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Sex- and age-specific effects are superimposed on seasonal variation in mite parasitism in Eastern Fence Lizards (*Sceloporus undulatus*)

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Abstract.—The natural histories of parasites and their hosts are intertwined, and intensity of parasitism depends on parasite abundance and host behavior, as well as potential effects of sex/age. To characterize potential effects of parasite abundance and host sex/age on chigger mite (*Eutrombicula alfreddugesi*) ectoparasitism on Eastern Fence Lizards (*Sceloporus undulatus*), we measured (1) the abundance of mites in the environment as well as mite load and prevalence on lizards throughout the activity season; (2) sex- and age-specific patterns of ectoparasitism; and (3) week-to-week consistency of mite loads on lizards. Environmental mite abundance varied seasonally in close association with mean monthly temperatures and was the main driver of pronounced seasonal variation in mite loads on lizards. Mite loads were almost always higher on yearlings than adults and, somewhat unexpectedly, were never higher on adult males than any of the other age-sex classes. As adults, females had higher mite loads than males in June–July, but as yearlings, males had higher mite loads than females in July–September. Despite considerable week-to-week variation, rank-ordering of lizard mite loads was highly consistent. These findings indicate that (1) consistent age-specific sex biases are superimposed on strong seasonal variation in mite loads and (2) detrimental effects of mites are expected to be consistently stronger in some individuals than others.

Key words: Chiggers; Ectoparasites; Seasonality; Testosterone; *Trombicula*

Parasites have negative and positive effects within ecosystems (Hatcher et al., 2012) and can force substantial life-history trade-offs within hosts, such as decreased hematocrit, growth, and reproductive success (Salvador et al., 1996; Uller and Olsson, 2003; Gooderham and Schulte-Hostedde, 2011). In any host-parasite relationship, parasite infections depend on ecological, demographic, and physiological factors, including environmental abundance and life-stage of parasites, as well as sex, age, body size, and testosterone levels of hosts (Veiga et al., 1998; Pollock et al., 2012; Dudek et al., 2016). Thus, the natural histories of both parasites and their hosts must be taken into account to understand host-parasite relationships in natural communities.

In many host species, males are often more heavily parasitized than females (Zuk and McKean, 1996; Klein, 2004; Krasnov et al., 2005; Heredia et al., 2014), and this male-biased parasitism is often associated with sex differences in plasma testosterone (T) (Zuk and McKean, 1996; Grear et al., 2009). In free-ranging Striped Plateau Lizards (*Sceloporus virgatus*), for example, ectoparasitic mites are more abundant on males than females, and in experimental manipulations, parasite load is decreased by castration and restored by T replacement (Cox and John-Alder, 2007). Results of other studies are mixed, but two recent meta-analyses found administration of exogenous T causes an overall increase in parasitism (Roberts et al., 2004; Foo et al., 2017), although parasitism is not usually correlated with T in unmanipulated animals (Foo et al., 2017). Testosterone is thought to increase physiological susceptibility to parasitism through immunosuppression (Olsson et al., 2000; Poiani et al., 2000; Hughes and Randolph, 2001; Foo et al., 2017), and T may also increase ecological exposure to parasitism (Zippel et al., 1996; Bulté et al., 2009; Rubio and Simonetti, 2009). Males, however, are not always more heavily parasitized than females. Female-biased parasitism has been documented in several taxa (McAlpine, 1997; Christe et al., 2007; Pandit et al., 2011), whereas parasitism is apparently not sex-biased in others (Reardon and Norbury, 2004; de Carvalho et al., 2006; Halliday et al., 2014; Knapp et al., 2019).

Previous reports of sex-biased parasitism must be interpreted cautiously because of discrepancies among studies, including between, on a single host species (compare Klukowski and Nelson, 2001; Klukowski, 2004; Cox et al., 2005). Discrepancies can arise when a host species is studied in different locations or seasons, as well as from differences in the species of parasite at issue. For example, tick loads were higher on male than female Western Fence Lizards (*Sceloporus occidentalis*) during spring breeding months, but chigger mite loads were higher on females than males during fall months (Lumbad et al., 2011). Similarly, most studies have been conducted over limited time frames (e.g., Klukowski and Nelson, 2001; Cox and John-Alder, 2007; Pollock et al., 2012). As such, these studies fail to account for age-dependent seasonal variation in circulating T (Cox et al., 2005; John-Alder et al. 2009) and seasonal changes in environmental abundance of parasites (Clopton and Gold, 1993; Eisen et al., 2002). A failure to account for seasonality in abundance of parasites, coupled with potential sex- and age-related differences in host susceptibility, may contribute to discrepancies among studies. To clarify some of the discrepancies, we report ectoparasitism by chigger mites (*Eutrombicula alfreddugesi*) on adult and yearling male and female Eastern Fence Lizards (*Sceloporus undulatus*) throughout two-and-a-half activity seasons in the New Jersey pinelands. We hypothesized: (1) males have higher mite loads than females, regardless of age, and (2) adults have higher mite loads than yearlings, regardless of sex.

