Ichthyology & Herpetology 112, No. 2, 2024, 238–256

Courtship and Mating Behavior of the Rare, Rock-Crevice Dwelling Salamander *Plethodon petraeus* with a Review for Eastern North American Woodland Salamanders (Amphibia: Plethodontidae)

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I describe courtship and mating of the plethodontid salamander *Plethodon petraeus* (Pigeon Mountain Salamander), which is a member of the *P. glutinosus* group (PGG) of eastern species of *Plethodon* (EP). Individuals exhibit adaptions for enhanced climbing ability and inhabit moist crevices of rock outcrops and cave openings within a very limited range in northwestern Georgia (USA). Courtship involves a unique blend of behaviors known for species in the PGG, *P. cinereus* group (PCG), and *P. welleri* group (PWG) of EP. Compared to most species in the PGG, there are notable differences during both the tail-straddling walk (TSW) and the period that precedes the TSW ('pre-TSW phase'). Males exhibit both 'foot dance' and 'foot shuffle.' Frequent, high-amplitude mental-gland 'popping' by males during mental-gland sliding may be due to more-adhesive skin or mental-gland secretions. Olfactory delivery of pheromones is absent or rare because mental-gland contact to the female's nares is absent or very infrequent during the pre-TSW phase and absent (or rare) during the TSW. Two forms of the duet behavior 'female-first tail-straddling walk' (ffTSW) occur during the pre-TSW phase: a discontinuous form during most courtships and a continuous form during some courtships. Infrequent 'mouth grasping' by males may be a facultative behavior that promotes transdermal pheromone delivery to less-receptive females. Very similar to some species in the PCG and PWG, the female initiates contact leading to the TSW in most courtships via turning back during ffTSW. If mating occurs within the protection of rock crevices, then reduced predation pressure or mate competition may have permitted the evolution of the relatively prolonged courtship (mean about 5 h). Results indicate that the detailed study of additional species will help refine current ideas about the evolution of courtship behavior in EP and perhaps other plethodontid clades.

THE majority of extant salamander species have internal fertilization, but since males lack an intromittent organ, sperm transfer into the female's cloaca occurs via a spermatophore, which consists of a sperm cap that surmounts a gelatinous base attached to the substrate (Noble and Brady, 1930; Salthe, 1967). In salamanders of the family Plethodontidae, a stereotypical sequence of courtship behaviors increases the likelihood of successful sperm transfer (Houck and Arnold, 2003). After finding a potential mate via olfaction (Dawley, 1984; Dantzer and Jaeger, 2007a), salamanders exchange information via a combination of visual, tactile, and chemical cues, which likely allows each individual to assess the suitability of its potential mate (Dantzer and Jaeger, 2007b; Eddy et al., 2012; Staub et al., 2020). If the female is receptive to mating, then the pair engages in a tail-straddling walk (TSW), a duet behavior in which the female straddles the male's tail, with her chin on his tail base, as they walk forward until the male stops and deposits a spermatophore (Noble and Brady, 1930; Arnold, 1977). The TSW ensures that spermatophore deposition occurs directly in front of the female's snout (Arnold, 1977). The pair then performs a duet behavior where the male leads the female directly over the spermatophore as she maintains chin contact with his tail base. When the female detects the sperm cap at her vent, she stops walking forward and lowers her vent onto the sperm cap. During sperm cap retrieval, the male extends his hind-legs to lift his pelvis while his tail base remains beneath her chin (Houck and Arnold, 2003). Many researchers describe the period that precedes the TSW as either the 'persuasion phase' (in which the male 'persuades' the female to mate; Verrell, 1999) or the 'head-contact phase' of courtship (e.g., Staub et al., 2020). However, since such terminology could imply that the female is not an active participant in courtship (Staub et al., 2020) or that contact exclusively involves heads, I refer to behavioral interactions that precede the TSW as the 'pre-TSW phase' of courtship. In contrast to the highly conserved evolutionary history of behavior during the TSW and sperm-transfer phase, behavior patterns that occur during the pre-TSW phase exhibit relatively rapid evolutionary change in plethodontid salamanders (Arnold et al., 2017).

Although a combination of various signals is likely important for courtship in plethodontid salamanders (Arnold et al., 2017; Staub et al., 2020), research has focused primarily on the functional importance of mental-gland pheromones (Houck, 1986). The transfer (delivery) of courtship pheromones from glands on the chin of the male (mental gland) to the female can increase female receptivity and reduce courtship duration (Sever, 1976; Houck and Reagan, 1990; Eddy et al., 2012). Observational and experimental studies for species of *Desmognathus*, *Plethodon*, and *Aneides* demonstrate that a male can deliver mental-gland pheromones to the female in different ways (Arnold and Houck, 1982; Sapp and Kiemnec-Tyburczy, 2011). In some species, a male may indirectly introduce pheromones into the female's bloodstream via application of mental-gland secretions to her skin to allow diffusion through the epidermis (Houck and Reagan, 1990). In many species, the male can more directly introduce pheromones into the female's bloodstream by rubbing his mental gland over her skin while performing 'pulling' or 'snapping' movements to abrade her skin with premaxillary teeth, which is termed either 'vaccination' delivery (Arnold and Houck, 1982) or 'transdermal' delivery (Arnold et al., 2017). Similarly, in

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Submitted: 15 September 2023. Accepted: 9 April 2024. Associate Editor: D. S. Siegel.
 DOI: 10.1643/h2023077 Published online: 19 July 2024

some species of *Desmognathus*, the male can use specialized mandibular teeth to bite and hold the female while introducing pheromones through skin perforations (Promislow, 1987; Verrell, 1999). In some species of *Plethodon*, the male contacts the female's nares with his mental gland to transfer pheromones to her vomeronasal system, which is termed 'olfactory' delivery (Arnold and Houck, 1982). However, pheromone delivery is not required for courtship success, because *Desmognathus* and *Plethodon* males without mental glands (i.e., experimentally de-glanded) can still successfully court and mate (Houck and Reagan, 1990; Rollmann et al., 1999; Eddy et al., 2012). Nonetheless, because courtship duration is significantly longer for males without a mental gland, certain selective pressures in natural environments (e.g., mate competition and predation pressure) may often favor a reduced courtship duration that results from pheromone delivery (Houck et al., 1998; Eddy et al., 2012).

The mode and timing for delivery of mental-gland pheromones changed during the evolution of different lineages of *Plethodon* in eastern North America (i.e., species of eastern *Plethodon* hereafter referred to as EP; Houck and Arnold, 2003). Molecular analyses of mental-gland pheromones indicate sexual selection affects such courtship diversity (Palmer et al., 2005; Kiemnec-Tyburczy et al., 2009). Courtship descriptions are available for species within three clades of EP named the *P. cinereus* group (hereafter PCG), *P. welleri* group (PWG), and *P. glutinosus* group (PGG; Kozak et al., 2006; Fisher-Reid and Wiens, 2011). Two species in the PCG utilize pulling and snapping during the pre-TSW phase for transdermal delivery of pheromones (Arnold, 1972; Dyal, 2006). Because such transdermal delivery also occurs in *Aneides* and *Desmognathus*, this is likely the ancestral trait for EP (Arnold et al., 2017). In contrast, several species in both the PWG and PGG primarily use the olfactory delivery mode to stimulate vomeronasal neurons (Picard, 2005). However, the timing of olfactory delivery varies among species. Delivery occurs primarily during the pre-TSW phase for some species in the PWG (Picard, 2005; Dyal, 2006). For the PGG, the timing of delivery varies much among species (Arnold, 1972; Marvin and Hutchison, 1996; Arnold et al., 2017). One hypothesis is olfactory delivery during the TSW was ancestral in the PGG, but was reduced or lost in the evolution of some species and became common during the evolution of other species (Picard, 2005). Because observations of behavior during complete courtships with TSW and sperm transfer are available for less than 25% of EP, the detailed study of additional species will help to evaluate current hypotheses and possibly generate new hypotheses concerning the evolution of courtship behavior within this speciose clade.

The Pigeon Mountain Salamander (*P. petraeus*) is a member of the PGG (Wynn et al., 1988; Kozak et al., 2006; Fisher-Reid and Wiens, 2011). Because the species has a highly restricted range within topographical gulfs on the eastern flank of Pigeon Mountain in northwestern Georgia (USA), the state protects it as a 'rare' species (Jensen, 1999). Individuals are patchily distributed, but locally abundant, within moist crevices of rock (sandstone/limestone) outcrops and cave openings/vents (Jensen et al., 2002). In comparison to most EP, individuals have relatively long limbs, large feet with blunt toes and extensive webbing between the digits, which are likely adaptations that improve climbing ability (Wynn et al., 1988). As for many other EP, adults are sexually dimorphic with females reaching significantly larger body sizes than males (Wynn et al., 1988; Marvin, 1996, 2001, 2009; Jensen et al., 2002). Individuals become sexually mature at a body size of about 56 mm snout–vent length (SVL) for males and 65 mm SVL for females (Jensen et al., 2002). Based on seasonal variation in the morphology of testes and vasa deferentia, and in levels of activity for mature individuals in the field, Jensen et al. (2002) proposed that mating occurs during the late winter and/or spring. In the current study, I observed courtship behavior and mating to (1) confirm the mating season, (2) provide additional reproductive information that may be useful for species conservation (e.g., captive breeding), (3) investigate whether microhabitat specialization may affect courtship, and (4) further examine variability in courtship behavior among EP. Thus, I also provide a review of courtship behaviors previously described for EP. Due to the extreme difficulty of performing detailed observations of courtship in the field, I describe the behavior of individuals maintained in the laboratory. Observations for some EP indicate courtship behaviors are equivalent in the field and laboratory, except perhaps for minor differences in the frequency of some behaviors (Gergits and Jaeger, 1990; Dyal, 2006; Pierson et al., 2017).

MATERIALS AND METHODS

Animal collection and care.—I collected 24 adults (4 females and 4 males each year) of *P. petraeus* from mid-March to early May during 2013, 2014, and 2015. The mean standard body length (snout–vent length [SVL] measured from snout tip to posterior angle of the vent) was 77.7 mm (SE = 1.47, range = 68 to 85) for females and 72.6 mm (SE = 0.82, range = 69 to 78) for males. Mean body mass was 8.6 g (SE = 0.37, range = 6.3 to 9.9) for females and 6.5 g (SE = 0.13, range = 5.9 to 7.3) for males. Mean tail length was 83.7 mm (SE = 2.58, range = 64 to 92) for females and 80.3 mm (SE = 1.55, range = 67 to 89) for males.

At the University of North Alabama, I maintained salamanders inside environmental chambers at 16°C with a simulated natural photoperiod from mid-March to early July each year. I cared for animals in accordance with the ASIH Guidelines for Live Amphibians and Reptiles in Field and Laboratory Research (https://bit.ly/ASIH_Herps). I kept individual males in plastic shoeboxes (32 × 17 × 10 cm) and individual females in Plexiglas 'courtship arenas' (32 × 21 × 6 cm). I lined each salamander container with a clean, damp paper towel substrate each week. For prey, I placed two small crickets and many vestigial-wing *Drosophila* in each salamander container every week. I removed uneaten prey items from containers after 18 h.

Staging courtship encounters.—From early May to early July, I staged 16 courtship encounters each year (i.e., for 48 encounters in the study) by gently transferring a single male into the courtship arena of a female that had deposited body secretions and fecal pellets on the substrate for 4 d. I placed courtship arenas in front of a white-cardboard background with dark, vertical lines at 5 cm intervals. I used these vertical lines to estimate the distance between individuals and the distance traveled during tail-straddling walks. I began all courtship pairings at the start of the scotophase under indirect illumination from a 25 W incandescent white-light bulb positioned 1 m from the animals. I video recorded each courtship encounter for 13 h with a Sony HDR-SR12 digital HD video camera recorder using the low light (NightShot) recording mode.

I used individuals in more than one courtship pairing; however, each individual pair was unique. For salamanders that courted, the mean number of times that each individual courted was 1.6 for males (SE = 0.19, range = 1 to 3) and 2.0 for females (SE = 0.39, range = 1 to 4). The minimum time interval between successive pairings for each individual was 7 d. For individuals involved in multiple courtships, the mean time interval between successive courtships was 16.2 d for males (SE = 3.5, range = 7 to 38, $n = 7$) and 11.3 d for females (SE = 1.2, range = 7 to 17, $n = 10$). As required by scientific collecting permits, I released each individual at its capture locality following courtship observations each year. To reduce the potential risk of introducing pathogens into wild populations from individuals held in captivity, I disinfected salamander containers each week with 70% ethanol for at least 1 min.

Analysis of behavior and statistical comparisons.—For the description and analysis of behavior, I thoroughly reviewed video recordings of ten complete courtships with ≥1 TSW and spermatophore deposition, and ten incomplete courtships in which salamanders courted but did not mate. I quantified the frequency of each behavior and the duration for sustained behaviors that lasted ≥1 sec. I measured the duration of 'apart' periods when salamanders were more than about 2.5 cm apart after their initial encounter and the duration of 'close' periods when salamanders were within about 2.5 cm of each other but not in sustained contact via the mental gland. I measured the duration of the pre-TSW phase as the period from the initial encounter between salamanders to the beginning of the TSW, excluding total time apart. To examine possible differences between complete and incomplete courtships in the frequency or duration of behaviors during the pre-TSW phase of courtship, I statistically compared the frequency or total duration of each behavior per pre-TSW hour. I checked data for normality and equal variance and used non-parametric statistical tests when appropriate. I report means ±1 SE unless stated otherwise.

