# Mating Behavior, Reproductive Biology, and Development of *Phidippus princeps* (Araneae: Salticidae)

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# ABSTRACT

We studied the courtship and copulation of *Phidippus princeps* and described 14 courtship and copulatory behaviors for this species. *Phidippus princeps* males exhibit many behaviors typical of the Salticidae, such as leg raises, zig-zag movement to approach the female, and typical salticid copulatory position. When receptive, females are quiescent during courtship. Laboratory-reared females produced as many as three fertile egg sacs with clutch sizes decreasing in successive sacs and time required from oviposition to spiderling emergence increasing in successive sacs. *Phidippus princeps* males required fewer molts to mature than females, and carapace width and length and spiderling weight increased in each successive instar.

# INTRODUCTION

Biological communication is defined as actions on the part of one organism, sender, that alter the probability of response in another organism, receiver (Wilson, 1975). Courtship is a type of heterosexual communication that precedes copulation (Robinson, 1982), and it is generally elaborate within the Araneae (Suter and Renkes, 1984). Courtship function has been the center of much research and is generally thought to operate in conspecific recognition (Robinson and Robinson, 1980; Suter and Renkes, 1984) or serve as a forum for sexual selection (Forster, 1982). Male spiders engage in pre-copulatory displays, despite costs of time, energy, and visibility to predators, thus allowing females to assess male fitness (Jackson, 1981). The family Salticidae (jumping spiders) includes 4,400 described species, making it the largest family within the Araneae (Foelix, 1996); however, biological information on many species is lacking. Specifically, courtship behavior has only been described for a small fraction of salticid species (Jackson, 1978,

1982b). Our study provides the first description of the courtship and copulatory behavior of the salticid, *Phidippus princeps*.

Spiders typically produce multiple egg sacs, and the first egg sac usually has the largest clutch size (Preston-Mafham and Preston-Mafham, 1984). Male spiders are generally smaller than females and, therefore, require fewer molts to mature (Foelix, 1996). We examined the reproductive biology of *P. princeps*, which involved determining clutch size, time between oviposition events, and number of egg sacs produced. Lastly, since developmental data on *P. princeps* has not been previously described, we determined the developmental times of spiderlings from emergence to maturity and recorded the number of molts required to reach maturity. We measured carapace width and length and spiderling weight in each instar to determine whether these measurements are accurate predictors of instar. Hagstrum (1971) has shown carapace width to be an accurate indicator of instar in lycosid spiderlings.

## **METHODS AND MATERIALS**

We collected immature *P. princeps* from a restored prairie at the Rock Springs Center for Environmental Discovery, Macon County, IL from August - October 1997 and 1998. These spiders and all subsequent offspring were maintained in a laboratory at Millikin University. We housed each spider individually in a 12.0 cm diameter petri dish and, as spiders matured, we moved each one into a 15.0 cm diameter petri dish. We supplied water daily via a moist cotton ball and fed the spiderlings fruit flies, Drosophila melanogaster, and houseflies, Musca domestica, three times per week. Drosophila mela*nogaster* were provided to smaller spiders and *M. domestica* to larger spiders. Although we could not control how much prey each spiderling consumed, we offered each individual within an instar the same amount and type of prey (Table 1). Upon maturity of fieldcollected spiders, we exposed females to males daily until females were receptive. Unreceptive females retreated or lunged at males. In contrast, receptive females remained stationary as males approached. Upon receptivity of field-collected spiders, we introduced a virgin male into a virgin female's arena, and recorded all courtship and copulatory behaviors exhibited by males. Since receptive females were generally quiescent, only moving to keep males in their visual field, only male courtship was analyzed. We defined courtship as the behaviors preceding mating, and copulation as actual palpal insertion by males. We ended trials when physical contact between the pair was broken. We observed 34 mating pairs, and we did not use individual spiders more than once in mating trials. Following the procedure used to analyze linyphiid courtship (Willey and Adler, 1994), we transcribed behavioral acts into a first-order preceding-following transition matrix and calculated expected values and standard normal deviates for individual transitions. We used a binomial test to analyze standard normal deviates and determine which transitions occurred at a frequency greater than that expected by chance (Bishop, et al, 1975; Fagen and Young, 1978). We then constructed an ethogram on the basis of transitions with significance at P < 0.05.

