

CHIGGER MITES (*HANNEMANIA* CF. *DUNNI*) INFEST NORTHERN SLIMY SALAMANDERS (*PLETHODON GLUTINOSUS*) IN ALABAMA, USA

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Abstract.—Chiggers are the larval form of trombiculid and leeuwenhoekiiid mites that parasitize terrestrial vertebrates. With one exception, species of chiggers that infest amphibians burrow under the skin to encapsulate and feed. They are detected by the naked eye as moving red or orange dots, swollen nodules, lesions, or pustules. Alabama, USA, has only one previous report of a chigger infested salamander. We examined 45 Northern Slimy Salamanders (*Plethodon glutinosus*) from five localities in Jefferson or Shelby counties, Alabama and counted the number of chiggers in infested individuals. We found salamanders infested with mites at four of five localities, and we identified the mite as *Hannemania* cf. *dunni*. The overall prevalence of infestation among the five localities was 66.7%, the average abundance was 11.8 ± 2.1 (SE) and the mean intensity of infestation was 17.6 ± 2.6 (range, 1–52), which is the highest intensity reported in the *Plethodon glutinosus* complex. We found no relationship between body size (snout-vent length, distance between limbs or weight) and infestation levels. Mites were not distributed equally across body regions; rather, the limbs and feet had more mites than either the tail or body. We found relatively fewer mites on the head, throat, and cloacal regions. Our report represents a new host and the second record of this chigger for Alabama. Infestation reportedly negatively affects salamanders through physical damage to the limbs and body, reduces reproductive success, and may increase susceptibility to disease.

Key Words.—Acari; Amphibia; Caudata; Leeuwenhoekiiidae; parasite; Plethodontidae

INTRODUCTION

Chiggers are the six-legged larval form of trombiculid and leeuwenhoekiiid mites that parasitize terrestrial vertebrates worldwide (Sambon 1928; Hyland 1961; Loomis and Wrenn 1984; Shatrov and Kudryashova 2008). Chigger mites have a complex life cycle consisting of egg, deutovum (inactive larval stage), larva (parasitic, six-legged chigger stage), nymphochrysalis (inactive nymphal stage), nymph (free-living, eight-legged), imagochrysalis (inactive), and adult (free-living, eight-legged; Hyland 1950; Wharton and Fuller 1952; Sasa 1961). Chigger mite larvae require only one host, and after feeding (engorgement) they drop off the host to continue their life cycle in soil, leaf litter, grasses, decaying logs, tree snags, or bark (Ewing 1944; Loomis 1956). In most groups of vertebrate hosts, chiggers typically engorge in just a few days (Wharton and Fuller 1952; Mullen and OConnor 2009); however, in amphibians, chiggers often remain partially or completely embedded in the dermis for months, even after feeding (Ewing 1926a; Hyland 1961). Nymphs and adults are not parasitic; rather, they prey on other small arthropods and their eggs (Lipovsky 1951; Hyland 1961; Mullen and OConnor 2009).

In North America, mites from two genera, *Hannemania* and *Eutrombicula*, parasitize amphibians (Paredes-León et al. 2008; Walters et al. 2011). All of the approximately 27 species of *Hannemania* are amphibian specialists (Silva-de la Fuente et al. 2016); whereas, *Eutrombicula* is more speciose and parasitizes all vertebrate groups (Wrenn and Loomis 1984; Mertins et al. 2011; Walters et al. 2011). Eutrombiculan chiggers are familiar to herpetologists as they are easily seen between the scales of snakes, in the axilla of lizards (Ewing 1921; Benton 1987), or attached to the skin of turtles (Ewing 1926b, Jenkins 1948). They are also responsible for the characteristic itching and red welts that afflict many field biologists (Ewing 1921; Jenkins 1948; Bennett et al. 2014). In amphibians, larval *Eutrombicula* sp. stay attached on the surface of the skin and are visible as small orange or red dots (Torrence et al. 2007; Mertins et al. 2011). In contrast, *Hannemania* sp. use specialized chelicerae to burrow into the skin of amphibians where they feed and encapsulate (Sambon 1928; Crossley 1960; Hyland 1961). The capsule that surrounds the chigger is formed by the dermis and located in the stratum spongiosum (Hyland 1961; Grover et al. 1975). Feeding times are shorter than encapsulation times, which vary from at least three months to over a year in anurans (Ewing 1926a; Loomis 1956; Hyland

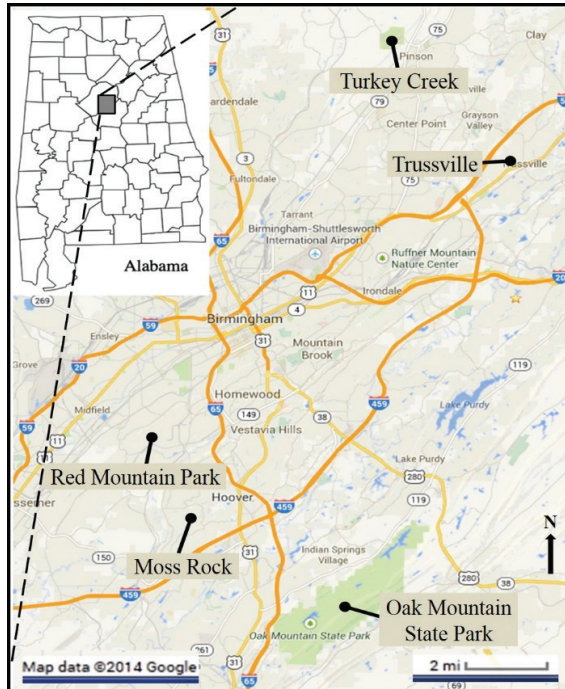


FIGURE 1. Collection localities for Northern Slimy Salamanders (*Plethodon glutinosus*) in Jefferson and Shelby counties, Alabama, USA. We derived the map from Google Maps.