For incomplete versus complete courtships, I compared: (1) the frequency of some male behaviors, (2) the total duration for some behaviors and periods, (3) the duration of mental-gland sliding on different anatomical regions, and (4) the frequency of some female behaviors. For some of these multiple statistical comparisons (#2 and 4 listed above), I used sequential Bonferroni adjustment (Rice, 1989) to conclude statistical significance for multiple probability values less than 0.05. To examine possible correlations between the frequencies and/or durations of some behaviors, I performed Pearson Product Moment correlations and then used sequential Bonferroni adjustment to conclude statistical significance for multiple probability values less than 0.05. For each sex, I compared body length (SVL) for individuals involved in complete versus incomplete courtships. To examine possible differences in body condition (i.e., mass in relation to body length) for individuals involved in complete versus incomplete courtships, I performed ANCOVA for log-transformed body mass with SVL as the covariate.

Review of courtship behaviors for EP.—For *P. petraeus*, the most closely related extant species may be *P. kentucki* (Kozak et al., 2006; Fisher-Reid and Wiens, 2011), and thus a comparison of courtship similarities and differences between these two species could help examine the evolution of some behaviors. To observe more closely some of the courtship behaviors for *P. kentucki* as part of my review for EP (i.e., behaviors similar to those observed in *P. petraeus* but not previously reported in detail), I digitized and reviewed videotape recordings for 12 randomly selected complete courtships from Marvin and Hutchison (1996). For 12 randomly selected courtships in *P. petraeus*, I compared the frequency of rear-leg movement during 'foot dance' to that observed during courtship in *P. kentucki*. In addition to providing descriptions of courtship behaviors for all EP studied to date (in the results and Appendix 1), I produced supplemental videos (see Data Accessibility for all supplemental videos) of most behaviors in *P. petraeus* and *P. kentucki* (listed in Appendix 2) to permit the visual comparison of courtship behaviors among plethodontid species (Arnold et al., 2017). I also reviewed the species occurrence of all courtship behaviors in EP (Table 1) for evaluation in a phylogenetic comparative context.

RESULTS

Mating season and body size comparisons for *P. petraeus*

Individuals of *P. petraeus* courted and mated in the laboratory from early May through early July. Thus, field data (Jensen et al., 2002) and my laboratory observations indicate that the mating season extends from late winter to early summer. For ten females involved in courtships, six engaged in complete courtships and seven engaged in incomplete courtships. For 12 males involved in courtships, nine engaged in complete courtships and seven engaged in incomplete courtships. For both females and males, there was no significant difference in body length for individuals that engaged in complete versus incomplete courtships (Mann-Whitney rank sum tests: $U = 16.5$, $T = 46.5$, $P = 0.534$ for females; $U = 30.0$, $T = 61.0$, $P = 0.915$ for males). There was no significant difference in body condition for males that engaged in complete versus incomplete courtships (ANCOVA: $F = 0.05$, $P = 0.826$ for intercepts; $F = 0.13$, $P = 0.725$ for slopes); however, body condition was significantly greater for females that engaged in complete courtships (ANCOVA: $F = 6.46$, $P = 0.029$ for intercepts; $F = 1.89$, $P = 0.202$ for slopes).

Catalogue of courtship behaviors for *P. petraeus*

Behaviors exhibited by both sexes.—**Nose-tap:** Individual taps the nasolabial region of its snout on the substrate, skin of another salamander, or a spermatophore (Supplemental Videos 1 and 29). **Move toward:** Individual moves toward and its head comes close to (i.e., within about 2.5 cm of) the other salamander (Supplemental Video 2). **Move away:** Individual moves away until its head is more than about 2.5 cm from the other salamander (Supplemental Video 1). **Stationary:** Individual does not move away when the other salamander moves toward and comes close or makes contact (Supplemental Video 2). **Head contact:** Head contacts the head of the other salamander (e.g., cheek-to-cheek or snout-to-cheek contact). **Nudge:** Individual moves its snout

Table 1. Courtship behaviors of eastern North American woodland salamander species (eastern *Plethodon*). Species groups: PCG = *P. cinereus* group, PWG = *P. welleri* group, and PGG = *P. glutinosus* group. Species: *ci* = *P. cinereus*, *ri* = *P. richmondi*, *we* = *P. welleri*, *an* = *P. angusticlavius*, *do* = *P. dorsalis*, *yo* = *P. yonahlossee*, *ke* = *P. kentucki*, *pe* = *P. petraeus*, *ou* = *P. ouachitae*, *ca* = *P. caddoensis*, *sh* = *P. shermani*, *cy* = *P. cylindraceus*, and *mo* = *P. montanus*. MG = mental gland, TSW = tail-straddling walk, F = female only behavior, M = male only behavior, FM = each sex exhibits behavior, and D = duet behavior with both female and male actions. *Rare or infrequent occurrence of behavior. [d]Behavior may differ from similar behavior in other species. ? = occurrence of behavior is uncertain due to absent or limited observations. Blank cell (–) = behavior not reported. See text and Appendix 1 for the description of each behavior.

	Groups and species of eastern *Plethodon*												
	PCG		PWG			PGG							
Behaviors	*ci*	*ri*	*we*	*an*	*do*	*yo*	*ke*	*pe*	*ou*	*ca*	*sh*	*cy*	*mo*
1. Nose-tap, 2. Stationary, 3. Move away	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM
4. Move toward, 5. Head contact, 6. Nudging	FM	FM	F*M	FM	F*M	F*M	FM	F*M	F*M	F*M	F*M	F*M	F*M
7. Bite	–	–	–	–	–	–	F*M	F*M	M	–	M	–	M
8. Foot dance	–	–	–	–	–	M*	M	M[d]	M	M	F*M	M	F*M
9. Foot shuffle	F	–	–	M	M	–	–	M*	–	–	–	–	–
10. Tail wagging	FM	FM	M	FM	FM	–	–	–	–	–	–	–	–
11. Rubbing/sliding, 12. Head rubbing	FM	FM	–	FM	M	–	–	–	–	–	–	–	–
13. Head swinging	M	M	–	–	–	–	–	–	M	M	–	–	–
14. Joint head swinging	–	D*	–	–	–	–	–	–	–	–	–	–	–
15. High amplitude head swinging	F	F	–	–	–	–	–	–	–	–	–	–	–
16. Cloacal nudging	FM	FM	–	FM	–	–	–	–	–	–	–	–	–
17. Cloacal rubbing	F	?	–	?	–	–	–	–	–	–	–	–	–
18. MG sliding (head sliding)	M	M	M	M	M	M	M	M	M	M	M	M	M
19. MG popping	–	–	–	–	–	–	M*	M	M*	–	M*	M*	M*
20. MG tap or swipe on snout *before 42*	–	–	–	–	M	–	M	–	–	–	M*	M*	M*
21. MG tap or swipe not on snout	–	–	–	–	–	–	M*	M*	–	–	–	–	–
22. Tail (or body*) flex *in response to 18*	–	–	–	–	–	–	–	F	–	–	–	–	–
23. Tail arch, 24. Undulate tail	FM	FM	M	FM	M	M	F*M	FM	M	M	F*M	M	F*M
25. High amplitude tail undulations	F	F	–	?	–	–	–	F	–	–	–	–	–
26. Snapping	M	M	–	–	–	–	–	–	–	–	–	–	–
27. Pulling	M	FM?	–	–	–	–	–	–	–	–	–	–	–
28. Mouth grasping	–	–	–	–	–	–	–	M	–	–	–	M	–
29. Snout high	–	–	–	–	–	–	F*	F	–	–	–	–	–
30. Chin-to-chin	–	–	–	–	–	–	D	–	–	–	D*	–	–
31. Tail straddle *for 32 or 33*	M	M	–	M	M*	–	–	M	–	–	–	–	–
32. Discontinuous, female-first TSW	–	–	–	–	–	–	D[d]*	D	–	–	–	–	–
33. Continuous, female-first TSW	D	D	–	D	D*	–	D[d]*	D	–	–	–	–	–
34. Turn back *during 18, 32, or 33*	F	F	–	F	–	–	F	F	–	–	F*	–	F*
35. Circling	D	D	–	D	–	–	D[d]*	D[d]	–	–	–	–	–
36. Snout under (lifting, crossing under)	M	M	M	M	M	M	M	M	M	M	M	M	M
37. Raise chin *in response to 36 or before 38*	F	F	F	F	F	F	F	F	F	F	F	F	F
38. Chin over	F	F	–	F	F	F*	F	F	F*	?	F*	F*	F*
39. Position for TSW	M	M	M	M	M	M	M	M	M	M	M	M	M
40. Turn around *after 39 or 53*	M	?	M	M	M	M	M	M	M	M	M	M	M
41. Tail straddle *to initiate 42*	F	?	F	F	F	F	F	F	F	?	F	F	F
42. Tail-straddling walk	D	?	D	D	D	D	D	D	D	?	D	D	D
43. Turn back *during 42*	M*	?	–	M*	–	M	M	–	–	?	M	M	M
44. Raise head *to receive 45*	–	?	–	–	–	–	F	–	–	?	F	–	F
45. MG slapping on snout *during 42*	–	?	–	M*	–	M	M	–	–	?	M	M	M
46. Vent sliding *at end of 42*	–	?	–	–	–	M	M	M	M	?	M	M	M
47. Spermatophore deposition	M	?	M	M	M	M	M	M	M	?	M	M	M
48. Lateral head movements *during 47*	–	?	F*	–	–	–	–	–	–	?	F*	–	F*
49. Lead female over spermatophore	D	?	D	D	D	D	D	D	D	?	D	D	D
50. Pass by spermatophore	F	?	?	F	F*	F*	F	?	F*	?	F*	F*	F*
51. Stop & lower vent, 52. Position on cap	F	?	F	F	F	F	F	F	F	?	F	F	F
53. Stationary with tail flexed	M	?	M	M	M	M[d]	M	M	M	?	M	M	M
54. Eat spermatophore cap and/or base	–	?	–	–	M	–	M	M	M	?	M	–	M
Species reference number for source(s)	1	2	3	4	5	6	7	8	9	10	11	12	13

Sources: [13]Organ, 1958; [12]Organ, 1960a; [3]Organ, 1960b; [13]MacMahon, 1964; [1,2,3,6,9,10,12,13]Arnold, 1972; [11,13]Arnold, 1976; [1]Gergits and Jaeger, 1990; [7]Marvin and Hutchison, 1996; [11]Houck and Arnold, 2003; [5]Picard, 2005; [1,2,4]Dyal, 2006; [11]Eddy et al., 2012; [6]Pierson et al., 2017; [7,8]current study against the lateral parts of the other salamander's body. **Tail arch:** Individual arches the tail base. Male often exhibits tail arch during 'position for TSW' (Supplemental Video 24) and the TSW (Supplemental Video 38). In response to contact by the male, the female exhibits tail arch before and during a 'female-first TSW' (ffTSW; Supplemental Videos 3, 5, 8, and 30). **Undulate tail:** Individual laterally undulates the tail, usually with tail arch. Male undulates his tail during position for TSW and the TSW, and occasionally during mental-gland sliding, foot dance, or foot shuffle (Supplemental Videos 4 and 24). Female undulates her tail before and during ffTSW (Supplemental Videos 5 and 30), and during 'position on sperm cap.' **Tail (or body) flex:** Individual flexes (i.e., greatly bends) the tail or body. Male flexes his tail during both 'lead female over spermatophore' and 'stationary with tail flexed' during sperm transfer (Supplemental Videos 28 and 35). Female may flex her tail or body in response to mental-gland contact by the male (Supplemental Videos 6, 7, and 17). **Tail straddle:** Individual steps astride the tail of the other salamander. Male performs tail straddle during ffTSW (Supplemental Video 8). To initiate the TSW, the female performs tail straddle in response to position for TSW by the male (Supplemental Video 9). **Bite:** Individual bites the other salamander (Supplemental Videos 10, 11, and 25).