MATERIALS AND METHODS

Seasonal Variation in Mite Loads.—Studies were conducted May to September of 2014 and 2015 and in June and July 2016 at Colliers Mills Wildlife Management Area (40.1° N, 74.4° W), an area of pinelands in Burlington County, New Jersey, USA. Colliers Mills is heavily managed for hunting and is characterized by edge habitat separating open fields from forested tracts of oak and pine (Fig. 1). Its forests tend to have relatively open canopy, sparse understory due to controlled burns, and a forest floor littered with abundant fallen trees and branches.

We captured adult and yearling lizards at monthly (2014, 2015) or weekly (2016) intervals by noosing or by hand. Upon capture, we measured snout-vent length (SVL, mm) and body mass (g) using a ruler and Pesola spring scale. Sex was determined by presence (male) or absence (female) of enlarged post-cloacal scales. Mites infesting each lizard (mite load) were counted by one investigator (NBP) using a 10x hand lens. We assessed accuracy of mite load counts by performing five repeated mite counts for 10 different lizards (mite loads ranging 10–129) and calculating a Pearson correlation coefficient (r) for each lizard. The repeated counts of mite load within individuals were highly correlated (mean correlation across all individuals = 0.996, SD = 2.10). We marked and identified lizards with unique toe-clip numbers and paint marks, allowing visual identification from a distance, facilitatiing recaptures and quantification of variation in ectoparasitism.

Seasonal Variation in Environmental Mite Abundance.—To quantify environmental mite abundance, we used a variation of the plate method described by Williams (1946) and modified by Klukowski (2004) and Schöler et al. (2006). Sampling was done at exact sites where lizards were captured during the 2015 activity season. We sampled between 0800–1240 h, because this time range was used in previous studies (Reed, 1977; Klukowski, 2004) and before high afternoon temperatures, which may reduce mite activity (Clopton and Gold, 1993). At each sampling site, we firmly placed nine black ceramic tiles (15x15 cm; Daltile, Cranbury, USA) on the substrate in a 3x3 grid format with approximately 1 cm between tiles. For 90 seconds, we counted mites as they crossed over the tiles and removed them with a small paintbrush. We used this methodology to estimate environmental mite abundance once per month in 2015.

Consistency of Mite Loads Among Lizards.—We investigated the consistency of mite loads among individuals by recapturing marked adult and yearling lizards at weekly intervals from 9 June to 14 July 2016 (6 wk). Methodology was the same as prior years, but the emphasis in 2016 was to maximize recaptures within a limited area (~3.5 ha) rather than to maximize all captures across a much broader area (~11.9 ha). The aim was to determine week-to-week consistency of absolute and ranked mite loads on individual lizards.

Statistical Analyses.—We combined data from 2014–2015 to provide sex- and age-specific mite loads throughout the activity season. This was done because: (1) sampling effort and the number of lizards captured between years was uneven and (2) after applying a Dunn-Sidak correction to control for the familywise error rate, we found no significant differences between 2014 and 2015 mite loads for any sex/age class in any month. We evaluated seasonal variation in environmental mite abundance and mite load by calculating mean environmental mite abundance, mite load, and mite prevalence (% lizards hosting ≥ 1 mite) for each month (May–September). For 2015 only, we used Spearman correlation (r_s) to determine if mite loads on individual lizards were correlated with environmental mite abundances at the sites of lizard capture (i.e., correlating a lizard's monthly mite load with the environmental mite abundance at the specific site of lizard capture).