1961; Welbourn and Loomis 1975). We did not find any records of encapsulation times for caudate hosts.

Larval *Hannemania* are seen by the naked eye as orange-colored lesions, swollen nodules, or vesicles that can be on any part of the body, but primarily are on the feet and ventral surfaces of the body (Sladky et al. 2000; Malone and Paredes-León 2005; Brown et al. 2006). An infested host may also have deformed limbs or be missing digits (Connior et al. 2016). While collecting Northern Slimy Salamanders (*Plethodon glutinosus*) for another study, we noticed that some were infested with chiggers. Hribar and Tyler (1989) first reported chigger infested amphibians in Alabama, USA. Here, we provide the second record of chiggers in any amphibian in Alabama. We report variation in parasitism by locality and body region and assess the relationship between body size and infestation.

MATERIALS AND METHODS

We collected 45 Northern Slimy Salamanders (*Plethodon glutinosus*) in June and July 2013 by searching underneath natural cover objects and in rock crevices in mixed hardwood-pine forests at five localities in Jefferson and Shelby counties in north-central Alabama, USA (Fig. 1). We placed each salamander into individual small plastic bags, transported them to the laboratory, and housed each in individual plastic containers with moist paper towels. We used digital

calipers to measure snout-vent length (SVL, tip of the snout to the posterior end of the cloaca) and distance between limbs (DBL, axilla to the anterior connection of the hind limb to the body) to the nearest 0.01 mm. We weighed each salamander to the nearest 0.01 g using a digital scale. We examined each salamander for chiggers and classified any as infested if they had lesions of orange to reddish pustules, swollen nodules, or vesicles (Sladky et al. 2000; Connior et al. 2016). We counted the number of chiggers on each of the following body regions: head and throat, body (dorsal and ventral surfaces), forelimbs and feet, hindlimbs and feet, cloaca, and tail. We also noted any missing digits, as mites have been found to deform the feet of parasitized salamanders (Connior et al. 2016). We released salamanders at their capture locations within a month.

We excised three mites from the tissues of a deceased salamander, stored them in 75% ethanol, briefly air dried them and then placed them directly into Hoyers Solution on standard (75 × 25 mm) microscope slides, applying a 12 mm coverslip. We dried the slides in a drying oven at 50° C for two weeks, then ringed with Glyptal (GC Electronics, Rockford, Illinois, USA). We identified the mites to genus using Brennan and Goff (1977), supplemented by Ewing (1931), Radford (1942), and Loomis (1956). We used Sambon (1928) and Hyland (1956) for species determination, consulting Goff et al. (1982) for the terminology used in chigger identification.

We used the definitions in Bush et al. (1997) to quantify parasite populations (prevalence, abundance, intensity) and visualized the distribution of chigger infestation using a histogram. Prevalence (number of infested hosts / number of examined hosts) and abundance (number of chiggers / total number of hosts) include infested and uninfested salamanders; whereas, intensity (number of chiggers / number of infested hosts) only includes infested salamanders. We tested the hypothesis that body size (as defined by SVL, DBL, and weight) predicts infestation status by conducting a logistic regression of SVL, DBL, and body weight against infestation status (0 if uninfested, 1 if infested) in R (R Core Team 2017). We followed this with a test of the hypothesis that our measures of body size (SVL, DBL, body weight) predict the extent of mite infestation for salamanders infested with chiggers. To accomplish this, we regressed overall counts of chiggers against the three previously described predictor variables using a Poisson generalized linear model in R. We used a Poisson regression because of its suitability in circumstances in which the response variable is count data (O'Hara and Kotze 2010). The coefficient of determination, r^2 , was calculated using the rsq package in R (Zhang 2018). We next tested the hypothesis that different body regions experienced differential degrees of infestation with a nonparametric

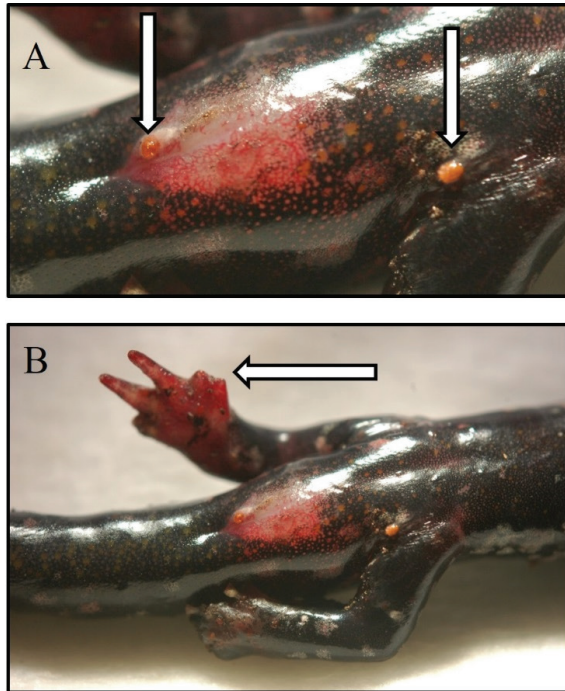


FIGURE 2. Chiggers (*Hannemania* cf. *dunni*) infesting Northern Slimy Salamanders (*Plethodon glutinosus*) from north-central Alabama, USA, burrowing into (A) the epidermis and (B) causing loss of digits. (Photographed by Kristin A. Bakkegard).