Behaviors exhibited by males only.—**Foot dance:** While stationary or moving very slowly toward the female with his venter in contact with the substrate, the male repeatedly raises and lowers his fore- and hind-limbs one at a time (Supplemental Videos 4 and 12). **Foot shuffle:** While stationary and close to the female, male alternately raises and lowers each rear foot (Supplemental Videos 13 and 14). Due to the inability to see the male's forelimbs clearly on occasions, I report the total occurrence of foot dance and foot shuffle as foot dance/shuffle. **Mental-gland sliding:** Male slides his mental gland on the female's skin (Supplemental Video 15). The equivalent behavior in other EP is often termed 'head sliding' (e.g., Arnold, 1972). On rare occasions, the male arches his head and may exert downward pressure during sliding (Supplemental Video 16). Male may perform foot dance, foot shuffle, tail arch, and undulate tail during sliding. **Mental-gland pop:** Occasionally during mental-gland sliding, when the male or female breaks contact, the mental gland abruptly pops away from the female's skin (Supplemental Videos 15, 17, and 18). The abrupt motion appears as if due to the breakage of an adhesive force. **Mental-gland tap:** Male taps his mental gland on the female's skin (Supplemental Video 19). However, unlike some other EP, male does not tap his mental gland on her nares. **Mental-gland swipe:** Male quickly swipes his mental gland on the female's skin (but not nares) with a sideways or backward motion (Supplemental Video 20). **Mouth grasp:** Male lightly grasps the female's head, body, leg, or tail with his jaws and maintains the grasp for one to several seconds (Supplemental Videos 21 and 22). **Snout under:** Male positions his snout under the slightly raised chin, body, or tail of the female (Supplemental Video 23). If he raises his head and makes contact with her chin, then she typically raises her chin higher to avoid the contact. Male then slowly crawls under her raised head and positions his tail base beneath her chin. Similarly, if there is sufficient space beneath the female's body or tail, then the male may perform snout under to the body or tail. 'Lifting' and 'crossing under' are the equivalent or very similar behaviors described in other EP (e.g., Arnold, 1972; Dyal, 2006). **Position for TSW:** If the female contacts the male either incidentally when moving or directly by tapping her chin on the male's dorsum during 'chin over,' then the male reflexively positions his arched tail beneath the female's chin (or against her body or tail) while slowly undulating his tail laterally (Supplemental Video 24). Sometimes the male walks forward very slowly with tail arched and undulating as he maintains contact with the female's skin. 'Stationary with tail arched and undulating' and 'moving forward with tail arched and undulating' are the equivalent or very similar behaviors described in other EP (e.g., Arnold, 1972). **Turn around:** After position for TSW, if the female does not move to maintain contact with the male's tail, then he typically turns around very slowly toward her with a U-shaped bend of his body, and moves toward her while often performing foot dance with tail arch and undulations. Also, turn around often follows 'position on sperm cap' by the female, but he does not perform foot dance or tail arch and undulate (Supplemental Videos 11 and 25). **Vent sliding:** During the final few seconds of TSW, the male lowers his vent and slides it in contact with the substrate before he stops walking forward (Supplemental Video 26), which may allow him to find an appropriate site to deposit the spermatophore (Arnold, 1972). **Spermatophore deposition:** Male stops walking at the end of TSW and remains stationary with his venter and vent in contact with the substrate and his head elevated (Supplemental Video 26). He continues to undulate his tail laterally as the female maintains chin contact with his tail base. Male's tail undulations increase in frequency and amplitude during spermatophore deposition. Male then stops undulating his tail, arches it upward, and lifts his vent free of the spermatophore (Supplemental Video 27). **Stationary with tail flexed:** If the female stops and lowers her vent on or near the spermatophore (during 'lead female over spermatophore'), the male stops walking and, while stationary with his tail flexed, extends and flexes his hind-legs (i.e., performs 'pelvic lifting') as she maintains her chin contact with his tail base (Supplemental Video 28). Male eventually stops flexing his rear legs and remains motionless with his rear legs extended and tail flexed to one side. **Eat spermatophore:** If the male locates an intact spermatophore or the gelatinous base of a spermatophore via nose-tapping, then he typically eats the sperm cap and/or base (Supplemental Video 29).

Behaviors exhibited by females only.—**High-amplitude tail undulations:** When the male's chin contacts the female's tail or sacral region, she may undulate her tail in a slow, wavelike motion while her tail is either in full contact with the substrate or with the tail base arched (Supplemental Video 30). **Snout high:** Female raises her snout high above the substrate such that her head forms about a 60 to 80° angle with the substrate (Supplemental Video 31). Snout high occurs occasionally in response to mental-gland sliding or during ffTSW. **Turn back:** As the male rests his mental gland on the female's tail base, she turns back toward him with a U-shape bend of her body (Supplemental Video 32). Turn back may occur during mental-gland sliding or ffTSW. Such behavior during ffTSW is very similar to the 'circling' behavior of some EP (Dyal, 2006); however, the female does not straddle the male's tail immediately after turn back. **Raise chin:** Female raises her chin before or after turn back, or in response to snout under by the male (Supplemental Video 23). **Chin over:** Female positions her snout above the male and usually taps her chin once or several times on his dorsum. Chin over typically occurs after turn back by the female (Supplemental Video 33) but may also occur in response to snout under by the male (Supplemental Video 34). Male typically responds to such contact with position for TSW. **Stop and lower vent:** During 'lead female over spermatophore,' the female stops walking forward and lowers her vent onto or close to the spermatophore (Supplemental Video 35). **Position on sperm cap:** After lowering her vent onto the sperm cap of a spermatophore, the female slightly undulates the base of her tail laterally (Supplementary Video 28). Female may or may not successfully retrieve the sperm cap. If successful, she retains the sperm cap in her cloaca as she raises her vent off the gelatinous base. Female may move away immediately after sperm-cap retrieval while male remains stationary with tail flexed.

*Duet behaviors with both female and male actions.—***Continuous, female-first TSW (ffTSWc):** While the male straddles the female's tail and continually rests his mental gland on her tail base or sacral region, the pair slowly walks forward in tandem as she laterally undulates her tail base continuously beneath his chin (Supplementary Videos 5 and 36). Female may keep her tail base very slightly arched as the pair walks forward without breaking contact. Pair performs tight turns to avoid obstructions (e.g., side of courtship arena) during ffTSWc. **Discontinuous, female-first TSW (ffTSWd):** Behavior is similar to ffTSWc, but contact between the pair, the forward movement of the pair, and the female's tail undulations are discontinuous. The female's walking is sporadically faster than the male's, which causes his chin contact to break; however, she stops moving forward after taking a few steps. Female's tail undulations and forward movement only occur when the male's chin rests on her sacral region or tail. In contrast to ffTSWc, lateral undulations of the female's tail are less frequent and larger in amplitude, which may cause the male's chin contact to break. In addition, flex or arch of the female's tail is typically greater. When the male's chin contact is lost, it often takes several seconds to re-establish contact (Supplemental Video 37). In some courtships, the pair may transition from ffTSWd to ffTSWc and vice versa. **Tail-straddling walk:** Following position for TSW, if the female steps astride the male's tail (Supplemental Video 9), the female walks slowly forward in tandem with the male while continually resting her chin on his tail base. Male continuously undulates his tail base laterally beneath her chin and keeps his tail base arched and head elevated above the substrate as the pair walks forward (Supplemental Videos 36 and 38). Male apparently adjusts his walking speed in response to the position of the female's chin on his tail (i.e., he walks more slowly if she contacts his tail more distally and vice versa). Pair performs tight turns to avoid obstructions (e.g., side of courtship arena) during TSW. **Lead female over spermatophore:** Female rests her chin on the male's tail base as he walks forward after spermatophore deposition with his vent raised and tail flexed to one side. Female walks over the spermatophore with her venter raised just high enough that the sperm cap slightly touches her venter (Supplemental Video 35).

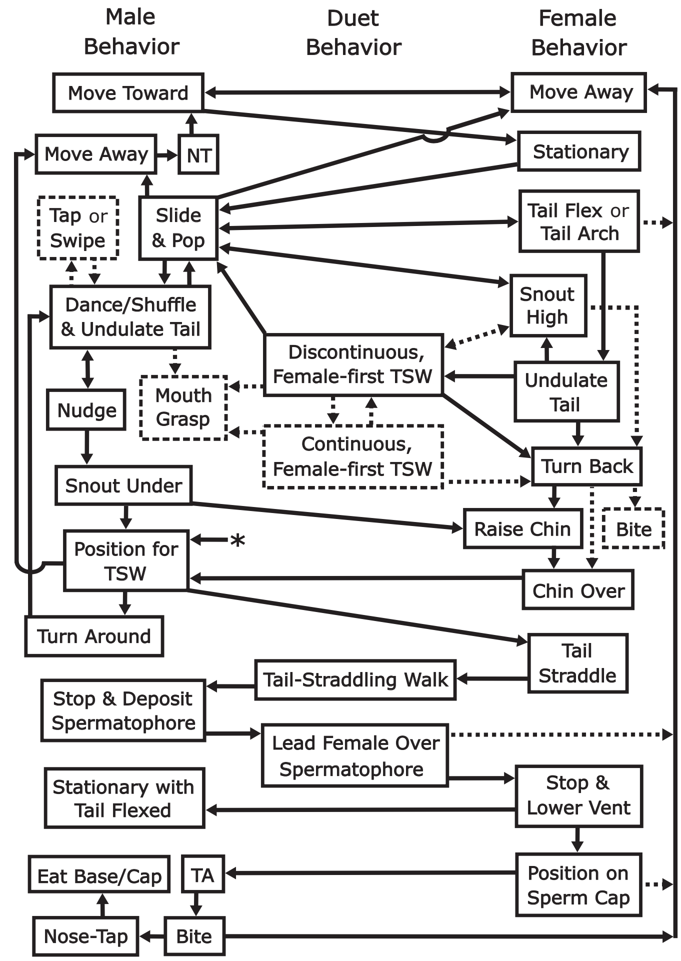

Fig. 1. Ethogram for many of the transitions between behaviors during courtship and mating in the salamander *Plethodon petraeus*. Data are from 20 individually unique pairs that engaged in ten incomplete courtships, which did not proceed to a tail-straddling walk (TSW), and ten complete courtships with TSW and spermatophore deposition. Line with arrowhead at both ends indicates transition in either direction. A solid line indicates the transition occurred in ≥65% of courtships, whereas a dotted line indicates the transition occurred in <65% of courtships (with $n = 20$ and 10 courtships prior to and after female tail straddle, respectively). NT = nose-tap. TA = turn around. Dance/Shuffle = foot dance and foot shuffle. See text for description of behaviors. *Incidental contact to the male during female movements of her feet, tail, or body often elicited position for TSW well before the occurrence of snout under or chin over. In each complete courtship, female turn back and chin over preceded the first successful position for TSW. Ethogram does not include a few male behaviors (stationary, head contact, tale arch, and tail straddle) and very infrequent female behaviors (nose-tap, move toward, head contact, and nudge).

Temporal organization of courtship, behavior frequency, and behavior duration for *P. petraeus*

*Initial courtship encounters.—*The ethogram summarizes many of the transitions between behaviors during courtship and mating in *P. petraeus* (Fig. 1). Initially the male nose-tapped the substrate frequently as he explored the courtship arena. When the male located the female, he often kept his venter in contact with the substrate as he moved toward her very

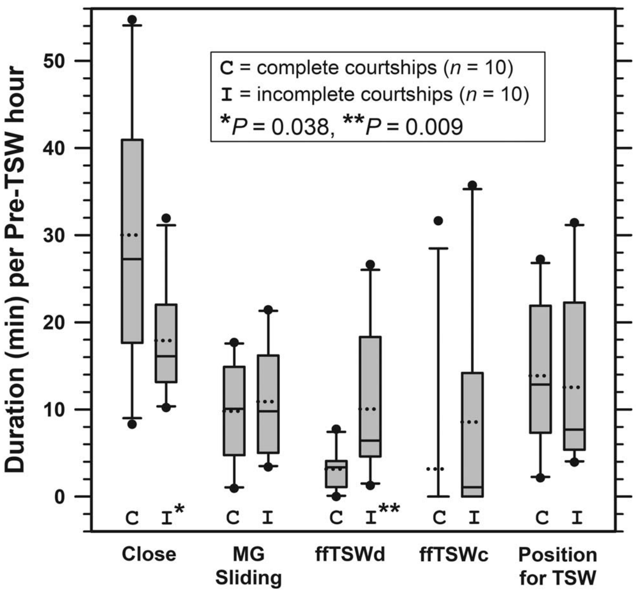

Fig. 2. Duration of some behaviors and periods during the preliminary (pre-TSW) phase of courtship in the salamander *Plethodon petraeus*. Data are from 20 individually unique pairs that engaged in ten incomplete courtships, which did not proceed to a tail-straddling walk (TSW), and ten complete courtships with TSW and spermatophore deposition. See text for description of behaviors. Close = salamanders within about 2.5 cm of each other but not in sustained contact via the mental gland (e.g., includes periods with male foot dance/shuffle, tail undulation, nudging, and snout under). MG Sliding = mental-gland sliding on the skin of the female. ffTSWd = discontinuous, female-first TSW. ffTSWc = continuous, female-first TSW. Position for TSW = attempted male solicitation of TSW. Box plots show minimum, maximum, median (solid horizontal line), mean (dotted horizontal line), and percentiles (10th, 25th, 75th, and 90th). *, **Probability values from Mann-Whitney rank sum tests demonstrate a significant difference between complete and incomplete courtships for the duration of both close and ffTSWd.