In 2014–2015, we recorded 1342 mite loads recorded from 677 different lizards. For analyses of the effects of month, sex, and age (and interactions) in 2014–2015, we used a Poisson generalized linear mixed model with individual lizard as a random effect (SPSS, Armonk, USA). To compare monthly mite loads of adults versus yearlings within each sex and males versus females within each age class, comparisons were carried out using Dunn-Sidak corrections to account for multiple comparisons and to control for the familywise error rate (i.e., probability of making at least one Type I error).

In 2016, we recorded 733 mite loads from 198 different lizards. Mite load data from 2016 were used for a finer-grained analysis of sex and age differences in mite load and to analyze interindividual repeatability as a measure of the consistency of mite loads on individual lizards. We excluded the first week of the study (6–10 June 2016) because prevalence of mite parasitism was only 59%, and many lizards carried ≤ 1 mite. Individual consistency of mite loads was analyzed using Kendall's coefficient of concordance. To analyze effects of week, sex, and age (and interactions), we used a Poisson generalized linear mixed model with individual lizard as a random effect (SPSS, Armonk, USA). To compare weekly mite loads of adults versus yearlings within each sex and males versus females within each age class, comparisons were carried out using Dunn-Sidak corrections to account for multiple comparisons and to control for the familywise error rate (i.e., probability of making at least one Type I error). All Dunn-Sidak corrections and *P* values were considered significant at the $\alpha = 0.002$ level.

RESULTS

Mite Abundance, Mite Loads, and Prevalence of Mites.—Environmental mite abundance, mite loads, and mite prevalence exhibited pronounced seasonal variation (Table 1). Environmental mite abundance (measured in 2015) was low in May, high in June and July, and low in August and September ($F_{4,737} = 33.82$, $P < 0.001$). Mite prevalence was low in May (27%), but high thereafter (June: 91%; July: 99%; August: 99%; September: 98%). Mite loads increased from the lowest point in May to peak in July, and declined through August to an intermediate point in September (Wald $X^2 = 15748.48$; $P < 0.001$).

In 2014–2015, mite loads on lizards in July were positively correlated with environmental mite abundance in June ($r_s = 0.24$; $P = 0.015$) and July ($r_s = 0.27$; $P < 0.001$). Mite loads in August were positively correlated with mite abundance in July ($r_s = 0.18$; $P = 0.050$) and August ($r_s = 0.14$; $P = 0.046$). Correlations between mite load and environmental mite abundance were not significant for other months (May:May: $r_s = 0.06$; $P = 0.5957$; June:May: $r_s = 0.03$; $P = 0.833$; June:June: $r_s = 0.03$; $P = 0.680$; September:August: $r_s = 0.00$; $P = 0.991$; September:September: $r_s = 0.12$; $P = 0.246$).

Mite loads in 2016 weekly samples followed patterns similar to previous seasons (Table 2). Mite loads increased markedly from an overall average of 3.5 mites per lizard and 59% mite prevalence (similar in all age-sex classes) in early June to an average of 122 mites per lizard and 100% prevalence in mid-July. Individual loads were as high as 300 mites per lizard.

Sex- and Age-Biased Seasonal Variation in Mite Loads.—Despite the importance of month as a determinant of mite load in 2014–2015 (Wald $X^2 = 15748.48$; $P < 0.001$), interaction effects of month x age (Wald $X^2 = 355.03$; $P < 0.001$), month x sex (Wald $X^2 = 321.47$; $P < 0.001$), sex x age (Wald $X^2 = 23.23$; $P < 0.001$), and month x sex x age (Wald $X^2 = 95.31$; $P < 0.001$) resulted in significant monthly differences between age-sex classes. In females (Fig. 2A; Table 1), mite loads were higher on adults than yearlings in June (SE = 0.78; $P < 0.001$), but higher on yearlings than adults in July (SE = 1.46; $P = 0.003$), August

(SE = 1.20; *P* < 0.001), and September (SE = 0.90; *P* < 0.001). In males (Fig. 2B; Table 1), however, mite loads were higher on yearlings than adults in June (*SE* = 0.78; *P* < 0.001), July (SE = 1.63; *P* < 0.001), August (SE = 1.41; *P* < 0.001), and September (SE = 0.94; *P* < 0.001). In adults (Fig. 3A; Table 1), mite loads were higher on females than males in June (SE = 0.81; *P* < 0.001) and July (SE = 1.62; *P* < 0.001). In yearlings (Fig. 3B; Table 1), however, mite loads were higher on males than females in July (SE = 1.47; *P* < 0.001), August (SE = 1.27; *P* < 0.001), and September (SE = 0.94; *P* < 0.001).