Kruskal-Wallis test performed in R using untransformed mite counts per body region of infestation for infested salamanders. We followed this with Nemenyi's non-parametric pairwise rank test using the PMCMRplus package in R (Zar 1999; Pohlert 2018) to identify which regions differed. Ties were randomly broken prior to analysis, which allowed us to correct for multiple testing using a Bonferroni correction. We subsequently visualized the distribution of mites across the body using boxplots. Results were considered significant if $P \leq 0.05$.

RESULTS

We identified the mites (Fig. 2) as *Hannemania*

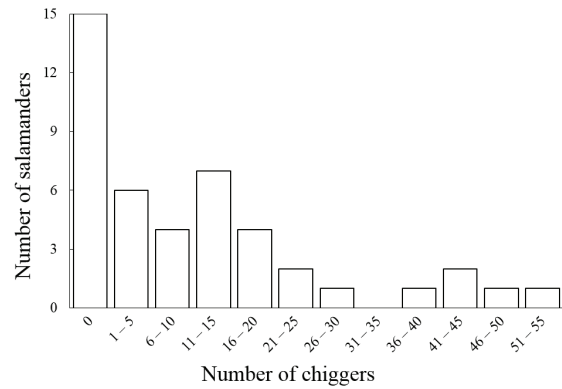


FIGURE 3. Distribution of abundance and intensity of infestation by *Hannemania* cf. *dunni* in Northern Slimy Salamanders (*Plethodon glutinosus*) from north-central Alabama, USA. Prevalence of infestation is 66.7%, median abundance is six chiggers and the median intensity is 14 chiggers.

cf. *dunni* (Acari: Leeuwenhoekiidae). We found salamanders parasitized with chiggers at four of five localities (Table 1), with none of the five salamanders captured at Red Mountain Park parasitized by mites. Total prevalence of infestation for salamanders ($n = 45$) from all five localities was 66.7%. Mean abundance was 11.8 ± 2.1 (standard error) and the mean intensity of infestation was 17.6 ± 2.6 (range, 1–52) with variation among localities and body region (Table 1, Table 2). Not all salamanders were infested by chiggers, and the data were not normally distributed; consequently, we followed the recommendation of Bush et al. (1997) and also report a median abundance (six chiggers) and intensity (14 chiggers; Fig. 3). The logistic regression revealed no relationship between SVL, DBL, or body weight and infestation status (Fig. 4A, C, E). Likewise, the Poisson regression revealed that the same three measures of body size do not predict the extent of infestation (Fig. 4B, D, F). Chiggers were not evenly distributed over the body ($H = 69.04$, $df = 5$, $P < 0.001$). Severity of infestation is greatest in limbs and feet, lowest on the head/throat and cloaca, and intermediate on the tail and body (Fig. 5, Table 3). We did not observe

TABLE 1. Sample size (n), percentage prevalence, mean abundance (± 1 standard error), mean intensity (± 1 standard error), and range of intensity, of parasite populations of Northern Slimy Salamanders (*Plethodon glutinosus*) infested with *Hannemania* cf. *dunni* by locality. The first four localities are in Jefferson County, Alabama, USA. Oak Mountain State Park is in Shelby County, Alabama, USA, and salamanders were collected at four different areas within the park. The abbreviation n indicates the number of salamanders examined for chiggers by locality and SE is standard error.

Locality	n	Prevalence (%)	Mean Abundance	Mean Intensity	Range of Intensity
Moss Rock	6	100.0	22.0 \pm 6.8	22.0 \pm 6.8	5–52
Red Mountain Park	5	0.0	0	0	0
Trussville	9	11.1	0.22 \pm 0.22	2	2
Turkey Creek	1	100.0	44	44	44
Oak Mountain State Park	24	91.7	14.6 \pm 2.6	16.0 \pm 2.7	1–47
Totals	45	66.7	11.8 \pm 2.1	17.6 \pm 2.6	1–52