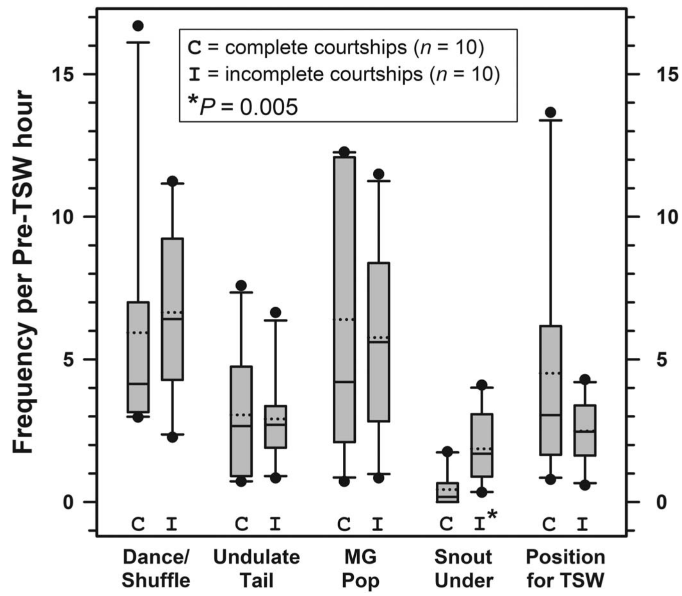

Fig. 3. Frequency of some male behaviors during the preliminary (pre-TSW) phase of courtship in the salamander *Plethodon petraeus*. Data are from 20 individually unique pairs that engaged in ten incomplete courtships, which did not proceed to a tail-straddling walk (TSW), and ten complete courtships with TSW and spermatophore deposition. MG = mental gland. See text for description of behaviors. Box plots show minimum, maximum, median (solid horizontal line), mean (dotted horizontal line), and percentiles (10th, 25th, 75th, and 90th). *Probability value from Mann-Whitney rank sum test demonstrates a significant difference between complete and incomplete courtships for the frequency of snout under.

slowly. During initial encounters, the male typically nose-tapped the female's tail. A male likely identifies the species, sex, and reproductive status of another salamander by olfaction during nose-tapping (Arnold, 1976; Dawley, 1984; Dantzer and Jaeger, 2007a, 2007b). If the female were non-receptive, she would move away from the male when he contacted her (Fig. 1). The male typically would soon relocate the female visually if she were moving or otherwise via olfaction. The male kept moving toward and contacting a non-receptive female until she eventually remained stationary (Fig. 1). In two incomplete courtships, the male bit the female when he first moved toward her; however, the male soon ceased aggressive behavior and began courtship.

Mental-gland sliding.—During the pre-TSW phase of courtship, the most frequent male behaviors were mental-gland sliding, mental-gland popping, foot dance/shuffle, tail arch, undulate tail, and position for TSW (Figs. 2, 3). The male typically initiated mental-gland sliding on the female's tail and then moved very slowly toward her head. If the male initially moved posteriorly during sliding, he would move anteriorly after reaching the tip of her tail. Total duration of sliding per pre-TSW hour was not significantly different between complete and incomplete courtships (two-way ANOVA on ranks, $F = 0.22$, $P = 0.64$) but significantly varied among the tail, body, and head ($F = 31.06$, $P < 0.001$; Supplemental Fig. A; see Data Accessibility). Duration was greater on the tail than on either the body ($t = 6.12$, $P < 0.001$) or head ($t = 7.36$, $P < 0.001$; mean = 7.71±1.06, 1.91±0.37, and 0.73±0.15 min/pre-TSW hour, respectively). Mental-gland sliding on the female's nares was momentary (usually <1 sec) and infrequent (3/10 complete and 5/10 incomplete courtships with mean = 0.27±0.06 times/pre-TSW hour; Supplemental Fig. B; see Data Accessibility), since the female would typically turn her head away when the male attempted to contact her snout. On very rare occasions, the female bit the male in response to sliding.

Close, foot dance/shuffle, tail arch, undulate tail, mental-gland pop, and mental-gland tap or swipe.—The male typically remained close to the female when he was not mental-gland sliding (Fig. 2). While close to the female or during sliding, the male would occasionally foot dance/shuffle, tail arch, and undulate tail (Fig. 3). For complete courtships, the male performed sliding and remained close to the female for about 17% and 45% of the pre-TSW phase, respectively (Table 2). For incomplete courtships, the total duration of close per pre-TSW hour was significantly less (Mann-Whitney rank sum test, $U = 22.0$, $T = 133.0$, $P = 0.038$; Fig. 2). For all courtships, mental-gland popping occurred often (Fig. 3) when the mental gland lost contact with the female's skin during sliding. The mean time elapsed before the initial mental-gland pop was 33±12 min (Fig. 4). For all courtships, there were significant, positive correlations between the frequency of female undulate tail and both foot dance/shuffle and mental-gland popping (Table 3). For

Table 2. Duration (min) of behaviors and phases during courtship and mating in the salamander *Plethodon petraeus*. Data are from ten individually unique pairs that engaged in complete courtship with tail-straddling walk (TSW) and spermatophore deposition. For Pair 3 courtship, there were two spermatophore depositions. (A) Apart = periods when salamanders were more than about 2.5 cm apart after their initial encounter. (B) Close = periods when salamanders were within about 2.5 cm of each other but not in sustained contact via the mental gland (e.g., includes periods with male foot dance/shuffle, undulate tail, mental-gland tap/swipe, nudge, and snout under). (C) Sliding = mental-gland sliding. (D) ffTSWd = discontinuous, female-first TSW. (E) ffTSWc = continuous, female-first TSW. (F) upTSW = unsuccessful position for TSW. (G) spTSW = successful position for TSW. (H) TSW = tail-straddling walk. (I) SD = spermatophore deposition. (J) LOS = lead female over spermatophore. (K) POC = position on sperm cap. *Successful retrieval of sperm cap. Total B to G = duration of pre-TSW phase of courtship. Total B to K = total duration of pre-TSW phase, TSW, and sperm transfer. Total A to K = total duration of courtship from the initial encounter between salamanders until the final attempted retrieval of sperm cap. Pearson Product Moment correlation coefficients (which do not include durations for behaviors from the second courtship sequence for pair 3): [1]$r = 0.952$, $P < 0.0001$ for Apart and TSW; [2]$r = 0.770$, $P < 0.01$ for Sliding and ffTSWd; [3]$r = 0.964$, $P < 0.00001$ for Sliding and upTSW; [4]$r = 0.765$, $P < 0.01$ for ffTSWd and upTSW.

		Pre-TSW phase						TSW & sperm-transfer phase						
Pair	(A)[1] Apart	(B) Close	(C)[2,3] Sliding	(D)[2,4] ffTSWd	(E) ffTSWc	(F)[3,4] upTSW	(G) spTSW	(H)[1] TSW	(I) SD	(J) LOS	(K) POC	Total B to G	Total B to K	Total A to K
1	29	152	5	3	0	3	3	31	7	0.4	0.5*	166	204.9	233.9
2	13	122	3	20	0	2	6	22	8	0.3	0.4*	153	183.7	196.7
3	9	69	19	3	0	73	2	23	7	0.4	0.8	166	197.2	
	2	66	3	0	0	17	5	26	8	0.6	0.5*	91	126.1	334.3
4	71	24	9	0	0	3	3	42	7	0.3	0.5*	39	88.8	159.8
5	172	45	35	26	170	35	12	223	9	0.3		323	555.3	727.3
6	12	69	33	6	0	17	15	20	8	0.4	0.8	140	169.2	181.2
7	8	36	33	7	0	42	1	26	8	0.3	0.7	119	154	162
8	29	119	68	15	0	73	10	43	7	0.5	0.6	285	336.1	365.1
9	8	323	48	32	0	88	12	32	6	0.4	0.9*	503	542.3	550.3
10	33	184	210	46	0	270	5	30	8	0.4	0.6*	715	754	787
Total	386	1209	466	158	170	623	74	518	83	4.3	6.3	2700	3311.6	3697.6
Mean	35.1	109.9	42.4	14.4	15.5	56.6	6.7	47.1	7.5	0.4	0.6	245.5	301.1	369.8
SD	49.4	86.7	59.3	15.1	51.3	77.2	4.7	58.8	0.8	0.1	0.2	202.3	218.6	237.3
% Total B to G		44.8	17.3	5.9	6.3	23.1	2.7							
% Total B to K		36.5	14.1	4.8	5.1	18.8	2.2	15.6	2.5	0.1	0.2			
% Total A to K	10.4	32.7	12.6	4.3	4.6	16.8	2.0	14.0	2.2	0.1	0.2			

incomplete courtships, there was a significant, positive correlation between the duration of close and the frequency of foot dance/shuffle (Table 4). Mental-gland tap or swipe to the female's head (but never nares), body, or tail was rare and infrequent (3/10 complete and 2/10 incomplete courtships with mean = 0.71±0.42 times/pre-TSW hour; Supplemental Fig. B; see Data Accessibility).

Female tail flex, tail arch, undulate tail, and snout high.—In response to continued mental-gland sliding, the female would eventually perform tail flex, tail arch, and undulate tail (Figs. 1, 5). Mean time elapsed before the initial tail flex was 72±16 min (Fig. 4). For all courtships, there was a significant, positive correlation between the duration of sliding and the frequencies of both foot dance/shuffle and female undulate tail (Table 4). In all courtships, snout high occurred occasionally during sliding (Fig. 5). Mean time elapsed before the initial snout high (118±23 min) was similar to that for initial female tail undulations (Fig. 4).

Snout under and position for TSW.—If the female contacted the male either incidentally when she moved or during snout under by the male, then the male reflexively exhibited position for TSW (Fig. 1). Thus, position for TSW occurred frequently (Fig. 3), including early in the courtship (Fig. 4), and the total duration was more than 10 min per pre-TSW hour (Fig. 2) and thus accounted for about 23% of the pre-TSW phase for complete courtships (Table 2). However, a position for TSW most often did not lead to TSW, and thus the male would typically turn around to continue foot dance/shuffle and sliding (Fig. 1). Occasionally, the male would move away from the female after an unsuccessful position for TSW but would soon relocate the female and continue sliding (Fig. 1). For complete courtships, there was a significant, positive correlation between the total duration of sliding and the total duration of unsuccessful position for TSW (Table 2). For all courtships, there were significant, positive correlations between the frequency of position for TSW and the frequencies of foot dance/shuffle, female undulate tail, and chin over (Table 3). For incomplete courtships, there was also a significant, positive correlation between the frequency of snout under and position for TSW (Table 3). Snout under occurred in 70% of courtships, and the mean time elapsed before its initial occurrence was 176±37 min (Fig. 4). The frequency of snout under per pre-TSW hour (Fig. 3) was significantly greater for incomplete courtships (Mann-Whitney rank sum test, $U = 13.0$, $T = 68.0$, $P = 0.005$).

Female-first tail-straddling walk.—In most courtships (19/20), the male would eventually (i.e., when female tail undulation occurred upon mental-gland contact to her tail base)

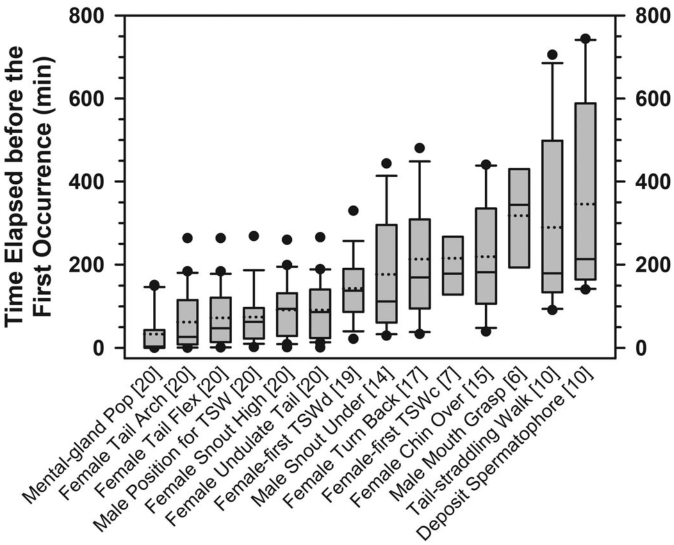

Fig. 4. Time elapsed before the first occurrence of some courtship behaviors in the salamander *Plethodon petraeus*. Data are from 20 individually unique pairs that engaged in ten incomplete courtships, which did not proceed to a tail-straddling walk (TSW), and ten complete courtships with TSW and spermatophore deposition. See text for description of behaviors. Number within brackets is the number of courtships with the behavior. Box plots show minimum, maximum, median (solid horizontal line), mean (dotted horizontal line), and percentiles (10th, 25th, 75th, and 90th).

step astride the female's tail during sliding, and the pair would engage in ffTSWd (Fig. 1). Mean time elapsed before the initial ffTSWd was 143±17 min (Fig. 4). The number of ffTSWd per pre-TSW hour did not significantly differ between incomplete courtships (mean = 1.66±0.44, median = 1.03, range = 0.17 to 4.07) and complete courtships (mean = 1.09±0.26, median = 0.95, range = 0 to 2.53; Mann-Whitney rank sum test, $U = 40.0$, $T = 95.0$, $P = 0.473$). However, the duration (min) of each ffTSWd during incomplete courtships (mean = 6.24±0.59, median = 4.16, range = 0.47 to 41.63) was significantly greater than during complete courtships (mean = 2.91±0.32, median = 2.24, range = 0.5 to 10.25; Mann-Whitney rank sum test, $U = 2005.0$, $T = 3495.0$, $P < 0.001$). Thus, the total duration of ffTSWd per pre-TSW hour (Fig. 2) was significantly greater for incomplete courtships (Mann-Whitney rank sum test, $U = 15.0$, $T = 70.0$, $P = 0.009$). For ten randomly selected ffTSWd in ten courtships (five complete, five incomplete), mean walking speed was 10.6±0.9 cm/min (range = 5.6 to 13.6).

