



Phenological variation in parasite load and inflammatory response in a lizard with an asynchronous reproductive cycle

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Abstract

We present the first study that compares phenological variation in parasite load and inflammatory response in a lizard with asynchronous male and female gonadal cycles. Other studies have used many species with seasonal and synchronous reproductive cycles, in which it is difficult to decouple the effects of internal and external factors that can affect parasite abundance in each sex. Species with asynchronous reproductive cycles provide the opportunity to study the effects of seasonality and reproductive condition separately, but few studies have documented variation in parasite abundance in these species. We made an extensive comparison of parasite load and inflammatory response of the lizard *Sceloporus torquatus*, a species with asynchronous reproductive cycles, throughout its active period. We hypothesized that the parasite load would be higher in the period of maximum gonadal activity for each sex, negatively related to body condition and inflammatory response. Our results partially support the hypothesis; males had more parasites in summer than in spring and autumn, while females had more parasites in spring and summer than in autumn; however, we do not find a relationship between parasite load, body condition and inflammatory response. Our results indicated that host-parasite interactions are complex and depend upon both environmental and internal factors. Therefore, longer-term studies may provide a more comprehensive picture of host-parasite dynamics in populations of wild lizards.

Keywords Parasite load · Inflammatory response · Gonadal cycle · Asynchronous cycle · *Sceloporus torquatus*

Introduction

Parasites draw resources and reduce the fitness of their hosts. Therefore, they can exert selective pressure on host populations, ultimately affecting the function of ecosystems

(Salathé et al. 2008; Artim et al. 2020). Parasite virulence, which is the proportion of the host's fitness reduced by parasitization, is generally associated with the intensity of the infection (Råberg et al. 2009). However, the outcome of an infection is also contingent on the co-evolutionary history

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between the host and the parasite (Hamilton and Zuk 1982; Gandon et al. 2002; Patterson and Ruckstuhl 2013). In this sense, the evolutionary arms race existing between parasites and hosts can also motivate the evolution of morphological, behavioral, physiological and/or molecular strategies in host populations that counteract the selective pressure exerted by parasites (Minchella 1985; Combes 1997).

Host body condition is an important life history trait that also influences the outcome of an infection and is a proxy for the energetic budget of vertebrates. Life history theory assumes that the energetic budget of organisms is limited, which forces trade-offs in resources allocation between important functions (Stearns 2000; Roff et al. 2002). A recent meta-analysis of 553 infection-body condition relationships, analyzed in 187 peer-reviewed studies in wildlife (birds, mammals, fish, reptiles, amphibians and other invertebrates), showed that the relationship between infection and the body condition of the hosts is generally negative, especially in experimental infections (Sánchez et al. 2018). This negative relationship could result from (i) trade-offs between body condition and mounting an immune response to fight off the infections; (ii) a higher susceptibility to infections of hosts with low body condition; and/or (iii) direct depletion of fat reserves due to the infections themselves (Guan and Han 2019). However, the authors also found a bias toward the publication of significant negative relationships, so there may be cases of positive correlations or nonsignificant correlations that are missing from the published literature.

Particularly in lizards, previous infection-body condition analyses have shown mixed relationships. Hematophagous mites are expected to have detrimental effect on lizards because they inflict micro-wounds and draw blood from the skin of lizards (e.g., Klukowski and Nelson 2001). In males of *Anolis brevirostris*, a higher mite load was associated with lower body condition, low dewlap display rate and less pigmented dewlaps (Cook et al. 2013). However, some studies in lizards found null or even positive relationships between ectoparasite load and body condition (Amo et al. 2005; Comas 2020; Paterson and Blouin-Demers 2020). To help explain these puzzling results, Paterson and Blouin-Demers (2020) suggested that long-term co-evolutionary histories between some parasites and lizards may have led in some populations to host-parasite co-adaptation and, hence, host tolerance. However, host-parasite relationships are dynamic and influenced by cycles of parasite virulence and host susceptibility (Hamilton and Zuk 1982; Balenger and Zuk 2014). In the latter case, the host vulnerability to infections may fluctuate along their reproductive cycle (Klukowski 2004; Šimková et al. 2005).

