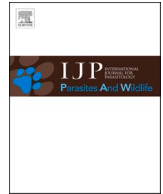


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Influence of biotic and abiotic factors on flea species population dynamics on *Lasiopodomys brandtii*

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ABSTRACT

Brandt's Vole (*Lasiopodomys brandtii*) is one of the most abundant rodent species in the grasslands of Inner Mongolia, China, and one of the main carriers of *Yersinia pestis*, the plague bacterium. There have been several instances of plague transmission among *L. brandtii*, and all of their dominant flea species are known carriers of plague. Little work has been done to understand the regulation of flea abundance on *L. brandtii* by biotic and abiotic factors. Here, we examine the impacts of host and climate variation on flea abundance on *L. brandtii* in May, July, and September of 2021 in the East Ujumqin Banner, Xilinhot City, Inner Mongolia Autonomous Region. We arrived at the following conclusions: 1) There were 8 flea species representing 2 families and 5 genera collected from *L. brandtii*, and *Frontopsylla luculenta*, *Neopsylla pleskei orientalis*, and *Amphipsylla primaris mitis* were most common. 2) Host body weight, host age, season, temperature, and humidity are key factors influencing flea abundance on *L. brandtii*. 3) Flea species vary in their respective responses to factors.

1. Introduction

Rodents are a primary vectors of zoonotic disease largely through their associated fleas (Stenseth et al., 2008; Bitam et al., 2010). Flea abundance is dictated by abiotic and biotic factors, such as host availability and body conditions (Colwell et al., 2012; Carlson et al., 2017; Hammond et al., 2019; Krasnov et al., 2021). Understanding these factors is critical for both predicting flea abundance and informing zoonotic disease management. Numerous biotic factors have been identified that impact flea abundance, including host age (Krasnov et al., 2006; Hawlena et al., 2007; Veitch et al., 2021), sex (Matthee et al., 2010; Kiffner et al., 2013; Kowalski et al., 2015), and body weight (Kiffner et al., 2013; Azrizal Wahid et al., 2019). There is also a correlation between the population densities of fleas and hosts (Krasnov et al., 2002; Young et al., 2015). Flea reproductive development, behavior, survival, and habitat are all impacted by abiotic factors such as temperature (Kreppel et al., 2016; Kamani et al., 2018; Hammond et al., 2019), precipitation (Eads and Hoogland, 2017; Eads et al., 2020), and season (Durden et al., 2005; Gálvez et al., 2017). As the impacts of climate change escalate in

many ecosystems, improving our understanding of the ecological factors that drive flea abundance and dispersal is essential for facilitating efforts to combat flea-borne diseases and relieve affected wildlife of the associated morbidity.

Responses to biotic and abiotic variation likely differs among flea species-to-species depending on their unique niches. For example, development time of *Synopsylla fonquerniei* was 1.79X longer and death time slightly shorter than that of *Xenopsylla cheopis* when the flea species were subjected to high temperature and low humidity (Kreppel et al., 2016). Two flea species, *Oropsylla montana* and *Hoplopsyllus anomalous*, found on the California ground squirrel (*Otospermophilus beecheyi*), have been shown to have different ecological niches (Smith et al., 2021). While *O. montana* is mainly found on adults during cool and humid early summer conditions, *H. anomalous* favors squirrel pups in hot and dry late summer conditions. Given the observed variability in responses to climatic variation by different species of fleas, it is a clear epidemiological imperative to further examine the roles of abiotic factors in governing abundance species-by-species.

Perhaps the most famous and historically significant zoonotic disease

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transmitted by rodent fleas is plague, a disease caused by the bacterium *Yersinia pestis*. With 12 natural plague host species, China has the highest number in the world, and there are four in Inner Mongolia (Li et al., 2021, 2022). Brandt's vole (*Lasiopodomys brandtii*), a primary carrier of plague in Inner Mongolia, is parasitized by fleas that are not host-specific but are potent vectors of plague (Wu, 1996; Zhang et al., 2015; Zhang, 2019). Thus far, research on *L. brandtii* fleas has been limited to examining flea community composition and detecting *Y. pestis* (Wu, 1996; Liu, 2015; Zhang et al., 2015; Zhang, 2019). There has not been any focus on the biotic and abiotic factors affecting flea abundance in *L. brandtii*.