We analyzed all reproductive and developmental data on the offspring of the above crosses using ANOVA. Where significant differences were detected, we performed posthoc comparisons using Tukey's HSD, a pairwise comparison within the testing group. To determine clutch size for each egg sac, we counted the number of unhatched eggs, num-

ber of embryos, and number of spiderlings from successive sacs. We recorded time between successive oviposition events and time required from oviposition until emergence of the first spiderling from each egg sac. We also recorded the number of molts required to reach maturity for males versus females and the length of time spent in each instar. We were unable to sex immature spiders since external reproductive structures do not become obvious until the penultimate (males) or adult (females) stage; therefore, data for immature spiders represent males and females combined. Within 36 hours of molting, we weighed each spiderling and measured its carapace width and length. Since the first instar is spent within the egg sac, we report all data for instars two – maturity.

## RESULTS

When males were introduced into a female's arena, the initial response of both spiders was to orient toward the conspecific. Following initial orientation, we described 14 behavioral acts associated with courtship and copulation of male *P. princeps* (Figure 1):

#### **Tap Palps on Female Silk**

Male alternately touches right and left palps to female's silk retreat.

#### Front Legs 90°

Male simultaneously raises front legs to a 90° angle from cephalothorax.

#### Tap Palps on Arena

Male alternately touches right and left palps to bottom of testing arena.

#### Front Legs 45°

Male simultaneously raises front legs to a 45° angle from cephalothorax.

#### Zig-Zag

Male simultaneously raises front legs to a 45° angle from cephalothorax and moves in a back-and-forth motion, while approaching the female and moving around her in a semicircle. Male intermittently adopts a hunched position between zig-zag motions.

#### **Initiate Leg Contact**

Male approaches female and contacts female cephalothorax with front legs. Front legs are held parallel in an out-stretched, frontal position. Male body is initially held in a low posture.

## **Climb on Female Dorsum**

Male climbs on female carapace or dorsum of abdomen and remains motionless.

#### Reverse

After male climbs on female abdomen, he turns 180° to position his cephalothorax over female abdomen; male and female are facing opposite directions.

#### **Rotate Female Abdomen**

Male grasps and lifts female abdomen with front legs while simultaneously turning abdomen clockwise or counter-clockwise. Female abdomen is rotated clockwise for insertion of left palp and counter-clockwise for insertion of right palp.

## **Insert Left Palp**

Male inserts left palp into female epigynum. Male and female are facing opposite directions with the male positioned over the female dorsum and leaning to his left.

## **Insert Right Palp**

Male inserts right palp into female epigynum. Male and female are facing opposite directions with the male positioned over the female dorsum and leaning to his right.

#### Crossover

Male removes palp, rotates female abdomen in opposite direction, and inserts other palp.

#### **Tap Palps on Female Abdomen**

Male alternately touches right and left palps to dorsum of female abdomen.

#### **Break Contact**

Male or female ends physical contact.

Female *P. princeps* oviposited up to three egg sacs. There were no significant differences in number of unhatched eggs (P = 0.192, F = 9.960, df = 2), number of embryos (P = 0.532, F = 0.652, df = 2), or number of spiderlings (P = 0.065, F = 3.15, df = 2) in successive egg sacs (Table 2); however, there was a strong trend for clutch size to decrease in successive sacs. There was a significant difference in the time between all oviposition events (P < 0.0001, F = 9.960, df = 2), and in time from oviposition to emergence of spiderlings (P < 0.001, F = 11.541, df = 2), with emergence time increasing in successive egg sacs (Table 3).