For all courtships, there was a significant, positive correlation between the frequency of snout under and the duration of ffTSWd (Table 4). For complete courtships, there were significant, positive correlations between the total duration of ffTSWd and the total duration of sliding and unsuccessful position for TSW (Table 2). For complete courtships, there was a significant, positive correlation between the frequency of mental-gland swipe and the duration of ffTSWd (Table 4). In some courtships, the pair would transition from ffTSWd to ffTSWc and vice versa (Fig. 1).

Mean time elapsed before the initial ffTSWc was 215±46 min (Fig. 4). Forty-one ffTSWc occurred in seven courtships with a mean duration of 23.89±7.16 min (median = 4.57, range 0.65 to 225.43). Mean total duration for ffTSWc was 16.8±5.8 min per pre-TSW hour. For seven randomly

Table 3. Pearson Product Moment correlation coefficients between the frequency of some male and female behaviors (i.e., occurrences per hour for each pair) during the preliminary (pre-TSW) phase of courtship in the salamander *Plethodon petraeus*. Data are from 20 individually unique pairs that engaged in ten incomplete courtships, which did not proceed to a tail-straddling walk (TSW), and ten complete courtships with TSW and spermatophore deposition. Dance/shuffle = foot dance and foot shuffle. MG = mental gland. See text for description of behaviors. [C]Coefficient for complete courtships, [I]coefficient for incomplete courtships, [A]coefficient for all courtships when both incomplete and complete courtships had very similar correlations. *$P < 0.025$, **$P < 0.015$, ***$P < 0.001$.

	Male behavior		Female behavior	
	Mouth grasp	Position for TSW	Undulate tail	Turn back
Male behavior				
Dance/shuffle		[A] 0.773***	[A] 0.660**	
Snout under		[I] 0.824**		
MG popping			[A] 0.548**	
Female behavior				
Tail flex	[I] 0.801**			
Undulate tail		[A] 0.507*		[C] 0.762**
Chin over		[A] 0.566**	[C] 0.793**	[A] 0.912***

selected ffTSWc from seven courtships, mean walking speed was 10.3±0.5 cm/min (range = 7.1 to 11.7). There was a trend for pairs to engage in ffTSWc more often during incomplete (6/10) than complete courtships (1/10; Fisher's exact test, $P = 0.057$). For incomplete courtships, there were significant, negative correlations between the duration of ffTSWc and the frequencies of foot dance/shuffle and mental-gland popping (Table 4).

The female occasionally exhibited snout high during ffTSWd (Fig. 1). Rarely, the female bit the male after turn back during ffTSW (Fig. 1). In many courtships, the female would turn back during ffTSWd or ffTSWc and exhibit raise chin and chin over (Figs. 1, 5). For all courtships, there was a significant, positive correlation between the frequencies of turn back and chin over (Table 3). Mean time elapsed before the initial chin over was 219±34 min (Fig. 4). The frequencies of turn back and chin over per pre-TSW hour (Fig. 5) were significantly greater for complete courtships (Mann-Whitney rank sum tests: $U = 17.0$, $T = 138.0$, $P = 0.014$ for turn back; $U = 20.0$, $T = 135.0$, $P = 0.025$ for chin over). For all courtships, if the female contacted the male during chin over, then the male often exhibited position for TSW (Fig. 1).

Mouth grasp.—Mouth grasping occurred infrequently during four complete and two incomplete courtships (mean = 0.98±0.35 times per pre-TSW hour; Supplemental Fig. B; see Data Accessibility) and always occurred at least 200 min after the courtship began (Fig. 4). For incomplete courtships, there were significant, positive correlations between the duration of time apart and the frequencies of mouth grasp and female tail flex (Table 4) and a significant, positive correlation between the frequencies of mouth grasp and female tail flex per pre-TSW hour (Table 3). The female sometimes bit the male in response to mouth grasping.

Initiation and duration of the TSW.—If the female did not step astride (i.e., tail straddle) the male's tail during position for

Table 4. Pearson Product Moment correlation coefficients between the duration and frequency of some behaviors during the preliminary (pre-TSW) phase of courtship in the salamander *Plethodon petraeus*. Data are from 20 individually unique pairs that engaged in ten incomplete courtships, which did not proceed to a tail-straddling walk (TSW), and ten complete courtships with TSW and spermatophore deposition. Duration = minutes per pre-TSW hour. Frequency = occurrences per pre-TSW hour. Apart = periods when salamanders were more than about 2.5 cm apart after their initial encounter. Close = periods when salamanders were within about 2.5 cm of each other but not in sustained contact via the mental gland. Dance/shuffle = foot dance and foot shuffle. MG = mental gland. See text for description of behaviors. [C]Coefficient for complete courtships, [I]coefficient for incomplete courtships, [A]coefficient for all courtships when both incomplete and complete courtships had very similar correlations. *$P < 0.02$, **$P < 0.01$, ***$P < 0.001$.

	Duration of period or behavior				
	Apart (> 2.5 cm)	Close (≤ 2.5 cm)	MG sliding	Discontinuous, female-first TSW	Continuous, female-first TSW
Male frequency					
Dance/shuffle		[I] 0.922***	[A] 0.528*		[I] −0.734*
MG popping					[I] −0.748*
MG swipe				[C] 0.704*	
Mouth grasp	[I] 0.856**				
Snout under				[A] 0.595**	
Female frequency					
Tail flex	[I] 0.806**				
Undulate tail			[A] 0.751***		

TSW, then courtship did not proceed to a TSW (Fig. 1). In each complete courtship, female turn back and chin over preceded the first successful position for TSW (i.e., male snout under never preceded the first TSW). However, for the courtship with two TSW, snout under preceded the second TSW. Mean time elapsed before the initiation of TSW was 290±66 min (Fig. 4). The duration of most TSW (8/11) ranged from 20 to 32 min (max. = 223, Table 2). There were significant, positive correlations between the duration of TSW and the total time apart and the total duration for ffTSW (i.e., both discontinuous and continuous forms combined; Fig. 6). Mean distance traveled during TSW was 3.93±0.65 m (range = 1.86 to 9.69, n = 11). Mean walking speed during TSW was 12.7±1.9 cm/min (range = 1.0 to 23.2).

Spermatophore deposition, sperm transfer, and the duration of complete courtships.—Mean time elapsed before the start of the first spermatophore deposition was 346±75 min (Fig. 4). Mean time for deposition was 7.5 min (Table 2). During deposition, the mean frequency of male tail undulations increased from 0.47±0.28 Hz at the beginning to 0.84±0.28 Hz at the end (range = 0.31 to 0.61 and 0.67 to 0.95, respectively). Mean time for lead female over spermatophore was 0.4 min (Table 2). Mean time for female position on sperm cap (including successful and unsuccessful cap-retrieval attempts) was 0.6 min (Table 2). Females retrieved the sperm cap from 55% (6/11) of spermatophores with a success rate of 60% per courtship (Table 2). In 80% of complete courtships, the male turned around and then bit or aggressively chased (e.g., repeatedly lunged and snapped at) the female either immediately after (4/10 courtships) or within 2 min after (4/10 courtships) position on sperm cap by the female (Fig. 1). For the 11 spermatophores, the male eventually ate the gelatinous base (n = 2), cap (n = 1), or entire spermatophore (n = 3).

The total duration of complete courtships from the first encounter between salamanders until the final attempted retrieval of a sperm cap ranged from 160 to 787 min (mean = 370, Table 2). Duration of the pre-TSW phase for these courtships ranged from 39 to 715 min (mean = 245, Table 2). Excluding periods when salamanders were apart after their initial encounter, total duration of courtship and mating ranged from 89 to 754 min (mean = 301, Table 2).

Review of some courtship behaviors for *P. kentucki*

The frequency (Hz) of rear-leg movement during foot dance in *P. kentucki* (mean = 0.532±0.055, median = 0.446, range = 0.370 to 0.840, n = 12; Supplemental Videos 44, 45, and 46) is significantly greater than for *P. petraeus* (mean = 0.229±0.012, median = 0.221, range = 0.151 to 0.299, n = 12; Mann-Whitney rank sum test, $U = 0.0$, $T = 78.0$, $P < 0.001$). Mental-gland popping (with very low amplitude; Supplemental Videos 47 and 48), snout high (Supplemental Video 46), ffTSWd, and ffTSWc are relatively infrequent (about 7 to 17% of courtships) in *P. kentucki*. Some female and male actions during ffTSW differ between the species. A female *P. kentucki* typically does not exhibit either tail flex or high tail arch during ffTSWd. A male *P. kentucki* does not straddle the female's tail during ffTSWd or ffTSWc but instead he walks alongside her tail as he rests his chin on her tail base (Supplemental Videos 53, 54, 57, 58, and 59). As observed in *P. petraeus*, a female *P. kentucki* may turn back and bite during ffTSW (Supplemental Video 59), and turn back during sliding to perform chin over to elicit male position for TSW (Supplemental Videos 60 and 61).

DISCUSSION

Comparison of foot dance, foot shuffle, mental-gland sliding, and olfactory pheromone delivery among EP.—All plethodontid species likely use a combination of chemical, visual, and tactile signals to exchange information during courtship; however, the context and relative importance of different signals may change during the evolution of different lineages (Arnold et al., 2017). For example, based on experiments with *P. shermani*, the foot dance is likely an important visual cue that may indicate male courtship intent and thus increase insemination success rate (Eddy et al., 2012). However, the relative importance of visual

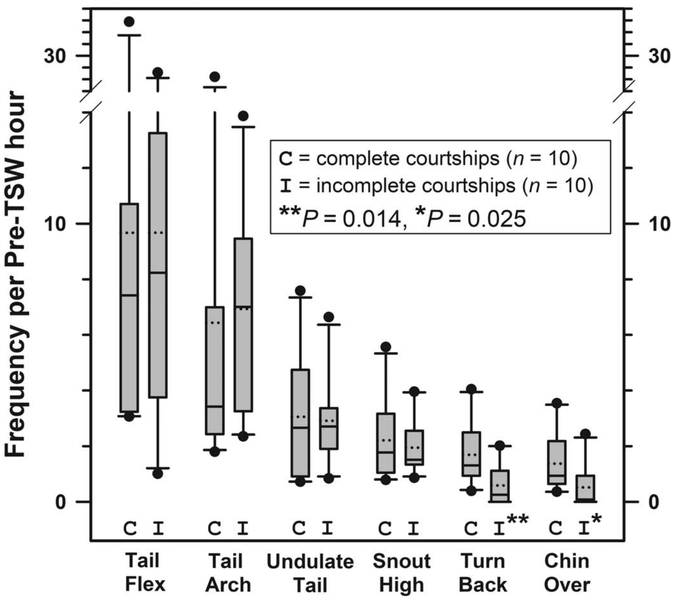

Fig. 5. Frequency of some female behaviors during the preliminary (pre-TSW) phase of courtship in the salamander *Plethodon petraeus*. Data are from 20 individually unique pairs that engaged in ten incomplete courtships, which did not proceed to a tail-straddling walk (TSW), and ten complete courtships with TSW and spermatophore deposition. See text for description of behaviors. Box plots show minimum, maximum, median (solid horizontal line), mean (dotted horizontal line), and percentiles (10th, 25th, 75th, and 90th). **, *Probability values from Mann-Whitney rank sum tests demonstrate a significant difference between complete and incomplete courtships for the frequency of both turn back and chin over.

