

Ecological correlates of ectoparasite load in a rodent: Complex roles of seasonality

Ling-Ying Shuai^{a,1}, Li-Qing Wang^{b,*}, Jian-Jun Wang^{c,1}, Yang Xia^a, Bin-Yan Zhai^a, Wen-Jie Xu^a, Xing-Ming Chen^a, Xiao-Yu Yang^a, Fu-Shun Zhang^b

^a College of Life Sciences, Huaibei Normal University, Huaibei, China

^b Grassland Research Institute, Chinese Academy of Agricultural Sciences, Hohhot, China

^c Inner Mongolia Autonomous Region Comprehensive Center for Disease Control and Prevention, Hohhot, China

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ABSTRACT

Understanding the mechanisms driving parasite distributions is not only important for understanding ecosystem functioning, but also crucial for disease control. Previous studies have documented the important roles of host sex, host body size, host behavioral trait (such as boldness and trappability), and seasonality in shaping parasite load. However, few studies have simultaneously assessed the roles of these factors, as well as their interactions. In spring and summer of 2021, we conducted live trapping in Hohhot, China, to collect ectoparasites on Daurian ground squirrel (*Spermophilus dauricus*), a small rodent widely distributed in East Asian grassland. We then used generalized linear models to explore the effects of several biological factors (sex, body weight, trappability, and reproductive status) and seasonality on the abundance of ticks and fleas in *S. dauricus*. Significant but inconsistent seasonal effects were observed: tick load was significantly greater in summer than in spring, while flea load was greater in spring than in summer. Seasons also significantly interacted with host trappability and body weight to affect tick abundance. Our results highlight the importance of considering seasonal changes in parasitism, as well as interactions between season and host biological traits in shaping parasite distributions.

1. Introduction

Parasitism is one of the most fundamental ecological processes and parasitic organisms are widespread both taxonomically and geographically (Carlson et al., 2020). Parasites can profoundly shape behavior, fitness and population dynamics of hosts, as well as community structure (Hatcher et al., 2014; Hudson et al., 1998; Milotic et al., 2020). Moreover, many ectoparasites feed on blood and act as effective transmitters of severe zoonoses such as plague and Lyme borreliosis. Understanding the mechanisms that influence the distribution patterns of parasites is thus crucial not only for a comprehensive understanding of ecosystem functioning, but also for human well-being, disease control, animal husbandry and livestock production (Craig, 2003; Perkins et al., 2003; Woolhouse et al., 1997).

At the population level, one of the most prevalent patterns in parasite ecology is that parasites are usually aggregated among host individuals

(Poulin, 2007; Shaw and Dobson, 1995). This phenomenon suggests that parasite load is often highly variable, and host individuals are considerably unequal in terms of exposure and/or susceptibility to parasites. For example, body size (often represented by body mass) is usually positively associated with parasite load (Butler et al., 2020; Chu et al., 2019; Harrison et al., 2010), as larger individuals may more likely to be targets for parasites (Shine, 1989), or simply can tolerate higher number of parasites (Mooring et al., 2004). Moreover, sex-biased infestation has also been frequently detected. Although not a universal rule (Kiffner et al., 2013; Warburton et al., 2016), male hosts are often more heavily parasitized than females (Harrison et al., 2010; Poulin, 1996), possibly because males are often larger than females, and/or suffer from immunosuppression associated with higher testosterone levels (Folstad and Karter, 1992). Finally, host behavioral traits or personality may also contribute to parasite infection. Bolder individuals are often associated with higher activity level or trappability, and may thus have better

* Corresponding author.

E-mail addresses: shuailingying@163.com (L.-Y. Shuai), lqwhohhot@163.com (L.-Q. Wang), erdoswang818@sina.com (J.-J. Wang), Xiexiamugeneral@163.com (Y. Xia), clover_zhai@163.com (B.-Y. Zhai), Cloris_xuwj@163.com (W.-J. Xu), cibaoer22@163.com (X.-M. Chen), yangxiaoyuyyx@163.com (X.-Y. Yang), zhangfushun2008@163.com (F.-S. Zhang).

¹ Ling-Ying Shuai, Li-Qing Wang and Jian-Jun Wang contributed equally to this work.

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chance of encountering parasites, especially in a heterogeneous environment (Boyer et al., 2010; Wilson et al., 1993). However, few studies have simultaneously assessed the relative importance of morphology, sex and behavioral traits in shaping host susceptibility to infestation.