Since there were no significant differences in the number of days spent within a particular instar for spiderlings of successive sacs (P = 0.07, F = 1.987, df = 2), we combined developmental data for all sacs. Upon analysis of combined data, there was a significant difference in the number of days spent in successive instars (P = 0.0001, F = 126.541, df = 4), with the exception of the second and third instars (P = 0.217, F = 126.541, df = 4) (Table 4). The fifth instar had the longest duration.

Carapace length (P < 0.0001, F = 2545.056, df = 8) and width (P < 0.0001. F = 1776.529, df = 8), as well as spiderling weight differed significantly among all instars (P < 0.0001, F = 1607.952, df = 8) (Table 5), with each successive instar being larger and heavier.

## DISCUSSION

Conspecific communication in spiders primarily occurs through olfactory, tactile, auditory, or chemical pathways with vision having a minor role in the courtship of most spiders (Jackson, 1978). Vision has a more prominent role in the salticidae (Land 1972, 1982, 1985; Forster, 1982). Salticids have one of the most highly developed visual senses among the invertebrates (Jackson, 1978), and their courtship signals are primarily visual (Forster, 1982). Salticids are sexually dimorphic with males often possessing elaborate morphological structures and bright colors, while females generally lack these features (Jackson, 1982b).

Evolutionary convergence is indicated by the similarity of salticid displays (Jackson, 1983). The behaviors described for *P. princeps* are characteristic of courtship behaviors described for heterospecific salticids. Salticids are noted for elaborate displays where males dance, gesture, and posture for females (Jackson, 1981). The zig-zag motion exhibited by *P. princeps* is characteristic of many heterospecific salticids. For example, males of Phidippus femoratus, Phidippus johnsoni, Habronattus captiosus, Hentzia palmarum, Marpissa marina, Mopsis mormon, Trite auricoma all zig-zag when approaching females (Jackson, 1978, 1982a, 1983; Forster, 1982; Richman, 1982; Cutler, 1988; Jackson et al., 1990). While zig-zagging, salticids exhibit species-specific movements such as raising the front legs, vibrating the palps, or twitching the abdomen (Jackson, 1978; Forster, 1982; Jackson and Whitehouse, 1989; Jackson et al., 1990; Richman and Jackson, 1992). *Phidippus princeps* raised both front legs at a 45° angle while zig-zagging. *Phidippus princeps* generally initiated courtship by tapping the palps on either the female's silk or on the arena floor. Female salticids typically respond to palpal tapping by orienting to males (Crane, 1949). Another behavior, extending the forelegs to initiate physical contact, frequently observed in P. princeps is also a common behavior in salticid courtship (Jackson, 1981).

Foelix (1996) defines four types of mating positions. In Type 3 courtship, the male is on top of the female dorsum and twists the female abdomen between consecutive palpal insertions. When the male switches palps, he turns the abdomen to the opposite side. The male climbs onto the female and positions his abdomen over the female cephalothorax. The male then turns the female's abdomen to insert a palp. When withdrawing the palp, the male does a "crossover" and turns the abdomen in the opposite direction to insert the other palp. These observations are all consistent with the courtship behavior of *P. princeps*.

Forster (1982) groups courtship behaviors of the salticid *Euophrys parvula* into three stages and hypothesizes that many salticid species exhibit these same broad categories. Stage 1 involves orientation of male and female toward each other with some initial posturing, stage 2 consists of those postures and movements that bring the pair closer together, and stage 3 includes pre-mounting postures common to all salticids. In addition to displaying stage 3 behaviors, *P. princeps* exhibited typical stage 1 behavior with orientation, leg posturing, and palpal tapping and stage 2 behavior with the zig-zag approach and leg posturing.