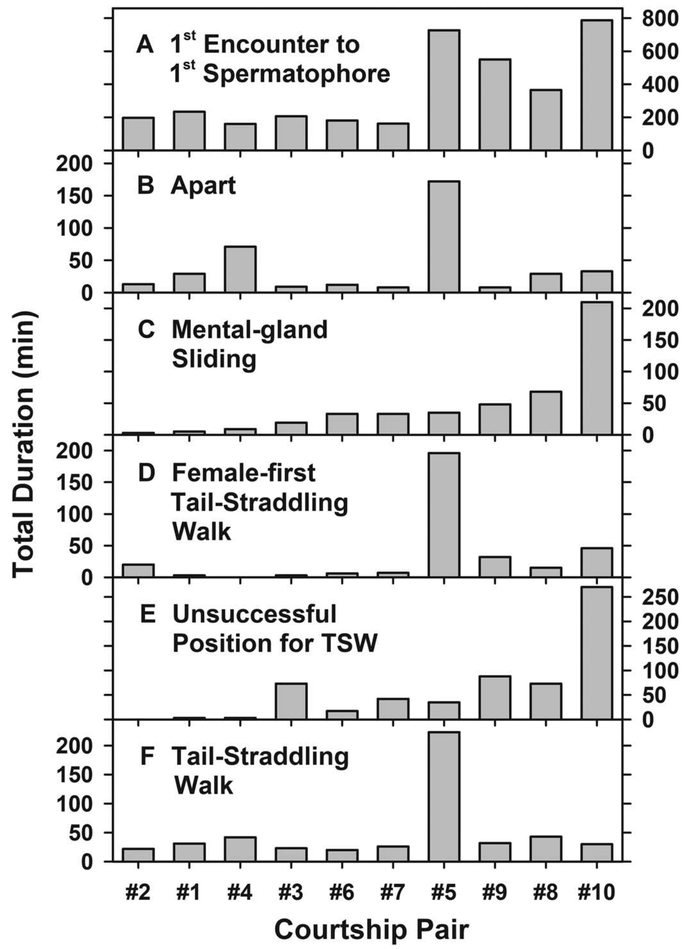

Fig. 6. Total duration (min) of some behaviors and periods during complete courtships in the salamander *Plethodon petraeus*. Data are from ten individually unique pairs that engaged in complete courtship with tail-straddling walk (TSW) and spermatophore deposition. For Pair 3 courtship, there were two spermatophore depositions, but this figure only includes data from the first spermatophore deposition. A = Courtship duration from initial close encounter between salamanders until the retrieval or attempted retrieval of the first spermatophore cap. B = Total of all periods when salamanders were more than about 2.5 cm apart after their initial encounter. D = Total duration for female-first TSW, which includes both discontinuous and continuous forms of the duet behavior. Pearson Product Moment correlation coefficients: r = 0.882, $P < 0.001$ for B and D; r = 0.952, $P < 0.0001$ for B and F; r = 0.964, $P < 0.00001$ for C and E; r = 0.961, $P < 0.00001$ for D and F. See Table 2 for additional data on the duration of other behaviors and periods.

signals delivered during foot dance may vary among species. The frequency (and perhaps amplitude) of rear-leg movement during foot dance is lower in *P. petraeus* relative to some species in the PGG such as *P. kentucki*. However, the relatively larger limbs and feet in *P. petraeus* might visually compensate for the lower frequency of foot movement. For *P. yonahlossee*, foot dance occurs more rarely (Pierson et al., 2017), which may indicate less importance for any visual signal(s) conveyed by the behavior. Similarly, other behaviors such as foot shuffle and tail wagging may serve as visual signals during the pre-TSW phase of courtship in the PCG and PWG (Arnold et al., 2017; Table 1). *Plethodon petraeus* is the only species to exhibit both foot dance and foot shuffle.

Similarly, the importance of mental-gland sliding to serve as a tactile signal and/or a means to deliver chemical signals (e.g., mental-gland pheromones) via diffusion across the female's skin may vary among plethodontid species. Dermal application of mental-gland pheromones increases female receptivity for mating in some species of *Desmognathus* (Houck and Reagan, 1990). Although mental-gland sliding is ubiquitous for EP (Table 1), experimental studies with *P. shermani* indicate dermal application of mental-gland pheromones does not influence female receptivity (Kiemnec-Tyburczy et al., 2011). Thus, current theory proposes pheromone delivery via dermal application is not important, whereas olfactory delivery is characteristically important for species in the PGG (Kiemnec-Tyburczy et al., 2011) and thus perhaps represents a plesiomorphic trait (Arnold et al., 2017). Alternatively, both delivery via dermal application and olfactory delivery could be ancestral for the PGG, but dermal application became unimportant during the evolution of some species (e.g., *P. shermani*).

Olfactory pheromone delivery both prior to and during the TSW might be a shared, ancestral trait for the PWG and PGG, but the timing of the delivery changed among different lineages (Picard, 2005). Based on observations for *P. dorsalis* and *P. angusticlavius*, olfactory delivery primarily occurs during the pre-TSW phase for species in the PWG (Picard, 2005; Dyal, 2006). For the PGG, the timing of delivery varies among species (Table 1, Fig. 7). In several species, delivery occurs primarily during the TSW (e.g., *P. montanus*, Arnold, 1976; *P. shermani*, Eddy et al., 2012; and *P. yonahlossee*, Pierson et al., 2017). In other species, delivery may be restricted to the pre-TSW phase (*P. ouachitae*; Arnold, 1972) or occur

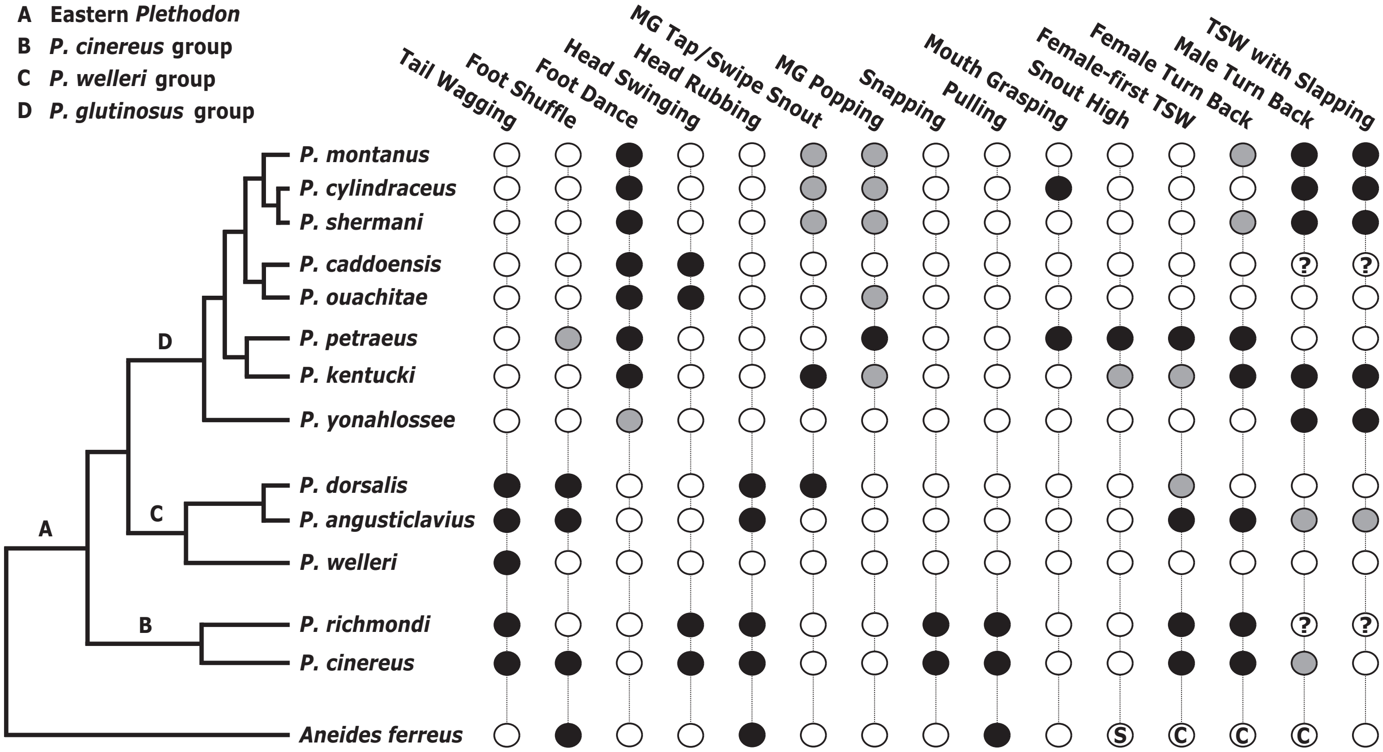

Fig. 7. Phylogenetic relationships for species of eastern *Plethodon* and *Aneides* presented with selected courtship behaviors. MG Tap/Swipe Snout = male mental-gland (MG) tap or swipe on the nasolabial region of the female's snout prior to the tail-straddling walk (TSW). See text for description of behaviors. Unshaded circle = behavior not reported; dark shaded circle = behavior reported; light shaded circle = rare or infrequent occurrence of behavior reported; ? = behavior during TSW has not been observed; S = similar behavior reported; C = circular TSW in *Aneides* includes similar behavior. Phylogenetic relationship between *Aneides* and eastern *Plethodon* inferred from mitochondrial data (Mahoney, 2001). Phylogenetic relationships among eastern species of *Plethodon* inferred from both nuclear and mitochondrial data (Kozak et al., 2006; Fisher-Reid and Wiens, 2011). Data for behavior occurrence obtained from Sapp and Kiemnec-Tyburczy (2011) and the sources listed in Table 1.

during both the pre-TSW and TSW phases (*P. kentucki*; Marvin and Hutchison, 1996). In contrast, olfactory pheromone delivery is probably not an important aspect of courtship in *P. petraeus* because mental-gland contact to the female's nares is often absent or very infrequent during the pre-TSW phase and absent (or perhaps very rare) during the TSW phase. Mental-gland tap and swipe to non-snout areas of the female at a very low frequency during the pre-TSW phase of some courtships in *P. petraeus* may be non-functional, vestigial behaviors for olfactory delivery. Because female *P. petraeus* typically turn away to avoid mental-gland contact to the nares whereas female *P. kentucki* often readily allow such contact (Supplemental Videos 49 and 55), species differences in female behavior may largely determine the variability among members of the PGG for the frequency of olfactory delivery during the pre-TSW phase.

As documented for *P. kentucki* (Marvin and Hutchison, 1996), mental-gland sliding constitutes a large portion of the pre-TSW phase for *P. petraeus* (Table 2, Fig. 2) with the duration about three times as long on the female's tail as on her body and head combined. If pheromone delivery via dermal application is not important for species in the PGG (Kiemnec-Tyburczy et al., 2011), then perhaps sliding primarily serves as a tactile signal and/or a way to assess female receptivity for mating. Although lacking a mental gland, the male slides his snout and chin on the female's skin during courtship in the plethodontid species *Pseudotriton ruber* (Arnold, 1972), *Gyrinophilus porphyriticus* (Beachy, 1997), and *Eurycea wilderae* ('Morph A' males; Kozak, 2003), which indicates this behavior, very similar to mental-gland sliding, could serve as a tactile signal and/or a means to evaluate female receptivity. Interestingly, on very rare occasions, a male *P. petraeus* arches his head and may exert downward pressure during sliding (Supplemental Video 16), which may be analogous or homologous to 'pressing' exhibited by male *Aneides ferreus* (Sapp and Kiemnec-Tyburczy, 2011).

Possible significance of mental-gland popping.—As initially implicated for female *P. cylindraceus* (Organ, 1960a), occasional popping of the mental gland from the female's skin during sliding may provide additional tactile stimulation for female *P. petraeus*. Alternatively, Arnold (1972, 1976) proposed that mental-gland popping in some EP (Table 1) is very infrequent and thus probably not an important tactile signal. Relative to other species, mental-gland popping in *P. petraeus* is more frequent and larger in amplitude (sometimes >2 cm from the female's skin). Perhaps a greater adhesiveness of skin or mental-gland secretions produces the high frequency and large amplitude of popping. Conceivably, natural selection favors more-adhesive skin secretions in the more-scansorial *P. petraeus* if such secretions enhance climbing ability. A comparative study of EP for the relative adhesiveness of skin and mental-gland secretions would help address this hypothesis. A more-concave ventral surface of the mental gland might also affect adhesion. Additionally, greater skin adhesion may allow for more-sustained mental-gland contact and thus a longer duration for tactile stimulation and dermal application of mental-gland secretions during sliding.

Possible significance of female snout high, tail arch, and undulate tail.—Although a female plethodontid salamander sometimes raises her head when the male attempts to contact her chin during courtship (e.g., Stebbins, 1949; Organ 1960a, 1960b; Arnold, 1972), the 'snout high' by female *P. petraeus* (and *P. kentucki*, Table 1) occurs when the male is not close to touching her chin. Perhaps snout high, tail arch, and undulate tail by females of *P. petraeus* serve as visual signals that indicate an increase in receptivity. These behaviors occurred more often later in the pre-TSW phase, typically while the male performed sliding on the tail or during ffTSW. Likewise, Staub et al. (2020) suggested that female tail undulation and/or raising of the head could serve as visual signals to the male prior to the TSW in some species of *Plethodon* and *Aneides*. Female *A. flavipunctatus* and *A. lugubris* elevate the chin before the TSW and this may signal female readiness for the TSW (Kiemnec-Tyburczy and Sapp, 2017). Such elevation of the chin and snout high may either be homologous or homoplastic traits in *Aneides* and EP (Fig. 7). Similarly, the duet behavior 'chin-to-chin,' which includes an almost vertical head raise by the female (Supplemental Video 55), often occurs immediately prior to female initiation of the TSW in *P. kentucki* (Marvin and Hutchison, 1996). While female tail arch and undulate in response to male contact to her tail occurs on very rare occasions in *P. montanus* (Arnold, 1976), females of *P. angusticlavius*, *P. cinereus*, and *P. richmondi* often tail arch and undulate prior to the TSW (Picard, 2005; Dyal, 2006). Female *A. flavipunctatus* undulate the tail if the male breaks contact, and this may help the male reorient toward the female (Kiemnec-Tyburczy and Sapp, 2017). In addition to a possible role as a visual signal, female tail undulations may serve as a tactile signal during ffTSW in *P. petraeus* and other EP, and during the circular TSW in *Aneides* (Picard, 2005; Dyal, 2006; Kiemnec-Tyburczy and Sapp, 2017).