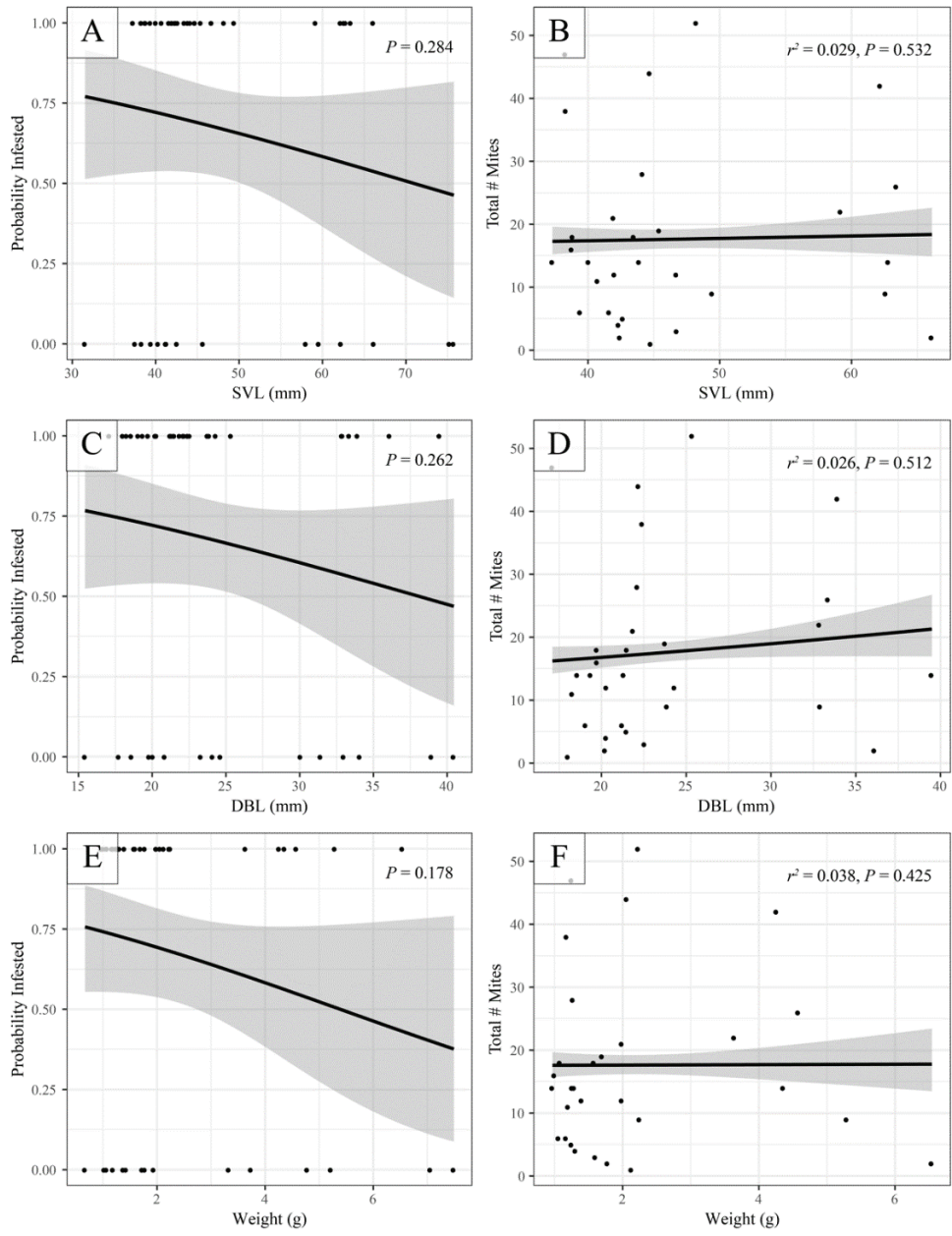


FIGURE 4. Relationships between body size measurements and chigger (*Hannemania* cf. *dunni*) infestation on Northern Slimy Salamanders (*Plethodon glutinosus*) collected in north-central Alabama, USA. Logistic regressions showing the relationship between body size and probability of infestation is plotted in A, C, and E; Poisson regressions showing the relationship between body size and extent of infestation is in B, D, and F.

any chiggers in or near nasolabial grooves. Only four salamanders were missing digits; three had lost a digit from a front foot and one was missing a digit from a front and hind foot.

DISCUSSION

Several species of chigger mites (*Hannemania* sp.) parasitize terrestrial and semiaquatic species of amphibians across the U.S. and Mexico (Paredes-León

et al. 2008; Walters et al. 2011; Connor et al. 2016), and salamanders from three families are known hosts of one or more species of these mites (e.g., *H. dunni*, *H. eltoni*, *H. hegeneri*, or *H. monticola*; Hyland 1961; Walters et al. 2011; Silva-de la Fuente et al. 2016). Parasitism of salamanders by species of *Hannemania* in Alabama, however, is either rare or seldom reported. For example, the only record of *H. dunni* parasitizing a species of salamander in Alabama is that of Hribar and Tyler (1989) who documented parasitism of the

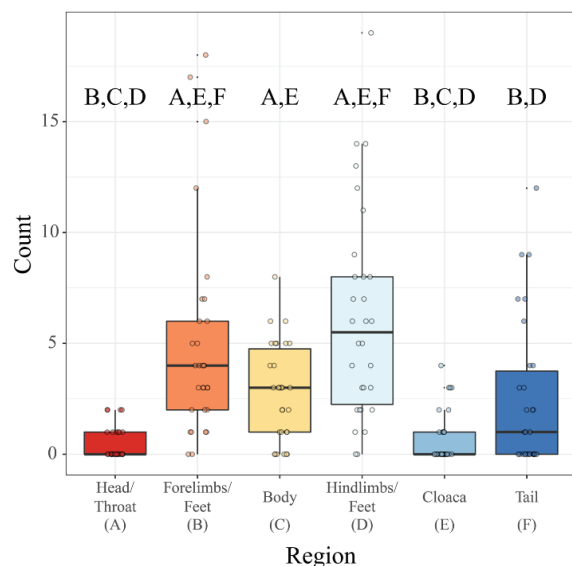


FIGURE 5. Distribution of chiggers (*Hannemania* cf. *dunni*) by body region for parasitized Northern Slimy Salamanders (*Plethodon glutinosus*) collected in north-central Alabama, USA. Significant differences ($P < 0.05$) by Nemenyi's non-parametric pairwise rank test is indicated with capital letters corresponding to letters below variable names. Corresponding P -values are in Table 3.