Fleas, hosts, and their surrounding environment are inextricably connected. Changes in either host conditions or surrounding environments will have consequences for flea population dynamics, and, as a result, also affect the occurrence and prevalence of flea-borne diseases (Davis et al., 2004; Wu and Yin, 2021). We investigated community structure of flea species populating *L. brandtii* and analyzed the effects on flea community structure and abundance by both biotic factors, including host gender, age, body weight, and population density, and abiotic factors, including season, temperature, and humidity. For this research, we make the following predictions: 1) flea abundance on *L. brandtii* is affected by many factors. 2) flea species vary in their responses to influencing factors and. 3) there are differences in abundance among the flea species hosted by *L. brandtii*.

2. Materials and methods

2.1. Overview of the study area

The research was conducted in Xilinhot City in the East Ujimqin Banner, Inner Mongolia Autonomous Region of China, at E 115°30'–116°30', N 44°42'–45°15' (Fig. 1). The habitat is typical grassland covered with a 10–20 cm layer of grass. The region is in the northern temperate continental climate zone. Regional climate is characterized by the Mongolian high-pressure system in winter, and both high precipitation and heat in summer. The average annual temperature is

1.6 °C, ranging from –18.9 °C in January to 21 °C in July. Maximum temperature is 39.7 °C, minimum –40.7 °C, and the daily average is 0.7 °C. The annual growth period (i.e., daily average > 5 °C) is 95 days, and the average frost-free period is 120 days. Annual precipitation is ~300 mm, 70% of which occurs June to August. Annual evaporation is more than 3000 mm, which is 7.5X precipitation. Rodents in this area include *Cricetulus barabebsis*, *Spermophilus dauricus*, and *Meriones unguiculatus*, but *L. brandtii* is the dominant species in abundance (Li et al., 2018).

2.2. Animal data collection

We surveyed animals over 4–5 days/month in three months representing all seasons except winter, in 2021. During each survey period, five sites were randomly selected for sampling. Fresh peanut rice was used as bait in live traps that were 27cm × 12.5cm × 12 cm in 10m × 10m mesh cages spaced at least 5m apart. Live traps were set during the night and checked every 4–6 h during the day. Trapped *L. brandtii* were sacrificed by cervical dislocation and placed into individual bags. We recorded sex, weight, and body size for each individual collected. Population density was calculated from the capture rate with the following formula:

$$P = N / (H \times n) \times 100\% \quad (1)$$

P is the capture rate, N represents the number of captured mice, H represents the total number of cages, and n represents the number of continuous cage days.

2.3. Environmental data acquisition

Hourly temperature and humidity during the survey period were obtained from the Huiju Atmosphere database (<https://airwise.hjhj-e.com>). Based on these data, the maximum temperature, average temperature, temperature change, maximum humidity, average humidity, and humidity change per day were calculated. Principal component analysis (PCA) was used to reduce the dimension of the data to generate

