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SHORT COMMUNICATION

Males respond to substrate-borne, not airborne, female chemical cues in the jumping spider, *Habronattus pyrrithrix* (Araneae: Salticidae)

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Abstract. Jumping spiders are known for complex courtship displays with both visual and vibratory components, but increasing evidence shows they also use chemoreception in intraspecific communication. We conducted two experiments using *Habronattus pyrrithrix* (Chamberlin, 1924) to assess male response to substrate-borne or airborne chemical cues produced by virgin females. First, we tested the effect of substrate-borne cues by allowing males to inspect two pieces of filter paper that had either been exposed to a female (thus covered in silk and/or excreta) or not (control). Second, we used a Y-tube olfactometer to test male response to female airborne cues versus a no-odor control in the absence of substrate-borne cues. Males responded to substrate-borne cues (spending more time traversing and palpating female-treated filter paper compared with the control) but did not respond to airborne cues alone. Together, these experiments suggest male *H. pyrrithrix* may use contact chemical cues from female silk to locate or assess females.

Keywords: Salticidae, chemical ecology, sexual selection, mate searching

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The study of animal sensory systems has long been susceptible to the bias of human perception, as evidenced by a widespread focus on animal vision and visual traits (Caves et al. 2019). While visual systems are crucial for survival and reproduction in many animals, other sensory modalities are often pivotal to an animal's success. One especially important but relatively understudied sensory modality is chemoreception (Yarmolinsky et al. 2009; Wyatt 2014; Li & Liberles 2015). Chemical ecology is a growing field of research that aims to elucidate the role of chemical interactions between organisms and their environment. Myriad animals use chemical cues in foraging, mate detection, mate attraction, and predator avoidance (Eisner & Meinwald 1996). Many of these animals have excellent vision or use other sensory modalities such as mechanoreception (auditory or vibratory) to perform some of the above functions yet also use chemoreception (Eisner & Meinwald 1996).

In species where males face the acute risk of pre-copulatory sexual cannibalism, such as many spiders (Elgar & Schneider 2004; Gav´ın-Centol et al. 2017), males might benefit from assessing female cues, as a female could be either a prospective mate or a potential predator. Thus, male spiders should be somewhat choosy if it means reducing the risk of being cannibalized before they can reproduce. It has been demonstrated that chemical cues produced by female spiders can contain information about female physiological state, which sometimes corresponds with female aggression (Roberts & Uetz 2005; Stoltz et al. 2007; Perampaladas et al. 2008; Johnson et al. 2011; Thomas 2011; Gav´ın-Centol et al. 2017). Thus, chemical cues could be one way for males to assess the likelihood of female aggression prior to approach. Supporting this idea, some male spiders alter their courtship behavior in response to chemical cues carried by air and/or in association with a mature female's silk (Schulz & Toft 1993; Aisenberg et al. 2010; Baruffaldi & Costa 2010, 2014; Johnson et al. 2011). It is possible that chemical cues play an important role in sexually cannibalistic spiders, even in species that largely rely on vision in courtship and foraging.

Jumping spiders (family Salticidae) often display colorful scales during energetic courtship dances, which are important in mate choice in some species (Li et al. 2008; Lim et al. 2008), but other sensory modalities are known to be involved in salticid courtship. In some species, females use mechanoreception to assess unique vibrations produced by males (Elias et al. 2004, 2005). Chemoreceptive capacity has been established in several salticid species (Jackson 1987; Clark & Jackson 1995; Clark et al. 2000; Hoefler 2007; Jackson & Cross 2011) but its behavioral role in courtship has been demonstrated most clearly in *Evarcha culicivora* Wesolowska & Jackson, 2003, a Kenyan mosquito specialist. *Evarcha culicivora* females prefer males that have recently fed on blood-filled female mosquitoes and are able to use airborne chemical cues to identify both mosquitoes that have recently ingested a blood meal and male conspecifics who have eaten such mosquitoes (Cross & Jackson 2009; Cross et al. 2009). *Evarcha culicivora* females appear to be unique in their reliance on male chemical cues; female salticids, in general, are less responsive to chemical cues produced by males than males are to chemical cues produced by females in most other species studied (Jackson 1987; Nelson et al. 2012). The predominance of chemical cue responsiveness in males suggests that most male salticids are not using chemical cues to attract mates but are perceiving and potentially using chemical cues produced by females during courtship.