Southern Two-lined Salamander (*Eurycea cirrigera*) in the southeastern Piedmont physiographic region of Alabama. Thus, our report of *Hannemania dunni* parasitizing the Northern Slimy Salamander represents both a new host record for Alabama and a new physiographic region (Valley and Ridge). Furthermore, our report represents the southern-most location of a species of *Hannemania* chiggers parasitizing a member of the Slimy Salamander species complex. Salamanders of the *Plethodon glutinosus* complex (Highton et al. 1989) parasitized by *Hannemania* (*dunni*, *hegeneri*, or unknown species) have been reported from Arkansas, USA (Duncan and Highton 1979; McAllister et al. 2002), Illinois, USA (Landewe 1960), North Carolina, USA (Mann 1932; Rankin 1937; Westfall et al. 2008), and Oklahoma, USA (Duncan and Highton 1979). *Plethodon glutinosus* is host to only one other species of chigger mite, *Eutrombicula lipovskiyana*, for which only one chigger was found on one salamander (Landewe 1960), indicating an uncommon occurrence. Our study does not eliminate the possibility that some of our salamanders could be infested by other species of *Hannemania*. Nearby records with the chigger identified to species are from Georgia, USA (*H. eltoni*, *H. hegeneri*; Crossley and Proctor 1971), and Florida, USA (*H. hegeneri*; Hyland 1956; McAllister et al. 2015).

We report the highest mean intensity of infestation by *Hannemania* sp. in the *P. glutinosus* complex, and the third highest mean intensity (17.6 chiggers/individual) for any salamander species in the USA. The next highest mean intensity was reported by Landewe (1960)

TABLE 2. Chigger location by body region (based on the total number of chiggers ($n = 529$) and the percentage of *Hannemania* cf. *dunni* infested Northern Slimy Salamanders (*Plethodon glutinosus*) by body region calculated with all salamanders in the sample ($n = 45$) and only those parasitized by mites ($n = 30$).

Body region	Mites by region (%)	All salamanders (%)	Parasitized only (%)
Head and throat	2.6	22.2	33.3
Body (dorsal and ventral sides)	15.9	42.2	63.3
Forelimbs/feet	28.5	62.2	93.3
Hindlimbs/feet	35.0	62.2	93.3
Tail (dorsal and ventral sides)	13.8	51.1	76.4
Cloaca	4.2	24.4	36.7

with seven *H. hegeneri*/salamander (range, 1 to 22) and by Mann (1932) with 6.4 *Hannemania* sp./salamander. It is unclear whether Rankin (1937) was reporting abundance (includes non-parasitized salamanders) or intensity (infested only), but he reported 3.2 parasites/host. Westfall et al. (2008) reported an abundance of 0.5 chiggers/salamander and Duncan and Highton (1979) and McAllister et al. (2002) provide only prevalence of infestation, which were less than 10%. The two species of salamander with higher mean intensities than ours were *Desmognathus brimleyorum* (21 chiggers per infested salamander) and *Plethodon ouachitae* (20 chiggers on average; Winter et al. 1986). Interestingly, Winter et al. (1986) found no infestation in any species from the *P. glutinosus* complex. Pope and Pope (1951), Duncan and Highton (1979), Anthony et al. (1994), and Connior et al. (2016) all report finding few to no infested individuals of *P. glutinosus* complex even when sympatric species had high infestation rates. This phenomenon is not limited to the *P. glutinosus* complex (Hribar and Tyler 1989; Regester 2001) but also occurs in

TABLE 3. Pairwise P -values from Nemenyi's non-parametric pairwise rank sum test comparing counts of *Hannemania* cf. *dunni* between body regions in Northern Slimy Salamanders (*Plethodon glutinosus*) from north-central Alabama, USA. All P -values were corrected for multiple testing using a Bonferroni correction; comparisons correspond to those in Figure 5.

	Head/Throat	Forelimbs/Feet	Body	Hindlimbs/Feet	Cloaca
Forelimbs/Feet	< 0.001	–	–	–	–
Body	0.001	0.647	–	–	–
Hindlimbs/Feet	< 0.001	0.964	0.176	–	–
Cloaca	1	< 0.001	0.002	< 0.001	–
Tail	0.227	0.017	0.550	< 0.001	0.241

anurans (Ewing 1926a; Brandt 1936; Loomis 1956; Jung et al. 2001). There is currently no good explanation for why some amphibian species are infested while others in the same habitat and locality are not. The maximum number of *Hannemania* chiggers infesting a salamander was 60 in *P. ouachitae* (Duncan and Highton 1979), but the population mean (most likely reporting abundance) was lower (5.9 ± 9.5 standard deviation), so we interpret this as a few individuals had a large number of chiggers, which we also observed in this study.