Based on weekly data of 2016, mite loads were influenced most significantly by week (Wald X^2 = 2315.75; *P* < 0.001). Age was also statistically significant (Wald X^2 = 86.65; *P* < 0.001), as were the interactions of sex x age (Wald X^2 = 115.56; *P* < 0.001), week x age (Wald X^2 = 81.70; *P* < 0.001), week x sex (Wald X^2 = 26.60; *P* < 0.001), and week x sex x age (Wald X^2 = 83.40; *P* < 0.001). In females, mite loads were higher on yearlings than adults during the last week of June (week 4: SE = 4.62; *P* < 0.001; Table 2), but higher on adults than yearlings during the first two weeks of July (week 5: SE = 5.39; *P* < 0.001; week 6: SE = 6.09; *P* = 0.005; Table 2). In males, mite loads were significantly higher on yearlings than adults during the last two weeks of June (week 3: SE = 3.35; *P* < 0.001; week 4: SE = 3.94; *P* < 0.001; Table 2) and during the first two weeks of July (week 5: SE = 4.03; *P* < 0.001; week 6: SE = 4.44; *P* < 0.001; Table 2). In adults, mite loads were significantly higher on females than males during the first two weeks of July (week 5: SE = 5.73; *P* < 0.001; week 6: SE = 6.37; *P* < 0.001; Table 2). In yearlings the opposite occurred: mite loads were higher on males than females during the fourth week of June (week 3: SE = 2.85; $P < 0.001$; Table 2) and during the first two weeks of July (week 5: SE = 3.54; $P < 0.001$; week 6: SE = 4.04; $P < 0.001$; Table 2).

Individual Consistency of Mite Loads.—Individual rankings of mite loads were fairly consistent week-to-week in 2016 (Fig. 4; Kendall's $W = 0.485$, $X^2 = 106.72$, $P < 0.0001$). Lizards were categorized into quintiles based on average mite loads calculated across the final five sampling points, and they tended to remain within those quintiles every week.

DISCUSSION

Our results indicate significant seasonality in mite load and environmental mite abundance in Eastern Fence Lizards, in addition to significant sex- and age-specific differences in mite load. Previous studies have documented seasonal variation in ectoparasite load (Goldberg and Bursey, 1991; Schall et al., 2000; Godfrey et al., 2008; Lumbad et al., 2011) or environmental ectoparasite abundance (Clopton and Gold, 1993; MacDonald and Briggs, 2016), but ours is one of the few to investigate seasonal variation in both ectoparasite load and abundance. We found a temporal association between mite load and environmental mite abundance across months. Furthermore, mite loads on lizards in July and August were correlated with environmental mite abundances measured at the specific localities where lizards were captured. These findings, along with strong significant effects of month and week, suggest abundance of mites in the environment is the primary determinant of host lizard mite load.

However, further studies are necessary to clarify relationships between host ectoparasite load and environmental ectoparasite abundance.

Two other studies on lizards have investigated seasonal variation in ectoparasite load and environmental abundance. In Collared Lizards (*Crotaphytus collaris*), Curtis and Baird (2008) found that seasonal variation in mite parasitism and environmental abundance were temporally dissociated, probably because abundance of nonparasitic adult mites was monitored instead of parasitic larval mites. Larval mites parasitized lizards after adult mites disappeared in early June, suggesting that adult mites descend into soil to oviposit in May, after which parasitic larvae emerge in June to feed on lizard hosts (Curtis and Baird, 2008). This could similarly explain the low mite loads and low environmental mite abundances we observed during May and early June. However, further investigations of the phenology of mite life cycles are needed (Shatrov and Kudryashova, 2006).

In contrast, Klukowski (2004) found an associated pattern similar to ours in his study of *S. undulatus* in Tennessee, where mite loads were low in May and August when environmental mite abundance was low, but high in June and July when abundance was high. However, environmental mite abundances, as well as mite loads, were high earlier and for a longer period of time in Tennessee than New Jersey. Differences in phenology of mite parasitism and environmental mite abundances can be attributed to geographical differences in climate. In south Texas, for example, Mather (1979) reported high mite loads and 100% infestation prevalence on *S. undulatus* in October and November, in sharp contrast to what has been found in California (Goldberg and Bursey, 1991; Lumbad, 2011), Tennessee (Klukowski, 2004), and New Jersey studies.

