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J. Burks Holland
University of Arkansas at Little Rock

J. Lanza
University of Arkansas at Little Rock, jxlanza@ualr.edu

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Geographic Variation in the Pollination Biology of *Passiflora lutea* (Passifloraceae)

J. Burks Holland[1,2] and J. Lanza[1,3]

[1]*Biology Department, University of Arkansas at Little Rock, 2801 South University, Little Rock, Arkansas 72204*
[2]*Present address: 3514 Steel Bridge Road, Benton, Arkansas 72015*

[3]Correspondence: jxlanza@ualr.edu

Abstract

Like most species of *Passiflora*, *P. lutea* is reported to produce one-day flowers with complicated floral movements and requires deposition of non-self pollen for fruit production. Medium sized bees are the most likely pollinators in central Texas. We report on a series of observations and experimental manipulations that compare the reproductive biology of *P. lutea* in central Arkansas to that reported previously from plants about 800 km distant in central Texas. We observed floral movements and floral visitors, compared fruit production of flowers available to pollinators versus flowers from which pollinators were excluded, and compared fruit production of flowers that were hand-pollinated with self pollen versus flowers that were hand-pollinated with non-self pollen. Floral movements were similar to those of other *Passiflora*, with flowers opening for one day and styles that usually deflexed to a level below the anthers, presumably facilitating cross-pollination. Some flowers (20%) had styles that did not fully deflex. Movement of floral parts of plants in central Arkansas occurred slightly earlier than in plants in central Texas. Unlike what was observed in a small sample in Texas, we observed a low level of self-compatibility in *P. lutea.* In contrast to the medium sized bees that were the important pollinators in central Texas, *Anthemurgus passiflorae*, a small specialized andrenid bee that only forages on *P. lutea*, was likely the most important pollinator in central Arkansas. Finally, fruit set of plants in central Arkansas was much higher than that reported for plants in central Texas. Thus, this species varies geographically in its reproductive biology.

Introduction

Although all passionflowers (*Passiflora* spp.) produce complex flowers with structural similarities, species vary substantially in flower color and in the detail of flower structure and behavior. All species in this tropical and subtropical speciose genus have at least one ring of filaments (the corona) around a vertical stalk that supports the stamens and styles (the androgynophore) (Vanderplank 1991). Flower colors include red (e.g., *P. coccinea*), purple (e.g., *P. menispermifolia)*, greenish-yellow (e.g., *P. coriacea*), and white (e.g., *P. costaricensis*). The corona may consist of one (e.g., *P. citrina*), or two (e.g., *P. biflora*), or more (e.g., *P. caerulea*) series of filaments; the filaments may be long (e.g., *P. quadrangularis*) or short (e.g., *P. coriacea*).

In most species, the reproductive parts change their orientation after the flower opens. In these cases, the styles point upward when the flower opens but later bend (deflex) so the stigmas move downward. These movements bring the stigmas near visiting pollinators and appear to promote outcrossing (Janzen 1968). The details of these movements differ among species. For example, style movements are completed within 20 min of opening in *Passiflora foetida* (Janzen 1968) but are not completed in a second unidentified species until about 5 h after opening (Janzen 1968). *Passiflora vitifolia* is intermediate to these two species, with styles that begin deflexing 30-180 min after opening and taking up to 2 h to finish moving (Janzen 1968).

The diversity in floral morphology is accompanied by a diversity in pollen vectors. The red flowers of *Passiflora vitifolia* (Janzen 1968, Snow 1982), *P. speciosa* (Varassin et al. 2001), and *P. coccinea* (Storti 2002) are pollinated by hummingbirds. In contrast, *P. foetida*, an ill-odored species producing small flowers (6 cm) that are white, pink, purple, or blue, is pollinated by large bees (*Ptiloglossa* spp.) (Janzen 1968, Amela Garcia 1998). Large bees also pollinate *Passiflora amethystina*, *P. miersii* (Koschnitzke and Sazima 1977), and *P. caerulea* (Amela Garcia and Hoc 1997). Bats pollinate *P. penduliflora* (Kay 2001), *P. galbana* (Varassin et al. 2001), and *P. mucronata* (Sazima and Sazima 1998, Varassin et al. 2001). *Passiflora incarnata*, with purple, mauve, or white flowers, is pollinated primarily by *Xylocopa* bees (May and Spears 1988).