We also found that chigger loads differed across body regions with feet and legs having more than other body locations, a result in agreement with Adler and Dennis (1962), Regester (2001), and Westfall et al. (2008). We also found no support for our hypothesis that body size is associated with parasite load; rather, our data indicate that salamanders of all sizes are, on average, infested by the same number of chiggers. Regester (2001) and Westfall et al. (2008) similarly found no relationship between SVL and load or abundance. Whether there is a threshold intensity associated with morbidity and mortality or whether smaller salamanders would show lower tolerance (sensu Simms 2000) than larger ones is unknown. We found, similar to Westfall et al. (2008), that infestation varies by locality. Attademo et al. (2012), working in mideastern Argentina, showed that a widespread frog species collected in agricultural fields had higher prevalence and mean abundance of *Hannemania* sp. than those from reference sites in native forest from the same area. Thus, we recommend further studies include, in addition to the microhabitat variables suggested by Westfall et al. (2008), land-use history as our sites experienced approximately 100 y of anthropogenic use including logging, mining (iron ore), steel production, and homesteading before becoming parks or nature preserves.

We join Regester (2001) and Westfall et al. (2008) in proposing further study on whether infestation by chiggers affects survivorship, fitness, or contributes to population decline. Chigger-parasitized salamanders are inferior competitors for food and territories (Maksimowich and Mathis 2000) and in addition to causing physical damage to the skin through burrowing, encystment, and emergence, they deform limbs, damage toes, and in plethodontids, the nasolabial groove (Anthony et al. 1994; Connior et al. 2016). Damaged appendages and toes would decrease mobility, including climbing behaviors (McEntire 2016; Button 2018). Chiggers also modify the behavior of salamanders, especially those that communicate via pheromones (Maksimowich and Mathis 2001; Dalton and Mathis 2014), which could reduce the mating success of individuals with a high parasitic load. Additionally, mechanical damage to the skin is certainly a pathway for a secondary bacterial or fungal infections, especially considering the length of

time (at least one year) that *Hannemania* can remain encysted. Whether chigger mites transmit pathogens in amphibians, as they do in other vertebrates (including humans), is currently unknown (Van der Geest et al. 2000), but is a possibility, and worthy of further study. We encourage field biologists to continue reporting encounters with chigger-parasitized amphibians in the herpetological literature whenever possible.

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LITERATURE CITED

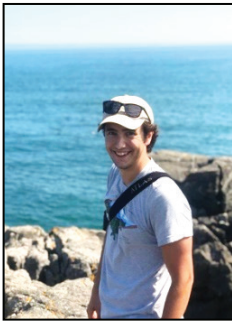
- Adler, K.K., and D.M. Dennis. 1962. *Plethodon longicrus*, a new salamander (Amphibia: Plethodontidae) from North Carolina. Special Publication of the Ohio Herpetological Society 4:1–14.
- Anthony, C.D., J.R. Mendelson III, and R.R. Simons. 1994. Differential parasitism by sex on plethodontid salamanders and histological evidence for structural damage to the nasolabial groove. *American Midland Naturalist* 132:302–307.
- Attademo, A.M., P.M. Peltzer, R.C. Lajmanovich, C. Junges, A. Bassó, and M. Cabagna-Zenklusen. 2012. Trombiculid mites (*Hannemania* sp.) in *Leptodactylus chaquensis* (Amphibia: Anura) inhabiting selected soybean and rice agroecosystems of Argentina. *Journal of Zoo and Wildlife Medicine* 43:579–584.
- Bennett, S.G., D.A. Crossley, Jr., L.A. Durden, and M.L. Goff. 2014. *Eutrombicula cinnabaris* (Ewing, 1920) (Acari: Trombiculidae) is the common pest chigger mite of the Eastern United States. *Journal of Entomological Science* 49:413–414.
- Benton, M.J. 1987. Host parasite coevolution. The mite pockets of lizards. *Nature* 325:391–392.
- Brandt, B.B. 1936. Parasites of certain North Carolina Salientia. *Ecological Monographs* 6:491–532.
- Brennan, J.M., and M.L. Goff. 1977. Keys to the genera of chiggers of the western hemisphere (Acarina: Trombiculidae). *Journal of Parasitology* 63:554–566.
- Brown, J.D., M.K. Keel, M.J. Tabsley, T. Thigpen, and J.C. Maerz. 2006. Clinical challenge. *Journal of Zoo and Wildlife Medicine* 37:571–573.
- Bush, A.O., K.D. Lafferty, J.M. Lotz, and A.W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* 83:575–583.