Possible significance of the female-first tail-straddling walk.—Six EP exhibit ffTSW (Table 1) at different frequencies: *P. kentucki* (2/30 complete courtships), *P. dorsalis* (1/8 courtships), *P. cinereus* (1/4 complete and 9/9 incomplete courtships), *P. angusticlavius* (2/2 complete courtships), *P. richmondi* (5/5 incomplete courtships), and *P. petraeus* (9/10 complete and 10/10 incomplete courtships). The mean total duration (min) for ffTSW per pre-TSW hour of courtship is similar for *P. petraeus* (10.3±2.5), *P. cinereus* (7.7±3.4), and *P. angusticlavius* (11.4±6.6) but may be less for *P. richmondi* (2.8±1.8). As in *P. petraeus* and *P. kentucki*, both discontinuous and continuous forms of ffTSW may occur in other EP because Dyal (2006) noted that slower female walking later in a courtship better allowed the maintenance of contact between partners during ffTSW. Data from *P. cinereus* and *P. petraeus* indicate that ffTSW is more frequent or lasts longer during courtships with less-receptive or more-choosy females. For *P. cinereus*, the proportion of courtships with ffTSW is significantly greater for incomplete than for complete courtships (9/9 vs. 1/4, Fisher's exact test, $P = 0.014$; Dyal, 2006). For *P. petraeus*, the duration of ffTSWd is significantly greater for incomplete than for complete courtships (Fig. 2). Perhaps less-receptive, non-reproductive females are unable to reach a threshold level of receptivity required to engage in TSW, which leads to longer duration for ffTSW. In some EP, fewer than half of mature females reproduce each year because more than one foraging season is required to accumulate sufficient adipose tissue for reproduction (Marvin, 1996). Variation in body condition indicates some female *P. petraeus* that engaged in incomplete courtships may have lacked sufficient lipid stores for reproduction.

In addition, perhaps an inverse relationship between female receptivity and the frequency or duration of ffTSW benefits each sex. The ffTSW may allow a less-receptive or more-choosy female to better assess male persistence or courtship performance, which could indicate male fitness. Sexual selection for greater male persistence ('stubbornness') may be important in the evolution of courtship behavior in some animal species (e.g., Jackson, 1978, 1992; Fattoruso et al., 2021). If a female can evaluate a male's quality based on courtship persistence, then female choice may drive selection in favor of 'stubborn' males that persist in long courtships (Fattoruso et al., 2021). In the salamander family Salamandridae, continued male pursuit of a less-receptive female is important during courtship in some species (Halliday, 1974). In both *P. petraeus* and *P. kentucki*, turn back and bite by the female during ffTSW in some courtships (Fig. 1) indicates that a female can terminate courtship at this stage, perhaps based on information obtained during ffTSW. This duet behavior may also help promote the transfer of chemical and tactile signals. Similar to males, females in some plethodontid species have glands at the base of the tail (i.e., caudal glands), which could produce chemical signals during courtship (Sever, 1989; Mary and Trauth, 2006; Sever and Siegel, 2015; Rollins and Staub, 2017; Rupp and Sever, 2018). Thus, a female may transfer chemical signals from her caudal glands to the male during ffTSW in some EP (Staub et al., 2020) as may occur during the circular TSW in *Aneides* (Cupp, 1971; Sapp and Kiemnec-Tyburczy, 2011). A long duration for ffTSW may also benefit the male because it allows sustained mental-gland contact and thus greater opportunity for tactile stimulation and dermal application of chemical signals.

Variation among EP for initiation of the TSW and male turn back during TSW.—Females and males of different EP vary in the proclivity to initiate the TSW. The male usually initiates the TSW via snout under (lifting) in *P. dorsalis*, *P. montanus*, *P. shermani*, and *P. cylindraceus* (Arnold, 1972; Picard, 2005). In contrast, females of *P. kentucki* and *P. petraeus* initiate contact leading to the TSW in the majority of courtships (i.e., directly via chin over without snout under; Marvin and Hutchison, 1996; current study). Likewise, in *P. cinereus* and *P. angusticlavius*, the female often initiates the TSW (Gergits and Jaeger, 1990; Dyal, 2006). For species with ffTSW, turn back by the female during ffTSW often directly leads into the TSW (i.e., *P. cinereus*, *P. angusticlavius*, and *P. petraeus*; Dyal, 2006; current study). Phylogenetic relationships among these species (Kozak et al., 2006; Fisher-Reid and Wiens, 2011) suggest that this behavioral sequence (female turn back during ffTSW leading into TSW) may be ancestral for EP (Fig. 7).

Arnold et al. (2017) proposed that male turn back toward the female during the TSW to deliver courtship pheromones is likely an ancestral trait for plethodontids because it occurs in many genera. If so, then the trait was lost in the evolution of *Pseudotriton*, *Gyrinophilus*, *Ensatina*, and some EP (Arnold et al., 2017). Male turn back during the TSW is either absent or rare for species in the PCG and PWG. Turn back may be absent in *P. dorsalis* and *P. welleri* but is rare in *P. angusticlavius* (Arnold, 1972; Picard, 2005; Dyal, 2006). Dyal (2006) did not describe turn back for *P. cinereus* but did report (in table 1 of that publication) the behavior as present. Thus, here I consider the behavior rare for *P. cinereus* (Fig. 7). Male turn back during the TSW may be ancestral for the PGG because it occurs in most (5/7) species but may have been lost or become very infrequent in both *P. ouachitae* and *P. petraeus* (Fig. 7).

Courtship duration for EP.—In comparison to other EP, courtship is often lengthy for pairs of *P. petraeus* due to a prolonged duration of both the pre-TSW and TSW phases. The mean time elapsed from their initial encounter until the initiation of the TSW for pairs of *P. petraeus* (290 min, Fig. 4) is much longer than for *P. kentucki* (96 min; Marvin and Hutchison, 1996) and *P. montanus* (56 min; Arnold, 1976). Likewise, the duration (min) of the TSW for pairs of *P. petraeus* (mean = 47, range 20 to 223) is often longer than for *P. kentucki* (mean = 20, range 1 to 73; Marvin and Hutchison, 1996), *P. yonahlossee* (range 15 to 29; Pierson et al., 2017), and *P. cinereus* (mean = 16, range 2 to 58; Dyal, 2006). Olfactory delivery of mental-gland pheromones reduces the duration of the TSW and thus the overall length of courtship in *P. shermani* (Houck et al., 1998, 2008; Rollmann et al., 1999; Eddy et al., 2012). Thus, the rare and infrequent application of mental-gland secretions to the female's nares during the pre-TSW phase and the absence of such transfer during the TSW in *P. petraeus* may partly explain the long duration of most courtships. For *P. shermani*, the more time a pair spends in the pre-TSW phase, the less time they spend in the TSW (Eddy et al., 2012). This inverse relationship could reflect the importance of information exchange between salamanders whereby a reduction in exchange during a shorter pre-TSW phase necessitates an increase in exchange during a longer TSW (Eddy et al., 2012). Such a relationship may explain the significant, positive correlation between the total duration of time apart and the duration of the TSW in *P. petraeus* (Fig. 6). Courtship duration is very long in *A. ferreus*, perhaps because the microhabitats utilized by individuals (i.e., trees and crevices which may provide protection from predators) reduce the effect of predation pressure on courtship length (Sapp and Kiemnec-Tyburczy, 2011). Similarly, if mating in *P. petraeus* often occurs within the protection of rock crevices, then reduced predation pressure or mate competition might have allowed the evolution of its lengthy courtship.

Comparison of spermatophore deposition, sperm transfer, and spermatophore consumption among EP.—The frequency of multiple spermatophore depositions for *P. petraeus* courtships (10%) is greater than for *P. montanus* (3% of 30 courtships; Arnold, 1976) but less than for *P. kentucki* (43% of 30; Marvin and Hutchison, 1996) and *P. cinereus* (75% of four; Dyal, 2006). Insemination success per spermatophore deposition is 55% ($n = 11$), 55% ($n = 31$), 56% ($n = 36$), and 27% ($n = 11$) in these species, respectively. Insemination success per complete courtship is 60% ($n = 10$), 57% ($n = 30$), 77% ($n = 30$), and 75% ($n = 4$) in these species, respectively. Thus, insemination success per complete courtship may be slightly greater for EP with a higher frequency of multiple spermatophore depositions. For male *P. petraeus*, the frequency of tail undulations during spermatophore deposition (mean = 0.84 Hz at end of deposition) is lower than frequencies (about 1.2 Hz) reported for other EP (Marvin and Hutchison, 1996; Pierson et al., 2017). The times required for spermatophore deposition (4 to 9 min) and sperm transfer (about 1 min) are highly conserved among EP (Marvin and Hutchison, 1996; Dyal, 2006; Table 2). Behavior is also highly conserved during sperm transfer (Table 1), but slight differences in male leg movement during pelvic lifting may occur in some species (Pierson et al., 2017). Male consumption of spermatophores occurs in many species of the PGG but may be rare for species in the PCG and PWG (Table 1). Such behavior, which is likely comparable in function to an individual eating its shed skin (pers. obs.), could reduce the loss of energy and nutrients by males during the mating season.

Facultative changes in courtship behavior for EP.—In some plethodontid species, variability in courtship behavior during the pre-TSW and/or TSW phase may reflect facultative changes in response to variation in partner receptivity. For example, the male of EP typically initiates mental-gland sliding on the female's tail, but eventually he increases contact time with her body and head (Arnold, 1972; Marvin and Hutchison, 1996; present study). A less-receptive female may be more likely to allow sustained contact to her tail than to her body or head. If courtship progresses and the female becomes more receptive or habituated to touch, then she may allow the sustained contact to her head required for initiating and maintaining the TSW. Another example is the occurrence of two forms of TSW, either with or without olfactory delivery of pheromones via mental-gland slapping, in several species of the PGG (Table 1). These two forms of TSW likely represent facultative changes in male behavior in response to variation in female receptivity, where TSW with slapping may occur more often with a less-receptive female, perhaps to test or enhance her receptivity (Arnold, 1977; Marvin and Hutchison, 1996).

My observations indicate additional changes in behavior may occur for some species in response to variation in partner receptivity. Although the frequency and duration of many behaviors of *P. petraeus* during the pre-TSW phase are very similar during both incomplete and complete courtships, some significant differences may result from facultative changes in behavior. During incomplete courtships, females perform turn back and chin over less frequently, while males perform snout under more frequently (Figs. 3, 5). Thus, perhaps a male occasionally benefits from attempting to initiate the TSW more frequently with a less-receptive or more-choosy female. Per pre-TSW hour, the total duration of close is less, whereas the total duration for ffTSWd is longer during incomplete courtships (Fig. 2). Lower courtship receptivity may often result in more time moving away from the potential mate (i.e., more time apart and a lower duration for close). When female receptivity is lower (or choosiness is higher), greater ffTSW duration could provide possible benefit(s) for each sex as summarized earlier. Thus, some behavioral differences between complete and incomplete courtships in *P. petraeus* may reflect facultative responses to less-receptive partners.

Similarly, among complete courtships, individual variation in courtship receptivity or ability may explain the significant, positive correlation between time apart during the pre-TSW phase and TSW duration (Table 2). Correspondingly, the less often a male *P. shermani* performs foot dance during the pre-TSW phase, the more time the pair spends in TSW (Eddy et al., 2012). Significant, positive correlations among the durations for sliding, ffTSWd, and unsuccessful positioning for TSW (Table 2), and between the total duration of all ffTSW (both discontinuous and continuous forms) and TSW duration (Fig. 6), may also reflect facultative behavioral changes in response to variable female receptivity or choosiness. For all courtships in *P. petraeus*, variation in female receptivity may also explain the significant, positive correlation between the frequency of snout under and the duration of ffTSWd (Table 4).

Tail or body flex by a female *P. petraeus* in response to mental-gland contact may occur when she is somewhat receptive but not receptive enough to allow sustained contact by the male. If so, then the behavior might be similar to that of a less-receptive female raising her head when the male attempts to contact her chin (e.g., Pierson et al., 2017). Similarly, a less-receptive female *P. richmondi* may curl her tail away from male contact (tail rubbing) to prevent or delay the initiation of ffTSW (Dyal, 2006). The infrequent 'mouth grasp' of the female by male *P. petraeus* (and *P. cylindraceus*, Table 1) is likely a facultative response to a less-receptive female. Males of *P. petraeus* perform mouth grasping only after at least 200 min of courtship (Fig. 4), and it occurs more frequently during incomplete courtships with a greater total duration of time apart for salamanders and a higher frequency of female tail flex (Table 4). Perhaps this behavior allows the male to puncture or abrade the female's skin, which increases the opportunity for mental-gland pheromones to enter her blood circulation. If so, mouth grasping may accomplish the same function (i.e., transdermal pheromone delivery) as pulling and snapping behaviors in *Desmognathus* (Verrell and Mabry, 2000), *Aneides* (Kiemnec-Tyburczy and Sapp, 2017), *P. cinereus* and *P. richmondi* (Dyal, 2006), and biting in some species of *Desmognathus* (Promislow, 1987; Houck and Sever, 1994; Verrell, 1999).