In many species, investment in reproduction during the breeding season is physiologically demanding (Stearns 2000; Roff et al. 2002). Therefore, reproduction is expected to induce reallocation of resources in the body, and thus, trade-offs in energy allocation, especially when reproduction takes

place in scenarios of food shortage (French et al. 2007a). Hormonal peaks, particularly of testosterone and estradiol, induce gonadal activity in lizards (Díaz et al. 1994; Feria-Ortiz et al. 2001). Testosterone has antagonistic effects. It increases male attractiveness through its stimulatory effect on secondary sexual traits, but it also can have immunosuppressant effects, which likely arise through trade-off pathways (Zahavi 1975; Folstad and Karter 1992). Similarly, the development of follicles and embryos are highly demanding processes that can compromise the immune response in female lizards (French et al. 2007b). Thus, hormonal or reproductive status, and/or host body condition may influence parasite abundance during infestations (Klukowski and Nelson, 2001; Amo et al. 2004; Curtis and Baird 2008; Pollock et al. 2012; Dudek et al. 2016; Argaez et al. 2020).

Besides these intrinsic factors, environmental or seasonal shifts are also associated with seasonal fluctuation in parasite abundances (Clopton and Gold, 1993; Araujo Filho et al. 2017). For example, the intensities of hematic parasites and hematophagous mites in the lizard *Psammotromus algirus* have opposite abundance patterns with elevation, likely reflecting changes in temperature and humidity (Álvarez-Ruiz et al. 2018). Similarly, vegetation cover and elevation predicted prevalence of ticks and mites, with contrasting patterns, in the lizard *Zootoca vivipara* (Wu et al. 2019). In addition, mite abundances infesting *Aspidoscelis tigris* were higher in seasons with high environment temperature and humidity (Jackson and Bateman 2018), which can be explained by the seasonal variation in the abundance of lizard-seeking mites in the environment (Klukowski 2004; Pollock and John-Alder 2020).

The Wiegmann's Torquate Lizard (*Sceloporus torquatus* Wiegmann, 1828) has an asynchronous gonadal cycle; males produce gametes in summer during the period of maximum testicular activity (June and July). Their testicles regress during the autumn (September), but they store sperm in the vas deferens until females are fertile in autumn (November) (Feria-Ortiz et al. 2001; Aldridge et al. 2020). Given this asynchronous cycle, *S. torquatus* represents an excellent model to study phenological shifts in host susceptibility associated with its reproductive cycle and distinguish them from seasonal changes in parasite abundance. This species naturally occurs over a wide altitudinal range in central Mexico (1500–3500 m above sea level, asl; González-Morales et al. 2015). We hypothesize that lizards experience trade-offs between inflammatory response and gonadal cycle, but these will occur asynchronously in males and females (Sheldon and Verhulst 1996). We predict that mite loads will be higher in females during autumn and during summer in males, which would reflect trade-offs between gamete production and immune function. We also expect that the number of mites will be negatively correlated with body condition and inflammatory response during autumn in females

and during summer in males. The latter would reflect trade-offs between fat storage, anti-parasitic defenses and reproductive investment during peaks of gonadal activity.

Materials and methods

Ethics Statement

All experimental procedures were carried out following the guidelines of the Universidad Autónoma del Estado de México (UAEM), as well as Mexican Federal Regulation for Animal Experimentation and Care (NOM-062-ZOO-2001; governmental approval SGPA/DGVS/02407/13).

Study site

Lizards were captured in Texcalyacac (19°07'37'' N, 99°29'41'' W; 2500 ± 1.64 m asl), a mountain region of central México. This site has a sub-humid temperate climate with summer rains until autumn. The average annual rainfall is 1150 mm, and the average temperature is 13 °C. The habitat of the lizards is dominated by pine trees and igneous extrusive rocks (INEGI 2009). We calculated monthly means of both temperature and precipitation using data from a nearby meteorological station 2.7 km away from our study site (station ID = 00,015,295; CONAGUA 2021).

Sampling

During autumn of 2018 (September to November) and spring to summer of 2019 (March to October), we captured 151 *Sceloporus torquatus* lizards by hand or lasso. Sampling was performed in autumn (53 males and 19 females), spring (18 males and 15 females) and summer (28 males and 18 females). We did not observe active lizards in winter, so we do not present data for this period. We used only adult animals (identified by having snout-vent length > 70 mm). The presence of blue ventral coloration in the males was used as an additional indicator of sexual maturity (Liner and Olson 1973). No pregnant females were used in this study. All lizards were marked by toe clipping for permanent identification; however, we did not capture any individual lizard more than once during the same year. Lizards were transported (1.5 h drive) in cloth bags to the Laboratorio de Ecofisiología de Fauna Silvestre at the Instituto para la Conservación de la Cordillera Neovolcánica ante el Cambio Climático (ICCoNeCC) A.C., where each lizard was maintained in an individual terrarium (23 × 41 × 21; width × length × height, respectively). A natural light source was supplied to enable natural circadian physiological processes (light–dark cycle 12:12) and a heat source (heat bulb) and rocks were put in one corner of each