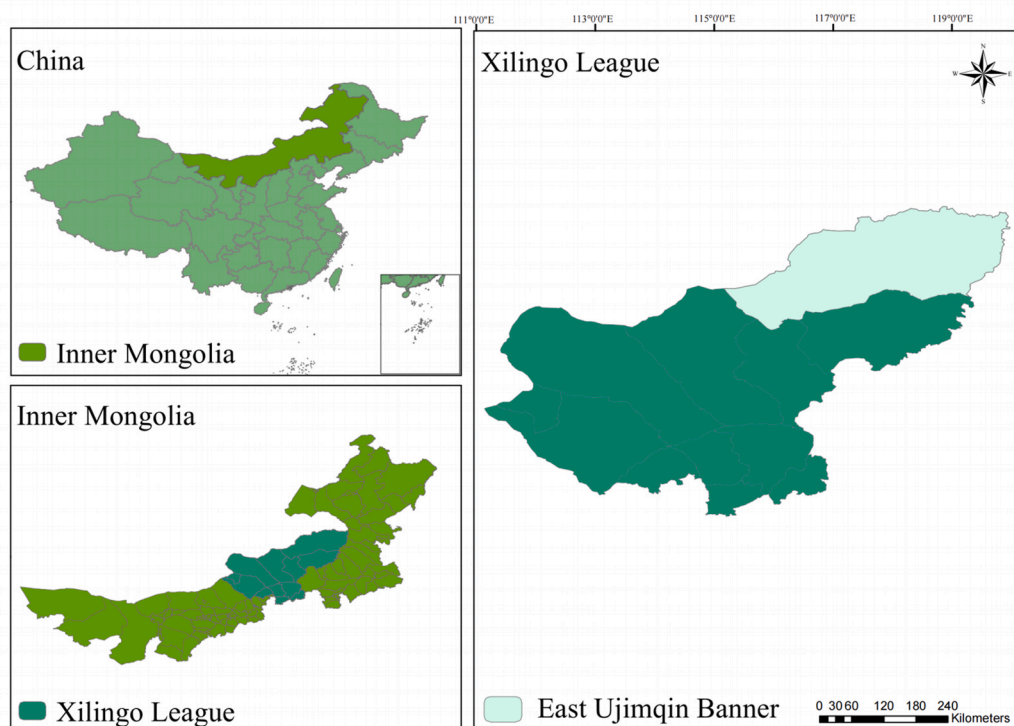


Fig. 1. Map of the study area.

a smaller number of unrelated variables that can be included in analytical models. The first (PC1; positively correlated with the maximum and average values of temperature and humidity), second (PC2; the strongest positive correlation with humidity changes), and third principal components (PC3; the strongest positive correlation with temperature changes) together explained 94% of the total variation (or individually 46%, 26% and 22%, respectively) (Table 1). These were considered as fixed effects in the model.

2.4. Data collection and identification of fleas in vitro

Combs and tweezers combined with white porcelain plates were used to collect fleas by examining the backs, abdomens, limbs, genitals, and tails of *L. brandtii*. *L. brandtii* and fleas were stored in individual bottles of 95% ethanol. Fleas were identified after being dehydrated, sliced, and preserved using a sealing solution of neutral resin with added xylene (Wu, 2007).

2.5. Data analyses

From both a Shapiro test and visual inspection of the data, we noted that the flea count data were non-normal. Therefore, in order to examine the factors affecting flea abundance, a generalized linear mixed model (GLMM) was constructed for the both the total set of fleas infesting *L. brandtii* and also a subset that included the three most common species. For this, we used the 'nbinom2' function in the glmmTMB package of R.4.2.2 version. (Fantozzi et al., 2022). Before constructing these models, we evaluated explanatory variables for multicollinearity by calculating VIF and GVIF values using the 'vif' function in the R package 'car' (Fox and Weisberg, 2018). Factors with VIF and GVIF values greater than 10 were eliminated. Finally, we considered as fixed effects interactions between 1) host gender, host age, host weight, population density, season (spring, summer, autumn), and climate (i.e., PC1, PC2, and PC3), 2) host gender, age, and weight, and 3) the interaction between season and climate factors. Site was used as a random effect. Best fit models were selected by gradually removing insignificant factors ($p < 0.05$) and comparing the fitted models with Akaike 's information criterion (Akaike, 1974). A likelihood ratio test (LRT) was used to compare the optimal model in the $\Delta AICc < 2$ model. All continuous fixed effects were standardized to facilitate the comparison of different variables.

3. Results

3.1. Brandt's vole flea community

From 917 *L. brandtii*, we collected 832 total fleas composed of 8 species belonging to 5 genera and 2 families (Table 2). Among them were *Frontopsylla luculenta*, *Neopsylla pleskei orientalis*, and *Amphipsylla primiaris mitis*, where are the main native vectors of plague found on *L. brandtii* on the Xilingol Plateau. The abundance of fleas in spring was higher than summer and autumn, and it was lowest in summer. *Rhadinopsylla rothschildi* was only detected in autumn (Fig. 2).