Most species of *Passiflora* appear to require animal pollination and to be self-incompatible. May and Spears (1988) excluded insect visitors from 52 flowers of *P. incarnata*; fruit production in these flowers was 0%, in contrast to a fruit production rate of 17% in flowers open to insect visitors. They also hand-pollinated flowers with self and non-self pollen. None of the flowers pollinated with self-pollen produced fruit, but 80% of the flowers pollinated with non-self pollen produced fruit. Similarly, Snow (1982) saw no fruit set in 30 self-pollinated flowers of *P. vitifolia*, and Varassin et al. (2001) saw no fruit production in self-pollinated flowers of *P. alata* (*N* = 27), *P. galbana* (*N* = 25), *P. mucronata* (*N* = 56), and *P. speciosa* (*N* = 18). Animal pollinators are also required in *P. coccinea* (Storti 2002), *P. alata* (Koschnitzke and Sazima 1997), *P. amethystina,* and *P. moersii* (Koschnitzke 1997). In contrast, *P. suberosa* and *P. capsularis* (Koschnitzke and Sazima 1997) and *P. foetida* (Amela Garcia and Hoc 1998) are self-compatible. *Passiflora caerulea* exhibits a "low degree of self-compatibility" (Amela Garcia and Hoc 1997).

In addition to between-species variation, some species of *Passiflora* exhibit substantial within-species variation in floral morphology and behavior. For example, *P. incarnata* varies in color from lavender to mauve to white. Although most flowers of this species open in late morning, in some flowers the stigmas immediately begin to deflex while in other flowers the stigmas never deflex (May and Spears 1988). The cultivated *P. edulis* also varies in self-compatibility; the purple strain is self-compatible but the yellow strain is not (Vanderplank 1991).

Because it is a widely distributed species (from Pennsylvania to Kansas and south to Texas and Florida) (Vanderplank 1991), *Passiflora lutea* L. (Passifloraceae) provides a good test species for assessing geographic variation in floral behavior. This herbaceous vine produces small, greenish-yellow flowers. Its pollination biology has been studied in Austin, Texas (Neff and Rozen 1995). Like other *Passiflora*, *P. lutea* produces stigmas that usually deflex after the flowers open; however, Neff and Rozen (1995) noted the styles in some flowers never deflex, suggesting that these flowers never receive pollen and are therefore functionally male. Using indirect evidence, they concluded that medium-large bees (*Bombus*, *Xylocopa*, *Colletes*) pollinate *P. lutea.* Neff (2003) later concluded that *P. lutea* probably relies on a "mix of medium sized bees and wasps" for pollination. They experimentally showed that *P. lutea* requires an animal pollen vector and is self-incompatible. Our study provides a look at the pollination biology of *P. lutea* in another part of its geographic range (central Arkansas, approximately 800 km from the study site of Neff and Rozen). We examined the diurnal movement of flower organs, assessed which animal visitors were likely pollinators, and tested if *P. lutea* is normally cross-pollinated and if it is self-compatible.

Methods

Passiflora lutea grew at sites located both on the campus of the University of Arkansas at Little Rock and throughout the city. Because *P. lutea* spreads vegetatively, we considered each "clump" a single individual. We conducted observations of pollinators in June-August 1994 and 1997; we conducted experimental manipulations in June-August 1994-1996; we conducted additional observations of style movements in July 2005. All times are Central Daylight Savings Time.