The genus *Habronattus* F.O. Pickard-Cambridge, 1901 is one of the most speciose genera of salticids and is known for its wide array of elaborate courtship displays (Maddison & Hedin 2003a). Visual and vibratory signaling has been well-explored in *Habronattus* (Elias et al. 2004, 2005, 2012; Taylor et al. 2011, 2014), but so far there has been no work on chemoreception in this genus. We conducted two experiments in *Habronattus pyrrithrix* (Chamberlin, 1924) by assessing male response to chemical cues from virgin females. We designed these experiments to determine whether males respond to chemical cues at all and, if so, how these stimuli may be transmitted through the environment (e.g., whether they are airborne vs. substrate-borne). This information will serve as the foundation for future work on more biologically interesting questions, such as male preference for – or ability to distinguish between – chemical cues from different spider sources. Here, we first tested whether males responded to substrate-borne cues, such as may be detected from physically

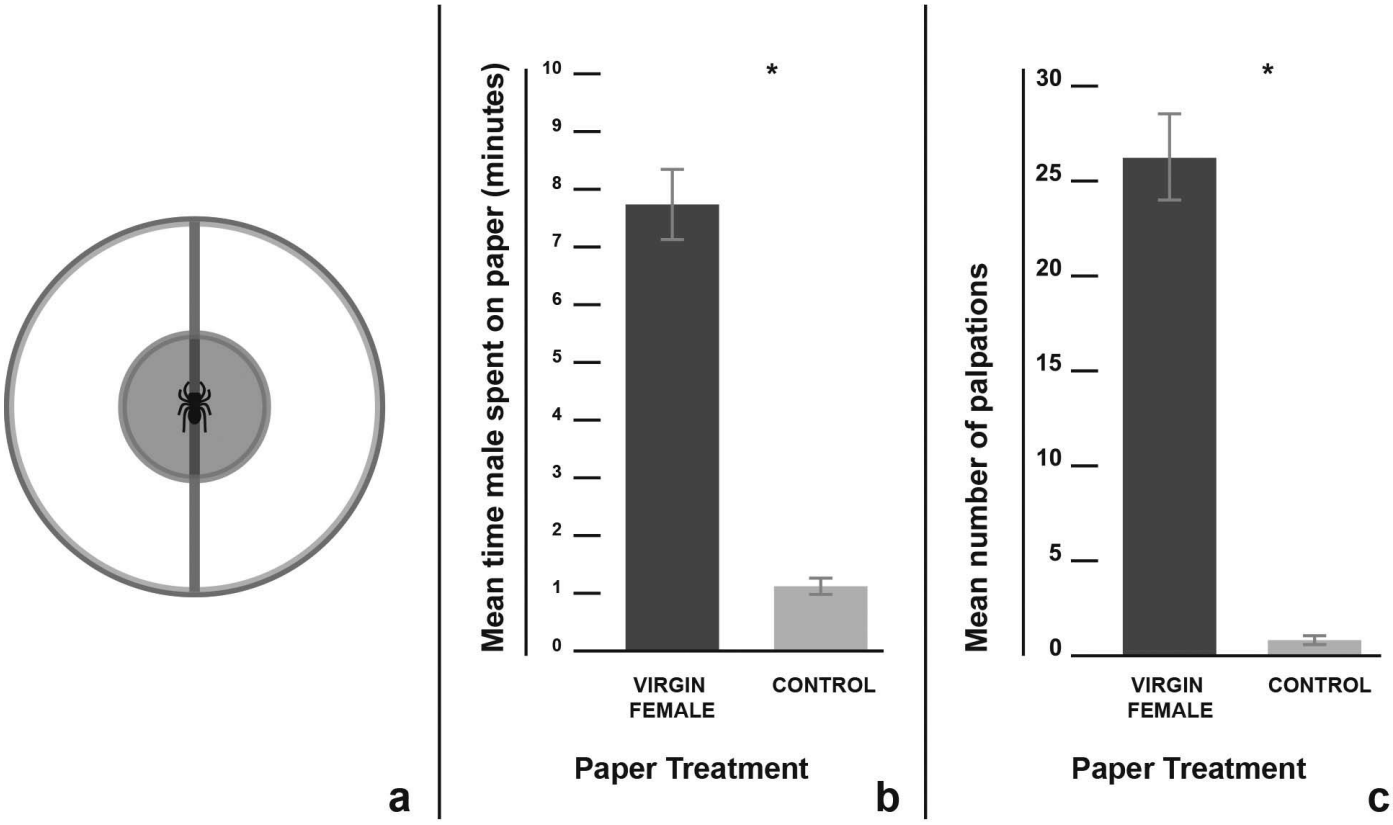

Figure 1.—(a) Experiment 1 arena used to test male *H. pyrrithrix* response to female chemical cues on filter paper vs. a no-odor control. Male shown in starting position in small 3 cm dish within large 9 cm dish; note that the placement (left vs. right) of the control and female-treated filter paper was randomized for each trial; (b) Results of Experiment 1 showing male response to virgin female chemical cues measured by time males spent (mean 6 SE) on female-treated filter paper vs. untreated (control) filter paper; and (c) the number of male palpation behaviors (mean 6 SE) on female-treated filter paper vs. untreated (control) filter paper. Asterisks indicate significant differences between treatment groups.

contacting female silk or excreta. Second, we tested whether males responded to airborne cues.

Because the role of chemoreception is not known in this genus, we began with an approach to determine whether males responded to substrate-borne chemical cues produced by virgin females (Experiment 1). We first provided male spiders with a surface they could traverse, half of which had previously been occupied by a virgin female; the other half, untreated. Because we could not disentangle the role of substrate-borne cues from airborne cues using this method, we then narrowed our scope to determine whether males could detect chemical cues via airborne cues exclusively. Our second experiment (Experiment 2) was performed using an olfactometer to test male response to virgin female airborne cues alone. Both experiments were conducted using different groups of *H. pyrrithrix* collected in Queen Creek, Arizona (n ¼ 223; 138 females, 85 males). All females used in these experiments were captured as juveniles or penultimates and maintained in the lab until maturity, thus ensuring their status as virgins. Virgin females were used in experiments when their ages ranged from 7–14 days post-maturity, as this appears to be the period in which females of this species are highly receptive (L. Taylor; M. Ihle, unpublished data). We chose to use virgin females in both experiments because virgin female cues have been shown to elicit the strongest male response in other salticid species when tested against other spider-produced chemical cues (Jackson 1987; Clark & Jackson 1995; Hoefler 2007; Cross & Jackson 2009). It should be noted that the video analyses for both experiments were conducted blind, as trial identifiers contained no information to reveal the treatment of each side, and treatments were randomly assigned to each side when preparing each trial. When data were input during video analysis, each observation was recorded as 'right' or 'left' rather than 'female' or 'control'. Only after all videos were analyzed did we sync the individual observations to the database metadata and generate totals for each treatment by trial.

In Experiment 1, we conducted trials to test male response to substrate-borne chemical cues produced by virgin females vs. a no-odor control. Male spiders (n ¼ 34) were placed in the center of a 9 cm petri dish with two half-pieces of filter paper (one female-treated and one control) (Fig. 1a). The female-treated paper was prepared by placing a virgin female spider (n ¼ 17) in a clean, unused petri dish lined with filter paper upon which she could deposit silk and other excreta for 24 hours (following methods in Persons et al., 2001). Immediately after the filter paper was removed from the female's dish, it was cut in half and divided between two clean, unused 9 cm petri dishes and paired with a piece of clean filter paper (no-odor control). The two halves of filter paper were separated by 2 – 4 mm to ensure female chemical cues were not transferred to the no-odor control paper. Each of these new 9 cm dishes constituted a test arena. Each female provided treated paper for two trials, but because each male was only used for one trial, no male-female pairing was repeated. The side of the dish (left vs. right in relation to the camera) to which each paper treatment was assigned was randomized in each trial to ensure there was no side bias. Trials were conducted within 5 minutes of arena preparation. A male spider was placed in a smaller 3 cm lidded petri dish which was then placed in the center of the larger petri dish, allowed 1 minute for acclimation, and released. The bottom of the 3