terrarium to allow normal thermoregulation behavior. Water and food (*Tenebrio molitor* larvae) were provided ad libitum. One day after capture, we measured the body mass of each lizard using a balance (accuracy: 0.01 g) and the snout-vent length (SVL) using a digital caliper (accuracy: 1 mm). A body condition index (BCI) was estimated as the residuals of the regression between the log₁₀-transformed scores of both body mass and SVL (Schulte-Hostedde et al. 2005).

Quantification of parasites

During either their second or their third days of captivity in the laboratory, we examined the lizards carefully under a stereoscope (VE-S1, VELAB, Mexico) at 20 × magnification and counted the total mites per lizard. In order to avoid observer effects, mite counts were always performed by the same person (JRR). The percentage of infested individuals was recorded and the intensity of infestation was calculated as the total number of mites in infested individuals (Margolis et al. 1982; Rózsa et al. 2000).

Inflammatory response

On the fourth day, we quantified in vivo inflammatory response by injecting a mitogen phytohemagglutinin-P lectine of the red kidney bean *Phaseolus vulgaris* (PHA; Sigma L8754). This method has been widely used in lizards (Martín et al. 2008; Huyghe et al. 2010; Sacchi et al. 2014). This lectine stimulates local lymphocyte T cells from the adaptative and innate immune systems, causing inflammation at the injection site. Greater inflammation indicates a stronger immune response (Belluire et al. 2004; Martin et al. 2006). We injected 20 µL solutions containing 50 mg of PHA in 10 mL phosphate buffered saline (PBS) in the lizards' right hindlimb foot pad. Thickness of pad was measured before injection and 24 h later (fifth day in captivity), using a spessimetre (Mitutoyo, accuracy: 0.01 mm). The left back pad was used as control; we injected only 20 µL of PBS. A small ink non-toxic mark was placed next to the measurement site to ensure that the same site was used in all measurements.

After we completed data collection from each lizard, they were kept from an additional day in laboratory conditions before they were released at their capture site. Each lizard therefore spent a total of seven days in captivity.

Statistical analyses

Normality and homogeneity of the meteorological data and morphological variables were examined prior to data analysis (Zuur et al. 2010). We used one-way ANOVA to compare environmental temperature and precipitation by season.

We used two-way ANOVA to compare body mass, BCI and inflammatory response between sex and season. Body mass required \log_{10} transformation to comply with the parametric assumptions of normality and homoscedasticity. To test for an effect of season on infestation intensity, we used generalized linear models (GLM) with Poisson distribution and log as linking function. Season (three levels), sex (two levels) and their interaction were set as independent factors; BCI and inflammatory response were used as continuous covariates. When we detected significant effects, we performed Bonferroni post hoc comparisons. All the analyses were performed with R 4.0.1 (R Core Team 2017).

Results

Data from the nearest meteorological station to our field site showed that the environmental temperature is higher in spring than any other season ($F_{3,12} = 12.70$, $P = 0.002$). Precipitation is higher in summer than spring or winter, whereas autumn had intermediate precipitation values between those of summer and those of spring and winter ($F_{3,12} = 8.99$, $P = 0.006$; Fig. 1).

We found a significant effect of season on the BCI of the lizards ($F_{2,145} = 18.48$, $P < 0.001$), but no significant effect of sex ($F_{1,145} = 0.07$, $P = 0.78$). The interaction sex*season was significant ($F_{3,145} = 18.07$, $P < 0.001$): male BCI did not vary among the seasons, while females had greater body condition in autumn than in either spring or summer (Fig. 2a). Body mass differed between seasons ($F_{2,145} = 10.13$, $P < 0.001$) and sexes ($F_{1,145} = 23.68$, $P < 0.001$), with no significant effect of the interaction between sex and season ($F_{3,145} = 2.56$, $P = 0.08$). Lizards of both sexes tended to be heavier in autumn than in spring (Fig. 2b); males were heaviest than females (males: 27.4 ± 0.73 , females: 21.4 ± 0.80 , $P = 0.001$). Males were longer than females (males: 88.1 ± 0.74 ; females: 81.0 ± 0.98 , mean \pm SE; $F_{1,145} = 27.52$, $P = 0.001$).