We observed floral movements in 1994 and 2005. For three days in 1994, observations began 30 min before sunrise and ended 30 min after dark. During the course of the day, we watched the plant in 2-3 h shifts, with 30-60 min breaks between observation periods. During this time, we recorded the movement of floral parts through drawings. In 2005, we observed *Passiflora lutea* flowers to assess the percentage of flowers with non-descending (non-deflexing) styles. Between 1230 and 0130, we counted and categorized styles on seven plants as fully deflexed (stigmas below the anthers), partially deflexed (stigmas at the same level as the anthers), and non-deflexed (stigmas above the anthers).

For three weeks in 1994, we observed and counted flower visitors at 0700, 1000, 1200, 1600, and 1900. We noted the behavior of flower visitors and captured samples of each species for later identification. In 1997, we again observed the behavior of flower visitors, concentrating on the behavior of *Anthemurgus passiflorae*. Voucher specimens of *A. passiflorae* and *Megachile concinna* were deposited in the US National Pollinating Insect Collection with the USDA Bee Biology and Systematics Laboratory at Utah State University.

The first test of the breeding system was done to determine if *Passiflora lutea* normally requires a floral visitor for fruit production. First, we tagged flower buds that were about to open—50 buds on one vine in 1994, 50 buds on a second vine in 1995, and 20 buds on each of three different vines in 1996. Half of the flowers on each plant were bagged with bridal veil to test whether the plant could spontaneously self-pollinate and set fruit. The remaining flowers were left unbagged, to be visited by pollinators. The individual flower buds in both groups were tagged and monitored for fruit production.

The next experiment tested if *P. lutea* was self-compatible. Flower buds were bagged several days before they opened. We bagged 50 buds on one vine in 1994, 50 buds on a second vine in 1995, and 20 buds on each of three different vines in 1996. As each flower opened, we manually pollinated it, using a cotton swab. Half of the flowers were pollinated with their own (self) pollen and half were pollinated with a mixture (non-self) of pollen from two other vines. After hand pollination, all flowers were rebagged and monitored for fruit production.

We measured rates of fruit set in 1997 by counting the number of fruits on stems versus the number of flower scars on a total of 25 stems from plants at eight sites. For a given shoot, we made observations between the fruit closest to the meristem and, working away from the meristem, the first ripe (blue) fruit; this procedure allowed us to eliminate potential fruit sites that were too young to have enlarged fruit and sites that had lost ripened fruits through dispersal.

Results

Passiflora lutea flowers remained open for only one day. Before opening, the styles were vertical and pointed upward and the filaments and anthers were vertical and pointed downward. The petals began to open around 0700 and most were fully open by 0800. As the petals opened, the 5 free filaments moved upward until they were horizontal and the 5 anthers hung vertically from the filaments. In late morning, there was a drastic change in style and anther position. Most styles, originally vertical and pointing upward, descended (deflexed) until they were below the filaments. At the same time, the anthers curled upward until they paralleled the base of the flower. Most flowers completed this shift by 1200 and remained in this position for most of the afternoon. At approximately 1600, the petals began to close, the filaments and anthers began to abscise and the styles began to move upward. This process continued until the styles were again vertical and pointed upward, the filaments and anthers were vertical and pointed downward and the flower was closed. By sunset, all flowers were closed. These organ movements were not induced by pollination. The same movements were observed in both the unbagged flowers that were visited by insects and in the bagged flowers that were not visited.

Although most flowers (80%) behaved in the manner describe above, styles of some flowers did not deflex completely. By 1230, 14.3% of the styles had deflexed until the stigmas were at the same level as the anthers and 5.7% of the styles remained vertical with the stigmas pointing upward.

Insect activity began as early as 0700 and few insects visited after 1700 (Fig. 1). Most visits occurred between 0800 and 1300. The peak in activity was approximately 1000.