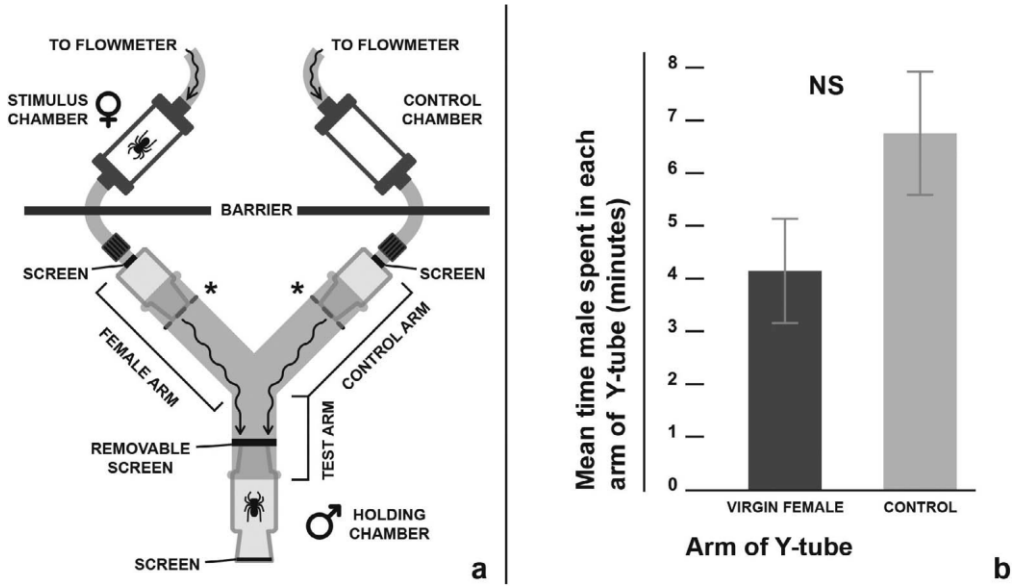

Figure 2.—(a) Experiment 2 olfactometer (not drawn to scale) used to test male *H. pyrrithrix* response to airborne female chemical cues vs. a no-odor control. Male is shown in the starting position in the holding chamber before the removable screen was raised to release male into the test arm. Asterisks indicate a visually identifiable boundary at which the spider was considered to have entered the female arm or control arm. Note that the position of the stimulus (female) and control chambers were randomized for each trial; (b) Results of Experiment 2 showing the time males spent (mean 6 SE) in the female-treated stimulus arm vs. the no-odor control arm of a Y-tube olfactometer. NS indicates no significant difference between the two arms.

cm petri dish remained in the center of the larger one, providing a cue-free starting point (Fig.1a).

These tests were recorded for video analysis to determine whether males responded to chemical cues produced by females. A trial began once the spider left the 3 cm petri dish and touched either piece of filter paper (Fig. 1a). Videos were analyzed for 30 minutes after that time point. We measured the total time that males spent on each filter paper treatment and the instances of palpating behavior per paper treatment to determine male preference. An instance of palpating behavior was recorded each time the male used both pedipalps (which are known to possess sensory hairs (Gaskett 2007)) to probe the substrate, and typically involved the male alternating between pedipalps for 1–3 seconds before moving to a new location. This behavior has been observed by males in relation to female nest silk in other salticid species (Jackson 1987; Jackson & Macnab 1989), lycosids (Hebets et al. 1996), and several other taxa (reviewed in Gaskett 2007). Once a male ceased palpation or changed location, any subsequent palpation was recorded as a separate instance. There was no evidence of male courtship behavior observed during trials. The time males spent on the rim or lid of the arena was not recorded, as female spiders had never contacted these surfaces.

All 34 males contacted both pieces of filter paper at some point during the 30-minute trials; 32 (94%) did so within the first 15 minutes. Males spent significantly more time on the female-treated paper (7.7 6 0.61 minutes) versus the no-odor control (1.1 6 0.14 minutes; paired t-test, t_{33} ¼ 0.9, P , 0.0001; Fig. 1b). Males also exhibited more instances of palpating behavior on the female-treated paper (26 6 2.3 palpations) than they did on the control paper (0.82 6 0.23 palpations; paired t-test, t_{33} ¼ 11, P , 0.0001; Fig. 1c). This suggests that males were able to detect and were motivated to explore chemical cues laid down in female silk and excreta.

