

The “jack-in-the-box” stamens of *Heliconia wagneriana* (Heliconiaceae)

While sessile, plants exhibit a surprising variety of adaptive movements in response to environmental stimuli. Examples of rapid floral movements are increasingly well documented, challenging conventional ideas of plant behavior (see Whippo and Hangarter (2009) and Ruan and da Silva (2011) for reviews). For example, Bynum and Smith (2001) demonstrated that corollas of *Gentiana algida* (Gentianaceae), an alpine herb common to the Rocky Mountains, USA, close minutes before afternoon monsoons to protect pollen from rain. Dean and Smith (1978) suggested that the nightly folding of *Machaerium arboreum* (Fabaceae) leaflets reduces water accumulation during nightly rains, thereby reducing rates of pathogenic infection. Other documented floral movements (i.e., changes in the positions of floral whorls relative to each other), may improve pollen transfer and deposition through increasing contact of the androecium or gynoecium with pollinator bodies (Ruan and da Silva 2011). Darwin (1862) described how orchids of the genus *Catasetum* use a hair-triggered mechanism to shoot their sticky pollinium onto bee pollinators. Other examples include the style movements of *Mimulus aurantiacus* (SCROPHULARIACEAE) that reduce interference between male and female structures (Fetscher 2001) and the spring-loaded stamens of *Cornus canadensis* (Cornaceae) that catapult pollen into the air at more than 3 m/s (Edwards et al. 2005).

In January–April 2017, we performed hand-pollination experiments on *Heliconia* (Heliconiaceae) species in the Coto Brus region of Costa Rica representing a range of floral morphologies and ecological strategies to test for cryptic pollinator specialization sensu Betts et al. (2015). During pollination experiments, *Heliconia wagneriana* Petersen demonstrated an intriguing example of plant movement, which, to our knowledge, has not previously been described.

Heliconiaceae is a monogeneric family that consists of 200–250 species occurring primarily in the Neotropics. Members of the genus are commonly known as lobster claws or false bird of paradise. *Heliconia* are largely hummingbird pollinated and have alternating, boat-shaped bracts that come in shades of red, pink, yellow, and green. Floral morphologies among *Heliconia* spp.

are diverse and exhibit classic examples of pollination syndromes and morphological fitting, specifically in relation to hummingbird bill length and curvature (Stiles 1975, Gill 1987, Temeles and Kress 2003). The flowers are composed of six petaloid tepals, five of which are fused into a cylindrical perianth, the sixth a lip-like structure that, upon anthesis, exposes a narrow opening that extends nearly the length of the floral tube.

Unlike many *Heliconia* species, the flowers in *H. wagneriana* do not noticeably wilt or decay by the second day after opening, nor do they abscise and fall to the ground as do the flowers of species with pendent inflorescences or those with flowers that extend above the bracts. Identification of mature flowers for use in hand-supplementation experiments required close scrutiny of flower characteristics. On inflorescences that were open to hummingbird visits, we observed flowers with exerted stamens. However, inflorescences that were covered with mesh bags to exclude hummingbird visitation did not have exerted stamens during a 4-d observation period ($N = 11$ unbagged, $N = 12$ bagged).

Further investigations of the flowers on bagged versus unbagged ramets revealed that stamen extension was triggered by bird visitation and insertion of the bill into the corolla (Fig. 1b). By maintaining a tightly sealed corolla, the stamens appear to be coiled and pressed into the curvature of the perianth (Fig. 1a), which may create elastic potential energy released upon physical separation of the tepals (Fig. 1b). We were able to manually trigger the response by opening the floral tube of a bagged flower using forceps to simulate a bird attempting to reach the nectary (Fig. 1c, videos S1 and S2).

There could be several adaptive advantages to this plant’s “jack-in-the-box” approach to pollen transfer. First, the spring-loaded action of the stamens has the potential to increase the force and area of contact with hummingbird pollinators by actively pushing the stamens against the feeding hummingbird’s bill and head, thereby promoting pollen transfer. In comparison to other plants with spring-loaded floral mechanisms (e.g., *C. canadensis* stamens), *H. wagneriana* stamens extend slowly. However, in ~62 h of video observation (PlotWatcher™), we counted 68 visits to focal flowers where birds could be seen feeding. Birds spent on average 2.1 ± 0.2 SE seconds drinking. This is roughly the amount of time required for full stamen extension (Fig. 1c).