Lizards had greater inflammatory responses in autumn than spring or summer ($F_{1,73} = 21.86$, $P < 0.001$; Fig. 3). We did not find different seasonal patterns in each sex (interaction sex*season: $F_{2,73} = 0.48$, $P = 0.61$), nor did we find any relationship between mite counts and inflammatory response across seasons (spring: $r = -0.08$, $P = 0.67$; summer: $r = 0.18$, $P = 0.31$; autumn: $r = 0.10$, $P = 0.62$).

Mite prevalence was 100% (99/99) for males and 98% (51/52) for females. Mean \pm SE mite abundance for the entire period was 196.26 ± 12.8 mites per lizard (range = 0–765). Intensity differed by sex ($\chi^2 = 1321$, $df = 1$, $P < 0.001$) and season ($\chi^2 = 1558$, $df = 2$, $P < 0.001$). Overall, males had higher infection intensities than females. Both male and female lizards had their highest infection intensities in the summer, but males had their lowest infection intensity in

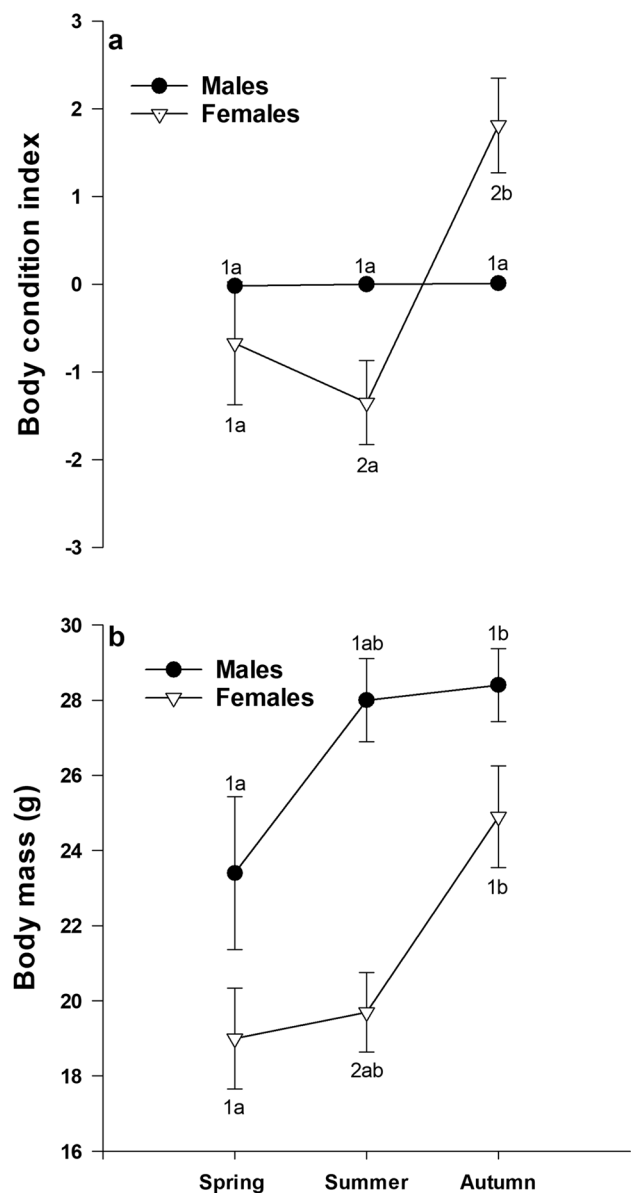


Fig. 1 Mean environmental temperature and mean environmental precipitation at the nearest meteorological station to the study site by month

spring, whereas females' lowest infection intensity occurred in the autumn (interaction sex*season: $\chi^2 = 1133$, $df = 2$, $P < 0.001$; Fig. 4; Table S1). The relationship between mite intensity and body condition was not significant ($r = -0.002$, $P = 0.98$).