- Button, S.T. 2018. *Plethodon glutinosus* (Northern Slimy Salamander). Climbing behavior. Herpetological Review 49:91–92.
- Connior, M.B., C.T. McAllister, L.A. Durden, S.E. Trauth, and H.W. Robison. 2016. New chigger (Acari) records from Arkansas amphibians (Caudata, Anura) and reptiles (Sauria). Journal of the Arkansas Academy of Science 70:263–267.
- Crossley, D.A., Jr. 1960. Comparative external morphology and taxonomy of nymphs of the Trombiculidae (Acarina). University of Kansas Science Bulletin 40:135–321.
- Crossley, D.A., Jr., and C.W. Proctor, Jr. 1971. New records of chigger species (Acarina: Trombiculidae) in Georgia. Journal of the Georgia Entomological Society 6:176–184.
- Dalton, B., and A. Mathis. 2014. Identification of sex and parasitism via pheromones by the Ozark Zigzag Salamander. Chemoecology 24:189–199.
- Duncan, R., and R. Highton. 1979. Genetic relationships of the eastern large *Plethodon* of the Ouachita Mountains. Copeia 1979:95–110.
- Ewing, H.E. 1921. Studies on the biology and control of chiggers. U.S. Department of Agriculture Bulletin 986:1–19.
- Ewing, H.E. 1926a. The life history and biology of the Tree-toad Chigger, *Trombicula hylae* Ewing. Annals of the Entomological Society of America 19:261–267.
- Ewing, H.E. 1926b. The common box-turtle, a natural host for chiggers. Proceedings of the Biological Society of Washington 39:19–20.
- Ewing, H.E. 1931. A catalogue of the Trombiculinae, or chigger mites, of the new world, with new genera and species and a key to the genera. Proceedings U.S. National Museum 80:1–19.
- Ewing, H.E. 1944. The trombiculid mites (chigger mites) and their relation to disease. Journal of Parasitology 30:339–365.
- Goff, M.L., R.B. Loomis, W.C. Welbourn, and W.J. Wrenn. 1982. A glossary of chigger terminology (Acari: Trombiculidae). Journal of Medical Entomology 19:221–238.
- Grover, J.J., D.W. Duszynski, and B.C. Bogan. 1975. Histochemistry of the tissue capsule surrounding intradermal mites, *Hannemania* spp. (Acarina: Trombiculidae) in New Mexico amphibians. Journal of Parasitology 61:382–384.
- Highton, R., G.C. Maha, and L.R. Maxson. 1989. Biochemical evolution in the Slimy Salamanders of the *Plethodon glutinosus* complex in the eastern United States. Illinois Biological Monographs 57:1–153.
- Hribar, L.J., and P.J. Tyler. 1989. *Hannemania dunnii*, a chigger parasitizing the Two-lined Salamander in Alabama. Melsheimer Entomological Series 37:28.
- Hyland, K.E. 1950. The life cycle and parasitic habits of the chigger mite *Hannemania dunnii* Sambon, 1928, a parasite of amphibians. Journal of Parasitology 36 (suppl.):32–33.
- Hyland, K.E. 1956. A new species of chigger mite, *Hannemania hegneri* (Acarina; Trombiculidae). Journal of Parasitology 42:176–179.
- Hyland, K.E. 1961. Parasitic phase of chigger mite, *Hannemania hegneri*, on experimentally infested amphibians. Experimental Parasitology 11:212–225.
- Jenkins, D.W. 1948. Trombiculid mites affecting man I. Bionomics with reference to epidemiology in the United States. American Journal of Hygiene 48:22–35.
- Jung, R.E., S. Claeson, J.E. Wallace, and W.C. Wellbourn, Jr. 2001. *Eleutherodactylus guttillatus* (Spotted Chirping Frog), *Bufo punctatus* (Red-spotted Toad), *Hyla arenicolor* (Canyon Tree Frog), and *Rana berlandieri* (Rio Grande Leopard Frog). Mite Infestation. Herpetological Review 32:33–34.
- Landewe, J.E. 1960. Helminth and arthropod parasites of salamanders from southern Illinois. M.S. Thesis, Southern Illinois University, Carbondale, Illinois, USA. 47 p.
- Lipovsky, L.J. 1951. Collembola as food for chiggers (Acarina: Trombiculidae). Journal of Parasitology 37:324–326.
- Loomis, R.B. 1956. The chigger mites of Kansas (Acarina, Trombiculidae). University of Kansas Science Bulletin 37:1195–1443.
- Loomis, R.B., and W.J. Wrenn. 1984. Systematics of the pest chigger genus *Eutrombicula* (Acari: Trombiculidae). Pp. 152–159 In Acarology VI 1. Griffiths, D.A., and C.E. Bowman (Eds.). Ellis Horwood, Chichester, UK.
- Maksimowich, D.S., and A. Mathis. 2000. Parasitized salamanders are inferior competitors for territories and food resources. Ethology 106:319–329.
- Maksimowich, D.S., and A. Mathis. 2001. Pheromonal markers as indicators of parasite load: parasite-mediated behavior in salamanders (*Plethodon angusticlavius*). Acta Ethologica 3:83–87.
- Malone, J.H., and R. Paredes-León. 2005. Characteristics of chigger mite (*Hannemania* sp.) parasitism on *Eleutherodactylus marnockii* (Amphibia: Leptodactylidae). Texas Journal of Science 57:345–358.
- Mann, D.R. 1932. The ecology of some North Carolina salamanders with special reference to their parasites. M.S. Thesis, Duke University, Durham, North Carolina, USA. 51 p.
- McAllister, C.T., C.R. Bursley, M.B. Connior, S.E. Trauth, and L.A. Durden. 2015. New host and geographic-distribution records for helminth and arthropod parasites of the Southern Toad, *Anaxyrus terrestris* (Anura: Bufonidae), from Florida. Southeastern Naturalist 14:641–649.