Besides the host-related factors described above, parasite-related factors also contribute to the distribution pattern of parasites. As parasitism has evolved independently in various taxa, significant differences often exist among parasites in terms of morphology, life history and host exploitation strategies (Carlson et al., 2020; Matthee and Krasnov, 2009). In this scenario, even on the same host, different parasites may also differ in their distribution pattern, as well as the underlying mechanisms. Comparisons of patterns of abundance (and its biological correlates) among different parasites feeding on the same host should help us to disentangle the effects of host-related factors from that of parasite-related factors (Matthee and Krasnov, 2009). Such studies, however, are relatively rare (but see Krasnov et al., 2010; Luguterah and Lawer, 2015; Matthee and Krasnov, 2009).

In this study, we explored the roles of sex, body weight and behavioral traits in shaping abundance of ticks and fleas on the same host species, Daurian ground squirrels (*Spermophilus dauricus*). *S. dauricus* is a intermediate-sized rodent (ca. 250 g in body mass) widely distributed in North China, often viewed as an important reservoir of zoonoses such as plague. Besides the effects of body weight and sex, we also tested for the effect of trappability, an important behavioral trait highly associated with boldness, activity and exploration (Boyer et al., 2010). In addition to test for the association between these biological factors and parasite load, we also aimed to address the following questions: (1) is there seasonal difference in regards to biological correlates of parasite load? And (2) whether ticks and fleas would differ in patterns of abundance, as well as the related biological correlates?

2. Material and methods

2.1. Study area

In the spring (late May to early June) and summer (late July to early August), 2021, we conducted live-trapping in the grassland located within the Experiment Demonstration Base, Grassland Research Institute, Chinese Academy of Agricultural Sciences (40°36' N, 111°45' E), ca. 30 km south of Hohhot, Inner Mongolia, China. This grassland was featured with a continental temperate monsoon climate, with annual mean temperature of ca. 6.9 °C and average annual precipitation of ca. 400 mm. The vegetation here was characterized by several dominant species including *Leymus chinensis*, *Stipa capillata*, *Cleistogenes squarrosa* and *Medicago sativa*. In terms of small mammals, *S. dauricus* was the dominant species in recent years, although striped hamster (*Cricetus barabensis*) and Mongolian gerbil (*Meriones unguiculatus*) were also occasionally captured. In the study area, *S. dauricus* are generally active between early May and late September. However, weather in early May and late September is often instable and windy, and frequent rainfalls in early July may cause difficulty for conducting consecutive live-trapping. The two study periods we selected are characterized by relatively stable weather and represent the local weather conditions in late spring (temperature range: 8.5–23.1 °C) and mid-summer (temperature range: 16.4–28.9 °C).

2.2. Rodent and ectoparasite sampling

We selected 6 sites (3 sites for each season, and each site had an area of ca. 1 ha) from the grassland, with a minimal interval of 300 m among sites. To reduce the potential effects of vegetation structure on parasite distributions or infestation (Chepkwony et al., 2021; Randolph et al., 2000), all the sites were comparable in terms of vegetation coverage (ca. 30–40%) and height (ca. 10 cm). In each site, 100 Sherman live traps baited with fresh peanuts were arranged in a 10 × 10 grid, with 10-m intervals between neighboring traps. The trapping session for each

season included 15 consecutive days. On each day, traps were open between 07:00 and 18:30 (Beijing time), during which ground squirrels were most active. We checked all the traps every 2 h. During each check, we used new traps to replace the occupied traps and rebaited the traps when necessary.