Second, by keeping the stamens and stigma retracted within the floral tube, these sensitive flower parts may be protected from insect herbivory prior to pollination. Herbivory of reproductive organs has previously been identified as a driving force in shaping the evolution of floral morphology in this species (Wootton and Sun 1990). Bracts fill with fluids produced by the plant as a

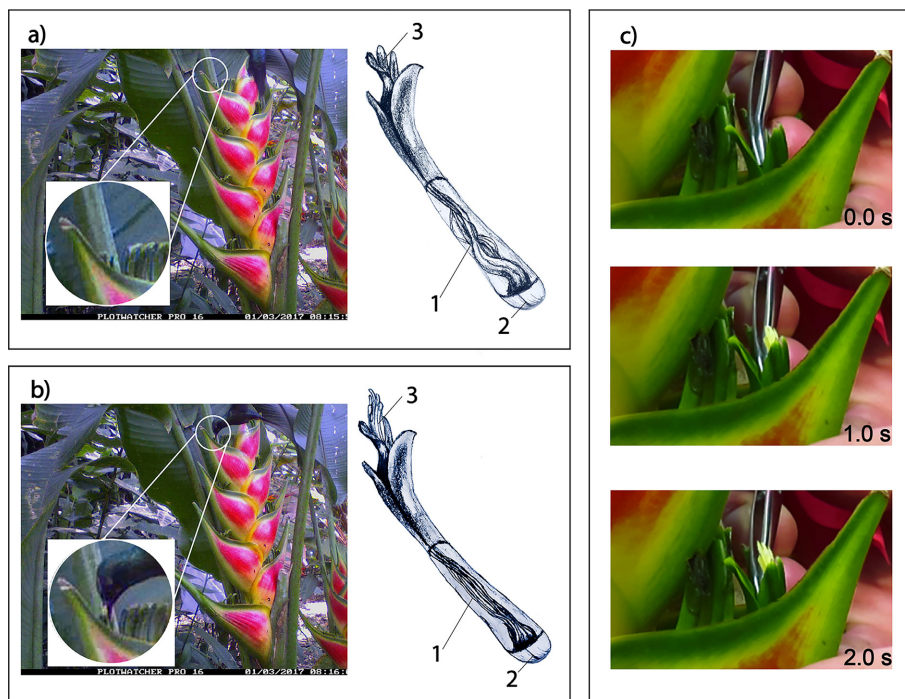


FIG. 1. (a) Before a hummingbird visit, the stamens of a mature flower in bract seven of a focal plant are retracted. The drawing to the right shows a flower with a window cut into the side of the cylindrical perianth to display the stamens coiled in a position of elastic potential energy (arrow 1). Arrow 2 shows the location of the nectary, and arrow 3 the closed tepals of the perianth. (b) During a visit from a male green hermit (*Phaethornis guy*), the stamens straighten and extend (arrow 1) to contact the bird's forehead. Arrow 2 again points to the nectary on the drawing, and arrow 3 shows stamens and anthers extended above the tip of the perianth. (c) A time-lapse series derived from Video S2 shows author D.G. triggering the jack-in-the-box stamens using forceps.

moat-like defense against herbivores. The constant aqueous environment within the bracts may also help to maintain the turgor necessary to create the potential energy released upon tepal separation.

We propose an additional potential benefit to maintaining retracted stamens prior to pollinator visitation; pollen desiccation has long been thought to reduce the longevity and viability of pollen, and dry weather conditions as well as the average travel time from anther to stigma may pose selective pressures on mechanisms to protect pollen from dehydration and subsequent degradation (Proctor 1998). Both its flowering ecology and biology indicate that risk of pollen desiccation is likely to be particularly severe in *H. wagneriana*. *Heliconia* possess exineless pollen, meaning the pollen lacks a tough outer layer that protects the viability of pollen grains in many flowering plants (Kress et al. 1978). The vulnerability of *H. wagneriana* pollen became apparent during pollination experiments. Pollen failed to stick to the stigma of the receiving flower ~20 min after triggering the extension and exposing the pollen (Dustin G. Gannon, *personal observation*), suggesting a persistent risk of desiccation.

Desiccation risk is likely exacerbated by the reproductive ecology of *H. wagneriana*, which flowers primarily during Central America's dry months (Stiles 1975) when

days with rain are reduced and winds increase. Furthermore, this species is almost exclusively pollinated by traplining hummingbirds that tend to move long distances between flowers. We counted 42 visits to focal inflorescences (68 total flower visits) in PlotWatcher™ videos, 93% of which were visits from violet sabrewings (*Campylopterus hemileucurus*) and 5% from green hermits (*Phaethornis guy*), both of which exhibit traplining foraging behaviors. These data are consistent with previous observations by Stiles (1975) at La Selva Biological Station, Heredia, Costa Rica, who reported that trapliners accounted for 96% of visits ($N = 51$ visits). With such a disparity between the number of visits from traplining and territorial hummingbirds, we expect the mean time since leaving the anther to the time pollen is deposited on a stigma to be considerably longer for pollen of *H. wagneriana* than pollen of a species regularly visited by territorial hummingbirds.

Rapid stamen extension following pollinator visits is a new example of specialized pollination biology in *Heliconia*, and suggests a number of hypotheses regarding the adaptive significance of the movement. The flower movements we observed may be a strategy to ensure both pollen transfer and preserve pollen viability until pollinators are present. Experiments with exposing

anthers and quantifying relative rates of pollen desiccation, flower damage, and successful pollen transfer would enable explicit testing of the potential ecological benefits of jack-in-the-box stamens. Future experiments may also include testing the effect of reduced water turgor on the speed of stamen extension to address hypotheses of the mechanisms underlying the movement presented here.

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