Discussion

In many species, reproductive cycles are seasonal and synchronous between males and females (Gadsden et al. 2008; Boretto and Ibarguengoytía 2009; Medina and

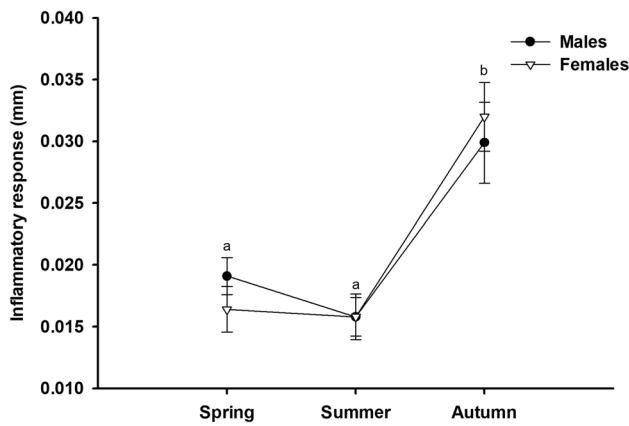


Fig. 2 Body condition (a) and body mass (b) of *Sceloporus torquatus* by sex and season. Letters show differences by season for the same sex. Numbers show differences by sex during the same season. Values are mean ± SE

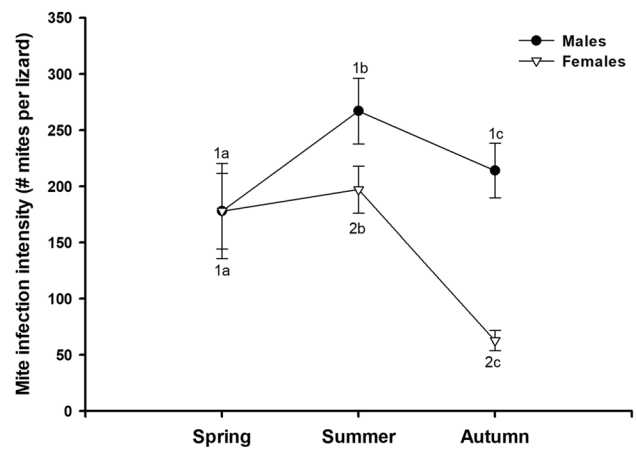


Fig. 4 Intensity of mite infestations in *Sceloporus torquatus* by sex and season. Letters show differences by season for the same sex. Numbers show differences by sex during the same season. Values are mean ± SE

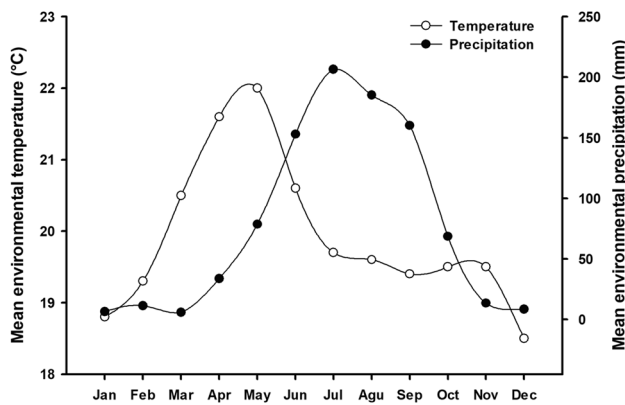


Fig. 3 Inflammatory response of *Sceloporus torquatus* by sex and season. Since we did not find differences by sex, the letters show differences by season. Values are mean ± SE

Ibargüengoytía 2010; see Aldridge et al. 2020), so it is difficult to decouple the effects of internal (e.g., reproductive status and body condition) and external factors (e.g., environmental temperatures and humidity). Species with asynchronous reproductive cycles provide the opportunity to study the effects of seasonality and reproductive condition separately.

This is the first study that compares phenological variation in parasite load and inflammatory response in a lizard with asynchronous gonadal cycles. We found that female and male Torquate lizards had different parasite loads and inflammatory responses depending on the season. We hypothesized that lizards would experience trade-offs between inflammatory response and gonadal cycle; however, this idea is only supported in males, in whom we found a coincidence of minimum inflammatory response and maximum mite infestation during the period of maximal testicular activity (summer).

However, in females the maximal gonadal activity coincides with maximum inflammatory response and with a reduction in mite infestation. Furthermore, female *S. torquatus* had the highest body condition in autumn.

To try to explain this we suggest two complementary scenarios: (i) gonadal activation, which in females takes place in autumn, is physiologically demanding and only those females that already had the lowest infestations were able to remain active during this season. (ii) mite infestation is costly to lizards, and those females with a better body condition and inflammatory response were able to control and reduce their mite load during the critical period of gonadal activation. Body mass is a determinant of reproductive investment in females *Sceloporus* (Weiss 2006; Weiss et al. 2009) and mites can reduce the increase in body mass of free-ranging lizards (Klukowski and Nelson 2001). Thus, mites might exert selective pressure on this population because females with more visible (ecto-) parasites and/or low body condition may either be less often chosen by high quality males or have lower fitness due to a lower reproductive output (Weiss et al. 2011; Kopena et al. 2020). However, the high prevalence of mites in the sample suggested that females controlled their infestation only until certain level because a strong inflammatory response can also compromise the investment of female lizards in the clutch (Uller et al. 2006). The latter also being in line with the idea that phenotypes of intermediate resistance to parasites can be a more stable evolutionary strategy than phenotypes of total resistance (e.g., Olsson et al. 2005; Råberg et al. 2009).

