflexively and instinctively to specific sensory stimuli, like Braitenberg Vehicles[12], producing complex outcomes using simple rules. We expect the truth to be some interesting and surprising combination, because in biology, the answer is (almost) always both hypotheses.

The rigorous investigation of behavioral phenomena, applying good experimental design and modern tools thoughtfully, gets us closer to understanding the basic algorithms by which the brain coordinates behavior. Moreover, this paper reminds us why we got into biology — and maybe why you are reading this journal — because of some appealing natural mystery. This research may make you pause and marvel the next time you are caught by a spider's web.

REFERENCES

1. Corver, A., Wilkerson, N., Miller, J., and Gordus, A. (2021). Distinct movement patterns generate stages of spider web building. Curr. Biol. *31*, 4983–4997.
2. Mathis, A., Mamidanna, P., Cury, K.M., Abe, T., Murthy, V.N., Mathis, M.W., and Bethge, M. (2018). DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. Nat. Neurosci. *21*, 1281–1289.

3. Pereira, T.D., Aldarondo, D.E., Willmore, L., Kislin, M., Wang, S.S., Murthy, M., and Shaevitz, J.W. (2019). Fast animal pose estimation using deep neural networks. Nat. Meth. *16*, 117–125.
4. Anderson, D.J., and Perona, P. (2014). Toward a science of computational ethology. Neuron *84*, 18–31.
5. Gomez-Marin, A., Paton, J.J., Kampff, A.R., Costa, R.M., and Mainen, Z.F. (2014). Big behavioral data: psychology, ethology and the foundations of neuroscience. Nat. Neurosci. *17*, 1455–1462.
6. Hunter, P. (2018). The revival of the extended phenotype: After more than 30 years, Dawkins' Extended Phenotype hypothesis is enriching evolutionary biology and inspiring potential applications. EMBO Rep. *19*, e46477.
7. Hall, Z.J., Meddle, S.L., and Healy, S.D. (2015). From neurons to nests: nest-building behaviour as a model in behavioural and comparative neuroscience. J. Ornithol. *156*, 133–143.
8. Weber, J.N., Peterson, B.K., and Hoekstra, H.E. (2013). Discrete genetic modules are responsible for complex burrow evolution in Peromyscus mice. Nature *493*, 402–405.
9. Yartsev, M.M. (2017). The emperor's new wardrobe: Rebalancing diversity of animal models in neuroscience research. Science *358*, 466–469.
10. Knaden, M. (2019). Learning and processing of navigational cues in the desert ant. Curr. Opin. Neurobiol. *54*, 140–145.
11. Mischiati, M., Lin, H.T., Herold, P., Imler, E., Olberg, R., and Leonardo, A. (2015). Internal models direct dragonfly interception steering. Nature *517*, 333–338.
12. Braitenberg, V. (1984). Vehicles, Experiments in Synthetic Psychology (MIT Press).

Evolution and development: From the pet shop to the pelagic zone

Florian Maderspacher
Florian Maderspacher is *Current Biology*'s Senior Reviews Editor
Correspondence: florian.maderspacher@current-biology.com
https://doi.org/10.1016/j.cub.2021.10.039

Flying fish and some of their relatives have evolved the ability to elegantly escape predators by gliding through air. A new study — involving a pet shop zebrafish mutant — offers glimpses into how fins might have been modified to enable this stunt.

> "There are these two young fish swimming along, and they happen to meet an older fish swimming the other way, who nods at them and says 'Morning, boys. How's the water?' And the two young fish swim on for a bit, and then eventually one of them looks over at the other and goes 'What the hell is water?'"
>
> David Foster Wallace — *This Is Water*.

Sure enough, there are fish for whom being out of the proverbial water is part of a lifestyle: there are mudskippers that hang out on tidal flats, or lungfish that can hole up in the ground to weather long droughts, but none escape their element more elegantly than flying fish. The 70 or so species of flying fish are found in the family Exocoetidae, part of the larger order of Beloniformes, which, among the halfbeaks, contains a few additional air-gliding fish[1]. Exocoetids break through the water surface propelled by their fast beating tail (Figure 1). With their ventrally enlarged hypoceral tail fin still in the water, they then taxi above the surface to pick up speed before they fully take to the air and glide on the airfoil afforded by their extended pectoral fins. The most accomplished flying fishes use four wings including enlarged pelvic fins to glide 50 or more meters before they have to taxi again[2]. With multiple rounds of flying and taxi, a fish can fly several hundred meters, outpacing large predators that haunt the waters underneath. Exocoetids are formidably adapted to this volant lifestyle: they have ultrafast muscles wagging their tails to propel them out of the water, a modified shoulder girdle and muscle system that lets them spread their 'wings', as well as an enlarged vestibular system to ensure balance in air and eyes that work well in both media; but their most obvious adaptation are their wing-like fins, whose evolutionary and developmental genetics are the focus of a new study by Jacob Daane, Matthew Harris and colleagues[3] in this issue of *Current Biology*.

With their wing-like fins, flying fish look like straight out of a Hieronymus Bosch painting and are a testament to the weird and wonderful awesomeness of nature and its — for want of a better word — creativity. But what makes flying fish so fascinating from an evolutionary perspective is that their aerial acrobatics — at least superficially — evoke an evolutionary transition — taking to the air — that has revolutionized the history of life on Earth. Only three vertebrate lineages — birds, bats and pterosaurs — have accomplished powered flight, and in each case conquest of airspace has led to spectacularly successful evolutionary radiations. Many more species, however, among them rodents, snakes or lizards, can glide, which is often invoked as a prelude to full flight. No wonder then that flying fish have captured the imagination of Charles Darwin, who mused that they "might have been modified into perfectly winged