Captured ground squirrels were immediately placed in separate cotton bags and then transferred to our laboratory for subsequent examinations. Each ground squirrel captured for the first time was anesthetized by an intraperitoneal injection with 10% chloral hydrate. Chloral hydrate was administered at 350 mg per kg of body weight, a moderate dose according to a study on rats with a similar body size (Field et al., 1993). Using a comb and small tweezers, we carefully scanned body surface of each ground squirrel and the bag for the presence of ticks or fleas. The ticks and fleas collected from a ground squirrel were immediately stored in ethanol (95%) contained in a separate centrifugal tube. After collecting ectoparasites, we recorded body weight, sex and reproductive status (scrotal males, and lactating or pregnant females were considered reproductively active) for each ground squirrel. All the ground squirrels were then individually marked by commercially available black hair dye (SAVOL, Zhanghua Ltd., Taizhou). Briefly speaking, the body surface of a ground squirrel was virtually divided into several regions (including shoulder, tail, left foreleg, right foreleg, left hindleg, right hindleg, and back), and a unique combination of those regions were painted black for each individual. To minimize the potential effects of marking on individuals, the marks on each ground squirrel was smaller than 8 cm² in total area. After these handling procedures, each ground squirrel was maintained in a plastic rat box (370 × 270 × 170 mm) with access to beddings, *ad lib* water and food (alfalfa and commercial food pellets for hamsters) for recovery and observation. All the ground squirrels recovered within 2 h post injection, without showing any obviously abnormal signs. In the next morning, each ground squirrel was released at the location where it was caught. We also recorded trapping history (times of trapping event during our live-trapping) of each individual. An individual's trappability was therefore categorized as either trap-happy (trapped at least twice during the trapping session) or trap-shy (trapped only once during the trapping session). The ectoparasites collected were later identified based on morphology using dichotomous keys (Deng, 1978; Liu and Shi, 2009). We also recorded the life stage (larva, nymph or adult) of each tick collected, using the guidance provided by Emel'yanova and Hoogstraal (1973).

2.3. Statistical analyses

All the statistical analyses were performed in R version 3.5.3 (R core team, 2019). We used negative binomial generalized linear mixed-effects models (GLMM) for tick load and flea load separately. Fixed terms of each model included the main effects of sex, season, body weight (centralized), trappability and reproductive status, as well as the two-way interactions between season and other factors (except for the season-reproductive status interaction, as no reproductively active individuals were recorded during summer). Site (nested within season) was included as a random term. We used the function 'glmer.nb' from the R package 'lme4' to build negative binomial GLMMs (Bates et al., 2014). We used the function 'vif' from the R package 'car' to evaluate the level of multicollinearity. If any term within the model had a degree of freedom larger than 1, generalized variance inflation factors (GVIF, also adjusted for the dimension of the confidence ellipsoid) were calculated (Fox and Weisberg, 2011). Otherwise, variance inflation factors (VIF) were calculated. Factors with VIF (or GVIF) larger than 10 (suggesting a high level of multicollinearity) were dropped and the modeling process was repeated using the remaining terms, until all the terms included in the model had a VIF (or GVIF) less than 10. As a result, we removed all the interactive terms from the model on flea load to reduce multicollinearity. Model selection was performed based on corrected Akaike Information Criterion (AIC_c) using the function 'dredge' from the R

package ‘MuMin’ (Bartoń, 2016). As no single best model (with delta AIC_c larger than 2.00) could be determined, conditional model averaging was performed using the function ‘model.avg’ from the R package ‘MuMin’ (Bartoń, 2016).

3. Results

A total of 105 ground squirrels (48 and 57 individuals caught in spring and summer, respectively) were captured, with a total of 2370 ticks (spring: mean $4.02 \pm \text{s.d.} 5.18$ ticks per ground squirrel, including 181 adults, 7 nymphs and 1 larva; summer: mean 38.19 ± 36.05 ticks per ground squirrel, including 343 adults, 1813 nymphs and 25 larvae) and 320 fleas (spring: mean $4.67 \pm \text{s.d.} 6.50$ fleas per ground squirrel; summer: mean $1.68 \pm \text{s.d.} 2.50$ fleas per ground squirrel) collected. The diversity of ectoparasites was low, with only one tick species (*Haemaphysalis verticalis*) and two flea species (*Citellophilus tesquorum mongolicus*, $n = 317$; and *Neopsylla bidentatiformis*, $n = 3$) recorded. Among these ground squirrels, 85.71% ($n = 90$) and 58.10% ($n = 61$) of individuals were infested by ticks and fleas, respectively.

Based on our criterion described above, 34.29% ($n = 36$) of ground squirrels were categorized as ‘trap-happy’. Trap-happy individuals were marginally heavier than trap-shy individuals (Mann-Whitney U test: $P = 0.063$). In spring, 78.38% (29 out of 37) of females were found lactating or pregnant, and 36.36% (4 out of 11) of males were found scrotal. No reproductively active individuals were captured in summer.

According to the results of conditional model averaging, flea load showed a significant seasonal difference, with flea load in summer significantly lower than in spring. By contrast, tick load in summer was significantly higher than in spring. Furthermore, we detected an interactive effect on tick load between season and body weight (Fig. 1A), with tick load positively related to host body weight in spring, and negatively related to host body weight in summer. Season also interacted with host trappability to affect tick load (Fig. 1B). In summer, trap-shy individuals had higher tick load than trap-happy individuals; in spring, however, trap-happy individuals had higher tick load than trap-shy individuals.