In light of the finding that female silk and/or excreta elicited a significant male response, we proceeded to examine the role of airborne cues in a second experiment (Experiment 2) using a new group of *H. pyrrithrix*. We used a Y-tube olfactometer (Fig. 2a) similar to those used in previous salticid studies (e.g., Jackson et al. 2005; Cerveira & Jackson 2011) set at a flow rate of 1.2 L/minute (CADS-4Push 4-Port Clean Air Delivery System, Sigma Scientific LLC, Micanopy, FL, USA). This flow rate did not appear to disrupt normal spider behavior or locomotion. All olfactometer components were connected by ¼-inch polyethylene tubing. We used transparent casing from universal clear-view in-line fuel filters (Part # 33318-10, Moeller Marine Products, Inc., Sparta, TN, USA) as stimulus and control chambers, as these are hollow, airtight, and could be easily removed, disassembled for cleaning, and replaced using push-to-connect ¼-inch tube fittings. We used a smoke wick to visually confirm that airflow was lamellar, and that the apparatus was free of leaks. Clean, filtered air was pushed through two separate flowmeters into a stimulus chamber and a control chamber, then into the corresponding source arms of the Y-tube and down into the central test arm. This airflow was maintained for one minute prior to introducing a spider to ensure that air entering the Y-tube at the onset of trials had been exposed to the source chambers.

We prepared stimulus chambers by placing adult virgin female spiders (n ¼ 29) inside with a strip of filter paper one week prior to tests to allow sufficient time and surface area for nest-building and the accumulation of chemical cues. We fed females twice during this preparation phase, briefly removing them from chambers each time to prevent the introduction of prey odorants. Their diet consisted of newly emerged crickets *(Gryllodes sigillatus)* amounting to each spider's approximate mass. Control chambers contained a strip of filter paper only (with no spider). We connected each chamber to a flowmeter and a source arm of the Y-tube one minute prior to each trial. These chambers were hidden behind an opaque barrier to block them from the test spider's view. We placed one male spider (n¼ 29) in a glass holding chamber fitted with screens to allow airflow while preventing escape and placed this at the stem end of the Y-tube (test arm). Treatment and control arms were randomly assigned in each trial to ensure there was no side bias. No males or females were used more than once in Experiment 2.

The trial began once we removed the screen barrier between the test arm and the holding chamber to release the spider after a one-minute

acclimation period. We recorded each trial for 30 minutes, after which the entire apparatus was dismantled and cleaned with deionized water and 80% ethanol (per Jackson & Cross, 2011) to ensure residual chemical cues did not interfere with future trials. We then analyzed the videos to determine the total time each male spent in the stimulus (female) arm vs. the control (odorless) arm. The time a spider spent in an arm was recorded from the moment it crossed a visually identifiable boundary located at a ground glass joint 2.5 inches up the length of the arm (62.5% total length of arm) (Fig. 2a). One trial was omitted because the spider did not enter either source arm. Because it is uncertain how accurately jumping spiders can detect and trace an odor source, we ran two separate paired t-tests, one including all spiders and one which only included spiders that entered each source arm at least once. We did this to ensure that males had sampled both options in case they were unable to follow the scent up the Y-tube into the corresponding arm and were entering the first arm at random and staying there.

We observed no difference between the time males spent in the female arm (4.1 6 0.99 minutes) versus the control arm (6.8 6 1.2 minutes; paired t-test, t_{28} = 1.5, P = 0.15; Fig. 2b) when considering all males. Only 15 of 29 male spiders visited both arms during the 30-minute trials. Of the 15 males that visited both arms at least once, there was no difference in the time spent in the female arm (4.7 6 0.91 minutes) and the control arm (7.05 6 1.3 minutes; t_{14} = -1.5, P = 0.17). The first arm entered appeared to be random (Chi-square, goodness-of-fit, X^2 = 0.31; P = 0.58). This suggests that males did not respond to female airborne chemical cues in this context. This appears to be a true null result and not just an undetected weak effect, as they were in the direction opposite expectation (i.e., in the direction of more time in the control arm compared with the female arm). Moreover, our sample sizes matched or exceeded those used in many similar studies with highly significant results (Clark et al. 2000; Jackson & Cross 2011; Cerveira & Jackson 2013). Further, the manufacturer of the olfactometer (Sigma Scientific, LLC, Micanopy, FL, USA) reviewed the recording of the smoke test we performed and confirmed that the instrument exhibited proper lamellar flow, so this result is unlikely to be due to improper performance of the equipment.