Table 1

Principal component analysis on all climate variables used in the study.

Coefficient	PC1	PC2	PC3
Maximum Temperature	0.752	-0.608	0.234
Mean Temperature	0.728	-0.676	0.077
Variance in Temperature	0.315	0.225	0.867
Maximum Humidity	0.864	0.394	-0.296
Mean Humidity	0.75	0.216	-0.564
Variance in Humidity	0.525	0.717	0.331
Eigenvalues	2.779	1.595	1.327
S.D.	1.97	0.95	0.95
Proportion of Variance	0.46	0.26	0.22

Table 2

The *Lasiopodomys brandtii* flea species community.

Family	Genera	Species
Ctenophthalmidae	<i>Neopsylla</i>	<i>Neopsylla bidentatiformis</i> <i>Neopsylla pleskei orientalis</i>
	<i>Rhadinopsylla</i>	<i>Rhadinopsylla rothschildi</i>
Leptopsyllidae	<i>Frontopsylla</i>	<i>Frontopsylla luculenta</i> <i>Frontopsylla elata taishiri</i>
	<i>Ophthalmopsylla</i>	<i>Ophthalmopsylla kukuschkini</i>
	<i>Amphipsylla</i>	<i>Amphipsylla primiaris mitis</i>
		<i>Amphipsylla marikovskii marikovskii</i>

3.2. Factors influencing flea abundance

We present model selection results in Table 3. The overall abundance of fleas had a significant positive correlation with host body weight and a significant negative correlation with host population density (Table 4). Among the environmental factors, the overall abundance of fleas had a significant positive correlation with spring and a significant negative correlation with both summer and autumn (Table 4). Overall flea abundance also had a significant positive correlation with PC1 (mean temperature and humidity) and a significant negative correlation with PC2 (humidity change; Table 4).

The abundance of *F. luculenta* had a significant positive correlation with host body weight and host age, favoring pups and subadults (Table 4). Among the environmental factors, the abundance of *F. luculenta* was significantly negatively correlated with spring and autumn (Table 4). The abundance of *F. luculenta* also had a significant positive correlation with the interaction term of autumn and PC2 (Table 4).

There was a significant positive correlation between *N. pleskei orientalis* abundance and host body weight (Table 4). Among the environmental factors, the abundance of *N. pleskei orientalis* was significantly negatively correlated with summer and autumn (Table 4). *N. pleskei orientalis* abundance also had a significant positive correlation with PC1 and a significant negative correlation with PC2 (Table 4).

The abundance of another common flea, *A. primiaris mitis*, was positively correlated with host body weight and negatively correlated with host population density (Table 4). There were no significant correlations in species abundance with environmental factors (Table 4).

4. Discussion

4.1. Investigation on flea presence on *L. brandtii*

There were 2 families, 5 genera, and 8 species of fleas detected on *L. brandtii* throughout the study, and the most common species were *F. luculenta*, *N. pleskei orientalis*, and *A. primiaris mitis*. The flea species we collected were all known to be plague vectors in China, except *A. marikovskii marikovskii* and *F. elata taishiri* (Liu and Shi, 2009; Liu and Gu, 2011; Liu, 2015). We found different results from previous reports on both the dominant flea species on *L. brandtii* in the Hebei Province and the overall composition of the flea community (Liu et al., 2003; Wang et al., 2006). Flea species are known to be shared across sympatric hosts (Yensen et al., 1996; Goldberg et al., 2020). Whether flea species are generalists across hosts or specialists on specific host species is situationally-dependent. Specialists will choose unsatisfactory hosts if necessary (Krasnov et al., 2004; Liu and Shi, 2009). Our study area and that in the Hebei Province have different primary carriers of plague in *L. brandtii* and *Meriones unguiculatus*, respectively (Kang et al., 2022). Differences in the dominant rodent species and host structures also contribute to the variation in observed flea communities between our study and previous ones (Li et al., 2001; Kang et al., 2022).