Geographic variation in patterns of seasonal mite loads is likely the result of climate differences between regions and subsequent impacts on abundance of mites in the environment. Environmental mite abundances are highest in areas with high humidity and moderate temperatures (Zippel et al., 1996), and mite activity is determined by a combination of temperature and humidity, rather than by either of these variables alone (Clopton and Gold, 1993). In New Jersey, variation in mean monthly temperatures recorded at the Rutgers Pinelands Field Station (RPFS, 2015) is closely associated with monthly environmental mite abundances. Environmental mite abundance is low during months in which mean monthly temperatures are less than 20 °C, but high during months in which mean monthly temperatures are greater than 20 °C.

Seasonal variation in mite abundance is likely an overarching cause of variation in mite load, but superimposed on this are consistent differences in mite load among sex and age classes. Based on commonly observed sex effects and previously reported relationships between T and parasitism, and because plasma T is always higher in males than in females of *S. undulatus* (Cox et al., 2005; John-Alder et al., 2009), we predicted mite loads would be higher on males than females and would show an association with seasonal variation in plasma T. However, our findings only partially support these predictions. Although mite loads were consistently higher on yearling males than other age/sex classes during the latter half of the activity season, loads in adult males were never highest and were often lowest among all classes. Furthermore, the majority of studies investigating effects of age on parasitism in reptiles have found higher parasite loads on older individuals (Amo et al., 2004; Reardon and Norbury, 2004; Dudek et al., 2016), but this was not the case in the present study.

The absence of mites in the environment can explain why mite loads on adult males are lower in May than at other times of year (Fig. 5), despite this being the time of high plasma T and peak investment in reproductive activity. Even if T and high activity cause males to be highly susceptible to parasitism, ecological exposure is simply too low for mites to be of any consequence. By the time mites become abundant in the environment, reproductive activity and plasma T have declined in adult males. Generational differences in the seasonality of activity and plasma T (Fig. 5) may help to explain why mite loads are lower on adult than yearling males during the latter half of the activity season, when environmental mite abundance is high. In yearling males, plasma T reaches its seasonal peak in July as they approach sexual maturity and begin to expand their home ranges. In effect, yearling males behave and have high plasma T in July and August much as adults do in the spring. Differences in mite load between adult and yearling males can be attributed to the difference in phenology between these age classes and associated differences in exposure and susceptibility to mites.

Similarly, phenological differences in activity may help to explain the unexpected result of higher mite loads on adult females rather than males. Adult males have much larger home range areas than females (Haenel et al., 2003;

Cox et al., 2005), and if home range size is positively associated with exposure to mites, then adult males would be expected to have greater mite loads than females. However, in European Common Lizards (*Zootoca*, formerly *Lacerta*, *vivipara*), parasite loads are negatively correlated with activity (Clobert et al., 2000). Furthermore, ectoparasites exhibit preferences for particular habitats depending on temperature, humidity, and precipitation (Clopton and Gold, 1993; Eisen et al., 2002; Zippel et al., 1996), and we have shown that mite load is correlated with mite abundance at the lizard capture site. Thus, despite being less active than adult males, females could be spending more time in microhabitats preferred by mites (Rubio and Simonetti, 2009). This behavior of females, coupled with heightened susceptibility as a result of reproductive investment, could help to explain the higher mite loads of adult females in comparison to adult males.

In yearlings, we found no clear differences in mite loads between males and females until July, when plasma T in males and environmental mite abundance are high (Fig. 4; Cox et al., 2005). This male-biased pattern of parasitism is in accordance with other studies on lizards (Salkeld and Schwarzkopf, 2005; Cox and John-Alder, 2007; Heredia et al., 2014; Dudek et al., 2016). As yearlings approach reproductive maturity during the latter half of the activity season in New Jersey, males but not females expand their home range areas and daily movement distances (John-Alder, pers. obs.). The male bias in yearling mite loads from July–September may be a result of sex differences in microhabitat use and yearling males expanding their home ranges and taking up residence in microhabitats abundant with mites.

Alternatively, high plasma T in yearling males may increase physiological susceptibility through immunosuppression (Duffy et al., 2000; Belliure et al., 2004; Tripathi and Singh, 2014), allowing more mites to feed and survive (Veiga et al., 1998; Poiani et al., 2000; Hughes and Randolph, 2001). However, several studies have failed to find a suppressive effect of T alone on immune function (Hasselquist et al., 1999; Greenman et al., 2005; Ruiz et al., 2010; Roved et al., 2017), and natural seasonal elevations in T are not generally associated with immunosuppression (Foo et al., 2017). Further studies are required to examine the interplay between T and immune response with ectoparasites of reptiles.