- McAllister, C.T., C.R. Bursey, and S.E. Trauth. 2002. Parasites of four species of endemic *Plethodon* from Arkansas and Oklahoma. *Journal of the Arkansas Academy of Science* 56:239–242.
- McEntire, K.D. 2016. Arboreal ecology of Plethodontidae: a review. *Copeia* 104:124–131.
- Mertins, J.W., S.M. Torrence, and M.C. Sterner. 2011. Chiggers recently infesting *Spea* spp. in Texas, USA, were *Eutrombicula alfreddugesi*, not *Hannemania* sp. *Journal of Wildlife Diseases* 47:612–617.
- Mullen, G.R., and B.M. O'Connor. 2009. Mites (Acari). Pp. 433–492 *In* Medical and Veterinary Entomology, 2nd Edition. Mullen, G.R. and L.A. Durden (Eds). Elsevier, Inc., Boston, Massachusetts, USA.
- O'Hara, R.B., and D.J. Kotze. 2010. Do not log-transform count data. *Methods in Ecology and Evolution* 1:118–122.
- Paredes-León, R., L. García-Prieto, C. Guzmán-Cornejo, V. León-Règanon, and T.M. Pérez. 2008. Metazoan parasites of Mexican amphibians and reptiles. *Zootaxa* 1904:1–166.
- Pohlert, T. 2018. PMCMRplus: Calculate Pairwise Multiple Comparisons of Mean Rank Sums Extended. R package version 1.4.1. <https://CRAN.R-project.org/package=PMCMRplus>.
- Pope, C.H., and S.H. Pope. 1951. A study of the salamander *Plethodon ouachitae* and the description of an allied form. *Bulletin of the Chicago Academy of Sciences* 9:129–152.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Radford, C.D. 1942. The larval Trombiculinae (Acarina, Trombididae) with descriptions of twelve new species. *Parasitology* 34:55–81.
- Rankin, J.S. 1937. An ecological study of parasites of some North Carolina salamanders. *Ecological Monographs* 7:169–269.
- Regester, K.J. 2001. Intradermal mite, *Hannemania* sp. (Acarina: Trombiculidae), infestations differ in populations of syntopic plethodontids in central Tennessee. *Herpetological Natural History* 8:69–73.
- Sambon, L.W. 1928. The parasitic acaridians of animals and the part they play in the causation of the eruptive fevers and other diseases of man. Preliminary considerations based upon an ecological study of typhus fever. *Annals of Tropical Medicine and Parasitology* 22:67–132.
- Sasa, M. 1961. Biology of chiggers. *Annual Review of Entomology* 6:221–244.
- Shatrov, A.B., and N.I. Kudryashova. 2008. Taxonomic rankings of major trombiculid subtaxa with remarks on the evolution of host-parasite relationships (Acariformes: Parasitengona: Trombiculidae). *Annales Zoologici* 58:279–287.
- Silva-de la Fuente, M.C., L. Moreno-Salas, and C. Castro-Carrasco. 2016. Review of the genus *Hannemania* (Acari: Leeuwenhoekiidae) with description the two new species in amphibians from Chile. *Zootaxa* 4200:580–590.
- Simms, E.L. 2000. Defining tolerance as a norm of reaction. *Evolutionary Ecology* 14:563–570.
- Sladky K.K., T.M. Norton, and M.R. Loomis. 2000. Trombiculid mites (*Hannemania* sp.) in Canyon Tree Frogs (*Hyla arenicolor*). *Journal of Zoo and Wildlife Medicine* 31:570–575.
- Torrence, S.M., L.M. Smith, and S.T. McMurry. 2007. Larval *Hannemania* sp. infestations of *Spea* spp. in the Southern High Plains, Texas, USA. *Journal of Wildlife Diseases* 43:742–746.
- Van der Geest, L.P.S., S.L. Elliot, J.A.J. Breeuwer, and E.A.M. Beerling. 2000. Diseases of mites. *Experimental and Applied Acarology* 24:497–560.
- Walters, B.L., J.O. Whitaker, Jr., N.S. Gikas, and W.J. Wrenn. 2011. Host and distribution lists of chiggers (Trombiculidae and Leeuwenhoekiidae), of North American wild vertebrates north of Mexico. Paper 697. Faculty Publications from the Harold W. Manter Laboratory of Parasitology, Lincoln, Nebraska, USA. 183 p.
- Welbourn, W.C., Jr., and R.B. Loomis. 1975. *Hannemania* (Acarina: Trombiculidae) and their anuran hosts at Fortynine Palms Oasis, Joshua Tree National Monument, California. *Bulletin of the Southern California Academy of Sciences* 74:15–19.
- Westfall, M.C., K.K. Cecala, S.J. Price, and M.E. Dorcas. 2008. Patterns of trombiculid mite (*Hannemania dunni*) parasitism among plethodontid salamanders in the western piedmont of North Carolina. *Southeastern Naturalist* 94:631–634.
- Wharton, G.W., and H.S. Fuller. 1952. A manual of the chiggers. The biology, classification, distribution, and importance to man of the larvae of the family Trombiculidae (Acarina). *Memoirs of the Entomological Society of Washington* 4:1–175.
- Winter, D.A., W.M. Zawada, and A.A. Johnson. 1986. Comparison of the symbiotic fauna of the family Plethodontidae in the Ouachita Mountains of western Arkansas. *Proceedings of the Arkansas Academy of Sciences* 40:82–85.
- Wrenn, W.J., and R.B. Loomis. 1984. Host selectivity in the genus *Eutrombicula* (Acari: Trombiculidae). Pp. 160–165 *In* *Acarology VI*, Volume 1. Griffiths, D.A., and C.E. Bowman (Eds.). Ellis Horwood, Chichester, UK.
- Zar, J.H. 1999. *Biostatistical Analysis*. 4th Edition. Prentice Hall, Inc., Upper Saddle River, New Jersey, USA.
- Zhang, D. 2018. Rsq: R-squared and related measures. R package version 1.1. <https://CRAN.R-project.org/package=rsq>.



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