Climatic factors can also affect population dynamics of major hosts and vectors (Li et al., 2021). Temperature and humidity have been repeatedly shown to have a significant effect on the growth and

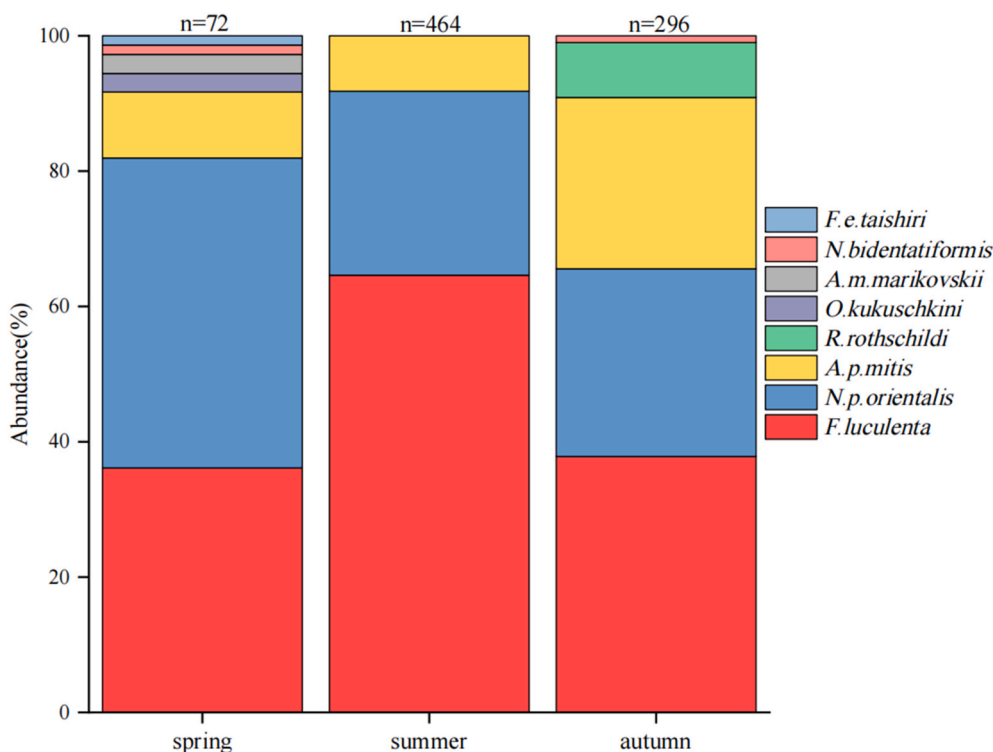


Fig. 2. Community structure of *Lasiopodomys brandtii* fleas by seasons. Three flea species were collected throughout the study meanwhile, *Rhadinopsylla rothschildi* was only detected in autumn. The top of each column indicates the number of samples for each season.

development of flea larvae. Flea species are impacted differently by temperature and humidity (Hu et al., 2001; Krasnov et al., 2001). Our study site was in a typical steppe habitat with a northern temperate continental climate, while that in the Hebei Province was a Bashang grassland with a monsoon climate. These habitats would be expected to contrast in temperature, humidity, extreme weather, and grassland types, and this contributes to differences in both rodent and flea communities. Climate change is impacting temperature and precipitation across the globe, and this will likely have consequences for reproduction, growth, and community structure of rodent and flea species (Niu et al., 2021; Zhang, 2021b). It would be valuable to clarify how spatial scales affect the role of *L. brandtii* and environmental factors as drivers of flea population dynamics (Pontifes et al., 2022).