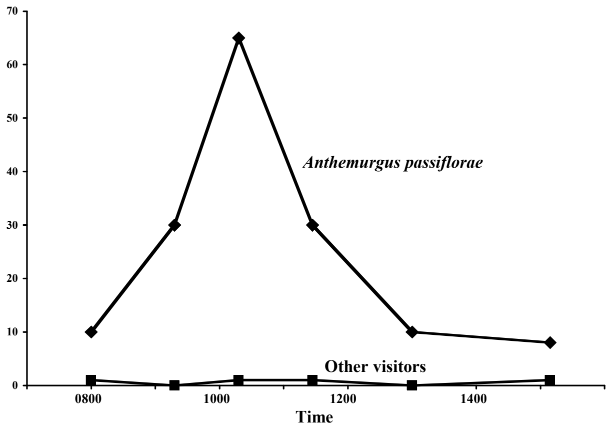

Figure 1. Total number of visitors observed at *Passiflora lutea* during 6 observation days. Each point represents visitors within 15 min before to 15 min after the time on the X-axis. Upper line is number of *Anthemurgus passiflorae;* lower line represents all other flower visitors combined.

Although there were several species of floral visitors, there was only one probable common pollinator, *Anthemurgus passiflorae*, an andrenid bee that has been observed only on *P. lutea* (Michener et al. 1994). A wasp, a bumblebee, a butterfly, and several species of flies and ants fed on nectar but probably did not pollinate the flowers because they did not contact the stigmas. A second bee, *Megachile concinna* (Megachilidae), was also a potential pollinator. Like other species of flower visitors, *A. passiflorae* and *M. concinna* collected nectar; unlike other species of flower visitors, these bees also collected pollen and, in doing so, contacted the stigmas. *Megachile concinna* was common at only one plant and this plant produced very few fruit (only two fruits of 60 possible). *Anthemurgus passiflorae* was most abundant between 1000 and 1200; by this time, floral movements had placed the stigmas and anthers close together and the bees contacted the stigmas as they collected pollen. *A. passiflorae* visited *P. lutea* in much greater numbers than did any of the other species. Thus, because of behavior and abundance, we concluded that *A. passiflorae* was the most important pollinator of *P. lutea*.

Fruits were abundant on open-pollinated plants in 1994-96. In 1997, when fruits were counted, fruit set ranged from 5% to 82% early in the season.

Passiflora lutea rarely set fruit without an insect vector. Only 3/25 (12%) bagged flowers in 1994, 2/25 (8%) bagged flowers in 1995, and 0/30 (0%) bagged flowers in 1996 produced fruit. In contrast, 20/25 (80%) unbagged flowers in 1994, 23/25 (92%) unbagged flowers in 1995, and 17/30 (56.7%) unbagged flowers in 1996 produced fruit. In 1994, 2 of the bagged flowers that produced fruit were found with dead bees in the bag. None of the other 3 bagged flowers that set fruit were likely to have been visited by insects. These results (chi square = 78.38, df = 1, $P < 0.001$) indicate that the plant almost always requires animals to visit and pollinate but that fruit production can occur in approximately 4% of the flowers without an insect vector.

Passiflora lutea was generally self-incompatible but there was a low level of self-compatibility. Only 2/25 (8%) flowers receiving self pollen in 1994, 6/25 (24%) flowers receiving self pollen in 1995, and 0/30 (0%) flowers receiving self pollen in 1996 produced fruit. In contrast, 18/25 (72%) flowers receiving non-self pollen in 1994, 21/25 (84%) flowers receiving non-self pollen in 1995, and 10/30 (33.3%) receiving non-self pollen in 1996 produced fruit. Considering the low number of fruit produced by the self-pollinated flowers (chi square = 45.81, df = 1, $P < 0.001$), it would appear that *P. lutea* usually requires another pollen source but that approximately 10% of the flowers can set fruit from self pollen.

Discussion

Although the floral biology of *Passiflora lutea* in central Arkansas was similar to that observed in central Texas, there were interesting differences.