The reproductive biology of salticids has not been as extensively studied as courtship behavior, but the development and reproductive biology of *P. princeps* is similar to that of other spiders. Although we found no significant differences in clutch sizes between consecutive egg sacs, our standard errors are large, due to the large range in clutch sizes (6 - 70) and the small numbers of second and third egg sacs produced. Additionally, our spiders received the same amount of prey daily while, in the field, prey decreases as the season progresses. Clutch sizes in *P. princeps* did show a trend of decreasing in con-

secutive sacs, as is typical of other spiders. Female *Silerella vittata* (Salticidae) oviposit 2 - 3 times after insemination, and clutch size decreases significantly between successive egg sacs (Miyashita, 1991). Decrease in clutch size could result from limiting factors such as sperm viability, number of eggs, female age, or limited foraging success.

Time from mating to oviposition of the first egg sacs was significantly shorter than time required for subsequent ovipositions, and less time was required for the third oviposition event than the second. Time from mating to first oviposition in *Frontinella pyramitelia* (Linyphiidae) was also significantly shorter than time of oviposition between successive sacs (Suter, 1990). Female *F. pyramitelia* synthesize yolk before insemination, therefore initial oviposition time is shorter than successive oviposition events. After the first oviposition, females must synthesize new yolk before subsequent ovipositions can take place. *Phidippus princeps* may also synthesize yolk before insemination, therefore requiring less time from insemination to first oviposition than that required for subsequent oviposition events. Time required for oviposition into third egg sacs decreased, but clutch sizes for third sacs also decreased which may have contributed to the shorter time interval. Time required for emergence of spiderlings from egg sacs increased significantly between successive egg sacs of *P. princeps*. Eggs produced later in the season may receive less resources from females as they age or as prey becomes scarcer, possibly causing spiderlings to remain within the protection of the egg sac longer.

Time between molts generally increased in each successive instar through the fifth instar and decreased in later instars. As spiderlings increase in size, the energy required for development also increases, and later instars may require more time to acquire the energy necessary for molting (Hallas, 1988). We changed prey from *D. melanogaster* to *M. domestica* at the start of the sixth instar In addition to *M. domestica* being a larger prey item, this is the first time spiders received variety in their diet, and these factors may influence instar length. Sample sizes were also lower in later instars since spiderlings in each instar experienced some mortality. The majority of mortality in all instars occurred during molting.

*Phidippus princeps* spiderlings undergo their first molt within the protection of the egg sac. Pre-emergence molting is also evident in *S. vittata*, with the second instar being the first observable stage (Miyashita, 1991). Female *P. princeps* required nine molts to mature, as compared to the 4-6 molts required by female *S. vittata* (Miyashita, 1991). To determine whether the number of molts varies within females of *P. princeps*, a larger number of spiders should be reared to maturity. Although we were unable to raise any males to maturity, we did raise seven males to the penultimate stage. Reaching the penultimate stage required five molts, indicating that these males would mature in six molts. This finding is consistent with the size dimorphism evident in most spiders, with females generally being larger than males (Foelix, 1996), therefore requiring more molts to mature.

*Phidippus princeps* increased significantly in carapace length and width and in spiderling weight between consecutive instars. Hagstrum (1971) showed that carapace width increased linearly as *Tarentula kochi* spiderlings developed and could therefore be used as an accurate indicator of instar. Carapace width is thought to be an accurate indicator of size because carapace size remains constant within an instar, only changing as a result of

molting. Weight is generally not an accurate indicator of instar because it is a more flexible measurement and varies within an instar as a result of prey intake. *Phidippus princeps* showed the same linear progression in spiderling weight as in carapace measurements demonstrating that weight is an accurate predictor of instar in some species. Using weight as an indicator of spider instar in the field may be less reliable since prey availability will vary.

Courtship behaviors of *P. princeps* are similar to those observed in other salticids. Type 3 courtship and the zig-zag display characteristic of salticids were exhibited by *P. princeps*. Similar to many spider species, females required more molts to obtain maturity than males, and clutch sizes decreased in subsequent egg sacs. Carapace width and length, as well as spider weight, were accurate indicators of instar in the laboratory. We are currently examining the reliability of leg spination as an indicator of instar since this character does not vary between laboratory-reared versus field spiders.