4.2. Factors influencing overall flea abundance

In our study, we evaluated the impacts of biotic and abiotic factors on flea abundance. Our results support our prediction that the abundance of fleas on *L. brandtii* is affected by many factors. (Krasnov et al., 2005b, 2006; Linardi and Krasnov, 2013). Among the biotic factors, there was a significant positive correlation between body weight and the overall flea abundance. Heavier hosts would be predicted to have larger surface areas that provide more habitat for fleas. Also, heavier hosts can provide more nutrition to fleas (Hawlena et al., 2005a; Gorrell and Schulte-Hostedde, 2008). While previous work found host sex and age impact flea presence (Hawlena et al., 2007; Kiffner et al., 2013; Kowalski et al., 2015; Veitch et al., 2021), we did not find this relationship to be significant in *L. brandtii*. There is an on-going debate about host gender bias by fleas (Krasnov et al., 2005a; Kiffner et al., 2013; Waterman et al., 2013; Kowalski et al., 2015). For those flea species that do not exhibit a host gender preference, it is speculated that differences in flea abundance may result from variability in spatial behavior, movement patterns, and immunity by male hosts (Kowalski et al., 2015). Flea species exhibiting host age bias may also be affected by differences in host species and environmental factors, which would also contribute to

contrasting research results (Hawlena et al., 2005b; Hawlena et al., 2006). We found a significant negative correlation between host population density and the overall abundance of fleas on *L. brandtii*, contrary to previous observations that reported the opposite trend (Kiffner et al., 2013; López-Pérez et al., 2018). This result may be due to both variability in host-parasitic dynamics and methodological differences for calculating population densities. Among the abiotic factors, we found that overall flea abundance was significantly positively correlated with spring and significantly negatively correlated with summer and autumn. Previous studies have suggested that the seasonal fluctuation of flea abundance will affect the seasonal characteristics of the plague epidemic (Zhao et al., 2016). Our work is the first to report on seasonal dynamics of flea populations on *L. brandtii* and our results provide both a good baseline and guideline for subsequent research. Climate variables are widely observed to be primary influencing factors affecting the flea population dynamics (Zhang et al., 1995; Khokhlova et al., 2009; Kreppel et al., 2016). We found that overall flea abundance was significantly impacted by abiotic factors, with a positive correlation with PC1 (max temperature and humidity) and negative correlation with PC2 (variability in humidity). Temperature and humidity directly affect flea development, survival, behavior, and reproduction (Krasnov et al., 2001, 2002; Tamara et al., 2011). It would be predicted that flea populations will increase when the temperature and humidity are suitable for the development and survival of eggs, pupae, and larvae (Silverman et al., 1981; Krasnov et al., 2001).

Little work has been done examining the factors influencing the presence of common flea species across the same host species. Our results suggest that the differences in biotic factors influencing the abundance of *L. brandtii* common flea species are mainly in host age and host population density. The abundance of *F. luculenta* was only affected by host age, with a significant positive correlation with the pup and sub-adults stages. The abundance of neither *N. pleskei orientalis* nor *A. primariaris mitis* was affected by host age. Overall these results are largely consistent with previous observations that flea abundance varies by host age (Schalk and Forbes, 1997; Knudsen et al., 2002; Mears et al.,

Table 3

Negative binomial mixed effect model (Δ AICc <2) explaining the biotic and abiotic factors associated with abundance of fleas found on *Lasiopodomys brandtii*.