A final point of discussion concerns the relative consistency in the rank ordering of mite loads on *S. undulatus*. Even while mite loads increased dramatically and exhibited considerable week-to-week variation, individual lizards held fairly consistent ranks in terms of mite loads relative to other lizards. Some of this consistency may reflect week-to-week autocorrelation due to continuing residence of individual mites. We do not know residence time for mites on *S. undulatus*, but residence times of 7–52 days have been reported for mites on other species of *Sceloporus* (Goldberg and Bursey, 1993). Thus, it is likely that some portion of mites were counted in consecutive weeks in the present study. However, given the consistent rank-ordering of lizards, even while mite loads increased through June, whether the mechanisms of inter-individual variation involve differences in exposure or differences in susceptibility, the differences among lizards are fairly consistent. This suggests that detrimental effects of mites are expected to be stronger in some individuals than others. For example, Knapp et al. (2019) found that consistently high tick loads were associated with decreased body condition and leukocyte counts in large-bodied iguanas, but not in small-bodied iguanas. Any inter-individual differences in detrimental effects of mites may depend on host susceptibility to ectoparasites and age-acquired immunity (Holland et al., 2007; Jackson et al., 2014).

In summary, sex biases in mite parasitism are dependent upon age and time of year in *S. undulatus*. Age biases in mite parasitism are dependent upon sex and time of year. The overriding determinant of mite load in yearlings and adults is seasonal variation in environmental mite abundance. Future studies should focus on detailed analyses of the physiological and behavioral mechanisms giving rise to seasonal patterns of male and female biased ectoparasite loads. Studies should also investigate direct and indirect effects of T and reproductive effort on immune function and activities and behaviors that may increase exposure to ectoparasites. Lastly, studies are needed to describe local population dynamics of mites and abiotic factors mediating local environmental mite abundance and mite prevalence on hosts.

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Table 1. Mean (± 1 SEM) mite loads (# of mites) for each *S. undulatus* age-sex class and environmental mite abundances (# of mites/90 sec) for the 2014–15 activity seasons at Colliers Mills. For mite loads, sample size (*n*), median mite load (Mdn), and prevalence of infestation (% of lizards with at least 1 mite) are given in parentheses (*n*, Mdn, %). For mite abundances, sample size (*n*) is the number of mite abundance sampling localities. See text for statistical analyses.

	May	**June**	**July**	**August**	**September**
Yearling male	0.29 ± 0.1 (50, 0, 20%)	28.5 ± 2.9 (102, 19, 85%)	117.4 ± 6.3 (93, 101, 100%)	86.0 ± 5.0 (102, 79, 100%)	30.0 ± 2.7 (60, 25, 98%)
Yearling female	0.32 ± 0.1 (74, 0, 11%)	29.4 ± 2.8 (111, 21, 94%)	92.4 ± 5.1 (103, 86, 100%)	73.3 ± 4.3 (95, 71, 99%)	17.5 ± 1.8 (47, 19, 98%)
Adult male	1.0 ± 0.3 (51, 0, 31%)	19.8 ± 3.5 (62, 11, 89%)	70.6 ± 8.3 (51, 51, 98%)	50.0 ± 4.8 (44, 42, 100%)	14.5 ± 2.2 (37, 12, 97%)
Adult female	1.8 ± 0.4 (60, 0, 42%)	34.4 ± 3.7 (102, 20, 93%)	86.3 ± 6.6 (70, 83, 99%)	46.8 ± 3.9 (69, 41, 97%)	11.9 ± 1.6 (27, 12, 100%)
Overall mite load	0.8 ± 0.1 (235, 0, 27%)	28.9 ± 1.6 (377, 18, 91%)	94.9 ± 3.3 (317, 87, 99%)	68.3 ± 2.5 (310, 63, 99%)	20.4 ± 1.3 (171, 15, 98%)
Mite abundance	1.1 ± 0.2 (112)	10.2 ± 1.1 (160)	9.2 ± 1.0 (160)	1.9 ± 0.3 (189)	0.1 ± 0.04 (121)

Table 2. Mean (± 1 SEM) mite load (# of mites) for each *S. undulatus* age-sex class and for all combined in 2016 at Colliers Mills. Sample size (*n*), median mite load (Mdn), and prevalence of infestation (% of lizards with at least 1 mite) are given in parentheses (*n*, Mdn, %). See text for statistical analyses.