Possible function of aggression and biting before courtship and after mating in some EP.—Aggression by some individuals of *P. petraeus* and other EP (Supplemental Videos 41 and 42) during their initial encounter may be misguided territorial behavior (Marvin and Hutchison, 1996). Territoriality is common among EP (e.g., Jaeger et al., 1982; Mathis, 1991; Marvin, 1998a, 1998b) and thus individuals might often benefit from aggression toward an unknown individual. Most male *P. petraeus* turned around and bit the female either immediately after or within two min after the attempted retrieval of the sperm cap by the female (Supplemental Videos 11 and 25). Such male aggression also occurs in other species of the PGG (Marvin and Hutchison, 1996). The possible selective advantage of male aggression after spermatophore deposition is unknown. Perhaps males benefit by chasing an inseminated female, or a female that is unsuccessful in retrieving the sperm cap, from the mating area because further courtship with that individual could be a waste of reproductive effort. In some species or populations, sexual interference among males (Arnold, 1976) may also select for aggressive behavior following spermatophore deposition. Such aggression could be beneficial for a male that might otherwise waste reproductive effort if he repeatedly performs TSW and spermatophore deposition with a male that engages in TSW like a female (Arnold, 1976).

Evolution of courtship behaviors in EP.—The evolutionary history of certain courtship behaviors is often summarized as a loss or gain of the trait for different EP (e.g., Picard, 2005; Arnold et al., 2017). Alternatively, perhaps the evolution of some behavioral traits involves a major decrease or increase in the behavior frequency instead of a loss or gain. For example, the apparent absence or loss of a given behavior in some species (e.g., mouth grasp, turn back during TSW) may sometimes result from a very low frequency of occurrence and limited courtship observations. Similarly, some behaviors (e.g., tail arch and undulate in response to contact, tail straddling) are not sex-specific but instead vary in frequency among species for each sex, perhaps due to sexual selection. Thus, it may often be more informative when researchers report behavior frequency (e.g., per hour or pre-TSW hour) in courtship descriptions.

Some behaviors may have evolved via a simultaneous or near-simultaneous expression of two other behaviors. For example, the duet behavior chin-to-chin, present in two species of the PGG (Table 1), may result from the simultaneous occurrence of raise chin (or snout high) by the female and mental-gland tapping by the male on her nares. The evolution of some behaviors may result from changes in the duration, timing and/or context of one or more behavioral traits. Foot shuffle may be ancestral for both *Aneides* and EP, but its context (and perhaps function) differs between these two clades (Sapp and Kiemnec-Tyburczy, 2011). The occurrence of both foot dance and foot shuffle in *P. petraeus* indicates that foot dance could have evolved from foot shuffle early in the evolution of the PGG (Fig. 7). Head swinging during courtship in several EP (Fig. 7) may be comparable to 'head sway' during aggressive interactions in *P. kentucki* and *P. glutinosus*, which could signal submissive (non-aggressive) intent and/or enhance chemoreception of volatile chemicals (Dawley, 1984; Marvin, 1998b; Dantzer and Jaeger, 2007b). The occurrence of ffTSW in some members of the PCG, PWG, and PGG indicates that the behavior could be a shared ancestral trait for EP (Fig. 7), and perhaps for *Aneides*. The circular TSW in some species of *Aneides* (Cupp, 1971; Kiemnec-Tyburczy and Sapp, 2017) may have evolved from sustained turning back by the female during ffTSW (i.e., as sustained circling behavior; Dyal, 2006) leading into the TSW. The downward arching of the male's head infrequently during sliding in *P. petraeus*, during snapping in *P. cinerus* and *P. richmondi*, and during pressing in *Aneides* may be analogous or divergent forms of a homologous behavior.

Arnold (1972) proposed that mental-gland slapping evolved from snapping. In contrast, Picard (2005) suggested that, after the evolutionary loss of snapping, head rubbing evolved into slapping. Similarly, I propose olfactory pheromone delivery evolved from sliding and brief contact of the mental gland on the female's nares. Perhaps a rapid, momentary application of mental-gland secretions onto her nares via mental-gland tapping and swiping (Supplemental Video 49) during the pre-TSW phase evolved to allow quick olfactory delivery when a female is not receptive enough to allow sustained head contact during sliding. In contrast to sustained sliding on her nares, quick olfactory delivery could occur during either the pre-TSW phase via tapping/swiping or turning back during the TSW via slapping, even with a less-receptive female. Picard (2005) proposed olfactory delivery during the TSW was ancestral in the PGG but was reduced or lost in the evolution of some species and became common during the evolution of other species. Similarly, I suggest olfactory delivery during both the pre-TSW and TSW phases was ancestral, became either more or less frequent in each phase for some species, and became very infrequent during both phases for *P. petraeus*.

Examples of possible avenues for future research on courtship in EP.—The detailed study of courtship and mating behaviors for additional EP is needed to advance our understanding of the evolution of the behavioral diversity within this speciose clade. Courtship and mating have not been described for any of the species (perhaps at least five; Felix et al., 2019) in the *P. wehrlei* group of EP. Based on the phylogenetic relationships of *P. websteri* and members of the *P. wehrlei* group to other EP (Kozak et al., 2006; Fisher-Reid and Wiens, 2011), research on these species could improve our understanding of the evolution of olfactory pheromone delivery and courtship behavior diversity. Similarly, based on phylogenetic relationships among members of the PCG (Kozak et al., 2006; Fisher-Reid and Wiens, 2011), the study of *P. serratus* may expand knowledge of the evolution of courtship behavior in this group. Because male behavior (e.g., tail straddle) during ffTSW may be comparable to behavior during male–male TSW that causes sexual interference in some species (Arnold, 1976), research that includes staged encounters between a female and two males could help examine possible links between the occurrence of ffTSW and male–male TSW among EP. Although behavior may often be similar for closely related species, the notable differences in courtship for *P. petraeus* and *P. kentucki* indicate that additional studies of somewhat closely related EP might produce unexpected and insightful observations. To investigate the possible inverse relationship between predation pressure and courtship duration for plethodontids, comparative studies of either different populations or closely related species that occupy disparate microhabitats may be useful. For example, the comparison of courtship for different populations of *P. kentucki* (e.g., which inhabit forest-floor versus rock-outcrop microhabitats) or closely related species within the *P. wehrlei* group (e.g., forest-floor populations of *P. wehrlei* versus rock-outcrop populations of *P. pauleyi* or cave-entrance populations of *P. dixi*; Felix et al., 2019) could be informative.

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/h2023077.

ACKNOWLEDGMENTS

I conducted this research under approval of the University of North Alabama (UNA) Institutional Animal Care and Use Committee, but the Committee does not issue protocol approval numbers. The Biology Department at UNA funded the research. The Georgia Department of Natural Resources issued scientific collecting permits 29-WBH-12-175 for 2012 (and a renewal for 2013), 29-WJH-14-3 for 2014, and 29-WBH-15-2 for 2015. J. Jensen and C. Camp provided specific locality information for salamander collection and collected some of the males in 2013. C. Camp, K. Kiemnec-Tyburczy, and J. Jensen provided many helpful comments and suggestions on the manuscript.

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APPENDIX 1

Description of behaviors for other species of eastern *Plethodon*

For *P. petraeus*, I did not observe the following behaviors, which occur in other species of eastern *Plethodon*. Table 1 summarizes the species occurrence for these behaviors and provides citations of sources. **Rubbing/sliding:** Individual moves its head in a side-to-side (rubbing) or forward-to-backward (sliding) motion while in contact with the body dorsum of the other salamander. **Head rubbing:** Head-to-head contact occurs with an individual making a side-to-side or forward-to-backward motion while its head is on top of the other individual's head. **Head swinging:** Male moves his head laterally in a side-to-side motion slightly above the substrate at about 15° arcs (Dyal, 2006) or with his mental gland in contact with the female's dorsum (Arnold, 1972). **High-amplitude head swinging:** Female swings her head side to side at approximately 45° arcs while either she is a short distance from the male or he is rubbing or nudging her back or tail. **Joint head swinging:** Duet behavior whereby both the male and female sway the head laterally, usually alternating sides relative to each other. Female's head moves in about 45° arcs while the male's head swings at about 15° arcs. Pair may either face one another or the male is on top of the female and facing in the same direction. **Cloacal nudging:** Snout of one individual contacts the cloacal region of the other individual. **Cloacal rubbing:** Female crawls over the male and rubs her cloaca with quick forward–backward movements while in contact with the male's dorsum. **Tail wagging:** During tail undulation, the distal portion (i.e., about one-half to one-third) of the tail wags back and forth. **Chin-to-chin:** Duet behavior whereby female raises her head in a near vertical position, often with forelegs extended. While facing the female, the male simultaneously raises his head in a near vertical position and taps his mental gland on her snout and/or chin. Female may walk forward in this position for several steps while the male steps backward. **Pulling:** Individual presses its chin against the other salamander's body and pulls the chin backward in contact with the skin. **Snapping:** Male arches his head downward, presses his chin against the female's skin, and then draws his chin backward very rapidly in a snapping motion. **Circling:** During ffTSW, the female turns back toward the male, and the pair forms a circle. If the female straddles the male's tail, then a circular form of TSW ensues, which later leads into a linear TSW. Although a female *P. petraeus* often exhibits turn back toward the male during ffTSW, she does not straddle his tail immediately after turn back. **Turn back during TSW:** During TSW, the male bends his body in a U-shape and positions his mental gland immediately above the female's snout or head. Male may then perform a mental-gland slap; however, sometimes he omits the slap, straightens his body, and resumes the TSW. **Mental-gland slapping during TSW:** After turning back toward the female during TSW, the male slaps his mental gland once on the female's snout or dorsum of her head (or eyes) while she remains astride his tail. If the female does not break contact and move away after a mental-gland slap, then the pair resumes TSW.

Raise head for mental-gland slap: As the male turns back toward the female during the TSW, she breaks chin contact with his tail base and raises her head above his tail as if to receive the mental-gland slap. Female lowers her head back onto his tail or retreats after receiving a mental-gland slap. **Lateral head movements:** Female moves her head laterally in synchronization with, but counter to, the lateral sacral and tail-base movements of the male during spermatophore deposition. **Pass by spermatophore:** Following spermatophore deposition, as the male leads female over the spermatophore, the female does not stop walking forward and passes by the spermatophore to continue TSW.

APPENDIX 2

Identification numbers for supplemental videos of courtship behaviors in the salamanders *Plethodon petraeus* and *Plethodon kentucki*. TSW = tail-straddling walk.

	Supplemental video identification number			
	P. petraeus		*P. kentucki*	
Behavior	Male	Female	Male	Female
Nose-tap	1, 29		39, 76	
Stationary		2, 15		40, 42
Move toward	2		40, 41, 42	
Move away	1	18	39	43, 67
Bite	11, 25	10	42	41, 59
Foot dance	4, 12		44, 45, 46	
Foot shuffle	13, 14			
Mental-gland sliding	4, 15, 16		46, 47, 48	
Mental-gland popping	15, 17, 18		47, 48	
Mental-gland tap/swipe on snout *(before TSW)*			49	
Mental-gland tap/swipe not on snout *(before TSW)*	19, 20		50	
Tail (or body) flex *in response to mental-gland sliding*		6, 7, 17		
Tail arch and undulate tail	4, 24, 38	3, 5, 8	51, 52	53, 54
High amplitude tail undulations		30		
Mouth grasping	21, 22			
Snout high		31		46
Chin-to-chin			55, 56	55, 56
Tail straddle *for female-first TSW*	8			
Discontinuous, female-first TSW	37	37	57, 58, 59	57, 58, 59
Continuous, female-first TSW	5, 36	5, 36	53, 54	53, 54
Turn back *during mental-gland sliding or female-first TSW*		10, 32		59, 60, 61
Snout under	23, 34		62, 64	
Raise chin *in response to snout under or before chin over*		23		63, 64
Chin over		33, 34		60, 61, 63
Position for TSW	24		60, 61, 62	
Turn around *after position for TSW or sperm cap retrieval*	11, 25		75	
Tail straddle *to initiate TSW*		9		61
Tail-straddling walk	36, 38	36, 38	51, 52	51, 52
Turn back *during TSW*			65, 66, 67	
Raise head *to receive mental-gland slap during TSW*				66
Mental-gland slapping on snout *during TSW*			65, 66, 67	
Vent sliding *at end of TSW*	26		68, 69	
Spermatophore deposition	26, 27		70, 71	
Lead female over spermatophore	35	35	71, 72	71, 72
Stop and lower vent		35		73, 74
Position on sperm cap		28		73, 74
Stationary with tail flexed	28		73, 74	
Eat spermatophore cap and/or base	29		76	