4. Discussion

In the present study, we explored the relationships between several ecological factors and abundance of two ectoparasites in a ground squirrel. Our results did not support the frequently documented relationships between parasite load and body weight, nor significant sex-biased parasitism. Significant seasonal differences were found, while

fleas and ticks differed in directions of seasonal effect. Significant interactions between season and other factors were also detected, suggesting that the relationships between host biological traits and parasite infestation were rather complex.

Parasite abundance often varied temporarily, and seasonal variations in parasite load have been frequently recorded (Krasnov et al., 2005; Le Coeur et al., 2015). In our study, pronounced seasonal differences in parasite burdens were also detected, but in distinct patterns for fleas and ticks. Tick load was generally higher in summer, while flea load was generally higher in spring. This difference in seasonal patterns should be related to differences in life history and behavior between fleas and ticks. Fleas are sensitive to variations in temperature and humidity (Blagburn and Dryden, 2009; Silverman et al., 1981), and the relatively high temperature in summer may thus help to decrease their survival rate, as well as the average flea load. Unlike many tick species, *H. verticalis* inhabits burrows of *S. dauricus* in each of its developmental stages, and seldom parasitises animals other than small mammals (Emel'yanova and Hoogstraal, 1973). Our results also confirm a previously found pattern of *H. verticalis*, with adults dominant in spring and nymphs dominant in summer (Emel'yanova and Hoogstraal, 1973). Considering these facts, the seasonal change in abundance of *H. verticalis* may largely reflect a result of reproduction.

Host body size is a frequently documented correlate of ectoparasite load, and larger-sized individuals are often associated with a higher ectoparasite load (Butler et al., 2020; Chu et al., 2019; Mooring et al., 2004). Such a pattern was not supported in our study, as we detected no significant relationship between host body weight and ectoparasite load. Nevertheless, we did find a significant interaction between season and host body weight (Table 1). We detected a positive relationship between body weight and tick load in spring, and a negative association between body weight and tick load in summer (Fig. 1A). Seasonal changes in host behavior and population structure may help to explain this seasonal change in the role of body weight. In our study system, many adult ground squirrels were social and reproductively active in spring. In this scenario, larger individuals may have advantages in competition for mates and thus have more chances to contact other individuals, increasing their chances of encountering ticks. Meanwhile, as invests on reproduction may cause loss of immunocompetence, larger males may also be more susceptible to parasites in the breeding season (Folstat and Karter, 1992). Such mechanisms should not take effect in summer, as ground squirrels were all reproductively inactive and became solitary. Moreover, juveniles constitute a large part of the population in this season (Han et al., 2005). In this sense, individuals with poorer body condition (e.g. juveniles with lower body weight) may be associated