Like other species of *Passiflora* (Vanderplank 1991), and like *P. lutea* in central Texas (Neff and Rozen 1995), *P. lutea* in central Arkansas produced one-day flowers that opened in the morning and closed before dark. Throughout the day, the movement of reproductive organs was consistent among flowers and similar to those of other *Passiflora* species (Vanderplank 1991). However, the timing of flower opening differed slightly. Because Austin is farther west in the time zone than Little Rock, we compared floral movements to time since sunrise (United States Naval Observatory 2006). Neff and Rozen (1995) write that in Austin, "flowers typically open between 0800 and 0900" or 1.5-2.5 h after sunrise while our data show that in Little Rock flowers open between 0700-0800, or 1-2 h after sunrise. Similarly, the timing of style movements differed slightly between the sites. In Austin, stigmas "typically do not descend to anther levels until after 1200"—5.5 h after sunrise—while in Little Rock, this movement was completed by 5 h after sunrise.

Fruit set of *Passiflora lutea* was much higher in Arkansas than in Texas. Fruits were abundant in Arkansas in 1994-1996. In 1997, when fruit set rate was quantified, nearly half the flowers set fruit ($\bar{x}$ = 48.5%, S. D. = 29.9). In contrast, Neff and Rozen (1995) saw no fruit set at all.

Another geographic difference in the pollination biology of *Passiflora lutea* was that the probable pollinators in the two areas differed. In central Arkansas, *Anthemurgus passiflorae* was the most important pollinator of *P. lutea*, based on both behavior and abundance. Working in central Texas, Neff and Rozen (1995) considered the pollination role of *A. passiflorae* "limited," partially because of the bees' "modest size." Writing in 2003, Neff concluded that the habits of *A. passiflorae* suggest it "may be a highly effective pollinator of *P. lutea*" but doubted that it contributes significantly to pollination of *P. lutea* because it is "probably a rare bee"; he continued to argue that *P. lutea* probably depends on medium sized bees and wasps for pollination. Our observations showed, however, that because of the flower design and the anatomy *of A. passiflorae*, these bees were able to land on the flower and collect both nectar and pollen efficiently. The stigmas of the flowers we observed in Little Rock were well positioned to contact the bee and receive pollen as the bee crawled over the anthers. In Austin, however, female *A. passiflorae* "very rarely contact the stigmas while harvesting pollen" (Neff and Rozen 1995) and may be related to the earlier deflexing of styles in central Arkansas. The high fruit set of plants we observed further demonstrates the presence of successful pollinators in Arkansas.

The relatively large bees (e.g., *Bombus*, *Xylocopa*, *Augochloropsis* and *Colletes*) considered likely pollinators in central Texas by Neff and Rozen (1995) were not likely pollinators in central Arkansas. These bees were not probable pollinators in central Arkansas because: (1) flower visitors other than *Anthemurgus passiflorae* were rare and (2) most other flower visitors did not contact both anthers and stigmas. The only other flower visitor that contacted both anthers and stigmas was *Megachile concinna*. We observed this bee consistently on only one plant and this plant set very few fruit (3%), whereas plants visited by *A. passiflorae* had higher fruit set. We conclude that *Megachile concinna* only rarely pollinates *P. lutea* in central Arkansas. A photograph in Neff (2003) clearly shows that *Colletes latitarsis*, a medium-sized bee, can contact both stigmas and anthers and at least occasionally pollinate *P. lutea*.

Although most species of *Passiflora* appear to require an animal pollen vector and non-self pollen for fruit set (Snow 1982; May and Spears 1988; Koschnitzke and Sazima 1997; Amela Garcia and Hoc 1998; Varassin et al. 2001; Storti 2002), *P. lutea* in central Arkansas set a limited number of fruits without animal vectors and with self pollen. *P. caerulea*

(Amela Garcia and Hoc 1997), *P. foetida* (Amela Garcia and Hoc 1998), *P. suberosa* and *P. capsularis* (Koschnitzke and Sazima 1997) show limited self-compatibility. In contrast, Neff and Rozen (1995) observed no fruit set from 18 hand-pollinations with self pollen.

This study demonstrated that *P. lutea* varies in its pollination biology between two points approximately 800 km apart. There were slight differences in the timing of flower opening and style movements, much higher fruit set in Arkansas, and different probable pollinators. Perhaps other differences occur in the more eastern and northern parts of its range. In addition, this study demonstrated that *P. lutea* appears to be slightly self-compatible.

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