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Instar	No. of Prey Presented	Prey Species
2-3	1	Drosophila melanogaster
4	2	D. melanogaster
5	3	D. melanogaster
6-7	1	Musca domestica
8 - 10	2	M. domestica

Table 1. Feeding regime of laboratory-reared Phidippus princeps in instars 2-10: instar 1is spent within the egg sac.

Table 2. Clutch sizes  $(\bar{x} \pm SE)$  of consecutive egg sacs constructed by *Phidippus princeps*.

Egg Sac Number	No. Sacs	No. Unhatched Eggs	No. Embryos	No. Spiderlings
Sac #1	15	$29.52 \pm 31.94$	$5.20 \pm 9.34$	$38.03 \pm 24.04$
Sac #2	5	$10.20 \pm 10.71$	8.40 ± 5.37	$19.20 \pm 7.50$
Sac #3	3	$3.67 \pm 2.51$	$1.67 \pm 1.53$	$11.00 \pm 2.65$

Table 3. Days  $(\bar{x} \pm SE)$  between sequential ovipositions and from oviposition to emergence of spiderlings from egg sacs of *Phidippus princeps*.

Oviposition Events	No. Sacs	No. Days Between Oviposition Events	No. Days From Oviposition to Emergence
Mating – Sac #1	15	$14.19 \pm 1.16$	$41.60 \pm 0.80$
Sac #1 – Sac #2	5	$47.23 \pm 3.62$	$47.38 \pm 2.14$
Sac #2 – Sac #3	3	$23.57 \pm 3.22$	$61.00 \pm 0.00$

$11.97 \pm 0.39$
$14.43 \pm 0.67$
22.64 ± 2.98
43.17 ± 6.41
33.34 ± 2.35
$37.80 \pm 5.56$
$24.00 \pm 0.00$
$21.00 \pm 0.00$
2

Table 4. Days  $(\bar{x} \pm SE)$  required for development of *Phidippus princeps* from instar 2 – maturity; instar 1 is spent within the egg sac.

Table 5. Carapace width and length  $(\bar{x} \pm SE)$  and spiderling weight  $(\bar{x} \pm SE)$  of *Phidip*pus princeps from instar 2 – maturity; instar 1 is spent within the egg sac.

Instar	No. Spiders	Carapace Width (mm)	Carapace Length (mm)	Weight (mg)
2	320	$0.63 \pm 3.90 \times 10^{-3}$	$0.89 \pm 4.80 \times 10^{-3}$	$1.00 \pm 1.27 \times 10^{-3}$
3	175	$0.84 \pm 6.20 \times 10^{-3}$	$1.13 \pm 9.98 \times 10^{-3}$	$2.00 \pm 3.59 \times 10^{-3}$
4	134	$1.07 \pm 9.20 \text{ x } 10^{-3}$	$1.45 \pm 0.011$	$3.00 \pm 7.45 \times 10^{-3}$
5	105	$1.32 \pm 8.80 \times 10^{-3}$	$1.83 \pm 0.014$	$6.00 \pm 1.19 \times 10^{-3}$
6	51	$1.50 \pm 0.012$	$2.09 \pm 0.017$	$10.00 \pm 2.58 \times 10^{-3}$
7	27	$1.73 \pm 0.034$	$2.30 \pm 0.034$	$14.00 \pm 4.07 \times 10^{-3}$
8	6	$2.18 \pm 0.037$	$2.72 \pm 0.083$	$23.00 \pm 2.00$
9	5	$2.27 \pm 0.101$	$3.03 \pm 0.113$	$40.00 \pm 5.00$
10	4	$2.82 \pm 0.083$	$3.07 \pm 0.112$	$70.00 \pm 9.00$

Figure 1. Ethogram of courtship acts for *Phidippus princeps*, showing significant behavioral transitions (P < 0.05). Values beside arrows indicate frequency of 34 pairs showing a specific transition.