Taken together, our findings from both experiments suggest that *H. pyrrithrix* males were able to detect chemical cues produced by females, but that males did not respond to airborne cues alone. Other salticid species (e.g., *Portia fimbriata* (Doleschall, 1859), *Portia labiata* (Thorell, 1887), *Portia schultzi* Karsch 1878, *Lyssomanes viridis* (Walckenaer, 1837), *Cyrba algerina* (Lucas, 1846)) have been shown to respond to airborne cues produced by conspecific females using methods similar to those used in our study (Jackson 1987; Pollard et al. 1987; Willey & Jackson 1993), so this result was unexpected. However, the taxa in which this response has been demonstrated are largely arboreal Old World species which tend to remain sessile and likely rely on airborne compounds to locate conspecifics from a distance (Nelson et al. 2012). Thus, it has been hypothesized that use of olfaction may be reduced in the roving Salticoid clade, of which *Habronattus* is a member (Nelson et al. 2012). We cannot conclude that male spiders responded solely to substrate-borne cues, as airborne cues were almost certainly present (and perhaps abundant) in the filter paper experiment (Experiment 1). Whether spiders responded to these airborne cues cannot be determined from these experiments, and it is possible that males responded to the combination of substrate-borne and airborne chemical cues rather than either in isolation.

The lack of male response in the olfactometer experiment is also consistent with an alternative hypothesis, which is that males responded to the physical structure of the silk itself rather than the chemical cues embedded therein. This tactile attraction to spider silk, known as sericophily (Fischer 2019), could be disentangled from chemoreception with additional behavioral assays, such as testing male response to female silk with or without chemical cues (i.e., unwashed silk vs. silk washed with a solvent to remove cues). Alternatively, the possibility of sericophily might be addressed by testing male response to silk produced by females we would expect, *a priori,* to differ in attractiveness (e.g., conspecific vs. heterospecific, mated vs. virgin, etc.), though a positive response to both cues could be due to either sericophilly or that both cues are perceived as equally attractive. Steps are being taken to determine which properties of female silk/excreta are relevant to males in a closely related congener, *Habronattus brunneus* (Peckham & Peckham, 1901). Initial tests indicate males can adeptly and consistently discriminate between two superficially similar silk samples produced by female spiders of different treatment groups (unpublished data). Although this finding concerns a different species, we submit that the close phylogenetic proximity of *H. brunneus* to *H. pyrrithrix* allows us to say with some confidence that male *H. pyrrithrix* in this study were likely responding to chemical cues produced by females.

Habronattus pyrrithrix males may use substrate-borne chemical cues incorporated in the dragline silk deposited by females to locate potential mates, or even to assess characteristics of the female who deposited the silk, as has been observed in other spider taxa. Wolf spiders (Family: Lycosidae) use chemical cues from other spiders' dragline silk to identify conspecifics (Roberts & Uetz 2004), distinguish adult females from juvenile females and males (Bell & Roberts 2017), assess the feeding history of a predatory lycosid species (Searcy et al. 1999), and even determine whether a conspecific female had recently interacted with that predator (Sweger et al. 2010). Chemical cues allow males to discern coarse information such as the sex and species that produced the cues, but they could also allow males to assess a female's receptivity or other features of her physiology. This information could allow males to avoid courting females that are more likely to attack and potentially cannibalize them. Interestingly, male *Habronattus* have been observed to misdirect courtship toward heterospecific females in the lab and in the field (Taylor et al. 2017), yet it is unclear what sensory information is used to make these courtship decisions. The interaction of chemical cues with stimuli of other sensory modalities (e.g., female visual and/or vibratory cues) warrants further investigation. The finding that *H. pyrrithrix* males can detect chemical cues produced by virgin females is the first step in understanding the role of chemoreception in this charismatic genus, which has recently become a well-studied model for understanding the evolution of multimodal courtship displays (Maddison & Hedin 2003b; Elias et al. 2005, 2006, 2012; Hebets & Maddison 2005; Taylor et al. 2011, 2014, 2017; Zurek et al. 2015; Leduc-Robert & Maddison 2018).

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DATA AVAILABILTY

All raw data from this study are freely available on Dryad, online at https://doi.org/10.5061/dryad.c59zw3r65

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