Response Variable	Best model	AICc	Δ AICc	K	Wi
Overall flea abundance	Mass + Season + Density + PC1 + PC2	2304.82	0.00	9	0.31
	Mass + Season + Density + PC1 + PC2 + Season * PC1 + Season * PC2	2305.72	0.91	13	0.20
	Mass + Season + Density + PC1 + PC2 + PC3 + Season * PC1 + Season * PC2	2305.83	1.02	14	0.19
	Mass + Season + Density + PC1 + PC2 + Season * PC2	2305.91	1.10	11	0.18
	Mass + Season + Density + PC1 + PC2+PC3+ Season * PC1 + Season * PC2+ Season * PC3+Mass*Sex + Mass*Age + Sex*Age (full model)	2320.12	15.31	27	0.00
	Mass + Age + Season + Density + PC2 + Season * PC2	1578.13	0.00	13	0.32
	Mass + Age + Season + Density + PC1+ PC2 + Season * PC2	1578.30	0.17	14	0.30
F. luculenta abundance	Mass + Age + Season + PC2 + Season * PC2	1579.17	1.04	12	0.19
	Mass + Season + Density + PC1 + PC2+PC3+ Season * PC1 + Season * PC2+ Season * PC3+Mass*Sex + Mass*Age + Sex*Age (full model)	1592.37	14.23	27	0.00
	Mass + Season + PC1 + PC2	1098.33	0.00	8	0.40
	Mass + Age + Season + Density + PC1 + PC2	1099.24	0.91	12	0.25
	Mass + Season + Density + PC1 + PC2	1099.56	1.23	9	0.22
	Mass + Season + Density + PC1 + PC2+PC3+ Season * PC1 + Season * PC2+ Season * PC3+Mass*Sex + Mass*Age + Sex*Age (full model)	1119.22	20.89	27	0.00
	Mass + Density	722.58	0.00	5	0.34
N. p. orientalis abundance	Mass + Density + Season	723.56	0.99	7	0.21
	Mass + Density + Season + PC2	724.29	1.71	8	0.14
	Mass + Season + Density + PC1 + PC2+PC3+ Season * PC1 + Season * PC2+ Season * PC3+Mass*Sex + Mass*Age + Sex*Age (full model)	748.45	25.87	27	0.00
	Mass + Season + PC1 + PC2	1098.33	0.00	8	0.40
	Mass + Age + Season + Density + PC1 + PC2	1099.24	0.91	12	0.25
	Mass + Season + Density + PC1 + PC2	1099.56	1.23	9	0.22
	Mass + Season + Density + PC1 + PC2+PC3+ Season * PC1 + Season * PC2+ Season * PC3+Mass*Sex + Mass*Age + Sex*Age (full model)	1119.22	20.89	27	0.00
A. p. mitis abundance	Mass + Density + Season	723.56	0.99	7	0.21
	Mass + Density + Season + PC2	724.29	1.71	8	0.14
	Mass + Season + Density + PC1 + PC2+PC3+ Season * PC1 + Season * PC2+ Season * PC3+Mass*Sex + Mass*Age + Sex*Age (full model)	748.45	25.87	27	0.00
	Mass + Season + PC1 + PC2	1098.33	0.00	8	0.40
	Mass + Age + Season + Density + PC1 + PC2	1099.24	0.91	12	0.25
	Mass + Season + Density + PC1 + PC2	1099.56	1.23	9	0.22
	Mass + Season + Density + PC1 + PC2+PC3+ Season * PC1 + Season * PC2+ Season * PC3+Mass*Sex + Mass*Age + Sex*Age (full model)	1119.22	20.89	27	0.00

Table 3 Note: Sites were included as random effects in the models. AICc: the information criteria corrected the small sample size; K: number of parameters; Wi: model weights.

2002; Hawlena et al., 2007; Smith et al., 2021). The effect of host age on the abundance of fleas varied among different host-parasite flea relationships (Yin et al., 2020). *A. prairieensis* abundance was significantly negatively correlated with host population density, which suggests that previous conclusions about relationships between host population density and flea abundance may have been biased by individual species of the flea community.

Common flea species also exhibited significant responses to abiotic variation. The abundance of both *F. luculenta* and *N. pleskei orientalis* differed not only in seasonal dynamics, but also in temperature and humidity-related factors. Studies have suggested that the abiotic factors affecting flea abundances vary from host to fleas (Silverman et al., 1981; Krasnov et al., 2001; Osacar-Jimenez et al., 2001; Hammond et al.,

Table 4

Generalized linear mixed model (GLMM) analysis of the biotic and abiotic factors associated with flea abundance on *Lasiopodomys brandtii*.