However, another possible explanation of our results is that rainy season is not favorable for lizards but good for mites. We find the lowest inflammatory response and higher mite infestation in summer (rainy season). We also find an

increase in **inflammatory response** and a reduction in mites in autumn, which appears to be a better season for lizards generally and also probably better for production of offspring by females (Clopton and Gold 1993; Jackson and Bateman 2018; Arguez et al. 2020). Perhaps gonadal development in males is less expensive than in females and they can face that cost in a less favorable season (Trivers 1972; French and Moore 2007; Hayward and Gillooly 2011).

Furthermore, we do not find relationships between mites and body condition or inflammatory response, which could indicate that the cost of this parasite is not high for lizards (Graham et al. 2012; Heredia et al. 2014; Wieczorek et al. 2020). In that case, lizards may show changes in immune response across seasons in relation to environmental factors unrelated to mite prevalence (Leceta and Zapata 1986; Huyghe et al. 2010; Hudson et al. 2020).

As commented, the evolution of parasite virulence is a dynamic process (Hamilton and Zuk 1982; Balenger and Zuk 2014) and fighting off parasites is an energetically demanding process that can impair other important functions in the host (e.g., Meylan et al. 2013). Thus, our results are in line with the idea that some host populations may co-evolve with their parasites toward strategies of intermediate resistance, resulting in a co-adaptive scenario for both hosts and parasites (Råberg et al. 2009). This would explain why, despite nearly 100% of the lizards being infested by mites, with infestations up to 765 mites in a single lizard, we found no significant relationship of mites with the body condition of the lizards.

Male *S. torquatus* had more parasites than females in summer and autumn; they also had a high inflammatory response in autumn, similar to that of females. In line with our predictions, summer coincides with the period of maximal gonadal development in males of this species (Feria-Ortiz et al. 2001; Rubio-Blanco et al. unpublished data). As in other vertebrates, the increase of testicular volume may be associated with a significant rise of testosterone levels (Moore 1986; Díaz et al. 1994). In lizards, an increase in the locomotor activity and agonistic behavior of male lizards has been observed by experimental increasing of testosterone (Marler and Moore 1989; Cox et al. 2005), which could explain how despite having an inflammatory response similar to that of females, the activity and behavior of males could cause them to have higher mite loads compared to females during autumn (More 1986; Olsson et al. 2000; Sinervo et al. 2000). Since the energy budget of organisms is finite, the energy depleted in locomotor activities may trade off with anti-parasitic defenses, which can result in increased load of hematophagous mites in lizards (Barrientos and Megía-Palma 2021).

Our results could be interpreted as a coevolution between host and parasites toward strategies of intermediate resistance, an adaptation of both, parasites and host; however,

environmental changes across seasons appear to be a plausible explanation too. Mites increase in humid conditions. The observed increase of mite loads in males might also result from the increase of precipitation and number of rainy days in autumn (see Fig. 1), which might also favor the proliferation of mites in the environment (Clopton and Gold 1993; Rieff et al. 2014; Jackson and Bateman 2018; Arguez et al. 2020). The plausible co-occurrence of the seasonal increase in lizard-seeking mites in the environment with a period of high host susceptibility to infections opens questions on the role of mites and other parasites potentially transmitted by them on the mating system in this population of *S. torquatus*, all of which warrants further investigation in this system.

In conclusion, we found that parasite load and inflammatory response differs between sexes and seasons in *S. torquatus*. We suggest that analyzing host-parasite interactions between sexes and seasons may provide a comprehensive picture of these dynamics in lizards and perhaps in other taxa with asynchronous gonadal cycles.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00114-022-01793-x>.

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Author contribution JRR, VF and JM designed research; JRR and JCGM performed research; JM and VF supervised project; JRR and RMP analyzed data; JRR, RMP, JCGM and VF wrote manuscript with contributions from JM and EB. All authors edited and approved the final manuscript.

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Data availability Data will be made available upon request.

Code availability Not applicable.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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