	Week 1 **June 9–10**	**Week 2** **June 14–15**	**Week 3** **June 22–24**	**Week 4** **June 29–30**	**Week 5** **July 6–7**	**Week 6** **July 13–14**
Yearling male	2.2 ± 0.8 (41, 1, 56%)	15.3 ± 1.0 (35, 13, 91%)	75.1 ± 2.1 (55, 60, 100%)	110.9.8 ± 2.6 (50, 83, 100%)	115.5 ± 6.5 (44, 98, 100%)	148.6 ± 2.9 (36, 130, 100%)
Yearling female	2.6 ± 0.6 (21, 3, 57%)	10.3 ± 0.8 (31, 13, 84%)	59.2 ± 1.9 (41, 62, 100%)	121.9 ± 2.8 (43, 86, 100%)	91.5 ± 2.4 (42, 86, 100%)	122.0 ± 2.8 (36, 102, 100%)
Adult male	4.2 ± 1.1 (15, 4, 75%)	12.3 ± 1.3 (22, 3, 82%)	47.7 ± 2.6 (26, 35, 100%)	62.9 ± 3.0 (22, 54, 100%)	66.1 ± 3.1 (23, 38, 100%)	77.0 ± 3.3 (18, 92, 100%)
Adult female	7.1 ± 3.5 (17, 2, 53%)	13.4 ± 1.6 (18, 3.5, 72%)	62.4 ± 3.5 (26, 58, 100%)	68.6 ± 3.7 (22, 76, 100%)	117.0 ± 4.8 (23, 96, 100%)	147.6 ± 5.4 (18, 133, 100%)
All	3.5 ± 0.8 (94, 1, 59%)	12.7 ± 0.6 (18, 3.5, 72%)	60.3 ± 1.4 (148, 56, 100%)	87.4 ± 1.7 (138, 82, 100%)	95.1 ± 1.7 (136, 85, 100%)	119.8 ± 1.9 (111, 84, 100%)

Fig. 1. Survey areas of *S. undulatus* (outlined in white) at Colliers Mills Wildlife Management Area, an area of pinelands in Burlington County, New Jersey. The survey areas were selected due to the relatively open canopy and forest floor, abundant with fallen trees and branches.

Fig. 2. Mite loads recorded on female (A: red = adults, pink = yearlings) and male (B: dark blue = adults, light blue = yearlings) *S. undulatus* during the 2014 and 2015 activity seasons at Colliers Mills. Circles represent mite loads of individual lizards. Horizontal bars represent mean monthly mite loads. Environmental mite abundances are shown in orange, with circles representing individual localities and horizontal bars representing mean monthly abundances. See text for statistical analyses.

Fig. 3. Mite loads recorded on adult (A: red = females, blue = males) and yearling (B: red = females, blue: males) *S. undulatus* during the 2014 and 2015 activity seasons at Colliers Mills. Circles represent mite loads of individual lizards. Horizontal bars represent mean monthly mite loads. Environmental mite abundances are shown in orange, with circles representing individual localities and horizontal bars representing mean monthly abundances. See text for statistical analyses.

Fig. 4. Mite loads recorded on individual *S. undulatus* at weekly intervals from 13 June to 14 July 2016 at Colliers Mills. Each line connects an individual lizard's mite loads for each of these 5 wks. Lines are color-coded by categories of overall mite ranks based on the mean mite count of each lizard over the 5-wk period. Mite loads exhibited a consistent rank order throughout the weeks of study. This consistency is evident in the segregation of colors in the figure. See text for statistical analyses.

Fig. 5. Asynchronous seasonality between *S. undulatus* males and chigger mites at Colliers Mills. The solid line (dark blue circles) represents plasma T in adult males (John-Alder et al., 2009), and the dashed line (light blue circles) represents plasma T in yearling males (Cox and John-Alder, 2005). For adults, 100% = 53 ng/ml; for yearlings, 100% = 33 ng/ml. The orange shaded region represents the period when mites infested lizards during the 2014–2016 activity seasons. The thick black-to-gray horizontal bar represents the activity season of *S. undulatus* in New Jersey.