Response Variable	Coefficient	Estimate \pm S.E.	z value	p-value	
Overall flea abundance	(Intercept)	2.64 \pm 0.79	3.347	< 0.001	
	Mass	0.31 \pm 0.05	5.695	< 0.001	
	Density	-0.20 \pm 0.07	-2.757	0.006	
	Season [summer]	-6.05 \pm 1.59	-3.799	< 0.001	
	Season [autumn]	-3.27 \pm 0.86	-3.796	< 0.001	
	PC1	2.36 \pm 0.61	3.88	< 0.001	
	PC2	-1.37 \pm 0.35	-3.908	< 0.001	
	F. luculenta abundance	(Intercept)	-2.17 \pm 0.58	-3.763	< 0.001
	Mass	0.50 \pm 0.09	5.707	< 0.001	
	<i>F. luculenta</i> abundance	Age [adult]	0.44 \pm 0.24	1.801	0.072
Age [teenager]		0.65 \pm 0.30	2.181	0.029	
Age [baby]		1.35 \pm 0.51	2.665	0.007	
Density		-0.16 \pm 0.09	-1.743	0.081	
Season [summer]		0.88 \pm 0.51	1.731	0.083	
Season [autumn]		-2.07 \pm 0.80	-2.601	0.009	
PC2		0.33 \pm 0.30	1.109	0.267	
Season [summer] : PC2		-0.59 \pm 0.34	-1.754	0.079	
Season [autumn] : PC2		1.86 \pm 0.71	2.602	0.009	
<i>N. p. orientalis</i> abundance		(Intercept)	2.34 \pm 1.29	1.816	0.069
	Mass	0.34 \pm 0.09	3.808	< 0.001	
	Season [summer]	-7.10 \pm 2.68	-2.647	0.008	
	Season [autumn]	-4.32 \pm 1.40	-3.086	0.002	
	PC1	2.46 \pm 1.02	2.41	0.015	
	PC2	-1.50 \pm 0.60	-2.484	0.012	
<i>A. p. mitis</i> abundance	(Intercept)	-2.28 \pm 0.21	-10.628	< 0.001	
	Mass	0.24 \pm 0.11	2.084	0.037	
	Density	-0.29 \pm 0.13	-2.238	0.025	

Table 4 Note: Sites were included as random effects. Significant results are in bold. Model results were selected using the lowest AIC and a likelihood ratio test.

2019). Here we show that flea abundance varies by species in responses to both biotic and abiotic factors. One potential issue with our study design is that it does not account for precipitation. Previous accounts found that likely due to warmer and wetter periods, increased numbers of voles led to higher *A. prairieensis* abundance (Li et al., 2001; Liu et al., 2001; Zhang, 2021a).

In summary, we determined that there were differences between both the overall parasitic flea abundance and the factors influencing abundance of the most common flea species. Previous investigations only considered overall flea abundance as a response variable (Goldberg et al., 2020; Pontifes et al., 2022; Shuai et al., 2022). Here we found *F. luculenta* abundance varied with host age, but the effect was not reflected by overall flea abundance. However, we note that while we can report the correlation. We cannot make a claim about whether this is caused by host age itself or if it was another correlated factor for which we did not account. We can conclude that future investigations should also model abundances of individual flea species as well as overall numbers to properly assess biotic and abiotic drivers of populations. *F. luculenta* and *N. pleskei orientalis* are generalists that can carry *Y. pestis*

(Wang et al., 2006). Therefore, it is an imperative to strengthen the monitoring of flea species that are most important for plague transmission, and to consider changes in the biotic and abiotic factors governing flea species abundances in predictive models aiming to mitigate the risk of plague spillover.

5. Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

6. Ethics statement

The animal study was reviewed and approved by Research Ethics Review Committee of Inner Mongolian Agricultural University (NND2023081).

7. Author contributions

MM XL and HPF: analyzed the data and wrote the manuscript. TL, HTZ and NSMK: collected data and samples in the field. XDW and SY: mapped out the manuscript. All authors contributed to the article and approved the submitted version.

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10. Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

11. Publisher's note

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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.2023.05.006>.

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