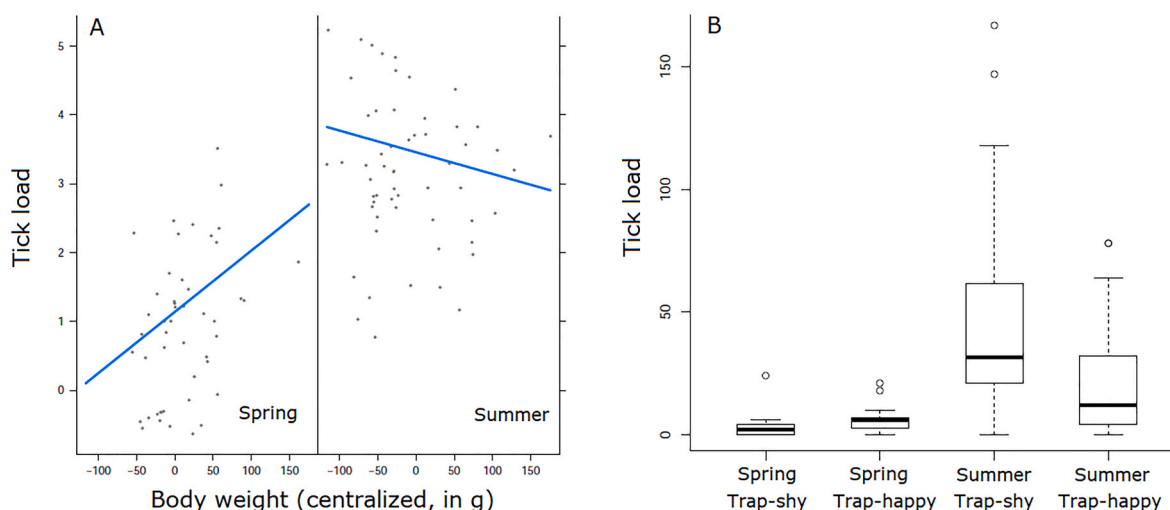


Fig. 1. Interactive effects of season and body weight (centralized) on tick load in *S. dauricus* (A); and interactive effects of season and trappability on tick load in *S. dauricus* (B).

Table 1
Results of conditional model averaging, based on negative binomial generalized linear mixed-effects model on ectoparasite load (whole data set) of Daurian ground squirrels (*Spermophilus dauricus*). Values of body weight were centralized prior to regressions. Significant terms were marked by asterisks. Terms in brackets show reference categories for categorical factors.

Dependent variable	Factor	Estimate	Standard error	Z value	P value
Flea load (theta = 0.56)	Intercept*	2.13	0.96	2.20	0.03
	Season (spring)*	−1.02	0.37	2.77	<0.01
	Sex (female)	−0.52	0.35	1.47	0.14
	Trappability (trap-shy)	0.60	0.32	1.87	0.06
	Body weight	0.00	0.00	1.01	0.31
	Reproductive status (inactive)	−0.27	0.50	0.52	0.60
	Season ×Weight*	−0.01	0.00	2.43	0.02
Tick load (theta = 1.17)	Intercept	−1.88	1.29	1.45	0.15
	Season (spring)*	2.75	0.67	4.07	<0.001
	Sex (female)	0.13	0.68	0.18	0.85
	Trappability (trap-shy)*	3.11	1.57	1.97	0.05
	Body weight	0.02	0.01	1.57	0.12
	Reproductive status (inactive)	−0.62	0.36	1.71	0.09
	Season ×Weight*	−0.01	0.00	2.43	0.02
	Season	−1.87	0.80	2.33	0.02
	×Trappability*				
	Season ×Sex	0.49	0.52	0.92	0.36

with higher parasite load.

Differences in trappability may reflect differences in behavioral traits such as space use (Biro and Dingemanse, 2009), and can in turn lead to differences in encounter rate of parasites. As a result, we should expect individuals with a higher trappability have a higher parasite load (Boyer et al., 2010). In our study, we detected significant interactions between host trappability and season, suggesting that the relationship between trappability and ectoparasite load was inconsistent. The positive relationship between trappability and tick load was only detected in spring, while trap-shy individuals had even higher tick load than trap-happy individuals in summer (Fig. 1B). We think a plausible reason is that larger individuals may outcompete smaller ones to get access to more traps (higher trappability), given that our baits are attractive food for ground squirrels. Since larger individuals were generally less heavily infested by ticks in summer, it would be reasonable to expect that trap-happy individuals should be associated with lower tick load in this season. Further experiments are required to testify these speculations.

In summary, our results highlighted the role of seasonality in shaping ectoparasite load in rodents, as well as seasonal changes in the roles of some biological traits of hosts. This study also suggested that different parasites could differ significantly in terms of distribution pattern, as well as its underlying mechanisms. Since fleas and ticks showed distinct seasonal patterns on the same host species, it would also be interesting to explore whether inter-specific competition exists between these parasite species.

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Availability of data and materials

The dataset used for analyses in this study can be found in the supplementary file.

Contributions

Ling-Ying Shuai: Conceptualization, Methodology, Writing-Reviewing and Editing. Li-Qing Wang: Methodology, Funding acquisition, Writing-Original draft preparation. Jian-Jun Wang: Methodology, Investigation, Data curation. Yang Xia: Investigation, Data curation. Bin-Yan Zhai: Investigation. Wen-Jie Xu: Investigation. Xing-Min Chen: Investigation. Xiao-Yu Yang: Investigation. Fu-Shun Zhang: Conceptualization, Funding acquisition.

Ethics approval and consent to participate

The experimental procedures were approved by the Grassland Research Institute, Chinese Academy of Agricultural Sciences (Permission No. 21-02), following the Regulations of the Animal Welfare Committee of Beijing Veterinarians of the Agriculture Ministry of China (Beijing, China).

Consent for publication

Not available.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijppaw.2022.06.006>.

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